# Ecology and management of range edge populations: the case of toothfish species at the South Sandwich Islands

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This thesis is dedicated to Nick

Father, playwright and master lobster fisherman

## **Declaration of Originality**

I, James Oliver Roberts, declare that this thesis is my own work. I collected much of the data myself while working on fishing vessels in the South Georgia and South Sandwich Islands longline fisheries. Additional data were collected by scientific observers and this is acknowledged in the text. All analyses of data are my own. I have acknowledged all other contributions and sources used and have received permission to cite where necessary.

#### Abstract

Current theory suggests that the life history of a species will vary in a predictable way from the range centre where habitat is likely to be optimal, to range peripheries where it is not. Moving towards cold water, high-latitude range edges, life history theory contends that individuals should exhibit reduced growth rates to an increased average maximum length, with delayed maturation and reduced somatic condition. In addition, increased recruitment variability should be observed towards range edges.

Toothfish species *Dissostichus eleginoides* and *D. mawsoni* are large deep-water finfish predators of the Southern Ocean region. Both are found at the South Sandwich Islands in the South Atlantic Ocean, where they are situated on the edge of their distributional range. In this study, data collected on board commercial fishing vessels were used to describe the ecology, life history and dispersal patterns of range-edge toothfish populations, compared with those of range centre populations (South Georgia *D. eleginoides* and Ross Sea *D. mawsoni*). Two main research questions were addressed:

- What limits the distribution of toothfish species populations at the South Sandwich Islands and how do range edge life history and population dynamics differ from those of range centre populations?
- 2. How can we use this information to more effectively manage the toothfish fishery at the South Sandwich Islands and other fisheries on range edge populations?

A bioregional analysis made use of commercial longline data to resolve the position of the ecotone between the Antarctic and Subantarctic bioregions at the South Sandwich Islands. An abrupt transition was observed between the two bioregions around Saunders Island and this was spatially coincident for finfish and invertebrate communities, indicating a dramatic change in habitat type at this location. A correlative modelling analysis suggested that the formation of toothfish species range edges is influenced by the extent of sea ice cover and winter seawater temperature near the surface. However, differences between threshold values of ice and temperature at the South Sandwich Islands and the Ross Sea suggest that regional patterns in hydrography and topography may lead to the formation of range edges

that do not necessarily correspond with niche requirements, with implications for studies evaluating species redistributions in response to climate change.

Some, though not all of the hypothesised high latitude range edge life history traits were observed in South Sandwich Islands *D. eleginoides*. Increased maximum size was observed, though initial growth rates were similar to those of individuals at South Georgia and growth is clearly not a factor limiting productivity towards the high latitude range edge. There was no evidence at all for gonad maturation to spawning condition and this appears to relate to improved somatic condition, which would not normally be expected in range edge individuals. Highly episodic recruitment, also assumed to be a feature of range edge populations, was observed in South Sandwich Islands *D eleginoides* population and this is unlikely to be self-sustaining. This appears to be confirmed by an analysis of the otolith chemistry of *D. eleginoides*, where a similar chemical signature was observed at the cores of otoliths extracted from individuals captured at South Georgia and South Sandwich Islands.

In addition a mark-recapture model was developed to estimate the migration rates of postrecruitment *D. eleginoides* between South Georgia and the South Sandwich Islands. Sexbiased migration of males away from the cold water range limit were also evident from an analysis of the sex ratio of the South Sandwich Islands population and have a considerable impact on resident population age structure. Accounting for the emigration of males greatly improved the accuracy of estimates from a CASAL assessment of the South Sandwich Islands *D. eleginoides* population. However the episodic nature of recruitment negatively impacted on the sustainable yield that could be taken according to CCAMLR harvest decision rules, which do not appear to be appropriate for this and other range edge toothfish stocks.

Some aspects of range edge life history, including decreased growth rates, delayed maturation and episodic recruitment will impact on the productivity of a population such that it will be increasingly vulnerable to the impacts of exploitation. Where generalised patterns in range position effects on life history can be discerned, this information can be used to make predictions about the life history of exploited stocks that are otherwise data poor and also will allow for improved predictions as to how species will respond to changes in the environment such as those arising from climate change.

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## Acronyms and Abbreviations

ACC	Antarctic Circumpolar Current
AGFP	Antifreeze glycoprotein
AIC	Akaike Information Criterion. A measure of the relative goodness of fit of a statistical model
ANOVA	Analysis of variance
BANZARE	British, Australian and New Zealand Antarctic Research Expedition (Bank)
BIDE	Birth, Immigration, Death, Emigration (model)
<i>B</i> <sub>0</sub>	Virgin spawning stock biomass
CASAL	C++ algorithmic stock assessment laboratory
CCAMLR	Commission for the Conservation of Antarctic Marine Living Resources
CPUE	Catch per unit effort. In this study either the number of individuals caught per 1000 hooks or the weight of individuals per 1000 hooks
CV	Coefficient of Variation
EEZ	Exclusive Economic Zone
ENSO	El Niño-Southern Oscillation
FAO	Food and Agriculture Organization of the United Nations
GAM	Generalised additive model. A statistical model for blending properties of generalised linear models with additive models
GLM	Generalised linear model. A flexible generalisation of ordinary least-squares regression
GMI	Gonad Maturity Index
GSGSSI	Government of South Georgia and the South Sandwich Islands
GSI	Gonadosomatic Index
IUU	Illegal, Unreported and Unregulated (fishing)
LA-ICP-MS	Laser Ablation-Inductively Coupled Plasma-Mass Spectrometry

MANOVA	Multivariate Analysis of Variance
MCMC	Markov Chain Monte Carlo
MRAG	Marine Resources Assessment Group
NIST	National Institute of Standards and Technology
NMDS	Non-metric Multidimensional Scaling
РСА	Principal Components Analysis
PFP	Plasma Freezing Point
Q-Q plot	Quantile–quantile plot. A graphical method of comparing two probability distributions by plotting their quantiles against each other.
RSG	Ross Sea Gyre
SAM	Southern Annular Mode
SB	Southern Boundary (of ACC)
SG	South Georgia
SSB	Spawning Stock Biomass
SSI	South Sandwich Islands
SST	Sea Surface Temperature
ТАС	Total Allowable Catch
UPGMA	Un-weighted pair-group method using Arithmetic averages
VME	Vulnerable Marine Ecosystem
WG	Weddell Gyre
WF	Weddell Front
WSC	Weddell Scotia Confluence
WG–FSA	CCAMLR's Working Group on Fish Stock Assessment
WG–SAM	CCAMLR's Working Group on Statistical Assessment Methods
YCS	Year Class Strength

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### Chapter 1

### Introduction

#### **1.1** Population dynamics at the range edge

Range position effects population dynamics have attracted considerable attention in recent years. This has largely been driven by the requirement to more accurately predict how populations will adapt or otherwise to anthropogenic changes in habitat and environment (Sexton, McIntyre et al. 2009). Recent reviews highlight the lack of comprehensive studies in this field, *i.e.* they tend to examine a restricted range of life history parameters and provide only partial explanations as to why range edges form (Parmesan, Gaines et al. 2005; Gaston 2009; Sexton, McIntyre et al. 2009).

Distributional ranges are, in effect, an expression of a particular species' ecological niche in space. Contemporary theory suggests a number of processes by which range limits may arise. Ultimately these processes relate in some way to changes in local population size and, in reviewing the causes of range limits, Gaston (2009) considered their influence on the different terms of the BIDE (Birth, Immigration, Death, Emigration) model:

$$N_{t+1} = N_t + b + i - d - e$$
 eqn 1.1

Where *N* is the population size, *b* is births, *i* is immigration, *d* is deaths and *e* is emigration. Many marine species including toothfish have planktonic early life stages (North 2002), and the processes of immigration and recruitment (a proxy for births) may be intrinsically linked. As such, it is convenient to consider the two together.

#### **Births and Immigration**

A number of species exhibit reduced reproductive capacity or total reproductive failure towards range peripheries and this is commonly identified to be a primary factor in defining range limits (Gaston 2009). A variety of parameters may be implicated, relating to reproductive biology (Berrigan and Charnov 1994; Gaston 2009) and behaviour (Sexton, Andrews et al. 1992). Impaired reproductive capacity is thought to result from the reduced availability of food resources, exacerbated by the increased metabolic demands for maintenance in suboptimal habitat, where both factors serve to limit the availability of somatic resources for reproductive development (Gaston 2009).

The distributional ranges of most species are dispersal limited (Gaston 2009) and physical barriers to dispersal will often prevent a particular species from realising its fundamental (or theoretical) niche. These barriers may be temporary in nature, such that immigration (or recruitment) to a recipient meta-population may be episodic or intermittent (Parmesan, Gaines et al. 2005; Gaston 2009). This dynamic is often most pronounced in species with passively dispersed life-stages, *e.g.* wind-borne seeds or plankton phase eggs and larvae, where the physical structuring of air or water currents prevent immigration to suitable habitat (Gaylord and Gaines 2000). Alternatively, favourable current regimes may distribute individuals to regions where habitat is suboptimal. Here, deaths may exceed births and in, extreme cases, unproductive sink populations may be entirely supported by recurrent immigration from source populations located elsewhere (Pulliam and Danielson 1991; Gilman 2006).

#### **Deaths and Emigration**

A few studies have sought empirical evidence for the impacts of emigration on the formation of range limits. These have mostly reported increased rates of dispersal in range edge meta-populations (Thomas, Bodsworth et al. 2001; Parmesan, Gaines et al. 2005), though few studies have directly explored the role of range contraction away from suboptimal habitat in the formation of range boundaries (Gaston 2009).

Range edges may also form where suboptimal habitat and lack of adequate resources impair biological function, impacting on the survival rates of individuals. Rates of outright mortality may be difficult to quantify in study populations and proxies are often used, such as: individual growth rate, reproductive development, or somatic condition. Where the functioning of a key biological process is observed as abnormal or suboptimal then this is taken as evidence for reduced fitness (Dekker and Beukema 1993; Ungerer, Ayres et al. 1999). However, while empirical studies tend to support climatic/habitat limitation of abundance at range boundaries, reductions in fitness are just as likely as not to be observed towards range edges (Gaston 2009; Sexton, McIntyre et al. 2009). Availability of resources may also be diminished by competition with other species, *e.g.* 23 out of 26 studies found support for the role of competition in shaping range limits in one meta-analysis (Sexton, McIntyre et al. 2009). As such, inter-specific competition may be a key factor in the resolving of distributional range edges. Often the locations of low latitude range limits are found to be heavily influenced by competitive interactions, whereas high latitude limits are mediated by thermal tolerance and this macroecological pattern has been observed in a wide range of marine and terrestrial species (MacArthur 1972; Hersteinsson and Macdonald 1992; Kaufman 1998).

#### **Population size**

Hence all of the demographic terms in the BIDE population model (Eqn. 1.1) may be affected in some way towards range edges. There is also a tendency towards increased temporal variation in each term, such that range edge meta-populations can exhibit substantial variation in abundance and temporal extinction events may occur (Gaston 2009) (Fig. 1.1). Reduced fitness, impaired reproductive biology and inter-specific competition for resources should all serve to decrease population density towards range edges, as per the 'abundant centre hypothesis' (Brown, Mehlman et al. 1995). However, empirical studies are more likely to find evidence for increased population fragmentation towards range peripheries, resulting in decreased density across wider areas (Sagarin and Gaines 2002; Sexton, McIntyre et al. 2009).



Figure 1.1 Schematic representation of range position effects on the population dynamics of a species. Size of circle reflects relative size of each population; boundaries between areas of habitat quality are illustrative and may be more gradual or structurally complex in reality.

#### 1.2 Problem statement

For no one species is there a comprehensive understanding of why range limits arise (Gaston 2009). However a number of studies have found evidence for range position effects in all four parameters of the BIDE model (Eqn. 1.1). As such, because studies tend to look for change in only one or two of the model parameters (and often only one aspect of a particular parameter) the inferences for range limitation that come from these studies are limited (Gaston 2009; Sexton, McIntyre et al. 2009). Hence there is a need for studies which document changes in all of the BIDE parameters towards range edges, so that interactions and tradeoffs between these processes can also be explored.

#### Significance for fisheries management

Theoretical models suggest a number of mechanisms through which range limits arise, though most remain empirically untested (Gaston 2009; Sexton, McIntyre et al. 2009). However, there is some empirical evidence for range position effects on life history

parameters of fish populations, including increased variation in recruitment (Philippart, Henderson et al. 1998; Brunel and Boucher 2006; Watanabe 2007) and impaired gonad or and somatic growth (Brunel and Dickey-Collas 2010). Uncertainty around estimates of recruitment variability, growth and maturity parameters and dispersal dynamics all compromise the accuracy of population assessments and increase uncertainty about the status of the target resource and the impacts of resource exploitation (Hart and Reynolds 2002). Even so, few if any studies have sought to understand in detail the potential effects of range edge life history on population assessment and the implications for management of exploitation of range edge populations.

#### Toothfish as a case study

Toothfish (*Dissostichus spp.*) are large predatory fishes of the family *Nototheniidae* and are endemic to cold waters of the Southern Hemisphere. Three species have been described, though only two are abundant and commercially important: Patagonian toothfish (*D. eleginoides*) and Antarctic toothfish (*D. mawsoni*) (De Witt, Heemstra et al. 1990) (Fig. 1.2).

Fisheries for toothfish species are generally thought to be well-managed according to the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) principals of marine resource exploitation (Agnew 2004). Toothfish species are caught across a broad range of latitudes and, though regional differences in toothfish biology have been observed (Collins, Brickle et al. 2011), the underlying mechanisms that cause variation in population parameters and which ultimately drive distribution patterns, such as recruitment or growth rate, are not well understood. From a management perspective, the poor understanding of range edge population dynamics is likely to compromise predictions about how toothfish populations will respond to large scale disturbances, such as those arising from fishing pressure or climate change – a particular concern for Antarctic marine ecosystems (Trathan and Agnew 2010).

However, toothfish fisheries are extremely data-rich when compared with most deepwater fisheries and it has been possible to construct data-intensive age-structured population models for a number of the key stocks (Hillary, Kirkwood et al. 2006; Candy and Constable 2008). These assessments have been informed by the implementation of mark-recapture programs and the routine collection of detailed biometric data, which are necessarily most intensive in the exploratory phase of development. The broad distributional range, isolated nature of a number of key stocks and extensive data collection programs make toothfish species ideally suited for the study of range position effects on life history and population dynamics as well as the potential implications for fisheries management.

#### **1.3 Toothfish species**

*D. eleginoides* and *D. mawsoni* are similar in appearance and body size, though the latter has several physiological adaptations for life in sub-zero temperatures. These include the presence of circulatory antifreeze glycoproteins (AFGPs) which prevent freezing of blood plasma (Chen, Cheng et al. 2008) and cold-stable eye lens crystallins that maintain transparency of lenses at very low temperatures (Kiss, Mirarefri et al. 2004). The two species have a different chromosomal organisation (Ghigliotti, Mazzei et al. 2007) and are thought to have diverged almost 15 million years ago (Near 2004). Hence there are likely to be many other physiological differences between the two species, though the general biology and life-history characteristics are broadly similar (Eastman and DeVries 2000; Horn 2002).



Figure 1.2 Typical specimens of *D. mawsoni* (top) and *D. eleginoides* (bottom) caught in the South Sandwich Islands longline fishery. These individuals would have weighed approximately 30 kg and 10 kg, respectively.

#### **1.3.1** Toothfish lifecycle

Toothfish individuals are distributed across a broad bathymetric range throughout their lifecycle. Pelagic larvae are occasionally recovered close to the surface, while adults are most abundant over continental slopes and may be observed as deep as 2,500 m (Evseenko, Kock et al. 1995) (Fig. 1.3). Although the general biology of toothfish species is well-studied compared with other deepwater species, there are still large gaps in our understanding of early life behaviour and processes, particularly relating to development and dispersal of eggs, larvae and juvenile fish (North 2002).

*D. eleginoides* and *D. mawsoni* are the most fecund of the nototheniids, with large individuals producing up to 500,000 eggs in one breeding cycle (Evseenko, Kock et al. 1995). Both toothfish species spawn during the southern winter (Agnew 1999; Hanchet 2006). Toothfish eggs are assumed to be pelagic, though few have ever been recovered (Evseenko, Kock et al. 1995). Hatching is likely to occur from early November to mid-December and larvae are initially pelagic (North 2002). These then settle over shelf habitat, where 1+ (of age between exactly 1 and 2 years old) individuals are captured by the annual groundfish trawl survey at South Georgia (Belchier and Collins 2008). Toothfish undergo a distinct ontogenetic down-slope migration with growth (Belchier and Collins 2008) and adults are predominantly found over continental slopes at depths of more than 700m, where they are targeted by longline fisheries (Agnew 2004).



Figure 1.3 Simplified toothfish lifecycle. From Collins et al. (2011).

Large-scale environmental phenomena, such as the El Niño-Southern Oscillation (ENSO) are thought to have a significant effect on the abundance, development and dispersal patterns of toothfish early life stages, causing temporal variation in annual recruitment, which may have a cyclical nature. Recruitment to the *D. eleginoides* population in the Patagonian shelf region is thought to pulse over an approximate four-year cycle (Laptikhovsky, Arkhipkin et al. 2008) and recruitment to the South Georgia population has been found to correlate with sea surface temperature and the resulting strong cohorts may be detected in exploited adult populations many years later (Belchier and Collins 2008).

#### 1.3.2 Toothfish diet and distribution

As with many other bathyal fish species (500 to 2,000 m depth in the Southern Ocean), toothfish species are known to occupy a wide geographic distribution (Rogers, Morley et al. 2006). *D. eleginoides* are most abundant around the sub-Antarctic Islands of the Southern Ocean and the southern cone of South America (De Witt, Heemstra et al. 1990). Antarctic toothfish have a number of adaptations to life at very cold water temperatures and are endemic to the seasonal pack-ice and high Antarctic zones surrounding the Antarctic Continent (De Witt, Heemstra et al. 1990) (Fig. 1.5). Populations of the two species are known to overlap at only a few locations, including the BANZARE (British, Australian and

New Zealand Antarctic Research Expedition) Bank in the Southern Indian Ocean (McKinlay, Welsford et al. 2008), over seamounts in the northern Ross Sea (Horn 2002; Hanchet 2009) and around the South Sandwich Islands in the South Atlantic, where they are targeted by a deep water longline fishery (Roberts, Xavier et al. 2011; presented in Annex A) (Fig. 1.5).

Both toothfish species are primarily piscivorous at all life stages, though will scavenge a wide range of prey taxa depending on their availability (McKenna 1991; Garcia del la Rosa, Sanchez et al. 1997; Pilling, Purves et al. 2001; Goldsworthy, Lewis et al. 2002; Xavier, Rodhouse et al. 2002; Arkhipkin, Brickle et al. 2003; Hoff 2004; Collins, Ross et al. 2007; Roberts, Xavier et al. 2011). Juveniles are, in turn, predated on by fur, elephant and Weddell seals (Collins, Ross et al. 2007). Owing to their large size, adult toothfish have few natural predators, though their remains are often found in the stomachs of sperm whales and elephant seals (Collins, Ross et al. 2007) and there is good evidence that they may predate on and be predated by colossal squid of different life stages (Roberts, Xavier et al. 2011).

#### **1.4** Development of fisheries for toothfish species

Toothfish were initially taken as bycatch in trawl fisheries operating over the shelf regions of Patagonia, South Georgia and the Kerguelen Plateau in the late 1970s and early 1980s (Kock 1992). They were first targeted by deep set longline gear around Chile in the mid-1980s (Collins, Brickle et al. 2011). Targeted fisheries for toothfish species then rapidly emerged about the Patagonian shelf and around sub-Antarctic Islands including South Georgia, Kerguelen and Heard Island. Reported catches of *Dissostichus* spp. peaked at around 30-40 thousand tonnes per annum between 1992 and 2003 and subsequently declined to around 25,000 tonnes (Fig. 1.4) (Collins, Brickle et al. 2011).



Figure 1.4 Annual reported landings of toothfish species. From Collins et al. (2011).

The lesser sub-Antarctic islands were first subject to exploratory fishing for *D. eleginoides* in the 1990s, including a number of islands in the Southern Indian Ocean: Heard Island, the Prince Edward Islands and Ob and Lena Sea-banks (Abellan 1999; Abellan 2005). Of these, only Heard Island currently supports a fishery of economic significance, while the stock at the Prince Edward Islands has been greatly depleted by illegal, unreported and unregulated (IUU) fishing (Agnew 2000).

The Antarctic Peninsula was first explored for toothfish in 1998 and was found to support populations of both *D. eleginoides* and *D. mawsoni*, though at very low densities (Arana and Vega 1999). *D. mawsoni* stocks fringe the Antarctic Continent and extend across the seasonal pack ice zone. A mixed *Dissostichus* spp. fishery operates in the Ross Sea (FAO Subareas 88.1 and 88.2) with a combined species annual yield of approximately 3,000 tonnes, though this is dominated by catches of *D. mawsoni* with much smaller take of *D. eleginoides* (<50 t per annum) mainly captured over northern seamounts (Hanchet 2009).

The first reported fishing for toothfish at the South Sandwich Islands (FAO Statistical Subarea 48.4) was by a single Ukrainian longliner vessel in early 1990 (CCAMLR 2011), though this and other exploratory trips in the 1992/93 season experienced low catch rates (Rubilar, Moreno et al. 1993). A single trip in 2005 was more successful and fishing has occurred at the South Sandwich Islands in all seasons since, focussed on gathering the data requirements for a robust assessment of toothfish biology and population size to inform the management of the fishery (Roberts and Agnew 2009a).



Figure 1.5 CCAMLR Convention area and approximate *Dissostichus* spp. distribution. South Georgia (FAO Statistical Subarea 48.3) and South Sandwich Islands (48.4) highlighted by yellow box. From CCAMLR website (<u>http://www.ccamlr.org/Pu/e/conv/map.htm</u>).

At the South Sandwich Islands, longline operations have been heavily constrained by research fishing objectives, such that effort has been spread evenly across the fishable area and a broad bathymetric range (GSGSSI 2009). Scientific Observers have been present on all vessels, with intensive data collection on catch rates and biological observations of target and bycatch species. The observer data collection procedure was based on the recommended sampling protocol for CCAMLR observers (CCAMLR 2005) and further biological sampling and observations were made according to the data requirements for management and development of an exploratory fishery. As such the data available for assessments of toothfish life history and dispersal are of extremely good quality for a deepwater stocks at such an early stage of exploitation (Roberts and Agnew 2009a).

#### 1.5 Project aims

The South Sandwich Islands are one of only a few areas where populations of both toothfish species are found. Here both species are targeted by an exploratory fishery with continuous effort since 2005. Empirical studies on range position effects on life history and also on deep water populations are often compromised by a lack of quality data, which may be difficult or costly to obtain (Gaston 2009; Sexton, McIntyre et al. 2009). From the outset, the longline fishery at the South Sandwich Islands has proceeded within a research framework aimed at providing the data requirements for assessment of toothfish biology, dispersal and population size. At present, the total depletion incurred by the target stock is likely to be minimal (Roberts, Mitchell et al. 2011).

The opportunity is taken to assess range position effects on the life history and population dynamics of toothfish populations at the edge of their distributional range, with the aim of answering two main research questions:

## **1.** What limits the distribution of D. eleginoides at the South Sandwich Islands and how do range edge population dynamics differ from those of range centre populations?

Here, the research is focussed on a number of sub-questions designed to explore the extent to which the current theory on range edge population dynamics is demonstrated empirically in South Sandwich Islands toothfish populations (Table 1.1). Table 1.1 Research questions relating to range edge formation

General question	Research questions	Chapters
To what extent are bathyal	What are the general patterns of fish and	2
taxa of the Southern Ocean	invertebrate taxonomic composition at the	
delineated in to different	South Sandwich Islands and what are the	
bioregions and what are the	likely environmental drivers of community	
main physical drivers of	change?	
ecosystem change? (Arntz,		
Thatje et al. 2005).		
How do changes in deepwater	To what extent are toothfish species range	3
fish distribution relate to	limits correlated with critical values of	
changes in habitat type and	environmental variables such as seawater	
are the same relationships	temperature or sea ice coverage? How might	
observed in different regions?	these range limits shift with regional climate	
(Stefansdottir, Solmundsson et	change?	
al. 2010)		
What changes in life history	Do we see range position effects on toothfish	4
strategy do we see towards	life history and to what extent are differences	
range limits and do we see	in growth, gonad development and	
empirical evidence for	recruitment inter-related?	
reduced fitness? (Gotthard		
and Nylin 1995; Sexton,		
McIntyre et al. 2009)		
How important are	To what extent are toothfish species range	5
immigration and emigration	limits created by dispersal effects at larval	
events in shaping the range	and adult life stages? How does this relate to	
edges of deepwater fish	range position effects on life history?	
species? (Bahn, O'Connor et		
al. 2006; Goldberg and Lande		
2007)		

## 2. How can we use this information to more effectively manage the toothfish fishery at the South Sandwich Islands and on other range edge populations?

Here, life history parameters estimated for the range edge toothfish population at the South Sandwich Islands are used to estimate population size and sustainable yield. The effects of range centre versus range edge population dynamics on fisheries management are explored with discussion as to how this research informs the management of deep water and range edge stocks elsewhere (Table 1.2).

Table 1.2 Research questions	relating to t	he management	of range edge	fisheries
Table 1.2 Research questions	relating to t	ine management.	of range euge	IISHCIICS

General question	Research questions	Chapter
How do range edge	How does incorporation of range edge	4,5&6
population dynamics effects	population dynamics effect population and yield	
assessment of range edge	assessments for toothfish species at the South	
populations? (Gaston 2009)	Sandwich Islands?	
What are the likely	How might population assessments need to be	6
consequences of range edge	modified to account for range edge population	
population dynamics for	dynamics? Is the CCAMLR management	
management of resource	framework appropriate for management of	
exploitation?	range edge toothfish populations?	

## **1.6 Chapter organisation**

An array of analytical methods are used to address the aims stated above, ranging from computational modelling of fishery data to forensic techniques for the analysis of biological samples (Fig. 1.6). These analyses primarily use data and samples collected during commercial fishing operations. The methods used are described in the chapter descriptions below and then in more detail in the relevant chapters.


Figure 1.6 Methodological framework for this project

#### Chapter 2 Bioregionalisation analysis of the bathyal South Sandwich Islands using data from an exploratory longline fishery

Previous studies have not managed to define the location of the boundary between Subantarctic and Antarctic bioregions to a particularly high resolution and are most deficient at the South Sandwich Islands where historic data collection has been minimal. Here catch and effort data from the exploratory longline fishery at the Sandwich Islands were used to describe the distributional patterns of abundant finfish and invertebrate species of the bathyal zone. Hierarchical clustering and ordination analyses were used to conduct a bioregionalisation analysis to evaluate changes in fish (including toothfish) and invertebrate communities along the island arc. Changes in taxonomic composition were related to changes in marine environment such that the mechanistic drivers of community change might be identified.

# Chapter 3 Distribution of toothfish species comparing South Sandwich Islands and the Ross Sea populations

Toothfish form a near continuous distribution over the bathyal region of the Southern Ocean seafloor, with a transition in species dominance occurring between 55°S and 65°S, depending on longitude. Longline catch and effort data were used to predict the distribution of toothfish species relative to environmental correlates. Generalised linear models (GLMs) were used to predict toothfish spp. catch rates and species composition of catch in response to an array of habitat-related explanatory variables, including depth, temperature and ice cover. This was used to identify which variables had a critical effect on toothfish species distribution and, hence, where likely to influence the formation of range limits. The model was then used to predict toothfish species distribution in the Ross Sea and the causes of discrepancies between predicted and observed distributions were discussed.

#### Chapter 4 Range edge effects on the life history of toothfish species *Dissostichus eleginoides* and *D. mawsoni* at the South Sandwich Islands

Toothfish biometric data collected from the longline fishery at the South Sandwich Islands were used to estimate key life history parameters for the assessments conducted in Chapter 6. A variety of analytical methods were adopted in order to determine stock age structure and temporal recruitment strength, von Bertalanffy growth parameters, length at maturity and length-mass relationships. In order to test the hypothesis of reduced fitness towards range edges, comparison was made between life history parameters of South Sandwich Islands populations with range centre populations at South Georgia (*D. eleginoides*) and the Ross Sea (*D. mawsoni*).

#### Chapter 5 Dispersal patterns of South Georgia and South Sandwich Islands toothfish from otolith microchemistry and mark recapture studies

The otolith microchemistry of Patagonian toothfish was analysed to determine the geographical origin of South Sandwich Islands toothfish and the degree of mixing with other

populations of the South Atlantic. Inferences from the otolith chemistry analysis were compared with those from genetic analyses conducted previously on the same individuals (Fitzcharles 2007). In addition, mark-recapture data from the longline fisheries at South Georgia and the South Sandwich Islands were used to estimate adult migration rates between the two populations. The model was constructed to estimate the most likely migration rates using a simple two-area assessment using mark-recapture observations. Current theory suggests that dispersal rates should be increased towards range edges, though studies have been biased towards evaluating evidence for range expansion. This study evaluated empirical evidence for the role of range contraction in the formation of range limits, while sex-effects on dispersal rates were also explored.

# Chapter 6 Exploitation of range edge populations: population assessment and yield estimation of South Sandwich Islands *D. eleginoides*

The effects of range edge population dynamics on population assessment of Patagonian toothfish at the South Sandwich Islands were explored. CASAL (C++ algorithmic stock assessment laboratory) stock assessment software was used to estimate population size and sustainable yield for the Patagonian toothfish fishery in the Northern Management Area of the South Sandwich Islands. This model made use of the life history and dispersal parameters estimated in Chapters 4 and 5. This was followed by a discussion of the effects of range edge life history and population dynamics on population assessment and yield estimation and the implication for management of range edge stocks.

#### Chapter 2

## Bioregionalisation analysis of the bathyal South Sandwich Islands using data from an exploratory longline fishery

"The most horrible coast in the world... a Country doomed by nature never once to feel the warmth of the Sun's rays" Captain James Cook on discovering the South Sandwich Islands in 1775.

#### 2.1 Introduction

The South Sandwich Islands remain of the most poorly described regions of the Southern Ocean (Ramos 1999; Arntz, Thatje et al. 2005). Previous studies have found finish and invertebrate species typical of Subantarctic and Antarctic bioregions are present here (Arntz and Brey 2003; Arntz, Thatje et al. 2005) and, as such, it is likely that a number of species are situated on their distributional range edge. In this chapter a bioregionalisation analyses was conducted to define the spatial boundaries between finfish and invertebrate communities about the island arc, using data collected from the exploratory longline fishery. The extent and location of community change was then compared with the spatial patterns environmental variables in order to identify the potential causes of any observed bioregionalisation.

#### 2.1.1 Bioregionalisation

Bioregions are large areas of the Earth's biosphere, where a particular set of environment conditions pervade, supporting a resident flora and fauna community of a distinctive composition (Grant, Constable et al. 2006). Often physical structuring of the marine environment by topography or large-scale forces such as atmospheric and oceanic currents can cause steep gradients in environmental variables which impact on the biological function of organisms (Grant, Constable et al. 2006; Murphy, Watkins et al. 2007). In extreme cases this can lead to the development of abrupt ecotones, where a community typical of one bioregion merges into another (Grant, Constable et al. 2006; O'Hara, Rowden et al. 2011).

A bioregionalisation is an analytical process where broad areas are partitioned into distinct bioregions, using a range of environmental and biological information (Grant, Constable et al. 2006). Bioregionalisation analyses have a broad range of uses from evolutionary studies to conservation planning (Spellerberg and Sawyer 1999; Lourie and Vincent 2004). Bioregionalisation analyses can vary greatly in their approach and degree of objectivity. A more subjective analysis may be based on expert opinion or might for example define bioregional boundaries through visual inspection of the spatial distributions of a number of species (Pawson 1995). A similar approach may be taken to define bioregions from spatial patterns in the biogeochemical environment and this may complement analyses using species distributions (Longhurst 1998). Statistical techniques such as non-metric multidimensional scaling (NMDS) ordination and hierarchical multivariate clustering analyses can be used to group different samples according to taxonomic similarity (Hargrove and Hoffman 1999; Griffiths and Linse 2009; Last, White et al. 2011). The latter of these is considered to be more objective than ordination for defining biogeographical boundaries (Clarke 1993; Grant, Constable et al. 2006), though a judgement must still be made to as to what level of dissimilarity between two community types constitutes a bioregional boundary and this tends to vary between studies (Clarke 1993). As such a variety of different analytical techniques are often used and the inferences compared (Last, White et al. 2011).

#### 2.1.2 Biogeography of the Atlantic Southern Ocean

The biogeography of the Southern Ocean is characterised by spatial heterogeneity in biological productivity and a north to south graduation in temperature and environmental correlates (*e.g.* mean sea ice coverage) which may be abrupt close to major hydrographic fronts (Murphy, Watkins et al. 2007). High latitude finfish and invertebrates must adapt to very cold water temperatures, seasonal ice cover and extreme temporal variation a range of environmental variables (Eastman 1990; Arntz, Thatje et al. 2005). The three Southern Ocean ichthyofaunistic bioregions proposed by Kock (1992) were based on patterns in sea ice formation (from north to south): **The Ice-free Zone**, between the Antarctic Convergence and the northern limit of the pack ice zone; **The Seasonal Pack-ice Zone**; and **The High-Antarctic Zone**, fringing the Antarctic Continent. Species typical of the latter two zones are often referred to as Antarctic species, the former being Subantarctic. A latitudinal zonation has also been observed in a variety of finfish and benthic invertebrate species distributed along the Scotia Arc, with species representative of both Antarctic and Subantarctic

bioregions found at the South Sandwich Islands (Arntz 1999; Arntz and Brey 2003; Arntz, Thatje et al. 2005) (Fig. 2.1).



Figure 2.1 (left) Biogeographical divisions of the Southern Ocean based on shelf and upper slope fish fauna; I Antarctic Region; 1 – South Polar Province; A – East Antarctic District; B West Antarctic District; 2 – South Georgian Province; II Sub-Antarctic Region; Thick line represents flow of the Antarctic Circumpolar Current (Gon and Heemstra 1990); and (right) distribution of one Subantarctic nototheniid: *Dissostichus eleginoides* and one Antarctic nototheniid *Lepidonotothen kempi* along the Scotia Arc (Arntz and Brey 2003).

Observations from limited survey sampling at the South Sandwich Islands suggest that resident invertebrate and finfish communities are dominated by a low biomass and diversity of opportunistic taxa (Ramos 1999; Arntz and Brey 2003; Linse, Brandt et al. 2007; Griffiths, Linse et al. 2008) that are likely to have been shaped by frequent disturbance events from local volcanic and seismic activity (Kaiser, Barnes et al. 2008). The postulated north to south zonation of Antarctic and Subantarctic species along the Scotia Ridge has been demonstrated for a number of finfish and invertebrate species (Lopez Abellan and Balguerias 1994; Arntz and Brey 2003), though the low spatial resolution of survey sampling effort has not until now permitted a detailed analysis of the location and mechanism of barriers to dispersal around the South Sandwich Islands, where the Weddell Front (WF) bisects the Scotia Ridge (Arntz and Brey 2003). In addition, sampling of benthic communities deeper

than 600 m has been extremely sparse and the bathyal ecosystems of the South Sandwich Islands remain poorly described (Ramos 1999; Arntz, Thatje et al. 2005).

#### 2.1.3 Marine environment of the South Sandwich Islands

The South Sandwich Islands comprise a 368 km long north to south oriented arc of eleven caldera located on the Scotia Ridge in the Atlantic Southern Ocean. The seafloor extends to >2,000 m depth between caldera and the island arc is isolated from South Georgia located 550 km to the northeast and the South Orkney Islands to the southwest by even deeper saddles in the Scotia Ridge (>3,000 m depth in places) (Holdgate and Baker 1979) (Fig. 2.2). Volcanic eruptions are frequent and activity has been detected at all except two islands over the past 100 years: Cook Island (Thule group); and Vindication (Candlemas group) (Allen and Smellie 2008; Leat, Tate et al. 2010). Benthic sediments of the bathyal zone are primarily composed of coarse basaltic pebbles and boulders, with volcanic sandy silt in places (Goodell 1964).



Figure 2.2 (left) Major water bodies, frontal systems and bathymetry of the Weddell Sea and Scotia Sea, taken from Murphy et al. (2007), 1,000 and 3,000 m depth contours shown. Labels are "ACC" – Antarctic Circumpolar Current; "PF" – Polar Front; "SB" – Southern Boundary of ACC; "WG" – Weddell Gyre; "WSC" – Weddell Scotia Confluence; and (right) mean September temperature at 1,000 m depth (Schlitzer 2006) and location of small island areas use in bioregionalisation analysis. Labels are island areas: "Br" – Bristol; "Ca" – Candlemas; "MS" – Montagu Seamount; "Mo" – Montagu; "Pr" – Protector Shoal; "Sa" – Saunders; "Th" – Thule; "Va" – Visokaya; "Vi" – Visokoi; and "Za" – Zavadovski.

The hydrography of the Southern Ocean is dominated by the eastward flowing Antarctic Circumpolar Current (ACC), which encircles the Antarctic Continent between 45°S and 60°S (Orsi, Whitworth et al. 1995). The ACC Southern Boundary (SB) separates the ACC from the cold water Weddell Gyre (WG) and Ross Sea Gyre (RSG) circulating adjacent to Antarctica. The hydrography of the South Sandwich Islands is not well described, though is likely to be quite complex. After flowing through Drake's Passage, the ACC is diverted northwards by the Scotia Ridge and the winter formation of sea-ice from the South, such that the warm waters of the ACC do not reach the South Sandwich Islands in most years (Orsi, Whitworth et al. 1995). In the southwest Atlantic, the ACC is separated from the Weddell Gyre by a third water body, the Weddell-Scotia Confluence (WSC) (Whitworth, Nowlin et al. 1994). The Weddell Front, which forms the northern boundary of the WG, bisects the South Sandwich Islands in the region of Saunders and Montagu Islands (Orsi, Nowlin et al. 1993) (Fig. 2.2). Elevated primary production and changes in temperature and marine biota are observed at each of these major frontal systems (Murphy, Watkins et al. 2007).

#### 2.1.4 Biogeography from longline catch and effort data and chapter aims

A small number of studies have made use of commercial fisheries data to describe the regional biogeography of the marine environment (Pawson 1995; Reygondeau, Maury *et al.* 2011). These may include quite subjective analyses, such as that conducted by Pawson *et al.* (1995), where the spatial distribution of catch or landings per unit effort was plotted for a number of commercially exploited species in the English Channel and North Sea, many of which were captured together in multi-species fisheries. These species were then grouped visually according to similarity of distributional range to inform the identification of appropriate multi-species management areas. A far more objective approach was adopted by Reygondeau, Maury *et al.* (2011) who conducted a bioregionalisation analysis of tuna and billfish communities through quantitative statistical analyses of pelagic longline catch and effort data. Hierarchical clustering analyses were used to define nine distinct communities that could be related to biogeochemical provinces, such that the tropical oceans could be divided in to a mosaic of community types.

Relative to studies using fisheries data, analyses using biological survey data will tend to benefit from improved data quality and the ability to tailor the sampling protocol to optimise a bioregionalisation analysis. However, analyses using fisheries data may benefit from an increased spatial and temporal resolution of sampling effort, and also a wide geographic spread of observations such that, despite decreases in data quality and biases introduced by inconsistent fishing practises (Reygondeau, Maury et al. 2011), gradients in community change can be observed across time and space to a higher resolution.

The South Sandwich Islands demersal toothfish longline fishery has operated in all seasons since 2005 with a wide bathymetric (700 m to 2,000 m) and spatial (55.5°S to 60°S) distribution of effort (Roberts and Agnew 2009a). Industry and observer catch and effort data from longline fishing operations at the South Sandwich Islands were used to conduct a bioregionalisation analysis of the bathyal environment at a much higher resolution than has previously been possible from survey data. Observed patterns were then related back to environmental correlates to identify the potential mechanisms that drive the north-to-south regionalisation of bathyal megafauna at the Subantarctic-Antarctic boundary, in a region where previous sampling effort has been particularly sparse and benthic communities are extremely poorly described (Ramos 1999; Arntz and Brey 2003; Arntz, Thatje et al. 2005).

#### 2.2 Methods

#### 2.2.1 Data collection

Catch and effort data were obtained from longline vessel operations at the South Sandwich Islands from 2005 to 2010. All vessels deployed an autoline gear configuration with lines typically consisting of 4,000 to 10,000 hooks, baited with squid. Catch rates of finfish by-catch species were esiimated from line observation data collected by Scientific Observers, monitoring a random sample of more than 20 % of hooks hauled, according to the protocol described in the CCAMLR Scientific Observer Manual (CCAMLR 2005). Catch rates of toothfish species were estimated from vessel-reported catch and effort data (CCAMLR 2011).

Data on catch rates of invertebrate species were not collected on every trip. From 2005 to 2008, observers recorded invertebrate catches during random line sampling (as CCAMLR 2005). From 2009 onwards, observers collected data on Vulnerable Marine Ecosystem (VME) taxa during designated sampling periods (CCAMLR 2009), though some observers continued to collect data on non-VME invertebrate taxa, including starfish (asteroids) and non-VME brittlestars (ophiuroids) during regular hook observation periods. During this period, data

from these two sources were combined where effort data (in terms of hooks observed) were available. Comparative data on VME and other invertebrate taxa catch rates were collected by CCAMLR scientific observers on longliners operating at South Georgia (2006 to 2009) and UK-flagged vessels operating in the Ross Sea (2008 to 2010) (data used with permission from Argos Fishing).

Species were identified to the lowest possible taxonomic level. A range of materials were used to assist with species identification including CCAMLR observer guides and species identification sheets (CCAMLR 2005; CCAMLR 2009). Fish species identifications were verified by observations of diagnostic features relating to anatomy and otolith structure (Gon and Heemstra 1990; Williams and McEldowney 1990).

Prior to 2008, fishing operations were limited to the region north of 57.4°S. All island areas were explored during this period, though a greater proportion of effort was expended over the Protector Shoal, where catch rates of *D. eleginoides* were initially greatest (Fig. 2.4). A more even spread in the spatial distribution of effort was observed following the expansion of fishing into the Southern Area. The bulk of fishing has operated seafloor between 1,000 and 1,800 m depth, similar to the depth distribution of the fishery data sample from the North of the Ross Sea though slightly deeper than at South Georgia or in the Central, Southern or eastern regions of the Ross Sea (Fig. A2.1).

#### 2.2.2 Taxon distribution

Catch per unit effort (CPUE) (frequency per hook set or observed) was used as a proxy for abundance for finfish and invertebrate by-catch taxa. There are a number of potential sources of bias which may impact on the extent to which catch rates reflect true abundance, and these may relate to: the morphology or behaviour of the resource, environmental factors (Bigelow, Boggs et al. 1999) and fishing practices – all of which may exhibit some degree of temporal or spatial variation (Maunder, Sibert et al. 2006). Some of the biases may be controlled for through CPUE standardisation (Maunder and Punt 2004), though that was not done here as fishing methods and data collection protocols were spatially and temporally consistent at the South Sandwich Islands. Also a high degree of variability in catch rates of most taxa had previously been observed by location and with depth (Figs. Table 2.2 and Figs. A2.2, A2.3 & A2.4) such that other sources of variability would be unlikely to totally obscure the effects of location of capture.

Spatial plots used data aggregated to a 0.2-degree square resolution while depth data were aggregated in to 200 m depth categories as this allowed for sufficient sampling effort in each area or depth partition. In each instance, the line position was taken as the mean of the start and end of line setting positions, as reported by the Scientific Observer. Baiting percentages were nearly always >95 % and therefore no adjustment of catch rates was made to account for empty hooks.

#### 2.2.3 Bioregionalisation analysis

Plots of taxonomic hotspot regions for the main taxa (Figs. 2.4 & 2.6) were defined as grid squares where CPUE was a minimum of 10 % of the maximum for any one grid square for a given taxon. The 10% level was found to result in the identification of a number of hotspot areas for most finfish and invertebrate taxa and spatial trends that could be explained by environmental gradients about the fishable area.

Clustering and ordination analyses were undertaken to identify finfish and invertebrate bioregions moving from north to south along the South Sandwich Islands. This was focussed on testing the hypothesis that the islands would be divided in to Subantarctic and Antarctic bioregions based on the taxonomic composition of macrofauna in longline catches. In addition the location and gradient of community change was also identified and related back to potential environmental drivers of regionalisation. For the clustering and ordination analyses (Figs. 2.8 & 2.9), catch and effort data were aggregated to determine the proportion of lines on which a particular fish or invertebrate taxon was present in an island area (Fig. 2.1) and depth category (400 – 800 m; 800 – 1,200 m; 1,200 – 1,600 m; 1,600 – 2,000 m). Trends with Depth and location of capture had previously been seen in the catch rates of all taxa encountered (Table 2.2 and Figs. A2.2, A2.3 & A2.4). This was then used to construct a resemblance matrix of Bray-Curtis similarity coefficients and subjected to non-metric multidimensional scaling ordination and hierarchical clustering analysis (un-weighted pair-group method using arithmetic averages – UPGMA) using the *vegan* package in *R* opmenytopme (Oksanen, Blanchet *et al.* 2011; R Core Development Team 2011).

#### 2.3 Results

#### 2.3.1 Finfish catch composition

A total of 485 tonnes of toothfish species have been caught in longline fishing operations since 2005, including individuals that were subsequently released. This comprises 69.0 % of the total catch weight of finfish from all seasons combined. Large catches of *D. mawsoni* were only made once the fishery extended south of 57.4°S, where they were much more abundant (Fig. 2.4). Macrourids and rajids dominated finfish by-catch, comprising 11.5 % and 19.0 % of total catch weight, respectively, though the majority of rajid by-catch was released alive immediately following capture. The remaining by-catch species, including *Antimora rostrata*, Muraenolepidids, nototheniids and icefish comprised less than 0.5 % of the total catch weight (Table 2.1).

