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Update on the global spatial dynamics archival tagging project - 2011

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Abstract

As part of the CCSBT Scientific Research Program (SRP), Australia initiated the Global Spatial Dynamics project in 2003. This project involved the archival tagging of juvenile (2–4 year old) SBT throughout their range (i.e. from South Africa to New Zealand) with the objective of estimating movement and mixing rates, and periods of residency in different parts of this range. The project is now close to completion and we provide a brief summary of the main results. The final report should become available towards the end of 2011, and will then be distributed to interested parties in the CCSBT.

Introduction

The project “Spatial Interactions Among Juvenile Southern Bluefin Tuna at the Global Scale: a large-scale archival tag experiment” was initiated in 2003 by Australia as part of the CCSBT SRP. The project involved the archival tagging of juvenile (2–4 year old) SBT throughout their range (i.e. from South Africa to New Zealand). The primary objective of the project is the estimation of movement and mixing rates, and periods of residency in different parts of this range. The project has been implemented as a collaborative project between New Zealand (NZ), Taiwan and Australia. The project is now nearing completion and this paper therefore presents only a brief summary of the main results. Detail about some aspects of the project have been presented in previous CCSBT documents (Basson et al. 2010, Basson et al. 2009, Polacheck et al. 2008, Polacheck et al. 2007, Polacheck et al. 2006a, Polacheck et al. 2006b, Polacheck et al. 2005, Polacheck et al. 2003) and the final report with substantially more detail should be publicly available towards the end of 2011 for more thorough consideration at the 17th meeting of the CCSBT-ESC in 2012.

1. Global Spatial Dynamics Project - Overview

As noted in Basson et al (2010) a multi-year, large-scale electronic tagging project was initiated by the CSIRO in 2003 to improve our understanding of the global spatial dynamics of juvenile southern bluefin tuna (SBT). Electronic tags that are recovered from tagged fish provide a fishery independent dataset of horizontal and vertical movements. The project also aimed to provide an understanding of the implications of SBT spatial dynamics for the analyses of conventional tag return data, CPUE data, and SBT stock assessments, and management advice.

The first objective was to release at least 450 archival tags on juvenile SBT over a period of 3 years throughout the full range of habitats (Section 2). The second objective included the estimation of daily positions based on light and depth data (Section 3). The third objective relates to an analysis of the evidence for temporal changes in the spatial dynamics of juvenile SBT (Section 4). Another major objective of the project is to “Provide critical information and contribute to developing a framework for incorporating the archival tag and conventional tagging data within the SBT stock assessment model”. In this context, “conventional tagging data” can in future also be gene-tagging or pit-tagging data, for example. We have developed and simulation tested a framework for integrating archival and conventional tag data. Although not an explicit objective of this project, we have used the archival tag data together with conventional tag data from the 1990’s and the 2000s to illustrate how the framework might be applied to SBT (Section 5 and Appendix 1). We note though that the actual values of parameter estimates from these analyses must be interpreted cautiously due to a number of reasons discussed in Appendix 1.

Several additional objectives were originally formulated in terms of the interpretation and standardisation of CPUE data. The potential impact of unreported catches on longline CPUE, together with concerns about spatial coverage of longline fleets, and changes in fleet behaviour has led to the objectives being modified to focus more directly on the modelling of habitat use and residency of SBT rather than the standardisation of CPUE. Results related to these objectives will be included in the final report.

2. Archival tag releases and recaptures

The tag deployment component of the project was completed in 2009. The number of release years was extended from the original goal of 3 years (2004-2006) to 6 years (2004-2009), and the project exceeded its minimum goal in terms of number of archival tag releases, with 568 releases as of May 2009 (last release 28 May 2009). Archival tags have been released in 5 locations in collaboration with this project:

1. in high seas in the central Indian Ocean
2. off the south west of West Australia (WA)
3. in the Great Australian Bight (GAB)
4. off New Zealand
5. off South Africa

Training programs in tag deployment for the partner nations, New Zealand and Taiwan, were completed in the early years of the project. Detailed summaries of the archival tag releases by year and area, together with recaptures were given in CCSBT-ESC/1009/Info3 (Basson et al. 2010). A more concise summary of the total number releases and of returned tags by recapture area is given in Table 1a,b. All tags released under this project were Wildlife Computers MK9 tags. The project was unsuccessful in its early attempts to have fish tagged off South Africa (Polacheck et al. 2007). However, during the latter part of 2007 and the early part of 2008, the program was successful in having 27 SBT archival-tagged in waters close to South Africa by observers stationed on Taiwanese vessels. To date there have been no recaptures from these releases.

Table 1a. Numbers of archival tagged SBT by RELEASE area, together with corresponding numbers of recaptures from those releases. (Only fish tagged as part of the Global Spatial Dynamics project, from 2004 to 2009, are included.)

Year	Data	Indian Ocean	WA	GAB	Tasman Sea	South Africa	Total
Total	No. released	159	175	122	85	27	568
	No. recaptured	17	20	33	5	0	75[a]

a) the actual number returned to us is 73

Table 1b. Numbers of SBT archival recaptures by RECAPTURE area and recapture year.

