

## A HYPOTHETICAL LIFE CYCLE FOR ANTARCTIC TOOTHFISH (*DISSOSTICHUS MAWSONI*) IN THE ROSS SEA REGION

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### Abstract

Aspects of the reproduction, size distribution and movements of Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region are reviewed. Based on the presumed location and timing of spawning and the probable early life-history characteristics of toothfish, the drift of eggs and larvae over a 6–24 month period were investigated using an oceanic circulation model linked to the high-resolution global environmental model (HiGEM). Model outputs indicated that the locations of toothfish larvae after an 18–24 month period were moderately consistent with the distribution of the smallest toothfish taken in the toothfish fishery.

The hypothesis presented is that *D. mawsoni* in CCAMLR Subareas 88.1 and 88.2 spawn mainly on the ridges and banks of the Pacific-Antarctic ridge to the north and east of the Ross Sea. The spawning appears to take place during the austral winter and spring. Depending on the exact location of spawning, eggs and larvae become entrained by the Ross Sea gyres, and may move west, settling out around the Balleny Islands and adjacent Antarctic continental shelf; south onto the Ross Sea shelf; or eastwards with the eastern Ross Sea gyre, settling out along the continental slope and shelf to the east of the Ross Sea in Subarea 88.2. As the juveniles grow in size, they move west back towards the Ross Sea shelf and then move out into deeper water. As they mature, the fish gradually move deeper out onto the continental slope where they gain condition before undergoing a northwards spawning migration to the Pacific-Antarctic Ridge to start the cycle again. Toothfish probably remain in the northern area for 6–18 months before migrating back to the slope to regain condition.

### Résumé

Divers aspects de la reproduction, la distribution de tailles et les déplacements de la légine antarctique (*Dissostichus mawsoni*) de la région de la mer de Ross sont examinés. À partir du lieu et de l'époque présumés de la reproduction et des caractéristiques probables des stades précoces du cycle vital de la légine, la dérive des œufs et des larves sur une période de 6 à 24 mois est étudiée au moyen d'un modèle de circulation océanique couplé à un modèle global de l'environnement à haute résolution (HiGEM). Les résultats des modèles indiquent qu'à l'issue d'une période de 18 à 24 mois, l'emplacement des larves de légine correspond moyennement à la répartition des légines de la plus petite taille capturées dans la pêcherie de légine.

Dans l'hypothèse présentée, *D. mawsoni* des sous-zones 88.1 et 88.2 de la CCAMLR se reproduit principalement sur les dorsales et les bancs de la ride Pacifique-Antarctique, au nord et à l'est de la mer de Ross. La reproduction semble se dérouler pendant l'hiver et le printemps australs. Selon l'emplacement exact de la reproduction, les œufs et les larves sont entraînés par les tourbillons de la mer Ross et vont se développer soit vers l'ouest, autour des îles Balleny et du plateau continental antarctique adjacent, soit au sud sur le plateau de la mer de Ross, ou encore vers l'est, emportés par le tourbillon est de la mer de Ross qui les déposera le long de la pente et du plateau continental à l'est de la mer de Ross, dans la sous-zone 88.2. En grandissant, les juvéniles se dirigent vers l'ouest pour revenir vers le plateau de la mer de Ross avant de descendre en eau plus profonde. Durant la période de maturité, les poissons s'enfoncent progressivement le long de la pente continentale où ils se préparent à la migration de reproduction vers le nord pour rejoindre la ride Pacifique-Antarctique et démarrer un nouveau cycle. La légine passe probablement 6 à 18 mois dans la région nord avant de rejoindre la pente où elle reconstitue ses réserves.

#### Резюме

Рассматриваются вопросы воспроизводства, размерного распределения и перемещения антарктического клыкача (*Dissostichus mawsoni*) в районе моря Росса. На основании предполагаемых места и времени нереста, а также возможных характеристик начальных стадий жизненного цикла клыкача исследовался перенос икры и личинок за период 6–24 месяцев с использованием модели океанической циркуляции, связанной с глобальной моделью окружающей среды с высоким разрешением (HiGEM). **Результаты моделирования показали, что местонахождение личинок клыкача по прошествии 18–24 месяцев более соответствовало распределению самых мелких особей клыкача, полученных в ходе промысла клыкача.**

Выдвигается гипотеза о том, что *D. mawsoni* в подрайонах АНТКОМа 88.1 и 88.2 нерестятся в основном на хребтах и банках Тихоокеанско-Антарктического хребта к северу и востоку от моря Росса. Нерест, **по-видимому, происходит во время австралийской зимы и весны. В зависимости от точного места нереста икра и личинки захватываются круговоротами моря Росса и могут перемещаться на запад (оседая вокруг о-вов Баллени и прилегающего континентального шельфа Антарктиды), на юг к шельфу моря Росса или на восток с восточным течением моря Росса (оседая вдоль континентального склона и шельфа к востоку от моря Росса в Подрайоне 88.2).** По мере роста, молодь возвращается на запад к шельфу моря Росса, а затем перемещается на большую глубину. По мере достижения половозрелости рыба постепенно перемещается глубже, на континентальный склон, где она набирает вес перед нерестовой миграцией на север к Тихоокеанско-Антарктическому хребту, что служит началом следующего жизненного цикла. Клыкач, по-видимому, остается в северном районе в течение 6–18 месяцев, прежде чем вернуться на склон для восстановления веса.

#### Resumen

Se han examinado algunos aspectos pertinentes a la reproducción, distribución de tallas y desplazamiento de la austromerluza antártica (*Dissostichus mawsoni*) en la región del Mar de Ross. Sobre la base de la supuesta zona y época de desove y las características más probables de los primeros estadios de vida de las austromerluzas, se utilizó un modelo de circulación oceánica acoplado a un modelo del medio ambiente mundial de alta resolución (HiGEM) para estudiar la deriva de huevos y de larvas durante un período de 6–24 meses. Los resultados del modelo indicaron que los lugares donde se encontrarían larvas de austromerluza después de un período de 18–24 meses concordaban moderadamente con la distribución de la austromerluza más pequeña extraída en la pesquería de este recurso.

La hipótesis planteada es que *D. mawsoni* en las Subáreas 88.1 y 88.2 de la CCRVMA desova principalmente en las crestas y bancos de la Dorsal Pacífico-Antártica, al norte y este del Mar de Ross. Aparentemente, el desove ocurre durante el invierno y la primavera austral. Dependiendo de la ubicación exacta del desove, los huevos y larvas son arrastrados por los giros del Mar de Ross, y pueden moverse hacia el oeste, asentándose alrededor de las islas Balleny y de la plataforma continental antártica adyacente; o hacia el sur en la plataforma del Mar de Ross; o hacia el este arrastrados por el giro este del Mar de Ross, asentándose a lo largo del talud y plataforma continental al este del Mar de Ross en la Subárea 88.2. A medida que los juveniles crecen se desplazan hacia el oeste, de vuelta a la plataforma del

Mar de Ross y luego a aguas más profundas. A medida que maduran, los peces se mueven gradualmente a aguas más profundas en el talud continental donde su condición mejora antes de emigrar hacia el norte para desovar en la Dorsal Pacífico-Antártica y comenzar nuevamente el ciclo. Las austrormerluzas probablemente permanecen en la zona norte durante 6–18 meses antes de emigrar de vuelta al talud para recuperar su estado físico.

Keywords: Antarctic toothfish, *Dissostichus mawsoni*, modelling larval drift, life history, Ross Sea, CCAMLR

## Introduction

A longline fishery for Antarctic toothfish (*Dissostichus mawsoni*) has been operating within CCAMLR Subarea 88.1 since the 1996/97 summer season when a single vessel fished there. Since that time this exploratory fishery has expanded, with a peak of 21 vessels fishing in 2003/04, 13 vessels in 2005/06, and 15 in 2006/07. The exploratory fishery has also extended into Subarea 88.2 (Hanchet et al., 2007) and a research trip was carried out into Subarea 88.3 (Patchell, 2005).

