

FACTORS THAT MAY INFLUENCE THE ACCURACY OF ABUNDANCE ESTIMATES FROM CCAMLR TAG-RECAPTURE PROGRAMS FOR *DISSOSTICHUS* SPP. AND BEST PRACTICE FOR ADDRESSING BIAS

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Abstract

The Lincoln-Petersen equation, the simplest form of an abundance estimator using tag-recapture data, was used to identify processes that may introduce bias into abundance estimates derived from tag-recapture programs. The methods that have been used in CCAMLR tag-recapture programs to mitigate such biases, or to account for their effects in stock assessments for *Dissostichus* spp. are also summarised. In nearly all cases, examples of at-sea or model-based approaches are available from established *Dissostichus* spp. tag-recapture programs to reduce these biases. Estimates of post-capture mortality, tag-detection rates and, where it occurs, post-release depredation rates are a priority for new assessments that use tag-recapture data. Due to the complexity of toothfish movements throughout their life cycle, as well as the spatial structure of release and recapture efforts by fishing and research vessels, development of spatially explicit modelling approaches is also an important next step for *Dissostichus* spp. assessments that use tag-recapture data.

Introduction

Tag-recapture programs are a powerful tool for researching population dynamics and providing estimates of population size. In the CCAMLR area, tagging programs have existed in some fisheries for toothfish (*Dissostichus* spp.) for more than a decade. For example, tagging from commercial fishing vessels commenced in the fishery at Heard Island and the McDonald Islands (Division 58.5.2) in 1998 (Williams et al., 2002) and at South Georgia (Subareas 48.3) and in the Ross Sea (Subarea 88.1) in 2000 (Marlow et al., 2003; SC-CAMLR, 2011a, 2011b).

Data from these programs have been used to estimate movement (Agnew et al., 2006b; Hanchet et al., 2008; Marlow et al., 2003; Welsford et al., 2011; Williams, 2002), growth rates (Candy et al., 2007; Marlow et al., 2003) and mortality rates (Candy, 2011b) of toothfish. The use of tag-recapture data as an integral part of stock assessments is a relatively recent development in fisheries worldwide (Maunder, 1998; Polacheck et al.,

2010), however, it is routinely used as a key input into integrated assessments of the *D. eleginoides* fishery in South Georgia and the northern part of Subarea 48.4 (Hillary et al., 2006; SC-CAMLR, 2010), the *Dissostichus* spp. fisheries in the Ross Sea (Mormede et al., 2011; SC-CAMLR, 2011b) and the *D. eleginoides* fishery inside the Australian exclusive economic zone (EEZ) at Macquarie Island (Fay and Tuck, 2011; Tuck et al., 2003). Based on these achievements, establishing tag-recapture programs has been a high priority for CCAMLR in areas where routine stock assessments have not yet been established.

In 2011, the Scientific Committee emphasised the importance of applying international best practice in tagging programs and tag-based research (SC-CAMLR, 2011c). Here, the events and processes in a tagging program that may lead to biases in tag-based abundance estimates, and methods that may be implemented to address these biases across the tag-recapture programs that are currently active in CCAMLR are identified.

Methods

A variety of methods exist for estimating abundance using tag-recapture data from fisheries (see review by Polacheck et al., 2010). For example, stock assessment model frameworks such as CASAL (Bull et al., 2012) can integrate tagging data as an index of abundance. However, they all share features in common with the simplest form of an abundance estimator, known as the Lincoln-Petersen equation (LPE) (Lincoln, 1930; Petersen, 1896). This study focuses on the LPE to discuss the processes that may affect any tagging program or may need to be addressed when estimating stock abundance based on data derived from a tagging program.

The LPE states that the ratio of all tagged animals to the total population in a closed and fully mixed population will be equal to the ratio of tagged animals in a sample to the total sample size:

$$\frac{M}{N} = \frac{R}{C} \quad (1)$$

where M is the total number of tagged animals released that are available for recapture, N is the total population vulnerable to capture, R is the total number of tagged animals recaptured in a sample, and C is the total number of animals caught in a sample and scanned for tags. This equation can be transposed to estimate N by:

$$N = \frac{C}{R} \times M \quad (2)$$

Deriving an accurate value for N using this estimator is based on a variety of assumptions with respect to M , R and C . Where these assumptions are not met, parameter estimates may be biased, and if not accounted for in a stock assessment context, there is a risk of over- or underestimating the true N by the estimate \hat{N} (i.e. $\hat{N} > N$ or $\hat{N} < N$), with potential consequences for any management advice based on these estimates.