Recapture Year	Data	Indian Ocean	WA	GAB	Tasman Sea	South Africa	Total
2004	No. recaptured	1		1			2
2005	No. recaptured			13			13
2006	No. recaptured			23		1	24
2007	No. recaptured	2	1	15			18
2008	No. recaptured	2		4		1	7
2009	No. recaptured	1		7			8
2010	No. recaptured				1		1
Total	No. recaptured	6	1	63	1	2	73

A total of 75 tags had been recaptured as of May 2011, 73 of which have been returned to CSIRO (Table 1b). We anticipate that additional archival tags have been recaptured and are in the farms in South Australia and look forward to these being returned during the harvesting operations. We will continue to process tags, upload the data to the database and, as funding allows, analyse the data even after this project has formally ended.

The percentage recoveries by release year are: 25% for 2004, 26% for 2005, 10% for 2006, 3% for 2007 and 5% for 2008. The recoveries from the releases in the Indian Ocean and Tasman Sea (New Zealand) are the first-ever recoveries of archival tags from releases in these two areas. As expected, the majority of the (reported) recaptures have come from the GAB (63 of the 73 tags, 86%). Of the remaining recaptures, 6 have come from the central Indian Ocean, 2 from South Africa, 1 from SW-West Australia and 1 from the Tasman Sea (Table 1b).

In addition to the tags released under this project, we have access to data from tags released under previous projects (Table 2). Some of these tags were Wildlife Computers MK7 tags. These additional tags extend the time-frame back to 1998, though the earlier releases generally have shorter deployment times than the more recent releases, making them suitable only for some types of analysis.

Table 2. Numbers of recaptures from WA and the GAB for tags released in 1998 to 2003

	Release Year						
Recapture location	1998	1999	2000	2001	2002	2003	Total
WA	0	0	0	3	0	3	6
GAB	29	8	9	0	2	0	48
Total	29	8	9	3	2	3	54

The number of tags used varies depending on the analysis. Reasons for having to leave out tags include lack of geolocation estimates (see below), very short deployment periods, and a few occurrences of problems with sensors, tag damage (e.g. data not retrievable), or the tag recaptured but not actually returned (so data could not be downloaded). The maximum number of tags for potential use consists of 68 returns from this project, plus tags released under previous projects: 54 tags from releases between 1998 and 2003, and 26 from releases between 1993 and 1995.

Each tag recorded date/time, light, depth, internal temperature and external temperature. The sampling interval varied according to tag type and capability; some of the early tags recorded data at 4-minute or 1-minute intervals; the more recent tags were set to record every 20 seconds.

Even simple summaries of the data over all tags are informative. Table 3 shows a) day-time and b) night-time summaries over all tags by month. Average sea surface temperature (AVG_SST) was calculated as average external temperature for depths less than 5m and proportion of time at the surface (PROP_SURF) was calculated as the proportion of depth values less than 10m. From these summaries we can see that juvenile SBT are found deeper on average during the day, spend less time at the surface during the day (particularly in the winter months), and on average maintain an internal temperature of ~4.5°C warmer than the external temperature in the day and ~5°C warmer at night.

Summary of main results

- The project has demonstrated the feasibility and viability of conducting archival tagging from longline vessels and using trained observers to do the tagging; there were 17 recaptures made from the 159 fish tagged by Taiwanese observers in the central Indian Ocean, and 1 recapture out of 6 releases by observers in New Zealand.
- The return rate of tags, including several multi-year deployments, supports the evidence from previous studies of the success of deployment methods.

Table 3a. DAY-TIME summaries of archival tag data by month. Data summarized over all MK7 and MK9 tags, excluding time in farms and excluding tags with obvious temperature drift.

MONTH	AVG_ INT_TEMP	AVG_ EXT_TEMP	AVG_ SST	AVG_ DEPTH	MAX_ DEPTH	PROP_ SURF
1	22.7	18.0	18.6	50.8	180.7	0.44
2	23.4	18.8	19.6	51.6	160.6	0.40
3	23.6	18.7	19.6	50.9	159.3	0.35
4	23.0	17.4	18.2	68.2	179.3	0.29
5	22.0	16.1	16.9	78.2	190.5	0.25
6	21.5	15.8	16.7	85.8	202.7	0.24
7	20.4	15.6	16.5	102.0	228.2	0.22
8	19.8	15.3	16.1	112.5	255.0	0.15
9	20.1	15.0	15.8	106.4	265.0	0.18
10	21.2	15.7	16.4	80.9	252.0	0.29
11	21.7	16.5	17.2	62.0	236.9	0.40
12	22.0	17.2	17.8	60.9	222.4	0.46
ALL	21.78	16.7	17.6	76.02	210.7	0.30

Table 3b. NIGHT-TIME summaries of archival tag data by month. Data summarized over all MK7 and MK9 tags, excluding time in farms and excluding tags with obvious temperature drift.