Over the past 10 years considerable amounts of data have been gathered from *D. mawsoni* caught in the fishery. The fishery has been characterised annually since 2000 providing a good understanding of the depth, location and size and age distribution of the *D. mawsoni* catch (e.g. Hanchet et al., 2003, 2007). This has also provided a moderately good understanding of its distribution and abundance (e.g. Dunn and Hanchet, 2006; Fenaughty, 2006), age and growth (Horn, 2002; Horn et al., 2003), diet (Fenaughty et al., 2003) and, to a lesser extent, reproduction (e.g. Patchell, 2001, 2002; Livingston and Grimes, 2005). Much of these data were recently reviewed and summarised by Hanchet (2006).

Despite a reasonable understanding of the fishery, and of many aspects of toothfish biology, knowledge of the spawning behaviour and early life history is poor. The spawning behaviour and life history have been identified as important gaps in current knowledge (e.g. Eastman and De Vries, 2000; Fenaughty, 2006; Hanchet, 2006). The key questions concerning these aspects of biology are: (i) where and how frequently (i.e. annual, biennial, triennial) do toothfish spawn? and (ii) where do the eggs and larvae go to? The answers to both of these questions have important implications for the management of toothfish in Subareas 88.1, 88.2 and 88.3.

There have been several attempts at developing a life cycle for *D. mawsoni*. Yukhov (1982) drew together unpublished and published material on *D. mawsoni* from the Ross Sea and other parts of the Antarctic to present a hypothetical life history

for this species (reported in Eastman and De Vries, 2000). This model divided the life cycle into three main stages: (i) larvae and small juveniles up to 12 cm which lived in the surface of the water column; (ii) older juveniles and sub-adults which lived on or near the seabed in coastal waters; and (iii) sexually mature adults (>90–100 cm) which migrated to the Antarctic Polar Front during the summer months where they fed on squid. Yukhov (1982) believed that the adult toothfish returned to coastal waters to spawn in late austral winter/early spring, and that this migration occurred repeatedly (although not necessarily every year) throughout their life cycle.

Eastman and De Vries (2000) summarised Yukhov's research and related it to their studies of *D. mawsoni* at McMurdo Sound. They noted that between September and December, toothfish gonads were in the resting stage and that they were feeding on Antarctic silverfish (*Pleuragramma antarcticum*) before the northward migratory phase of their life cycle. Hanchet et al. (2003) updated the life cycle with new data derived mainly from the toothfish fishery. They noted discrepancies between the hypothesised migrations and the observed fish distribution in the fishery. For example, adult toothfish are found throughout the Ross Sea shelf and slope during the summer months, which questions the idea of a large-scale northward migration to the Polar Front during the summer months. More recently, Fenaughty (2006) has highlighted significant biological differences between *D. mawsoni* found in the north on the Pacific-Antarctic Ridge and those in the south, found on the shelf and slope.

The objective of the current paper is to develop a plausible life history for *D. mawsoni* in the Ross Sea region, including aspects of distribution, reproduction, behaviour and movements, in order to answer some of the following key questions:

- Where and when do the toothfish spawn?
- Where do the eggs and larvae go?
- Where are the juvenile, sub-adult and adult toothfish?
- How do the adult toothfish get to the spawning grounds?

## Methods

### Biological data

Biological data (including length, sex, weight and gonad stage) for *D. mawsoni* have been collected by scientific observers since the Ross Sea toothfish fishery began in 1996/97 in accordance with the CCAMLR Scheme of International Scientific Observation (CCAMLR, 2006). Although the gonad stages have also been routinely recorded using the CCAMLR five-point staging system (Kock and Kellermann, 1991), these data have limited use because most fish are resting or maturing while the fishery takes place (Patchell, 2001, 2002). Since 2002/03, gonads have also been weighed on the vessels from New Zealand, usually on motion-compensated scales to the nearest 10 g. All data collected from the Ross Sea fishery since 1996/97 were extracted and, where possible, used in the analysis.

The weight data were used to calculate a gonadosomatic index (GSI) as follows:

$$\text{GSI} = (\text{gonad weight (kg)} / \text{wet body weight (kg)}) \times 100.$$

The analysis of GSI data was restricted to fish longer than 100 cm – the assumed length at 50% maturity for *D. mawsoni* (Hanchet, 2006). Separate analyses were made for the areas north and south of latitude 70°S following Fenaughty (2006). The data were plotted as density-distribution plots.

To illustrate the location where juvenile, sub-adult and adult toothfish occur in Subareas 88.1 and 88.2, the median length of fish caught in all sets in each small 20' latitude by 20' longitude cell was calculated. These median lengths were then grouped into one of five length categories and plotted.

An insight into movements of *D. mawsoni* has come from two tagging programs in Subarea 88.1. Over 4 500 *D. mawsoni* have been tagged since 1972 by US researchers in McMurdo Sound (Eastman and De Vries, 2000; A. De Vries, pers. comm.). In addition, over 15 000 *D. mawsoni* have now been tagged in Subareas 88.1 and 88.2 as part of a CCAMLR toothfish tagging program (Dunn et al., 2007). The location of released and recaptured toothfish from both tagging programs are presented and discussed to infer possible movements and migrations.

### Circulation model

There are no published records of *D. mawsoni* eggs or larvae (Hanchet, 2006). Circulation models

have been used elsewhere to provide some insight into plausible movement patterns of eggs and larvae of fish (Heath and Gallego, 1998; Adlandsvik et al., 2004). The aim here was to use ocean current simulations to identify probable patterns of dispersal from potential spawning grounds for the first 6–24 months of the *D. mawsoni* life cycle.

In order to be able to integrate trajectories, the circulation is taken from a high-resolution global environmental model (HiGEM) recently run on the Earth Simulator in Japan as part of a joint research project with the Hadley Centre at the UK Meteorological Office ([www.higem.nerc.ac.uk](http://www.higem.nerc.ac.uk)). There are many sources of climatological and real-time ocean circulation models presently available, but HiGEM has the advantages of being fully global (and hence covering the whole of the Ross Sea except that part under the Ross Ice Shelf), being coupled to an atmosphere and sea-ice model, and having relatively good spatial resolution for the area of interest. HiGEM includes a sea-ice model that interacts with both the ocean and atmosphere components of the climate model, but does not model interactions with ice shelves. Hence, the model currents include sea-ice influences, but not effects due to ice shelves. Further details of the model and model validation are given in Rickard et al. (2007).

### Predicted circulation patterns from HiGEM

The circulation pattern produced by HiGEM has two gyre systems (Figure 1). A smaller gyre system (the western Ross Sea gyre) is centred at about 65°S 170°E and rotates clockwise around the Balleny Islands ridge. It is separated by slightly deeper water from a second much larger gyre to the east (the eastern Ross Sea gyre), which is centred at about 165°W 70°S. Water in this gyre is transported to the northeast in the Antarctic Circumpolar Current (ACC), before being deflected south towards the Antarctic coast and then west as part of the Antarctic coastal countercurrent. This countercurrent connects the southern edge of both gyres, and continues to the west beyond the western Ross Sea gyre.

Rickard et al. (2007) noted that the location and peak transport of the eastern gyre, predicted by the HiGEM model, agreed reasonably well with recent modelling by Assmann and Timmermann (2005) and Chu and Fan (2007). However, neither model had the western gyre predicted by HiGEM, whilst Assmann and Timmermann (2005) had an additional weaker 'far eastern gyre'. Rickard et al. (2007) concluded that simulation of the Ross Sea gyre was sensitive to the model choice and forcing.