Rajid by-catch was dominated by *Raja georgiana*. Rajid species normally observed in longline by-catch at South Georgia, including *Bathyraja meridionalis* and a deep water variant of *A. georgiana*, were not observed at the South Sandwich Islands (Endicott 2011). Large catches of *Bathyraja maccaini* were captured on shallow set lines. Two nototheniid taxa, identified as *Lepidonotothen kempi* and *Notothenia* sp. were also captured on shallow set lines (Table 2.2). Macrourid by-catch was dominated by *Macrourus whitsoni* while a cryptic *Macrourus* species has also been tentatively identified from genetic sampling of macrourids captured south of Saunders Island (E. Fitzcharles 2011, unpub. data). Muraenolepidid by-catch was mostly identified as *Muraenolepis microps* (Table 2.1).

Taxon	2004/05	2005/06	2006/07	2007/08	2008/09	2009/10	All
D. eleginoides	13.37	3.98	7.56	9.00	3.66	3.04	5.34
D. mawsoni	0.00	0.03	0.01	0.01	1.43	1.60	0.80
Macrouridae	23.01	17.33	27.29	22.56	32.19	24.17	25.73
A. rostrata	1.88	0.21	0.56	0.53	0.62	0.69	0.62
Muraenoelpididae	0.01	0.13	0.09	0.14	0.95	0.72	0.51
Nototheniidae (other)	0.00	0.34	0.19	0.09	0.28	0.01	0.17
Channichthyidae	0.00	0.00	0.00	0.00	0.01	0.00	0.01
A. georgiana	3.72	12.95	8.68	10.18	5.92	1.83	9.89
B. maccaini	0.00	0.00	0.00	0.88	0.00	0.00	0.16

Table 2.1 Annual CPUE (*n* per 1,000 hooks observed) of finish taxa.

Table 2.2 Finfish CPUE (*n* per 1000 hooks) by depth category. Bars represent proportion of maximum CPUE for any one taxon.

Depth bin mid (m)	B. maccaini	Other nototheniid sp.	M. microps	A. georgiana	D. eleginoides	D. mawsoni	M. whitsoni	A. rostrata
300 500 700 900 1100 1300 1500	50.7 3.2 1.9 0.0 0.0 0.0 0.0	0.7 5.3 3.8 0.1 0.2 0.0 0.0	<ul> <li>0.0</li> <li>1.8</li> <li>0.4</li> <li>0.1</li> <li>0.6</li> <li>0.3</li> <li>0.2</li> </ul>	<ul> <li>0.0</li> <li>1.9</li> <li>9.6</li> <li>14.0</li> <li>13.9</li> <li>8.9</li> <li>9.4</li> </ul>	0.0       0.2       2.3       4.5       4.6       6.0       5.9	1     0.0       0.0     0.0       0.0     0.2       0.6     0.5       1.5	<ul> <li>0.0</li> <li>4.8</li> <li>8.9</li> <li>16.7</li> <li>29.1</li> <li>27.6</li> <li>24.6</li> </ul>	<ul> <li>0.0</li> <li>0.0</li> <li>0.1</li> <li>0.0</li> <li>0.2</li> <li>0.6</li> <li>0.6</li> </ul>
1700 1900	0.0	0.0	0.1	10.1 7.1	2.9 3.0	0.5	38.8 31.6	0.9



Figure 2.3 Finfish by-catch species at the South Sandwich Islands: a) *Lepidonotothen* cf. *kempi*; b) *Amblyraja georgiana*; c) *Notothenia* cf. *rossii*; and d) *Chaenocephalus aceratus*.

#### 2.3.2 Finfish distribution

Both toothfish species were distributed widely across the fishable area of the South Sandwich Islands, with an abrupt transition in species dominance occurring around Saunders and Montagu Islands, between 57.5°S and 58.5°S. Small catches of *D. eleginoides* were made to the south of this point, mainly along west-facing slopes fringing the Scotia Sea, while *D. mawsoni* were captures to the north were extremely rare.

Macrourids were widely distributed, with decreases in catch rates observed around island caldera south of 58°S. These are thought to be the areas where the cryptic *Macrourus sp.* were most abundant (E. Fitzcharles 2010, pers. comm.). *R. georgiana* were also distributed throughout the fishable area though were more abundant over west-facing slopes to the north of 57.5°S. Muraenolepidids (*Muraenolepis* cf. *microps*) were most abundant south of 57.5°S with occasional catches on east-facing slopes to the north of this, *i.e.* in all the areas where *R. georgiana* are not abundant. Nototheniids (other than *Dissostichus* spp.) were mainly caught in the north, though few shallow sets (where catch rates were highest) were conducted in the Southern Area. *Antimora rostrata* were more abundant in the north though very high catch rates were also observed over the large submerged caldera to the east of Montagu Island (Fig. 2.4).

Nototheniids and the rajid *B. maccaini* dominated catches on lines set shallower than 600 m. All other major finfish by-catch species were distributed deeper, including *R. georgiana*, which was most abundant shallower than 600 m at South Georgia (Endicott 2011), though was rarely captured on lines set shallower than this at the South Sandwich Islands. The two toothfish species had a similar distribution with depth and were most abundant between 1,000 m and 1,800 m depth, where the bulk of fishing effort was distributed. *A. rostrata* peaked in abundance at depths deeper than those operated by the fishery (Table 2.2).



Figure 2.4 Spatial distribution of effort (top left) and CPUE distribution of *Dissostichus* spp. (top right); major finfish by-catch species (bottom left); and minor finfish by-catch species (bottom right) at the South Sandwich Islands.

#### 2.3.3 Invertebrate catch composition

A wide variety of invertebrate species interacted with longline fishing gear at the South Sandwich Islands. As at South Georgia and the Ross Sea, invertebrate by-catch was dominated by cnidarians (including actiniaria and cold water coral species), echinoderms and king crabs (*Lithodidae*) (Fig. 2.5). Catch rates of the main echinoderm taxa – asteroids and ophiuroids (574 and 264 per million hooks, respectively) – were similar to those observed at the Ross Sea (1,524 and 264 per million hooks) and were much less abundant at South Georgia. By comparison, holothurians were more abundant at South Georgia. Catch rates of actiniarians at the South Sandwich Islands were higher than all cold water coral taxa combined (343 compared to 113 per million hooks) and gorgonians were much less abundant here than at South Georgia (78 and 744 per million hooks) (Table A2.1). Tentative identifications were made of a selection of gorgonian colonies, with *Thourella* and *Metafanyella* species comprising 8 out of 15 colonies identified to genus level (M. Taylor 2009, pers. comm.). No scleractinian corals were observed at the South Sandwich Islands, though actiniarians (anemones) were abundant and may be dominated by a small number of unidentified species (Table A2.1).

Mobile invertebrate fauna were dominated by ophiuroids and asteroids, though species identifications were not made of either of these taxa. King crabs were rarely captured south of 57°S and all observer identifications to species level suggest that *Paralomis formosa* are the only species present at the depths targeted by the longline fishery (Table A2.1).



Figure 2.5 Two suspension feeding invertebrate taxa entangled on longline gear at the South Sandwich Islands: a) *Thourella* sp.; b) large *Actiniarian* sp.; and two mobile invertebrate taxa attracted to squid bait: c) large predatory asteroids and d) *Paralomis formosa*.

#### 2.3.4 Benthic invertebrate distribution

Catch rates of sedentary suspension feeding organisms were greatest at locations where mobile fauna were less abundant. The former, dominated by actiniarians and gorgonian corals were most abundant over Protector Shoal and Zavadovski in the north, around Saunders Island at the centre and over Visokaya Bank in the South. Mobile fauna, dominated by asteroids and ophiuroids (cf. *Ophiocamax gigas*) were much more abundant over the slopes of Montagu, Bristol and Thule Islands (Figs. 2.6, A2.2 & A2.3).



Figure 2.6 Spatial CPUE distribution of sedentary feeding (left) and mobile invertebrate taxa (right) at the South Sandwich Islands.

A separation in the distribution of the main suspension feeding taxa was observed with depth. Gorgonians and sponges were most abundant shallower than 600 m, while actiniarians are found across a broad range of depths and were most abundant between 800 m and 1,000 m depth. Hence in the South, low fishing effort shallower than 800 m may partly explain the reduced catch rates of gorgonian corals and sponges, though catch rates of other suspension feeding organisms (particularly actiniarians) were also low. Likewise, the reduced catch rates of coldwater corals and sponges at the South Sandwich Islands relative to South Georgia may reflect the low proportion of sets shallower than 800 m (Figs. A2.1 & A2.4).

Large north-south gradients were observed in the CPUE of mobile fauna. The combined CPUE of asteroids and ophiuroids was much greater in the south than in the north when comparing the same depth categories (ranging from 1,324 to 4,323 individuals per million hooks between 800 and 1,800 m depth over 200 m classes in the North, compared to 82 to 399 in the South over the same depth range). In the northern area, a bimodal distribution in asteroid CPUE was observed with depth, suggesting that different taxa dominate in shallow

and deep areas of seafloor. Catch rates of stone crabs (*P. formosa*) were greatest in the 800 m - 1,400 m depth range (Fig. A2.4).

#### 2.3.5 Bioregionalisation analysis

An abrupt change in finfish and crab catch composition was observed south of Saunders Island, at approximately 58°S. Catch and effort data indicate that this area is the southern extent of abundant populations of Subantarctic species, including: *D. eleginoides, A. georgiana* and *P. formosa*. This location is also the northern distributional extent of two typically Antarctic species known to have antifreeze glyco-proteins: *D. mawsoni* and *M. microps* (Fig. 2.7). The multidimensional scaling ordination produced two distinct clusters based on catch composition of fish taxa with all locations to the south of Candelmas in one 'Antarctic' cluster and all to the north in a 'Subantarctic' cluster (Fig. 2.8). The hierarchical clustering analysis allocated the two same groups to discrete clusters at the 30 % level of dissimilarity. The species composition of sites to the north of Saunders were very similar, regardless of depth band (<15 % dissimilarity) (Fig. 2.9).



Figure 2.7 High CPUE regions for finfish taxa (left) and invertebrate taxa (right). Positives indicate 0.2 degree grid squares where CPUE was greater than 10% of the maximum for any one grid square.

A steep gradient in abundance was also observed in invertebrate taxa moving from north to south. Some of these taxonomic groupings are likely to be quite diverse in species composition and may comprise both Subantarctic and Antarctic species. Hence gradients in abundance are likely to reflect changes in habitat type. Sessile, suspension feeding taxa (including *gorgoniidae*, *actiniaria*, *porifera* and *alcyonacae*) were most abundant to the north of 58°S, over the submerged caldera to the east of Montagu Island and to the South of the Thule Island group. Asteroids appear to be highly abundant in all regions where the suspension feeding organisms were not (Fig. 2.7). The ordination analysis based on invertebrate catch composition grouped all locations to the south Candlemas Island together. The distinction between the invertebrate communities, suggesting a more gradual north to south change in taxonomic composition of invertebrates, though the degree of overlap between the two areas was minimal (Fig. 2.8). The clustering analysis separated the two areas at the 40 % level of dissimilarity, with a maximum similarity of approximately 20 % between any two island areas (Fig. 2.9).



Figure 2.8 Non-metric multidimensional scaling ordination based on the probability of presence of fish (left) and invertebrate taxa (right) on longlines set at different island areas and depth ranges at the South Sandwich Islands. Labels are island areas: "Br" – Bristol; "Ca" – Candlemas; "MS" – Montagu Seamount; "Mo" – Montagu; "Pr" – Protector Shoal; "Sa" – Saunders; "Th" – Thule; "Va" – Visokaya; "Vi" – Visokoi; and "Za" – Zavadovski. Islands to the south of Candlemas labelled blue; all others are red.



Figure 2.9 Cluster analysis (UPGMA) of different island area/depth band combinations based on taxonomic composition of fish (left) and invertebrates (right) captured in different small islands areas and depth bands (invertebrates –1,200 to 1,600 m depth band only). Arbitrary 30 % and 40 % similarity level delineates northern and southern regions of the South Sandwich Islands based on fish and invertebrate catch rates, respectively. Labels are island areas: "Br" – Bristol; "Ca" – Candlemas; "MS" – Montagu Seamount; "Mo" – Montagu; "Pr" – Protector Shoal; "Sa" – Saunders; "Th" – Thule; "Va" – Visokaya; "Vi" – Visokoi; and "Za" – Zavadovski.

#### 2.4 Discussion

The analysis presented here provided a detailed description of the spatial distribution of toothfish species and major by-catch species (macrourids, rajids and muraenolepidids) as well as of less frequently caught finfish taxa (Fig. 2.4). Catch rates of invertebrate were comparatively low, though the spatial distribution of effort and quality of data collected by observers allowed a coherent bioregionalisation of the bathyal slopes of the South Sandwich Islands based on invertebrate and finfish catch rates.

#### 2.4.1 Benthic habitat and invertebrate distribution

Previous sampling of benthic fauna had been extremely limited at the South Sandwich Islands, particularly in the bathyal zone, where species composition is typically very different from that of shelf regions (Ramos 1999; Arntz and Brey 2003; Rex, Etter et al. 2006). Previous benthic surveys of the Scotia Ridge have noted the presence of both Subantarctic and Antarctic species of finfish and benthic invertebrates at the South Sandwich Islands, though the number of sample sites here had been low and it has not, up to this point, been possible to describe the fine-scale distribution of species around the islands (Ramos 1999; Arntz and Brey 2003).

Sedentary suspension feeding invertebrates, including actiniarians, cold water corals and sponges were much more abundant over the Protector Shoal region to the north east of Zavadovski, where current speeds may be comparatively high. In the north Atlantic, Lophelia pertusa reefs and sponges are found in regions with moderate current speeds (25 cm s<sup>-1</sup>), where there is sufficient supply of food particles and exposure of hard substrate for attachment (OSPAR 2008). The lack of sedentary species to the south suggests that current speeds are insufficient for successful colonisation and development. Compared with South Georgia and the Ross Sea, these taxa were rarely entangled on gear at the South Sandwich Islands (Table A2.1). The particularly low catch rates of slow-growing scleratinian corals and certain hydroid taxa (e.g. anthoathecatae) and the increased abundance of more opportunistic actiniarians suggest that benthic communities at the South Sandwich Islands experience relatively high levels of disturbance. This is consistent with reports from previous surveys conducted along the Scotia Ridge (Ramos 1999; Arntz and Brey 2003). The most recent eruption at Protector Shoal in 1962 (Gass, Harris et al. 1963) is likely to have obliterated local benthic communities and smothered distant regions of seafloor in volcanic ash. Given that all except two of the islands have erupted over the last 100 years, early successional taxa would be likely to predominate throughout the South Sandwich Islands, though reduced current speeds may also constrain their successful colonisation in regions to the south of Protector Shoal.

Ordination and clustering analyses both indicate an abrupt change in habitat for invertebrate taxa moving from north to south, approximately coincident with Saunders Island. Elevated catch rates of mobile ophiuroids and predatory asteroids to the south were also observed in the Southern Ross Sea (located to the south of the ACC) (Fig. A2.3). Their increased abundance may be typical of Antarctic bathyal communities, where current speeds are insufficient for colonisation by sessile suspension feeding organisms. A similarly abrupt demarcation in benthic invertebrate composition has been observed over shelf regions of the Antarctic Peninsula and islands of the Southern Scotia Ridge, where spatial temperature distribution at the seafloor and relative position the ACC and WG water masses were also thought to be highly influential (CCAMLR 2007).

Previous studies have found enhanced primary production at the South Sandwich Islands in surface waters stabilised by sea-ice melt water (Perissinotto, Laubscher et al. 1992) and, so, changes in benthic habitat to the south may indirectly relate to increased sea ice formation. The maximal extent of sea ice cover varies dramatically by season and the 15 % ice cover contour has been observed between Candlemas and Saunders Islands in warmer years (Murphy, Watkins et al. 2007) (Fig. A2.5). As such, inter-annual consistency in sea ice cover may influence the location of the bioregional boundary between invertebrate and fish taxa at the South Sandwich Islands and elsewhere along the Antarctic-Subantarctic frontier.

#### 2.4.2 Temperature and finfish distribution

Temperature is one of the key abiotic determinants of the distribution of fish species with cold temperature stress limiting the southward range expansion of a number of Southern Ocean species (Eastman 1990). The abrupt bioregional boundary between Subantartctic and Antarctic species at Saunders Islands is coincident with the northernmost location along the island arc where mean winter temperature near the surface dips below -1 °C (Fig. 3.10). This is the approximate temperature at which fish blood plasma freezes in the absence of antifreeze glycoproteins (De Vries and Wohlschlag 1969). Antarctic fish species, such as Antarctic toothfish (D. mawsoni), the striped-eye notothen (L. kempi) and blackfin icefish (C. aceratus) were much more frequently caught to the south of this location (Fig. 2.4) and all are known to have plasma antifreeze glycol proteins or produce additional antifreeze molecules (De Vries and Wohlschlag 1969; Devries 1971; Wöhrmann 1996). Increased catch rates of *M. muraenolepis* in the south would indicate that this species is also able to synthesis plasma antifreeze molecules though this has not yet been verified. All except one of eleven C. aceratus reported in industry catch data between 2005 and 2010 were captured over Visokaya Bank at the Southern limit of the fishable area; all 9 L. kempi identified by observers were captured at Bristol Island or over Visokaya Bank; and the cryptic species of Macrourus was only encountered south of Saunders Island (E. Fitzcharles 2011, unpub. data). These 'Antarctic' finfish species were all more abundant over east-facing slopes, where the influence of the Weddell Gyre is likely to be greatest (Fig. 2.4).

Subantarctic teleosts that are known to lack plasma antifreeze proteins, including *D. eleginoides*, were rarely captured to the south of Saunders Island (Fig. 2.4). Southward expansions of this species are likely to be constrained by ambient temperature and competition with *D. mawsoni* (Roberts, Xavier et al. 2011). Similarly, southward movements *A. georgiana* and *P. formosa* king crab beyond Saunders Island are likely to be constrained by cold temperatures (Arana 1999; Arntz, Thatje et al. 2005) (Figs. 2.4 & 2.6), though the Weddell Front may also form an effective barrier to the southward dispersal of pelagic life stages from regions where growth and reproductive development of organisms are not compromised by cold temperature.

#### 2.4.3 Bioregionalisation

An abrupt partitioning is observed in the taxonomic composition of finfish and invertebrate catches at the South Sandwich Islands moving from north to south, with Subantarctic taxa dominant in the north and Antarctic taxa in the South. Here, the transition in fish and invertebrate taxa was found to coincident in space and a number of factors may influence whether Subantarctic or Antarctic fauna will be dominant in any one area. These might include: ambient seawater temperature; patterns in sea ice formation and related impacts on biological productivity (Perissinotto, Laubscher et al. 1992); and seafloor substrate and topography.

Antarctic finfish species, including *D. mawsoni* and *M. microps* and *L. kempi* are rarely if ever captured to the north of Saunders Island (Fig. 2.4), the northernmost location where 15 % cover of sea ice regularly occurs in September (Murphy, Watkins et al. 2007). Hence, northward expansion of Antarctic finfish and invertebrate species may be constrained by a lack of sea ice cover in some years. However a number of studies have found that competitive interactions with species adapted to warmer habitat frequently define the position of low latitude range limits (MacArthur 1972; Hersteinsson and Macdonald 1992; Kaufman 1998), such that northward expansions of Antarctic fish, *e.g. D. mawsoni*, may be constrained by the presence of Subantarctic species, *e.g. D. eleginoides*, distributed to the north.

Subantarctic fauna at the South Sandwich Islands, including *D. eleginoides* and *P. formosa* appear to tolerate a degree of ice cover in some seasons, though cold temperatures do appear to limit the reproductive capacity of *D. eleginoides* (Figs. 4.5 & 4.6). Subantarctic fauna of the South Sandwich Islands are geographically isolated from the nearest sizable

populations at South Georgia, though dispersal from South Georgia spawning grounds to the South Sandwich Islands may be facilitated by the ACC. This normally flows to the north of the South Sandwich Islands (Orsi, Whitworth et al. 1995), though southward incursions of the ACC are likely to occur in some years. Hence, the southward expansions of Subantarctic species may be limited by the northern limit of sea ice cover and also the southern limit of incursions of the ACC. Competitive interactions are also likely to influence the southern and northern range limits of Subantarctic and Antarctic taxa, respectively in regions where habitat is mutually suitable, sharpening the boundary between the two bioregions.

#### 2.4.4 Conclusions and future work

This study found a low abundance and diversity of sessile suspension feeding organisms at depths less than 600 m which is likely to relate to volcanic disturbance of benthic ecosystems. However, surface waters are productive (Perissinotto, Laubscher et al. 1992; Allen and Smellie 2008) and high catch rates of bathyal finfish, particularly of macrourids and rajids, and of mobile invertebrate fauna in the south suggest that benthic communities may be dominated by relatively abundant taxa at depths where the impacts of volcanic disturbance are less pronounced. However it is recognised that longline gear will be relatively selective in terms of which species are preferentially captured. Other types of evidence, including deep water trawl surveys, video cameras mounted on longlines (Kilpatrick, Ewing et al. 2011) and baited lander gear (Bagley, Priede et al. 2004; King, Bagley et al. 2006) could be used to validate the spatial patterns in benthic fauna observed here and evaluate the extent to which the organisms most frequently captured on longline gear, *e.g.* ophiuroids and predatory asteroids in the south, are actually the dominant fauna of a particular bioregion.

This is the first study to conduct such a fine-scale bioregionalisation of the bathyal zone at the Subantarctic-Antarctic frontier. The north-to-south transition in abundance of fauna representative of the two bioregions is likely to be more abrupt than previously thought, with a virtual 'oil-and-water' interface observed at the South Sandwich Islands. A number of factors may mediate whether Subantarctic or Antarctic fauna will dominate, including sea ice effects on productivity, as well as temperature and other environmental correlates. However, the lack of biological data from the South Sandwich Islands is matched by a general lack of *in situ* physicochemical measurements which may be used to explain the causes of the abrupt bioregionalisation observed here. It is clear that progress in this area would improve our predictions of how Antarctic marine organisms are distributed in space and also how they may redistribute with changes to the marine environment.

Further advances could be made through an assessment of the biological characteristics of the dominant fauna which may lead them to present in a particular bioregion. This could focus on hypothesised physiological adaptations to changes in the marine environment moving from north to south, *e.g.* physiological tolerance to cold water temperatures and relative metabolic requirements, such that changes in community type might be related back to changes in the marine environment. Where there are trophic/competitive interactions between species, the occurrence of one organism will influence the abundance and distribution of others, and in extreme cases, could affect an apparent bioregionalisation. As such, advances in our understanding of the biology and ecosystem relationships of benthic macrofauna would allow for the development of a mechanistic rationale for understanding why species appear to bioregionalise and allow predictions of how species or whole bioregions might redistribute with changes to the marine environment.

#### Chapter 3

## Distribution of toothfish species comparing South Sandwich Islands and the Ross Sea populations

#### 3.1 Introduction

In the previous chapter, data collected from the longline fishery at the South Sandwich Islands were used to show how the composition of finfish and invertebrates communities changes abruptly moving from north to south along the island arc, with *D. eleginoides* and other Subantarctic species dominant in the north and *D. mawsoni* and typically Antarctic species dominant in the south. Here, correlative habitat modelling was used to identify the key environmental variables that lead one species of toothfish to be dominant over the other.

#### 3.1.1 Correlative niche modelling of species distributions

Predictive habitat distribution models have a long history and remain the most common type of investigation of the factors that cause range-edges (Guisan and Zimmermann 2000; Sexton, McIntyre et al. 2009). A number of different tools have been used, including: Bioclimate Envelope Modelling (Bioclim) (Busby 1991); Maximum Entropy Analysis (Maxent) – a program for modelling species distributions from presence-only data (Phillips, Anderson et al. 2006) and regression models, *e.g.* generalised linear/additive models (GLMs/GAMs), which can be used to predict distributions from a variety of species data types. In each case, niche habitat is identified through correlative modelling of observed patterns in species' distribution with those of environmental data. Correlative niche modelling is increasingly used as a tool to predict species distributions from environmental data and has utility for predicting where species will be distributed in data poor areas and also how distribution patterns will alter with changes in habitat quality through time (Guisan and Zimmermann 2000).

In the world of fisheries, GLMs are the most commonly used statistical tool for standardising catch and effort data, though usually with the aim of developing standardised CPUE series

through time for determination of stock status (Maunder and Punt 2004; Venables and Dichmont 2004). Examples of their usage for the niche modelling of fish species are much more limited, though they are sometimes used for this purpose in pelagic fisheries where distribution pattern may change through time (Bigelow, Boggs et al. 1999; Nishida and Chen 2004; Hobday and Hartmann 2006) and exploratory/deep water fisheries, where the distribution of the species of interest is not well described or the data are of poor quality (Katsanevakis, Maravelias et al. 2009; Stefansdottir, Solmundsson et al. 2010). GAMs have also been used to model the diversity of deepwater fish species relative to environmental correlates including surface chlorophyll, temperature, depth and slope (Bailey, Collins et al. 2009; Priede, Godbold et al. 2010; Stefansdottir, Solmundsson et al. 2010).

#### **3.1.2** Toothfish species distribution and niche separation

Toothfish species, *D. eleginoides* and *D. mawsoni* are endemic to cold waters of the Southern Hemisphere. Their general distributional patterns were discussed in the introduction (see Section 1.3), with *D. mawsoni* most abundant in regions fringing the Antarctic continent and *D. eleginoides* more abundant in Subantarctic and cold temperate waters to the north. The distributions of the two species are known to overlap in the Ross Sea (Horn 2002; Hanchet 2006) and over the BANZARE Bank (McKinlay, Welsford et al. 2008) and at the South Sandwich Islands (Roberts, Xavier et al. 2011). Both *D. eleginoides* and *D. mawsoni* undergo ontogenetic down-slope migrations and tend to occupy a similar bathymetric distribution at each life stage.

Differences in toothfish species' distributional ranges are likely to relate to known differences in physiology. *D. mawsoni* and most other Antarctic fish species, have AFGPs, while *D. eleginoides* do not (De Vries and Wohlschlag 1969; Eastman 1990; Wöhrmann 1996). In the absence of AGFPs fish plasma freezes at around -0.9 °C, reduced to -2.0 to -2.1 °C when AGFPs are present, below the freezing point of seawater (-1.9 °C) (De Vries and Wohlschlag 1969; De Vries, Komatsu et al. 1970). Hence cold water temperatures are likely to be the key factor limiting southward expansion of distribution in *D. eleginoides* (Collins, Brickle et al. 2011), while Eastman (1990) suggested that *D. eleginoides* were unlikely to occur in water cooler than 2°C. Roberts *et al.* (2011) found a large degree of diet overlap of toothfish species at the South Sandwich Islands which suggested that the range limit between the two species may also be influenced by competitive interactions. The

distributional patterns of *D. mawsoni* have been well described in the Ross Sea, where the occurrence of *D. eleginoides* in the north coincides with a decrease in *D. mawsoni* catch rates (Hanchet 2006; Hanchet, Rickard et al. 2008). Cheung *et al.* (2008) used Bioclim to predict changes in *D. mawsoni* distribution (using presence data) in response to projected climate change and predicted that the species would become extinct within 30 years, largely as a result of retreating sea ice coverage. However, as yet, no attempt has been made to identify threshold values of temperature-related variables, *e.g.* seawater temperature and degree of ice cover, which lead to the formation of range limits or for one species to dominate over the other.

GAMs and GLMS have previously been used to model catch rates of toothfish species and, although they have incorporated habitat variables, including depth and region of capture, they have been configured to produce time series of standardised CPUE for the assessment of stock status, rather than understanding the environmental factors that influence distributional patterns. Even so, these models often found significant effects of depth and location of capture on catch rates, suggesting that their distribution is quite heterogenous about bathyal slopes in response to spatial variation in the marine environment (Agnew 1999; Agnew 2005; Lord, Duhamel et al. 2006; Agnew, Edwards et al. 2009).

#### 3.1.3 Chapter aims

All previous studies of the diet of the two species have been on widely separated populations. At the South Sandwich Islands *D. mawsoni* and *D. eleginoides* overlap in distribution, providing an almost unique opportunity to identify levels of abiotic factors that lead to local species dominance and the formation of range edges at the species interface.

In this Chapter, GLMs were developed to model toothfish catch rates (a proxy for population density) in response to environmental correlates at the South Sandwich Islands, including: depth; seawater temperature at depth in the summer and winter; and midwinter sea ice cover. The different models were then used to predict toothfish distribution in the Ross Sea area. This analysis was designed to address three main research questions:

1. What are the key environmental variables that lead to the formation of toothfish species range limits?

- 2. Where key environmental variables are identified, what are the critical values of each that lead one species to dominate over another at a particular space and time?
- 3. Are the critical values of key environmental variables consistent when comparing toothfish species populations of different areas and what might be inferred from between-area discrepancies?

The potential implications of climate change on toothfish species distribution were discussed given the results of this analysis. The potential influences of competition and hydrography on the formation of range limits were also considered.

#### 3.2 Methods and materials

#### 3.2.1 Environmental data sources and post processing

Toothfish catch was modelled in response to an array of environmental variables. Seawater temperature at depth was derived from World Ocean Atlas 2009 data (WOA09 - National Oceanographic Data Center, Silver Springs, MD, USA) using Ocean Data View software (Schlitzer 2006). Mean values at a 1-degree resolution, were obtained from warmest (February) and coldest (September) time periods, to test the degree to which the distributional range of each species is shaped by seasonal extremes in temperature. Temperature at depth (50 m and 1050 m) was averaged over a 100 m depth range – the reported depth being the mid-point (50 m or 1,050 m). A standard deviation of less than 0.1 <sup>o</sup>C was predicted for each grid square, which was considered small enough to ignore for the purposes of this analysis.

Sea ice concentration data from the International Satellite Land Surface Climatology Project (ISLSCP) for years 1986 to 1995 (Armstrong and Knowles 2010) were used to estimate mean sea ice cover percentages for in the month of September, to a quarter-degree resolution. Levels of error in sea ice concentration data are generally assumed to be less than 5% on average (Armstrong and Knowles 2010), though were expected to be smaller than this in the time averaged dataset. Data from the ETOPO1 global relief model were used to derive bathymetry datasets for the two study areas, to a one-sixth degree resolution (Amante and Eakins 2008).

#### 3.2.2 Toothfish catch and effort data

Line-by-line catch and effort data were made available from four vessels, fishing at the South Sandwich Islands and the Ross Sea. For each area there was a good coverage by vessel and latitude for each season (Tables A3.1 to A3.4). Catch per unit effort was estimated from Scientific Observer data from line hauling observation periods and was estimated here as frequency of individuals of each species captured per thousand hooks observed. Differentiation between toothfish species in catch was made by scientific observers either during hook line observation periods or during biological sampling of randomised selections from the catch (CCAMLR 2005). Full permission was granted from Argos Fishing for the use of the Ross Sea data in this analysis.

#### 3.2.3 Toothfish CPUE GLMs

Generalised linear models (GLMs) in *R* (R Core Development Team 2011) were used to predict *D. eleginoides* CPUE (catch *n* per 1000 hooks set, cube-root transformed) in response to abiotic variables (*e.g.* temperature and depth at the location of line setting) and fishing operation-related variables (*e.g.* line soak time and vessel identifier). Explanatory variables were binned to account for non-linear responses. As expected, there is was a high degree of correlation between temperature-related explanatory variables: winter and summer sea temperature and 50 m and 1050 m and also September Ice cover % (for any combination – Pearson's correlation coefficient > 0.75; *d.f.* = 645; *p* < 0.001; Table A3.5). As such, each model was constructed to incorporate only one of each variable in turn and the preoptimisation model had the following form:

#### CPUE ~ depth.bin \* temp.variable.bin + soak.bin \* vessel \* year eqn 3.1

The model configuration with the lowest Akaike Information Criterion (AIC) was selected as the optimal configuration, though information on the percentage of explained deviance and significant of explanatory terms are also presented here. The optimal model structure is presented in the results section (Tables 3.1 & 3.2). The "predict" function in *R* (R Core Development Team 2011) was then used to predict average CPUE (and standard error) using Ross Sea environmental data while keeping variables relating to fishing operation constant (*e.g.* soak time of 1.25days + vessel1 \* year2009).

#### 3.3 Results

#### 3.3.1 Marine environment at the South Sandwich Islands and raw toothfish CPUE

The spatial extent of suitable habitat for slope-phase toothfish populations is relatively high at the South Sandwich Islands (26.7 thousand km<sup>2</sup> between 500 and 2000 m depth, compared with 43.0 thousand km<sup>2</sup> at South Georgia), though is extremely limited for shelfphase juveniles (0.15 thousand km<sup>2</sup> shallower than 500 m depth and 44.30 thousand km<sup>2</sup> at South Georgia, respectively). Regions deeper than 2,000 m are only observed between Candlemas and Saunders Islands and, given that toothfish are primarily distributed shallower than 2,000 m depth (Agnew 1999; Hanchet, Rickard et al. 2008), the degree of connectivity between areas of suitable habitat is likely to be high (Fig. 3.1).



Figure 3.1 Spatial distribution of modelled habitat variables around the South Sandwich Islands, including (clockwise from top-left): bathymetry, mean September sea ice % coverage, mean September temperature at 1,050 m depth and at 50 m depth.

Pack ice extends past the northernmost island Zavadovski in most years, though a steep gradient in ice cover percentage is observed from north to south in midwinter (September mean), ranging from 70 % over the Visokaya Bank in the South to less than 20 % over the Protector Shoal in the North. In warmer years, the northernmost extent of pack ice formation occurs between Saunders and Candlemas Islands (Fig. A2.5), corresponding with the position of the mean 50 % ice cover contour in September. North to south gradients were also observed in seawater temperature near to the surface and in the bathyal zone, with decreased temperatures and increased temperature gradient with latitude closer the

surface (ranging from -1.6  $^{\circ}$ C to -0.8  $^{\circ}$ C at 50 m depth compared with 0.3  $^{\circ}$ C to 1.0  $^{\circ}$ C at 1050 m) (Fig. 3.1).

Both *D. eleginoides* and *D. mawsoni* have been captured by longline fishing vessels since the resumption of fishing at the South Sandwich Islands in 2005. Prior to 2009, fishing operations were restricted to the area north of 57.4 °S where *D. eleginoides* dominate catch species composition and are likely to be much more abundant. Subsequently, operations expanded to the southern area, where *D. mawsoni* dominate toothfish catches. The degree of overlap in the species' distributions was minimal with significant catches of both species occurring only around Saunders and to the north of Montagu Island. Patterns in distribution are also observed with longitude, particularly in the Southern Area, where increased *D. mawsoni* catch rates were observed over east-facing slopes fringing the Weddell Sea and occasional catches of *D. eleginoides* are taken over western slopes facing in to the Scotia Sea (Fig. 3.2).



Figure 3.2 Observed CPUE distributions of toothfish species from 2005 to 2010. 1,000 m depth contours displayed.

Catch rates of both species were greatest between 1000 m and 1600 m depth, with occasional captures on lines set as shallow as 400 m and up to 2000 m depth. The rapid

north to south transition in species dominance which occurs at Saunders Island coincided with the 50 % mean September ice cover contour and -1.4 °C and 0.6 °C winter isotherms at 50m and 1050 m depth, respectively (Fig. 3.3).



Figure 3.3 Toothfish species CPUE *n* distribution at the South Sandwich Islands with depth, September ice percentage coverage, 50m and 1,050 m September seawater temperature. *D. eleginoides* top row; *D. mawsoni* bottom row.

Minimal overlap was observed in the spatial distributions of toothfish species both at the South Sandwich Islands and in the Ross Sea (Fig. 3.2 and Fig 3.8). The temperature range over which both species comprised more than 10 % of catch *n* was 0.5 °C or less regardless of depth and season (Fig 3.4Figure ). The transition in toothfish species dominance occurred at a lower winter near-surface seawater temperature and an increased winter sea ice cover at the South Sandwich Islands than at the Ross Sea (50-60% ice cover and -1.4 to -1.2°C at 50m depth at the South Sandwich Islands; 10-20% and > -0.1°C in the Ross Sea). A similar pattern was observed in winter temperature at 1,050 m depth at the South Sandwich Islands, though *D. eleginoides* were not dominant at any temperature at this depth in the Ross Sea (Fig 3.4).



Figure 3.4 Proportion of *Dissostichus* spp. catch *n* at the South Sandwich Islands and the Ross Sea comprised of *D. eleginoides* in response to temperate and ice cover. Points show median values and boxes the inter-quartile range of all lines.

#### 3.3.2 South Sandwich Islands D. eleginoides model

Predictive GLM models were developed using *D. eleginoides* catch and effort data from the South Sandwich Islands longline fishery and were later used to predict their distribution in the Ross Sea. The top two model configurations included only one interaction term between vessel and year and comprised more than 90% of the total weighting of all assessed (Table 3.1). Both of these models explained more than 69% of the total deviance and the optimal model configuration was as follows:

For the best-fitting model, incorporating September temperature at 50m depth, all main effects and interactions had a significant effect on *D. eleginoides* CPUE (Tables 3.2 & 3.3). The use of a cube-root transformation of CPUE resulted in a normal error distribution with no sign of heteroscedasticity of errors, despite an irregular fit at lower values (Fig. 3.5).
Table 3.1 Comparison of model configurations used to describe *D. eleginoides* CPUE at the South Sandwich Islands (best-fitting model rank 1).

Rank	Depth	lce cover	Soak time	Vessel	Year	Depth * Ice	Soak * Vessel	Soak * Year	Vessel * Year	Soak * Vessel *	Deviance explained	δΑΙϹ
1	+	+	+	+	+				+		69.7%	0.0
2	+	+		+	+				+		69.2%	1.9
3	+	+	+	+	+	+			+		72.1%	5.0
4	+	+	+	+	+						69.1%	6.8
5	+	+		+	+	+			+		71.6%	7.9
6	+	+		+	+						68.6%	9.5
7	+	+	+	+	+	+					71.7%	10.7
8	+	+	+	+	+		+		+		70.1%	14.3
9	+	+		+	+	+					71.0%	16.3
10	+	+	+	+	+		+				69.6%	20.0

Table 3.2 Comparison of models incorporating different temperature related variables (best-fitting model rank 1)

Rank	Model	df	Deviance explained	δΑΙϹ
1	Temp 50m Sep	27	69.8%	0.0
2	Ice Sep	29	69.7%	5.6
3	Temp 50m Feb	29	66.8%	64.9
4	Latitude	24	64.3%	101.5
5	Temp 1050m Sep	27	63.1%	129.0
6	Temp 1050m Feb	27	61.9%	149.5



Figure 3.5 Model diagnostic plots for the optimal GLM model describing *D. eleginoides* distribution at the South Sandwich Islands (model rank 1 in Table 3.2).

Table 3.3 ANOVA table for the optimal GLM describing *D. eleginoides* CPUE at the South Sandwich Islands (model rank 1 in Table 3.2).

Variable	d.f.	Resid d.f.	Resid. Deviance	F	p	
NULL		646	4.13			
Depth	7	639	3.96	12.57	< 0.001***	
Temp 50m Sep	4	635	1.49	306.45	< 0.001***	
Vessel	3	632	1.39	17.26	< 0.001***	
year	5	627	1.30	8.87	< 0.001***	
Soak	4	623	1.28	2.48	0.043*	
Vessel:Year	2	621	1.25	6.89	0.001**	
(***) 0 001 (**)	0.04 (*)	0.05				

'\*\*\*' = 0.001; '\*\*' = 0.01; '\*' = 0.05

Models that incorporated ice cover percentage and winter surface water temperature had a lower AIC than the others. Both models had a similar low value of AIC and explained more than 69 % of the total deviance in *D. eleginoides* CPUE at the South Sandwich Islands. Models incorporating deep water temperature variables explained a similar amount of

deviance as the model incorporating latitude and did not fit nearly as well as either of the surface temperature variables or surface ice cover percentage (Table 3.2). Term plots using the optimal model (model rank 1 in Table 3.2) predicted a parabolic response of *D. eleginoides* CPUE to depth and a rapid decrease in catch rates in regions where surface temperatures fall below -1.4°C in mid-winter (Fig. 3.6).



Figure 3.6 Term plots for optimal GLM model describing *D. eleginoides* CPUE at the South Sandwich Islands (bars represent one standard error).

#### 3.3.3 Application of GLM model to Ross Sea environmental data

In the Ross Sea, a large proportion of the *D. mawsoni* population are distributed over the comparatively deep shelf area and continental slope fringing Antarctica. To the north of 65°S, areas suitable for toothfish colonisation (shallower than 2,000 m) are limited to numerous elevations of the seafloor associated with the southern Pacific-Antarctic ridge. Winter pack ice extends as far north as this ridge in most years and is at least 80% ice coverage is observed over a large proportion of the Ross Sea area in September (Fig. 3.7).

The oceanography of the Antarctic zone of the Ross Sea is dominated by two cyclonic gyres, either side of the 180° meridian (Hanchet, Rickard et al. 2008). During the austral winter,

near surface and bathyal water temperature may drop below -2°C toward the centre of these gyres, with a small increase in temperature between as warmer water is entrained from the north. The ACC dominates waters to the north of the Pacific-Antarctic ridge where surface seawater temperature rarely drops below 0°C. Bathyal water temperatures of the ACC are similar to the Ross Sea Gyres though are much warmer at the surface (>0.5 °C) and are also warmer than at all depths at the South Sandwich Islands (Figs. 3.1 & 3.7).



Figure 3.7 Spatial distribution of modelled habitat variables in the Ross Sea, including (clockwise from top-left): bathymetry, mean September sea ice percentage cover, mean September temperature at 1,050 m depth and at 50 m depth.

The majority of the Ross Sea fishing effort used in this analysis was concentrated along shallow slope regions between  $160^{\circ}E$  and  $200^{\circ}E$  and from  $230^{\circ}E$  to  $245^{\circ}E$ ; and along the Pacific-Antarctic ridge region to the north of  $67^{\circ}S$ . *D. mawsoni* dominated catches in all areas, with catch rates of >10 fish 1000 hooks observed in most areas south of  $-65^{\circ}S$ . Increased *D. eleginoides* catch rates was observed to the north of this, though they were still much lower than at the South Sandwich Islands (<2 fish per 1000 hooks set in the northern Ross Sea, compared to >10 fish per 1000 hooks at the South Sandwich Islands). *D.* 

*eleginoides* were occasionally captured further south than  $70^{\circ}$ S, though were never observed in the region to the east of 230°E (comparing Fig. 3.2 & 3.8).

A slightly different distribution with depth was observed with *D. mawsoni* in the Ross Sea, with greatest catch rates between 600-1400 m depth, compared with 1000-1600 m at the South Sandwich Islands. In comparison, *D. eleginoides* were rarely captured shallower than 800 m depth. *D. mawsoni* catches remain high in regions where September ice coverage was greater than 30%. This coincides with the September -0.7 <sup>o</sup>C isotherm at 50 m depth. No substantial drop off in CPUE is observed across the range of temperatures at 1,050 m depth though *D. mawsoni* catch rates may be increased where the temperature was less than 0.6<sup>o</sup>C. *D. eleginoides* catch rates are much lower by comparison and they are only caught consistently in areas where sea ice coverage is less than 20 % in September, coincident with the -0.6<sup>o</sup>C near-surface and 1.6 <sup>o</sup>C bathyal isotherms (Figs. 3.4 & 3.8).



Figure 3.8 *D. eleginoides* (top) and *D. mawsoni* (bottom) CPUE distribution from longline operations in the Ross Sea area.

There was a good agreement between the observed and predicted spatial distributions of *D. eleginoides* CPUE based on September sea ice coverage and temperature at 50 m depth. However the agreement with predicted distribution from winter temperature at 1,050 m was poor. This model predicted high catch rates across all slope areas deeper than 1,000 m depth (Fig. 3.9).

As such, surface temperature and ice formation both appear to be plausible factors limiting the southward range expansion of *D. eleginoides* in the Ross Sea. However, the model incorporating surface temperature predicted that a reduced population density could persist further south, particularly in the region of 75°S, where winter surface temperature is greater than immediately to the north (Fig. 3.7) and *D. eleginoides* are indeed occasionally captured

this far south of the transition in species dominance (Fig. 3.8). All three predictive models suggest that at least small populations should be encountered in the eastern Ross Sea, though they were never observed in the catches of this area (Figs. 3.8 & 3.9).



Figure 3.9 Predicted *D. eleginoides* CPUE in the Ross Sea from GLM models fit to catch and effort data at the South Sandwich Islands. From top to bottom: predicted CPUE distribution using September sea ice % coverage; from September seawater temperature at 50 m depth and; from September seawater temperature at 1,050 m depth.

# 3.4 Discussion

#### 3.4.1 Temperature, ice formation and toothfish species distribution

A distinct north to south gradient in abundance was observed in toothfish species at both the South Sandwich Islands and the Ross Sea. This was evident from the spatial distribution of observed toothfish species catch rates and from species composition in catch, which was dominated by *D. eleginoides* to the north of Saunders Islands and *D. mawsoni* to the south. The transition in species dominance was abrupt and is spatially coincident with a transition in fish species community composition with Antarctic species *e.g. Muraenolepsis microps* and a currently undescribed species of *Macrourus* (E. Fitzcharles 2011, pers. comm.) dominant to the south and Subantarctic species are known to produce plasma antifreeze molecules (De Vries and Wohlschlag 1969; Wöhrmann 1996) and it is likely that the shared range limits of the two toothfish species are to some extent mediated by ice formation and sea water temperature (Eastman 1990; Collins, Brickle et al. 2011), which decreased abruptly moving from the ACC in the north to the Weddell Sea and Ross Sea Gyres in the South.