MONTH	AVG_ INT_TEMP	AVG_ EXT_TEMP	AVG_ SST	AVG_ DEPTH	MAX_ DEPTH	PROP_ SURF
1	22.6	18.1	18.4	30.1	165.2	0.40
2	23.2	19.1	19.4	28.1	149.2	0.40
3	23.3	19.2	19.5	28.7	151.4	0.39
4	22.6	18.0	18.0	35.4	186.9	0.40
5	21.4	16.5	16.5	42.6	223.4	0.41
6	20.9	16.2	16.3	47.2	238.7	0.40
7	20.0	16.1	16.1	50.2	243.2	0.36
8	19.5	15.6	15.6	46.1	247.2	0.38
9	19.6	15.4	15.5	44.2	253.0	0.36
10	20.6	16.0	16.3	40.8	246.5	0.37
11	21.5	16.9	17.1	33.8	217.6	0.42
12	22.0	17.5	17.7	30.9	194.3	0.47
ALL	21.4	17.0	17.2	38.3	210.0	0.40

3. Geolocation estimates

Geolocation estimates for archival tags are based on light data; essentially, on the difference between midday and GMT-noon (longitude), and the length of day and characteristics of the light curve (over time) at dawn and dusk (latitude). We previously commented on the difficulties involved in light-based geolocation (Basson et al. 2010). One important issue is the fact that latitude estimates are inherently much more uncertain than longitude estimates. This is particularly true for the two equinoxes (March and September) and several days either side of these dates. We applied the TrackIt software (Nielsen and Sibert 2007) to all returned tags, including the historic tag returns prior to this project. Although this approach provides estimates of uncertainty in location, an important weakness of TrackIt for application to SBT is that it does not take landmasses into account. Some estimates of location, particularly when SBT are in the GAB, are therefore on land. We obviously know these are unrealistic and discard these latitudes. However, even without latitude estimates, the longitude estimates alone are still of great value. Out of the 122 tags, we obtained estimated tracks for 91 tags. The 31 that failed did not converge to a solution although several options for parameter starting values and "phasing" in the optimisation were tried.

TrackIt location estimates, i.e. for all 91 tags, including those that fall on land, are shown in Figure 1. Closer inspection reveals that most of the extreme latitudes (very high or very low) are in fact at or around the March and September equinoxes). Each estimate has an associated covariance matrix, but the figure becomes cluttered when the uncertainty is also included. A plot of just the estimated longitudes over time is given in Figure 2.

External to this project, we developed a new likelihood-based method which represents a substantial step forward in light-based geolocation. This allows us to look at the statistical likelihood of any point on the globe for a particular dawn-dusk light curve. By combining this output with a model of individual SBT movement we are able to produce statistically robust tracks. Unlike Kalman filter based methods such as TrackIt, in this method, space is discretized into a set of grid squares and movements can only be between these grid squares. This approach allows for straightforward incorporation of land, therefore constraining movement paths to the ocean. However the size of grid is limited by computational demands. In the case of SBT, which move such large distances, this is not a major concern and we have found it is feasible to run these models at a 1 degree size grid square. This works builds on initial models (Pedersen et al. 2011), and was presented at the Biologging IV conference in Hobart, March 2011. We have also applied this approach to all tags, particularly those data sets that failed to yield viable location estimates with the TrackIt software.

Figure 1. TrackIt estimates of location for 91 tags, colour-coded by month, and covering years from 1998 to 2008. Estimates on land are obviously unrealistic, but this is because the TrackIt software is unaware of land. Uncertainties of locations estimates are not shown.