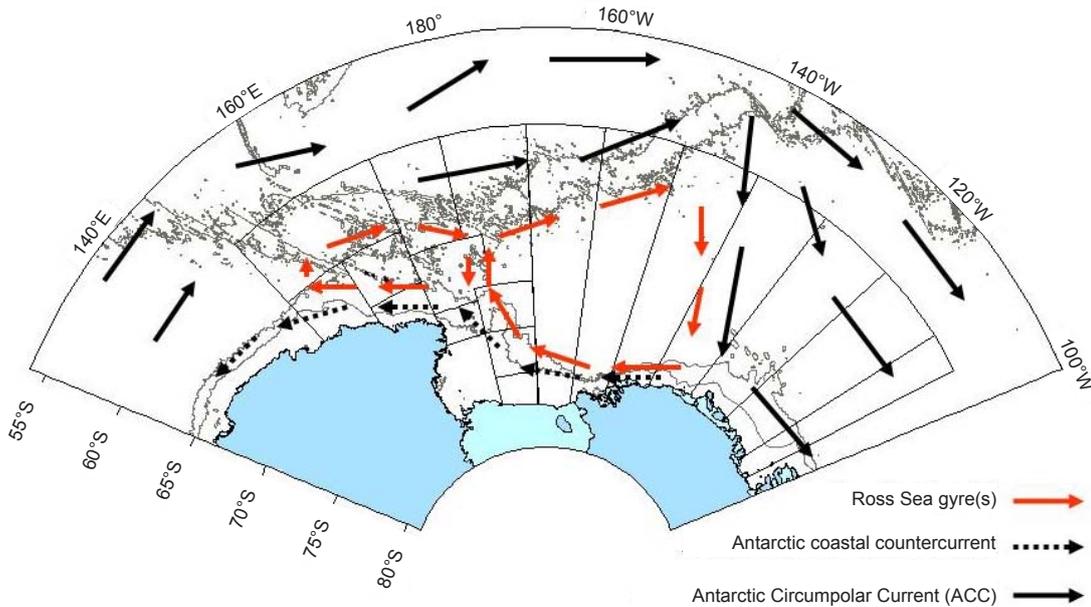


Figure 1: Schematic of the annual mean HiGEM depth-averaged circulation showing modelled locations of the Antarctic Circumpolar Current, Antarctic coastal countercurrent and Ross Sea gyres. Depth contours at 1 000 and 3 000 m.

### Modelling egg and larval drift

To model egg and larval drift requires: location, date and depth of spawning; buoyancy of the eggs and the egg development time; and depth and period of passive larval drift.

#### Location, date and depth of spawning

The approximate location and timing of spawning was obtained from the biological data (see 'Results'). For the purpose of the modelling it was therefore assumed that spawning occurs between June and November on the topographic features in the area immediately to the north of the Ross Sea. The depth of spawning in *D. mawsoni* is unknown. Although *D. eleginoides* in Subarea 48.3 spawn in depths of about 1 000 m (Agnew et al., 1999), most of the northern hills are deeper than 1 000 m. So, assuming that spawning takes place on the bottom, spawning in *D. mawsoni* is more likely to be in depths of 1 000–1 600 m.

#### Buoyancy of the eggs and the egg development time

There appear to be no published records of *D. mawsoni* eggs from plankton samples, and only a few records of *D. eleginoides* eggs (North, 2002). Eight eggs were recorded by Kellermann (1989), whilst seven eggs of about 4.5 mm diameter were sampled offshore to the north of South Georgia in

the upper 700 m of the water column by Evseenko et al. (1995). Evseenko et al. (1995) and North (2002) considered that *D. eleginoides* eggs were most likely to be pelagic, but did not rule out the possibility that they could initially be demersal, as suggested by Zhivov and Krivoruchko (1990).

The egg development time for *D. mawsoni* has not been reported. However, La Mesa (2007) identified presumed hatching checks and first feeding checks in the core region of sagittal otoliths from *D. mawsoni* collected around the South Shetland Islands. By counting the micro-increments since the presumed hatching check, La Mesa estimated the hatching dates to range from November to February with a peak in December. The timing of spawning at the South Shetland Islands is unknown, but assuming a winter–spring spawning time with a peak in July/August would suggest an egg development time of 4–5 months. This is similar to the egg development time for *D. eleginoides*, which has been reported as 3–3.5 months (Evseenko et al., 1995; North, 2002).

#### Depth and period of passive larval drift

There appear to be no published records of *D. mawsoni* larvae from plankton samples. More data are available for the larval and early juvenile stages of *D. eleginoides* (North, 2002). *Dissostichus eleginoides* larvae at South Georgia are believed to hatch at around 15 mm SL in November/December. The

smallest (18 mm SL) larva was caught in 16–62 m depth over a bottom depth of 1 500 m. Most of the 43 larval and early juvenile stages (18–63 mm SL) were caught at night and in the upper 250 m, with over 50% taken at the sea surface (upper 3 m).

The period of passive larval drift is unknown but is likely to last several months, with the post-larvae/young juveniles starting to swim more actively during late summer/autumn.

#### Simulating egg and larval drift

Using interpolated, monthly mean, HiGEM velocity fields, eggs and larvae (here referred to as floats) have been seeded and then tracked to provide estimates of dispersal in space and time. An area between 160°E and 175°W, and between 72.5°S and 62.5°S, has been uniformly populated with floats (here 3 888 of them, comprising 72 columns and 54 rows) (see Figure 5). This region spans suggested toothfish spawning sites (see above). Because of uncertainty over the depth of release and subsequent transport of toothfish eggs and larvae (see above), dispersal was modelled at four different model depth levels: 25, 146, 530 and 1 376 m.

For the simulations reported here, the floats were released at the end of June and the locations of the floats were plotted after periods of 6, 12, 18, 24 and 36 months. The drifting period was extended to 36 months to determine potential long-term trajectories, even though post-larval toothfish are unlikely to be drifting passively after a period of 18–24 months.

## Results

### Timing and location of spawning

The timing and location of spawning was recently reviewed by Hanchet (2006) and Fenaughty (2006). GSI data collected from the fishery up to 2004/05 for all fish >100 cm were presented by Hanchet (2006). These data are presented as distribution plots in Figure 2. Based on the steady increase in the gonadosomatic index (GSI) of both males and females during the season from December to May, it can be concluded that spawning is unlikely to start until at least June. Some ovaries collected at the beginning of December from the northern area show signs of having recently spawned (Fenaughty, 2006). Therefore, spawning is believed to occur at least during the winter and spring probably extending from June to November.

The currently available evidence also suggests that there is very little spawning on the Ross Sea

shelf or slope. The GSI of both males and females remained very low to the south of 70°S, but increased steadily during the season on the hills, banks and ridges to the north of 70°S (Figure 2).

### Distribution of juvenile, sub-adult and adult *D. mawsoni*

No small juvenile toothfish (<40 cm) have been caught in the Ross Sea toothfish fishery. Larger juveniles (40–80 cm) show quite localised distributions, being found around the Balleny Islands in SSRU 881E, in the south of SSRUs 882A and 882F, as well as being scattered across the shelf in SSRUs 881H, 881J and 881L (Figure 3). Although most of these locations are typically in relatively shallow water of <800 m depth, the fish found in SSRU 882F were in 1 000–1 500 m depth (Hanchet et al., 2007). Research fishing carried out on the continental slope further east in Subarea 88.3 also caught predominantly small fish ranging from 40–80 cm (Arana and Vega, 1999; Patchell, 2005).

Sub-adult toothfish (80–100 cm) tend to be found mainly on the Ross Sea shelf and around the Balleny Islands (Figure 3). They appear to be the main size group found in SSRU 881L, and are also found around Scott Island and in Terra Nova Trench in SSRU 881J at about 1 000 m depth. They also appear to be scattered along the 1 000 m depth contour in SSRUs 881H and 881K, with isolated occurrences in SSRUs 881F and 882G.

Maturing toothfish (100–120 cm) predominate in deeper water beyond the 1 000 m depth contour on the continental slope of the Ross Sea (Figure 3). The largest adult toothfish are more consistently caught on the banks, ridges and hills in SSRUs 881A–G and 882E in depths of 1 000–1 800 m. Larger fish are clearly found deeper and further north throughout most of the area.

### Movement and migration of *D. mawsoni*

Over 4 500 *D. mawsoni* have been tagged in the vicinity of McMurdo Sound by US scientists since 1972 (Eastman and De Vries, 2000). Of these, 17 have been recaptured at McMurdo Sound (A. De Vries, pers. comm.) and five have been recaptured by commercial fishing vessels (Dunn et al., 2007). Of these, one fish was recaptured on the continental slope in SSRU 881H, three were recaptured on the banks and ridges to the north of the Ross Sea (SSRU 881C), whilst the fifth was recaptured a distance of 2 300 km to the northeast in SSRU 882E (Figure 4). All five recaptured fish were sexually mature.