Eastman (1990) suggested that *D. eleginoides* are limited to regions of seawater warmer than 2°C. However, this analysis did not consider temperature differences with depth, which can exceed 2°C across the depth range inhabited by toothfish species at both the Ross Sea and the South Sandwich Islands (Fig. 3.10). Considering the 1,000 m – 1,100 m depth range where *D. eleginoides* catch rates are close to their maximum (Fig. 3.3), the transition in toothfish species dominance at the Ross Sea occurs where the average mid-winter temperature is approximately  $2.0^{\circ}$ C. The corresponding temperature at the South Sandwich Islands predicted a more southerly distribution at the Ross Sea when using temperature at bathyal depth, than was actually observed (Fig. 3.9). As such, it seems unlikely that temperatures experienced by slope-phase individuals are limiting the southward range expansion of Ross Sea *D. eleginoides* populations beyond the transition in species dominance; unless there are significant physiological differences between individuals of Ross Sea and South Sandwich Islands populations.

Closer between-area agreement is observed in the critical winter temperature at 50 m depth at the location of transition in species dominance; -0.6 to -0.8 °C at the Ross Sea and -1.4 °C at the South Sandwich Islands (Fig. 3.4). These temperatures are close to the point at which fish plasma freezes in the absence of antifreeze molecules, which *D. eleginoides* are thought to lack (Eastman 1990). Hence, cold shallow water temperatures may limit southward expansion of juvenile planktonic and juvenile shelf-phase individuals of *D. eleginoides* which are most abundant at these depths (Belchier and Collins 2008; Hanchet, Rickard et al. 2008).

The degree of winter pack ice concentration was also similar at the point of species transition in dominance when comparing the two areas (10-30 % at the Ross Sea and 50-60 % at the South Sandwich Islands) (Fig. 3.4). Again, ice formation would more likely to influence the survival of larval and juvenile populations of *D. eleginoides*, assuming slope-phase individuals do not migrate up to surface waters. Adults of both species have occasionally been observed ascending to such shallow regions (Davis, Fuiman et al. 1999; Collins, Ross et al. 2007), although whether most individuals do so once recruited to slope habitat is not known. Tagging studies indicate that horizontal movements by slope-phase individuals (between 500 and 2,000 m depth) are generally quite limited (Agnew, Kirkwood et al. 2006) and archival tag studies on *D. eleginoides* suggest diurnal migrations of less than 50 m up and down the water column are common, though they were not observed in waters <200m depth (Williams, Tuck et al. 2002).



Figure 3.10 Mean September potential temperature at depth at different latitudes (see legends): at 28.5°W at the South Sandwich Islands (left) and; at 179.5°E in the Ross Sea (right). Temperatures interpolated from World Ocean Atlas 2009 data, using Ocean Data View (Schlitzer 2006). "PFP" = Plasma Freezing Point of teleost blood in the absence of antifreeze glycoproteins (Eastman 1990); profiles in bold with open circles are approximately at the location of transition in species dominance for the given longitude.

In this analysis, GLM models that included winter sea-ice or 50 m temperature had a lower AIC than those which incorporated temperature at 1,050 m depth or summer temperature in describing toothfish species CPUE or species composition in catch (Table 3.2). However, a high degree of correlation was observed between all temperature-related variables (Table A3.5) and all models explained a high percentage of observed deviance in toothfish CPUE (Table 3.2). Hence winter ice formation, temperature at the surface and at depth, are all plausible drivers of distribution patterns of toothfish species, while interaction effects (*e.g.* between temperature and ice cover) may also be important.

#### 3.4.2 Southerly populations of *D. eleginoides*

Given that *D. eleginoides* catch rates decreased rapidly in regions where *D. mawsoni* were abundant, the presence of isolated populations at the very south of the Ross Sea was

unexpected. this has been noted previous to this study with 14 fish captured on a single line set at 71°40'S at approximately 1,000 m depth (Stevenson, Hanchet et al. 2008). In this study, *D. eleginoides* were observed in the catch of 18 lines set south of 70°S (Fig. 3.8, top). At this location surface temperatures dip below  $-1^{\circ}$ C in mid winter, though are considerably warmer at approximately 1,000 m depth (0.6 to  $0.8^{\circ}$ C) (Fig. 3.10), similar to that observed at the Southern limit of *D. eleginoides* distribution at the South Sandwich Islands. Hence the GLM model fit to South Sandwich Islands data predicted that *D. eleginoides* should be distributed in the South of the Ross Sea, based on temperature at these depths (Fig. 3.9, bottom).

Species identifications were made by experienced scientific observers during hook line and biological sampling periods based on the physiological characteristics of captured fish. Hence these identifications should be treated with a moderate degree of confidence, even if they cannot be confirmed. Even so, records of D. eleginoides captured close to the coastline of Antarctica appear unlikely. Though, positive identifications of D. eleginoides have also been made over Visokaya Bank in the South of the South Sandwich Islands (59.9°S), where average winter temperature at 1,050 m depth falls below 0.3 °C (Fig. 3.2). Individuals of both species are capable of long distance migrations over short time periods (Agnew, Kirkwood et al. 2006; Hanchet, Rickard et al. 2008) and it is not known whether the southerly populations at the Ross Sea have persisted for more than one year. However, the fundamental niche of slope-phase D. eleginoides appears to extend some way to the south of the observed transition in species dominance. For planktonic and juvenile phase individuals, the southern extent of the fundamental niche approximately corresponds with the transition point. Pulling all of this information together, it appears that southward *D. eleginoides* dispersal from spawning grounds is initially limited by lethally cold temperatures in surface waters. Following ontogenetic movement in to warmer water at depth, they are then able to migrate long distances south of this point. This hypothesis is consistent with the observed patterns at the Ross Sea and the South Sandwich Islands, of an abrupt decrease in D. eleginoides abundance where surface temperatures are lethal and the presence of low density populations distributed some way to the south.

#### 3.4.3 Hydrography, competition and northward dispersal of D. mawsoni

Though not incorporated into the GLM models developed here, hydrography is also likely to play an important role in the formation of range limits, particularly in shaping the southern extent of *D. eleginoides* distribution. Individuals of the South Sandwich Islands population do not appear to reach spawning condition (Figs. 4.5 & 4.6) and may be dependent on dispersal from spawning grounds at South Georgia, carried by the ACC. As such, the episodic pattern in recruitment to this population (section 4.3.1) may coincide with variability in the southern position in the ACC (Billany, Swart et al. 2010). The apparent lack of *D. eleginoides* in the eastern Ross Sea could also relate to hydrography, where a previous analysis has indicated that the path of the western Ross Sea Gyre would be likely to advect the pelagic early life stages of individuals to the north of the eastern Ross Sea (Hanchet, Rickard et al. 2008).

*D. mawsoni* appear to actively disperse to deeper warmer regions in the north of the Ross Sea and South Sandwich Islands to spawn (Fig. 4.9) (Hanchet, Rickard et al. 2008), though very few individuals were observed to the north of the transition in species dominance. Perhaps the most northerly record for *D. mawsoni* is of a single individual caught at South Georgia in 2010 (J. Fenaughty 2010, pers. comm.) and this analysis shows that, at 1,000 m – 1,100 m depth, they are able to tolerate warmer regions of the Ross Sea than at the South Sandwich Islands (Fig. 3.4). As with *D. eleginoides*, there may be physiological differences between individuals of the two populations, which have been demonstrated to have a different genetic composition (Kuhn and Gaffney 2008).

Similarities in diet preference and competition with *D. eleginoides* (Roberts, Xavier et al. 2011) may also restrict northern range expansions in *D. mawsoni*. In addition the northern range limit of D. mawsoni at the South Sandwich Islands (Fig. 3.2) corresponds with the location of the inter-annual minimum in sea ice extent at the South Sandwich Islands (Fig. A2.5) and northern range expansions may also be constrained by a lack of ice cover in warmer winters. Hence, mean ice concentration in mid-winter may be less important to the habitat requirements of *D. mawsoni* than inter-annual consistency of ice cover.

#### 3.4.4 Climate change and toothfish species distribution

Near surface temperature and extent of sea ice formation, are likely to play an important role in deciding how *D. eleginoides* and *D. mawsoni* will be distributed. A trend of decreasing

extent of sea ice formation has been observed over the past few decades in the South Atlantic region of the Southern Ocean and this has been attributed to a general warming of this region (Vaughan, Marshall et al. 2003). Ice formation at lower latitudes is influenced by large-scale ocean circulation effects on the position of the ACC Southern Boundary (Nicol, Pauly et al. 2000) and a southward trend in the Southern Boundary has been observed in the Atlantic region in recent years (Billany, Swart et al. 2010). This contrasts with Increased sea ice formation in the western Ross Sea since the late 1970s (Comiso, Kwok et al. 2011), though it is thought that the observations in both regions can both be explained by variability in the Southern Annular Mode (SAM) and El Nino Southern Oscillation (ENSO) (Hall and Visbeck 2002; Stammerjohn, Martinson et al. 2008).

Given a continuation of these trends, the models constructed here would predict a southerly movement of the transition in species dominance in the Scotia Sea and a northward movement in the Western Ross Sea. However this simplistic view is complicated by ocean circulation patterns, which may maintain barriers to dispersal in the face of warming or cooling events. In the case of *D. eleginoides* at the South Sandwich Islands, we could expect less sporadic recruitment, as incursion of the ACC become more frequent. As temperatures increase resident populations may also begin to develop to spawning condition. There is greater concern for *D. mawsoni* populations, which are hemmed in by the Antarctic Continent and Cheung *et al.* (2008) used bioclimate envelope modelling to demonstrate that *D. mawsoni* would become extinct within 30 years if expected trends in warming were realised. The analysis conducted here shows that ontogenetic changes to distribution with depth will affect the spatial extent of the fundamental niche of both toothfish species and should be represented in mechanistic models that use biophysical observations to describe the fundamental niche of these and other deep water species.

#### 3.4.5 Conclusions and future work

Both toothfish species are captured at the South Sandwich Islands and the Ross Sea, with increased catch rates of *D. eleginoides* in the North. An abrupt north to south transition in species dominance was observed in both areas though *D. eleginoides* were occasionally captured a long distance to the south. A steep north to south gradient is observed in a number of temperature-related environmental variables moving from north to south, including: surface temperature, bottom temperature and percentage sea ice coverage in midwinter. These variables are spatially correlated and it unsurprising that all three were

found to have a significant effect on the proportion of toothfish catch comprised of *D. eleginoides*. However, differences were observed in the "critical values" of each variable at the point of transition in species dominance, when comparing the South Sandwich Islands and the Ross Sea and this may relate to the specific hydrographic conditions of each area. Hence, the models developed here may be improved through the incorporation of hydrographic data.

In the absence of antifreeze compounds, fish plasma freezes at around -1°C (Eastman 1990) and across much of the *D. mawsoni* range, temperatures only fall below this point at nearsurface depths. Here it is hypothesised that the southerly range limits of *D. eleginoides* are primarily caused by dispersal patterns and cold water mortality of juvenile fish. Warmer bathyal waters permit slope-phase *D. eleginoides* to range further south of the point of transition in species dominance. Northward dispersal of *D. mawsoni* at the South Sandwich Islands may be limited by consistent sea ice formation and competition with *D. eleginoides* populations, while rapid decreases in the extent of sea ice formation are likely to result in a southward movement of the distributional range edge of these and other Southern Ocean fish species. These hypotheses are difficult to test, though would be made easier if there was an improved understanding of the horizontal and vertical movement patterns of toothfish species at different life stages. This may be achieved through analysis of fishery mark recapture data, archival pop tag studies, or from *in situ* observations using underwater cameras.

However, between-area discrepancies in the critical values of key variables affecting toothfish species distribution suggest that other factors, such as regional bathymetry, hydrography, availability and competition for food resources are also likely impact on species distributions. As such, studies that use correlative modelling to predict how species will redistribute with climate change will be improved where they consider a wide range of factors in their analyses, even if they cannot easily be integrated directly in to correlative models.

# Chapter 4

# Range edge effects on the life history of toothfish species Dissostichus eleginoides and D. mawsoni at the South Sandwich Islands

# 4.1 Introduction

In this chapter data acquired during fishing operations are used to describe the biology and life history (*e.g.* growth and reproductive biology) of toothfish at the South Sandwich Islands, where both *D. eleginoides* and *D. mawsoni* are situated at their distributional range edge (Roberts, Xavier et al. 2011). Comparison is made with observations from the South Georgia *D. eleginoides* and Ross Sea *D. mawsoni* fisheries, where populations of each species are assumed to be closer to their respective range centres. In addition to testing some of the hypotheses in the literature relating to range position effects on life history (below), a number of the key biological parameters used in the South Sandwich Islands *D. eleginoides* 

#### **4.1.1** Range position effects on life history

The life history of an organism describes the scheduling of key developmental processes such as growth, sexual maturation and gonad development. Common life history metrics include age or size at first maturity, fecundity at age and size at age. The biological processes which underlie these metrics compete for a common somatic energy source and life history theory posits that evolutionary forces will optimise their scheduling, such that they will maximise the survival of offspring and hence increase the fitness of individuals within a population (Chisholm 1993).

According to the abundant centre hypothesis, a decreasing trend in population density will occur moving from the range centre towards range edges as suboptimal habitat or physiological tolerance limits the resources available for optimal biological function, or the ability of animals to utilise resources through loss of favourable physiological conditions (Brown, Mehlman et al. 1995). Eventually habitat quality will impair fitness to the extent

that populations cannot be sustained and a range edge is defined. However recent reviews have found that studies are just as likely as not to find evidence for reduced fitness towards range edges (Gaston 2009; Sexton, McIntyre et al. 2009). It has been argued in many cases that areas of favourable habitat merely become more fragmented towards range edges, rather than gradually decreasing in quality from centre to edge (Gaston 2009). Where local extinction events occur in low quality areas, decreased fitness may not be detected towards range edges because analyses are often biased towards the sampling of populations in more favourable range-edge habitat, which are no less fit than those present at the centre (Gaston 2009). Also, studies that sample populations at a single point in time may not capture the importance of periodic bad years which may critically decrease fitness over longer time periods (Sexton, McIntyre et al. 2009).

Appropriate measurements of fitness may be difficult to achieve in studies on wild populations. Perhaps the best metric of fitness is to measure survival rates of offspring, though it is often extremely challenging to link offspring and parent populations. Instead a large proportion of studies look for signs of impaired growth and reproductive function (Sexton, McIntyre et al. 2009), for which the data may be much easier to collect. However many of these studies are not sufficiently broad in focus to allow for consideration of life history tradeoffs, which may have a significant effect on realised fitness towards range edges (Gaston 2009).

A relatively small number of studies have characterised geographic variation in life history parameters of fished populations from range centre to range edge (Philippart, Henderson et al. 1998; Brunel and Boucher 2006; Watanabe 2007; Brunel and Dickey-Collas 2010) and the implications of range position are rarely discussed in the context of population assessment and fishery management even though the concept of stock identity and population distribution are fundamental to management assumptions (Hart and Reynolds 2002). At the South Sandwich Islands, both toothfish species are situated on the edge of their distributional range, with minimal species overlap, providing two examples of fish populations at range edges. Furthermore, the northern *D. eleginoides* has a centre range that is well described, at South Georgia and around South America.

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# 4.1.2 Range position and temperature effects on growth and reproductive biology

A short summary of the mechanisms by which spatial patterns in demographic parameters can lead to the formation of range edges is given in Chapter 1. In recent years a number of studies have examined the relationships between organism life history and ambient temperature, and have identified a number of macro-ecological patterns that hold true across a broad set of taxa. The best known of these is Bergmann's rule which states that individuals tend to be larger in colder environments. This pattern has been shown to arise through genetic selection and phenotypic plasticity and is often referred to as *the temperature size rule* (Atkinson, Begon et al. 1994; Atkinson and Sibly 1997). In a number of species, increased maximum body size appears to be associated with delayed onset of maturity, which allows individuals to invest energy in continued growth. This may actually increase mean fecundity through a life time because in some groups of animals, such as fish, larger individuals have a greater fecundity. Although delayed maturity is associated with reduced survival to maturity, where the benefits outweigh the costs natural selection will favour delayed maturation at a large body size (Roff 2000; Stearns 2000).

Geographical variation in growth rate, somatic condition and reproductive biology have also been observed in wild fish populations (Fenaughty 2006; Brunel and Dickey-Collas 2010). A study of 15 different North Atlantic herring (*Clupea harengus*) populations found increased longevity and maximum size (increased von Bertalanffy  $L_{inf}$  – see Eqn. 4.3) with increasing latitude, though they took a longer time to reach maximum size (reduced von Bertalanffy *K*) (Brunel and Dickey-Collas 2010). Patterns in growth parameters with temperature have also been observed in Atlantic cod populations (Taylor 1958). Significant geographic effects on size-at-age have also been demonstrated to be spatially correlated with bottom temperature in Atlantic cod (Campana, Mohn et al. 1995).

Studies on cultured populations allow for the adoption of a controlled experimental approach to finding optimal conditions for fish growth and body condition. These have demonstrated that a number of species are capable of short-term phenotypic adaptation of growth to variations in temperature. With other environmental factors controlled for, a number of species exhibit a dome-shaped response of growth coefficient (*K*) to temperature, including: cod (Pedersen and Jobling 1989; Bjornsson, Steinarsson et al. 2001),

turbot (Burel, PersonLeRuyet et al. 1996), Atlantic halibut (Jonassen, Imsland et al. 1999) and spotted wolfish (Imsland, Foss et al. 2006). Profiles of phenotypic expression to variable environmental conditions are often referred to as "reaction norms". The thermal reaction norms of laboratory-reared Atlantic cod have been demonstrated to vary with genotype, with potential consequences for the ability for different sub-populations to recovery from natural and anthropogenic disturbance (Hutchings, Swain et al. 2007).

#### 4.1.3 Range position and temperature effects on recruitment

Studies on the effects of recruitment variability on the formation of range limits often experience difficulty in separating the effects of a range of potential causes of this variability, including breeding failure, juvenile mortality and dispersal effects (Gaston 2009). However, increased recruitment variability towards range edges has been demonstrated empirically in a variety of North Atlantic fish species, including significant differences from range centre recruitment in both North Atlantic cod and sole (Brunel and Boucher 2006). Other studies have found inconclusive results or have even observed increased variability at the range centre (Leggett and Frank 1997; Philippart, Henderson et al. 1998), though it has been argued that these studies analysed populations from a narrow component of the overall distributional range (Brunel and Boucher 2006). The effects of range position (and temperature) may be confounded with those of stock exploitation, which can also increase recruitment variability where density dependent effects on the stock-recruit relationship are reduced at lower stock levels (Myers 2001). However, range position effects on recruitment variability have also been observed in well-exploited populations (Brunel and Boucher 2006).

### 4.1.4 Geographic patterns in toothfish life history

Toothfish species are widely distributed and populations of *D. eleginoides*, in particular, support commercial fisheries across a wide range of latitudes. The life history parameters of different toothfish stocks are typically estimated for the parameterisation of population assessment models. Fishing gear (and therefore size selectivity) as well as sampling and analytical methods can vary between areas, introducing different biases to parameter estimation. Even so, the size-at-age trajectory of *D. eleginoides* can be markedly different when comparing populations from different areas (Ashford 2001), suggesting the selection of different life history strategies optimised to different environmental conditions.

Despite often large differences in the size-at-age trajectories of a number of different managed stocks, the relationships between growth and ambient temperature are difficult to identify and may be masked by other factors influencing parameter estimation. Significant biases are likely to be introduced by differential size selectivity of fishing gears deployed in different areas (Collins, Brickle et al. 2011) as well as the bathymetric range of gear deployment, particularly given the tendency in toothfish populations of increasing size at depth (Agnew 1999; Hanchet, Rickard et al. 2008). This is likely to account for the very low value of *K* estimated for the Kerguelen *D. eleginoides* population (Table 4.1), where samples were collected from fish captured in the relatively shallow trawl fishery (Collins, Brickle et al. 2011). Size-at-maturity may be less affected by such biases and there is some evidence for decreasing  $L_{m50}$  towards the centre of the distributional range of this species, though there are large between-study estimates for the same population off the Southern coast of Chile (Table 4.1).

Currently the greatest catch biomass of *D. eleginoides* is taken from the Kerguelen Plateau and South Georgia stocks (Collins, Brickle et al. 2011) and, as such, these populations may be considered to be located towards the range centre. Here, mean ambient temperature ranges from 1.6°C to 2.2°C at 1,000 m depth (Schlitzer 2006). Even so, warmer regions to the north, including Falklands and Southern Chile populations (mean temperature at 1,000 m depth ranging from 2.9°C to 3.8°C), still support annual yields in excess of 1,000 tonnes (Collins, Brickle et al. 2011) and are still relatively productive even though they are situated closer to the low latitude range limit for this species.

Table 4.1 Von Bertalanffy growth and maturity parameter estimates for female *D. eleginoides* by region. Areas ordered by decreasing seawater temperature; annual mean temperature at 1,000 m depth from World Ocean Atlas accessed via Ocean Data View (Schlitzer 2006).

Population	Temp.	Fishing	К	L <sub>inf</sub>	t <sub>o</sub>	<i>L</i> <sub><i>m</i>50</sub>	Growth ref.	Maturity ref.
	1,000m	gear						
	(°C)							
Southern	3.8	Longline	0.064	209.7	-1.15	128.7	(Young et al.,	(Young et al.,
Chile						89.9	1992)	1992)
								(Arana 2009)
Macquarie	2.6	Trawl &	0.085	158.7	-0.35		(Horn 2002)	
& NZ EEZ		Longline						
Falklands	2.9	Longline	0.172	122	-0.001	90	(Agnew 2004)	(Laptikhovsky and
		& Trawl						Brickle 2005)
Kerguelen	2.2	Longline	0.110	103.5	-4.7	85	(Ashford,	(Lord, Duhamel et
		& Trawl					Duhamel et al.	al. 2006)
							2005)	
Heard	1.9	Trawl	0.039	197.6	-2.30	100	(Candy, Constable	(Constable, 1999,
Island							et al. 2007)	FSA-99/68)
South	1.6	Longline	0.080	132.0	-0.30	98.2	(Hillary, Kirkwood	(Everson and
Georgia							et al. 2006)	Murray 1999)

The environmental processes that effect toothfish recruitment strength are likely to be heavily influenced by the hydrographic, bathymetric and climatic systems prevalent in a particular region. As such, the range position effects on recruitment, perhaps a better measure of fitness, may be particularly difficult to assess. Large-scale environmental phenomena, including ENSO are thought to have a significant effect on the abundance and development of toothfish eggs and larvae and, subsequently, recruitment to fished populations (Belchier and Collins 2008). Recruitment to the South Georgia population, in terms of abundance of 1+ juveniles, was found to be inversely related to sea surface temperature experienced by pre-spawning adults the previous season (Belchier and Collins 2008). In addition, a four-yearly pulse in recruitment of *D. eleginoides* has been observed over the Patagonian shelf (Laptikhovsky and Brickle 2005), though no attempt was made to link recruitment periodicity to climatic variability (Belchier and Collins 2008) and range position effects on toothfish recruitment variability have yet to be examined.

# 4.1.5 Chapter aims

The longline fisheries for *D. eleginoides* at the South Sandwich Islands and South Georgia are operated by vessels deploying the same gear and a similar approach to fishing operations. In addition genetic (Fitzcharles 2007) and otolith chemistry studies (Chapter 5) both point to a minimal degree of physical separation of the two separately managed stocks. *D. mawsoni* populations at the Ross Sea and the South Sandwich Islands are likely to be genetically distinct (Kuhn and Gaffney 2008) though the basic approach to fishing operations and the biometric sampling methodology are similar when comparing the two areas. As such, the effects of gear selectivity, fishing behaviour and genetic variation on toothfish life history can more easily be separated from those of range position (*i.e.* centre versus edge) and temperature.

Here, biometric data collected by scientific observers during longline operations at South Georgia, the South Sandwich Islands and the Ross Sea were used to compare the life history of toothfish species at the range edge (South Sandwich Islands) with range centre populations (South Georgia for *D. eleginoides* and Ross Sea for *D. mawsoni*). The basic life history parameters were estimated for each population to assess the extent to which we see reduced fitness towards the range edge, expressed as:

- Decreased initial growth rate and increased average maximum size (Atkinson and Sibly 1997);
- Decreased somatic condition (Gaston 2009)
- Delayed onset of maturation (Roff 2000)
- Increased recruitement variability (Brunel and Boucher 2006)

In reviewing a wide range of life history parameters it is hoped it will be possible to evaluate whether only factor important in the formation of range limits, or if life history tradeoffs, such as between growth and gonad development (Roff 2000) are also be important.

# 4.2 Methods

## 4.2.1 Data and sample collection

Biometric data were collected from *D. eleginoides* randomly selected from the catch in all seasons since the resumption of fishing at the South Sandwich Islands in 2005. Data were only collected from a large sample of *D. mawsoni* following the expansion of fishing to the Southern Management Area (South of 57.4°S) from 2009, where this species is much more abundant than in the Northern Management Area (North of 57.4°S). *D. eleginoides* otoliths were also collected in all years, though age validation (2009) and microchemistry (2005) were limited to collections from a single year (Table 4.2). Of the 1,830 otoliths collected from South Sandwich Islands *D. eleginoides* from 2005 to 2010, 294 were from fish captured in the Southern Management Area. In addition biometric data were collected from *D. eleginoides* captured at South Georgia and *D. mawsoni* in the Ross Sea (Table 4.2). Full permission was given by the data owner (Argos Fishing) for the use of Ross Sea data and analyses conducted in this study.

Table 4.2 Biometric data collection of toothfish species at South Georgia, the South Sandwich Islands and Ross Sea by season. All data collected at the South Sandwich Islands and all data analysed from South Georgia and the Ross Sea.

Population	Year	Otolith	Total length	Somatic mass	Sex	Gonad Maturity Index	Gonad mass
S. sand. Isles D. eleginoides							
	2005	142	815	257	259	249	0
	2006	175	1,099	936	693	693	359
	2007	301	1,584	1,544	1,491	1,476	1,369
	2008	366	2,299	1,526	1,531	1,487	1,060
	2009	486	1,808	1,704	1,687	1,681	1,522
	2010	360	1,831	1,086	1,234	1,232	1,226
S. sand. Isles D. mawsoni							
	2005	0	0	0	0	0	0
	2006	9	10	10	10	10	2
	2007	3	6	6	6	6	5
	2008	8	9	9	9	9	1
	2009	450	1,129	972	1,104	1,096	846
	2010	320	1,099	716	845	845	619
Population	Year	Otolith	Total length	Somatic mass	Sex	GMI	Gonad mass
South Georgia D. eleginoides							
	2005	0	0	0	0	10,808	0
	2006	0	0	0	0	17,882	0
	2007	0	0	0	0	20,145	0
	2008	0	6,002	6,002	0	20,778	1,396
	2009	512	6,658	6,658	0	20,832	1,154
	2010	0	4,446	4,446	0	12,636	592
Ross Sea D. mawsoni							
	2005	0	188	188	0	0	188
	2006	0	0	0	0	0	0
	2007	0	590	590	0	0	585
	2008	0	473	473	0	0	472
	2009	0	844	844	0	0	0
	2010	0	827	827	0	0	279

#### 4.2.2 Somatic condition and reproductive biology

Seasonal effects on the length-mass relationship, body condition and gonad development of *D. eleginoides* and *D. mawsoni* were assessed, comparing range centre populations (*D. eleginoides* at South Georgia, *D. mawsoni* in the Ross Sea) and range edge populations of both *Dissostichus sp.* at the South Sandwich Islands.

Area differences in *D. eleginoides* and *D. mawsoni* somatic condition were assessed using Fulton's condition factor (*K*) which assumes an isometric length-mass regression and is calculated as:

$$K = W / L^3 \times 10^5$$
 eqn 4.1

Where W is the wet fish mass in kg and L is the total length in mm.

Scientific observers track gonad development by measuring the Gonad Maturity Index (GMI) of individual fish, which ranges from 1 (immature) to 5 (spent). The full definition of each GMI stage for both sexes is presented in Table A4.1. The Gonadosomatic Index (GSI) is considered a less subjective means of estimating gonad maturity status and was also calculated for all fish where both whole body and gonad mass were measured, as:

All measurements of whole fish and gonad mass were made using motion-compensated scales (± 10 g accuracy) with regular calibration against standard weights of different masses.

# 4.2.3 Age validation

In order to estimate catch at age and growth rates of *D. eleginoides* at the South Sandwich Islands, age validations were conducted on 218 otoliths extracted from individuals randomly selected from the catch during the 2009 fishing season (Fig. A4.1). Otoliths were dried and stored in paper envelopes prior to preparation and age validation at British Antarctic Survey, Cambridge.

Otoliths were baked whole in an oven at 250 °C for 10 minutes and were allowed to cool before embedding in clear-setting epoxy resin. Embedded otoliths were cut in to section of an average of 50  $\mu$ m width. The section containing the primordium was then mounted on a glass microscope slide and a cover slip adhered with another small layer of resin. Otoliths were examined under a light microscope at a minimum of 40-times magnification, viewed with transmitted light. The cohort of an individual was derived by counting dark annuli from the core to the otolith rim.

Some age-blurring is likely to have occurred as a result of miscounting of annuli, though for the purpose of growth curve parameter and relative year class strength (YCS) estimation, all age validation estimates are assumed to be correct.

# 4.2.4 Length-frequency, growth parameters and year class strength estimation

The von Bertalanffy size-at-age relationship was used to describe the growth trajectory of age-validated *D. eleginoides* at the South Sandwich Islands. The von Bertalanffy equation expresses length, *L*, as a function of the age of the fish, *t*, as follows:

$$L_{t} = L_{inf} (1 - e^{(-k(t-t0))})$$
 eqn 4.3

Where  $L_t$  is the total length, K is the growth rate coefficient,  $L_{inf}$  is the asymptotic length and  $t_0$  is the theoretical age at zero length. Unreasonable estimates of  $t_0$  were made when this was left free, so it was decided to constrain it to a value of -0.3, the latest estimate for the South Georgia toothfish population (Collins, Brickle et al. 2011). Using  $t_0 = -0.3$ ,  $L_{inf} = 132$  and K = 0.079 as in Hillary, Kirkwood *et al.* (2006), the predicted length at the time of hatching was 3.1 cm, suggesting that the value of  $t_0$  is appropriate for this population. The growth curve parameters were estimated using the least squares method of the differences between observed and predicted values of total length, given different values of  $L_{inf}$  and K.

The catch-weighted length frequency of toothfish species was analysed as a means of understanding the population age structure at the South Sandwich Islands through time. Length frequency observations in a 5 cm length interval  $(n_l)$ , were catch weighted as follows:

$$n_l = \frac{n_c}{n_m}$$
eqn 4.4

Where  $n_c$  is the total reported catch *n* reported for an individual haul and  $n_m$  was the total catch *n* measured for the same haul. Estimates of  $n_l$  were then summed across all hauls in one year to estimate total annual catch *n* for each 5 cm length interval.

# 4.3 Results

#### 4.3.1 Size and age structure

It was apparent form a visual examination of the progression of the catch-weighted length frequency distribution through time that the vulnerable population of *D. eleginoides* is likely to be dominated by a small number of cohorts, which have grown in size over the course of the fishery (Fig. 4.1). That modal length of this group of this cohort (or group of cohorts) appears to have increased in size as the fishery progressed, from 91-95 cm in 2005 to 116-120 cm in 2010. At least two other large recruitment events are likely to have occurred in recent years, as indicated by the presence of a large mode (which increased in size from 130-134 cm in 2006 to 155 cm in 2009) and the emergence of a smaller mode in 2006, which comprised a greater proportion of the catch as it continued to recruit in subsequent seasons (from 66-70 cm in 2006 to 81-84 cm in 2010). *D. mawsoni* were much more frequently captured after the expansion of the fishery in to the Southern Management Area in 2009. A modal length category of 156-160 cm was observed in both 2009 and 2010 and few fish smaller than 120 cm were captured in any season (Fig. 4.1).



Length category (standard length cm)

Figure 4.1 Catch-weighted length frequency distribution of *D. eleginoides* (left) and *D. mawsoni* (right) at the South Sandwich Islands from 2005 to 2010. Dashed lines highlight 25 cm length divisions.

Large area effects were observed in the size structure of both *D. eleginoides* and *D. mawsoni*. The large 100 to 140 cm mode dominated the vulnerable population of *D. eleginoides* of both the northern and southern management areas of the South Sandwich Islands. A much smaller size distribution was observed at South Georgia. The small mode of 66-90 cm *D. eleginoides* was not observed in the Southern Management area of the South Sandwich Islands. The catch size distribution of *D. mawsoni* at the South Sandwich Islands was similar, if slightly larger, to that observed in the northern area of the Ross Sea (north of 70°S and west of 160°W) (Fig. 4.2).



Figure 4.2 a) *D. eleginoides* captured aboard the San Aspiring at the South Sandwich Islands in 2009 (note similar size of fish captured); and b) area effects on catch-weighted length-frequency of *D. eleginoides* and *D. mawsoni* in 2010.

The length frequency of fish randomly selected for age validation was representative of the catch length frequency (Fig. 4.1). Only 15 out of 218 of otoliths (7%) could not be accurately read and these were omitted from YCS analyses (Fig. 4.3). Otolith ageing confirmed that recruitment to the South Sandwich Islands *D. eleginoides* population is likely to be highly episodic, with a large proportion of the captured population dominated by 15+, 16+ and 17+ individuals, hatching in years 1991, 1990 and 1989, respectively (111 of 203 successful age validations). Most fish of 96-130 cm total length were found to belong to one of these three cohorts. Fish smaller than this were mostly comprised of individuals from cohorts 6+ to 10+ (hatching in 1985). However, low levels of recruitment were likely to have occurred in all other years, with a minimum of one individual observed in each cohort ranging from ages 6+ to 32+ (Table A4.2).



Figure 4.3 Examples of otolith preparations used for age validation: a) ventral view of otolith from 75 cm male, read as 9+, with primordium (hollow circle) and first six translucent bands (filled circles) highlighted; and b) annual growth rings on dorsal side of otolith, extracted from 162 cm female, read as 27+ (Scale bars are 1 mm).

In the Northern Area of the South Sandwich Islands, the three dominant cohorts in the 2009 catch (15+, 16+ and 17+) comprise 56% of the total sampled population, compared with 36% of the South Georgia sample in 2009 (7+, 10+ and 11+). Very few fish younger than 10+ were likely to have been captured in the Southern Area of the South Sandwich Islands (Fig. 4.4), where catches of *D. eleginoides* are mostly limited to the slopes of Saunders Island (Fig. 6.1), and the three dominant cohorts (16+, 17+ and 18+) comprised 57% of the sampled population.



Figure 4.4 Age distribution of otolith aged *D. eleginoides* captured in 2009, comparing fish captured at South Georgia and the Northern and Southern management areas of the South Sandwich Islands.

### 4.3.2 Condition and gonad maturation

Previous studies have indicated that the main spawning event of South Georgia *D.* eleginoides occurs in late-July and August (Agnew 1999), with an  $L_{m50}$  of approximately 93 cm total length and age 10-14 (Hillary, Kirkwood et al. 2006). Taking a subset of individuals at South Georgia sampled in this study of >100 cm total length, no fish were observed to have a GSI of > 0.08 in April, compared with 49 % in July, reduced by spawning to 8.5 % in August. A very different pattern was observed at the South Sandwich Islands, where all fish had a GSI of < 0.08 in any month where sampling occurred, including 509 fish sampled in July, when GSI is typically greatest at South Georgia (Fig. 4.5).



Figure 4.5 GSI distribution of *D. eleginoides* at South Georgia and the South Sandwich Islands by month. All measured individuals > 100 cm total length; sample size in parentheses.

The lack of gonad development suggests that few fish at the South Sandwich Islands undergo development to maturity in any one season. This is confirmed by analysis of GMI data. At South Georgia, in the months of May through to August, the proportion of *D. eleginoides* with GMI of 3 or greater (developing, gravid or spent gonads) is normally between 0.3 and 0.6 in any one season (Fig. 4.6). At the South Sandwich Islands, this proportion was less than 0.05 during April, May and July in all seasons fished except for one (July 2005), though gonad mass data were lacking from this period to provide a more objective measure for comparison (Fig. 4.6). Given the lack of gonad development it was not possible to estimate the length at maturity relationship for the South Sandwich Islands *D*.

*eleginoides* population. However, many animals were larger than the South Georgia  $L_{m50}$  points, so the expectation should be that they could have matured.



Figure 4.6 Proportion of *D. eleginoides* with GMI of 3-5 by month, comparing South Georgia and South Sandwich Islands populations

The gradient of the length-mass parameters estimated for the Western South Georgia *D. eleginoides* population in April was similar to that of the Northern Management Area of the South Sandwich Islands, though smaller than that of the Southern Management Area (both axes log-transformed; SG = 3.186; SSI North = 3.193; SSI South = 3.294) (Fig. 4.7). The median Fuller's condition factor (*K*) of the South Sandwich Islands Northern Area *D. eleginoides* was greater than 1 in all months assessed and always greater than that of the South Georgia population, in which maximum somatic condition was observed in July. Even greater values of median *K* were observed in the Southern Management Area (April *median*  $K_{SG} = 0.928$ ; *median*  $K_{SSI N} = 1.031$ ; *median*  $K_{SSI S} = 1.052$ ) (Figs. 4.5 and 4.8).



Figure 4.7 Length-mass relationship of *D. eleginoides* captured in April at South Georgia and the South Sandwich Islands. "SG Shag" = South Georgia west of 40 °W; "SSIs North" = South Sandwich Islands north of 57.4°N and; "SSIs South" = South Sandwich Islands south of 57.4°N. Trend lines labelled with linear equations.



Figure 4.8 Monthly condition factor (Fulton's *K*) of *D. eleginoides* captured at South Georgia and at the South Sandwich Islands (left) and *D. mawsoni* at the Ross Sea and the South Sandwich Islands (right)

The reproductive biology of South Sandwich Islands *D. mawsoni* appears to be similar to that observed in the northern Ross Sea, which is thought to be the main spawning area for the Ross Sea population (Hanchet, Rickard et al. 2008). Biometric data were available for South Sandwich Islands *D. mawsoni* captured in March and April only, though the very low proportion of individuals with GSI of less than 0.08 (26.2 % and 24.5 % in March and April, respectively) suggests that a large component of the vulnerable population reached spawning condition in both seasons fished in the Southern Management Area (Fig. 4.9).



Figure 4.9 Monthly GSI distribution of *D. mawsoni* at the northern Ross Sea and South Sandwich Islands (minimum length of 100 cm total length; sample size in parentheses)

The somatic condition (K) of South Sandwich Islands *D. mawsoni* was similar to that of the northern Ross Sea population, though the two fisheries tend to operate at slightly different times of the year and data were available from both areas in March only, when median condition was approximately 1.1 on both areas (Fig. 4.9).

#### 4.3.3 Growth

Estimates of *D. eleginoides* size-at-age were made from otolith-based age validations of 218 individuals captured in the South Sandwich Islands fishery in 2009. As is usually reported for *D. eleginoides*, females were found to grow to a greater  $L_{inf}$  than males (187.0 cm, compared to 148.8 cm). Few males greater than 20 years of age were picked at random from the catch and included in this analysis, so the estimate of  $L_{inf}$  is less certain, though there was still no overlap in the 95% confidence intervals for the two sexes (171.9 to 207.1 cm and 136.8 to

170.8 cm for females and males, respectively). The mixed sex  $L_{inf}$  of 180.2 cm (95 % CIs – 167.1 to 191.5 cm) for the South Sandwich Islands population is far greater than that currently assumed for the South Georgia population 132.0 cm (Agnew and Belchier 2009). The corresponding mixed-sex growth coefficient for South Sandwich Islands *D. eleginoides* (*K* = 0.060; 95% CIs – 0.054 and 0.070) was much lower than estimated for the South Georgia population (0.079) (Agnew and Belchier 2009) and the divergence in predicted length at age occurs between 80 and 100 cm total length, approximately corresponding with the  $L_{m50}$  for *D. eleginoides* at South Georgia of 93 cm total length (Hillary, Kirkwood et al. 2006) (Fig. 4.10 and Table A4.3).



Figure 4.10 Length at age for *D. eleginoides*, comparing South Sandwich Islands and South Georgia populations (left) and length at age of South Sandwich Islands *D. eleginoides* comparing males and females. South Georgia length at age from growth parameters in Agnew and Belchier (2009);  $L_{inf} = 132$ , K = 0.079,  $t_0 = -0.3$ . Dashed line represents 95% confidence intervals around estimates for South Sandwich Islands populations.

# 4.4 Discussion

# 4.4.1 Adaptive plasticity of *D. eleginoides* to cold water

A recent genetic study has shown that the *D. eleginoides* population at the South Sandwich Islands is genetically very similar to the South Georgia population (Fitzcharles 2007) and analysis of otolith microchemistry (Chapter 5) has suggested that they are likely to have migrated from juvenile foraging grounds located close to each other. The lack of gonad development in South Sandwich Islands *D. eleginoides* observed here adds further weight to the argument that this population is likely to be supported by emigration of individuals from spawning grounds located elsewhere, rather than from resident spawning activity. As such, a unique opportunity is provided to study plasticity in *D. eleginoides* phenotype from the range centre (South Georgia) to the southern distributional range limit, where I hypothesise that cold temperature and environmental covariates are limiting factors to further southward dispersal.

This study finds large differences in the life histories of the two *D. eleginoides* populations that are indicative of adaptive phenotypic plasticity (Gotthard and Nylin 1995). At the South Sandwich Islands, the growth phase of *D. eleginoides* is more rapid than at South Georgia and more prolonged and development to spawning condition was not observed in any year from 2005-2010 (Fig. 4.6). The life history characteristics of South Sandwich Islands D. eleginoides are consistent with the temperature size rule (Atkinson and Sibly 1997). However, assuming that South Sandwich Islands and South Georgia population are genetically identical, the contrasting life histories observed here are likely to have resulted from the adaptive plasticity of *D. eleginoides* rather than through selective adaptation. However, it should also be noted that South Georgia D. eleginoides has been exploited for more than 20 years (Agnew 2004) and this may have changed the life history characteristics in the remaining population. Exploitation tends to lead to decreased age and length at maturity and a curtailed estimated growth curve. As such the size-at-age relationship of the current South Georgia stock may be quite from the historic natural range centre population. For instance, Aguayo et al. (1992) estimated very different von Bertalanffy growth parameters for the South Georgia population in 1992 than those estimated in 2006 (Hillary, Kirkwood et al. 2006) (combined sex estimates in 1992 - K = 0.062,  $L_{inf} = 216.1$ ,  $t_0 = -0.877$ ; 2006 - K = 0.08,  $L_{inf} = 132$ ,  $t_0 = -0.3$ ), though the older estimate was based on ring counts on scales rather than otoliths and there may be differences in the ages acquired using the two different methods.

In addition, South Sandwich Islands *D. eleginoides* are characterised by improved somatic condition relative to individuals at South Georgia and this may relate to the lack of gonad maturation in the former population, as life history theory predicts that this will be compromised by the energetic demands of gonad development (Roff 2000). Ambient

temperature may be the cue that triggers gonad development and it appears to be too cold at the South Sandwich Islands for this to occur. However *K* continued to increase moving south across the South Sandwich Islands, even though there is no real evidence for gonad maturation in *D. eleginoides* across the entire island arc and there may another, potentially more direct mechanism by which temperature and condition interact that has not been considered here (Fig. 4.8). The linkages between feeding ecology, somatic condition, gonad development and growth have been discussed previously in Ross Sea populations of *D. mawsoni* (Fenaughty, Eastman et al. 2008), though not in the context of adaptive plasticity and life history optimisation.

Life history theory suggests that prolonged growth of *D. eleginoides* populations at the South Sandwich Islands would occur at the expense of gonad maturation, which competes with growth for somatic energy stores. However, this could also be supported by the acquisition of additional food, particularly where prey increase in abundance (Angilletta, Steury et al. 2004). This would not normally be expected towards range edges where conditions would be assumed to be suboptimal, though diet studies of toothfish species indicate relatively high rates of prey occurrence at the South Sandwich Islands relative to South Georgia (Roberts, Xavier et al. 2011). Also, reduced population density of *D. eleginoides*, as inferred from longline catch rates comparing South Sandwich Islands and South Georgia fisheries (Roberts and Agnew 2009a), may reduce potential density-dependent effects on growth rate. This may also explain the rapid growth rate of South Sandwich Islands *D. eleginoides* (Fig. 4.10), given that the reverse is normally observed at the early life stages of cold water populations.

Reduced population density of North Atlantic herring populations has been found with increasing latitude and the effects of reduced density dependence on growth patterns were also considered to be important for this species (Brunel and Dickey-Collas 2010). Departures from classic life history theory can sometimes be explained by complications arising from covariation between temperature change and occurrence rates of predators and prey. This picture can be further complicated by the effects of intra-specific competition for resources and these complex interactions deserve more consideration in the context of life history studies (Angilletta, Steury et al. 2004).
#### 4.4.2 Reproductive biology and recruitment towards range edges

Reproductive failure has been recorded in the range edge populations of a number of species and often appears to be more important than survival rates of offspring in shaping distributional range limits (Gaston 2009). However, it is rarely observed in wild fish populations, possibly because fish do not often survive for long in conditions sufficiently adverse to interfere with reproductive biology. The observed lack of gonad development in the South Sandwich Islands D. eleginoides population suggests that reproductive failure is common and it is likely that most individuals do not reach spawning condition in most seasons. Studies of *D. eleginoides* genetics and otolith microchemistry (Fitzcharles 2007) (Chapter 5) strongly suggest that the resident population is supported by recruitment of individuals from spawning grounds located upstream, most probably from the region of South Georgia. Long distance migrations would be required and these may be assisted by the Antarctic Circumpolar Current, which normally flows to the north of the South Sandwich Islands (Orsi, Whitworth et al. 1995), though southward incursions of ACC water are likely to occur in warmer years. Hence, resultant immigration (and recruitment to the fishery) would be expected to be highly sporadic, as expected for any range edge population where soft barriers to dispersal temporarily restrict migration.