To assist with assessing the impact of bias in estimating these parameters, this study has identified the processes that may lead to bias in estimates of estimates of the parameters of the LPE (M , R and C) in each of the three phases of a tag-recapture program:

- (i) initial capture, tagging and release of fish
- (ii) the period while tagged fish are at liberty
- (iii) recapture and landing of fish.

It is noted that issues overlapping all three phases result from the spatial distribution of tagged fish, movement and mixing post-release, and the spatial distribution of recapture effort can interact to introduce bias, and so these processes were considered separately.

This study also attempted to assess how likely it is that a process may occur given existing tagging program designs and management measures, its impact on \hat{N} , and the priority for addressing the source of the bias. The assessment of priority is based on the rationale that avoiding bias that may lead to overestimation of the size (and potentially the productivity) of the stock, and the consequent risk of overfishing, is a higher priority issue than maximising the catch during the development of a *Dissostichus* spp. fishery (Table 1). Finally, this study also attempted to identify where a method has already been employed to mitigate (prevent or reduce the effect occurring in the first place) or remediate (account for the effect after it has occurred, such as through correcting a parameter estimate) potential sources of bias.

Results and Discussion

Several processes may occur during the first phase that have the potential to bias the parameters of the LPE and \hat{N} (Table 2). Transcription errors, such as noting the incorrect tag colour, does not affect the estimated number of tagged fish, but can reduce the number of recaptures because it may be impossible to correctly allocate the recaptured fish to a release event. For analyses that require every individual to be uniquely identified, such as for estimating growth or movement, transcription errors are a substantial problem. The use in recent years of standardised tags and increasingly sophisticated methods for data grooming and matching tags of the centralised database at the CCAMLR Secretariat (CCAMLR Secretariat, 2011; Dunn and Middleton, 2009) led to the conclusion that the occurrence of transcription errors in CCAMLR fisheries currently has a relatively low likelihood. Similarly, while anecdotal evidence indicates that some duplicate tag numbers have been released in CCAMLR toothfish fisheries in the past, the use of a single manufacturer (Hallprint) that maintains

Table 1: Schema for assessing the priority for addressing potential sources of bias in tag-recapture programs based on their likelihood of occurrence and impact on estimates of the vulnerable population \hat{N} derived from the Lincoln-Petersen equation (LPE) compared to the true vulnerable population N .

Likelihood	Impact on \hat{N}	
	$\hat{N} > N$	$\hat{N} < N$
Low	Medium priority	Low priority
High	High priority	Medium priority

Table 2: Processes that may occur during the release phase of a tagging program and their impact on parameters of the Lincoln-Petersen equation (LPE) and the estimated vulnerable population abundance (\hat{N}) compared to the true vulnerable population abundance (N), likelihood of the process occurring, assessment of relative priority of remediating the issue (see Table 1), and potential mitigation or remediation measures. M and \hat{M} are the true and estimated total number of tagged animals released that are available for recapture, and R and \hat{R} are the true and estimated total number of tagged animals recaptured in a sample.

Process	Impact on LPE parameters	Impact on \hat{N}	Likelihood	Priority	Mitigation	Remediation
Transcription errors	$\hat{R} < R$	$\hat{N} > N$	Low	Medium	Use standard tags with consecutive numbers At-sea data checking methods	Tag matching/data grooming processes, including photo verification of recaptures
Duplicate tag numbers released	$\hat{R} < R$	$\hat{N} > N$	Low	Medium	Standard tags from a single source, preventing issuing of duplicates	
Selection of fish that are not representative of the catch (e.g. size of fish)	$\hat{M} > M$	$\hat{N} > N$	Low	Medium	Release tagged fish that are representative of the catch	Size-specific \hat{M}
Release rate of tagged fish higher in areas of low population abundance relative to the overall population	$\hat{M} > M$	$\hat{N} > N$	High	High	Tag fish in proportion to the catch, spread tags across the experimental area	Use spatially explicit model
Release rate of tagged fish higher in areas of high population abundance relative to the overall population	$\hat{M} > M$	$\hat{N} < N$	High	Medium	Tag fish in proportion to the catch, spread tags across the experimental area	Use spatially explicit model

a database of tag numbers issued, as well as the CCAMLR Secretariat as the primary point of issue of tags, reduces the likelihood that release of duplicate tags, will impact current tagging programs.