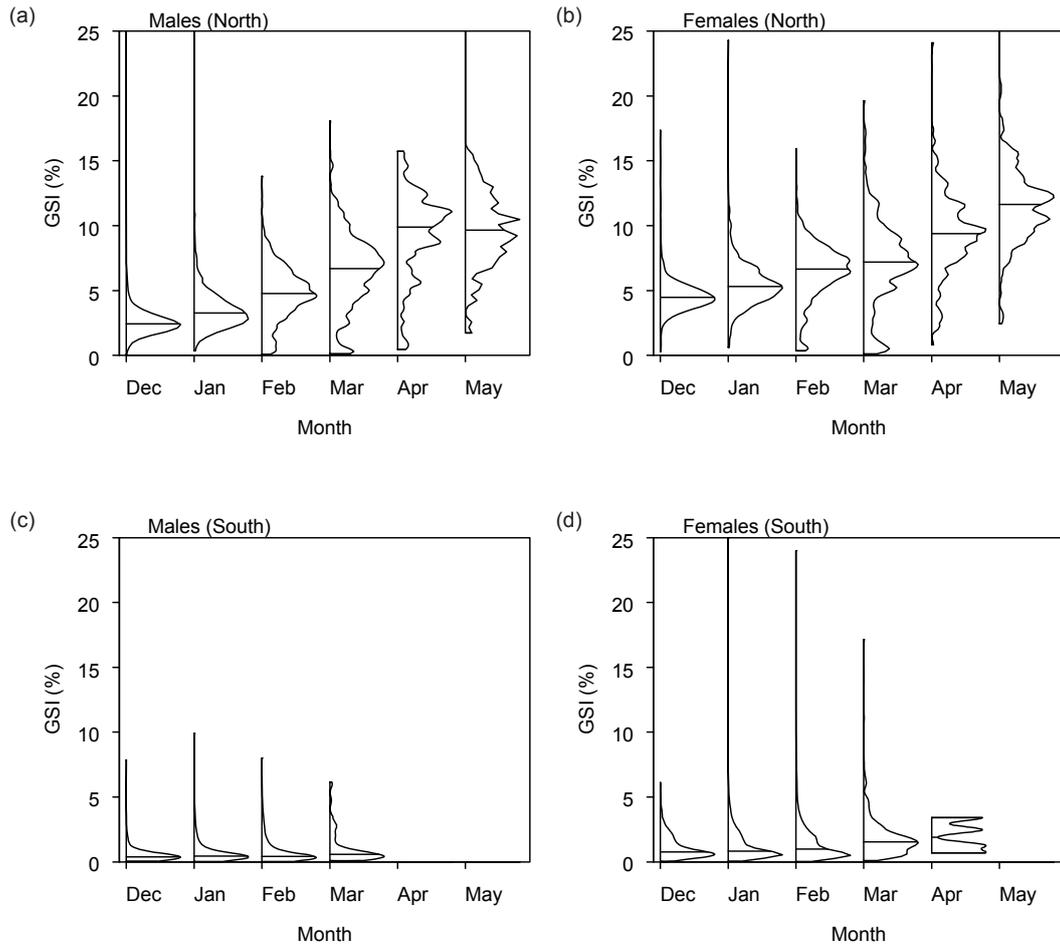


Figure 2: Distribution (and median) of the gonadosomatic index (percent) for male and female *Dissostichus mawsoni* to the north and south of 70°S from December to May for all years and all vessels.

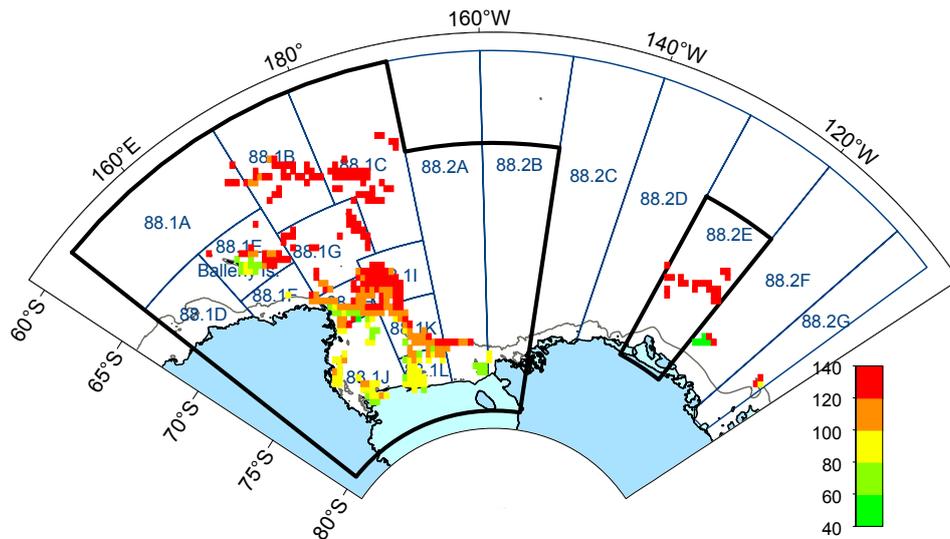


Figure 3: Median length categories of *Dissostichus mawsoni* caught in Subareas 88.1 and 88.2 by location, 1997–2007. Also shown are the Ross Sea and SSRU 88.2E areas (bounded regions), the small-scale statistical research units (SSRUs), and the 1 000 m depth contour.

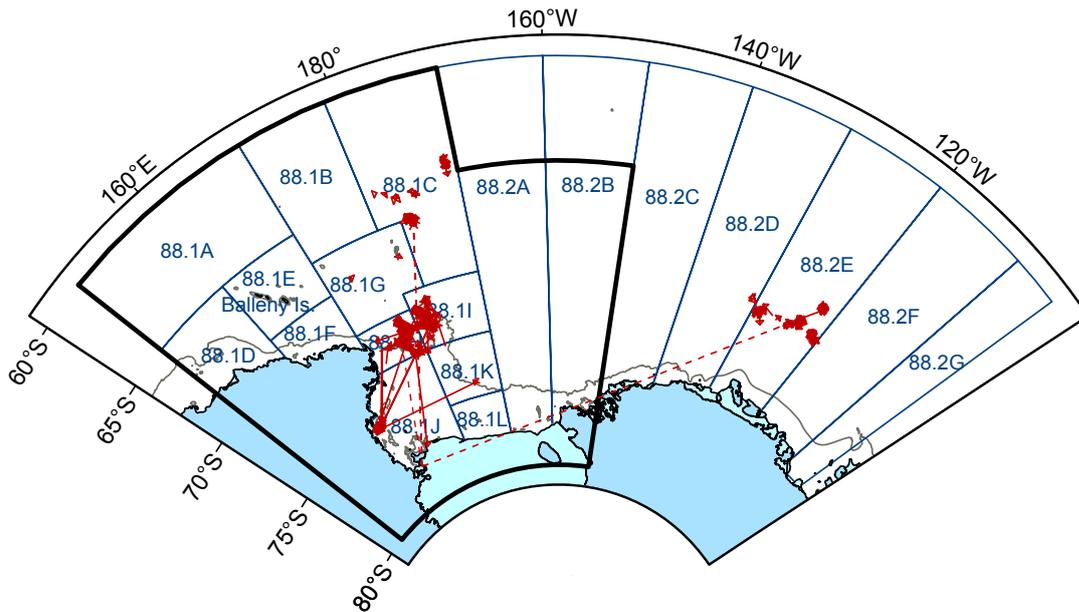


Figure 4: Movements of released and recaptured *Dissostichus mawsoni* for (solid lines) those released by commercial fishing operations, and (dashed lines) those released at McMurdo Sound by US scientists.

Over 15 000 *D. mawsoni* have now been tagged in Subareas 88.1 and 88.2 as part of a toothfish tagging program, and 458 fish have been recaptured (Dunn et al., 2007). Despite the large numbers of tags that have been released and recaptured in this program, there have been few long-distance movements, and none matching the scale of movements seen in the McMurdo fish. During the 2007 season, six fish moved significant distances from the slope fisheries in SSRUs 881H, 881I and 881K to grounds off Terra Nova Bay and Ross Island in SSRU 881J. Other than these few longer-distance movements, most fish have moved short distances, typically less than 50 km. Juvenile and sub-adult fish of length <80 cm and 80–100 cm respectively showed the greatest average distances travelled by fish between release and recapture.