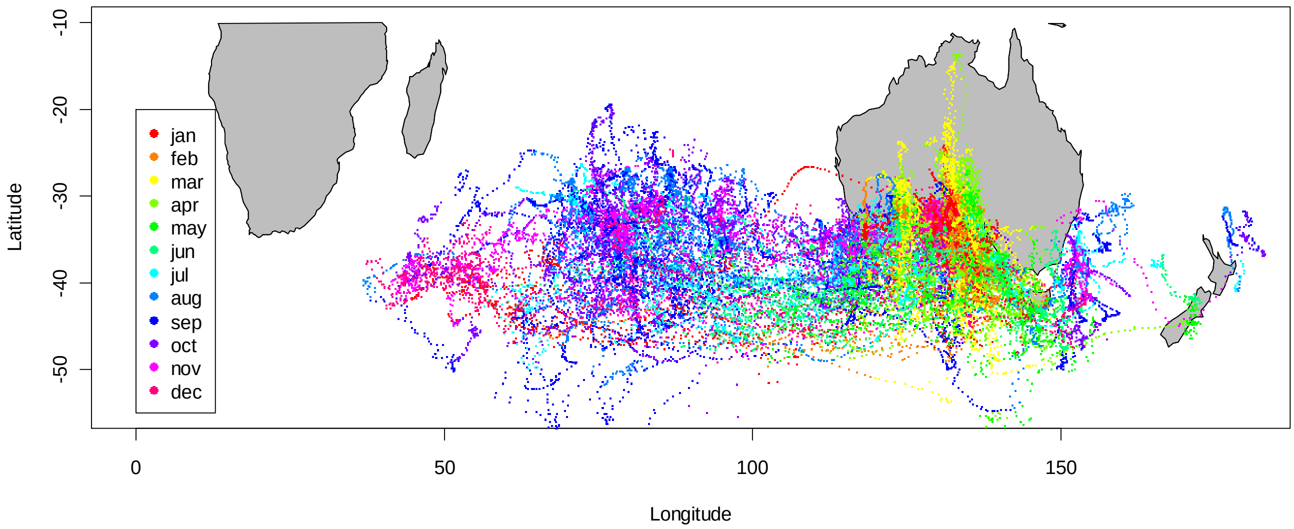
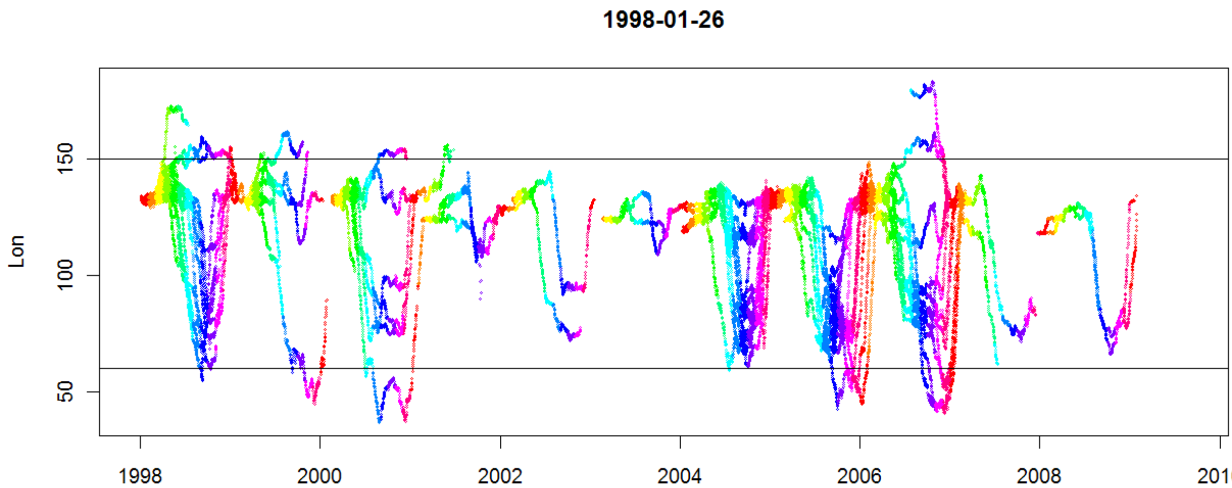


Figure 2. Longitude estimates from TrackIt software for 91 tags, colour-coded by month, starting on 26 January 1998. The horizontal line at 150° E is an approximate indicator of the Tasman Sea and that at 60° E indicates waters "off South Africa". The region in-between covers the Indian Ocean, WA and the GAB.



Summary of main results

Interpretation of the resulting tracks should be done with caution because of the large uncertainty in latitude estimates and the fact that the software is unaware of land. However, uncertainty in the longitude estimates is small enough that we can determine east-west movement with sufficient accuracy. Results from the estimated tracks indicate that:

- Juveniles are aggregated in the GAB over summer (January to March in particular) and disperse into the Indian Ocean and Tasman Sea in winter, but some juveniles spend their winters in WA or even in the GAB (presumably off-shore).
- There is large variability between animals in the timing of arrival into or departure from the GAB

- Animals that were tagged together, i.e. on the same day in the same location, may spend some further time together, but then generally follow very different subsequent tracks. This was the case for individuals tagged in the GAB and ones tagged in the Indian Ocean (IO).
- This suggests that after leaving the GAB there is a large degree of mixing of the tagged fish over the winter grounds.
- All individuals tagged in the IO in winter, came to the GAB the following summer and all, but one, individuals tagged elsewhere (WA, GAB, Tasman) returned to the GAB each summer.
- Only one individual (out of 91), tagged in the IO in winter, returned to the GAB the first summer after being tagged, but then returned to the IO and spent the next two summers in waters off South Africa (~ 40^{o}E).
- All other juveniles that were in waters off South Africa in winter and early summer made a return journey to the GAB even if that was in late summer (e.g. arriving in the GAB in February, March).
- Note, however, that we have NOT yet had returns from animals tagged in waters off South Africa. There is still the possibility that some juveniles never visit the GAB in summer.

4. Changes in spatial dynamics

Polacheck et.al. (2006a) reported changes in east-west movements of juvenile SBT between the 1990s and the 2000s, with fewer archival tagged fish moving into the Tasman or as far west towards South Africa in the 2000s as in the 1990s. The archival tags returned to date continue to support these changes to some extent; however, the picture has become more complicated. Up until 2001, all archival tagging of juvenile SBT took place in the GAB. Thus, for greatest comparability, we start by considering only archival tag releases in the GAB for all years. Figure 3 shows the longitude estimates from all GAB releases. There does appear to be a contraction in east-west movement of SBT after 2001, at exactly which point is difficult to say since the data are sparse between 2001 and 2004. Only 3.4% of tracks (1/29) from fish that were released in the GAB showed movement into the Tasman Sea (>150°E) during the months of May through November after 2001, compared to 22% (14/64) in prior years (Table 4). Although suggestive of a change, this difference is not statistically significant based on a chi-square test (p-value=0.1). Also, no tracks from fish that were released in the GAB moved into the more western part of the Indian Ocean (< 55°E) during the months of May through November since 2001, compared to 9.4% (6/64) previously (Table 5). Again, while suggestive of a possible change, this difference is not significant based on a chi-square test.