Selection of fish that are not representative of the catch can result in a lower than expected number of tagged fish available for subsequent recapture. Data from CCAMLR exploratory fisheries indicate that in the past some vessels have not always selected a random representative sample of the catch, but instead selectively tagged smaller fish from the catch (e.g. see Figure 3 in SC-CAMLR, 2009). These small fish tend to have low fishing selectivity and thus lower recapture probability. Remediation by accounting for size-specific releases, as implemented in the CASAL framework, can reduce, but not fully eliminate, biases from selectively tagging small fish (Ziegler, 2013). In CCAMLR toothfish fisheries, random representative sampling has been mandated in Conservation Measure (CM) 41-01, Annex C, since 2010/11, so this issue is largely limited to tag releases prior to 2010.

Releasing tags in low-density areas where there may be little incentive to return also may result in overestimates of the tagged and overall population vulnerable to recapture. Concentrating releases of fish in areas of higher or lower abundance also has the potential to bias the estimates of LPE parameters, particularly if insufficient mixing has occurred prior to the recapture effort (see below).

A number of processes may impact abundance estimates in the second phase of the tagging program while fish are at liberty (Table 3). The tagged population will be attrited by natural mortality requiring the number of tagged fish available for recapture to be corrected. The tagging process itself poses additional sources of mortality. Injuries associated with the capture and tagging process, such as multiple hooking wounds, can be common (e.g. see Figure 1 in SC-CAMLR, 2011a) and are likely to increase the mortality rate of fish that are tagged and released through blood loss, infection and lice attack. A study by Agnew et al. (2006a) found that injuries, as well as larger size and capture from deeper depths, were all factors decreasing the likelihood of post-capture survival of toothfish held in aquaria. CM 41-01 (CCAMLR, 2012) recommends that only fish in good condition are selected for tagging; toothfish are known to be relatively hardy and many survive the capture and tagging process

if carefully handled. For example, there are at least two individual toothfish in the Heard Island and McDonald Islands fishery that have been tagged, recaptured in trawls and re-released four times over a total of three years at liberty (D. Welsford, unpublished data), and recaptures after more than eight years have been recorded in the Ross Sea, South Georgia and Macquarie Island programs (Fay and Tuck, 2011; SC-CAMLR, 2011a, 2011b). In integrated assessments for South Georgia and the Ross Sea, an estimate of tag-release mortality has been included in addition to natural mortality to account for the poorer survivorship of tagged fish based on results from Agnew et al. (2006a) (SC-CAMLR, 2011a, 2011b).

In locations where orca (*Orcinus orca*) or sperm whales (*Physeter macrocephalus*) are present when longlines are retrieved, depredation of toothfish can result in substantially reduced catch rates (Moir Clark and Agnew, 2010; Tixier et al., 2010). If depredation also affects tagged fish when released, the actual number of tagged fish available for subsequent recapture can be substantially reduced. Current mitigation measures include leaving areas when whales are prevalent which may reduce the likelihood that tagged fish that are being released are eaten. There is also the potential to correct \hat{M} for depredation on tagged fish that may have occurred, however, we are unaware of such an adjustment having been implemented in a stock assessment for toothfish.

Depredation during hauling has also the potential to affect the numbers of observed recaptures, however, if tagged and untagged fish are taken out in similar proportions, this process is unlikely to cause a bias in \hat{R} . Similarly, fish that are hooked on gear that is subsequently lost, or that are caught in IUU gear, may result in unaccounted loss of tagged fish, but unless tagged fish are more likely to be caught in such gear than untagged fish, this is unlikely to cause a direct bias in the estimate of population abundance. However, in areas where these problems are prevalent, the probability of recapturing any tags may be reduced to very low levels, leading to a significant reduction in the precision of any tag-based abundance estimator.