#### Simulating egg and larval drift

The location of floats released at a model depth of 146 m at time zero, and after 6, 12, 18, 24 and 36 months are shown in Figure 5. In each figure, each frame is labelled with the depth at release, and the time elapsed in months since release. The colours of each float relates back to their initial position at time zero. The movements of the releases at 25 and 530 m are not shown but are referred to in the text and their locations after 24 months are summarised in Figure 6. The deeper releases at 1 376 m are not shown but showed similar but

slower dispersal patterns to those at 146 and 530 m (i.e. the floats went in the same direction but at a much slower rate).

For the green end of the spectrum of floats, the general dispersal is fairly independent of depth (Figure 5). The presence of an Antarctic coastal countercurrent is very clear to the west of the Ross Sea, with a number of floats swept in that direction. A number of these floats also found their way onto the Ross Sea continental shelf, especially for the shallower depths at 25 and 146 m, where the depth level does not intersect the continental shelf.

For the red end of the spectrum of floats, the majority is swept to the northeast at all depths (Figure 5); this flow is associated with the northern edge of the Ross Sea gyre. At 25 m, the floats continued to the east, where they eventually pile up at the edge of the integration domain used here. However, at the other depths, a significant proportion of the red floats veered to the south at around 62°S 150°W, coincident with the eastern end of the model's eastern gyre (see Figure 1). These floats then continue to drift southwards towards the coastline at the eastern end of the Ross Sea in Subarea 88.2. As floats approach the coastline, they become separated by the circulation, with some returning westwards into the Ross Sea on the southern side of the gyre, whereas the remainder became entrained in the eastward flowing component comprising the model extension of the ACC (see Figure 1).

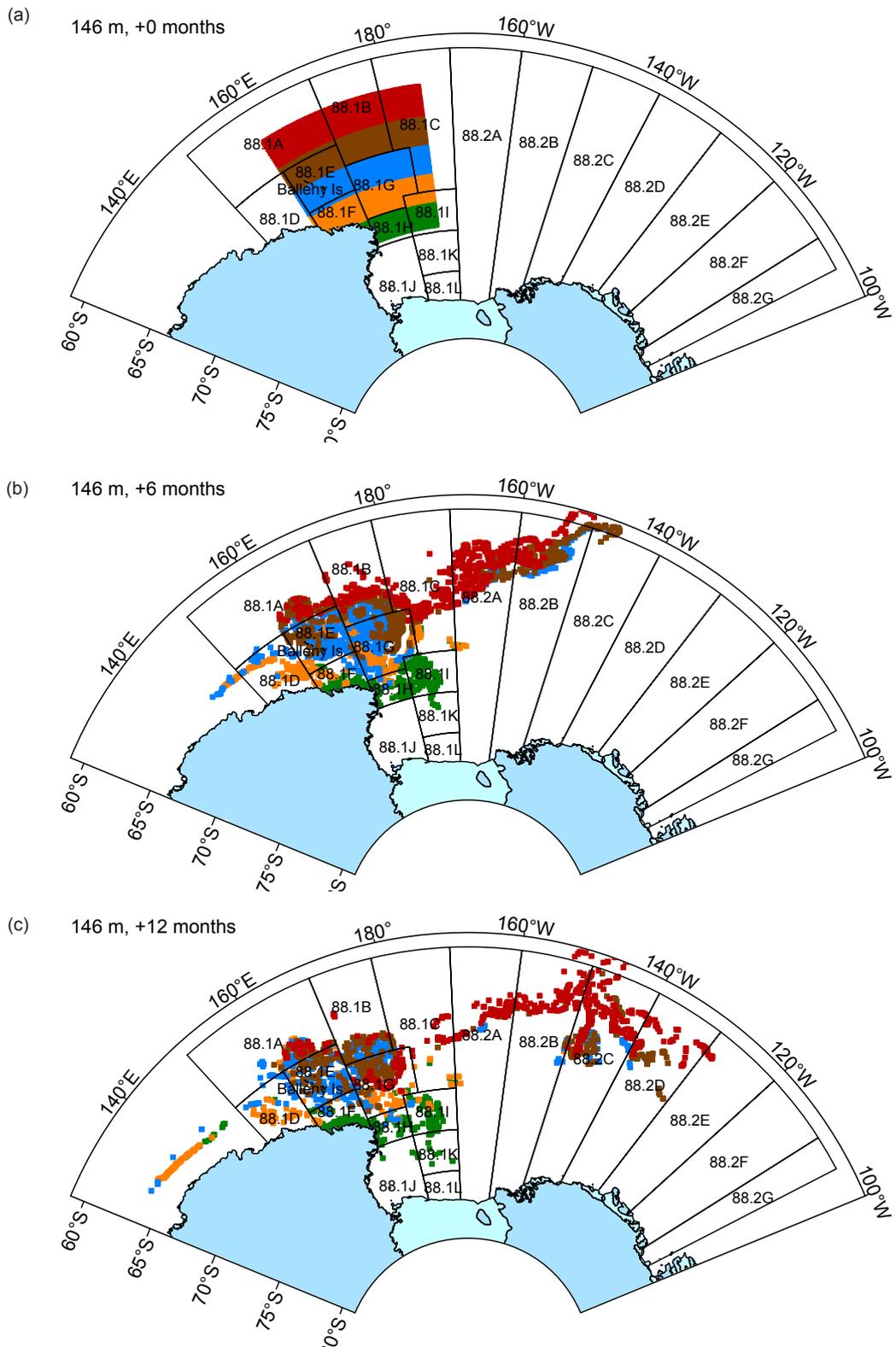


Figure 5: Dispersal pattern for initial positions at 146 m depth: (a) at time zero; (b) after 6 months; (c) after 12 months.

(continued)