The size and age structure of the South Sandwich Islands *D. eleginoides* vulnerable biomass suggest that it is dominated by a limited number of cohorts (15+, 16+ and 17+), of which just a single cohort may be most dominant, given that estimates by different readers can differ by up to four years when reading otoliths of this species (Kalish and Timmiss 1998). Older fish appear to be present in the population (oldest 35+) though are not nearly so abundant, assuming larger fish are equally selected for by the fishing gear as mid-sized fish. This is consistent with very low catch rates experienced by exploratory fishing conducted in the area in the early 1990s (Rubilar, Moreno et al. 1993). All the evidence suggests that recruitment to this range edge population is highly sporadic and it is possible that this species is not found here at all during cooler time periods. The appearance of at least one cohort, which began recruiting in to the fishery in 2006 is coincident with the appearance of two strong year classes at South Georgia (Agnew and Peatman 2009) and it possible that recruitment events to the two stocks are linked by climatic phenomena such as ENSO and SAM effecting large areas of the Southern Ocean.

#### 4.4.3 Comparative life history of D. mawsoni

The South Sandwich Islands population of *D. mawsoni* is also situated on the edge of its distributional range, with few ever captured to the north of Saunders Island. However, unlike *D. eleginoides*, their life history characteristics are more typical of the range centre population (Ross Sea). Age validation data were not available, though the catch length frequency distribution indicated that the population age structure was relatively even. The lack of fish smaller than 100 cm in longline catches is also observed in the northern Ross Sea. Juveniles and small adults dominate shelf regions in the southern Ross Sea and it is thought that fish migrate northwards down the slope as they mature to spawn grounds over the Pacific-Antarctic Ridge (Fenaughty 2006).

As in the northern Ross Sea, *D. mawsoni* gonad development at the South Sandwich Islands was advanced for the time of year and it is plausible that the South Sandwich Islands form the northern spawning grounds for the Weddell Sea population, which is known to be genetically distinct from the Ross Sea population (Kuhn and Gaffney 2008). *D. mawsoni* have occasionally been caught further south along the Scotia Arc, where they are typically much smaller in size (Arana 1999). The relatively close proximity of the South Sandwich Islands to the southern Scotia Arc appears to allow migration of *D. mawsoni* northward from this region. If the South Sandwich Islands population has indeed migrated up from the South, then range edge life history (increased von Bertalanffy *K* and reduced *Lm*50 at increased temperature) would not be expected for this population.

#### 4.4.4 Conclusions and future work

Some though not all of current theories of range position effects on life history were observed in *D. eleginoides*. Increased maximum size was observed towards the cold water range limit at the South Sandwich Islands, though initial growth rates are not any slower than those observed at South Georgia, assumed to be typical of range centre populations. Cold water temperatures appear to limit gonad maturation and the lack of reproductive development may leave more energy available for growth. This also appears to lead to improved somatic condition, which would not normally be expected in range edge individuals, where habitat should be suboptimal and food resources may be limited. Highly episodic recruitment, also assumed to be a feature of range edge populations (Philippart, Henderson et al. 1998; Brunel and Boucher 2006), was also observed in the South Sandwich

Islands *D. eleginoides* population and is likely to relate to impaired reproductive development of the resident population, which may not be self-sustaining (Fig. 4.3).

Table 4.3 Range edge life history	theory	and	extent	to	which	this	was	observed	in	South	Sandwid	:h
Islands D. eleginoides.												

Life history feature	Current theory (reference)	Theory reference	Observed in D. eleginoides
Maximum average size	Increased at low temperature	(Atkinson and Sibly 1997)	Yes
Initial growth rate	Decreased at low temperature	(Atkinson and Sibly 1997)	No
Somatic condition	Decreased towards range edge	(Gaston 2009)	No – the opposite response was observed of increased condition towards the range edge
Maturation	Delayed at low temperature	(Roff 2000)	No maturation observed at all, though delayed maturation may have occurred at a slightly warmer temperature
Recruitment variability	Increased towards range edges	(Brunel and Boucher 2006)	Yes

Several studies have highlighted differences in genetic composition when comparing different populations of *D. eleginoides* (Shaw, Arkhipkin et al. 2004; Rogers, Morley et al. 2006), with morphological differences also noted between populations segregated by major fronts of the Antarctic Circumpolar Current. These differences are likely to partly reflect selective adaptation to regional differences in habitat including temperature differences from north to south. It is clear that the productivity of the South Sandwich Islands *D. eleginoides* population is limited by temperature effects on reproductive biology, whereas somatic growth rates are rapid for a cold water population and this may relate to the lack of energetic investment in reproduction. Life history differences between genetically similar South Georgia and South Sandwich Islands populations also indicate that *D. eleginoides* may also demonstrate adaptive phenotypic plasticity and life history theory suggests that these reaction norms will be optimised to improve the fitness of individuals over shorter time scales than those affected by selective processes.

These are the observations for a single range edge population of *D. eleginoides* and similarly broad analyses on other high latitude populations (*e.g.* BANZARE bank, Heard Island) would allow an assessment of whether they are typical of other populations situated at their cold

water range limits. Expanding the analysis across a full distributional range would allow for a generalisation of range position effects on life history that would be informative for the management of data poor fisheries and for predictions of climate change impacts on life history and distribution.

#### Chapter 5

### Dispersal patterns of South Georgia and South Sandwich Islands toothfish from otolith microchemistry and mark recapture studies

#### 5.1 Introduction

The evidence for range position effects on toothfish species life history and population dynamics were examined in the previous chapter, which evaluated range position effects on the proxies for the births and deaths component of the BIDE population model (Eqn. 1.1). This chapter focuses on dispersal effects and more specifically, the effects of immigration and emigration on population size and demographics. An obvious question arises from the observation that *D. eleginoides* do not appear to reach spawning condition at the South Sandwich Islands: from where do they originate and how might this relate to the recruitment patterns observed in the resident population? Also can the position of range limits be explained by the dispersal patterns of adult fish and how might this relate the scheduling of life history processes? Finally, how might range edge dispersal patterns impact on population assessments for resource management and how might they be incorporated into an assessment; as conducted in Chapter 6?

#### 5.1.1 Dispersal effects on species distributions

The BIDE population model (Eqn. 1.1) stipulates that population size will vary as function of births (recruitment), deaths, immigration and emigration. The spatial extent of a species' fundamental niche will be defined by environmental conditions and the availability of fundamental resources. The "abundant centre hypothesis" (Brown, Mehlman et al. 1995) contends that population density will decrease from a range centre to the periphery in response to decreasing habitat quality (see Section 4.1.1). Biotic interactions, such as competition and disease will also impact on births and deaths and, so, define the extent to which the fundamental niche is realised, though there remains a general ignorance of the importance of dispersal effects on population size, distribution and the formation of range

edges (Guisan and Zimmermann 2000) largely due to a lack of good quality empirical field data on which to estimate rates of dispersal (Bahn, Krohn et al. 2008).

Experiences with invasive organisms have demonstrated that restrictions on dispersal can critically affect the extent to which the fundamental niche is realised – areas may not be occupied simply because they cannot be reached (Gaston 2009). Conversely, strong dispersive forces may distribute organisms in to areas with less favourable habitat, where deaths exceed births. In such areas, immigration can support sink populations (Pulliam and Danielson 1991), often referred to as "run off" stocks in the context of fisheries management. Variable dispersive forces and intermittent dispersal barriers can upset factors which equilibrate species distributions, such that the locations of range edges may shift through time (Gaston 2009).

Passive dispersal is powered by naturally occurring sources of kinetic energy such as wind or currents which propel the organism without energetic cost. This is also termed "density independent dispersal" because dispersal patterns are not responsive to the spatial distribution of resources or to population density. Passive dispersal is typical of marine organisms with a pelagic life phase, including the early life stages of toothfish species (Collins, Brickle et al. 2011), or the wind borne seeds of terrestrial plants. Gaylord and Gaines (2000) demonstrated how the prevailing pattern of currents can have a dominant affect on the spatial distribution of passively dispersed marine organisms, such that current flow fields create biogeographic boundaries that do not necessarily relate to a species' niche requirements.

Motile organisms are able to redistribute in response to gradients in habitat quality and competition for resources. This redistribution is also referred to as "density dependent" or active dispersal. Where this dominates over passive dispersal, population density should with time equilibrate to the spatial distribution of resources, such that the abundant centre distribution might arise where habitat at the range centre is optimal (Brown, Mehlman et al. 1995). Where the spatial distribution of resources remains constant through time, density dependent dispersal should tend to equilibrate a species' distribution. This contrasts with density independent dispersal, which may have a destabilising effect on species distributions and range edges, because the energy comes from current systems which may be subject to a high degree of temporal variation in path and intensity (Gaylord and Gaines 2000). This may

lead to increasingly episodic recruitment and uneven population age structure towards range edges (Gaylord and Gaines 2000) (see Chapter 4).

#### 5.1.2 Dispersal of toothfish at different life stages

Antarctic and Patagonian toothfish are endemic to the cold waters of the Southern Hemisphere, where they are both widely distributed as with many other bathyal fish species (Rogers, Morley et al. 2006). They also inhabit a broad range of depths depending on lifestage; eggs are pelagic, and are likely to spend several months in surface waters after hatching since larvae tend to be recovered close to the surface; large adults are found as deep as 2500 m (Evseenko, Kock et al. 1995).

Both toothfish species are thought to be broadcast spawners, producing pelagic eggs and larvae that drift in surface currents for several months before settling over shelf habitat (North 2002). The ecology and dispersal patterns of the earliest life stages are not well understood (North 2002). A small number of patchily distributed *D. eleginoides* eggs have been found in the waters surrounding South Georgia, mostly in the top 700 m of the water column. These were found both on and off the shelf, some more than 100km to the north of South Georgia (Evseenko, Kock et al. 1995; North 2002). Hence the dispersal potential of pelagic phase individuals may be high and will depend largely on the flow regime of local current systems. One study utilised a circulation model to demonstrate that *D. mawsoni* eggs and larvae can be distributed widely about the Ross Sea from discrete release sites. Here it was found that that location of spawning would have a large effect on whether eggs would remain in the vicinity of putative juvenile foraging habitat or advected out of the Ross Sea (Hanchet, Rickard et al. 2008).

The distribution of later life stages varies with age. Juveniles undergo a distinct ontogenetic migration in to deeper regions of the shelf, with a mean depth of 140 m for 1+ fish, compared with 209 to 240 m for 2+ to 4+ fish (Belchier and Collins 2008). At South Georgia, the youngest fish are tightly aggregated over shallow shelf regions surrounding Shag Rocks and 3+ fish are distributed over deep shelf regions, close to the shelf breaks surrounding South Georgia and Shag Rocks (Belchier and Collins 2008).

The dispersal patterns of *D. eleginoides* individuals can be inferred from differences in spatial distribution at each life stage. At ages 4+ to 6+, shelf juveniles migrate down over the

shelf break to join bathyal slope-phase adults. This is apparent from the disappearance of fish greater than 50 cm length from the shelf groundfish survey at South Georgia and the appearance of fish greater than this size in bathyal longline catches (Belchier and Collins 2008). One unpublished study suggested that South Georgia *D. eleginoides* continue to spread outward from the Shag Rocks region as they increase in size, so that they are more evenly distributed about the shelf habitat (D. Agnew 2011, pers. comm.). Mark recapture studies indicated that dispersal rates of slope-phase fish are relatively low, with most *D. eleginoides* and *D. mawsoni* recaptured with 50 km of the point of release (Agnew, Kirkwood et al. 2006; Hanchet, Rickard et al. 2008). Toothfish reach sexual maturity at approximately age 10 and the concentration of South Georgia *D. eleginoides* spawning activity at certain locations suggests that spawning migrations are likely (Agnew 1999).

Differences in ecology and behaviour will affect the dispersal potential of different life stages. Intuitively, the passive, density independent dispersal patterns of pelagic phase individuals advected by strong currents will be very different in character (speed, direction and potential for long distance dispersal) compared with those of the active, densitydependent dispersal patterns of shelf and slope phase individuals.

#### **5.1.3** Delineation of toothfish stocks

Population assessments for managed fisheries generally assume a closed population (Hillary, Kirkwood et al. 2006; Candy and Constable 2008), such that migration rates in and out of the stock are sufficiently low as to have a negligible effect on population size and structure. A number of analytical methods have been used to assess dispersal patterns of toothfish populations, including: mark-recapture experiments; genetic analyses; comparative morphology; taxonomic studies of endo-parasites; and otolith chemistry (Collins, Brickle et al. 2011).

Mark-recapture programs provide one of the more direct means of assessing the dispersal patterns of fish populations. All of the main *D. eleginoides* and *D. mawsoni* stocks are now the subject of extensive mark-recapture programs (Agnew, Kirkwood et al. 2006). Horizontal movement rates of slope-phase, post-recruitment individuals are thought to be low and may be greatest in juveniles and sub-adults (Hanchet, Rickard et al. 2008). With the exception of Kerguelen Plateau *D. eleginoides*, which supports major fisheries in French and Australian

maritime zones at Kerguelen and Heard Islands, mark-recapture movements between managed toothfish stocks appear to be rare (Welsford, Candy et al. 2011).

Inferences of toothfish population connectedness have also been made from examination of mitochondrial haplotype frequencies (Appleyard, Williams et al. 2004; Shaw, Arkhipkin et al. 2004; Rogers, Morley et al. 2006; Kuhn and Gaffney 2008) and the elemental chemistry of otoliths (Ashford, Arkhipkin et al. 2006; Ashford and Jones 2007; Ashford, Jones et al. 2008). Where large distances and geographic isolation limit the flow of genetic material between populations, significant differences in haplotype frequencies between populations may arise. Studies of D. mawsoni genetics have revealed that South Shetland Islands and Ross dependency populations are genetically distinct, despite a high overall degree of genetic similarity (Kuhn and Gaffney 2008). This genetic differentiation is speculated to have arisen from physical separation of these populations by the Antarctic Peninsula. Falklands and South Georgia populations of *D. eleginoides* have also been shown to be genetically distinct (Shaw, Arkhipkin et al. 2004; Rogers, Morley et al. 2006). Differences have also been observed between South Georgia and Bouvet populations, though Bouvet and nearby Ob populations were not significantly different (Rogers, Morley et al. 2006). Recent research has also pointed to genetic similarity between South Sandwich Islands and South Georgia D. eleginoides populations. Analysis of a 12S mitochondrial sequence showed that the South Sandwich Islands population comprised a mixture of two haplotypes, characteristic of populations resident to slope regions to the north or south of the Polar front. Only 9 out of 230 individuals were found to have the Northern Haplotype (as the Falklands population) compared with 221 with Southern haplotype (as the South Georgia population) (Fitzcharles 2007) (Fig. 5.1).



Figure 5.1 12S rRNA Sequence alignments for *D. eleginoides* captured at the South Sandwich Islands. The top two sequences correspond to Northern haplotype and others to the Southern haplotype. From Fitzcharles (2005).

The chemical composition of fish otoliths is thought to be strongly influenced by ambient seawater chemistry and this can vary by region, such that it can be used to infer a degree of stock delineation where the otolith chemistry of two populations is heterogeneous (Bath, Thorrold et al. 2000; Gillanders 2002). Existing studies of toothfish suggest a high degree of stock delineation in early (otolith nuclei) and later life (rims), with a strong degree of population structuring by major frontal systems of the Southern Ocean, particularly the Polar Front at the northern limits of the ACC (Ashford, Arkhipkin et al. 2006; Ashford, Arkhipkin et al. 2007). However, another study found the otolith nucleus microchemistry of separately managed stocks at the Falklands and Chilean EEZ to be quite homogenous (Ashford, Jones et al. 2008), though this does not necessarily imply a high degree of mixing between the two populations as this pattern may also arise where seawater chemistry of the two stock areas is not significantly different, as may be the case across the Patagonian shelf region.

This same study (Ashford, Jones et al. 2008) found within-population heterogeneity of nucleus microchemistry at South Georgia, which indicated a degree of physical structuring within a single managed stock that were not detected in previous genetic analyses (Rogers, Morley et al. 2006; Ashford, Jones et al. 2008). Within-stock heterogeneity of otolith nuclei may be observed where sub-populations originate from spatially discrete spawning grounds or juvenile feeding grounds where the ambient seawater chemistry is different, though intermingling of subsequent life stages might then mix genetic material across the managed stock, so that they there is not genetic variation across the wider population. Hence, otolith chemistry can be used to make some inferences about the physical structuring and delineation of different populations, though more complete inferences may be made through comparison of evidence from different methods, including: genetic analyses, analysis of otolith chemistry, and mark-recapture studies.

#### 5.1.4 Chapter aims

Catch rates of *D. eleginoides* decrease significantly on lines set below 2,000m (Agnew 1999) and it is likely that the deep seafloor (>3000m) between South Georgia and South Sandwich Islands presents a significant barrier to toothfish dispersal between these two areas. A similar barrier appears to limit the dispersal of South Georgia fish westwards beyond the 3000m deep trench between shag rocks and the eastern Scotia Arc (Shaw *et al.*, 2004). However, the abnormal reproductive development of South Sandwich Islands *D. eleginoides* (Figs. 4.5 & 4.6), coupled with the genetic analysis undertaken by Elaine Fitzcharles (Fig. 5.1), suggests that this population cannot be sustained without immigration from elsewhere. In

this study, otoliths were obtained from South Georgia D. eleginoides and also from South Sandwich Islands *D. eleginoides* which had previously been identified by Fitzcharles to have either a Northern or Southern haplotype (Fitzcharles 2007) and the microchemistry was analysed from core to rim. The primary aims of this study were:

- to evaluate the degree of stock delineation at different life stages; and where mixing between populations was detected; and
- to determine the approximate age at which long distance migrations occurred.

A secondary goal of this research was to evaluate patterns in otolith chemistry from core to rim that might relate to seawater chemistry with depth that would be experienced at different life stages. This was aimed at testing the extent to which the chemical composition of otoliths is likely to reflect ambient seawater chemistry and, at the same time, to assess the usefulness of this approach for assessing the horizontal movements of deep water species that may be difficult to elucidate by other means.

More than 20,000 *D. eleginiodes* have been tagged at South Georgia since 2000 and more than 1,000 at the South Sandwich Islands since the resumption of fishing in 2005. Here a mark-recapture migration model was developed to estimate migration rates of slope phase *D. eleginoides* between the two areas. In addition, the basic dispersal characteristics of both toothfish species were assessed using tag mark-recapture data to test the degree to which dispersal plays an important role in the formation of range limits at the South Sandwich Islands.

#### 5.2 Methods

#### 5.2.1 Stock delineation from otolith microchemistry

#### Sample selection

Otoliths were collected from *D. eleginoides* captured in longline operations at South Georgia (2009) and the South Sandwich Islands (2005). A total of 40 otoliths were analysed from fish comprising a combination of area of capture/haplotype groupings, including 10 fish captured in the gully region between the South Georgia and Shag Rocks shelves ("SG Gully"; from 39.5°W to 40.5°W); and 10 from east South Georgia ("SG East"; 34.0°W to 36.2°W). All fish

captured at South Georgia were assumed to be Southern Haplotype as had previously been found to be the case (Rogers, Morley et al. 2006). In addition, otoliths were sampled from 20 fish captured at the South Sandwich Islands, including 14 fish previously determined to be Southern haplotype ("SSI/Southern") and 6 Northern Haplotype fish ("SSI/Northern") (E. Fitzcharles *et al.* 2011, unpub. data) (Fig. A5.1). These were selected at random from a larger pool of otoliths, constrained to those extracted from females of between 90 and 110 cm total length, to exclude potential sex and size effects on otolith chemistry. Broken otoliths were removed from the random subsample and new otoliths randomly selected.

#### Sample preparation

Otoliths were baked in an oven at 250°C for 10 minutes and allowed to cool, before being in embedded in clear casting epoxy resin and allowed to set. Transverse sections of 80 mm width were made with a circular saw and sections containing primordia were identified and mounted on to petrographic slides. Eight otoliths, comprising a random sample of area/haplotype groupings, were mounted on each slide. The mounting resin was allowed to set for at least 12 hours prior to sonication in Milli-Q water. Plastic forceps and other vessels used to manipulate and contain the otoliths were first cleaned with hydrogen peroxide. Mounted samples were stored in sterile plastic jars prior to chemical analysis. All otoliths were cleaned with Anal-R Aristar grade 1% nitric acid + 0.5% hydrochloric acid for approximately 10 seconds immediately prior to ablation.

#### **Chemical sampling**

Chemical sampling of otoliths was undertaken at the British Geological Survey, Keyworth under the supervision of Dr Simon Chenery. A laser ablation inductively coupled mass spectrometer (LA-ICP-MS) was used to analyse the minor and trace element chemistry. All otoliths were analysed on one slide before moving on to the next to minimise any potential effects of drift in the measuring equipment.

Otoliths were sampled for lithium, sodium, magnesium, calcium, manganese, strontium and barium measuring the following isotopes: <sup>7</sup>Li, <sup>23</sup>Na, <sup>24</sup>Mg, <sup>55</sup>Mn, <sup>88</sup>Sr, and <sup>138</sup>Ba, each reported as a molar ratio to <sup>42</sup>Ca. The laser ablation microprobe used in this study consisted of a NewWave 193FX excimer laser operating in the far-UV spectrum (193 nm) with built in light microscopy allowing optical viewing via a video camera. The laser beam and optical viewing

were focused by a common objective lens. The otolith sections under investigation were placed in a plastic cell beneath the microscope, and the specimen illuminated in reflected light. The appropriate areas of the otolith were selected and the laser fired for 30 seconds producing an ablation crater of nominal  $35\mu$ m diameter. The ablated material was transported in a continuous flow of helium before mixing with argon gas to an Agilent 7500c ICP mass spectrometer where vapourisation and ionisation by the hot (6000 <sup>o</sup>K) argon plasma occurred. The quadrupole mass spectrometer filtered and counted the produced atoms.

Results were calibrated against two standard NIST (National Institute of Standards and Technology) glass reference materials (NIST 610 and 612), which were sampled five times at the beginning and end of each slide sampled. Otoliths were sampled a minimum of three times at each of four sites, corresponding approximately to the nucleus, the 3rd annulus, the 8th annulus and 100  $\mu$ m in from the otolith edge (rim) (Fig. 5.2). The laser was set to 75% power at a repetition rate of 5Hz and an energy density of 9.2 J/cm<sup>2</sup> as measured by the internal system, which gave rise to a crater of approximately 35  $\mu$ m diameter and 20  $\mu$ m depth. The embedding resin was also sampled to assess for potential sources of contamination, though none were detected.



Figure 5.2 Photographs of *D. eleginoides* otolith sections with LA-ICP-MS craters: a) standard sampling pattern and b) standard sampling with traverse.

#### Data analysis and statistics

The molar ratio of each element was taken as the median of three replicate samples taken at each annulus, to minimise the influence of potential outliers. Power transformations were applied to achieve univariate normality of each elemental variable, with power values estimated using Box Cox analyses (Table A5.1 & Fig. A5.2). Bartlett's test was used to assess homogeneity of variances. Multivariate normality was tested graphically with Q-Q plots of squared Mahalanobis distances ( $d^2$ ) (Fig. A5.4). Mn.Ca<sup>-1</sup>, Sr.Ca<sup>-1</sup> and Ba.Ca<sup>-1</sup> were all found to vary with area of capture and haplotype grouping and other elements were omitted from multivariate analyses. Multivariate outliers were detected using adjusted quantile plots of ordered squared robust Mahalanobis distances, though none of those identified were likely to have resulted from measurement errors and were left in as they did not compromise normality of error distributions and other fundamental assumptions of statistical tests applied.

Mixed effects models were used to assess the effects of haplotype and area of capture on the profile of elemental ratios to calcium with increasing age. The same basic model structure was applied for all elemental ratios:

#### Element:Ca ~ Age \* Haplotype + Area of capture + (1/Otolith) eqn 5.1

This was the most complex viable model incorporating these terms (models with an interaction term between age and haplotype did not converge). It was not always the most parsimonious model, though it was applied consistently to facilitate comparison between elemental ratios. The function "*pvals.fnc*" in *R* package "*languageR*" (Baayen 2011) was used to estimate *p*-values relating to different terms of the mixed-effects model.

Statistical analyses were designed to test for differences in otolith microchemistry that might reflect differences in foraging habitat of each area/haplotype grouping, at prerecruitment (ages 0+ and 1+) and post-recruitment (6+ and 7+) ages. A high degree of correlation was observed between Ba:Ca and Sr:Ca ratios, though correlation coefficients were not above 0.9 for either pre or post recruitment comparisons and both variables were retained in multivariate analyses. Type II MANOVA was used to conduct multivariate assessments of the effect of location of capture and haplotype on otolith microchemisry, to account for unbalanced sampling design and to negate the importance of term order. Type II ANOVAs were conducted to assess for area of capture and haplotype effects on individual elemental ratios. Principal components analyses were conducted in R using the "*prcomp*" function in the "*stats*" R package (R Development Core Team 2011). PCA1 and PCA2 accounted for more than 80% of the variance of both pre and post-recruitment age groupings.

#### 5.2.2 Mark-recapture procedures

Vessels at the South Sandwich Islands were required to tag and release a minimum of five individuals per tonne of fish landed. These fish were randomly selected from the catch and were allowed to rest in tanks with a circulating seawater supply. Those fish deemed to be in good condition were removed from the tank and tagged with two short dart tags, each labelled with a unique serial number. Biometric measurements were made (species, total length in mm and mass in grams) and tagged fish were released over the side of the boat and location (depth, latitude and longitude) and time/date at the point of release were recorded. Large fish were lifted from the water in an improvised net to minimise jaw damage on pulling heavy fish out of the water (Fig. 5.3).

On recapture, marked fish were set aside from the catch and a detailed set of biometric measurements were taken by the observer (species, total length, body mass, sex, GMI, gonad mass), the otoliths were removed and tag identification recorded. All recaptured fish were photographed with tags *in situ*, such that tag serial numbers could be read (Fig. 5.3). A matrix of all mark-recapture events by area and season is presented in Table 5.3.



Figure 5.3 Cradle used to land large fish for tagging (left) typical position of tags either side of dorsal fin in a recaptured *D. eleginoides* (right).

#### 5.2.3 Mark-recapture migration model

A standard methodology for estimating movement rates of fish populations from mark recapture data (Hilborn 1990) was adopted and developed to estimate migration rates of *D. eleginoides* between the South Sandwich Islands and South Georgia. The model had four components:

- A population dynamics and movement model which predicted the number of tagged fish in each area and time interval;
- 2. An observation model of mark recapture events in each area and time interval;
- 3. A function that gives the probability of observing a given number of mark recaptures in each area and time interval; and
- 4. A non-linear solver that maximises the fit of mark recapture observations to the model for a given annual between-area migration rate

Models that estimate migration rates from the South Sandwich Islands to South Georgia were defined using the following terms:

 $T_{iSSIt}$  = number of tag releases at the South Sandwich Islands in tag group *i* and year *t* 

T = matrix of all  $T_{SSIit}$  values

 $\hat{N}_{i \ SSI \ t}$  = predicted number of tagged fish of tag group *i* present at the South Sandwich Islands in year *t* 

**R** <sub>*i*</sub> <sub>*ssl*</sub> <sub>*t*</sub> = number of tag returns of tag group *i* recovered at the South Sandwich Islands in year t

 $R_{SSI}$  = matrix of  $R_{iSSIt}$  values

 $N_{iSGt}$  = predicted number of tagged fish of tag group *i* present at South Georgia in year *t* 

**R**<sub>iSG t</sub> = number of tag returns of tag group *i* recovered at South Georgia in year t

 $R_{SG}$  = matrix of  $R_{iSGt}$  values

 $\hat{R}_{iSGt}$  = predicted number of tag returns of tag group *i* recovered at South Georgia in year *t* 

 $\hat{R}_{sG}$  = matrix of  $\hat{R}_{isGt}$  values

x = vector of parameters of the population dynamics and movement model

y = vector of parameters of the observation model

P ssi sG = probability of movement from South Sandwich Islands to South Georgia

 $M_{SSI SG}$  = additional mortality associated with movement from South Sandwich Islands to South Georgia

 $B_{SGt}$  = vulnerable biomass *n* at South Georgia in year *t* 

H<sub>sGt</sub> = annual harvest rate (proportion n) at South Georgia

The tag group *i* is defined as the group of fish tagged in the same time and area, which is extended to include both sexes (mixed sex model), or males/females (sex partitioned model).

#### Population dynamics and movement model

A simple simulation model predicted the number of a tag release event in year *t* at the South Sandwich Islands surviving to year *n*.

$$\widehat{N}_{i\,SSI\,t+n} = T_{i\,SSI\,t} \times (1-U) \times e^{-(M+V)^{(n-t)}} - \sum_{i=t}^{t+n} R_{i\,SSI\,t} \qquad \text{eqn 5.2}$$

Where U = tagging induced mortality; M = natural mortality rate and V = tag shedding rate. Values for these parameters were taken from the *D. eleginoides* population assessment for South Georgia (Hillary, Kirkwood et al. 2006): M = 0.13; tag shedding rate = 0.0036 yr<sup>-1</sup> (all fish double-tagged with a shedding rate of 0.06 yr<sup>-1</sup> for a single tag); tagging induced mortality = 0.1; and tag reporting rate = 1.

The movement model took a proportion of the surviving tagged fish South Sandwich Islands and redistributed them to South Georgia.

$$\hat{N}_{i SG t+1} = \hat{N}_{i SSI t} \times P_{SSI SG} \times (1 - M_{SSI SG})$$
eqn 5.3

Where  $M_{SSISG}$  represented an additional mortality associated with the migration of individuals between the two areas, expressed as a proportion of the migrated population. Three migration mortality levels were trialled: 0, 0.25 and 0.5.

#### **Observation model**

The predicted number of tag recaptures at South Georgia was then estimated as follows:

$$\widehat{R}_{iSGt} = \widehat{N}_{iSGt} \times H_{SGt}$$
eqn 5.4

Where harvest rate was determined from CCAMLR catch statistics (CCAMLR, 2010) and estimates of vulnerable population n from a recent population assessment (Agnew and Peatman 2009). Population size for 2010 was derived by assuming the same depletion in vulnerable biomass (in tonnes) observed in the previous year.

#### Probability of observed recoveries

The binomial probability of the observed tag recapture matrix was then estimated given the predicted recapture matrix and probability of movement.

$$P\left(R_{SG} \mid \hat{R}_{SG} \mid P_{SSI SG}\right)$$
 eqn 5.5

Where binomial *n* and *p* were estimated as follows.

$$n = B_{i SG t} \times H_{SG t}$$
eqn 5.6

$$p = \hat{R}_{i SG t} \div B_{i SG t}$$
 eqn 5.7

This was repeated for a range of migration rates to generate a probability distribution, where the most likely migration rate had the greatest probability of observed recaptures given the data and model configuration. The 95% CIs were estimated as the migration rates which corresponded to 2.5 % and 97.5 % of the cumulative probability distribution.

Models of movement from South Georgia to the South Sandwich Islands substituted **SSI** for **SG** and **SG** for **SSI** in all above formulae.

#### 5.2.4 Drifter data analysis

Surface drifter buoy data were analysed to evaluate the potential routes for dispersal of toothfish between South Georgia and the South Sandwich Islands, as Matschiner, Hanel *et al.* (2009). Surface drifter buoy data (1994 to 2008) were obtained through the Fisheries and Oceans Canada surface drifter archive (<u>http://www.meds-sdmm.dfo-mpo.gc.ca</u>). Non-drogued drifters were omitted from the analysis to minimise the influence of surface winds on observed dispersal patterns.

#### 5.3 Results

#### 5.3.1 Otolith microchemistry

Significant trends with age were observed in the molar ratios of Sr, Ba, Na and Mn to Ca and these were observed in all area of capture/haplotype groupings (Table 5.1). Ratios of Ba and Sr to Ca approximately quadrupled between ages 1 and 13 and both increased significantly with age (Sr:Ca – *d.f.* = 1; *F* = 307.23; *p* < 0.001; Ba:Ca – *d.f.* = 1; *F* = 135.22; *p* < 0.01). The increase in Na:Ca with age was less pronounced, though was still significant (*d.f.* = 1; *F* = 32.77; *p* < 0.01). Mn:Ca was the only elemental ratio that decreased with age, though the rate of change was greatly reduced in Northern haplotype fish, where mean Mn:Ca at age 13 was greater than 1 µmol mol<sup>-1</sup>, compared with less than 0.5 µmol mol<sup>-1</sup> in all other area of capture/haplotype groupings (significant interaction effect between age and haplotype; *d.f.* = 1; *F* = 6.67; *p* < 0.01). Location of capture also had a significant effect on Sr and Ba ratios to Ca, where elevated levels were observed towards the otolith rims of fish captured at the South Sandwich Islands (Sr:Ca – *d.f.* = 1; *F* = 6.35; *p* < 0.05; Ba:Ca – *d.f.* = 1; *F* = 12.53; *p* < 0.01; Table 5.1, Fig. 5.4 & Fig. A5.3).

Table 5.1 Coefficients of mixed effect models predicting otolith microchemistry in response to area of capture, haplotype and annulus (all fixed effects) and fish ID (random effect). Significant effects highlighted in grey.

		Random effect			
Element	Annulus	Area of	Haplotype	Age*Haplotype	Fish ID
	(d.f. = 1)	capture	(d.f. = 1)	(d.f. = 2)	Proportion s.d.
		(d.f. = 2)			
Sr Ca <sup>-1</sup>	F = 307.23	F = 6.35	F = 1.96	F = 0.07	0.273
	p < 0.001***	p < 0.05*	p = 0.25	p = 0.79	
Ba Ca <sup>-1</sup>	F = 135.22	F = 12.53	F = 4.85	F = 2.38	0.345
	p < 0.01**	p < 0.01**	p < 0.01**	p = 0.12	
Mg Ca <sup>-1</sup>	F = 0.58	F = 0.38	F = 0.20	F = 0.45	-
	p = 0.75	p = 0.60	p = 0.50	p = 0.51	
Mn Ca <sup>-1</sup>	F = 80.34	F = 1.83	F = 6.53	F = 6.67	0.369
	p = 0.28	p = 0.41	p = 0.81	p = 0.01**	
Na Ca <sup>-1</sup>	F = 32.77	F = 0.13	F = 0.22	F = 0.09	0.426
	p < 0.01**	p = 0.66	p = 0.58	p = 0.76	
Li Ca <sup>-1</sup>	F = 0.76	F = 0.34	F = 5.21	F = 0.80	0.616
	p = 0.24	p = 0.40	p = 0.02*	p = 0.37	

Microchemistry towards otolith edges should reflect the ambient seawater chemistry at the location where they were captured. Between-area of capture differences were most obvious when comparing post-recruitment age groupings. The increase in Sr and Ba ratios to Ca was much more pronounced in fish captured at the South Sandwich Islands, while Mn to Ca ratios decreased to a much lesser degree in the same fish (Fig. 5.4).

Multivariate analyses (based on Sr Ca<sup>-1</sup>, Ba Ca<sup>-1</sup> and Mn Ca<sup>-1</sup>) indicated no significant difference in core (pre-recruitment ages 0+ and 1+) microchemistry based on area of capture (Manova Type II, Pillai's trace; *d.f.* = 1; *F* = 1.19; *p* = 0.33) or haplotype (Manova Type II, Pillai's trace; *d.f.* = 1; *F* = 1.97; *p* = 0.14). However mean Sr Ca<sup>-1</sup> was greater in Falklands haplotype fish captured at the South Sandwich Islands, than in all other groupings (2.12 mM Sr  $\cdot$  M Ca<sup>-1</sup> and 1.60 to 1.76 mM Sr  $\cdot$  M Ca<sup>-1</sup> for all other groupings). This was also the case for Ba Ca<sup>-1</sup> (2.21  $\mu$ M Ba  $\cdot$  M Ca<sup>-1</sup> and 0.92 to 1.24  $\mu$ M Ba  $\cdot$  M Ca<sup>-1</sup>, respectively). Haplotype was found to have a significant effect on Sr Ca<sup>-1</sup> at pre-recruitment ages (Anova Type II; *d.f.* = 1; *F* = 4.68; *p* < 0.05), while haplotype effects on Ba Ca<sup>-1</sup> were close to significant (Anova Type II; *d.f.* = 1; *F* = 3.75; *p* = 0.06) (Table 5.2), suggesting that Northern haplotype fish have a slightly different core microchemistry to that of South Georgia haplotype fish. Area of capture was not found to have an effect on Sr Ca<sup>-1</sup>, Ba Ca<sup>-1</sup> and Mn Ca<sup>-1</sup> at pre-recruitment ages, indicating

that Southern haplotype fish captured at the South Sandwich Islands have a very similar core chemistry to fish captured at South Georgia (Table 5.2).



Figure 5.4 Pre-recruitment (ages 1+ and 2+; horizontal bars) and post-recruitment (ages 6+ and 7+; black triangles) otolith microchemistry of different area of capture/haplotype groupings. Error bars represent one standard error.

Multivariate analyses indicated a highly significant effect of area of capture on microchemistry at post-recruitment ages (Manova Type II, Pillai's trace; d.f. = 1; F = 7.79; p < 0.001), where univariate analyses also found significant area of capture effects on Sr Ca<sup>-1</sup>, Ba Ca<sup>-1</sup> and Mn Ca<sup>-1</sup> (Table 5.2). The effects of haplotype were insignificant in the multivariate analysis (Manova Type II, Pillai's trace; d.f. = 1; F = 1.97; p = 0.14), though small but insignificant effects of haplotype were observed on Mn Ca<sup>-1</sup> (Anova Type II; d.f. = 1; F = 3.07; p = 0.09) (Table 5.2).

Table 5.2 Results of ANOVA (Type II) comparison of location of capture and haplotype of *D. eleginoides* based on otolith microchemistry at pre-recruitment and post-recruitment ages. South Georgia captures all one group.

Age	Molarity ratio	Area of capture	Haplotype			
		(d.f. = 1)	(d.f. = 1)			
Pre-recruitment	Sr:Ca	F = 1.14; p = 0.29	F = 4.68; p < 0.05*			
(0+ and 1+)	Ba:Ca	F = 2.46; p = 0.13	F = 3.75; p = 0.06·			
	Mn:Ca	F = 0.36; p = 0.55	F = 0.65; p = 0.43			
Post-recruitment	Sr:Ca	F = 4.48; p < 0.05*	F = 0.80; p = 0.38			
(6+ and 7+) Ba:Ca		F = 11.52; p < 0.01**	F < 0.01; p = 0.97			
	Mn:Ca	F = 5.39; p < 0.05*	F = 3.066; p = 0.09·			

PCA analyses were conducted on area of capture/haplotype groupings, based on microchemistry of pre and post recruitment ages. The first two components of the PCA of core microchemistry (PCA1 and PCA2) accounted for 83.1% of the total variance of pre-recruitment individuals and 97.2% of post-recruits. A two dimensional plot of PCA1 and

PCA2 scores for each otolith, revealed a minimal degree of separation between area of capture/haplotype groupings. A greater separation was observed in the analogous plot for post-recruitment microchemistry, with an almost complete separation of South Sandwich Islands captured/Northern haplotype fish and fish captured at South Georgia. There was a large degree of overlap between the two South Georgia groupings in both pre and post-recruits (Fig. 5.5).



Figure 5.5 PCA1 and PCA2 scores of different area/haplotype groupings at pre-recruitment (left) and post-recruitment ages (right). SSI/Northern haplotype – orange squares; SSI/Southern haplotype – pink circles; SG Gully – green diamonds; SG East – blue stars.

#### 5.3.2 Basic dispersal patterns from mark-recapture data

Mark release-recapture data were analysed to investigate the basic dispersal patterns of *D. eleginoides* about the South Sandwich Islands. More than 70% of 54 recapture events were within 10km of the point of release and > 81% within 20 km (Fig. A5.5). There were no obvious patterns in the direction of movements greater than 20 km, with almost as many in a northerly direction as moving to the South (Fig. 5.6). To date no *D. eleginoides* tagged in the north have been recaptured south of  $57^{\circ}$  30S (*i.e.* have moved from the Northern to Southern Management Area), though 7 have been recaptured at South Georgia (6 males and 1 female). This result may be unexpected given the long distance between South Georgia and the South Sandwich Islands (700 km) and the deep saddles in the Scotia Ridge between these two areas (>3,000 m depth), given that *D. eleginoides* are typically most abundant between the 500-2,000 m depth range (Agnew 1999). Also, this is deeper than the saddle

between Saunders Islands and the Candlemas Island group to the north (approx 2,500 m), which appeared to be an effective barrier to dispersal for slope-phase *D. eleginoides*.



Figure 5.6 *D. eleginoides* tag recaptures linked to point of release. All recaptures to 2010; where arrow is not visible the point of recapture was within 20 km of the point of release; 1,000 m depth contours shown.

#### 5.3.3 Migration rates from mark recapture data

Mark-recapture matrices are given in Table 5.3. The combined-sex *D. eleginoides* mark recapture movement model was used to estimate an annual migration rate from South Sandwich Islands to South Georgia of 0.089 of the total estimated vulnerable population (95% CIs 0.04 to 0.20), though with considerable variability in estimates from different tag release years. Migrations rates were doubled when an additional 0.5 migration-related mortality was applied.

(	Combined sex Males																	
Releases at SSI North					Recaptures at South Sandwich Islands							Recaptures at South Georgia						
Release	/r Relea	ses N	/I:F rat	tio	2006	20	07	2008	200	9 20	010	2006	2007	7 20	008	2009	2010	
2005	49		0.255	5	0	(	)	2	1		0	0	0		0	0	0	
2006	134	1	0.356	5	0	(	)	2	0		1	0	1		1	0	0	
2007	292	1	0.343	3	na	(	)	6	7		1	na	0		0	0	2	
2008	504	1	0.282	2	na	n	а	0	0		5	na	na		0	0	0	
2009	344	1	0.302	2	na	n	а	na	0		2	na	na	I	าล	0	2	
											Fema	ales						
					Recap	tures	at So	uth Sa	andwi	ch Isla	ands	Recaptures at South Georgia						
Release	/r				2006	20	07	2008	200	92	010	2006	2007	7 20	008	2009	2010	
2005					0	(	)	0	1		0	0	0		0	0	0	
2006					0	2	2	5	4		1	0	0		0	0	0	
2007	S	ee abo	ove		na	(	)	6	5		0	na	0		1	0	0	
2008					na	n	а	0	8		3	na	na		0	0	0	
2009					na	n	а	na	3		5	na	na	1	าล	0	0	
Scanned numbers (millons - combine					ed sex)							0.488	0.45	53 0	.508	0.503	0.385	
Releases at South																		
Geor	gia			F	Recaptu	res at	South	n Geor	gia			Recap	tures	at Sou	th Sar	ndwich I	slands	
Release yr I	Releases	2000	2001	200	2 2003	2004	2005	2006	2007	2008	2009	2005	2006	2007	200	8 2009	2010	
2000	135	na	0	0	0	1	2	0	0	1	1	0	0	0	0	0	0	
2001	347	na	na	0	0	14	4	10	6	6	8	0	0	0	0	0	0	
2002	401	na	na	na	0	0	0	15	10	9	4	0	0	0	0	0	0	
2003	355	na	na	na	na	0	0	17	13	13	6	0	0	0	0	0	0	
2004	2914	na	na	na	na	na	103	132	116	108	53	0	0	0	0	0	0	
2005	3844	na	na	na	na	na	na	194	153	145	119	na	0	0	0	0	0	
2006	4848	na	na	na	na	na	na	na	230	198	138	na	na	0	0	0	0	
2007	4782	na	na	na	na	na	na	na	na	237	167	na	na	na	0	0	0	
2008	4575	na	na	na	na	na	na	na	na	na	229	na	na	na	na	0	0	
2009	3495	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	0	
Scanned numbers (thousands) 2.69 1.37 4.09 6.12 3.39 2										2.07								

Table 5.3 *D. eleginoides* mark recapture matrices for South Georgia and the South Sandwich Islands

The large male to female sex ratio of South Sandwich Islands to South Georgia mark-recapture events was reflected in the migration estimates obtained from sex-partitioned mark-recapture models, where approximately a quarter of the male component of the vulnerable biomass was estimated to migrate to South Georgia each year (0.241; 95 % CIs 0.10 to 0.50), compared with less than 2% of the female component (0.018; 95 % CIs 0 to 0.11) (Fig. 5.7 and Table A5.2). The male migration rate is much higher than might be expected and lower estimates were obtained using the CASAL population model of approximately 0.10 (see Section 6.3.2.1), at the lower 95% CI of the mark-recapture estimate. Currently, no mark recapture movements have been detected in the direction of South Georgia to the South Sandwich Islands. The mark-recapture model estimated an upper 95% confidence interval for annual combined-sex migration from South Georgia to

South Sandwich Islands at 0.0015 of the vulnerable population at South Georgia (Table A5.2 & Fig. A5.6).



Figure 5.7 Probability of observed *D. eleginoides* tag recaptures from the South Sandwich Islands to South Georgia given different migration rates

Sex-biased dispersal was also inferred through analysis of sex ratio distribution with age and location. At South Georgia, the male to female sex ratio remains stable between 0.4 to 0.5 regardless of age, whereas at the South Sandwich Islands the ratio decreased from 0.35 at ages 6+ to 10+ down to less than 0.1 of fish greater than 20 years of age (Fig. 5.8). Sex ratio

also varied with location, though this was only evident in fish greater than 120 cm total length, where male to female sex ratio was less than 0.15 on all lines set at the South Sandwich Islands to the north of 57<sup>o</sup> 30S, compared with approx 0.35 for fish smaller than this. At South Georgia, the male to female ratio of fish younger than 20+ does not vary much across the fishing grounds, though the sex ratio of fish older than this increased to more than 0.6 along eastern slopes and to less than 0.4 in the Shag Rocks region to the west (Fig. 5.8).