Tag shedding operates in a similar way as tag-release mortality and depredation by reducing the true number of tagged fish available to recapture. Tag shedding is largely mitigated by double-tagging

Table 3: Processes that may occur during the phase of a tagging program while tagged fish are at liberty and their impact on parameters of the Lincoln-Petersen equation (LPE) and the estimated vulnerable population abundance (\hat{N}) compared to the true vulnerable population abundance (N), likelihood of the process occurring, assessment of relative priority of remediating the issue (see Table 1), and potential mitigation or remediation measures. M and \hat{M} are the true and estimated total number of tagged animals released that are available for recapture respectively, and R and \hat{R} are the true and estimated total number of tagged animals recaptured in a sample respectively.

Process	Impact on LPE parameters	Impact on \hat{N}	Likelihood	Priority	Mitigation	Remediation
Tagged fish die of natural mortality	$\hat{M} > M$	$\hat{N} > N$	High	High		Correct \hat{M} based on natural mortality
Tagged fish have a lower survivorship than the overall population due to release condition	$\hat{M} > M$	$\hat{N} > N$	High	High	Select fish in good condition likely to survive the tagging process	Correct \hat{M} based on estimated tag-release mortality
Fish are depredated post-release	$\hat{M} > M$	$\hat{N} > N$	High ^a	High ^a	Avoid areas with high depredation	Correct \hat{M} based on estimated depredation rate
Tag shedding	$\hat{M} > M$	$\hat{N} > N$	High ^b	High ^b	Double-tagging, passive integrated transponder (PIT) tagging	Correct \hat{M} based on estimated tag-shedding rate
Tagged fish grow out of the size range selected by the fishery	$\hat{M} > M$	$\hat{N} > N$	Low	Medium		Estimate size-specific \hat{M} , taking account of growth rate of tagged fish

^a Depredation of longline-caught fish has been reported in Subareas 48.3 (South Georgia), 58.6 (Prince Edward and Marion Islands) and 58.7 (Crozet Islands) and Divisions 58.4.4 (Ob and Lena Banks) and 58.5.1 (Kerguelen Islands).

^b Some tag shedding is likely in all programs and may differ with size. For example, anchoring the standard size of CCAMLR T-bar tags between the pterygiophores at the base of the dorsal fin may be more difficult in larger fish than for smaller fish. Anecdotal reports also suggest that, where cachaloterias are used to mitigate toothed whale depredation, these may abrade tags and increase shedding rates at the time of recapture.

in all CCAMLR tag programs, and fish tagged at Heard Island and the McDonald Islands also have passive integrated transponder (PIT) tags inserted under the skin on the back of the head. These measures reduce the overall probability that fish will shed all tags before recapture. In addition, double-tagging also provides data to estimate rates of tag shedding through the comparison of rates of recaptures of single- and double-tagged fishes (Candy, 2011a; Dunn et al., 2011), which can then be applied to correct as in the South Georgia and Ross Sea assessments (SC-CAMLR, 2011a, 2011b).

Growth of tagged toothfish has the potential to lead to overestimates of M if fish grow out of

the size range selected by the fishing gear used to recapture fish. Tagging a range of sizes of fish is likely to mitigate this, and the effect of growth can be remediated by estimating size- or age-based estimates of LPE parameters. Slowing of growth due to tagging can also be accounted for as is done in the assessments for South Georgia and the Ross Sea (SC-CAMLR, 2011a, 2011b).

Processes that may impact abundance estimates in phase 3 at recapture include scanning rates and tag-detection probability (Table 4). Scanning rates and detection rates of tagged fish being recaptured on board a fishing vessel are likely to be high, since every individual fish is handled multiple times

Table 4: Processes that may occur during the recapture phase of a tagging program and their impact on parameters of the Lincoln-Petersen equation (LPE) and the estimated vulnerable population abundance (\hat{N}) compared to the true vulnerable population abundance (N), likelihood of the process occurring, assessment of relative priority of remediating the issue (see Table 1), and potential mitigation or remediation measures. R and \hat{R} are the true and estimated total number of tagged animals recaptured in a sample respectively, and C and \hat{C} are the true and estimated total number of fish caught and scanned for tags respectively.