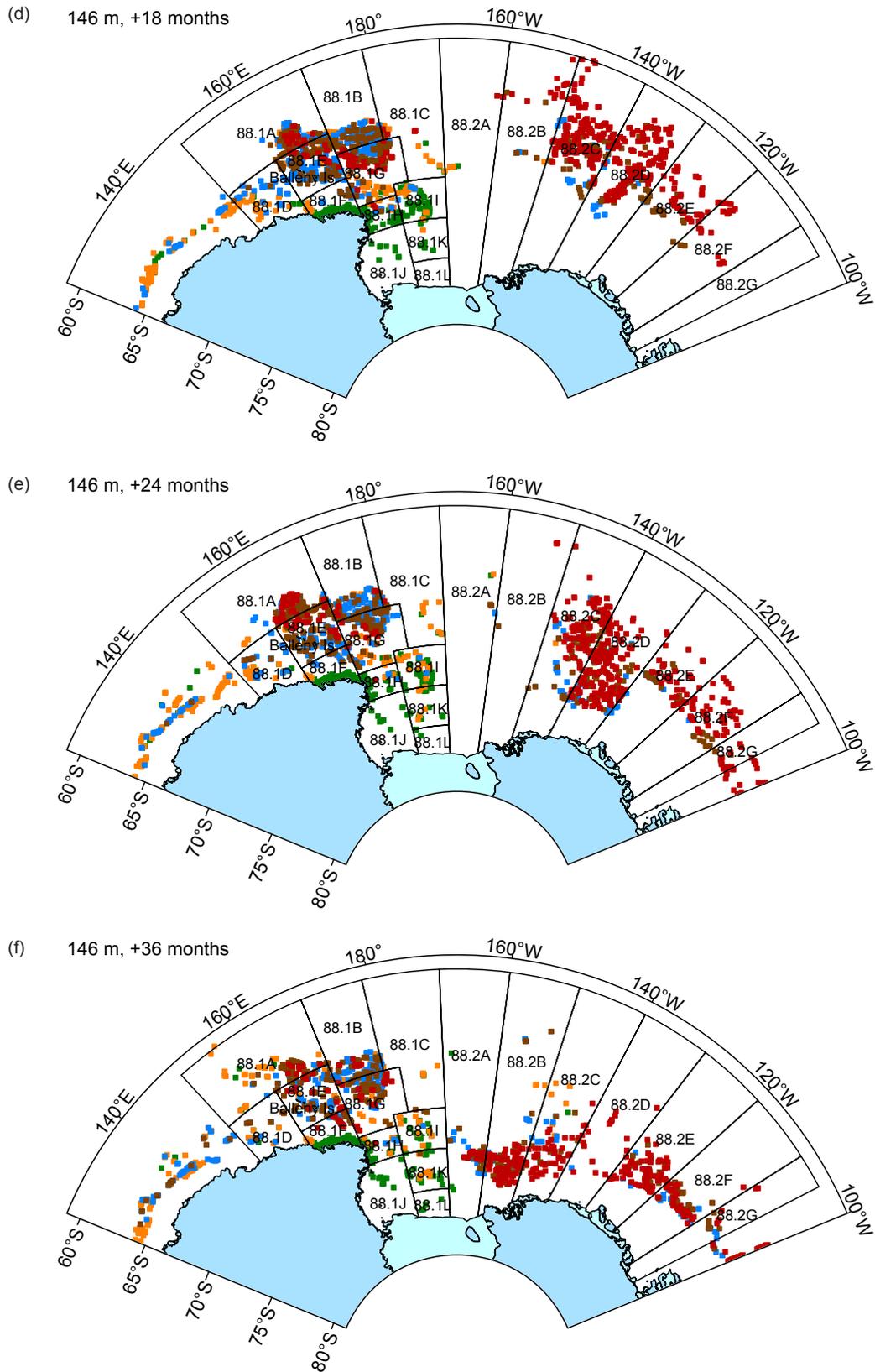


Figure 5 (continued): Dispersal pattern for initial positions at 146 m depth: (d) after 18 months; (e) after 24 months; and (f) after 36 months.

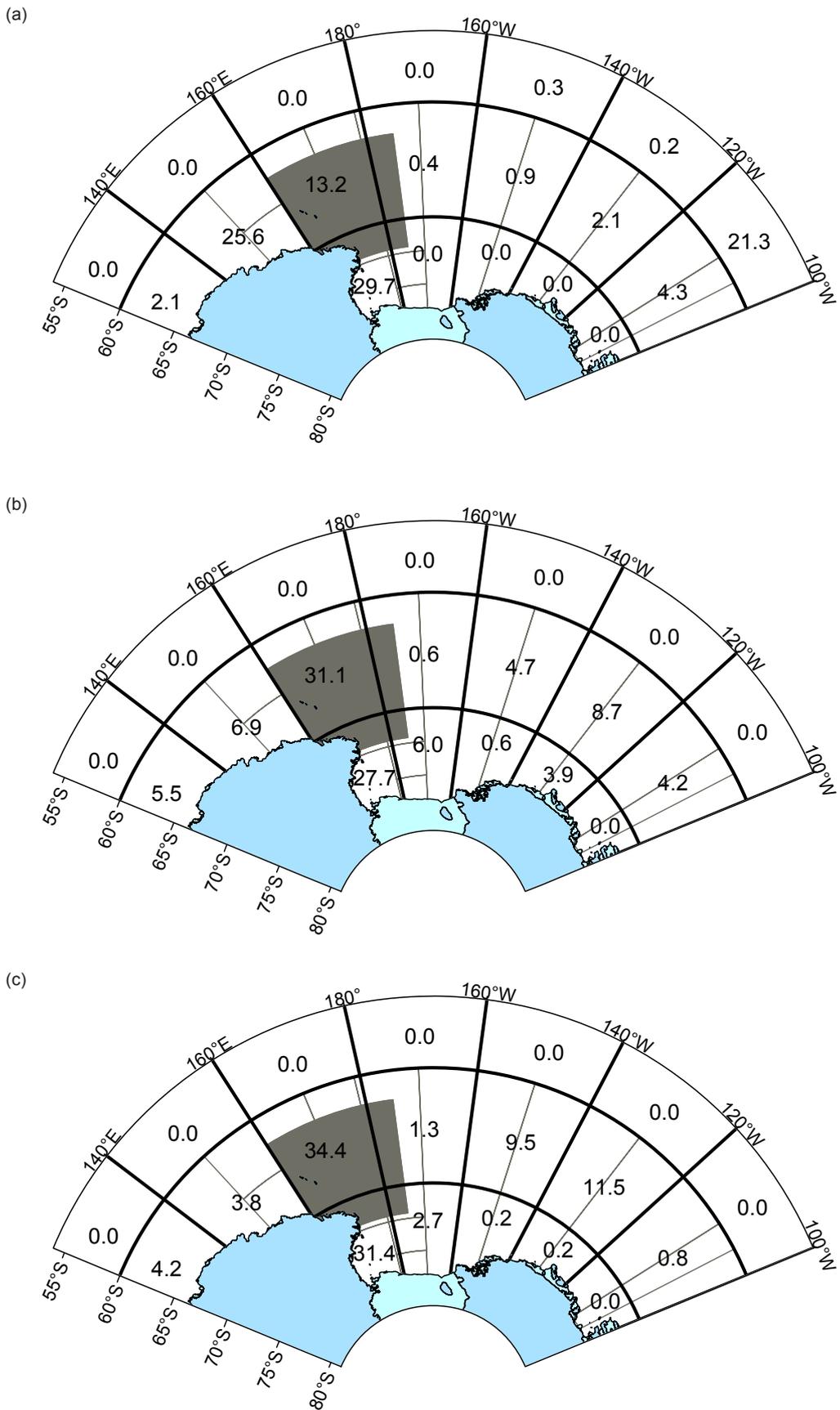


Figure 6: Percentage distribution of floats in each of 19 sub-regions at the end of the two-year simulation period for floats released at depths of: (a) 26; (b) 146; and (c) 530 m. The shaded area shows the area of release.

At a release depth of 146 m, these red floats take about two years to reach the continental shelf at the eastern end of the Ross Sea (Figure 5). At deeper release depths, the floats take slightly longer to reach the same location. This suggests that a vertical shear in the horizontal model currents is acting to separate out the near-surface floats from the rest, and is setting this time delay for the floats deeper in the water column.

After two years the majority of floats released at 25 m had left the area from where they were released. At the other depths, however, a relatively larger number are still recirculating in the vicinity of the release area. This is because many of the floats have been released over a region spanning the eastern and western Ross Sea gyres in the model. Each gyre is bounded to the north by the main circulation in the ACC, and to the south by coastline and/or bathymetry and flow in the Antarctic counter-current. A number of floats below the surface are clearly being retained by the complex model flow pattern in this region.

#### Seasonal effects

The floats detailed previously were all released at the end of June. However, the spawning time probably lies between June and October (see above). The time of release could be relevant if there is an obvious seasonality to the flow speeds in the Ross Sea gyre and environs. Seasonal model transport anomalies were explored by Rickard et al. (2007), but were found to be insignificant over the time period in question.

#### Cumulative float statistics

Figure 5 is clearly not detailed enough to show the distribution of all the released floats. Therefore, cumulative float statistics are provided for 19 sub-regions, each 10° in latitude and 20° in longitude. The number of floats per sub-region after two years from release was counted, and then plotted as percentages of the total number of floats at each release depth (Figure 6a–c). Note that floats which reach the boundary of the model (i.e. 130°E or 100°W) accumulate in the appropriate region.

The plot shows that over 25% of the floats released at 25 m depth had been swept eastwards by the main body of the ACC and out of the area, almost 30% had moved west on to the continental slope, and almost 30% had moved south on to the Ross Sea shelf (Figure 6a). The region covering the area where most of the floats are released is

relatively depleted, and none of the floats ended up on the slope or shelf to the east of the Ross Sea.

Of the floats released at 146 m depth, about 30% were retained in the area of release, about 12% moved west with the western Ross Sea gyre, almost 35% moved south onto the Ross Sea shelf (Figure 6b). The remaining 25% were spread out to the east with about 5% reaching the continental slope to the east of the Ross Sea.

Of the floats released at 530 m depth, almost 35% of the floats had remained in the area of release and almost 35% had moved south on to the Ross Sea shelf (Figure 6c). As discussed earlier, floats released at 530 m (and 1376 m) tended to lag behind those released at 146 m depth and have moved shorter distances. Thus, of those deeper floats which became entrained in the eastern Ross Sea gyre, there is a higher proportion between 60°S and 70°S and lower proportions between 70°S and 80°S compared to floats released at 146 m. Floats which become entrained in the western Ross Sea gyre have a shorter distance to travel, so the numbers of floats in the regions of the Antarctic coast to the west of the Ross Sea were more similar between the three deeper releases.