If we include releases from all areas, our sample sizes for the 2000s become much larger. Figure 4 shows the longitude estimates from all tags. In this case, 4% of tracks (3/75) showed movement into the Tasman Sea (>150°E) during the months of May through Novem ber after 2001, compared to 21% (14/67) in prior years. Given the larger sample sizes, this difference is now statistically significant (chi-squared test p-value=0.01). In terms of westward movement, including all releases actually makes the difference almost disappear, with 6.7% of tracks going further west than 55°E after 2001 compared to 9% in prior years. This is because several of the fish that were tagged in the Indian Ocean ventured west towards South Africa.

Taking all of the above into consideration, the data lends reasonably strong support for a contraction in eastward movement after 2001; there is less support for a contraction in westward movement. However, a further complicating factor is that 77% of fish tagged in 1993-2000 were ages 3 and 4 (23% age 2), whereas only 32% of fish tagged after 2000 were ages 3 and 4 (16% age 1 and 48% age 2). It is possible that there is a greater tendency for older fish to migrate further and this is part of the reason for the observed differences.

Warming in surface temperatures has occurred in the eastern GAB and Tasman Sea between the periods 1993-2000 and 2003-2008, and we are completing investigations about whether or not warming, or other environmental covariates, may have influenced juvenile SBT migration patterns.

[1] Note that 2 of the 3 tags were released in the Tasman.

Table 4. Number of tracks that go further east than 150°E in May-Dec of each year based on fish tagged in the GAB. (Note that an individual fish can be counted in more than once if its track extends across several years.)

Year	Total	>150 E	Percent
1993	2	0	0.0
1994	8	2	25.0
1995	15	3	20.0
1996	1	1	100.0
1998	17	4	23.5
1999	10	2	20.0
2000	10	1	10.0
2001	1	1	100.0
2002	2	0	0.0
2004	9	0	0.0
2005	9	0	0.0
2006	9	1	11.1

Table 5. Number of tracks that go further west than 55°E in May-Nov of each year based on fish tagged in the GAB. (Note that an individual fish can be counted in more than once if its track extends across several years.)

Year	Total	<55 E	Percent
1993	2	0	0
1994	8	2	25.0
1995	15	0	0
1996	1	0	0
1998	17	1	5.9
1999	10	2	20.0
2000	10	1	10.0
2001	1	0	0
2002	2	0	0
2004	9	0	0
2005	9	0	0
2006	9	0	0

Figure 3. Longitude estimates from archival tags released in the GAB. The horizontal red lines mark 150°E and 55°E.

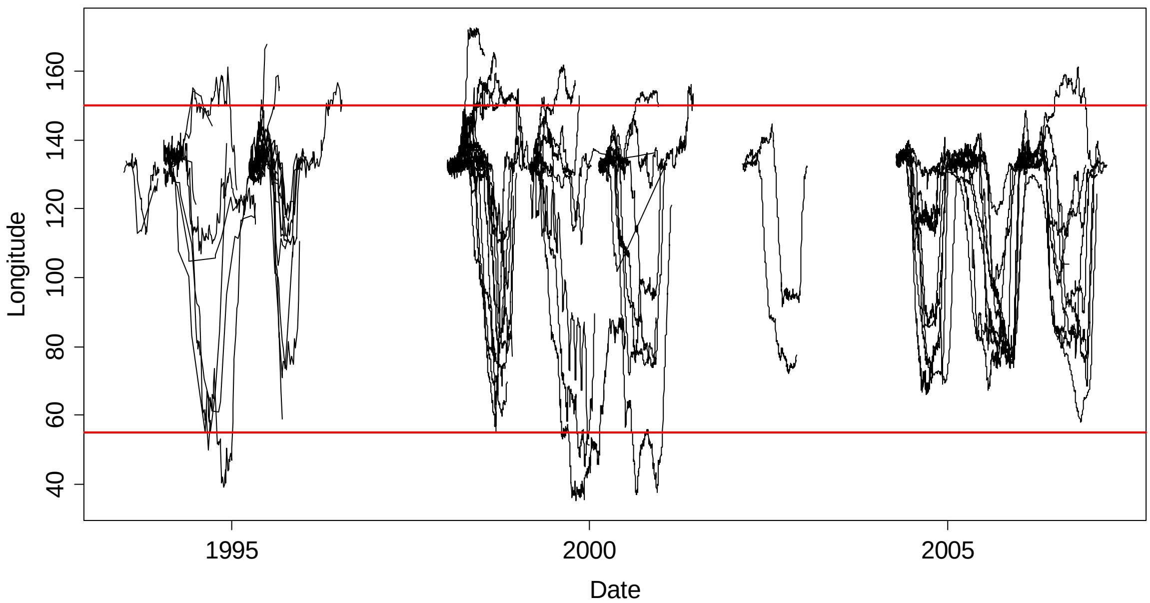
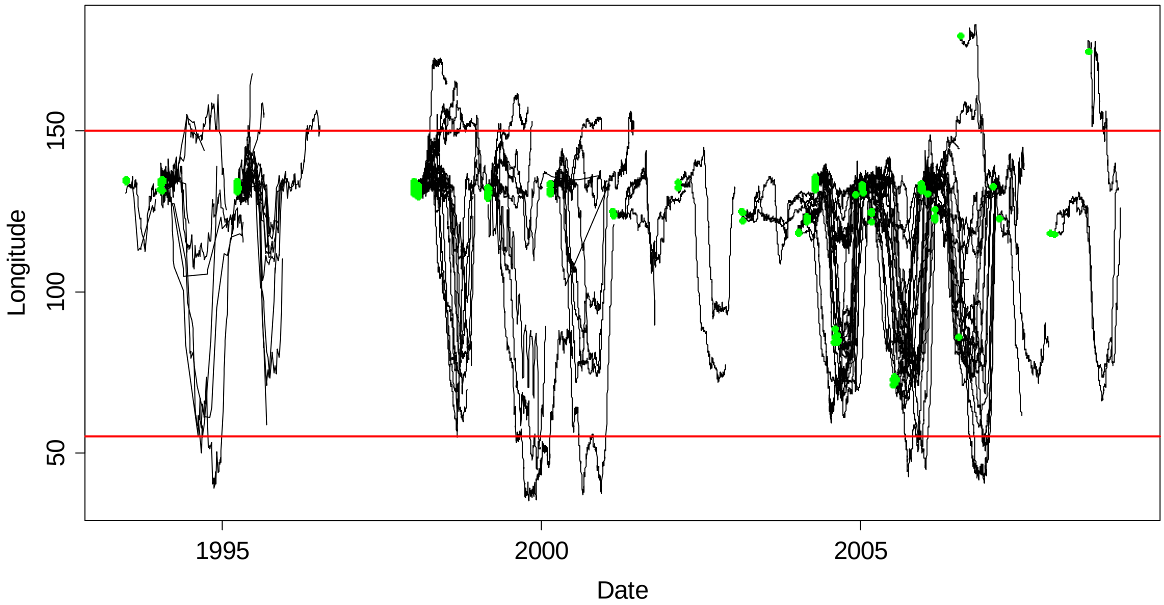