Process	Impact on LPE parameters	Impact on \hat{N}	Likelihood	Priority	Mitigation	Remediation
Not all fish are scanned	$\hat{C} > C$	$\hat{N} > N$	Low	High	Make fishing crews aware of the need to check all fish, provide incentives to report tags, use automatic passive integrated transponder (PIT) tag detectors	Correct \hat{C} to account for unscanned fish
Not all tagged fish are detected	$\hat{R} < R$	$\hat{N} > N$	High	High	Make fishing crews aware of the need to check all fish, provide incentives to report tags, use automatic passive integrated transponder (PIT) tags detectors	Correct \hat{R} to account for undetected fish
Tagged fish are poorly selected by recapture effort	$\hat{R} < R$	$\hat{N} > N$	Low	High	Overlap recapture effort with areas where tagged animals have been released, use same gear for recaptures as for releases	Include estimates of area-/size-specific \hat{R} , growth and movement in assessment models

between being landed, processed and stored. However, both scanning and detection rates are unlikely to be 100% across all vessels. Lower than expected scanning rates can lead to an overestimation of C , while low detection rates can lead to substantial underestimation of R . Both will result in an overestimation of the true vulnerable population N .

The use of automatic PIT tag readers on board trawlers in the Division 58.5.2 (Heard Island and McDonald Islands) fishery provides a useful comparison of methods that rely on human detection only, and indicates an average detection probability of over 95% for trawl-caught fish when both methods were used (Candy and Constable, 2008). There is also evidence from the Ross Sea (Subareas 88.1 and 88.2) that some vessels report lower number of tags than other vessels fishing in the same area (Mormede and Dunn, 2012). Rewards for reporting tags have also been used to provide incentives to the crew to achieve high tag-detection rates

(Agnew et al., 2006b), however such schemes may be difficult to sustain as tagging programs mature and increasing numbers of tag recaptures are reported. As a remediation measure, estimates for scanning and tag-detection rates across a fleet have been included into the tag-based stock assessments of Subareas 48.3 and 88.1 (SC-CAMLR, 2011a, 2011b).

The fish movements post-release and the timing and location of recapture effort can also strongly influence the results of the LPE during all three phases of a tagging program. Tag-recapture data from long-established tag programs indicate that toothfish generally move less than 50 km yr⁻¹, although individuals can make large-scale movements (100s or 1 000s of km) during their life span, migrating to deeper waters or moving to and from spawning grounds (Agnew et al., 2006a; Appleyard et al., 2002; Hanchet et al., 2008; Marlow et al., 2003; Welsford et al., 2011). Where toothfish have

insufficient time to mix through the population, the overlap between the release site of individual fish and the exact location of subsequent recapture effort has the potential to strongly impact on recapture rates (Figure 1). Focusing recapture effort in locations where a higher density of tagged fish are vulnerable to recapture can lead to underestimation of N . This seems to be the case in the trawl grounds in Division 58.5.2, where tagged fish may be recaptured within days of release, leading to a substantial underestimation of vulnerable biomass when compared to trawl survey data (Candy and Constable, 2008). Conversely, if the recapture effort does not return to areas where tagged fish were released, e.g. due to sea-ice cover at the time, lower than expected recaptures will lead to overestimation of N .

Spreading the spatial release of tagged fish in proportion to the catch over the entire fishing area can mitigate this problem. Such a spread has not always been achieved in exploratory toothfish fisheries in the past (e.g. SC-CAMLR, 2009, Figure 2), which is likely to impact on analyses including these releases in \hat{M} , however, recent focus on achieving the intent of CM 41-01, Annex C, has seen improvements in spreading tags across the locations where catches were taken in exploratory fisheries. The effects of incomplete mixing can be remediated by excluding tag recaptures that occur within a certain period (Hillary et al., 2006; SC-CAMLR, 2011a, 2011b; Tuck et al., 2003). Developing spatial models that attempt to estimate the movement of toothfish and the spatial distribution of size and age classes (e.g. Dunn and Rassmussen, 2008; Fay and Tuck, 2011) have potential to remediate some of the issues related to uneven distribution of tag releases and the consequences for tag-recapture programs, however, these remain to be implemented for any toothfish assessments used by CCAMLR.