## Discussion

By considering the various pieces of information, and including further material from recent studies of its biology (e.g. Fenaughty, 2006; Hanchet, 2006) it is possible to start to piece together a tentative life cycle for *D. mawsoni* in Subareas 88.1, 88.2 and 88.3. This can also identify gaps in our knowledge which could be investigated through further research.

#### Spawning and early life history

All the evidence presently suggests that *D. mawsoni* mainly spawn on the hills, banks and ridges to the north of 70°S (Patchell, 2002; Fenaughty, 2006; Hanchet, 2006). However, as can be seen from the modelling work, the precise location and depth of spawning and the location of the eggs and larvae in the water column are important for determining egg and larval drift. If the fish spawn further north, and the eggs and larvae are in the surface waters, then modelling suggested that as much as 30% of the eggs and larvae could be advected out of the Ross Sea area by the ACC. Whereas, if the fish spawn further south, the eggs and larvae appear more likely to be entrained by the western Ross Sea gyre and be advected to the south and west of the

spawning area onto the Ross Sea shelf and onto the continental shelf and slope to the west of the Ross Sea.

The early life-history stages of *D. mawsoni* seem particularly elusive. There have been three main studies of the ichthyoplankton and pelagic fish fauna in the Ross Sea region (De Witt, 1970; Vacchi et al., 1999; Donnelly et al., 2004). Using a variety of plankton nets and fine mesh mesopelagic trawls, these studies have sampled widely across the Ross Sea shelf and slope and out to the east as far as 130°W (SSRU 882E) and down to 1 000 m depth. Despite catching a wide range of larval, postlarval and juvenile fish (ranging from 8 to 150 mm SL) from over 20 pelagic species, they have not caught a single *D. mawsoni*. Extensive ichthyoplankton surveys from the Antarctic Peninsula region have also failed to catch any of the early life-history stages of *D. mawsoni* (see Kellermann, 1996 and references therein). Limited data are also available on the whereabouts of post-larval and pelagic juvenile *D. mawsoni* (Yukhov, 1971; Roshchin, 1997). Yukhov (1971) recorded the occurrence of 11–12 cm long juveniles captured by midwater trawl in the surface layers (0–50 m) in the Weddell Sea, Amundsen Sea and off Wilkes Land. Roshchin (1997) noted that 4–15 cm long *D. mawsoni* juveniles have been consistently caught in midwater trawls by vessels fishing aggregations of krill and *P. antarcticum* south of about 64°S throughout the Indian Ocean sector. These fish were generally caught in the surface waters (0–100 m) over depths of 1 000–4 000 m.

#### Benthic juveniles and sub-adults

It is believed that *D. mawsoni* have become benthic by a length of about 15 cm (Roshchin, 1997; Near et al., 2003). Based on the recent studies of juvenile growth by La Mesa (2007), this is likely to be in autumn (March–May) about 1 year and 9 months after the eggs were spawned. The location of small benthic juvenile *D. mawsoni* in the Ross Sea region is unknown. Despite sampling using a wide range of sampling gears (including bottom trawls, trammel nets, gill nets, drop lines and longlines), no *D. mawsoni* less than 40 cm have been caught on the Ross Sea shelf or slope (O'Driscoll et al., 2004; Hanchet, 2006). Yukhov (1971) reported 20–40 cm long toothfish caught by set net, rod and line, and otter trawl from depths of 20–300 m in several areas adjacent to the Antarctic continent. Around the South Orkney Islands, Elephant Island, the South Shetland Islands, and west of the Antarctic Peninsula, individual juvenile *D. mawsoni* (10–50 cm long) have been regularly caught (albeit in low numbers) by bottom trawl surveys in depths of 50–500 m (e.g. Jones et al., 2003). In the Indian

Ocean sector, 30–75 cm long *D. mawsoni* have been commonly caught by Ukrainian bottom trawlers targeting Wilson's icefish (*Chaenodraco wilsoni*) (Roshchin, 1997).

Very few *D. mawsoni* less than 50 cm have been caught in the Ross Sea toothfish fishery (Hanchet et al., 2007). Although large hooks (between size 12 and 15) are used in the fishery, these hooks do catch very small icefish and macrourids, and so this is probably a consequence of the smaller fish being absent from the grounds. Catches of the smallest toothfish have been localised to the shelf and slope in SSRUs 882A and 882F, and to a lesser extent in Subarea 88.3, whilst catches of sub-adults have been concentrated in the southern Ross Sea itself. This suggests there may be an ontogenetic movement of juvenile toothfish from east to west as they grow and develop, but more data are required to substantiate this.

As the sub-adult toothfish grow, they move into slightly deeper water – they are found both in deeper areas of the Ross Sea shelf and on the Ross Sea slope. They probably remain there for a further 2–3 years before they gain sufficient size and body condition for maturation of the gonads. The length- and age-at-sexual-maturity of *D. mawsoni* is uncertain. The smallest female toothfish undergoing vitellogenesis has been 90 cm (Patchell, 2001). For modelling purposes, it is currently assumed that 50% of the population of both sexes is mature at 100 cm (range 85–115 cm), which is equivalent to an age of 9–10 years (Dunn and Hanchet, 2006). However, Livingston and Grimes (2005) considered that length-at-maturity is likely to be greater than this and is almost certainly different between sexes.

#### Adult toothfish – and closing the loop

In general, there is a direct relationship in toothfish between length and depth (Hanchet et al., 2003). The maturing adult toothfish (100–120 cm) are typically found on the continental slope of the Ross Sea in 800–1 500 m, whilst the large mature adult toothfish (>120 cm) are mainly caught by the fishery in the deeper waters (1 000–1 800 m) of the continental slope and banks, ridges and hills to the north of the Ross Sea. Whilst this is the general pattern observed in the fishery, larger adults can occasionally be caught in shallower waters on the Ross Sea shelf (Eastman and De Vries, 2000; Hanchet et al., 2007). Although they are caught on bottom longlines, they have also been shown at times to have a more pelagic existence. Using a video camera mounted on the head of Weddell seals (*Leptonychotes weddellii*), large adult toothfish have

been seen in McMurdo Sound in the top 200 m of the water column over a bottom depth of 570 m (Fuiman et al., 2002). They have also been found in sperm whale (*Physeter macrocephalus*) stomachs, which had been taken over deep waters, from an area extending from 150°E to 100°W and from 60°S to 78°S (Yukhov, 1971).

From an analysis of five years of data from the toothfish fishery, Fenaughty (2006) showed that fish collected from the northern area (north of 70°S) differ substantially from those in the southern area in several key respects: length-frequency distribution, sex ratio and condition. Briefly, this analysis showed that the modal length distributions of the fished population differed between the two areas – being clearly unimodal in the north with the average value for all years occurring at about 141 cm for males and 152 cm for females. Most of the fish in the north were greater than 120 cm with very few fish recorded as being less than 100 cm. In contrast, the southern distribution was multimodal and included a much higher proportion of sexually immature fish. The sex ratio was also skewed with a higher proportion of males north of 70°S and a higher proportion of females south of 70°S, although the proportion of females in the catch in the north increased in April/May – possibly as females move northward to spawn. Fenaughty (2006) also showed a significant difference in mean weight-at-length in the northern area from the south with the male fish showing the largest difference. These fish were emaciated and are referred to as ‘axe handles’ by longline crews, because of their large heads and thin bodies.

Our interpretation of these regional differences is that toothfish migrate to the northern areas for spawning. The spawning season appears to extend from June to November. However, it is unknown whether a single individual will spawn one or more batches of eggs during this time period. Patchell (2001) noted that ovaries collected during March contained two size groups of vitellogenic oocytes measuring about 0.6 mm and 1.8–3.0 mm in diameter. He noted that these were larger than those seen by Eastman and De Vries (2000) during spring and suggested that both size groups of vitellogenic oocytes could be maturing to spawn during the coming season. However, in many other Antarctic fish species, vitellogenesis is a prolonged process and sexually mature fish have yolked oocytes at all times of the year (Kock and Kellermann, 1991; Kock, 1992). *Dissostichus mawsoni* clearly makes a relatively large investment in reproductive tissue during spawning. Maximum GSI of 43 and 30% have been reported for males and females respectively (Patchell, 2002; Fenaughty, 2006). Other fish

close to spawning have also had high GSI indices (15–20%) (see Figure 2). The high investment in reproduction, combined with the very poor physical state of fish found in the north, suggests that many fish are unlikely to spawn annually. It is therefore suggested that after spawning fish migrate back to the continental slope (and possibly shelf) of the Ross Sea for a period of ‘reconditioning’.