Figure 5.8 Sex ratio by age at the South Sandwich Islands (left) and sex ratio with size and latitude (right).



Figure 5.9 Area effects on sex ratio with size at the South Sandwich Islands (left) and with age at South Georgia (right). Error bars represent 95% confidence intervals.

#### 5.4 Discussion

## 5.4.1 Otolith microchemistry and the distribution of *D. eleginoides* at different life-stages

*D. eleginoides* are known to undergo a distinct ontogenetic down-slope migration with development, such that juveniles are found over shelf regions and adults are much more abundant over continental slopes (De Witt, Heemstra et al. 1990; Collins, Brickle et al. 2011). As such, differences in otolith microchemistry might be expected moving from the core to the rim, particularly of trace minerals which have a more variable seawater concentration with depth. This was observed in a number of elements, including Sr.Ca<sup>-1</sup>, Ba.Ca<sup>-1</sup>, Mn.Ca<sup>-1</sup> and Na.Ca<sup>-1</sup>, while large increases in Sr.Ca<sup>-1</sup> and decreases in Mn.Ca<sup>-1</sup> after the 4+ and 5+ annuli (Fig. A5.3) were coincident with *D. eleginoides* timing of recruitment to slope habitat (Collins, Brickle et al. 2011). Reduced Mn.Ca<sup>-1</sup> towards otolith rims is consistent with the approximate four-fold decrease in dissolved manganese concentration with depth (Bender, Klinkhammer et al. 1977). Seawater barium concentration tends to increase with depth, mirroring the distribution of minerals depleted by surface primary production (Chan, Drummond et al. 1977) and Ba.Ca<sup>-1</sup> was increased substantially in post-recruitment fish.

Seawater distributions of dissolved strontium and magnesium are relatively uniform with depth (Brass and Turekian 1972; Brass and Turekian 1974). Rates of accumulation of strontium are generally thought to increase with decreasing ambient seawater temperature and this has been demonstrated in two deepwater grenadier species (*Macrouridae*) (Gauldie, West et al. 1995). Therefore, the increased Sr.Ca<sup>-1</sup> towards otolith rims might reflect the ontogenetic migration of *D. eleginoides* in to colder water at depth.

#### 5.4.2 Delineation of *D. eleginoides* populations from otolith chemistry

Previous studies have demonstrated the potential of using otolith chemistry to delineate *D. eleginoides* populations to the north and south of the South Atlantic Polar Front, based on core (Ashford, Arkhipkin et al. 2006) and rim chemistry (Ashford, Jones et al. 2008). As would be expected, the elemental composition of South Georgia fish in this study is very similar to measurements from previous studies (approximate values at core – Sr.Ca<sup>-1</sup> = ~1,400; Ba.Ca<sup>-1</sup> = ~1.2; Mn.Ca<sup>-1</sup> = ~1.4; and rim – Sr.Ca<sup>-1</sup> = 4,500 to 5,000; Ba.Ca<sup>-1</sup> = 3-4; Mn.Ca<sup>-1</sup> = 0.2-0.3; all μmol:mol Ca) (Ashford, Arkhipkin et al. 2006; Ashford, Jones et al. 2008) (cross-referenced with Fig. 5.4). The methods for samples preparation used here were based on those developed for these previous studies and the reproducibility of results adds validity to the application of this type of analysis for stock identification.

This study found that South Georgia East and South Georgia Gully populations could not be distinguished based on the otolith chemistry of pre or post-recruitment annuli. This agrees with genetic studies which have found very low levels of variation in 12S rRNA sequences in the South Georgia D. eleginoides population (Rogers, Morley et al. 2006). Thus it is likely that the South Georgia population is relatively homogeneous and migration rates between this and other stocks, particularly to the north of the Polar Front, are low (Rogers, Morley et al. 2006). However, distant populations at Ob and Lena in the Southern Indian Ocean have been found to have an identical haplotype to South Georgia fish and it is possible that these seamounts, and some of the other small seamount populations, may be supported by larval or benthopelagic life-stage migration events from the South Georgia population located upstream (Rogers, Morley et al. 2006). The lack of gonad development and genetic similarity with the South Georgia stock suggests that the South Sandwich Islands population is also dependent on migration of individuals from the region of South Georgia. Here, the prerecruitment chemistry of South Georgia haplotype fish captured at the South Sandwich Islands was very similar to those captured at South Georgia (Fig. 5.4) with no significant differences observed based on multivariate or univariate analyses.

The otoliths of Northern haplotype fish had a slightly different chemistry of pre-recruitment annuli, with significantly increased Sr.Ca<sup>-1</sup> and a close to significant increase in Ba.Ca<sup>-1</sup>, suggesting a different natal origin from the Southern haplotype fish, if not a clear delineation of populations. Ashford *et al.* (2006 & 2008) characterised the chemistry of populations to the north of the Polar Front as having decreased Sr.Ca<sup>-1</sup> and Ba.Ca<sup>-1</sup> and increased Mn.Ca<sup>-1</sup> relative to populations to the South. This suggests that the Northern haplotype fish originated from locations to the south of the Polar Front. Given that this haplotype is not observed in South Georgia population, they may have originated from spawning locations over the Northern Scotia ridge, where Shaw *et al.* (2005) found that *D. eleginoides* to be entirely comprised of northern haplotype individuals. The absence of Northern haplotype fish from the South Georgia population suggests that intermingling of Northern and Southern haplotype individuals occurs to the northeast of South Georgia from

where they would be advected to the east of the South Georgia plateau (Fig. 5.10). The genetic structure of D. eleginoides at the Maurice Ewing Bank to the north of South Georgia has not yet been analysed though Northern haplotype fish may also be located here and would be less distant from the South Sandwich Islands and, so, may also be considered a putative source of migrants from up-current.

Significant differences in the otolith chemistry of post-recruitment annuli of fish captured at South Georgia and the South Sandwich Islands, suggested a clear delineation of the two populations following recruitment. South Sandwich Islands fish were characterised by: increased Sr<sup>-</sup>Ca<sup>-1</sup>, which is typical of cold water populations; increased Ba<sup>-</sup>Ca<sup>-1</sup>, which increases in seawater concentration moving from Sub-Antarctic to Antarctic waters; and increased Mn<sup>-</sup>Ca<sup>-1</sup>. Deep water manganese concentration is known to increase around hydrothermal vent systems (Klinkhammer, Rona et al. 1985) and these have been found at different locations across the South Sandwich Islands, a region with frequent tectonic activity (Barker 2001). In contrast to previous studies (Ashford, Arkhipkin et al. 2007; Ashford, Jones et al. 2008), Mg<sup>-</sup>Ca<sup>-1</sup> was relatively homogenous across study populations and appeared to have limited utility for the delineation of *D. eleginoides* populations located to the south of the Polar Front.

#### 5.4.3 Timing and route of migration to the South Sandwich Islands

The lack of recaptures at the South Sandwich Islands of fish tagged at South Georgia and different growth characteristics between the two regions suggests that immigration to the South Sandwich Islands occurs at ages prior to recruitment, or on recruitment itself. This might be passive dispersal of pelagic eggs and larvae or active dispersal of juvenile fish. In the first scenario eggs would only be transported between the two areas when specific hydrographic regimes were in place. The ACC is the most obvious route for transportation between the two areas and has previously been identified as a probable source of larvae for South Sandwich Islands finfish populations (Kaiser, Barnes et al. 2008). Using the approach adopted by Matschiner, Hanel *et al.* (2009), plots of drifter position data showed that most eggs produced at South Georgia would probably be advected to the north of the South Sandwich Islands (Fig. 5.10), though southern incursions of the ACC may occur in warmer years. The length of time taken by drifters to make this journey was within the 3-4 months

developmental period postulated for toothfish eggs (North 2002) without even accounting for the pelagic larval phase of development.



Figure 5.10 Drogued drifter movement around South Georgia and the South Sandwich Islands since 1994 and toothfish species CPUE at the South Sandwich Islands: a) All drifters moving through the South Georgia maritime zone; b) All drifter passing close to the South Sandwich Islands. Points are 4-daily positions. Drifter data acquired via Fisheries and Oceans Canada data portal at http://www.meds-sdmm.dfo-mpo.gc.ca.

This study found a departure in the otolith chemistry of *D. eleginoides* captured at South Georgia and at the South Sandwich Islands between pre-recruitment (0+ and 1+) and post recruitment (7+ and 8+ ages) life stages (Fig. 4.14). Increased Sr.Ca<sup>-1</sup> and Ba.Ca<sup>-1</sup> at ages 3+ through to 5+, in South Sandwich Islands captured fish are consistent with the hypothesis that migration is coincident with recruitment from shelf to slope habitat. Mark-recapture studies have found increased movement rates of juvenile toothfish relative to mature adults (Hanchet, Rickard et al. 2008) which may relate to the dispersal of juveniles from spatially discrete locations on the shelf to slope habitat.

The South Sandwich Islands are surrounded by abyssal and hadal depths and the principal source of recolonisation of shelf and upper slope habitats are deep or distant. Hence, a protracted period of pelagic drifting and swimming would be necessary for migration from South Georgia to the South Sandwich Islands at later life stages, which are generally thought to more benthic in habit (Collins, Brickle et al. 2011). A preliminary study indicated that juvenile D. eleginoides at South Georgia are primarily clustered over the Shag Rocks shelf and that they do not disperse to slopes surrounding the South Georgia shelf until reaching

ages 5+ to 8+ (D. Agnew 2011, pers. comm.). Thus migrations between South Georgia and the South Sandwich Islands may actually occur just after post-recruitment. At this age a proportion of the migrated population would almost certainly have been tagged, though may be too few in number to be detected in catches at the South Sandwich Islands.

Successful dispersal of later life stages may also be effected by hydrography, where the path of the ACC would be favourable for between-area migrations in some years more than others. As such, hydrographic variation may be the main driver of highly variable recruitment in the South Sandwich Islands toothfish populations (Section 4.3.1), regardless of the precise life stage at which migration occurs. As such an assessment of the impacts of large scale climatic phenomena (such as El Nino Southern Oscillation or the Southern Annular Mode) on recruitment patterns at the South Sandwich Islands would be worth pursuing with a longer time series of data.

#### 5.4.4 Range contraction of *D. eleginoides*

As of the end of 2011, no tag recaptures have been recorded in the direction of South Georgia to the South Sandwich Islands. It appears unlikely that adult migration rates in this direction are very high (upper 95% CI migration rate of 0.0015, corresponding to 75 tonnes of a 50 thousand tonne biomass at South Georgia) and are probably insufficient to support the current South Sandwich Islands population (approx. 1,000 tonnes vulnerable biomass – see Section 6.3.2.3) through the migration of post-recruitment fish alone.

The lack of mark-recapture events in this direction might suggest that the deep saddle in the Scotia ridge between South Georgia and the South Sandwich Islands (>3,000 m depth) comprises a significant barrier to the dispersal of slope phase individuals between the two areas. However, a number of fish have now been observed moving in the reverse direction: from the South Sandwich Islands to South Georgia and the migration rates, particularly of males, are of significance to fisheries management. Sex-biased migration is also evident from the residual sex ratio of *D. eleginoides* at the South Sandwich Islands, where females dominate older age classes and very few males older than age 20+ remain (Fig. 5.8). A simplistic explanation for the range contraction of males may be a reduced tolerance to low temperature resulting in northward redistribution. A number of the fish that were recaptured had gonads in an advanced stage of maturation (J. Roberts 2012, unpub. data) and, so, this migration may be timed with the onset of maturity. The reproductive biology of

South Sandwich Islands *D. eleginoides* appears to be repressed by cold water temperature (Figs. 4.5 & 4.6), though normal functioning is resumed once ambient temperatures are sufficiently warm. Alternatively, the maturation of males may be the cue for migrations to warmer water spawning grounds at South Georgia.

Sex-biased dispersal has been observed in a wide range of vertebrate species, where there are behavioural differences of males and females, including Ross Sea *D. mawsoni* (Pusey 1987; Hanchet 2009). This study finds that mark-recapture studies complement studies of spatial demographics in providing an independent means of assessing sex-biased dispersal patterns. The independence of the two approaches has particularly value for analyses of fisheries-dependent data, where there may also be some sex-biased selectivity of fishing gear.

#### 5.4.5 Conclusions and future work

The processes of *D. eleginoides* colonisation at the South Sandwich Islands and subsequent redistribution to South Georgia are likely to be heavily influenced by prevailing hydrographic conditions, *e.g.* the flow and path of the ACC and the position of the ACC Southern Boundary is known to respond variability in ENSO and the Southern Annular Mode (Billany, Swart et al. 2010). As such, the southern range limit of *D. eleginoides* at the South Sandwich Islands is likely to be quite dynamic and natural fluctuations in distribution and population size should be expected through time (Fig. 5.11).



Figure 5.11 Hypothesised paths of *D. eleginoides* dispersal between South Georgia and South Sandwich Islands populations. ACC highlighted in light red; "SAF" = Sub-Antarctic Front; "SB" = Southern Boundary of ACC; "WF" = Weddell Front; Base image from (Murphy, Watkins et al. 2007).

Previous studies of dispersal patterns towards range limits have been biased towards finding evidence for increased capacity for dispersal towards range edges (Gaston 2009). At the South Sandwich Islands, movement rates of *D. eleginoides* are similar to those observed at South Georgia (Fig. A5.5), though there is also good evidence for range contraction away from the range edge. Immigration and emigration events occur at different life stages, though both appear to be triggered by biological/behaviour changes: immigration of juveniles on recruitment to slope habitat and; emigration to spawning grounds on reaching maturity. The extent to which this is typical of other range edge populations is not known, though mark recapture programs have now been initiated on a large number of stocks and these data can be used to evaluate between-stock migration patterns.

Assuming that South Sandwich Islands *D. eleginoides* comprise a closed population would compromise the accuracy of population assessments. It is fairly clear that the productivity of the resident population is largely if not wholly dependent on immigration and that

population size will be dependent on the spawning stock from where these fish originate and dispersive regime between the two regions, rather than on the resident spawning population. Emigration of adult males will further diminish the probability of successful spawning events and reduce the effective yield per recruit and would ideally be accounted for in the modelling process in order to improve model fits and the accuracy of model outputs. Between-stock migrations are often assumed to be so low as to have a negligible effect on population size and age structure and, as such, dispersal patterns are often not represented in population assessments. However, dispersal effects *can* have a significant impact on population structure and this may be accentuated in range edge stocks. As such, where between stock migrations are detected they should be incorporated in to assessment models so that they produce more robust estimates for the purposes of fisheries management.

#### **Chapter 6**

# Exploitation of range edge populations: population assessment and yield estimation of South Sandwich Islands *D. eleginoides*

#### 6.1 Introduction

Historically commercial fishing has tended to operate on relatively abundant species which commonly occupy a broad distributional range. This is particularly true of deepwater fisheries, where target species may have an extremely broad spatial distribution (Rogers, Morley et al. 2006). The range position effects on biology, life history and dispersal have been discussed in Chapters 4 and 5. Moving from the range centre to edge, generalised patterns in fitness, specifically growth, fecundity, and survivorship have been hypothesised that may be correlated with abiotic variables, such as temperature (Gaston 2009; Sexton, McIntyre et al. 2009). However, such patterns are rarely considered in the context of resource management, where the exploited stocks may be situated towards range peripheries.

#### 6.1.1 Exploitation of range edge populations

The management of exploitation on fish populations is informed by stock assessments, of which there are many different approaches, varying in structural complexity and data requirements (Hart, 2002). Compared to production models and other methods which may require only a time series of catch and effort data, age-structured population assessments are data intensive and may incorporate an array of data including: a time series of catch-at-age; catch-at-size as well as information on size-at-age; maturity-at-age, the relationship between spawning stock size and average recruitment and others. However, where data are sufficient they allow for a robust means of modelling the exploited population through time and for estimating a sustainable yield (Hart, 2002). Where information on the biology of population is limited, a common approach is to use data or parameters gathered from better-described populations (Punt and Smith 2011), though the values of key biological parameters may vary across a distributional range (Fig. 4.1). However, if trends in range position effects on life history can be described, then this knowledge can be used to inform

population assessments and management of data poor stocks, which may include a large proportion of range periphery and the majority of deepwater fish stocks (Japp and Wilkinson 2006).

Growth and fecundity with age have a large impact on the relative productivity of a population and predictable trends in each have been observed moving from high to low latitudes. Both processes compete for a common somatic energy resource and increased maximum body size at higher latitudes – the temperature-size rule (Atkinson, Begon et al. 1994; Atkinson and Sibly 1997) – often corresponds with a delayed onset of maturation, which allows individuals to invest energy in continued growth. Hence, evolutionary pressures optimise life history to environmental conditions which vary across the distributional range (Roff 2000).

The age structure of adult toothfish populations and variations in year class strength provide a good indication of the stability (or variability) of recruitment. Such information is required for robust assessments of sustainable yield, which typically use the Beverton-Holt stock recruit relationship to estimate the number of recruits from the spawning biomass (Beverton and Holt 1957). Increased temporal variation in gonad maturation, reproductive success and also passive dispersal-mediated immigration all contribute to increased recruitment variability towards range edges (Gilman 2006; Gaston 2009) (see Chapters 4 & 5) and this has been demonstrated in a number of fish species (Philippart, Henderson et al. 1998; Brunel and Boucher 2006). Reductions in habitat quality and increased competition are also likely to result in reduced fitness or survivorship towards range edges (Dekker and Beukema 1993; Ungerer, Ayres et al. 1999; Sexton, McIntyre et al. 2009), while trends in dispersal patterns across distributional ranges have yet to be properly explored, though are also likely to impact on population size and age structure towards range peripheries (Gaylord and Gaines 2000; Bahn, O'Connor et al. 2006).

Hence, predictable trends have emerged in range position effects on growth, reproductive biology and recruitment and may also exist for mortality and dispersal and these should have predictable impacts on productivity and sustainable yield across a distributional range. Here the life history and dispersal parameters estimated in Chapters 4 & 5 are used to parameterise a population assessment, inform assessment model structure and estimate sustainable yield for the South Sandwich Islands *D. eleginoides* population. This population is
located on the high latitude limit of the distributional range of this species (Roberts, Xavier et al. 2011) and the effects of range position life history and dispersal on the assessment process were discussed.

#### 6.1.2 CCAMLR approach to population and yield assessment

South Georgia and the South Sandwich Islands are located to the South of the Polar Front. Here marine resources are exploited within the CCAMLR management framework. Article II of the Convention describes the CCAMLR approach to the conservation of Antarctic marine living resources:

"Any harvesting and associated activities in the area to which this Convention applies shall be conducted in accordance with the provisions of this Convention and with the following principles of conservation:

- *i.* prevention of decrease in the size of any harvested population to levels below those which ensure its stable recruitment. For this purpose its size should not be allowed to fall below a level close to that which ensures the greatest net annual increment;
- *ii.* maintenance of the ecological relationships between harvested, dependent and related populations of Antarctic marine living resources...; and
- iii. prevention of changes or minimisation of the risk of changes in the marine ecosystem which are not potentially reversible over two or three decades..."

This article embodies two important concepts relating to resource management: firstly **the precautionary approach**, which has implications when working with uncertainty in information, for instance when the actual size of exploited stocks is not known precisely, or when new stocks are being targeted; and secondly **the ecosystem approach** which seeks to minimise the risk of fisheries adversely effecting 'dependent and related species'.

Article II is implemented through a three-part decision rule for estimating sustainable yield as a proportion of pre-exploitation biomass (*y* or "gamma"):

 The recruitment criterion - choose a yield (y1) so that the probability of the spawning biomass dropping below 20% of its median pre-exploitation level over a 35-year harvesting period is 10%

- **2.** The predator criterion choose a yield ( $\gamma$ 2) so that the median escapement at the end of a 35 year period is 50% of the median pre-exploitation level; and
- 3. Select the lower of  $\gamma 1$  and  $\gamma 2$  as the yield.

The CCAMLR Working Group of Fish Stock Assessment (CAMLR-WG-FSA) conducts biannual stock assessments for the main toothfish stocks. These aim to maintain spawning stock biomass above a fraction of the virgin biomass ( $B_0$ ), according the above harvest decision rule.

Yield estimation for the South Georgia *D. eleginoides* stock is currently conducted using an age-structured population model constructed in CASAL (Bull, Francis et al. 2005). This is a single-area, combined-sex population assessment (Peatman, Mitchell et al. 2011) and is integrated such that values of free parameters (which might include *B*<sub>0</sub>, growth parameters and YCS) are estimated during the model fitting procedure through maximisation of the likelihood of observational data, such as catch-at-age time series, mark recapture, or size-at-age observations. A Markov Chain Monte Carlo (MCMC) sampler is used to generate values of free parameters including future recruitment such that the impacts of different yields on the projected population can be assessed. The stochastic nature of this assessment means that application of the three-part decision rule can be applied by estimating depletion probabilities as the proportion of the total sample with Spawning Stock Biomass (*SSB*) in the 35<sup>th</sup> year of the projection below a certain proportion of the virgin spawning biomass.

# 6.1.3 History of management of the toothfish fishery at the South Sandwich Islands

Exploratory fishing at the South Sandwich Islands commenced in 1992, following notifications from Chile and the USA to fish using demersal longline gear. A "precautionary" catch limit of 240 tonnes approved by the CCAMLR Scientific Committee, based on fishable area comparisons with South Georgia (CCAMLR 1992). The following season, two vessels fished around the northern islands, with a combined *D. eleginoides* catch of only 40 tonnes and *D. mawsoni* were not encountered (CCAMLR 1993; Rubilar, Moreno et al. 1993). CAMLR-WG-FSA used the data collected from these two trips to estimate a stock size of 235 tonnes and the annual catch limit was revised to 28 tonnes (CCAMLR 1993). This applied only to the "Northern Management Area", defined as the area north of 57.4° S, though there

was no further regulated fishing activity until 2005, when the UK conducted a pilot tagging program aboard the UK-flagged fishing vessel *Argos Helena*. This vessel caught 27 tonnes of *D. eleginoides*, with catch rates comparable to those experienced at South Georgia, increasing interest in development of the toothfish fishery at the South Sandwich Islands (Payne and Agnew 2006).



Figure 6.1 Historic toothfish longline catch and effort at the South Sandwich Islands (CCAMLR 2011); and CPUE distribution of toothfish species at the South Sandwich Islands in 2009. Lines are 500m depth contours.

At the end of 2005, CCAMLR agreed to a proposal from the UK to implement a three-year tagging program in the Northern Management Area to allow for a more robust assessment of toothfish population structure, size, movement and growth than had been possible in 1993 (Payne and Agnew, 2005). The Northern Area catch limit was temporarily increased to 100 t from 2006 to 2008 and 75 t in 2009 to allow for increased numbers of tagged fish releases (CCAMLR 2008). By the end of 2009, sufficient data were available for a robust population assessment conducted in CASAL (Roberts and Agnew 2009a). Assessments indicated a sustainable catch of 41 t in 2010, 39 t in 2011, according to CCAMLR 2011).

In addition, a tagging experiment was initiated in the Southern Management Area (between 57.4°S and 60°S) in 2009 with a combined catch limit of 75 t for *D. eleginoides* and *D. mawsoni* (Roberts and Agnew 2009b), though data from this Southern Area experiment were not included in the assessment presented here.

#### 6.1.4 Aims

The South Sandwich Islands Longline fishery has operated in all years since 2005. Since then, the tagging program and biometric data collected by scientific observers have provided the data requirements for the development of an assessment that can be used to evaluate the impacts of exploitation on this population. Here an age-structured population assessment was constructed for the range edge *D. eleginoides* population at the South Sandwich Islands. This incorporated life history parameters and information on dispersal rates estimated in previous chapters. This model was used to assess:

- the consequences of range edge recruitment, growth and dispersal patterns on population assessment and sustainable yield according to CCAMLR harvest control rules; and
- the implications for exploitation and assessment of range edge fish populations.

A similar model structure was used to that developed for the South Georgia *D. eleginoides* assessment (Hillary, Kirkwood et al. 2006) to facilitate an evaluation of the effects of range position on life history and population dynamics (including though not limited to growth, recruitment variability and dispersal dynamics) on optimal model structure, stock productivity and yield estimation.

#### 6.2 Methods

#### 6.2.1 Model structure and estimation

#### 6.2.1.1 Base case model

The CASAL software package (Bull, 2005) was used to construct a sex-partitioned, singlearea, three-season model using data collected from the South Sandwich Islands *D*. *eleginoides* fishery in the Northern Management Area, with seasons (a fraction of the year) defined as follows:

- Season 1 (from 1 December to 30 April) with recruitment at the start then natural mortality;
- Season 2 (from 1 May to 31 August) when fishing and spawning takes place; also natural mortality (half before spawning and half after);
- Season 3 (remainder of the year) natural mortality only.

The model was run from 1990 to 2011 with an initial unexploited equilibrium age structure. The model used a multinomial likelihood to fit to a time series of catch-at-length, catch-at-age and size-at-age observations as well as mark release-recapture observations. The length frequencies of catch-at-length and mark-release and recapture observations ranged from 20 to 220 cm in 10 cm length bins. The estimated numbers of scanned fish for each length class relevant to those in the recapture data were calculated using the total catch biomass, the catch-at-length proportions and the mean weight of the fish captured in each length class.

Two penalties were included in the model: one which constrained the harvest rate from exceeding a value of 1 and a tagging penalty reduced the likelihood of populations estimates that were too low to allow the reported number of fish to be tagged (as Roberts and Agnew 2009a; SC-CAMLR 2009).

The input files used to drive the base-case assessment are displayed in Appendix B.

#### 6.2.1.2 Yield estimation

Yield was estimated according to the three-part decision rule described in the introduction. A constant catch was applied to a sample of 1,000 35 year projections of the population model. The Beverton-Holt model (Beverton and Holt 1957) was used to estimate recruitment from resident spawner biomass, with log normal error and a CV of 1.0. This was greater than the value currently adopted for the South Georgia *D. eleginoides* assessment of 0.6 (Peatman, Mitchell et al. 2011), to account for the increased recruitment variability observed at the South Sandwich Islands (Chapter 4).

The depletion probability (relating to the recruitment criterion) was calculated as the proportion of samples from the Bayesian posterior, where the predicted future SSB was below 20% of the median  $B_0$  in the respective sample of any one year, for each year in the 35-year projection period. The level of escapement (relating to the predator criterion) was calculated as the proportion of samples from the Bayesian posterior, where the projected future status of the SSB was below 50% of median  $B_0$  in the respective sample, at the end of the 35-year projection period. The maximum catch which resulted in a depletion probability >0.1 and a level of escapement of >0.5 was taken as the yield estimate.

#### 6.2.2 Summary of input parameters

A number of key biological parameters used in the South Sandwich Islands *D. eleginoides* population model used estimates derived in Chapters 4 & 5. Where these could not be estimated for this stock, such as those relating to the mark-recapture experiment and maturity-at-age, values from the latest South Georgia assessment were used in their place (Peatman, Mitchell et al. 2011). In addition, a number of key biological parameters were left free for the model to estimate, including  $B_0$ , selectivity parameters, Von Bertalanffy growth parameters and YCS. In each instance bounded priors and error distribution were supplied (Table 6.1). Recruitment variability is represented by *'sigma-r'* which gives the standard deviation around the log of YCS and is used to estimate a projected time series of recruitment from the spawning biomass. The current South Georgia assessment assumes a value of 0.6 (Peatman, Mitchell et al. 2011), though two different values were used in the South Sandwich Islands CASAL model to assess the impacts of recruitment variability on yield: including 0.6 and 1.0 – to reflect the increased recruitment variability observed in this population based on otolith age readings from fish captured in 2009 (Section 4.3.1).

Table 6.1 List of parameter values used in the South Georgia and South Sandwich Islands *D. eleginoides* CASAL population models

		South			Link to South
	South	Georgia	Prior	Upper/lower	Sand. Isles
Parameter	Sandwich	(Hillary,	distribution	bounds	parameter
	Islands	Kirkwood et			estimation
		al. 2006)			section
B <sub>0</sub>	Free	Free	Uniform-log	500 / 5,000	
VB K	Free	Free	Uniform	0.03 / 1.50	
VB L <sub>inf</sub>	Free	Free	Uniform	110 / 250	
VB t <sub>0</sub>	Free	Free	Uniform	-2 / 0	
Size-weight a	2.71e-8	2.54e-8			4.3.2
Size-weight b	2.8	2.8			4.3.2
Recruitment	1	0.6	N/A	N/A	4.3.1
S.D.					
YCS	Free	Free	Log-normal	0.001 / 20	
Steepness (h)	0.75	0.75	N/A	N/A	
М	Male 0.24	Male 0.13	N/A	N/A	5.3.3
	Female 0.13	Female 0.13			
Maturation	Constrained	Constrained	N/A	N/A	
ogive	as South	(male &			
	Georgia	female)			
Tag loss rate	0.0064	0.0064	N/A	N/A	
Tag mortality	0.1	0.1	N/A	N/A	
rate					
Tag detection	1	1	N/A	N/A	
probability					
Selectivity a <sub>1</sub>	Free	Free	Uniform	1 / 50	
Selectivity S <sub>L</sub>	Free	Free	Uniform	0.05 / 50	
Selectivity $S_R$	Free	Free	Uniform	0.05 / 500	

Sex-biased migration of males to South Georgia appears to have a large impact on the age structure of the residual population at the South Sandwich Islands. Male to female sex ratio of the South Sandwich Islands population was shown to decrease dramatically with increasing age, such that few males of age greater than 20+ remain in the population (Fig. 5.8). Here the migration of males was simulated by increasing the value of male mortality used by the CASAL model until the best model fit was achieved (measured as the CV around the virgin biomass estimate). The mark-recapture study indicated that the female migration rate is likely to be low (Fig. 5.7) and female mortality was maintained at 0.13, as currently assumed for all major *D. eleginoides* stocks in the CCAMLR area (Hillary, Kirkwood et al. 2006; Candy and Constable 2008).

#### 6.2.3 Fishery observations

The CASAL model was fit to annual catch-at-length (2005-2008 and 2010-2011) and catch-atage (2009 only) observations (detailed in Section 4.3.1). *D. eleginoides* catch-at-length and catch-at-age observations in the Northern Area of the South Sandwich Islands are presented in the plots of model fits (Figs. 6.4 & 6.5).

In addition the model estimates were fit to observations from the South Sandwich Islands *D. eleginoides* mark recapture experiment. Tag-release events for years 2005 to 2010 were incorporated into the model with recaptures used from years 2006 to 2011 (within-season captures were ignored). A total of 1,742 *D. eleginoides* have been tagged and released in the Northern Management Area of the South Sandwich Islands in all seasons from 2005 to 2011 and 107 of these have now been recaptured, of which 3 were within-season recaptures and so were omitted from the population model analysis (Table 6.2). In all season, the spatial and length distribution of *D. eleginoides* tagging effort was similar to that of catch (Roberts, Mitchell et al. 2011).

Table 6.2 <i>D</i> .	eleginoides	tag recapture	matrix fo	or the	Northern	Management	Area	of the	South
Sandwich Islands, relating tag recaptures to year of release. Annual catch in parentheses.									

			Recaptures by Season (catches in parentheses)						
Release Season	Tag releases (rate)	2005 (26.8t)	2006 (18.3t)	2007 (54.0t)	2008 (97.5t)	2009 (58.9t)	2010 (39.6t)	2011 (35.9t)	All Seasons
2005	42	0	0	0	2	2	0	1	5
2006	134	-	0	2	8	4	2	1	17
2007	291	-	-	0	13	12	1	4	30
2008	504	-	-	-	0	8	8	8	24
2009	344	-	-	-	-	3	7	9	19
2010	232	-	-	-	-	-	0	12	12
2011	195	-	-	-	-	-	-	0	0
All	1,742	0	0	2	22	29	18	35	107

#### 6.2.4 Simple Petersen population estimation

Independently of the CASAL population model, mark-recapture observations were used to estimate vulnerable biomass using the simple Petersen method (Seber 1982). This method assumes a closed population and is biomass (*N*) is estimated as follows

$$N = \frac{n_1 \times n_2}{m_2}$$
eqn 6.1

where:

 $n_1$  = Total number of fish tagged and released in the tagging season

 $n_2$  = Total weight of all fish caught in the recapture season

 $m_2$  = total number of tag recaptures in the recapture season

The value of  $n_1$  was adjusted to estimate the number of tagged fish remaining at the beginning of each tag recapture season ( $n_1^*$ ) as follows:

$$n_1^* = n_1(1-t)(1-f)e^{-M^y}$$
 eqn 6.2

where:

t = tag induced mortality rate

**f** = tag failure rate

**M** = natural mortality rate

y = years at liberty between the tagging season and the recapture season

Parameter estimates were consistent with those used in the CASAL population models and a natural mortality of 0.13 was assumed. Variance on the biomass estimates returned was estimated as the shortest 95% confidence interval for  $N/\lambda$ , based on the Poisson distribution (Chapman 1948).

# 6.3 Results

#### 6.3.1 Simple Petersen population estimates

Simple Petersen estimates of vulnerable biomass should not be very different from those estimated by the population model. Including only year of release-recapture combinations with 4 or more recaptures, vulnerable biomass ranged from 547-2,922 t, though a large proportion of estimates were between 900-1,800 t (Table 6.3). These estimates were similar to those from the model which estimated a decline in vulnerable biomass from 1,566 t in 2005 to 1,036 t in 2011. There is some evidence for a decline in vulnerable biomass in the latest season. A decline in vulnerable biomass was also observed in CASAL estimates of vulnerable biomass (Fig. 6.8), though this was more gradual and the reduced estimate based purely on mark-recapture observations will be more strongly effected by the spatial distribution of fishing and tagging effort in particular year of release recapture combinations.

Season released	Season recaptured	Tag recaptures	Median stock estimate	95% CI Lower (tonnes)	95% CI Upper (tonnes)	
			(tonnes)	()		
2006	2008	8	1,125	473	2,304	
2007	2008	13	1,719	894	2,971	
2006	2009	4	1,190	328	3,474	
2007	2009	11	1,074	520	1,949	
2008	2009	8	2,922	1,230	5,985	
2008	2010	8	1,720	724	3,523	
2009	2010	7	1,534	601	3,317	
2007	2011	4	1,377	380	4,066	
2008	2011	8	1,363	567	567	
2009	2011	9	945	417	1,846	
2010	2011	12	547	276	964	

Table 6.3 Results of simple Petersen vulnerable biomass estimates. Only year release/recapture combinations with 4 or more tagged fish recaptures are shown.

#### 6.3.2 CASAL integrated model

#### 6.3.2.1 Estimating Natural mortality and emigration

As single-area assessment configuration was retained despite evidence for emigration of individuals to South Georgia and it was decided instead, as the South Georgia population was not being modelled, to express this as increased male mortality in the South Sandwich Islands assessment (above the value of 0.13 currently assumed for *D. eleginoides* assessments). The optimal level of mortality was estimated by examining the effect of varying *M* on the CV around the estimate of  $B_0$ , such that best-fit was observed where  $B_0$  CV was minimised. A large decrease in uncertainty around the biomass estimate was observed when male mortality was increased from 0.13. The lowest CV around  $B_0$  was obtained when male *M* was set between 0.2 and 0.3. This was by some higher than the 0.10 – 0.13 range in female *M* which resulted in the lowest CV around  $B_0$  (Fig. 6.2).



Figure 6.2 CV around CASAL virgin biomass estimate in response to natural mortality rate (*M*) of males (left) and females (right).

A comparison of observed sex ratio with age from otolith readings against estimated sex ratio under different mortality scenarios indicated male mortalities within the 0.2 to 0.3 range which minimised  $B_0$  CV would adequately reflect migration of males out of the South Sandwich Islands population. The 'optimal' male morality rate of M = 0.24 was retained within the optimal CASAL model (Fig. 6.3). With male mortality constrained to this value, female mortality rates of between 0.10 and 0.13 were found to result in the lowest

uncertainty around the virgin biomass estimate and the widely-used natural mortality rate of M = 0.13 was retained for females in the CASAL model.



Figure 6.3 Projected *D. eleginoides* sex ratio under different male mortality scenarios (female mortality constrained to M = 0.13) compared with observed sex ratio at age of aged otoliths. Aggregated in to 5-year categories and labelled with sample size.

#### 6.3.2.2 Year Class Strength, growth and model fits to fishery observations

The CASAL model outputs indicated that the bulk of the vulnerable biomass was comprised of a single year class estimated to have spawned in 1992 (selected in all 1,000 runs of the stochastic sampler), with a much smaller peak of recruits spawned in the early 2000s, possibly over 2-3 years (Fig. 6.8). The resulting dominant year class is visible in the catch-atage and catch-at-length fits (Fig. 6.6). The YCS CV at the South Sandwich Islands was estimated at 2.36, compared with 0.71 for the South Georgia population (calculated as the median C.V. of 1,000 CASAL sampler estimates of YCS).

The CASAL model used the size-at-age observations, though also incorporated information from catch-at-size and catch-at-length observations. As expected, the CASAL estimate of female  $L_{inf}$  was greater than for males (202 cm and 174 cm respectively). Both estimates were greater than those from size-at-age observations only (187 cm and 149 cm, respectively) and were much higher than previously estimated for the South Georgia *D. eleginoides* population (141 cm and 111 cm) (Agnew and Belchier 2009). Estimates of *K* were negatively correlated with  $L_{infr}$ , whereas  $t_0$  (-0.2 males; -0.3 females) was very close to those from size-at-age observations from the South Georgia D. eleginoides population (Table 6.4). Table 6.4 Summary of VB growth parameters for *D. eleginoides* populations at South Georgia and the South Sandwich Islands. Mortality values used in South Sandwich Islands population assessment: Male M = 0.24; Female M = 0.13. "LS" – Least squares estimation. South Georgia CASAL estimates from Agnew & Belchier (2009).

Population	Sex	Model	L <sub>inf</sub>	K	t <sub>0</sub>
South Georgia	Male	CASAL	111	0.105	-0.1
South Sand. Is.	Male	LS	149	0.083	-0.3*
South Sand. Is.	Male	CASAL	174	0.058	-0.2
South Georgia	Female	CASAL	141	0.072	-0.3
South Sand. Is.	Female	LS	187	0.057	-0.3*
South Sand. Is.	Female	CASAL	202	0.047	-0.3

Model fits to catch-at-length data were very good. Good fits in all years and across a broad range of length classes indicate that the estimated growth and selectivity parameters were appropriate for this population (Fig. 6.4). Catch-at-age fits were also good, though were affected by the level of male natural mortality adopted. With male and female mortality both set to 0.13, the model overestimated the proportion comprised of males and underestimated the proportions of females across all ages. Better fits were achieved when male *M* was increased to 0.24, to simulate emigration of males out of the South Sandwich Islands population (Fig. 6.5). Model fits to mark recapture observations were also good and frequency of tag recaptures was generally within the binomial standard error (Fig. 6.6).



Figure 6.4 Sex-partitioned model fits to catch-at-length observations. Solid line = observed, dotted line = fit. Male M = 0.24; Female M = 0.13.



Figure 6.5 Sex-partitioned model fits to catch-at-age observations with different levels of natural mortality. Solid line = observed, dotted line = fit.



Figure 6.6 Fits to tag data with catch-at-length model. Solid line (triangles) = fit, dotted line (circles) = observed. 95% binomial CIs are shown as dotted lines. Male M = 0.24; Female M = 0.13.

#### 6.3.2.3 Biomass estimate

The CASAL estimate of  $B_0$  was 1,407 t, with most of the information coming from tag release recapture observations, observed as increased contrast in the likelihood estimates of different components of fishery observations (*e.g.* mark releases in 2005, or catch-at-age in 2009) with constrained values of  $B_0$  ranging from 400 to 4,000 tonnes (Fig. 6.7). The CASAL model best-fit was obtained at the  $B_0$  where the sum of likelihoods from all sets of observations was minimised. The strongest signal informing the CASAL estimate of  $B_0$  came from 2008 tag releases for which the maximum likelihood was observed at a  $B_0$  of approximately 2,000 t, while 2010 tag releases, catch-at-age data as well as priors and penalties all pushed the biomass estimate to a smaller value (Fig. 6.7).



Figure 6.7 Likelihood profiles for the virgin biomass estimate from tag, catch-at-length, catch-at-age data and priors and penalties.

Estimates of harvest rate increase from <0.02 in 2005 and 2006 to between 0.03 and 0.07 in subsequent years. The CASAL output suggests that vulnerable biomass was increasing prior to the resumption of fishing in 2005, as the dominant cohorts reached sizes where they would be vulnerable to fishing gear. The subsequent decrease will have resulted in part from fishing pressure and also from natural mortality of the dominant cohorts once they were fully recruited to the fishery. Spawning stock biomass follows a similar trajectory, though South Georgia maturity-at-age was used in the absence of maturation of the South Sandwich



Islands population (Figs. 4.5 & 4.6) and the true SSB is likely to be much lower and possibly close to zero (Fig 6.8).

Figure 6.8 CASAL estimates of biomass, year class strength and harvest rate of D. eleginoides in the Northern Area of the South Sandwich Islands. Upper and lower lines on biomass plots are the medians of 50% and 20% of virgin biomass, respectively.

#### 6.3.2.4 Yield estimation

For the best fit model configuration (sex-partitioned model with male M of 0.24 and female M of 0.13), the future catch limit was constrained by the recruitment criterion ( $\gamma$ 1 of Section 6.1.2), such that at higher yields SSB would be less than 20% of median  $B_0$  in more than 10% of model runs. This becomes more probable when recruitment variability is increased, as was observed in the South Sandwich Islands population. Assuming the Beverton-Holt stock recruitment relationship and steepness parameters (0.75) are relevant to this stock, the

MCMC projections indicated a sustainable yield of 57 t from 2012 to 2047. The predator criterion ( $\gamma$ 2 of Section 6.1.2) was also close to being triggered at this catch level, such that increasing the yield by much would decrease median SSB below 50% of the median estimate of  $B_0$ . Hence, although yield was essentially limited by increased recruitment variability in this range edge *D. eleginoides* population, if this were decreased the estimated yield would not be greatly increased. With *sigma-r* (the standard deviation of log YCS, describing the variability of projected recruitment estimates from spawning biomass) reduced to 0.6, as used in the South Georgia *D. eleginoides* assessment of Hillary, Kirkwood et al. (2006), sustainable yield was increased to 64 t (Fig. 6.9).



Figure 6.9 Stock projections for the period 2012-2046 with sigma-r = 1.0 yield of 57 t (left) and *sigma-r* = 0.6 yield of 64 t (right). Solid lines represent the median and dashed lines represent the 80% credible interval; upper and lower lines are the medians of 50% and 20% of virgin biomass, respectively.

#### 6.4 Discussion

An age structured population assessment was conducted for an exploratory deep water stock of *D. eleginoides*, situated on the distributional range edge of the species. Fishery observations were available and used from the resumption of fishing in 2005, when the stock may be considered to have been almost entirely unexploited. As such, this presented an almost unique opportunity to assess the effects of range edge life history and dispersal traits on population assessment and yield estimation. Good estimates of population size were achieved (low CV) and biological parameters estimated by the model were credible, such that the model constructed was likely to be a fair representation of the true population. As a result of this the model will have accurately represented the growth of recruited fish and relative depletions from fishing pressure.

#### 6.4.1 Maturity and projected recruitment

In order to project the modelled population forwards in time and estimate sustainable yield, the CASAL model applied the Beverton Holt equation (with stochasticity) to the SSB to estimate YCS from 2012 to 2046. SSB was estimated from a maturity-at-age relationship applied to the modelled population at age through time. However, the lack of gonad maturation in South Sandwich Islands D. eleginoides (Figs. 4.5 & 4.6) and evidence from genetic and otolith chemistry studies (link to dispersal chapter) suggest that recruitment to this population is not dependent on resident spawning biomass, as has been observed in seamount populations of other species (Boehlert and Sasaki 1988). Here, the maturity-atage relationship estimated for the South Georgia population was taken from the South Georgia assessment (Peatman, Mitchell et al. 2011) in order to generate a projected recruitment series. True recruitment should not respond to reductions in resident SSB caused by fishing pressure, though with the CASAL model mean recruitment would be responsive to SSB. However, the CCAMLR harvest control rules ensured that estimated yield would rarely (<0.1) deplete SSB below 20% of B<sub>0</sub>, where mean recruitment was still 0.75 of the rate at  $B_0$  (steepness = 0.75). As such the generated recruitment series would tend to slightly underestimate recruitment, though not by much so long as the CCAMLR harvest control rules were adhered to.

A more conservative model configuration may have set the maturity-at-age proportions to zero. It would then have been possible to determine the level of depletion caused by different constant yields on the current population, in the absence of future recruitment. Yield would then be selected based on the level of escapement after a designated time period. The causes of recruitment variability at the South Sandwich Islands are unknown though are likely to be influenced by temporal climatic variation, as has been demonstrated for the South Georgia population (Belchier and Collins 2008). Correlations between YCS and SST or position of climatic oscillations such as ENSO and SAM may allow development of environmental predictors of recruitment, particularly where the physical mechanisms affecting spawning success and migration can be determined (Francis 2006; Belchier and

Collins 2008). Identification of the precise location of origin of individuals which recruit to the South Sandwich Islands stock may also allow for improved predictions of recruitment strength.

#### 6.4.2 Range edge effects on stock productivity

Generalised patterns in life history have been observed moving towards high latitude range peripheries, including decreased growth rates (not observed in *D. eleginoides*) to a greater maximum size and increased age at maturity. These life history traits may be optimised for low ambient temperature in the sense that they maximise fecundity (Roff 2000). However, the delayed maturation of low latitude populations should make them increasingly vulnerable to fishing pressure, where contractions in population age distribution resulting from extractions will remove a greater proportion of the virgin spawning biomass relative to similar extractions at the range centre.