Conclusion

This study focused on the processes and parameters that have the potential to influence any tag-based estimates of abundance, and where possible identified examples of studies from CCAMLR toothfish fisheries where measures have been established to ensure these issues are addressed, either through practical mitigation measures or by remediating bias by providing estimates for these parameters. Considerable effort has gone into implementing tagging programs and developing

tag-based assessment methods in the Convention Area that explicitly address many of the issues that have the potential to cause bias in tag-based assessments for fisheries, such as in the assessments in Subareas 48.3, 88.1 and 88.2. Based on the existing examples, there is great opportunity for tagging programs that currently exist or are planned to rapidly develop to a point where they could be considered to be achieving best-practise.

The work that remains outstanding includes the development of stock-, gear- and/or vessel-specific estimates of important parameters such as post-capture survival, tag detection, and where it occurs, depredation on fish post-release. Furthermore, the development of size- and age-based models for areas without assessments, such as the exploratory toothfish fisheries in Subareas 48.6 and 58.4, remains urgent. The development of spatially explicit models that account for toothfish behaviour, as well as the behaviour of the fishing fleet, is also likely to improve all assessments of *Dissostichus* spp. stocks in the CCAMLR area.

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References

- Agnew, D.J., J. Moir Clark, P.A. McCarthy, M. Unwin, M. Ward, L. Jones, G. Breedts, S. Du Plessis, J.V. Heerdon and G. Moreno. 2006a. A study of Patagonian toothfish (*Dissostichus eleginoides*) post-tagging survivorship in Subarea 48.3. *CCAMLR Science*, 13: 279–289.
- Agnew, D.J., G.P. Kirkwood, J. Pearce and J. Clark. 2006b. Investigation of bias in the mark-recapture estimate of toothfish population size at South Georgia. *CCAMLR Science*, 13: 47–63.
- Appleyard, S.A., R.D. Ward and R. Williams. 2002. Population structure of the Patagonian toothfish around Heard, McDonald and Macquarie Islands. *Ant. Sci.*, 14: 364–373.

- Bull, B., R.I.C.C. Francis, A. Dunn, A. McKenzie, D.J. Gilbert, M.H. Smith, R. Bian and D. Fu. 2012. CASAL (C++ algorithmic stock assessment laboratory): CASAL User Manual v2.30-2012/03/21. *NIWA Technical Report 135*: 280 pp.
- Candy, S.G. 2011a. Models of tag shedding for double tagging as a function of time at liberty and approximate solutions for the single tagging model in CASAL. Document *WG-SAM-11/12*. CCAMLR, Hobart, Australia: 17 pp.
- Candy, S.G. 2011b. Estimation of natural mortality using catch-at-age and aged mark-recapture data: a multi-cohort simulation study comparing estimation for a model based on the Baranov equation versus a new mortality equation. *CCAMLR Science*, 18: 1–27.
- Candy, S.G. and A.J. Constable. 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., A.J. Constable, T. Lamb and R. Williams. 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. 2012. *Schedule of Conservation Measures in Force 2012/13*. CCAMLR, Hobart, Australia: 236 pp.
- CCAMLR Secretariat. 2011. Developments in the CCAMLR tagging program. Document *WG-FSA-11/06*. CCAMLR, Hobart, Australia: 6 pp.
- Dunn, A. and S. Rasmussen. 2008. Development of a spatially explicit age-structured statistical catch-at-age population dynamics model for modelling movement of Antarctic toothfish in the Ross Sea. Document *WG-SAM-08/14*. CCAMLR, Hobart, Australia: 31 pp.
- Dunn, A. and D.A.J. Middleton. 2009. Identification of data quality metrics for tagging data selection. Document *WG-SAM-09/19*. CCAMLR, Hobart, Australia: 14 pp.
- Dunn, A., M.H. Smith, D.J. Agnew and S. Mormede. 2011. Estimates of the tag loss rates for single and double tagged toothfish (*Dissostichus mawsoni*) fishery in the Ross Sea. Document *WG-SAM-11/18*. CCAMLR, Hobart, Australia: 14 pp.
- Fay, G. and G.N. Tuck (Eds). 2011. *Development of a multi-gear spatially explicit assessment and management strategy evaluation for the Macquarie Island Patagonian toothfish fishery*. Australian Fisheries Management Authority and CSIRO Marine and Atmospheric Research, Wealth from Oceans Flagship, Hobart: 178 pp.
- Hanchet, S.M., G.J. Rickard, J.M. Fenaughty, A. Dunn and M.J. Williams. 2008. A hypothetical life cycle for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region. *CCAMLR Science*, 15: 35–53.
- Hillary, R.M., G.P. Kirkwood and D.J. Agnew. 2006. An assessment of toothfish in Subarea 48.3 using CASAL. *CCAMLR Science*, 13: 65–95.
- Lincoln, F.C. 1930. Calculating waterfowl abundance on the basis of banding returns. *United States Dept. of Agriculture Circular*, 118: 1–4.
- Marlow, T.R., D.J. Agnew, M.G. Purves and I. Everson. 2003. Movement and growth of tagged *Dissostichus eleginoides* around South Georgia and Shag Rocks (Subarea 48.3). *CCAMLR Science*, 10: 101–111.
- Maunder, M.N. 1998. *Integration of tagging and population dynamics models in fisheries stock assessment*. Unpublished PhD thesis. University of Washington: 306 pp.
- Moir Clark, J. and D.J. Agnew. 2010. Estimating the impact of depredation by killer whales and sperm whales on longline fishing for toothfish (*Dissostichus eleginoides*) around South Georgia. *CCAMLR Science*, 17: 163–178.
- Mormede, S. and A. Dunn. 2012. The development of spatially and temporally controlled measures of survival and tag-detection for the CCAMLR tagging program. Document *WG-SAM-12/30*. CCAMLR, Hobart, Australia: 14 pp.