Figure 4. Longitude estimates from all archival tags. The horizontal red lines mark 150°E and 55°E, and the green dots mark the release points.



5. Approaches for combining archival and conventional tag data

One of the main objectives of this project is to use the information provided by archival tags on the mixing rates of juvenile SBT between the major SBT fishing areas to inform the analyses of the conventional tagging data. A fundamental assumption in estimation of mortality rates and abundance from tag data is that tagged and untagged animals are fully mixed throughout the range of the population. For SBT, this can be difficult to achieve since they are distributed over such a large geographic area. If complete mixing is not achieved, then spatial heterogeneity in survival and capture probabilities can lead to biased estimates of mortality rates and abundance, if not accounted for.

Basson et al. (2010) provided details of work under this objective of the project. One of the key outcomes has been a framework for the integration of archival tag data into a spatial mark-recapture model developed for conventional tag data to estimate fishing mortality, natural mortality and movement rates. Abundance can also be estimated if catch data are included. Results from applying this integrated spatial model to simulated data were presented. Some preliminary results from analysing the SBT archival and conventional tag data from the 1990s and 2000s were also presented, but for a model without catch data.

Further analyses of the SBT data, such as the inclusion of catch data, have subsequently been undertaken. The advantage of including catch data is that it allows for abundance by region to be estimated, whilst also contributing information to the fishing mortality estimates. Comparisons between fishing mortality estimates from a spatial and non-spatial model can only be made for the case where catches are included (see Appendix 1). However, the inclusion of catch data is seriously complicated by the issue of unreported catches.

The integrated spatial model requires sufficient overlap in release years of archival and conventional tags, which unfortunately did not exist for SBT in the 1990s. Instead, we applied a two-stage approach to data from the 1990s, in which archival tag data were used to estimate movement parameters that were then input directly into the spatial model (which was applied to conventional tag and catch data). For the 2000s, there was sufficient overlapping archival and conventional tag data for applying the integrated model. Details are provided in Appendix 1.

Summary of main results

From simulations:

- Archival tag data used together with conventional-type tag data in the spatial mark-recapture model can greatly improve the precision of movement estimates, and many fishing mortality estimates, particularly for situations, such as the case for SBT, where fish can only realistically be tagged in some areas.
- Archival tag data can inform and improve the structure of the spatial mark-recapture model used to estimate harvest rates and other relevant quantities.
- Even a modest number of archival tags can lead to significant improvements in the precision of many parameter estimates, as quantified by the simulation study. These results can be used to plan future mark-recapture programs.
- When tags cannot be released in all regions and time periods, there are many situations for which not all parameters of the model can be estimated using conventional tags alone but CAN be estimated if archival tags are included.

From application to SBT:

Reminder: The main objective of our application to SBT data was to illustrate the effect that using archival tag data to inform the movement rates can have on all of the parameter estimates; the actual values of parameter estimates are likely to be biased and must be interpreted cautiously (due to a number of reasons discussed in Appendix 1).