The predicted, and in this case observed, increasingly episodic recruitment towards range peripheries will cause fluctuations in population size through time that are not related to fishing pressure. This will result in lower yields where stock projections account for uncertainty of future recruitment (Fig. 6.9). In extreme cases this would be likely to lead to temporal fluctuations in sustainable yield which may be commercially undesirable. In addition, harvest control rules which limit stock depletions to a fraction of the unexploited spawning biomass (as in CCAMLR waters) will be increasingly inappropriate where episodic or intermittent recruitment causes large variations in population size and age structure. Therefore there may be an increased importance of adopting age-structured assessments for the management of exploitation of range edge populations so that recruitment patterns are adequately represented within the modelling framework.

The adoption of a long-term harvest quantity is likely to be inappropriate for this population, because constant recruitment is assumed and recruitment to the South Sandwich Islands *D. eleginoides* population (and other range edge stocks) is highly episodic and may have an intermittent nature if recruitment patterns are correlated with climatic oscillations. A key management recommendation stemming from this should be that the expectation of a sensible, predictable long term harvest strategy based on a long-term yield is unlikely to be appropriate for this or other range edge toothfish stocks, such as at BANZARE Bank in the Southern Indian Ocean, where there are concerns as to the status of the stock and an

estimate of sustainable of yield has yet to have been delivered (McKinlay, Welsford et al. 2008).

#### 6.4.3 Accounting for emigration and natural mortality

In a previous analysis, the mark-recapture data were used to estimate annual migration rates from the South Sandwich Islands to South Georgia of males (0.241; 95 % CIs 0.10 to 0.50; 6 recaptures) and females (0.018; 95 % Cls 0 to 0.11, 1 recapture; Section 5.3.3). Here the migration of males accounted for by increasing male M above the value of 0.13, the natural mortality rate commonly used in D. eleginoides population assessment models (Hillary, Kirkwood et al. 2006; Candy and Constable 2008). The observed response in CV around the estimate of  $B_0$  related to goodness of fit between observed catch-at-age and the modelled catch-at-age, both of which were sex-partitioned. A decline in male to female sex ratio was observed with increasing age such that that very few males of greater than 20+ age are observed in the catch (Fig. 6.3). The best model fit (lowest CV around  $B_0$ ) was obtained with a male M of 0.24. This represented natural mortality (assumed to be 0.13) as well as migration and suggested that the annual migration rate was considerably lower than 0.24 year<sup>-1</sup> estimated from the mark-recapture data. This value was estimated from a small number of tag recaptures (6 males and 1 female – though female migration was assumed to be zero) and the true migration rate may be closer to 0.1, at the lower 95% CI end of the mark recapture estimate.

The dispersal dynamics of *D. eleginoides* between the South Sandwich Islands and South Georgia may be more accurately represented with an area-partitioned assessment, such that migration rates between the two sub-populations can be specified in the model and could use migration rate estimates from analyses of mark-recapture data, or sex-ratio with age. The model could also be configured such that recruitment to the South Sandwich Islands population was dependent on spawning biomass of the South Georgia sub-population. However, despite genetic similarities between the two stocks the precise origin of recruits to the South Sandwich Islands is unknown. Even so, the current single-area population model, which combines emigration and natural mortality, deals with migration sufficiently for the purposes of yield estimation.

The observed dispersal patterns suggest a sex-biased migration of males, resulting in range contraction away from high latitude, lower temperature regions to warmer regions where

spawning grounds are located. There is a general lack of empirical studies of range position effects on dispersal patterns (Guisan and Zimmermann 2000; Bahn, Krohn et al. 2008) and it is not known to what extent the patterns observed her in *D. eleginoides* are typical of other fish species. Even so, increased migration rates might be expected and mark-recapture experiments provide a particularly useful means of assessing dispersal patterns of range edge stocks. Where mark recapture is not possible and dispersal is sex-biased, population sex ratio with age and location can also be used to estimate mortality rates with some assumptions and can at least be used to validate estimates from mark-recapture analyses.

Previous studies have found limited evidence for reduced survivorship towards range edges (Gaston 2009; Sexton, McIntyre et al. 2009). The effects of range position on natural mortality rate was not assessed here and future analysis might look for evidence of increased *M* towards range limits and mark-recapture data could be used to achieve this once a sufficient number of tagged fish have been recaptured. This might also be used to assess temporal variation in mortality rates which also may increase towards range peripheries.

#### 6.4.4 Sex-partitioned assessment of range edges stocks

A combined-sex assessment is appropriate where the two sexes do not differ much in terms of biology or behaviour, or where there is insufficient data for both males and females. Sexaggregated assessments are currently used to estimate yield for both South Georgia (Hillary, Kirkwood et al. 2006) and Heard Island *D. eleginoides* (Candy and Constable 2008) fisheries. Sex-disaggregated assessments have previously been produced for the South Georgia *D. eleginoides* population, the latest of these by Peatman *et. al* (2011), though have never been used to estimate sustainable yield for the fishery. However, differences in biology are frequently observed in a number of species, such as increased size-at-maturity (Everson and Murray 1999) and greater  $L_{inf}$  of female *D. eleginoides* (Agnew and Belchier 2009). Large differences in size-at-age were observed in the two sexes South Sandwich Islands population (Table 6.4) and emigration rates to South Georgia were strongly sex-biased (Fig. 6.3).

Sex biased-dispersal has been observed in a variety of vertebrate species (Pusey 1987). Small differences in the niche requirements of the two sexes could potentially result in large differences in distributional range and this pattern might be accentuated in highly mobile species where individuals are better able to redistribute in to more suitable habitat areas.

Sex-biased tolerance to harsh environmental conditions might also be manifested as accentuated difference in life history towards range edges, particularly relating to growth and reproductive biology. In order to account for differences in tolerance and behaviour, sex-partitioned assessments may be more appropriate where they improve model fits to observational data and reduce uncertainty around estimates obtained from population models of range periphery stocks.

#### 6.4.5 Conclusions and future work

A primary criticism of the population assessment assembled for South Sandwich Islands D. eleginoides is that the application of a Beverton-Holt spawning stock recruitment relationship is probably inappropriate given that recruits appear to be migrating in from somewhere else and so are independent of resident spawning stock size. Such non-breeding sink populations may be increasingly commonplace towards range edges where environmental conditions are not suitable for development to sexual maturity or current flow regimes do not lead to the entrainment of eggs and larvae to suitable juvenile feeding grounds. Currently there is a considerable gap in the knowledge of dispersal patterns and how these affect population dynamics from range centre to range edge (Bahn, Krohn et al. 2008). Advances in this area would be particularly informative for population assessments and management of range edge stocks, particularly in data-poor fisheries such as most deep water stocks (Japp and Wilkinson 2006). Specifically research might address sex-biased dispersal and impacts on population assessment, *i.e.* moving towards range peripheries is recruitment increasingly reliant on immigration from range centre spawning grounds? Also, is the sex-biased range contraction observed in South Sandwich Islands typical of other range edge species?

In addition there is a need to resolve generalised patterns of range position effects on life history and to consider their effects on population dynamics such that it will be possible to predict the impacts of resource exploitation on range periphery stocks relative to those at the range centre. Where temperature is the key abiotic factor driving variation in life history strategy, this might also be considered within the context of climate change effects on stock productivity and sustainable yield.

# Chapter 7

# Synthesis and discussion

The South Sandwich Islands are extremely remote and have been subject to limited historical fishing pressure, such that the marine ecosystem can be considered to have been pristine when exploratory fishing commenced in 2005. The mark-recapture experiment for toothfish species was the primary focus of the research fishing, though detailed biological measurements of toothfish and finfish and invertebrate bycatch data were also collected from the outset, allowing an almost unique opportunity to describe the ecology of a largely unexplored region of the Southern Ocean.

This study was broad in focus, including: a description of the bathyal ecology of the South Sandwich Islands; an analysis of the abiotic factors which limit toothfish distribution; and an analysis of range position effects on toothfish life history. These then informed an evaluation of the consequences of range edge population dynamics for the management of resource exploitation, taking the example of South Sandwich Islands toothfish species populations.

### 7.1 Biogeography of the Southern Ocean

Prior to this study the South Sandwich Islands were one of the least well-described regions of the Southern Ocean, with virtually no data from the upper bathyal zone (from 500 to 2,000 m depth) (Ramos 1999; Arntz and Brey 2003; Linse, Brandt et al. 2007; Griffiths, Linse et al. 2008). The South Sandwich Islands are unique in that they comprise the only region of continuous bathyal seafloor spanning the transition between Subantarctic and Antarctic zones of the Southern Ocean. These two bioregions are characterised by differences in seawater temperature with depth, hydrographic characteristics and biological productivity (Orsi, Whitworth et al. 1995; Murphy, Watkins et al. 2007). A number of trawl surveys have been conducted along the Scotia Arc, though these have tended to sample only a few locations and have adopted different sampling gear and methods, making it difficult to combine information from different sources (Ramos 1999; Arntz and Brey 2003; Malyutina 2004; Griffiths, Linse et al. 2008). As such, previous bioregionalisation studies have failed to resolve the precise location of the boundary between Subantarctic fauna and

compositionally different Antarctic fauna, fringing the Antarctic Continent (Gon and Heemstra 1990; Arntz, Thatje et al. 2005).

Longline operations are typically more selective than commercial or research trawls in terms of the species that are captured or impacted through mechanical disruption. Even so, the relatively high levels and even spread of longline fishing effort about the island arc allowed for an informative analysis of the distributions of the more abundant megafauna in an area where very little was previously known (Figs 2.4 & 2.6). An abrupt transition in catch composition was observed in both finfish and invertebrate taxa around Saunders Island (Figs. 2.2 & 2.7). To the south of this, mobile invertebrates and fish species known to have plasma AFGPs were much more abundant, whereas Subantarctic species were dominant to the north. The bioregionalisation analysis resolved the position of this boundary at the South Sandwich Islands, where it falls along the path of the Weddell front dividing cold waters of the Weddell Gyre to the south from the Weddell Scotia Confluence and Antarctic Circumpolar Current located to the north (Figs. 2.2, 2.8 & 2.9). The north to south transition in finfish communities was coincident with that of invertebrate taxa, suggesting a dramatic change in habitat south of this location, which may relate to decreased temperature, increased sea ice cover and associated increases in biological productivity (Murphy, Watkins et al. 2007).

Future studies might focus on validating the bioregionalisation analysis conducted here. The longline rig adopted by vessels collecting data for this study is thought to be relatively selective and it would be informative, where possible, to conduct trawl surveys close to longline sampling points to calibrate the selectivity of the gear. This would facilitate a more thorough assessment of the benthic ecology of this region and also of the impacts of the fishery. Cameras have been successfully deployed on longline gear in the Southern Ocean (Kilpatrick, Ewing et al. 2011) and may be used at the South Sandwich Islands to observe predicted differences in seafloor habitat moving across the ecotone at the Weddell Front, which delineates Subantarctic and Antarctic fauna. Where the spatial coverage of effort is sufficient, studies might adopt a similar approach to the one used here to describe the biogeography of other regions of the Southern Ocean.

This bioregionalisation analysis was complemented by an evaluation of the environmental factors that impact on toothfish distribution. Both toothfish species are present at the South

Sandwich Islands, including the Subantarctic *D. eleginoides* and the Antarctic *D. mawsoni*. Correlative modelling of toothfish species distribution suggested that winter surface seawater temperature and sea ice cover were both good predictors of which species are dominant at a particular location (Table 3.2), such that cold water extremes appear to limit the southward incursion of *D. eleginoides*. However a considerable overlap in diet of *D. eleginoides* and *D. mawsoni* indicates that competitive interactions may also impact on distribution patterns towards the species interface (Roberts, Xavier et al. 2011; Annex A).

Discrepancies between threshold values of ice cover and temperature when comparing the Ross Sea and South Sandwich Islands populations suggest that topographic and hydrographic features play an important role in deciding where the ecotone between the two bioregions will occur (Fig. 3.4), such that current flow fields create biogeographic boundaries that do not necessarily relate to species and possibly whole community niche requirements (Gaylord and Gaines 2000). Thus, species redistributions in response to climate change will respond not just to changes in temperature – they will also be strongly influenced by local bathymetry and prevailing current systems. As such, predictions of how species will redistribute in response to changes in climate or habitat will have improved accuracy where the spatial organisation of dispersive forces and potential barriers to dispersal are also accounted for.

#### 7.2 Range position effects on life history & dispersal

Previous studies have sought evidence for the role of declining fitness in range periphery meta-populations for the formation of distributional range edges (Gaston 2009; Sexton, McIntyre et al. 2009). The evidence from these studies has been equivocal, and reviews have concluded that the relevant analyses have tended to suffer from a lack of completeness. Studies tend to focus either on growth, sexual development or fecundity and rarely on all of these at once, so that interactions and potential life history tradeoffs cannot be properly investigated (Gaston 2009).

Current theory suggests that the life history of a species will vary in a predictable way from the range centre where habitat is likely to be optimal, to range peripheries where it is not. Moving towards cold water, high-latitude range edges, life history theory suggests that individuals should exhibit reduced growth rates to an increased average maximum length (Atkinson and Sibly 1997; Angilletta, Steury et al. 2004), with delayed maturation (Roff 2000; Stearns 2000) and reduced somatic condition (Gaston, 2009). In addition, increased recruitment variability should be observed towards range edges. Some, though not all, of these hypothesised range edge traits were observed in South Sandwich Islands *D. eleginoides*. Increased maximum size was observed, though initial growth rates were similar to those of individuals at South Georgia and growth is clearly not a factor limiting productivity towards the high latitude range edge. There was no evidence at all for gonad maturation to spawning condition and this appears to relate to improved somatic condition, which would not normally be expected in range edge individuals. Highly episodic recruitment – also assumed to be a feature of range edge populations (Philippart, Henderson et al. 1998; Brunel and Boucher 2006) – was observed here and the South Sandwich Islands population does not appear to be self-sustaining (Table 4.3).

In the case of South Sandwich Islands *D. eleginoides* it is likely that cold-water stress impairs normal reproductive function and this is likely to be a key factor limiting southward range expansions of this species. The extent to which these observations are representative of other high latitude range edge populations is unknown. To this end, a meta-analysis might be conducted of range position effects on the life history of a variety of species with different life history traits. This could also explore trends with different taxonomic or distributional groupings (*e.g.* pelagic versus demersal; deep water versus shallow water; tropical versus polar).

The life history patterns observed in South Sandwich Islands *D. eleginoides* may be typical of species where dispersive forces distribute organisms beyond the realms of their fundamental niche – defined as the region where normal reproductive development occurs. The extent to which this pattern is likely to occur would be informed by population genetic and otolith microchemistry studies and the application of other approaches for assessing dispersal rates and connectedness between stock components, so that that the life cycles of toothfish and other deep water species are better understood.

The genetic composition of South Sandwich Islands and South Georgia populations indicated a high degree of mixing between the two populations (Fig. 5.1). This is supported by the otolith microchemistry analysis which found similarities in the chemistry of otolith nuclei suggesting a similar point of origin of South Georgia individuals and the bulk of the South Sandwich Islands population. Some individuals of the latter population were found to have a different (Northern) haplotype and a different chemical composition was observed in the otolith cores of these individuals, suggesting a different location of origin (Section. 5.4.2). While the microchemistry analysis conducted here was informative, the small sample size and limited number of study groups constrained the inferences that could be made. However, the high level of reproducibility of the results suggests that follow-on analyses could append results to those generated as part of this study in order to better understand the life cycle and dispersal dynamics of toothfish and other deep water species.

The influence of dispersal patterns on range edge formation is rarely explored owing to a general lack of empirical data (Bahn, Krohn et al. 2008). The results of the mark-recapture model for estimating *D. eleginoides* migration rates between South Georgia and the South Sandwich Islands indicated that range contractions of *D. eleginoides* occur in adults, possibly in response to maturation, though this was primarily observed in males. Hence active migration may redistribute individuals passively migrated to unsuitable habitat areas, though differences in behavioural ecology may affect the extent to which this occurs in the two sexes.

Increasingly accurate estimates will come from the mark-recapture migration model as future recaptures become available to update this analysis. Even so, sufficient data were already available to describe the basic trend of sex-biased range contraction away from the range edge and this was validated by analyses of residual sex ratio at age of the resident population. The general lack of empirical data for other populations means that it is currently not possible to speculate about whether the patterns observed here are typical of range edge populations. However, mark-recapture studies have now been conducted on a large number of fish and other vertebrate species, principally for the estimation of population size, and these could also be used to generalise about dispersal effects on the formation of range edges.

# 7.3 Exploitation of range edge stocks

Fisheries management is often hampered by the poor quality and insufficient quantity of data available for population assessment. As such, it would be useful to be able to make predictions about the biology and population dynamics of the target resource based on range position, particularly as range edge stocks may be among the especially data poor.

A number of the range edge life history traits listed above, including reduced growth rates at higher latitudes and impaired reproductive biology, will negatively impact on the productivity of a stock, such that exploited populations will take a longer time to return to their initial biomass. However, the growth characteristics of the South Sandwich Islands population – rapid growth to a large average maximum size – actually lead to increased productivity. Emigration will also negatively impact on productivity and this may be sexbiased, such that sex-partitioned models may be more appropriate for range periphery stocks to improve model fits to fishery observations and so reduce uncertainty around model estimates.

Having constructed a population model to adequately account for range edge population dynamics, there may be further impacts of range edge life history and reproductive success on estimates of sustainable yield, though this will depend on the nature of the harvest control rule that is used. The South Sandwich Islands *D. eleginoides* fishery is managed according to CCAMLR harvest control rules which, in order to avoid recruitment overfishing, aim to keep the probability below 0.1 that *SSB* will fall below 20% of  $B_0$ . As a result of this, predicted *D. eleginoides* yield is inversely related to recruitment variability. The model configuration presented here adopted a Beverton-Holt stock recruitment relationship for producing a projected recruitment series. Though this was clearly inappropriate for this stock, it was likely to lead to conservative estimates of yield, assuming that the actual spawning population was not also being depleted.

Further complications arise from increased recruitment variability towards range edges, where this causes true  $B_0$  to fluctuate through time. As such, harvest control rules which aim to maintain *SSB* above a fraction of  $B_0$  may be increasingly less appropriate in range periphery stocks. This applies to the South Sandwich Islands, and to several other range edge occurrences of toothfish, particularly at BANZARE bank (McKinlay, Welsford et al. 2008). In CCAMLR waters, two reference points are used to maintain stock size above a fraction of  $B_0$ :

 $\gamma$ 1 which minimises the probability of recruitment overfishing; and  $\gamma$ 2 which maintains the *SSB* of toothfish (the largest finfish predator of the bathyal zone) above 50% of  $B_0$  (see Section 6.1.2). If it can be proven that South Sandwich Islands *D. eleginoides* do in fact comprise a sink population, then  $\gamma$ 1 can be ignored. The second rule,  $\gamma$ 2, will maintain ecosystem relationships between predators and prey, though yield will still depend on the size of  $B_0$  immediately prior to fishing, even though this may fluctuate through time. A more conservative approach may be to estimate the levels of stock depletion imposed by different constant catch levels, assuming no future recruitment. The  $\gamma$ 2 rule would then be applied to maintain predator biomass above a fraction of  $B_0$ .

#### 7.4 Conclusion

This study demonstrates that predictions can be made about how the life history of vertebrate species is optimised moving across a distributional range, and the implications of these gradients for management. Much of the theory concerning range edge species is currently untested, though studies such as this one, examining a broad range of life history and population dynamic parameters, allow for an evaluation of how different life history processes may be traded off against each other. Some aspects of range edge life history, particularly relating to growth, reproductive success and recruitment, will impact on a species' productivity such that they may be increasingly vulnerable to the impacts of exploitation. Where generalised patterns in range position effects on life history can be discerned, this information can be used to make predictions about the life history of exploited stocks that are otherwise data poor, such as many deepwater stocks, and will also allow for improved predictions as to how species will respond to changes in the environment, particularly relating to climate change.

References

- Abellan, L. (1999). Results of a longline survey on seamounts in the southeast Atlantic and in CCAMLR Subarea 48.6 (Atlantic Ocean) and division 58.4.4 (Indian Ocean). *CCAMLR Science*, 6, 99-116.
- Abellan, L. (2005). Patagonian toothfish in international waters of the southwest Indian Ocean (Statistical Area 51). *CCAMLR Science*, 12, 207-214.
- Agnew, D. (2000). The illegal and unregulated fishery for toothfish in the Southern Ocean, and the CCAMLR catch documentation scheme. *Marine Policy*, 24, 361-374.
- Agnew, D. (2004a). Fishing south: History and management of South Georgia fisheries. The Penna Press, St Albans, UK.
- Agnew, D. & Belchier, M. (2009). Adding catch at age and survey data to the 48.3 toothfish CASAL assessment. *CCAMLR WG-SAM*, 09/13, CCAMLR, Hobart, Australia.
- Agnew, D., Edwards, C., Hillary, R., Mitchell, R. & Abellan, L. (2009). Status of the coastal stocks of *Dissostichus* spp. In East Antarctica (Divisions 58.4.1 and 58.4.2). *CCAMLR Science*, 16, 71-100.
- Agnew, D. & Peatman, T. (2009). Preliminary assessment of toothfish in Subarea 48.3. *CCAMLR WG-FSA*, 09/28, CCAMLR, Hobart, Australia.
- Agnew, D. J., Kirkwood, G. P., Pearce, J. & Clark, J. (2006). Investigation of bias in the markrecapture estimate of toothfish population size at South Georgia. *CCAMLR Science*, 13, 47-63.
- Agnew, D. J. H., L.; Jones, C.; Watson, A.; Berkieta, K.; Pearce, J. (1999). Depth distribution and spawning pattern of *Dissostichus eleginoides* at South Georgia. *CCAMLR Science*, 6, 19-36.
- Agnew, D. J. K., G.P.; Payne, A.; Pearce, J.; Clarke, J. (2005). Parameters for the assessment of toothfish in Subarea 48.3. *CCAMLR WG-FSA*, 05/18, CCAMLR, Hobart, Australia.
- Agnew, D. J. P., L. V.; Orr, P. A.; Payne, A. G.; Zara, S; Beddington, J. R. (2004b). The Falkland Islands fisheries research report: 19 february 2004. London, UK: RRAG, Imperial College.

- Allen, C. S. & Smellie, J. L. (2008). Volcanic features and the hydrological setting of Southern Thule, South Sandwich Islands. *Antarctic Science*, 20, 301-306.
- Amante, C. & Eakins, B. W. (2008). Etopo1 1 arc-minute global relief model: Procedures, data sources and analysis, Boulder, CO, National Geophysical Data Center, NESDIS, NOAA, U.S. Department of Commerce.
- Angilletta, M., Steury, T. & Sears, M. (2004). Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, 44, 498-509.
- Appleyard, S. A., Williams, R. & Ward, R. D. (2004). Population genetic structure of Patagonian toothfish in the west indian ocean sector of the Southern Ocean. *CCAMLR Science*, 11, 21-32.
- Arana, P. (2009). Reproductive aspects of the Patagonian toothfish (*Dissostichus eleginoides*) off southern Chile. *Latin American Journal of Aquatic Research*, 37, 381-394.
- Arana, P. M. & Vega, R. (1999). Exploratory fishing for *Dissostichus* spp. in the Antarctic region (sub-areas 48.1, 48.2 and 88.3). *CCAMLR Science*, 6, 1-17.
- Arkhipkin, A., Brickle, P. & Laptikhovsky, V. (2003). Variation in the diet of the Patagonian toothfish with size, depth and season around the Falkland Islands. *Journal of Fish Biology*, 63, 428-441.
- Armstrong, R. L. & Knowles, K. (2010). ISLSCP II global sea ice concentration. In: Hall, F. G., Collatz, G., Meeson, B., Los, S., Brown de Coulstoun, E. & Landis, D. (eds.) ISLSCP initiative II Collection. Data set.
- Arntz, W. & Brey, T. (2003). The expedition ANTARKTIS XIX/5 (LAMPOS) of RV "Polarstern" in 2002. *Berichte Polarforsch Meeresforsch*, 462.
- Arntz, W. E. (1999). Magellan-Antarctic: ecosystems that drifted apart. Summary review. *Scientia Marina*, 63, 503-511.
- Arntz, W. E., Thatje, S., Gerdes, D., Gili, J. M., Gutt, J., Jacob, U., Montiel, A., Orejas, C. & Teixido, N. (2005). The antarctic-magellan connection: Macrobenthos ecology on the

shelf and upper slope, a progress report. *In:* IBMANT/ANDEEP International Symposium and Workshop, 2003, Ushuaia, Argentina. Inst Ciencias Mar Barcelona, 237-269.

- Ashford, J. (2001). In support of a rationally managed fishery: Age and growth in Patagonian toothfish (Dissostichus eleginoides). Ph.D., Old Dominion University, USA.
- Ashford, J., Duhamel, G., Jones, C. & Bobko, S. (2005). Age, growth and mortality of Patagonian toothfish (*Dissostichus eleginoides*) caught off Kerguelen. *CCAMLR Science*, 12, 29-41.
- Ashford, J. & Jones, C. (2007). Oxygen and carbon stable isotopes in otoliths record spatial isolation of Patagonian toothfish (*Dissostichus eleginoides*). *Geochimica Et Cosmochimica Acta*, 71, 87-94.
- Ashford, J. R., Arkhipkin, A. I. & Jones, C. M. (2006). Can the chemistry of otolith nuclei determine population structure of Patagonian toothfish *Dissostichus eleginoides? Journal of Fish Biology*, 69, 708-721.
- Ashford, J. R., Arkhipkin, A. I. & Jones, C. M. (2007). Otolith chemistry reflects frontal systems in the Antarctic Circumpolar Current. *Marine Ecology-Progress Series*, 351, 249-260.
- Ashford, J. R., Jones, C. M., Hofmann, E. E., Everson, I., Moreno, C. A., Duhamel, G. & Williams, R. (2008). Otolith chemistry indicates population structuring by the Antarctic Circumpolar Current. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 135-146.
- Atkinson, D., Begon, M. & Fitter, A. H. (1994). Temperature and organism size--a biological law for ectotherms? *Advances in ecological research*. Academic Press.
- Atkinson, D. & Sibly, R. M. (1997). Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology & Evolution*, 12, 235-239.
- Baayen, R. H. (2011). LanguageR: Data sets and functions with "Analyzing linguistic data: A practical introduction to statistics using R". Cambridge University Press, UK.

- Bagley, P. M., Priede, I. G., Jamieson, A. D., Bailey, D. M. & Battle, E. J. V. (2004). Lander techniques for deep-ocean biological research. *Journal of the Society for Underwater Technology*, 26, 3-12.
- Bahn, V., Krohn, W. & O'connor, R. (2008). Dispersal leads to spatial autocorrelation in species distributions: A simulation model. *Ecological modelling*, 213, 285-292.
- Bahn, V., O'Connor, R. & Krohn, W. (2006). Effect of dispersal at range edges on the structure of species ranges. *Oikos*, 115, 89-96.
- Bailey, D. M., Collins, M. A., Zuur, A. F. & Priede, I. G. (2009). Long-term changes in deepwater fish populations in the northeast Atlantic: A deeper reaching effect of fisheries? *Proceedings - Royal Society. Biological sciences*, 276, 1965-1969.
- Barker, P. F. (2001). Scotia Sea regional tectonic evolution: Implications for mantle flow and palaeocirculation. *Earth-Science Reviews*, 55, 1-39.
- Bath, G. E., Thorrold, S. R., Jones, C. M., Campana, S. E. & Mclaren, J. W. (2000). Strontium and barium uptake in aragonitic otoliths of marine fish. *Geochimica Et Cosmochimica Acta*, 64, 1705-1714.
- Belchier, M. & Collins, M. A. (2008). Recruitment and body size in relation to temperature in juvenile Patagonian toothfish (*Dissostichus eleginoides*) at South Georgia. *Marine Biology*, 155, 493-503.
- Bender, M. L., Klinkhammer, G. P. & Spencer, D. W. (1977). Manganese in seawater and the marine manganese balance. *Deep Sea Research*, 24, 799-812.
- Berrigan, D. & Charnov, E. (1994). Reaction norms for age and size at maturity in response to temperature a puzzle for life historians. *Oikos*, 70, 474-478.
- Beverton, R. J. H. & Holt, S. J. (1957). On the dynamics of exploited fish populations. *Fishery Investigations (2. Sea Fish.).* Ministry Agriculture Fisheries and Food G.B.
- Bigelow, K., Boggs, C. & He, X. (1999). Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. *Fisheries oceanography*, 8, 178-198.

- Billany, W., Swart, S., Hermes, J. & Reason, C. J. C. (2010). Variability of the Southern Ocean fronts at the Greenwich Meridian. *Journal of Marine Systems*, 82, 304-310.
- Bjornsson, B., Steinarsson, A. & Oddgeirsson, M. (2001). Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* I.). *ICES Journal of Marine Science*, 58, 29-38.
- Boehlert, G. W. & Sasaki, T. (1988). Pelagic biogeography of the armorhead, *Pseudopentaceros-wheeleri*, and recruitment to isolated seamounts in the North Pacific-Ocean. *Fishery Bulletin*, 86, 453-465.
- Brass, G. W. & Turekian, K. K. (1972). Strontium distributions in sea water profiles from the GEOSECS I (Pacific) and GEOSECS II (Atlantic) test stations. *Earth and Planetary Science Letters*, 16, 117-121.
- Brass, G. W. & Turekian, K. K. (1974). Strontium distribution in geosecs oceanic profiles. *Earth and Planetary Science Letters*, 23, 141-148.
- Brown, J., Mehlman, D. & Stevens, G. (1995). Spatial variation in abundance. *Ecology*, 76, 2028-2043.
- Brunel, T. & Boucher, J. (2006). Pattern of recruitment variability in the geographical range of the exploited northeast Atlantic fish species. *Journal of Sea Research*, 55, 156-168.
- Brunel, T. & Dickey-Collas, M. (2010). Effects of temperature and population density on Von Bertalanffy growth parameters in Atlantic herring: A macro-ecological analysis. *Marine ecology. Progress series*, 405, 15-28.
- Bull, B., Francis, R. I. C. C., Dunn, A., Mckenzie, A., Gilbert, D. J. & Smith, M. H. (2005). CASAL user manual v2.07-2005/08/21. NIWA, NZ.
- Burel, C., Personleruyet, J., Gaumet, F., Leroux, A., Severe, A. & Boeuf, G. (1996). Effects of temperature on growth and metabolism in juvenile turbot. *Journal of Fish Biology*, 49, 678-692.

- Busby, J. R. (1991). Bioclim a bioclimatic analysis and prediction system. In: Margules, C., Austin, M. (eds.) Nature conservation: Cost effective biological surveys and data analysis.CSIRO, Melbourne, Australia.
- Campana, S., Mohn, R., Smith, S. & Chouinard, G. (1995). Spatial implications of a temperature-based growth model for Atlantic cod (*Gadus morhua*) off the eastern coast of Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 2445-2456.
- Candy, S. G. & Constable, A. J. (2008). An integrated stock assessment for the Patagonian toothfish (*Dissostichus eleginoides*) for the Heard and McDonald Islands using CASAL. *CCAMLR Science*, 15, 1-34.
- Candy, S. G., Constable, A. J., Lamb, T. & Williams, R. (2007). A Von Bertalanffy growth model for toothfish at Heard Island fitted to length-at-age data and compared to observed growth from mark-recapture studies. *CCAMLR Science*, 14, 43-66.
- CCAMLR (1992). Report of the eleventh meeting of the Scientific Committee SC-CAMLR XI. CCAMLR, Hobart, Australia.
- CCAMLR (1993). Report of the twelfth meeting of the Scientific Committee SC-CAMLR XII. CCAMLR, Hobart, Australia.

CCAMLR (2005). CCAMLR scientific observer manual, CCAMLR, Hobart, Australia.

- CCAMLR (2007). Workshop on bioregionalisation of the Southern Ocean. In: *Report of the twenty-sixth meeting of CCAMLR Scientific Committee* (2007). CCAMLR, Hobart, Australia.
- CCAMLR (2008). Report of the twenty-seventh meeting of the Commission SC-CAMLR XXVII. CCAMLR, Hobart, Australia
- CCAMLR (2011). *Statistical bulletin, Vol. 23 (database version)*. Data set. CCAMLR. Hobart, Australia.
- Chan, L. H., Drummond, D., Edmond, J. M. & Grant, B. (1977). On the barium data from the Atlantic GEOSECS expedition. *Deep Sea Research*, 24, 613-649.
- Chapman, D. G. (1948). A mathematical study of confidence limits of salmon populations calculated by sample tag ratios. *International Pacific Salmon Fisheries Communications, Bulletin,* 2, 67-85.
- Chen, Z. Z., Cheng, C. H. C., Zhang, J. F., Cao, L. X., Chen, L., Zhou, L. H., Jin, Y. D., Ye, H., Deng,
  C., Dai, Z. H., Xu, Q. H., Hu, P., Sun, S. H., Shen, Y. & Chen, L. B. (2008).
  Transcrintomic and genomic evolution under constant cold in antarctic notothenioid
  fish. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 12944-12949.
- Chisholm, J. S. (1993). Death, hope, and sex life-history theory and the development of reproductive strategies. *Current anthropology*, 34, 1-24.
- Clarke, K. R. (1993). Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18, 117-143.
- Collins, M., Brickle, P., Brown, J. & Belchier, M. (2011). The Patagonian toothfish: biology, ecology and fishery. *Advances in Marine Biology 58*, 227-300.
- Collins, M. A., Ross, K. A., Belchier, M. & Reid, K. (2007). Distribution and diet of juvenile Patagonian toothfish on the South Georgia and Shag Rocks shelves (Southern Ocean). *Marine Biology*, 152, 135-147.
- Comiso, J. C., Kwok, R., Martin, S. & Gordon, A. L. (2011). Variability and trends in sea ice extent and ice production in the Ross Sea. *J. Geophys. Res.*, 116, C04021.
- Davis, R., Fuiman, L., Williams, T., Collier, S., Hagey, W. & Kanatous, S. (1999). Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science*, 283, 993-996.
- De Vries, A. L., Komatsu, S. & Feeney, R. (1970). Chemical and physical properties of freezing point depressing glyco proteins from Antarctic fishes. *Journal of Biological Chemistry*, 245, 2901-2908.
- De Vries, A. L. & Wohlschlag, D. (1969). Freezing resistance in some Antarctic fishes. *Science*, 163, 1073-1075.

- De Witt, H. H., Heemstra, P. C. & Gon, O. (1990). Nototheniidae. *In:* Gon, O. & Heemstra, P.C. (eds.) *Fishes of the Southern Ocean.* Grahamstown: JLB Smith Institute of Ichthyology.
- Dekker, R. & Beukema, J. (1993). Dynamics and growth of a bivalve, *Abra-tenuis*, at the northern edge of its distribution. *Journal of the Marine Biological Association of the United Kingdom*, 73, 497-511.
- Devries, A. L. (1971). Glycoproteins as biological antifreeze agents in Antarctic fishes. *Science*, 172, 1152-1155.
- Eastman, J. T. (1990). The biology and physiological ecology of notothnioid fishes. *In:* Gon, O.
  & Heemstra, P. C. (eds.) *Fishes of the Southern Ocean.* Grahamstown: JLB Smith Institute of Ichthyology.
- Eastman, J. T. & Devries, A. L. (2000). Aspects of body size and gonadal histology in the Antarctic toothfish, *Dissostichus mawsoni*, from McMurdo Sound, Antarctica. *Polar biology*, 23, 189-195.
- Endicott, M. (2011). *The impact of the toothfish longline fishery on skate populations around South Georgia*. Ph.D., Imperial College London.
- Everson, I. & Murray, A. (1999). Size at sexual maturity of Patagonian toothfish (*Dissostichus eleginoides*). CCAMLR Science, 6, 37-46.
- Evseenko, S. A., Kock, K. H. & Nevinsky, M. M. (1995). Early-life history of the Patagonian toothfish, *Dissostichus eleginoides* Smitt, 1898 in the Atlantic sector of the Southern-Ocean. *Antarctic Science*, 7, 221-226.
- Fenaughty, J. M. (2006). Geographical differences in the condition, reproductive development, sex ratio and length distribution of antarctic toothfish (*Dissostichus mawsoni*) from the Ross Sea, Antarctica (CCAMLR Subarea 88.1). CCAMLR Science, 13, 27-45.
- Fenaughty, J. M., Eastman, J. T. & Sidell, B. D. (2008). Biological implications of low condition factor "axe handle" specimens of the Antarctic Toothfish, *Dissostichus mawsoni*, from the Ross Sea. *Antarctic Science*, 20, 537-551.

- Fitzcharles, E. (2007). *Genetic diversity of deep-sea fish around the Southern Ocean*. Institute of Zoology, Regents Park, London.
- Francis, R. (2006). Measuring the strength of environment-recruitment relationships: The importance of including predictor screening within cross-validations. *ICES Journal of Marine Science*, 63, 594-599.
- Garcia Del La Rosa, S., Sanchez, F. & Figueroa, D. (1997). Comparative feeding ecology of Patagonian toothfish (*Dissostichus eleginoides*) in the southwestern Atlantic. *CCAMLR Science*, 4, 105-124.
- Gass, I. G., Harris, P. G. & Holdgate, M. W. (1963). Pumice eruption in the area of the South Sandwich Islands. *Geological Magazine*, 100, 321-330.
- Gaston, K. (2009). Geographic range limits: Achieving synthesis. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1395-1406.
- Gauldie, R. W., West, I. F., Coote, G. & Merrett, N. (1995). Strontium variation and the oxygen-isotope water temperature record in the otoliths of the deep-water fishes *Trachyrincus-murrayi* and *Coryphaenoides-mediterraneus*. *Comparative Biochemistry and Physiology A-Physiology*, 110, 271-280.
- Gaylord, B. & Gaines, S. (2000). Temperature or transport? Range limits in marine species mediated solely by flow. *The American Naturalist*, 166, 769-789.
- Ghigliotti, L., Mazzei, F., Ozouf-Costaz, C., Bonillo, C., Williams, R., Cheng, C. H. C. & Pisano, E.
   (2007). The two giant sister species of the Southern Ocean, *Dissostichus eleginoides* and *Dissostichus mawsoni*, differ in karyotype and chromosomal pattern of ribosomal RNA genes. *Polar Biology*, 30, 625-634.
- Gillanders, B. M. (2002). Temporal and spatial variability in elemental composition of otoliths: Implications for determining stock identity and connectivity of populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 669-679.
- Gilman, S. E. (2006). The northern geographic range limit of the intertidal limpet *Collisella scabra*: a test of performance, recruitment, and temperature hypotheses. *Ecography*, 29, 709-720.

- Goldberg, E. & Lande, R. (2007). Species' borders and dispersal barriers. *American Naturalist, The,* 170, 297-304.
- Goldsworthy, S. D., Lewis, M., Williams, R., He, X., Young, J. W. & Van Den Hoff, J. (2002). Diet of Patagonian toothfish (*Dissostichus eleginoides*) around Macquarie Island, South Pacific Ocean. *Marine and Freshwater Research*, 53, 49-57.
- Gon, O. & Heemstra, P. (1990). *Fishes of the Southern Ocean,* Grahamstown, South Africa, J.L.B. Smith Institute of Ichthyology.
- Goodell, H. G. (1964). Marine geology of the Drake Passage, Scotia Sea, and South Sandwich Trench. *Sedimentology Research Laboratory Contribution*, 7. 277 pp. Department of Geology, Florida State University, Tallahassee.
- Gotthard, K. & Nylin, S. (1995). Adaptive plasticity and plasticity as an adaptation a selective review of plasticity in animal morphology and life-history. *Oikos*, 74, 3-17.
- Grant, S., Constable, A., Raymond, B. & Doust, S. (2006). Bioregionalisation of the Southern Ocean: Report of experts workshop. Hobart: WWF-Australia and ACE CRC.
- Griffiths, H. & Linse, K. (2009). Towards a generalized biogeography of the Southern Ocean benthos. *Journal of Biogeography*, 36, 162-177.
- Griffiths, H. J., Linse, K. & Barnes, D. K. A. (2008). Distribution of macrobenthic taxa across the scotia arc, Southern Ocean. *Antarctic Science*, 20, 213-226.
- GSGSSI (2009). Vessel guidelines for research fishing in 48.4. CCAMLR season 2008/09. Government South Georgia & South Sandwich Islands, UK.
- Guisan, A. & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135, 147-186.
- Hall, A. & Visbeck, M. (2002). Synchronous variability in the Southern Hemisphere atmosphere, sea ice, and ocean resulting from the annular mode. *Journal of Climate*, 15, 3043-3057.
- Hanchet, S. M. (2006). Species profile for Antarctic toothfish (*Dissostichus mawsoni*). *CCAMLR WG-FSA*, 06/26, CCAMLR, Hobart, Australia.

- Hanchet, S. M. (2009). A characterisation of the toothfish fishery in Subareas 88.1 and 88.2 from 1997/98 to 2008/09. CCAMLR WG-FSA, 09/36, CCAMLR, Hobart, Australia.
- Hanchet, S. M., Rickard, G. J., Fenaughty, J. M., Dunn, A. & Williams, M. J. H. (2008). A hypothetical life cycle for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region. *CCAMLR Science*, 15, 35-53.
- Hargrove, W. W. & Hoffman, F. M. (1999). Using multivariate clustering to characterize ecoregion borders. *Computing in science & engineering*, **1**, 18-25.
- Hart, P. J. B. & Reynolds, J. D. (2002). *Handbook of fish biology and fisheries* Oxford, Blackwell Publishing.
- Hersteinsson, P. & Macdonald, D. W. (1992). Interspecific competition and the geographicaldistribution of red and arctic foxes *Vulpes-vulpes* and *Alopex-lagopus*. *Oikos*, 64, 505-515.
- Hilborn, R. (1990). Determination of fish movement patterns from tag recoveries using maximum-likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences*, 47, 635-643.
- Hillary, R. M., Kirkwood, G. P. & Agnew, D. J. (2006). An assessment of toothfish in Subarea 48.3 using CASAL. *CCAMLR Science*, 13, 65-95.
- Hobday, A. & Hartmann, K. (2006). Near real-time spatial management based on habitat predictions for a longline bycatch species. *Fisheries Management and Ecology*, 13, 365-380.
- Hoff, J. (2004). A comparative study of the cephalopod prey of Patagonian toothfish (*Dissostichus eleginoides*) and southern elephant seals (*Mirounga leonina*) near Macquarie Island. *Polar biology*, 27, 604-612.
- Holdgate, M. W. & Baker, P. E. (1979). The South Sandwich Islands: I. General description. British Antarctic Survey Scientific Reports. British Antarctic Survey, Cambridge, UK.

- Horn, P. L. (2002). Age and growth of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D-mawsoni*) in waters from the New Zealand Subantarctic to the Ross Sea, Antarctica. *Fisheries Research*, 56, 275-287.
- Hutchings, J., Swain, D., Rowe, S., Eddington, J., Puvanendran, V. & Brown, J. (2007). Genetic variation in life-history reaction norms in a marine fish. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1693-1699.
- Imsland, A., Foss, A., Sparboe, L. & Sigurdsson, S. (2006). The effect of temperature and fish size on growth and feed efficiency ratio of juvenile spotted wolffish *Anarhichas minor. Journal of Fish Biology*, 68, 1107-1122.
- Japp, D. & Wilkinson, S. (2006). Deep-sea resources and fisheries. *Report and documentation* of the expert consultation on deep-sea fisheries in the high-seas. Bangkok, Thailand.
- Jonassen, T. M., Imsland, A. K. & Stefansson, S. O. (1999). The interaction of temperature and fish size on growth of juvenile halibut. *Journal of Fish Biology*, 54, 556-572.
- Kaiser, S., Barnes, D. K. A., Linse, K. & Brandt, A. (2008). Epibenthic macrofauna associated with the shelf and slope of a young and isolated Southern Ocean island. *Antarctic Science*, 20, 281-290.
- Kalish, J. M. & Timmiss, T. A. (1998). Determination of Patagonian toothfish (*Dissostichus eleginoides*) age, growth and population characteristics based on otoliths. *CCAMLR WG-FSA*, 98/40, CCAMLR, Hobart, Australia.
- Katsanevakis, S., Maravelias, C., Damalas, D., Karageorgis, A., Tsitsika, E. & Anagnostou, C. (2009). Spatiotemporal distribution and habitat use of commercial demersal species in the eastern Mediterranean sea. *Fisheries Oceanography*, 18, 439-457.
- Kaufman, D. M. (1998). The structure of mammalian faunas in the new world: From continents to communities., Univ. of New Mexico.
- Kilpatrick, R., Ewing, G., Lamb, T., Welsford, D. & Constable, A. (2011). Autonomous video camera system for monitoring impacts to benthic habitats from demersal fishing gear, including longlines. *Deep-sea Research. Part 1. Oceanographic Research Papers*, 58, 486-491.