- Mormede, S., A. Dunn and S.M. Hanchet. 2011. Assessment models for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea for the years 1997–98 to 2010–11. Document WG-FSA-11/42. CCAMLR, Hobart, Australia: 42 pp.
- Petersen, C.G.J. 1896. The yearly immigration of young plaice into the Limfjord from the German Sea. *Rep. Dan. Biol. Sta.*, 6: 5–84.
- Polacheck, T., J.P. Eveson and G.M. Laslett. 2010. Classifying tagging experiments for commercial fisheries into three fundamental types based on design, data requirements and estimable population parameters. *Fish Fish.*, 11 (2): 133–148.
- SC-CAMLR. 2009. Report of the Working Group on Fish Stock Assessment. In: *Report of the Twenty-eighth Meeting of the Scientific Committee (SC-CAMLR-XXVIII)*, Annex 5. CCAMLR, Hobart, Australia: 223–357.
- SC-CAMLR. 2010. Report of the Working Group on Fish Stock Assessment. Fishery Report: *Dissostichus eleginoides* and *Dissostichus mawsoni* South Sandwich Islands (Subarea 48.4) In: *Report of the Twenty-ninth Meeting of the Scientific Committee (SC-CAMLR-XXIX)*, Annex 5, Appendix N. CCAMLR, Hobart, Australia.
- SC-CAMLR. 2011a. Report of the Working Group on Fish Stock Assessment. Fishery Report: *Dissostichus eleginoides* South Georgia (Subarea 48.3) In: *Report of the Thirtieth Meeting of the Scientific Committee (SC-CAMLR-XXX)*, Annex 7, Appendix G. CCAMLR, Hobart, Australia.
- SC-CAMLR. 2011b. Report of the Working Group on Fish Stock Assessment. Fishery Report: Exploratory fishery for *Dissostichus* spp. in Subareas 88.1 and 88.2. In: *Report of the Thirtieth Meeting of the Scientific Committee (SC-CAMLR-XXX)*, Annex 7, Appendix R. CCAMLR, Hobart, Australia.
- SC-CAMLR. 2011c. *Report of the Thirtieth Meeting of the Scientific Committee (SC-CAMLR-XXX)*. CCAMLR, Hobart, Australia: 454 pp.
- Tixier, P., N. Gasco, G. Duhamel, M. Viviant, M. Authier and C. Guinet. 2010. Interactions of Patagonian toothfish fisheries with killer and sperm whales in the Crozet Islands Exclusive Economic Zone: an assessment of depredation levels and insights on possible mitigation strategies. *CCAMLR Science*, 17: 179–195.
- Tuck, G.N., W.K. de la Mare, W.S. Hearn, R. Williams, A.D.M. Smith, X. He and A. Constable. 2003. An exact time of release and recapture stock assessment model with an application to Macquarie Island Patagonian toothfish (*Dissostichus eleginoides*). *Fish. Res.*, 63: 179–191.
- Welsford, D.C., S.G. Candy, T.D. Lamb, G.B. Nowara, A.J. Constable and R. Williams. 2011. Habitat use by Patagonian toothfish (*Dissostichus eleginoides* Smitt 1898) on the Kerguelen Plateau around Heard Island and the McDonald Islands. In: G. Duhamel and D.C. Welsford (Eds.). *The Kerguelen Plateau: Marine Ecosystem and Fisheries*. Société française d'ichtyologie, Paris.
- Williams, R., G.N. Tuck, A.J. Constable and T. Lamb. 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.
- Ziegler, P.E. 2013. Influence of data quality and quantity from a multiyear tagging program on an integrated fish stock assessment. *Can. J. Fish. Aquat. Sci.*, 70: 1031–1045.