The timing of these migrations and residence time in the northern area is uncertain. The change in sex ratio during the season suggests that females may be migrating onto these hills during the austral autumn months just prior to spawning. Spawning itself may be protracted lasting several months from June to November. Most recoveries of tagged toothfish from the northern grounds have been males caught either within season or after one year at liberty, with few fish caught after two or more years (Dunn et al., 2007).

This agrees with Fenaughty (2006) who concluded that a likely cause of the generally poorer condition of *D. mawsoni* in the northern area was deterioration of physical condition following, or during, spawning. He also considered that this condition could be aggravated by the effects of migration to the northern hills over areas of open ocean (waters deeper than 2 500 m), and the effect of the strong tidal influences, that are characteristic of these northern geological features, combined with lower productivity. However, Fenaughty (2006) also noted that the poor physical condition was not universally consistent in the northern sample and probably indicated different entry times into the spawning population.

#### Plausible life cycle

*Dissostichus mawsoni* probably spawn on the underwater topographic features in the north of the Ross Sea (north of about 70°S). Spawning begins in early June, peaking in July/September and continues until at least November. Because of the large spawning area, and complex hydrology in the spawning ground, the eggs and larvae are widely dispersed. Some eggs and larvae drift east in the eastern Ross Sea gyre and prevailing ACC, across the northern edge of the Ross Sea, and into the shelf and slope of Subarea 88.2. Other larvae become entrained in the western Ross Sea gyre, and settle out on the shelf and slope of the Antarctic continent to the west of the Ross Sea. Some larvae may also move south onto the Ross Sea shelf itself. This egg and larval drift period probably lasts for up to at least 9–12 months until the toothfish juveniles reach a length of 4–8 cm. These juvenile *D. mawsoni* are pelagic, feeding mainly on a range of crustaceans

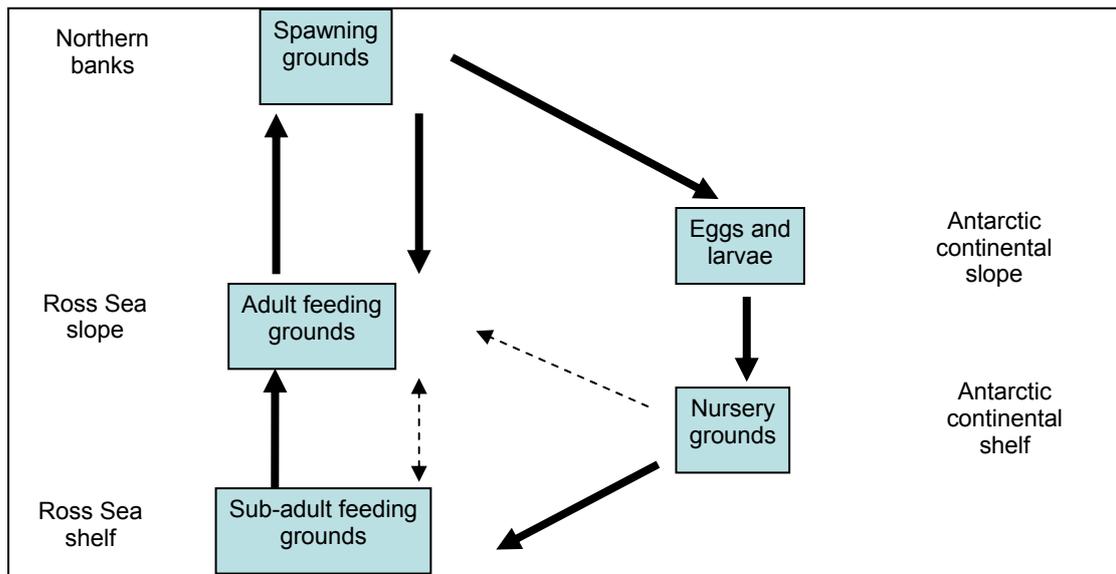


Figure 7: Hypothetical life history of *Dissostichus mawsoni* in the Ross Sea region.

including various early life stages of krill. They live mainly in the surface waters and may occur over depths of 3 000–4 000 m. As they grow during this period, they move steadily south onto the shallow continental shelf and slope in Subareas 88.1 and 88.2. They spend a further 6–9 months in pelagic schools in the surface waters. By the following autumn, after reaching a length of about 15 cm, and an age of about 21 months, they become more benthic. For the next 3–4 years these small fish (15–60 cm long) probably remain mainly in shallow waters (50–600 m) on the continental shelf and slope around Antarctica, including the continental shelf (and slope) of Subarea 88.2, the shallow banks of the Ross Sea, and on the narrow shelves around the Balleny Islands and Scott seamount. As the toothfish grow they gradually move into deeper water, so that as sub-adults (80–100 cm) they are mainly found in 600–800 m depth on the Ross Sea shelf and adjacent slope areas.

Fish mature at a length of 100–120 cm, at an age of 8–12 years, by which time they have moved deeper and are found between 800–1 800 m on the continental slope of the Ross Sea. They become neutrally buoyant and spend more time feeding in the water column. As adults, their growth rate slows down and they put more energy into reproduction. Once they have gained sufficient condition, the adults migrate to the hills, ridges and banks to the north of the Ross Sea. The migration and subsequent spawning on these grounds results in a loss of body condition as the fat reserves in the fish are utilised for production of gonad material. The adult fish may remain on these grounds for 1–2 years, feeding at times on benthic fish such as

rattails (Macrourids) and blue antimora (*Antimora rostrata*), but at other times in the pelagic zone on squid. After a maximum of 2–3 years, most fish return to the continental slope of the Ross Sea, where there is a larger and more diverse food supply. Because of the considerable loss in body condition, toothfish may take more than one year to regain enough body condition to make this migration again. This hypothetical life history of *D. mawsoni* in the Ross Sea region is depicted in Figure 7.

## Conclusions

The present hypothesis is that *D. mawsoni* in Subareas 88.1 and 88.2 spawn mainly on the ridges and banks of the Pacific-Antarctic Ridge to the north and east of the Ross Sea. The spawning appears to take place during winter and spring, and may extend over a period of several months. Depending on the exact location of spawning, eggs and larvae become entrained by the Ross Sea gyres, and may either move west settling out around the Balleny Islands and adjacent Antarctic continental shelf, south onto the Ross Sea shelf, or eastwards with the eastern Ross Sea gyre settling out along the continental slope and shelf to the east of the Ross Sea in Subarea 88.2. As the juveniles grow in size, they move west back towards the Ross Sea shelf and then move out into deeper water (>600 m). The fish gradually move northwards as they mature, feeding in the slope region in depths of 1 000–1 800 m, where they gain condition before moving north onto the Pacific-Antarctic Ridge to start the cycle again. Spawning fish may remain in the northern area for up to 2–3 years. They then move southwards back onto the shelf and slope

where productivity is higher and food is more plentiful and where they regain condition before spawning.

It is clear that considerable uncertainty remains over the spawning dynamics and early life history of *D. mawsoni*. Much of the hypothesised life history is speculative as the data used in this study have been restricted in a seasonal and geographical extent. Therefore, most of the conclusions presented here are projections based on biological data collected over the austral summer and autumn period, and the theories on the reproductive behaviour and fish and larval movement at present can only be inferred rather than determined by direct observation. However, it is hoped that this may provide a focus for other researchers working on various aspects of the species' biology and behaviour to test the various hypotheses proposed. Further research should be carefully planned to address these uncertainties.

### Acknowledgements

Thanks to the many observers who collected the data presented in this paper and to the CCAMLR Member countries for releasing those data. We thank Malcolm Roberts at the Met Office (UK) for providing the model output from HiGEM. We would also like to thank the members of the New Zealand Antarctic Fisheries Stock Assessment Working Group for helpful discussions and Drs Kock and Everson for helpful comments on an earlier version of this paper. This project was funded by the New Zealand Ministry of Fisheries under project ANT2006/01.

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