- King, N. J., Bagley, P. M. & Priede, I. G. (2006). Depth zonation and latitudinal distribution of deep-sea scavenging demersal fishes of the mid-Atlantic ridge, 42 to 53 degrees N. *Marine Ecology Progress Series*, 319, 263-274.
- Kiss, A. J., Mirarefri, A. Y., Ramakrishnan, S., Zukoski, C. F., Cheng, C. H. C. & Devries, A. L.
   (2004). Characterisation of the eye lens crystallins from the Antarctic toothfish, Dissostichus mawsoni. Investigative Ophthalmology & Visual Science, 45, 3968.
- Klinkhammer, G., Rona, P., Greaves, M. & Elderfield, H. (1985). Hydrothermal manganese plumes in the mid-Atlantic ridge rift valley. *Nature*, 314, 727-731.
- Kock, K. H. (1992). Antarctic fish and fisheries, Cambridge University Press, Cambridge, UK.
- Kuhn, K. L. & Gaffney, P. M. (2008). Population subdivision in the Antarctic toothfish (*Dissostichus mawsoni*) revealed by mitochondrial and nuclear single nucleotide polymorphisms (snps). *Antarctic Science*, 20, 327-338.
- Laptikhovsky, V., Arkhipkin, A. & Brickle, P. (2008). Life history, fishery, and stock conservation of the Patagonian toothfish around the Falkland Islands. *Reconciling Fisheries with Conservation, Vols I and II,* 49, 1357-1363.
- Laptikhovsky, V. & Brickle, P. (2005). The Patagonian toothfish fishery in Falkland Islands' waters. *Fisheries Research*, 74, 11-23.
- Last, P., White, W., Gledhill, D., Pogonoski, J. & Lyne, V. (2011). Biogeographical structure and affinities of the marine demersal ichthyofauna of Australia. *Journal of Biogeography*, 38, 1484-1496.
- Leat, P., Tate, A., Tappin, D., Day, S. & Owen, M. (2010). Growth and mass wasting of volcanic centers in the northern South Sandwich Arc, South Atlantic, revealed by new multibeam mapping. *Marine Geology*, 275, 110-126.
- Leggett, W. C. & Frank, K. T. (1997). A comparative analysis of recruitment variability in North Atlantic flatfishes -- testing the species range hypothesis. *Journal of Sea Research*, 37, 281-299.

Linse, K., Brandt, A., Bohn, J. M., Danis, B., De Broyer, C., Ebbe, B., Heterier, V., Janussen, D., Gonzalez, P. J. L., Schuller, M., Schwabe, E. & Thomson, M. R. A. (2007). Macro- and megabenthic assemblages in the bathyal and abyssal Weddell Sea (Southern Ocean). Deep-Sea Research Part II-Topical Studies in Oceanography, 54, 1848-1863.

Longhurst, A. (1998). *Ecological geography of the sea*, San Diego, Academic Press.

- Lopez Abellan, L. J. & Balguerias, E. (1994). On the presence of *Paralomis spinosissima* and *Paralomis formosa* in catches taken during the Spanish survey ANTARTIDA 8611. *CCAMLR Science*, 1, 165-173.
- Lord, C., Duhamel, G. & Pruvost, P. (2006). The Patagonian toothfish (*Dissostichus eleginoides*) fishery in the Kerguelen Islands (indian Ocean sector of the Southern Ocean). *CCAMLR Science*, 13, 1-25.
- Lourie, S. A. & Vincent, A. C. J. (2004). Using biogeography to help set priorities in marine conservation. *Conservation Biology*, 18, 1004–1020.
- Macarthur, R. H. (1972). *Geographical ecology: Patterns in the distribution of species,* New Jersey, Princeton University Press.
- Malyutina, M. (2004). Russian deep-sea investigations of Antarctic fauna. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 51, 1551-1570.
- Maunder, M. & Punt, A. (2004). Standardizing catch and effort data: A review of recent approaches. *Fisheries Research*, 70, 141-159.
- Maunder, M. N., Sibert, J. R., Fonteneau, A., Hampton, J., Kleiber, P. & Harley, S. J. (2006). Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES Journal of Marine Science: Journal du Conseil*, 63, 1373-1385.
- Mckenna, J. (1991). Trophic relationships within the Antarctic demersal fish community of South Georgia island. *Fishery Bulletin*, 89, 643-654.
- Mckinlay, J. P., Welsford, D. C., Constable, A. J. & Nowara, G. B. (2008). An assessment of the exploratory fishery for *Dissostichus* spp. On BANZARE bank (CCAMLR division 58.4.3b) based on fine-scale catch and effort data. *CCAMLR Science*, 15, 55-78.

- Murphy, E. J., Watkins, J. L., Trathan, P. N., Reid, K., Meredith, M. P., Thorpe, S. E., Johnston, N. M., Clarke, A., Tarling, G. A., Collins, M. A., Forcada, J., Shreeve, R. S., Atkinson, A., Korb, R., Whitehouse, M. J., Ward, P., Rodhouse, P. G., Enderlein, P., Hirst, A. G., Martin, A. R., Hill, S. L., Staniland, I. J., Pond, D. W., Briggs, D. R., Cunningham, N. J. & Fleming, A. H. (2007). Spatial and temporal operation of the Scotia Sea ecosystem: A review of large-scale links in a krill centred food web. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362, 113-148.
- Myers, R. A. (2001). Stock and recruitment: Generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES Journal of Marine Science*, 58, 937-951.
- Near, T. J. (2004). Estimating divergence times of notothenioid fishes using a fossil-calibrated molecular clock. *Antarctic Science*, 16, 37-44.
- Nicol, S., Pauly, T., Bindoff, N. L., Wright, S., Thiele, D., Hosie, G. W., Strutton, P. G. & Woehler, E. (2000). Ocean circulation off East Antarctica affects ecosystem structure and sea-ice extent. *Nature*, 406, 504-507.
- Nishida, T. & Chen, D. (2004). Incorporating spatial autocorrelation into the general linear model with an application to the yellowfin tuna (*Thunnus albacares*) longline CPUE data. *Fisheries Research*, 70, 265-274.
- North, A. W. (2002). Larval and juvenile distribution and growth of Patagonian toothfish around South Georgia. *Antarctic Science*, 14, 25-31.
- O'hara, T. D., Rowden, A. A. & Bax, N. J. (2011). A Southern Hemisphere bathyal fauna is distributed in latitudinal bands. *Current biology*, 21, 226-230.
- Oksanen, J. F., Blanchet, G. & Kindt, R. (2011). *vegan: Community Ecology Package,* version 2.0-0. ed.
- Orsi, A., Nowlin, W. & Whitworth, T. (1993). On the circulation and stratification of the Weddell Gyre. *Deep-sea Research. Part I, Oceanographic Research Papers,* 40, 169-203.

- Orsi, A., Whitworth, T. & Nowlin, W. (1995). On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-sea research. Part I, Oceanographic research papers,* 42, 641-673.
- Ospar (2008). Descriptions of habitats on the OSPAR list of threatened and/or declining species and habitats. OSPAR, London, UK.
- Parmesan, C., Gaines, S., Gonzalez, L., Kaufman, D. M., Kingsolver, J., Townsend Peterson, A.
  & Sagarin, R. (2005). Empirical perspectives on species borders: From traditional biogeography to global change. *Oikos*, 108, 58-75.
- Pawson, M. G. (1995). Biogeographical identification of English Channel fish and shellfish stocks. *Fisheries Research Technical Report.*
- Payne, A. & Agnew, D. J. (2006). Results of the tagging experiment for *D. eleginoides* in Subarea 48.4. *CCAMLR WG-FSA*, 06/56, CCAMLR, Hobart, Australia.
- Peatman, T., Mitchell, R. E., G., P. & Agnew D. J. (2011). Preliminary assessment of toothfish in Subarea 48.3. *CCAMLR WG-FSA*, 11/33, CCAMLR, Hobart, Australia.
- Pedersen, T. & Jobling, M. (1989). Growth rates of large, sexually mature cod *Gadus morhua*, in relation to condition and temperature during an annual cycle. *Aquaculture*, 81, 161-168.
- Perissinotto, R., Laubscher, R. & Mcquaid, C. (1992). Marine productivity enhancement around Bouvet and the South Sandwich Islands (Southern-Ocean). *Marine Ecology Progress Series*, 88, 41-53.
- Philippart, C. J. M., Henderson, P. A., Johannessen, T., Rijnsdorp, A. D. & Rogers, S. I. (1998).
   Latitudinal variation in fish recruits in northwest Europe. *Journal of Sea Research*, 39, 69-77.
- Phillips, S. J., Anderson, R. P. & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological modelling*, 190, 231-259.

- Pilling, G. M., Purves, M. G., Daw, T. M., Agnew, D. A. & Xavier, J. C. (2001). The stomach contents of Patagonian toothfish around South Georgia (south Atlantic). *Journal of Fish Biology*, 59, 1370-1384.
- Priede, I. G., Godbold, J. A., King, N. J., Collins, M. A., Bailey, D. M. & Gordon, J. D. M. (2010).
   Deep-sea demersal fish species richness in the porcupine seabight, NE Atlantic ocean: Global and regional patterns. *Marine Ecology*, 31, 247-260.
- Pulliam, H. & Danielson, B. (1991). Sources, sinks, and habitat selection a landscape perspective on population-dynamics. *American Naturalist, The,* 137, S50-S66.
- Punt, A. & Smith, D. (2011). Among-stock comparisons for improving stock assessments of data-poor stocks: The "Robin Hood" approach. *ICES Journal of Marine Science*, 68, 972-981.
- Pusey, A. E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution, 2*, 295-299.
- Ramos, A. (1999). The megazoobenthos of the Scotia Arc Islands. *Scientia Marina*, 63, 171-182.
- Rex, M. A., Etter, R. J., Morris, J. S., Crouse, J., Mcclain, C. R., Johnson, N. A., Stuart, C. T., Deming, J. W., Thies, R. & Avery, R. (2006). Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Marine Ecology-Progress Series*, 317, 1-8.
- Reygondeau, G., Maury, O., Gregory, B., Fromentin, J., Fontenau, A. & Cury, P. (2011). Biogeography of tuna and billfish communities. *Journal of Biogeography*, 39, 114-129.
- Roberts, J. & Agnew, D. J. (2009a). Assessment of Patagonian toothfish population in the north of Subarea 48.4 using data from a four-year tagging experiment. *CCAMLR WG-FSA*, 09/17, CCAMLR, Hobart, Australia.
- Roberts, J. & Agnew, D. J. (2009b). Proposal for an extension to the mark recapture experiment to estimate toothfish population size in the south of Subarea 48.4. *CCAMLR WG-FSA*, 09/18, CCAMLR, Hobart, Australia.

- Roberts, J., Mitchell, R. & Wakeford, R. (2011). Population assessment of Patagonian toothfish in Subarea 48.4 2011 update. *CCAMLR WG-FSA*, 11/38, CCAMLR, Hobart, Australia.
- Roberts, J., Xavier, J. C. & Agnew, D. J. (2011). The diet of toothfish species *Dissostichus* eleginoides and *Dissostichus* mawsoni with overlapping distributions. *Journal of Fish Biology*, 79, 138-154.
- Roff, D. A. (2000). Trade-offs between growth and reproduction: An analysis of the quantitative genetic evidence. *Journal of Evolutionary Biology*, **13**, 434-445.
- Rogers, A. D., Morley, S., Fitzcharles, E., Jarvis, K. & Belchier, M. (2006). Genetic structure of Patagonian toothfish (*Dissostichus eleginoides*) populations on the Patagonian shelf and Atlantic and western Indian Ocean sectors of the Southern Ocean. *Marine Biology*, 149, 915-924.
- Rubilar, P. S., Moreno, C. A., Ashford, J. R. & Everson, I. (1993). An exploratory fishing expedition for *Dissostichus eleginoides* around the South Sandwich Islands, Antarctica. SC-CAMLR-XII/BG/4, CCAMLR, Hobart, Australia.
- Sagarin, R. D. & Gaines, S. D. (2002). The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters*, 5, 137-147.
- Schlitzer, R. (2006). *Ocean data view* [Online]. Available: <u>http://odv.awi.de/</u> [Accessed Feb 2011].
- Seber, G. A. F. (1982). The estimation of animal abundance, London, UK, Griffin.
- Sexton, J., Mcintyre, P., Angert, A. & Rice, K. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics,* 40, 415-436.
- Sexton, O. J., Andrews, R. M. & Bramble, J. E. (1992). Size and growth-rate characteristics of a peripheral-population of *Crotaphytus-collaris* (*sauria, crotaphytidae*). *Copeia*, 968-980.
- Shaw, P. W., Arkhipkin, A. I. & Al Khairulla, H. (2004). Genetic structuring of Patagonian toothfish populations in the southwest Atlantic ocean: The effect of the Antarctic

polar front and deep-water troughs as barriers to genetic exchange. *Molecular Ecology*, 13, 3293-3303.

- Spellerberg, I. F. & Sawyer, J. W. D. (1999). *An introduction to applied biogeography.* Cambridge University Press, Cambridge, UK.
- Stammerjohn, S. E., Martinson, D. G., Smith, R. C., Yuan, X. & Rind, D. (2008). Trends in Antarctic annual sea ice retreat and advance and their relation to El niño & southern oscillation and southern annular mode variability. *J. Geophys. Res.*, 113, C03S90.
- Stearns, S. (2000). Life history evolution: Successes, limitations, and prospects. *Naturwissenschaften*, 87, 476-486.
- Stefansdottir, L., Solmundsson, J., Marteinsdottir, G., Kristinsson, K. & Jonasson, J. (2010). Groundfish species diversity and assemblage structure in Icelandic waters during recent years of warming. *Fisheries Oceanography*, 19, 42-62.
- Stevenson, M. L., Hanchet, S. M. & Dunn, A. (2008). A characterisation of the toothfish fishery in Subareas 88.1 and 88.2 from 1997/98 to 2007/08. CCAMLR WG-FSA, 08/22, 1-20.
- Taylor, C. C. (1958). Cod growth and temperature. *Journal du Conseil*, 23, 366-370.
- R Core Development Team (2011). *R: A language and environment for statistical computing,* Vienna, Austria, R Foundation for Statistical Computing.
- Thomas, C. D., Bodsworth, E. J., Wilson, R. J., Simmons, A. D., Davies, Z. G., Musche, M. & Conradt, L. (2001). Ecological and evolutionary processes at expanding range margins. *Nature*, 411, 577-581.
- Trathan, P. N. & Agnew, D. (2010). Climate change and the antarctic marine ecosystem: an essay on management implications. *Antarctic Science*, 22, 387-398.
- Ungerer, M. J., Ayres, M. P. & Lombardero, M. J. (1999). Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (*coleoptera* : *Scolytidae*). *Journal of Biogeography*, 26, 1133-1145.

- Vaughan, D., Marshall, G., Connolley, W., Parkinson, C., Mulvaney, R. & Hodgson, D. (2003).
   Recent rapid regional climate warming on the Antarctic Peninsula. *Climatic change*, 60, 243-274.
- Venables, W. & Dichmont, C. (2004). GLMs, GAMs and GLMMs: An overview of theory for applications in fisheries research. *Fisheries Research*, 70, 319-337.
- Watanabe, Y. (2007). Latitudinal variation in the recruitment dynamics of small pelagic fishes in the western North Pacific. *Journal of Sea Research*, 58, 46-58.
- Welsford, D. C., Candy, S., Lamb, T., Nowara, G. B., Constable, A. & Williams, A. (2011).
  Habitat use by Patagonian toothfish (*Dissostichus eleginoides* Smitt 1898) on the Kerguelen Plateau around Heard Island and the McDonald Islands. *In:* Duhamel, G. & Welsford, D. C. (eds.) *The Kerguelen Plateau: Marine ecosystem and fisheries.* Paris: Société Française d'Ichtyologie.
- WG-FSA-CAMLR (2011). Fishery report: Dissostichus eleginoides South Georgia (Subarea 48.3). In: SC-CAMLR Report on the working group on fish stock assessment, appendix N. CCAMLR, Hobart, Australia.
- Whitworth, T., Nowlin, W., Orsi, A., Locarnini, R. & Smith, S. (1994). Weddell Sea shelf water in the Bransfield Strait and Weddell-Scotia Confluence. *Deep-sea Research. Part I, Oceanographic Research Papers,* 41, 629-641.
- Williams, R. & Mceldowney, A. (1990). A guide to the fish otoliths from waters off the Australian Antarctic Territory, Heard and Macquarie island. ANARE Research Notes, 1.
- Williams, R., Tuck, G. N., Constable, A. J. & Lamb, T. (2002). Movement, growth and available abundance to the fishery of *Dissostichus eleginoides* Smitt, 1898 at Heard Island, derived from tagging experiments. *CCAMLR Science*, 9, 33-48.
- Wöhrmann, A. P. A. (1996). Antifreeze glycopeptides and peptides in Antarctic fish species from the Weddell Sea and the Lazarev Sea. *Marine Ecology Progress Series*, 130, 47-59.

 Xavier, J. C., Rodhouse, P. G., Purves, M. G., Daw, T. M., Arata, J. & Pilling, G. M. (2002).
 Distribution of cephalopods recorded in the diet of the Patagonian toothfish (*Dissostichus eleginoides*) around South Georgia. *Polar biology*, 25, 323-330. Appendices

# **Appendix A**





Figure A2.1 Proportion of benthos sampling effort by South Sandwich Islands seafloor area and season (left) and at depth for different seafloor areas; "SG West" = South Georgia west of  $39.5^{\circ}$ W; "SG North" = north of  $54.5^{\circ}$ S; "SG South" = south of  $54.5^{\circ}$ S; "Ross Sea North" = North of  $65^{\circ}$ S; "Ross Sea Central" = from  $65^{\circ}$ S to  $70^{\circ}$ S; "Ross Sea South" = South of  $70^{\circ}$ S; "Ross Sea West" = west of  $160^{\circ}$ W) (right).

		CPUE (count per million hooks observed)								
Phylum	Taxon	South Sandwich Islands	South Georgia	Ross Sea						
Porifera										
	Unkown poriferan sp.	15	43	11						
Cnidaria										
	Gorgoniidae	78	744	132						
	Alcyonacea	27	78	2						
	Scleractinia	0	85	24						
	Anthipatharia	1	20	0						
	Hydroida	6	234	0						
	Actiniaria	343	60	86						
	Unkown cnidarian sp.	35	162	0						
Bryozoa										
	Unknown bryozoan	3	0	0						
Echinode	rmata									
	Crinoidea	4	8	6						
	Holothuroidea	5	219	5						
	Echinoidea	3	10	1						
	Asteroidea	574	59	1,524						
	Ophiuroidea	264	83	143						
	Unkown echinoderm sp.	10	8	36						
Arthropod	la									
	Lithodidae	147	320	19						
	Pycnogonidae	2	1	2						
Annelida										
	Unknown annelid	2	34	0						
Mollusca										
	Octopodidae	1	0	4						
Ascidiace	ae									
	Unknown ascidiaceae sp.	5	14	0						
Unknown	invertebrate	13	8	0						
Sampling	effort (million hooks)	1.28	16.49	4.05						

Table A2.1 Table catch composition benthos taxa; CPUE – numbers per million hooks.

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Figure A2.2 Catch rates of suspension feeding benthic fauna at South Georgia, the South Sandwich Islands and the Ross Sea.



Figure A2.3 Catch rates of mobile fauna at South Georgia, the South Sandwich Islands and the Ross Sea.



Figure A2.4 Depth effects on the CPUE of sedentary and mobile invertebrates, comparing Northern and Southern areas of the Sandwich Islands. Asterisks indicate that no effort was expended in this depth range/area combination.



Figure A2.5 Inter-annual variation in extent of sea ice formation in September – position of 15% sea ice concentration from 1986 to 1995. Mean position of 15 % ice cover in bold; mean cover between 5 and 15 % shaded in light blue. Data source – ISLSCP II Global Sea Ice Concentration (Armstrong and Knowles 2010).

	Season												
Vessel	2004/05	2005/06	2006/07	2007/08	2008/09	2009/10							
1	0	0	0	62	0	120							
2	0	0	0	0	97	0							
3	22	30	24	0	0	0							
4	0	40	56	40	94	62							

Table A3.1 South Sandwich Islands fishery observations: number of lines set by vessel and fishing season

Table A3.2 South Sandwich Islands fishery observations: number of lines set by vessel and latitude

	Degrees latitude												
	-59.5	-59.5 -59 to58.5 -58 to -57.5 to -57 to -56.5 to -56 to											
Vessel	to -60	59.5	to -59	-58.5	-58	-57.5	-57	-56.5	-56				
1	57	12	16	6	41	9	27	9	5				
2	29	10	13	0	11	2	15	10	7				
3	47	25	4	0	0	0	0	0	0				
4	108	43	23	20	29	16	27	13	13				

Table A3.3 Ross Sea fishery observations: number of lines set by vessel and fishing season

	Season											
Vessel	2003/04	2004/05	2005/06	2006/07	2007/08	2008/09	2009/10					
1	0	0	0	0	146	141	166					
2	0	0	85	132	79	143	68					
3	35	141	117	161	131	161	0					

Table A3.4 Ross Sea fishery observations: number of lines set by vessel and latitude

	Degrees latitude												
	-76 to74 to72 to70 to68 to66 to64 to62 to												
Vessel	78	76	74	72	70	68	66	64					
1	0	169	37	41	138	47	21	0					
2	31	21	95	112	126	49	73	0					
3	18	203	129	163	78	23	118	14					

Table A3.5 Correlation matrix between explanatory variables used to predict *D. eleginoides* catch rates at the South Sandwich Islands.

					COR			
Variable	coak	donth	lon	temp.50m.	temp.1050m	temp.50m.	temp.1050m.	ico %
	SOUK	ueptii	1011	sep	. sep	feb	feb	<i>ICE.7</i> 0
soak.bin	1.000							
depth.bin	0.115	1.000						
lon.bin	-0.084	-0.190	1.000					
temp.50m.sep.bin	-0.045	-0.121	0.827	1.000				
temp.1050m.sep.bin	-0.065	-0.471	0.635	0.771	1.000			
temp.50m.feb.bin	-0.026	-0.072	0.706	0.960	0.756	1.000		
temp.1050m.feb.bin	-0.068	-0.538	0.690	0.801	0.933	0.782	1.000	
ice.%.bin	0.046	0.144	-0.796	-0.967	-0.810	-0.962	-0.838	1.000

Table A4.1 Gonad Maturity Index descriptions used to identify maturity stage of *Dissostichus* species.

Code	Female	Male
1	Immature. Ovary small, firm, no eggs visible to the naked eye	Immature. Testis small, translucent, whitish, long, thin strips lying close to the vertebral column.
2	Maturing virgin or resting. Ovary more extended, firm, small oocytes visible, giving ovary a grainy appearance.	Developing or resting. Testis white, flat, convoluted, easily visible to the naked eye, about 1/4 length of the body cavity.
3	Developing. Ovary large, starting to swell the body cavity, colour varies according to species, contains oocytes of two sizes.	Developed. Testis large, opalescent white and convoluted, no milt produced when pressed or cut.
4	Gravid. Ovary large, filling or swelling the body cavity, when opened large ova spill out.	Ripe. Testis large, pure white, drops of milt produced when pressed or cut.
5	Spent. Ovary shrunk, flaccid, contains a few residual eggs and many small ova.	Spent. Testis shrunk, flabby, dirty white in colour.



Figure A4.1 Size distribution of age validation sample of D. eleginoides captured in 2009, compared with catch size distribution in the same season

Table A4.2 Distribution of annuli counts for *D. eleginoides* captured at the South Sandwich Islands in 2009, aggregated in to 5cm length bins

Length																Anı	nuli															
bin (cm)	Unsuccessful	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	Sample
61-65		2	2																													4
66-70		1																														1
71-75		1	1	2	2	1																										7
76-80	1		1	2				1																								5
81-85				2	1	2																										5
86-90	1		1		1				2																							5
91-95															1																	1
96-100							1				2	2	1	1																		7
101-105	1					1			1		3	1	4	2																		13
106-110	1				1						6	6	9	1		1																25
111-115	2						1		2	3	5	6	12	1	1																	33
116-120	4						1		1	1	5	9	9	1		1																32
121-125	1						1	1			2	6	7				1	1	1		1											22
126-130	1									1		7	5	1	2		1		1													19
131-135												1	1	1	3	1										1						8
136-140	1												2	1		1	1		1								1					8
141-145	2															1		1				1		1								6
146-150															1		1	2	1													5
151-155																		1			1				2							4
156-160																			3	1								1				5
161-165																							1			1						2
166-170																																0
171-175																																0
176-180																																0
181-185																															1	1
1	15	4	5	6	5	4	4	2	6	5	23	38	50	9	8	5	4	5	7	1	2	1	1	1	2	2	1	1	0	0	1	218

Table A4.3 Von Bertalanffy growth parameters estimates for different populations of *D. eleginoides*.

Population	L <sub>inf</sub>	k	t <sub>o</sub>	Reference
South Sandwich Islands Male	148.8	0.0832	-0.30*	This study
South Sandwich Islands Female	187.0	0.0566	-0.30*	This study
South Sandwich Islands All	180.2	0.0599	-0.30*	This study
South Georgia All	132.0	0.0790	-0.30	CCAMLR, 2009
Patagonian shelf Male	120.7	0.1300	-1.55	Ashford, 2001
Patagonian shelf Female	141.4	0.1500	-1.10	Ashford, 2001
South Chile Male	195.6	0.0742	-0.72	Young et al., 1992
South Chile Female	209.7	0.0641	-1.15	Young et al., 1992

\* Constrained value



Figure A5.1 Distribution of otolith LA-ICP-MS sampling by area of capture/haplotype groupings: (clockwise from top-left) estimated age distribution of fish sampled; age distribution of crater locations; and c) mean depth of capture.

Table A5.1 Power transformations applied to achieve univariate normality of elemental variables

Elemental ratio	Sr:Ca	Ba:Ca	Mg:Ca	Mn:Ca	Na:Ca	Li:Ca
Mixed effect modelling	0.19	0.10	-1.60	0.62	0.34	-0.32
Multivariate modelling (pre-recruitment)	-0.88	-0.20	N/A	0.31	N/A	N/A
Multivariate modelling (post-recruitment)	0.85	-0.14	N/A	0.62	N/A	N/A



Figure A5.2 Q-Q plots for power transformed otolith elemental ratios to calcium



Figure A5.3 Otolith microchemistry (Element:Ca) in response to age. Lines represent mean and 95% confidence intervals predicted by mixed effects models (continued on next page).



Figure A5.3 (continued) Otolith microchemistry (Element:Ca) in response to age. Lines represent mean and 95% confidence intervals predicted by mixed effects models.



Figure A5.4 *Q*-*Q* plot for assessing multivariate normality of Sr, Ba and Mn ratios to Ca at pre (left) and post-recruitment ages (right).



Distance of recapture from point of release

Figure A5.5 Distance of point of recapture from point of release of toothfish species at the South Sandwich Islands and South Georgia from 2005 to 2010. This includes 7 D. eleginoides that migrated to from South Georgia to the South Sandwich Islands.

Table A5.2 Estimated annual migration rates of *D. eleginoides* between the South Sandwich Islands to SouthGeorgia from mark recapture data

		SSIs to	o SG			SSIs to	o SG	
Grouping	Tag years	Median	Lower Cl	Upper Cl	Tag years	Median	Lower CI	Upper Cl
Mixed sex	All	0.089	0.040	0.200	All	0.00000	0.00000	0.00145
	2005	0.000	0.000	0.960				
	2006	0.434	0.070	0.740				
	2007	0.118	0.040	0.410				
	2008	0.000	0.000	0.130				
	2009	0.216	0.060	0.750				
Females	All	0.018	0	0.11				
	2005	0.000	0.000	0.960				
	2006	0.000	0.000	0.920				
	2007	0.068	0.020	0.870				
	2008	0.000	0.000	0.190				
	2009	0.000	0.000	0.560				
Males	All	0.241	0.100	0.500				
	2005	0.000	0.000	0.970				
	2006	0.489	0.120	0.730				
	2007	0.172	0.050	0.520				
	2008	0.000	0.000	0.710				
	2009	0.708	0.170	0.980				



Figure A5.6 Probability of zero *D. eleginoides* tag recaptures from South Georgia to the South Sandwich Islands given different migration rates (top) and with different tag release years (bottom).

### **Appendix B**

## **CASAL** population assessment input files

#### population.csl

**#INITIALSATION** 

@initialization B0 2000 **# PARTITION** @size\_based False @min\_age 1 @max\_age 50 @plus\_group True @sex\_partition True @mature\_partition False @n\_areas 1 @n\_stocks 1 @n\_tags 6 @tag names 2005Tags 2006Tags 2007Tags 2008Tags 2009Tags 2010Tags @tag\_shedding\_rate 0.0064 0.0064 0.0064 0.0064 0.0064 0.0064 # changed from 0.0036 after Candy SAM 2011 @tag loss props 0.4166667 0.3333333 0.25 0.0 @tag\_growth\_loss 2005Tags nogrowth\_period 0.5 # if tagged no growth for 1/2 year @tag\_growth\_loss 2006Tags nogrowth\_period 0.5 # if tagged no growth for 1/2 year @tag\_growth\_loss 2007Tags nogrowth\_period 0.5 # if tagged no growth for 1/2 year @tag\_growth\_loss 2008Tags nogrowth\_period 0.5 # if tagged no growth for 1/2 year @tag\_growth\_loss 2009Tags nogrowth\_period 0.5 # if tagged no growth for 1/2 year @tag growth loss 2010Tags nogrowth\_period 0.5 # if tagged no growth for 1/2 year **# TIME SEQUENCE** @initial 1990 @current 2011 @final 2046 @annual\_cycle time steps 4 recruitment\_time 1 spawning\_time 2 spawning\_part\_mort 0.5 spawning ps 1.0 aging\_time 4 # Dec1 May1 Sep1 M\_props 0.4166667 0.3333333 0.25 0.0 growth\_props 0.4166667 0.75 1.0 0.0 baranov False fishery\_names FSSI FSSIlength fishery\_times 2 2 @y\_enter 1 @standardise\_YCS True @recruitment YCS\_years 1989 1990 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010

YCS SR BH steepness 0.75 sigma\_r 1.0 #altered from sigma\_r 0.6 first free 1989 last free 2002 p\_male 0.5 # 50% of 'recruits' are males **# RECRUITMENT VARIABILITY** @randomisation method lognormal @first\_random\_year 2003 #MATURATION @maturity\_props # from Tom Peatman sex disaggregated model 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23+ # age male allvalues\_bounded 1 23 0.000 0.000 0.000 0.000 0.000 0.200 0.485 0.550 1.000 0.615 0.680 0.745 0.810 0.875 0.940 1.000 1.000 1.000 1.000 1.000 1.000 1.000 1.000 female allvalues\_bounded 1 23 0.000 0.000 0.000 0.000 0.000 0.030 0.000 0.000 0.000 0.100 0.170 0.240 0.310 0.380 0.450 0.520 0.590 0.660 0.730 0.800 0.870 0.940 1.000 **# NATURAL MORTALITY** @natural\_mortality male 0.24 # 0.24 produces the lowest CV around B0 female 0.13 # 0.11 produced lowest CV around B0 # FISHING @fishery FSSI years 2005 2006 2007 2008 2009 2010 2011 catches 0 0 0 0 58.8 0 0 U max 0.999 selectivity SelSSI @fishery FSSIlength years 2005 2006 2007 2008 2009 2010 2011 catches 26.8 18.3 54.0 97.5 0 39.6 35.8 U\_max 0.999 selectivity SelSSI future\_years 2012 2013 2014 2015 2016 2017 2018 2019 2020 2021 2022 2023 2024 2025 2026 2027 2028 2029 2030 2031 2032 2033 2034 2035 2036 2037 2038 2039 2040 2041 2042 2043 2044 2045 2046 future\_catches 57 **# SELECTIVITIES** @n\_quant 15 @selectivity\_names SelSSI @selectivity SelSSI all double\_normal 8.63 1.17 9.79 # SIZE AT AGE @size\_at\_age\_type von\_Bert @size at age dist normal @size\_at\_age k\_male 0.083 t0 male -0.3 Linf\_male 149 cv\_male 0.1 k\_female 0.057 t0\_female -0.3

Linf\_female 187 cv\_female 0.1 **# SIZE-WEIGHT** @size\_weight a 2.71e-8 b 2.8 verify\_size\_weight 150 30 50 # 150 cm fish weighs between 30 and 50 kgs **# TAGGING OBSERVATIONS** @tag 2005Tags tag\_name 2005Tags release\_type deterministic sex both year 2005 step 2 mature\_only False number 42 plus\_group False class\_mins 50 60 70 80 90 100 110 120 130 140 150 160 170 props all 0 0 0.048 0.333 0.476 0.119 0.024 0 0 0 00 mortality 0.1 ogive SelSSI @tag 2006Tags tag\_name 2006Tags release\_type deterministic sex both year 2006 step 2 mature\_only False number 134 plus group False class\_mins 50 60 70 80 90 100 110 120 130 140 150 160 170 0.022 0.000 0.000 0.000 props\_all 0.007 0.104 0.045 0.134 0.396 0.239 0.022 0.022 mortality 0.1 ogive SelSSI @tag 2007Tags tag\_name 2007Tags release\_type deterministic sex both year 2007 step 2 mature\_only False number 291 plus\_group False class\_mins 50 60 70 80 90 100 110 120 130 140 150 160 170 0.079 0.048 0.082 0.299 0.261 0.127 props\_all 0.055 0.031 0.017 0.000 0.000 0.000 mortality 0.1 ogive SelSSI @tag 2008Tags tag\_name 2008Tags release\_type deterministic sex both year 2008 step 2 mature\_only False number 504 plus\_group False class\_mins 50 60 70 80 90 100 110 120 130 140 150 160 170 props\_all 0.016 0.075 0.067 0.046 0.190 0.444 0.143 0.014 0.004 0.000 0.000 0.000

mortality 0.1 ogive SelSSI @tag 2009Tags tag\_name 2009Tags release\_type deterministic sex both year 2009 step 2 mature only False number 344 plus\_group False class\_mins 50 60 70 80 90 100 110 120 130 140 150 160 170 props\_all 0.003 0.089 0.139 0.092 0.059 0.279 0.036 0.021 0.000 0.003 0.166 0.113 mortality 0.1 ogive SelSSI @tag 2010Tags tag\_name 2010Tags release\_type deterministic sex both year 2010 step 2 mature\_only False number 222 plus\_group False class\_mins 50 60 70 80 90 100 110 120 130 140 150 160 170 0.108 0.0405 0.2117 0.238 0.1441 0.0495 0.00900 0 props\_all 0 0.0495 0.144 0.0045 mortality 0.1 ogive SelSSI

#### estimation.csl

# ESTIMATION @estimator Bayes @max\_iters 1000 @max\_evals 4000 @grad\_tol 0.002

@MCMC start 0 length 1100000 keep 1000 adaptive\_stepsize True adapt\_at 100000 200000 burn\_in 100 proposal\_t True df 4

# ESTIMATION PROFILING @profile parameter initialization.B0 n 10 I 400 u 4000

@catch\_at FSSIlengthCatch years 2005 2006 2007 2008 2010 2011 fishery FSSIlength at\_size True sexed False sum\_to\_one True plus\_group False class\_mins 40 70 20 30 50 60 80 90 100 110 120 130 140 150 160 170 180 190 2005 0.005305 0.009284 0.035809 0.091512 0.351459 0.233422 0.098143 0.071618 0 0 0 0.059682 0.009284 0.022546 0.01061 0 0 0.000906 0.007246 0.020833 0.004529 0.041667 0.251812 0.336957 0.137681 0.068841 2006 0 0 0.059783 0.03442 0.016304 0.008152 0.005435 0 2007 0.003776 0.00944 0.011957 0.030837 0.175582 0.346759 0.213971 0.082442 0 0 0  $0.063562\ 0.040906\ 0.012587\ 0.004405\ 0.000629\ 0$  $0.000435\ 0.002173\ 0.009996\ 0.022599\ 0.021295\ 0.113864\ 0.3103 \qquad 0.274229\ 0.117775$ 2008 0 0  $0.061278\, 0.039983\, 0.017818\, 0.005215\, 0.001738\, 0$ 2010 0 0 0 0.000531362 0.018211773 0.040591526 0.033182196 0.038604153 0.140317938 0.295507138 0.227820293 0.10408517 0.060404634 0.026238453 0.012312789 0.001659266 0.00053331 2011 0.018333 0.056667 0.048333 0.021667 0.058333 0.195000 0.276667 0.183333 0.086667 000 0 0.038333 0.013333 0.001667 0.001667 # new data added for 2011 needs checking dist multinomial N 2005 73 # reweights N 2006 123 # reweights N 2007 144 # reweights N\_2008 121 # reweights #N 2009 199 # reweights N\_2010 163 # reweights N\_2011 86 # reweights r 1e-11 @catch at FSSICatch years 2009 fishery FSSI at size False sexed True sum\_to\_one True plus\_group False min class 1 1 # 1 for males and 1 for females max\_class 36 36 # 36 for males and 36 for females # groups M1 > > M36 then F1 > > F36 0.041666667 #2009 0 0 0.041666667 0 0 0 0 0 0.0625 0.020833333 0.020833333 0.041666667 0.020833333 0 0.145833333 0.270833333 0.166666667 0.083333333 0.020833333 0 0 0 0.041666667 0 0 0 0.020833333 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0.025974026 0.019480519 0.025974026 0.012987013 0.019480519 0.019480519 0.012987013 0.025974026 0.025974026 0.103896104 0.162337662 0.266233766 0.032467532 0.045454545 0.032467532 0.025974026 0.032467532 0.032467532 0.006493506 0.012987013 0.006493506 0.006493506 0.006493506 0.012987013 0.012987013 0 0.006493506 0 0 0.006493506 2009 0 0 Ω 0 0 0 0 0.00990099 0.00990099 0.014851485 0.004950495 0.004950495 0 0.00990099 0.004950495 0.034653465 0.01980198 0.064356436 0.039603961 0.004950495 0 0 0 0.00990099 0 0 0 0 0 0.004950495 0 0 0 0 0 0 0 0 0 0 0 0.01980198 0 0.01980198 0.00990099 0.00990099 0.014851485 0.014851485 0.014851485 0.01980198 0.01980198 0.079207921 0.123762377 0.202970298 0.024752475 0.034653465 0.024752475 0.01980198 0.024752475 0.024752475 0.004950495 0.00990099 0.004950495 0.004950495 0.004950495 0.00990099 0.00990099 0 0.004950495 0 0 0.004950495

```
dist multinomial
```

N\_2009 203# 48 154 # 48 males; 154 females (sum of otoliths sampled as an approximation) r 1e-11

**# RELATIVITY CONSTANTS** 

@q\_method nuisance

# AGEING ERROR @ageing\_error type normal c 0.1

@estimate parameter initialization.B0 lower\_bound 500 upper\_bound 5000 prior uniform-log phase 1

@estimate parameter size\_at\_age.k\_male lower\_bound 0.03 #changed from 0.05 upper\_bound 0.15 prior uniform phase 1

@estimate parameter size\_at\_age.k\_female lower\_bound 0.03 #changed from 0.05 upper\_bound 0.15 prior uniform phase 1

@estimate parameter size\_at\_age.Linf\_male lower\_bound 110 upper\_bound 250 prior uniform phase 1

@estimate
parameter size\_at\_age.Linf\_female
lower\_bound 110
upper\_bound 250
prior uniform
phase 1

@estimate
parameter size\_at\_age.t0\_male
lower\_bound -2
upper\_bound 0
prior uniform
phase 1

@estimate
parameter size\_at\_age.t0\_female
lower\_bound -2
upper\_bound 0
prior uniform
phase 1

@estimate parameter selectivity[SelSSI].all lower\_bound 1 0.05 0.05 upper\_bound 50 50 500 prior uniform phase 1
@estima	ite											
paramet	er recruitr	ment.YCS										
#YCS_yea	ars 198	9 1990 1	991 1992	1993 199	94 1995 1	1996 1997	7 1998 19	99 2000	2001 200	2 2003 2	004 2005	
2006 20	07 2008 2	2009 2010										
lower_bo	ound	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	
	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001 0.0	01 0.001	
upper_b	ound	20	20	20	20	20	20	20	20	20	20	20
	20	20	20	20	20	20	20	20	20 20 20	1		
prior log	normal											
mu	1	1	1	1	1	1	1	1	1	1	1	1
	1	1	1	1	1	1	1	111				
CV	1	1	1	1	1	1	1	1	1	1	1	1
	1	1	1	1	1	1	1	111				
phase 1												
@catch	limit pen	alty										
label cate	ch limit	-										
log scale	e False											
fishery FS	SSI											
, multiplie	r 100											
@catch	limit pen	alty										
label cate	ch limit	,										
log scale	e False											
fisherv F	SSIlength											
, multiplie	r 100											
@tag_re	capture 2	005Tags										
tag nam	e 2005Tag	25										
sample s	ize	J-										
detection	n probabi	lity 1										
vears 200	06 2007 2	008 2009	2010 2011									
step 2												
proportio	on mortal	lity 1.0										
nlus gro	un True											
class mi	ns 40 50	60 70 80	90 100 1	10 120 13	0 140 150	160 170 1	80					
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step 2
proportion mortality 1.0
plus group True
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detection_probability 1
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step 2
proportion_mortality 1.0
plus group True
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do_bootstrap True
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tag_name 2008Tags
sample size
detection probability 1
years 2009 2010 2011
step 2
proportion mortality 1.0
plus group True
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do bootstrap True
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dispersion 9
@tag_recapture 2009Tags
tag_name 2009Tags
sample size
detection probability 1
years 2010 2011
step 2
proportion mortality 1.0
plus group True
class_mins 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180
# includes one fish with no length measurement - allocated to 110cm - the modal tag length group in 2009
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        80.25529 26.28711 3.740748 1.643072
do_bootstrap True
r 1e-11
dispersion 9
@tag_recapture 2010Tags
tag_name 2010Tags
sample size
detection_probability 1
years 2011
step 2
proportion_mortality 1.0
plus group True
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do_bootstrap True
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@fish_tagged_penalty
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@fish_ label 20 tagging multipl	tagged_p 008TagPe ;_episode ier 1	enalty nalty 2008Tags										
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	17	17	17	17	17	17	17	17	17	17	17	1/
	18	18	18	18	18	18	18	18	18	18	18	18
	18	18	18	18	18	18	18	18	18	18	18	18
	18	18	18	18	18	18	18	18	18	18	18	18
	18	18	18	19	19	19	19	19	20	20	20	20
	20	20	20	21	21	21	21	21	22	22	22	22
	25	23	23	29	30	30	31	31	33	36	8	8
	9	9	10	10	10	11	12	14	14	15	16	16
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sizes	18 63	18 70	19 19	19 74	19	19 71	20 87	24 83	24 73	32 74	85	85
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	118	125	102	109	111	124	98	117	119	99	101	107
	107	109	113	119	125	135	100	117	120	126	130	111
	102	109	115	118 111	119	122	122	123 120	120	138	100	102
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	111	112	113	114	115	119	119	120	120	122	123	124
	127	129	136	135	107	119	129	138	149	111	91	126
	131	132	132	106	137	116	133	144	121	128	140	147
	149	153	121	141	147	140	158	148	156	128	158	125

	154	144	162	142	155	152	134	163	159	183	63	76
	76	80	75	75	86	81	116	102	114	113	106	112
	98	108	112	118	119	109	109	115	118	118	119	109
	118	125	125	127	128	129	110	119	120	123	107	109
	110	122	104	105	98	113	126	124	127	140		
sexes	2	2	2	2	2	2	2	2	2	2	2	2
	2	2	2	2	2	2	2	2	2	2	2	2
	2	2	2	2	2	2	2	2	2	2	2	2
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# output.csl

@print
# estimation section stuff
parameters false
fits\_every\_eval false
objective\_every\_eval false
parameters\_every\_eval false
parameter\_vector\_every\_eval false
fits true
resids true
pearson\_resids true
estimation\_section true

# population section stuff
requests false
initial\_state false
state\_annually t
state\_every\_step true
final\_state true
results false

#output section stuff yields true unused\_parameters true covariance True

@quantities
all\_free\_parameters true
fishing\_pressures true
nuisance\_qs true
true\_YCS true
B0 true
R0 true
SSBs true
YCS true
actual\_catches false
ogive\_parameters selectivity[SelSSI].all

fits true normalised\_resids false tagged\_age\_distribution true

@print\_sizebased\_ogives\_at 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 105 110 115 120 125 130 135 140 145 150 155 160 165 170 175 180 185 190 195 200 205 210 215 220

@selectivity\_at SelSSI-at-age ogive SelSSI years 2005 2006 2007 2008 2009 2010 2011 step 2 proportion\_mortality 0.5 sexed False #sexed True

@abundance vulnerable biomass true mature\_only false step 2 proportion\_mortality 0.5 ogive SelSSI years 2005 2006 2007 2008 2009 2010 2011

# Annex A

**Roberts, J.,** Xavier, J. C. & Agnew, D. J. (2011). The diet of toothfish species *Dissostichus eleginoides* and *Dissostichus mawsoni* with overlapping distributions. *Journal of Fish Biology, 79*: 138-154.



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# The diet of toothfish species *Dissostichus eleginoides* and *Dissostichus mawsoni* with overlapping distributions

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The diets of Antarctic toothfish Dissostichus mawsoni and Patagonian toothfish Dissostichus eleginoides were examined around the South Sandwich Islands in the Southern Ocean, one of few regions with overlapping populations of the two species. Despite large differences in the proportion of stomachs containing prey (76.2% of D. mawsoni compared to 7.2% of D. eleginoides), diet composition was broadly similar (Schoener overlap index of 74.4% based on prey mass) with finfishes (particularly macrourids and muraenolepidids) and cephalopods (mainly Kondakovia longimana) comprising >90% of the prev mass of both species. Predation rates of the main fish prev, as mean counts per stomach sampled, were spatially correlated with their relative abundance around the islands derived from fishery by-catch data, suggesting a general lack of prey selectivity. This study supports the view that bathyal Dissostichus are opportunistic carnivores and finds that D. mawsoni and D. eleginoides occupy a similar trophic niche and are likely to compete for prey in regions where both are distributed. The large increase in rate of prey occurrence and size of prey in D. mawsoni stomachs relative to D. eleginoides suggests, however, species differences in feeding behaviour, which may reflect the increased metabolic demands of a cold-water adapted physiology. [Correction added after online publication 13 June 2011: spelling of species name corrected] © 2011 The Authors

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Key words: Antarctic; bathyal; CCAMLR; dietary overlap; prey distribution.