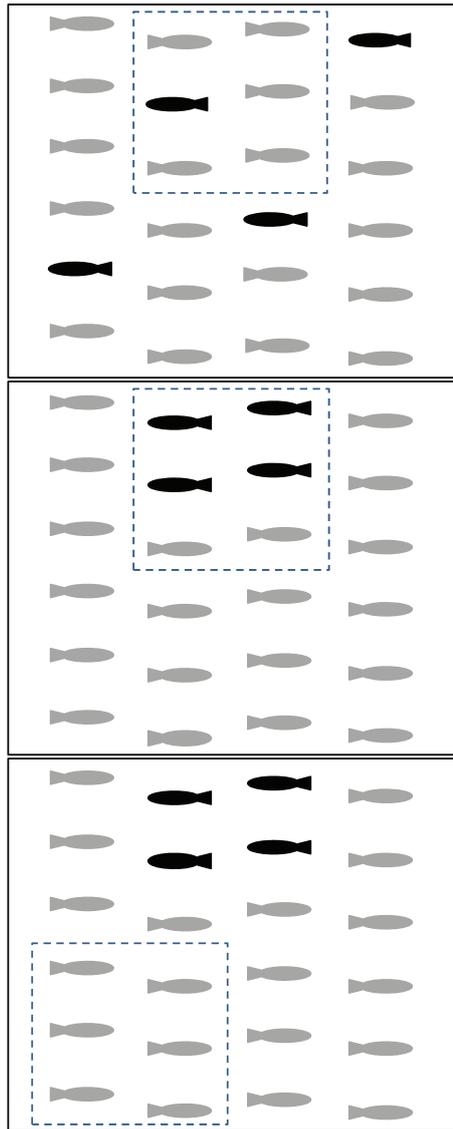


Figure 1: Diagram illustrating the effect of violating assumptions of complete mixing and spatial overlap of recapture effort with tagged fish at liberty. Untagged fish are represented by the grey symbols, tagged and released fish by the black symbols and recapture effort by the dotted line. The upper panel depicts the ideal situation where tagged fish are mixed throughout the untagged population, and so tag recaptures enable estimates of the parameters of the Lincoln-Petersen equation (LPE) to approximate their true value and produce an unbiased estimate of the vulnerable population (N). The centre panel depicts a situation where releases of tagged fish are localised and insufficient time has passed to permit mixing; consequently, recapture effort focused on this area may have a higher rate of recaptures than in the ideal situation, and consequently N will be underestimated by the LPE. The lower panel also depicts a situation where releases of tagged fish are localised and insufficient mixing has occurred; however, where recapture effort is focused in an area where few tagged fish are available for recapture, the rate of recapture may be lower than in the ideal situation and consequently N will be overestimated by the LPE.