- Comparison of spatial models with/without archival tag data for the 1990s: The archival tag data for the 1990s suggest essentially all juvenile SBT returned to South Australia (SA) at the end of winter, whereas the model without archival tags estimates that the majority of fish remain in their winter longline region for the summer. Including the movement parameters estimated from the archival tags into the spatial model led to fishing mortality estimates for the SA purse seine fishery that were smaller across most cohorts and ages, while those for fisheries off S. Africa became larger.
- Comparison of spatial models with/without archival tag data for the 2000s: The inclusion of archival tag data had a substantial effect on many of the parameter estimates, such as:
  - The movement probability estimates suggest most fish (91%) migrate from SA to the South-East Indian Ocean (SEIO) at the end of summer, as opposed to 24% migrating to the SEIO and 75% to S. Africa without archival tag data. At the end of winter, the movement estimates obtained with archival tag data suggest that almost all fish return from the SEIO to SA at age 1 and about 30% return from S. Africa and the Tasman. Without archival tag data, almost all fish are estimated to return from S. Africa at age 1, 85% from the SEIO and none from the Tasman. In both cases, these percentages decline with age.
  - The fishing mortality (F) estimates tended to be smaller in all regions except S. Africa when archival tag data were included; however, the estimates for ages 3 and 4 in SA (South Australia) are still very high (>0.6 for all cohorts except 2004).
  - The regional abundance estimates were much higher in the SEIO and SA regions and lower off South Africa when archival tag data were included, and the total age 1 abundance estimates were consistently higher (by roughly 0.2 million for each cohort; ~20% higher on average).
- Comparison of spatial model results with a **non-spatial** model for the 1990s data:
  - Generally, there is fairly good agreement between the fishing mortality estimates.
  - The age 1 natural mortality (M) estimates are similar from all the models, but the age 2+ M estimate from the non-spatial model is substantially higher (0.395 compared to 0.21 and 0.28 from the two spatial models).
  - The total age 1 abundance estimates from the non-spatial model are lower than the estimates from the spatial models for cohorts 1990-1992 but higher for cohorts 1993-1994.
- Comparison of spatial model results with a **non-spatial** model for the 2000s data:
  - There is a consistent tendency for average fishing mortality estimates from the spatial model that included archival tag data to be smaller than the non-spatial estimates (and also smaller than those from the spatial model without archival tag data).
  - The age 1 natural mortality (M) estimates are similar from all the models, but the age 2+ M estimate from the non-spatial model is somewhat higher (0.207 compared to 0.187 and 0.132 from the two spatial models).
  - The total age 1 abundance estimates from the non-spatial model are consistently smaller than those from the spatial model, both with and without archival tag data but particularly with.

6. Final report

There are two further components of the project that are being completed for the final report. The first is "habitat modelling". In the original proposal, habitat modelling was envisaged as "... integrating position, temperature and depth data from the tags with oceanographic data to develop a seasonal model of residence times and habitat use" with the aim to use this information to assist interpretation of catch and effort data, and monitoring strategies. The second component is to evaluate implications of the spatial dynamics of juvenile SBT for the management of the SBT resource (e.g. "the potential consequences and benefits of either ignoring or using spatially explicit management actions"). The final report will cover all aspects of the project and a "draft final report" will be submitted to the FRDC for review at the end of August 2011. The final report should be available by the end of the calendar year.

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Appendix 1.

Application of a spatial tag-based assessment model to juvenile southern bluefin tuna conventional and archival tag data

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Abstract

Two general approaches for incorporating archival tag data into a spatial mark-recapture model for estimating natural mortality, fishing mortality, movement and abundance were applied to data from juvenile southern bluefin tuna (SBT). A two-stage approach, in which archival tag data are used to estimate movement parameters that are plugged into the spatial model, was applied to data from the 1990s. An integrated approach, in which archival tag data are incorporated directly in the model through an additional likelihood component, was applied to data from the 2000s. The integrated model approach is preferable because all sources of data contribute to the estimation of all parameters (and their uncertainty), but requires sufficient overlap in release years of the archival and conventional tags, which did not exist for the 1990s. The main objective of this work was to illustrate the effect that using archival tag data to inform the movement rates can have on all of the parameter estimates; the actual values of parameter estimates are likely to be biased and must be interpreted cautiously (due to a number of reasons discussed in the text).

The results show that the movement parameters are strongly affected (improved) by incorporating archival tags, and this has a substantial effect on the regional fishing mortality and abundance estimates. For instance, for the 1990s, the archival tag data suggest essentially 100% of juvenile SBT return to South Australian waters (SA) at the end of winter, whereas the model without archival tags estimates that the majority of fish remain in their winter longline region for the summer. Plugging the movement parameters estimated from the archival tags into the spatial model led to fishing mortality estimates for SA (where the Australian purse seine fishery operates) that were lower across most cohorts and ages. For the 2000s, the majority of fish were estimated to migrate from SA to the south-east Indian Ocean (SEIO) at the end of summer when archival tag data were included in the model, as opposed to the majority of fish estimated to migrate to S. Africa in the model without archival tag data. The movement probabilities estimated for the end of winter were also more plausible when archival tag data were included in the model. The fishing mortality estimates tended to be smaller in all regions except off South Africa, and the abundance estimates were higher in the SEIO and SA regions and lower off South Africa, when archival tag data were included.