#### **INTRODUCTION**

Dissostichus spp. are large predatory fishes of the family Nototheniidae capable of attaining >2 m in total length ( $L_T$ ) and 100 kg in mass (Horn, 2002). They inhabit a broad range of depths depending on life stage. Pelagic larvae are occasionally recovered close to the surface and large adults are found as deep as 2500 m (Evseenko *et al.*, 1995). Patagonian toothfish *Dissostichus eleginoides* Smitt 1898 are most abundant around the sub-Antarctic Islands of the Southern Ocean and the Patagonian region of South America. Antarctic toothfish *Dissostichus mawsoni* Norman 1937 have a number of adaptations to very cold-water temperatures and are endemic to the seasonal pack-ice and high Antarctic zones surrounding the Antarctic

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continent (De Witt et al., 1990). Populations of the two species overlap at only a few locations, including the Banzare Bank in the southern Indian Ocean, over seamounts in the northern Ross Sea and around the South Sandwich Islands in the South Atlantic (McKinlav et al., 2008; Hanchet et al., 2009; Roberts & Agnew, 2009). [Correction added after online publication 13 June 2011: spelling of species name corrected]

The South Sandwich Islands form the only continuous region of bathyal seafloor spanning 55° S to 59° S in the Atlantic Southern Ocean. Both *Dissostichus* species are found here, though fishery catch data suggest that the north-south transition in Dissostichus species dominance is abrupt, occurring around Saunders Islands between  $57^{\circ}$  30' S and  $58^{\circ}$  00' S (Roberts & Agnew, 2009). This coincides with the point where the Weddell Front crosses the South Sandwich Islands, dividing the eastward-flowing Weddell-Scotia Confluence (WSC) to the north and Weddell Gyre to the south (Whitworth et al., 1994). These two water bodies are characterized by rather different hydrographic regimes and the observed distributions of Dissostichus species are likely to reflect north-south gradients in water temperature and habitat type (Fig. 1).

Over the past two to three decades, a number of deep-water longline fisheries have targeted Southern Ocean Dissostichus populations (Agnew, 2004), though the fishery at South Sandwich Islands has operated consistently only since 2005, taking a combined *Dissostichus* spp. catch of <150 t annually (Roberts & Agnew, 2009). The diet of the target species and its predators are often analysed as a first step in assessing the potential effects of fishing mortality on ecosystem trophic relationships (Goldsworthy et al., 2001; Pilling et al., 2001).

Previous studies on Dissostichus species diet have found that they are primarily piscivorous at all life stages, with the composition of prey species reflecting availability (McKenna, 1991; Garcia del la Rosa et al., 1997; Pilling et al., 2001;



FIG. 1. (a) Location of the South Sandwich Islands and general position of major frontal systems of the Scotia Sea [WF, Weddell Front (Orsi et al., 1993); SB, Southern Boundary of the Antarctic Circumpolar Current (Orsi et al., 1995); SACCF, Southern Antarctic Circumpolar Current Front (Orsi et al., 1995)]. Depth contours shown for 500 and 2000 m. (b) Mean sea surface temperature (Acker & Leptoukh, 2007) and spatial distribution of Dissostichus spp. catch per unit effort (CPUE) at the South Sandwich Islands (Roberts & Agnew, 2009). [Correction added after online publication 13 June 2011: pie chart shading corrected]

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Goldsworthy et al., 2002; Xavier et al., 2002; Arkhipkin et al., 2003; Hoff, 2004; Collins et al., 2007). Shelf juvenile populations, occasionally referred to as the shelf ontogenetic phase (Arkhipkin et al., 2003), mainly prey on small nototheniid fishes, such as Patagonotothen guntheri (Norman 1937) or Lepidonotothen spp. in D. eleginoides, and Pleuragramma antarcticum Boulenger 1902 in juvenile D. mawsoni. This may be supplemented with krill Euphausia superba, squid or pelagic fishes depending on spatial and temporal availability (Arkhipkin et al., 2003; Barrera-Oro et al., 2005; Collins et al., 2007). The range of prey sizes increases with development and large fishes such as macrourids, morids and rajids tend to dominate the diet of the upper slope ontogenetic phase (500-1000 m). In deeper waters, D. eleginoides are thought to be more opportunistic, consuming increasing quantities of deep-water shrimps (Caridea) and onychoteuthid squid, particularly Kondakovia longimana (Pilling et al., 2001; Xavier et al., 2002; Arkhipkin et al., 2003) and scavenged prey, such as penguin remains and fishery discards dropped from the surface (Stevens, 2004). The more recent studies on *D. mawsoni* diet have focused on Ross Sea populations (Fenaughty et al., 2003; Stevens, 2004) where Macrourus whitsoni (Regan 1913) was the dominant prey species.

All previous studies on the diet of the two species have been on widely separated populations. At the South Sandwich Islands, *D. mawsoni* and *D. eleginoides* overlap in distribution, providing a rare opportunity to compare the diet of the two close species. In this article, the evidence for niche overlap and separation of diet composition is examined. Comparison is also made with abundance estimates from industry catch and effort data of the main prey taxa also taken as by-catch, to assess *Dissostichus* species prey selectivity and the distribution of abundant macrofauna in an undersampled region of the Southern Ocean (Ramos, 1999; Arntz *et al.*, 2005).

#### **MATERIALS AND METHODS**

All samples were collected onboard the longliner F.V. *San Aspiring*, fishing at the South Sandwich Islands from March to April 2009. An autoline system was deployed with snoods set 1.4 m apart on the main line and hooks baited with New Zealand arrow squid *Nototodarus sloanii*. Samples were collected from lines set across the full range of latitudes and depths fished (from  $55 \cdot 7^{\circ}$  S to  $59 \cdot 9^{\circ}$  S and 917 to 1720 m, respectively). An integrated weight main line was used in all sets (50 g m<sup>-1</sup>), and it was assumed that all fishes became hooked while the line was situated close to the bottom. Line positions were estimated as the mean of the start and end line setting positions. The baited section of line ranged in length from 3600 to 15 600 m (2571–11 141 hooks).

Fishes were randomly selected from the catch for stomach sampling. Biometric measurements were taken from all sampled fish, including total length  $(L_T)$  mass and sex. Whole stomachs were collected and put into a deep freeze prior to dissection in the wet laboratory at BAS King Edward Point, South Georgia, in June 2009. All stomachs were fully defrosted and presence, frequency and wet mass were quantified for taxonomic groupings identified to the lowest possible level. Fishes were identified from morphological characteristics of the body and sagittal otoliths, where these were still present in the cranium (Gon & Heemstra, 1990; Williams & McEldowney, 1990; Reid, 1996). Provisional identification of cephalopod prey was made from tentacular club morphology (Fischer & Hureau, 1985). In addition, 193 cephalopod lower beaks were preserved in 90% ethanol for later identification to species level (Xavier & Cherel, 2009), including beaks extracted from buccal masses and those found free in stomachs, though the latter were not included (if not fresh) in mass calculations for respective prey taxa in order to avoid overestimation of the cephalopod component (Xavier *et al.*, 2003). The allometric equations, converting cephalopod beak size to mantle length and mass, were obtained from Xavier & Cherel (2009). All samples were photographed in the laboratory to a 10 megapixel resolution. Tentative taxonomic identifications of caridean shrimps were made from high-resolution photographs by the Oxford University Museum of Natural History (S. De Grave, pers. comm.).

Stomach content data were analysed using a combination of per cent frequency of occurrence (% *F*) and per cent mass (% *M*) (Pinkas *et al.*, 1971) of each prey taxon identified to the lowest possible level. Diet overlap between *Dissostichus* species and intraspecific groupings was estimated using the Schoener overlap index ( $R_0$ ) of the mass of prey items, calculated as:  $R_0 = 100(1 - 0.5 \sum_{i=1}^{n} |p_{x,i} - p_{y,i}|)$ , where  $R_0$  is the overlap index expressed as a percentage and  $p_{x,i}$  and  $p_{y,i}$  are the relative proportions of each food item *i* of *n* total items found in the stomachs of two species, or groups of animals, *x* and *y* (Schoener, 1970). Values of  $R_0 > 60\%$  indicated a high degree of overlap (Wallace & Ramsay, 1983). For comparison, the Spearman rank correlation coefficient ( $R_s$ ) was also calculated for the same predator groupings. This allowed for significance testing to compare diet composition in terms of % *M*, where *n* (17) was the number of pairs of prey taxon rankings compared. Avian prey items were combined into a single taxonomic group and unidentified tissue, bait, rocks, fishing gear and macroalgae were excluded from the analysis.

Industry catch data were used to derive plots of *Dissostichus* spp. catch per unit effort (CPUE) in terms of kg per hook set. By-catch CPUE estimates (as individuals per 1000 hooks set) were derived from hooks survey data collected by scientific observers on all trips from 2005 to 2009, monitoring a random sample of >20% of hooks hauled, according to the protocol described in the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Scientific Observer Manual (CCAMLR, 2005). MODIS Aqua sea surface temperature (11 micron day) plots were produced using the Giovanni online data system, developed and maintained by the U.S. National Aeronautics and Space Administration, Goddard Earth Sciences Information Center (NASA GES DISC) (Acker & Leptoukh, 2007).

#### RESULTS

A total of 775 *D. eleginoides* and 269 *D. mawsoni* were sampled around South Sandwich Islands (*D. eleginoides*, 55–178 cm  $L_T$  and 2.5:1 female to male ratio; *D. mawsoni*, 106–193 cm  $L_T$  and 1.2:1, respectively). For both species, the  $L_T$  frequency distribution and sex ratio of sampled fish was representative of the captured population. All fishing took place on continental slopes deeper than 900 m and shelf ontogenetic phase juveniles were not represented in the captured population. Catch rates demonstrated a separation in the distributions of the two species of *Dissostichus*, with overlap around Saunders and Montagu Islands only, at the approximate position of the Weddell Front (Fig. 1).

### PROPORTION OF STOMACHS CONTAINING PREY

A highly significant species effect was observed in the occurrence of prey items in *Dissostichus* species stomachs, with 76·2% of *D. mawsoni* stomachs containing prey compared to only 7·2% of *D. eleginoides* ( $\chi^2 = 506.8$ , d.f. = 1, P < 0.001) (Table I). The influence of location of capture on this difference was minimal, the frequency of prey occurrence ranging from 66·7 to 100% of *D. mawsoni* stomachs and 0 to 13·5% of *D. eleginoides* stomachs in half-degree grid squares where at least 10 fishes were sampled, though sampling was mostly restricted to the regions where each species was abundant [comparing Figs 1(b) and 2]. Where present, the mean prey mass per stomach was significantly greater in *D. mawsoni* (432 g) compared to *D. eleginoides* (111 g) (Mann–Whitney *U*-test = 11 435,  $n_1 = 203$ ,  $n_2 = 56$ , P < 0.001 one-tailed) (Table I).

	D. mawsoni	D. eleginoides
Stomachs sampled	269	775
Percentage containing prey	76.2	7.2
Mean mass of prey where present (kg)	0.432	0.111
s.D. mass of prey where present (kg)	0.511	0.181

 
 TABLE I. Summary of Dissostichus mawsoni and Dissostichus eleginoides stomach sampling at the South Sandwich Islands

In both species, the proportion of stomachs containing prey increased in response to increasing size of *Dissostichus*, though the proportion was still significantly greater in *D. mawsoni* when comparing the same  $L_T$  classes (0.60–0.78 compared to 0.11–0.16 of *D. eleginoides* from 130 to 160 cm, over 10 cm  $L_T$  classes) ( $\chi^2 = 37.9$ , d.f. = 1, P < 0.001). Occurrence of prey also increased with increasing depth of capture, while the effects of latitude were minimal (Fig. 3). Mean fish  $L_T$  varied little over the depth range included in this analysis (155–162 cm for *D. mawsoni* and 113–116 cm for *D. eleginoides* from 1000 to 1800 m, over 200 m depth classes).

#### SPECIES EFFECTS ON DIET COMPOSITION

Fishes dominated the prey mass of both *Dissostichus* species at the South Sandwich Islands (62.0 and 73.6% *M* in *D. mawsoni* and *D. eleginoides*, respectively).



FIG. 2. Spatial distribution of *Dissostichus* spp. stomachs sampled at the South Sandwich Islands and proportion containing prey items: (a) *Dissostichus mawsoni* and (b) *Dissostichus eleginoides*. (Size of circles represents number of fish sampled in each 0.5 degree grid square.)



FIG. 3. Proportion of *Dissostichus mawsoni* ( $\bigcirc$ ) and *Dissostichus eleginoides* ( $\bigcirc$ ) stomachs containing prey as a factor of (a) fish total length ( $L_T$ ), (b) line latitude and (c) fishing depth at the South Sandwich Islands. Sample sizes are indicated above points; only classes with a minimum of 10 samples are included.

Macrourids (*Macrourus cf. whitsoni*) were the dominant fish prey in both species and tended to be smaller than those taken as by-catch in the fishery (56% of fish from stomachs had snout to anus measurements <15 cm compared to 7% of captured fish). Eel cods *Muraenolepis cf. microps* Lönnberg 1905 (7.4 and 6.8% *M*) and rajids [*Amblyraja georgiana* (Norman 1938)] (5.9 and 5.2% *M*) were also preyed on by both *D. mawsoni* and *D. eleginoides* (Table II).

With the exception of some small portions of well-digested tissue, nototheniids were only present in *D. mawsoni* stomachs, with *Notothenia* spp. and *Lepidonotothen* spp. [*Lepidonotothen cf. kempi* (Norman 1937)] comprising the greatest mass (5·9 and 1·6% *M*, respectively). Icefish *cf. Chaenocephalus aceratus* (Lönnberg 1906) and daggertooth *Anotopterus cf. vorax* (Regan 1913) were also only found in *D. mawsoni* stomachs (6·0 and 1·0% *M*, respectively). *Antimora rostrata* (Günther 1878) and *Bathydraco joannae* DeWitt 1985 were found in *D. mawsoni* and *D. eleginoides*, though may be more important to the latter in terms of prey mass (Table II).

Cephalopods were present in large quantities in D. mawsoni and D. eleginoides stomachs (35.7 compared to 18.1% M) (Tables II and III). The few whole squid found were all identified from lower beak morphology as being Moroteuthis knipovitchi [Fig. 4(a)] and their range in size (368-703 g, n=6) was similar to that estimated from measurements of loose beaks identified as M. knipovitchi (342-982 g, n = 39) (unpubl. data). Most of the cephalopod mass comprises the brachial crowns and upper mantle sections of larger animals and the less well-digested specimens were tentatively identified from tentacular club hook and sucker arrangement as being Kondakovia longimana. In addition, one 80 cm long section of colossal squid arm (Mesonychoteuthis hamiltoni), identified by the presence of swivelling hooks [Fig. 4(b)], and a relatively fresh 78 cm section of a *M. hamiltoni* tentacle with tentacular club (manus length 17.5 cm) were found in D. mawsoni stomachs. Kondakovia longimana and M. knipovitchi also dominated cephalopods identified from beaks found in D. mawsoni and D. eleginoides, in terms of % F and % M. Other species only found in D. mawsoni stomachs included Psychroteuthis glacialis, Alluroteuthis antarcticus, Galiteuthis glacialis and Stauroteuthis gilchristi (Table III).

Caridean shrimps (*cf. Nematocarcinus* spp.) are likely to be the main crustacean prey of both *Dissostichus* species (Table II). They frequently occurred in *D. mawsoni* and *D. eleginoides* stomachs (7.3 and 23.2% F, respectively), though were

	D. m	awsoni	D. eleginoides		
Prey taxon	% F	% M	% F	% M	
Pisces					
Amblyraja georgiana	2.4	5.8	1.8	5.2	
Macrourus cf. whitsoni	39.0	23.8	21.4	30.7	
Unidentified nototheniid	6.3	1.5	3.6	0.8	
Notothenia spp.	6.3	5.9	_		
Lepidonotothen cf. kempi	4.9	1.6	_		
Muraenolepis cf. microps	12.7	7.3	16.1	6.8	
cf. Chaenocephalus aceratus	3.4	6.0	_		
Anotopterus cf. vorax	3.4	1.0	_		
Bathydraco joannae	1.0	0.1	5.4	2.0	
Antimora rostrata	0.5	0.0	1.8	7.7	
Borostomias antarcticus	_	_	1.8	0.2	
Lycenchelys sp.	_	_	1.8	0.2	
Unidentified myctophid	0.5	0.0		_	
Unidentified fishes	51.7	8.2	51.8	20.1	
Cephalopoda					
Teuthidae	50.2	35.4	10.7	18.0	
Octopoda			1.8	0.5	
Crustacea					
cf Nematocarcinus spp	7.3	0.1	23.2	1.5	
Thymons hirsteini	0.5	0.0			
Paralomis spinosissima				_	
Echinodermata					
Brittle stor	1.0	0.0			
	1.0	0.0			
Aves	2.4	1.5			
Pygoscelis antarcticus	2.4	1.5			
Unidentified petrel species	0.5	0.1			
Other					
Macroalgae	0.5	0.1			
Rocks	5.9	0.2	7.1	0.1	
Bait	5.4	0.5	14.3	6.2	
Fishing gear	0.5	0.0			
Unidentified prey	2.9	0.1			

TABLE II. Dissostichus mawsoni and Dissostichus eleginoides stomach contents at the South Sandwich Islands, in terms of per cent frequency of occurrence (% F) and per cent mass (% M)

small in size compared to other prey taxa (c. 10 g) and formed a low percentage of overall prey mass (0.1 and 1.5% M, respectively). With the exception of a single *Thymops birsteini* from a *D. mawsoni* stomach, benthic crustaceans were absent. Benthic invertebrates and other benthos species were represented by a small number of brittle stars in *D. mawsoni* stomachs (1.0% *F*). In addition, a number of scavenged prey were found in *D. mawsoni*, including the well-digested remains of six penguins, tentatively identified as *Pygoscelis antarcticus* [Fig. 4(c)] and a single unidentified petrel. Macroalgae (a large section of kelp) and fishing gear (a single

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	<i>D. m</i>	awsoni	D. eleginoides		
Prey species	% F	% M	% F	% M	
Kondakovia longimana	38.0	96.8	10.7	92.6	
Moroteuthis knipovitchi	18.5	2.6	7.1	7.4	
Psychroteuthis glacialis	3.9	0.4			
Alluroteuthis antarcticus	0.5	0.1			
Mesonychoteuthis hamiltoni	0.5	0.1			
Galiteuthis glacialis	2.4	>0.1			
Stauroteuthis gilchristi	0.5	>0.1			
Unknown sp. (eroded)	0.5	>0.1			

TABLE III. Cephalopod component of *Dissostichus mawsoni* and *Dissostichus eleginoides* stomach contents at the South Sandwich Islands, identified from fresh lower beaks (see Table II)

snood) [Fig. 4(d)] were also found. The mass of squid bait in *D. mawsoni* (0.5% *M*) was low relative to that found in *D. eleginoides* (6.2% *M*) (Table II).

More than 20% of prey items in *D. mawsoni* stomachs had a mass >250 g (*i.e.* prey over this mass were found) in both small [from 120 to 150 cm  $L_T$ ] and large



FIG. 4. The contents of four *Dissostichus mawsoni* stomachs: (a) *Macrourus* spp. and whole cephalopod (*cf. Moroteuthis knipovitchi*), (b) section of *Mesonychoteuthis hamiltoni* arm, (c) remains of chinstrap penguin (*Pygoscelis antarcticus*) and (d) cephalopod mantle tissue and upper and lower beaks, fish head and longline snood. (Scale bars are *c*. 200 mm.)

TABLE IV. Schoener diet overlap index ( $R_0$ ) for *Dissostichus mawsoni* and *Dissostichus eleginoides* at the South Sandwich Islands [Spearman rank correlation ( $R_s$ ) in parentheses with level of significance: \*, P < 0.05; \*\*, P < 0.01; *n*, the number of pairs of prey taxon rankings compared = 17]

Group 1	Group 2	$R_{\rm o}~(R_{\rm s})$
Interspecific D. mawsoni	D. eleginoides	74.4 (0.382)
Intraspecific	D mausoni South	68 2 (0 508*)
D. eleginoides North	D. eleginoides Central	62.2 (0.615*)
D. mawsoni Male	D. mawsoni Female D. mawsoni >160 cm	85·1 (0·925**) 84·1 (0·925**)
D. eleginoides $<120$ cm	D. eleginoides $>120$ cm	63.1 (0.724**)

fish (>150 cm  $L_T$ ). This compares to <10% of *D. eleginoides* from 120 to 150 cm  $L_T$  and smaller than this.

The  $R_o$  between *Dissostichus* species was high when comparing the mass of prey taxa (74.4%) (Table IV), though the  $R_s$  was low (0.382), indicating a moderate though insignificant level of diet overlap. In terms of % *F*, the primary interspecific differences in diet were in small prey (such as caridean shrimps) and large prey (nototheniids and squid) (Table II).

## SOAK-TIME EFFECTS ON OCCURRENCE OF PREY

Mean counts of macrourids and cephalopods per sampled *D. mawsoni* stomach were examined in response to increasing line soak time (Fig. 5). Predator size and line-depth effects were minimized by only including fish >150 cm caught on lines from 1200 to 1800 m depth. Over the shortest soak time (0.4-0.6 days), the count of macrourid prey per stomach was much higher than those of squid (means of 0.96 and 0.18, respectively). Macrourid counts per stomach were greatly reduced over longer soak times, ranging from 0.28 to 0.41 per stomach over 0.2 day soak intervals (from 0.6 to 1.6 days). Conversely, increased counts of cephalopods per stomach were observed over longer soak times (ranging from 0.33 to 0.53 individuals per stomach) (Fig. 5). Too few *D. eleginoides* stomachs contained prey items to allow a comparative analysis for this species.

### LENGTH AND SEX EFFECTS OF DIET COMPOSITION

The observed trends in stomach fullness suggested that other differences in diet might exist between small and large fish. The median  $L_{\rm T}$  of *D. mawsoni* was 160 cm and, so to investigate potential differences between large and small fish, two categories were created: < and > 160 cm. A large and significant overlap in diet was observed when comparing large and small *D. mawsoni* ( $R_0 = 84\cdot1\%$ ;  $R_{\rm s} = 0.925$ , n = 17, P < 0.01). The overlap was less pronounced between *D. eleginoides* size groupings (< and > 120 cm), though it was still significant ( $R_0 = 63\cdot1\%$ ;  $R_{\rm s} = 0.724$ , n = 17, P < 0.01), suggesting minimal ontogenetic shift in *Dissostichus* 



FIG. 5. Effect of line soak time on mean ± 95% C.I. count of macrourid (●) and cephalopod (O) prey in *Dissostichus mawsoni* stomachs (depth 1200–1800 m; total length ≥150 cm).

species diet once individuals have recruited to slope populations. The diet of male and female *D. mawsoni* was also very similar ( $R_0 = 85 \cdot 1\%$ ;  $R_s = 0.925$ , n = 17, P < 0.01) (Table IV), though too few male *D. eleginoides* contained prey to allow for a meaningful assessment of sex effects in this species.

# DEPTH AND AREA EFFECTS ON DIET COMPOSITION AND THE DISTRIBUTION OF PREY SPECIES

The main finfish prey taxa, such as: macrourids, muraenolepidids and nototheniids, and cephalopods were found in *Dissostichus* species caught across the full range of latitudes fished at the South Sandwich Islands. Macrourids and squid were found in stomachs wherever *D. mawsoni* were caught, though muraenolepidids and nototheniids appeared to be more heavily preyed on further south. This agrees with abundance estimates from longline data, where increases in CPUE (number per hook) of muraenolepidids and nototheniids were observed further south, while macrourid catch rates were stable across the fishing grounds. Cephalopods are not taken as bycatch though appear to be abundant throughout the islands, with perhaps an increased abundance on east-facing slopes in the south (Fig. 6, nototheniids not displayed).

The effect of depth on mean prey count was minimal for macrourids, nototheniids and cephalopods, though macrourids do appear to be less heavily preyed on at depths shallower than 1200 m, and muraenolepidids were rarely present in fishes caught deeper than 1600 m. A greater depth effect was observed on less frequently taken prey, such as *C. aceratus* (only found in fishes caught shallower than 1200 m) and *Anotopterus* sp. (mostly > 1600 m), though both were only found in fishes caught across a narrow range of latitudes (58° 00' to 58° 30' S) and their horizontal distribution may be quite patchy.

A large degree of diet overlap was observed when comparing prey species mass of *D. eleginoides* in the north and central regions of the South Sandwich Islands  $(R_0 = 62.2\%; R_s = 0.615, n = 17, P < 0.05)$  and *D. mawsoni* in the central and



FIG. 6. Spatial distribution of prey taxa (a), (d) *Macrourus* spp.; (b), (e) *Muraenolepis* spp. and (c) *Kondakovia longimana*, as: (a)–(c) counts per *Dissostichus mawsoni* stomach sampled ( $\Box$ , area where five or more stomachs were sampled;  $\times$ , areas where prey taxa were found in *Dissostichus eleginoides* stomachs) and (d)–(e) longline by-catch catch per unit effort (CPUE) in terms of number observed per 1000 hooks (areas with <5000 hooks sampling effort omitted).

southern regions ( $R_0 = 68.3\%$ ;  $R_s = 0.598$ , n = 17, P < 0.05) (north, from 55.5 to 56.5° S; central, from 56.5 to 58.5° S; and south, from 58.5 to 60.0° S). Few samples were obtained from *D. eleginoides* in south and *D. mawsoni* in north and these area groupings were omitted from diet overlap analyses (Table IV).

### DISCUSSION

This study provides a snapshot view of the diet of bathyal *Dissostichus* species populations of the Southern Ocean within a restricted area and period. The South Sandwich Islands are located inside the seasonal pack-ice zone, where hydrographic conditions vary considerably with location and season. Hence, temporal variation in *Dissostichus* diet would be expected at the South Sandwich Islands. This was observed in *D. eleginoides* populations off the coast of Chile where spring and summer diets were dominated by ophidiids and macrourids and cephalopods increased

in importance during the autumn and winter (Murillo et al., 2008). Also, temporal shifts in the diet of juvenile D. eleginoides populations over the Falkland shelf were thought to reflect seasonal cycling in the availability of key prey species (Arkhipkin et al., 2003). In this study (and many others of Dissostichus diet), samples were collected over a narrow period and the potential seasonal effects of Dissostichus diet are considered where relevant.

## FACTORS AFFECTING RATE OF PREY OCCURRENCE

The large species effect on the proportion of stomachs containing prey has been noted before (Fenaughty et al., 2003), though until this study, it had not been demonstrated in overlapping Dissostichus spp. populations over the same period. As such, these differences are likely to relate to the specific physiology and behaviour of the two close species, rather than regional or seasonal variations in prey availability. The rates of prey occurrence (76.2% of D. mawsoni and 7.2% of D. eleginoides) are comparable to those observed in longline caught D. mawsoni in the western Ross Sea (79.8%) (Stevens, 2004) and D. eleginoides at South Georgia (9.0%) (Pilling et al., 2001). The latter study found a significant increase in prey occurrence where fishes were captured in traps and linked decreased prev occurrence to stress-induced regurgitation of prey. Hence, decreases in prey occurrence may be expected with increasing line depth, though the reverse effect was observed in this study (Fig. 3). A few D. eleginoides stomachs were found to contain sea water and may have been flushed on hauling, though it seems unlikely that such low rates of prey occurrence were solely caused by flushing and regurgitation when c. three-quarters of D. mawsoni still contained prey.

Alternative explanations relate to differences in feeding behaviour. Large-bodied fishes, such as C. aceratus, are often found with a high proportion of empty stomachs (Kock, 1992) and seasonal variation is often observed in the diet and feeding intensity of a number of sub-Antarctic and Antarctic fish species. A two- to three-fold decrease in feeding intensity is common during winter months, often relating to the timing of spawning (Kock, 1992). Murillo et al. (2008) found that the percentage of D. eleginoides stomachs containing prev increased from 29% in autumn and winter months to 54% in spring and summer. As such, the high proportion of D. eleginoides with empty stomachs at the South Sandwich Islands may be explained by seasonally depressed feeding intensity. As with stress-linked regurgitation, however, D. mawsoni do not appear to be affected by this phenomenon to the same degree, despite both Dissostichus species appearing to spawn during the austral winter months (Agnew et al., 1999; Hanchet et al., 2008). Also, D. mawsoni tend to prey on a larger size fraction of prey regardless of body size (Fig. 3). Hence, the reduced rates of prey occurrence in D. eleginoides may relate to the increased gut clearance rates of smaller prev items.

Alternatively, the observed patterns could result from general species differences in feeding intensity. This may be expected given dissimilarities in the life history and physiology of the two species. Dissostichus mawsoni grow faster to a greater maximum length (Horn, 2002) and, unlike D. eleginoides, possess a number of physiological adaptations to very cold-water temperatures, including antifreeze glycopeptides and aglomerular kidney structure (Eastman, 1990). All of which likely to elevate metabolic energy demands and, so, feeding rates.

### DIET COMPOSITION AND ECOLOGY OF PREY SPECIES

Studies on adult *Dissostichus* species populations generally report that fishes are the most important prey taxon in terms of mass, with species composition dependent on area and season. Fishes are high in nutritional value and are often the most abundant prey item available over a certain size, so it is unsurprising that fishes tend to be the main prey species for Antarctic fishes >40-50 cm  $L_T$  (Kock, 1992). At the South Sandwich Islands, fish prey were dominated by macrourids, muraenolepidids, benthic icefish and medium-sized nototheniids (the last two only in *D. mawsoni*), all of which are typically assumed to be demersal in habit (Gon & Heemstra, 1990). Macrourids dominated the prey mass of both *Dissostichus* species and are also the main by-catch taxon in the longline fishery that operates there. They are likely to be locally abundant, while catch rates have a similar spatial and horizontal distribution to those of *Dissostichus* species (Roberts & Agnew, 2009), suggesting a preference for similar habitat types. This may explain why macrourid species are often found to dominate *Dissostichus* diet in other study regions and, as with *Muraenolepis cf. microps*, may provide a dependable year-round food source.

The variety of fish species found in stomachs reflects the broad range of latitudes encompassed by the island chain and the complex oceanography of the region. During some seasons, southward incursions of the Antarctic Circumpolar Current (ACC) bring relatively warm water to the northernmost islands. Further south, the well-mixed Weddell Scotia Confluence and more stratified Weddell Gyre offer markedly different nutrient and temperature profiles with depth (Whitworth *et al.*, 1994). This has led to predictions of north–south gradients in the abundance of different fishes, with Magellanic species dominating the north and increasing numbers of Antarctic species in the south (Arntz *et al.*, 2005). At the South Sandwich Islands, the distributions of *Muraenolepis* spp., *Lepidonotothen* spp. and *Notothenia* spp. CPUE were spatially correlated with rates of presence in *Dissostichus* stomachs. All these taxa appear to be more abundant in the south, which may explain their increased mass in *D. mawsoni* stomachs.

A recent groundfish trawl survey conducted at the South Sandwich Islands found *L. cf. kempi* to be the dominant finfish species of bathyal slopes (Arntz & Brey, 2003), though they are rarely taken as by-catch in the longline fishery. These differences are likely to relate in part to gear selectivity, though their reduced prey mass compared to *Macrourus* spp. suggests they are less abundant across the foraging habitat of *D. mawsoni*, possibly distributed shallower than the 700–1600 m depth range where *D. mawsoni* are targeted by the longline fishery. The presence of epimesopelagic *A. vorax* in a number of *D. mawsoni* stomachs suggests, however, that some individuals migrate up through the water column to forage shallower depths, as has been observed in McMurdo Sound populations (Eastman & Barry, 2002).

Cephalopods are an important constituent of the diet of both *D. mawsoni* and *D. eleginoides*, with *K. longimana* the dominant prey species (Tables II and III). *Kondakovia longimana* is commonly cited as the main squid prey of *Dissostichus* species populations except at Macquarie Island; this island is geographically positioned further north, closer to warmer waters, and therefore other squid species (such as *Histioteuthis eltaninae*) occur (Xavier *et al.*, 2002; Hoff, 2004). All cephalopod species found in their diet are typically Antarctic (Nesis, 1997; Xavier *et al.*, 2003) (Table III) and are also preyed upon by a wide range of other Antarctic predators

including seals, whales, albatrosses, penguins and sharks (Cherel & Klages, 1998; Cherel *et al.*, 2004; Xavier & Cherel, 2009).

It has been previously reported that a portion of D. mawsoni stomach contents arise from fish feeding on by-catch prior to becoming caught (Stevens, 2004). A large decrease in the mean count of macrourids per stomach was observed between 12 and 16 h of soak time, suggesting that at least some individuals were ingested some time prior to capture. Macrourids were found in a wide range of digestive stages and only one specimen appeared to be fresh. This contrasts with the mean counts of cephalopods, which increased markedly over the same soak time, remaining fairly constant thereafter. This may be explained by the comparative large size of cephalopod prey items, which may require a longer time to clear the stomach. It may also be caused by continued predation on new individuals lured by caught fishes, as evidenced by the presence of squid sucker marks about the head of a number of sampled fishes or of fish preying on squid that have become caught on hooks. Gashes were also observed along the flanks of some fishes that were thought to have resulted from attacks by large squid. Associations have been noted between M. hamiltoni and hooked Dissostichus species in other studies (Xavier et al., 2002; Fenaughty et al., 2003) and also here with the presence of a M. hamiltoni arm and a relatively fresh tentacle in separate D. mawsoni stomachs. Smaller individuals of this species are known to be preyed on by *Dissostichus* species, though this relationship may be reversed as colossal squid increase in size.

Scavenged items are likely to be an important food source for *Dissostichus* species. A number of the *K. longimana* beaks were estimated to have come from individuals >10 kg in total mass (unpubl. data). No *D. mawsoni* was found with >3 kg of stomach contents (1 kg in *D. eleginoides*) and the larger squid must have been consumed in sections, either torn from living animals or scavenged from the seafloor. The penguin and petrel carcasses found in stomachs must also have been scavenged from the seafloor. A number of chinstrap penguins *Pygoscelis antarcticus* were observed floating dead on the surface being scavenged by giant petrels *Macronectes* spp. and, given their large population at the South Sandwich Islands, may provide a significant input to the seafloor food web. Few benthos or benthic invertebrates were found in stomachs at the South Sandwich Islands. Limited benthic sampling at the South Sandwich Islands suggests a low diversity of benthic fauna dominated by a few opportunistic species (Ramos, 1999; Arntz & Brey, 2003). Benthos species tend to be relatively low in nutritional value and are unlikely to be an important component of *Dissostichus* species diets in bathyal populations.

# *DISSOSTICHUS* SPP. DISTRIBUTION AND NICHE DIFFERENTIATION

Previously the diets of *Dissostichus* species have been assessed in spatially discrete stocks and over different periods. This study shows that the diet of *Dissostichus* species are actually very similar when confronted with a broadly comparable prey composition. The small species differences in diet composition may largely be explained by north-south gradients in abundance of certain prey species, as observed in nototheniids, suggesting that prey selection by species is minimal in *Dissostichus*, *i.e.* predation rates will reflect availability. There is evidently, however, some selection based on prey size, with *D. mawsoni* stomachs containing a greater mass of

larger prey items, such as cephalopods compared to caridean shrimps (Tables I and II). Virtually no within-species variation in diet was detected between sexes and  $L_T$  classes, suggesting minimal ontogenetic shift in diet once recruited to slope populations.

The north-south transition in *Dissostichus* species distribution coincides with the approximate position of the Weddell Front at the South Sandwich Islands (Orsi et al., 1993). This point divides two rather different habitat areas and differences in temperature profile to the north and south are likely to constrain the viable ranges of the two Dissostichus species. Hence, the parapatric speciation of D. mawsoni to life in very cold water appears to create an effective barrier against interspecific competition at the South Sandwich Islands. The contiguous distribution of the two Dissostichus species populations suggests, however, that competition may occur across the narrow horizontal range where both species are able to persist. This would likely be temperature mediated, so called condition-specific competition, as previously demonstrated in experimental salmonid populations (Taniguchi & Nakano, 2000). Under this hypothesis, D. eleginoides would exclude submissive D. mawsoni to the north, either through direct interaction or indirectly through depletion of prey consumed by both species. This dynamic would be reversed to the south and the precise location of the transition in species dominance would depend on interannual difference in front position and ambient temperature. The consequences of fishing at the transition in species dominance may include range expansions of one *Dissostichus* species where the other is selectively removed (Hairston, 1980).

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#### References

- Acker, J. G. & Leptoukh, G. (2007). Online analysis enhances use of NASA earth science data. *Eos Transactions American Geophysical Union* 88, 14–17.
- Agnew, D. J. (2004). Fishing South: History and Management of South Georgia Fisheries. St Albans: The Penna Press.
- Agnew, D. J. H., Jones, C., Watson, A., Berkieta, K. & Pearce, J. (1999). Depth distribution and spawning pattern of *Dissostichus eleginoides* at South Georgia. *CCAMLR Science* 6, 19–36.
- Arkhipkin, A., Brickle, P. & Laptikhovsky, V. (2003). Variation in the diet of the Patagonian toothfish with size, depth and season around the Falkland Islands. *Journal of Fish Biology* 63, 428–441.
- Arntz, W. E. & Brey, T. (2003). The Expedition ANTARKTIS XIX/5 (LAMPOS) of RV "Polarstern" in 2002. Berichte zur Polar-und Meeresforschung 462, 1–120.
- Arntz, W. E., Thatje, S., Gerdes, D., Gili, J. M., Gutt, J., Jacob, U., Montiel, A., Orejas, C. & Teixido, N. (2005). The Antarctic–Magellan connection: macrobenthos ecology on the shelf and upper slope, a progress report. *Scientia Marina* 69, 237–269.
- Barrera-Oro, E. R., Casaux, R. J. & Marschoff, E. R. (2005). Dietary composition of juvenile *Dissostichus eleginoides* (Pisces, Nototheniidae) around Shag Rocks and South Georgia, Antarctica. *Polar Biology* 28, 637–641.

CCAMLR (2005). CCAMLR Scientific Observer Manual. Hobart: CCAMLR.

- Cherel, Y. & Klages, N. (1998). A review of the food of albatrosses. In *Albatross Biology* and Conservation (Robertson, G. & Gales, R., eds), pp. 113–136. Chipping Norton: Surrey Beatty.
- Cherel, Y., Duhamel, G. & Gasco, N. (2004). Cephalopod fauna of subantarctic islands: new information from predators. *Marine Ecology Progress Series* **266**, 143–156.
- Collins, M. A., Ross, K. A., Belchier, M. & Reid, K. (2007). Distribution and diet of juvenile Patagonian toothfish on the South Georgia and Shag Rocks shelves (Southern Ocean). *Marine Biology* 152, 135–147.
- De Witt, H. H., Heemstra, P. C. & Gon, O. (1990). Nototheniidae. In *Fishes of the Southern Ocean* (Gon, O. & Heemstra, P. C., eds), pp. 279–331. Grahamstown: JLB Smith Institute of Ichthyology.
- Eastman, J. T. (1990). The biology and physiological ecology of notothenioid fishes. In *Fishes* of the Southern Ocean (Gon, O. & Heemstra, P. C., eds), pp. 34–51. Grahamstown: JLB Smith Institute of Ichthyology.
- Eastman, J. T. & Barry, J. P. (2002). Underwater video observation of the Antarctic toothfish Dissostichus mawsoni (Perciformes: Nototheniidae) in the Ross Sea, Antarctica. Polar Biology 25, 391–395.
- Evseenko, S. A., Kock, K. H. & Nevinsky, M. M. (1995). Early-life history of the Patagonian toothfish, *Dissostichus eleginoides* Smitt, 1898 in the Atlantic Sector of the Southern-Ocean. Antarctic Science 7, 221–226.
- Fenaughty, J. M., Stevens, D. W. & Hanchet, S. M. (2003). Diet of the Antarctic toothfish (*Dissostichus mawsoni*) from the Ross Sea, Antarctica (subarea 88.1). CCAMLR Science 10, 113–123.
- Fischer, W. & Hureau, J. (1985). FAO Species Identification Sheets for Fishery Purposes, Southern Ocean: Fishing Areas 48, 58 and 88, CCAMLR Convention Area. Rome: FAO.
- Garcia del la Rosa, S. B., Sanchez, F. & Figueroa, D. (1997). Comparative feeding ecology of Patagonian toothfish (*Dissostichus eleginoides*) in the Southwestern Atlantic. *CCAMLR Science* **4**, 105–124.
- Goldsworthy, S., He, X., Tuck, G., Lewis, M. & Williams, R. (2001). Trophic interactions between the Patagonian toothfish its fishery, and seals and seabirds around Macquarie Island. *Marine Ecology Progress Series* 218, 283–302.
- Goldsworthy, S. D., Lewis, M., Williams, R., He, X., Young, J. W. & van den Hoff, J. (2002). Diet of Patagonian toothfish (*Dissostichus eleginoides*) around Macquarie Island, South Pacific Ocean. *Marine and Freshwater Research* **53**, 49–57.
- Gon, O. & Heemstra, P. (1990). Fishes of the Southern Ocean. Grahamstown: J.L.B. Smith Institute of Ichthyology.
- Hairston, N. (1980). The experimental test of an analysis of field distributions competition in terrestrial salamanders. *Ecology* **61**, 817–826.
- Hanchet, S. M., Rickard, G. J., Fenaughty, J. M., Dunn, A. & Williams, M. J. H. (2008). A hypothetical life cycle for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region. *CCAMLR Science* 15, 35–53.
- Hanchet, S. M., Dunn, A. & Mormede, S. (2009). A characterisation of the toothfish fishery in Subareas 88.1 and 88.2 from 1997/98 to 2008/09. *Document WG-FSA 09/36*. Hobart: CCAMLR.
- Hoff, J. (2004). A comparative study of the cephalopod prey of Patagonian toothfish (*Dissostichus eleginoides*) and southern elephant seals (*Mirounga leonina*) near Macquarie Island. *Polar Biology* 27, 604–612.
- Horn, P. L. (2002). Age and growth of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mawsoni*) in waters from the New Zealand subantarctic to the Ross Sea, Antarctica. *Fisheries Research* **56**, 275–287.
- Kock, K. H. (1992). Antarctic Fish and Fisheries. Cambridge: Cambridge University Press.
- McKenna, J. (1991). Trophic relationships within the Antarctic demersal fish community of South Georgia Island. *Fishery Bulletin* **89**, 643–654.
- McKinlay, J. P., Welsford, D. C., Constable, A. J. & Nowara, G. B. (2008). An assessment of the exploratory fishery for *Dissostichus* spp. on Banzare Bank (CCAMLR Division 58.4.3b) based on fine-scale catch and effort data. *CCAMLR Science* **15**, 55–78.

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- Murillo, C., Oyarzun, C. & Fernandez, I. (2008). Latitudinal and temporal variation in the diet of *Dissostichus eleginoides* Smitt, 1898 (Perciformes: Nototheniidae) in deep environments of the south and center coast of Chile. *Gayana* 72, 94–101.
- Nesis, K. (1997). Cephalopods of the World. Neptune City, NJ: TFH Publications.
- Orsi, A., Nowlin, W. & Whitworth, T. (1993). On the circulation and stratification of the Weddell Gyre. *Deep-Sea Research I* 40, 169–203.
- Orsi, A., Whitworth, T. & Nowlin, W. (1995). On the meridional extent and fronts of the Antarctic circumpolar current. *Deep-Sea Research I* **42**, 641–673.
- Pilling, G. M., Purves, M. G., Daw, T. M., Agnew, D. A. & Xavier, J. C. (2001). The stomach contents of Patagonian toothfish around South Georgia (South Atlantic). *Journal* of Fish Biology **59**, 1370–1384.
- Pinkas, L., Oliphant, S. & Iverson, I. (1971). Food habits of albacore, bluefin tuna and bonito in Californian waters. *Californian Fish and Game* 152, 1–105.
- Ramos, A. (1999). The megazoobenthos of the Scotia Arc islands. *Scientia Marina* 63, 171–182.
- Reid, K. (1996). A Guide to the Use of Otoliths in the Study of Predators at South Georgia. Cambridge: British Antarctic Survey.
- Roberts, J. & Agnew, D. J. (2009). Proposal for an extension to the mark–recapture experiment to estimate toothfish population size in the South of Subarea 48.4. WG-FSA-09/18. Hobart: CCAMLR.
- Schoener, T. W. (1970). Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* **51**, 408–418.
- Stevens, D. W. (2004). Stomach contents of the Antarctic toothfish (*Dissostichus mawsoni*) from the Western Ross Sea, Antarctica. *Document WG-FSA 04/31*. Hobart: CCAMLR.
- Taniguchi, Y. & Nakano, S. (2000). Condition-specific competition: implications for the altitudinal distribution of stream fishes. *Ecology* 81, 2027–2039.
- Wallace, H. J. & Ramsay, S. (1983). Reliability in measuring diet overlap. Canadian Journal of Fisheries and Aquatic Sciences 40, 347–351.
- Whitworth, T., Nowlin, W., Orsi, A., Locarnini, R. & Smith, S. (1994). Weddell Sea shelf water in the Bransfield Strait and Weddell-Scotia Confluence. *Deep-Sea Research I* 41, 629–641.
- Williams, R. & McEldowney, A. (1990). A guide to the fish otoliths from waters off the Australian Antarctic Territory, Heard and Macquarie Island. ANARE Research Notes 175, 1–173.
- Xavier, J. C. & Cherel, Y. (2009). Cephalopod Beak Guide for the Southern Ocean. Cambridge: British Antarctic Survey.
- Xavier, J. C., Rodhouse, P. G., Purves, M. G., Daw, T. M., Arata, J. & Pilling, G. M. (2002). Distribution of cephalopods recorded in the diet of the Patagonian toothfish (*Dissos-tichus eleginoides*) around South Georgia. *Polar Biology* 25, 323–330.
- Xavier, J. C., Croxall, J. P., Trathan, P. N. & Rodhouse, P. G. (2003). Inter-annual variation in the cephalopod component of the diet of wandering albatrosses *Diomedea exulans* breeding at Bird Island, South Georgia. *Marine Biology* 26, 20–26.