Introduction

As part of FRDC Project No. 2003/002 ("Spatial interactions among juvenile southern bluefin tuna (SBT) at the global scale: a large-scale archival tag experiment"), over 500 archival tags have been deployed on juvenile SBT throughout their known geographic range. One of the goals of the project is to acquire information about mixing rates of juvenile SBT between major fishing regions that can be used in analyses of conventional tagging data to get fishery-independent estimates of mortality rates. Several hundred archival tags were also deployed on juvenile SBT in the 1990s, but the distribution of releases was limited to coastal waters south of Australia, so the data from these tags may not provide a complete picture of mixing.

SBT have been subject to high exploitation rates since the 1950s. Recent stock assessments and stock indicators suggest that the spawning biomass is at a historically low level and that the numbers of recruits (i.e., young fish entering the population) have been worryingly low over the last two decades (Anon. 2009). Because the number of young fish in the population largely determines the number of spawners in the future (and, thus, the potential for stock-rebuilding), it is important for effective management of the fishery to have reliable estimates of recruitment numbers and harvest rates. Problems with interpreting catch per unit effort data as an index of abundance are well known. Additionally, catch data for SBT are known to be subject to biases due to under-reporting, potentially large (Anon. 2006). As such, more reliable, fishery-independent data for estimating juvenile abundance are in high demand.

Large-scale conventional tagging experiments have been carried out on juvenile SBT periodically over the past five decades, with the primary aim of estimating juvenile fishing mortality rates and, thereby, abundance. A fundamental assumption in the use of tagging experiments to estimate these quantities is that tagged and untagged animals are fully mixed throughout the range of the population. This can be difficult to achieve in wild populations, especially ones that are distributed over large geographic areas, such as SBT. If complete mixing is not achieved, then spatial heterogeneity in survival and capture probabilities, if not accounted for, can lead to biased estimates of mortality rates and abundance. Since it is known that capture rates differ significantly between major fisheries/fishing regions for juvenile SBT, it is important to consider a model that takes spatial heterogeneity into account when analyzing the tag-return data.

As part of FRDC project 2002/015 (Polacheck et al. 2006), a discrete-space, discrete-time model for estimating fishing mortality, natural mortality and movement rates from conventional tag-return data was developed. Abundance can also be estimated if catch data are included. The model was initially developed under a general spatial framework, but was subsequently modified to accommodate spatial and temporal dynamics resembling those of juvenile SBT (Polacheck et al. 2006, Appendices 11 and 16).

Having position estimates from archival tags that were released at the same time as conventional tags can improve the model in a number of ways. Namely, it can:

- provide valuable information about the appropriateness of the spatial and temporal structure being assumed;
- help determine whether the assumption that a fish has no memory with respect to its previous movements is reasonable, or whether an alternative hypothesis that fish show site-fidelity is more appropriate;
- provide information to help separate fishing mortality from movement, as this is difficult for the model to do with conventional tagging data alone.

Two general approaches can be used for including archival tag data in the model: 1) a two-stage approach, in which position estimates from archival tags are used to estimate movement parameters, which can then be plugged into the model as known or as priors (i.e. with uncertainty); 2) an integrated approach, in which data from archival tags are incorporated directly in the model through an additional likelihood component. For each recaptured archival tag, the data to be included in the likelihood is the region that the fish was in during each time period between release and recapture. The integrated spatial model is more statistically rigorous because the variance and, therefore, relative weighting of the archival tag data gets correctly accounted for. Plus, there is information not only about movement but also about mortality rates in the archival tag data that gets incorporated with the integrated approach. The integrated approach does, however, require that the archival tag releases correspond to the same release years and ages as the conventional tag data. This is not strictly required with the two-stage approach, provided that movement rates determined from the archival tag data are applicable to the conventional tag data (i.e. movement rates did not change significantly between the time of the archival tagging experiment and the conventional tagging experiment).

The archival tag data for SBT suggest changes in juvenile migration patterns have occurred between the 1990s and 2000s, with a contraction in eastward (and possibly the extent of westward) movement (Basson et al. 2009). Moreover, previous analyses of the conventional tag data from the 2000s have found that fishing mortality estimates derived from tags released at age 1 off the south coast of Western Australia are much lower than those derived from tags released at ages 2 and 3 in the Great Australian Bight (Polacheck and Eveson 2007). This difference was not observed in the 1990s conventional tag data, and the reason for it remains a puzzle (see Polacheck and Eveson 2007 for a thorough discussion). Thus, it made sense to analyse the data separately for these two periods.

For the 1990s, the amount of overlapping conventional and archival tag data is sparse (conventional tags were mostly released in the first half of the decade, and archival tags in the second half—see Table 1), so incorporating archival tag data directly into the model is not very useful. Thus we present results from applying the two-stage approach to the data from the 1990s. For the 2000s, the amount of overlapping conventional and archival tag data is much greater, so results from applying the integrated approach are presented.

Methods

SBT background

SBT are long-lived (age 30+) and highly migratory (Caton 1991). Mature adults (age 10+) spawn in the Indian Ocean south-east of Java, Indonesia during the months of September to April (Davis and Farley 2001). Newly spawned fish migrate down the west coast of Australia, with 1 year olds commonly found off the west and south coasts of Western Australia (WA) (Hobday et al. 2008). Juveniles predominantly of ages 2 to 4 congregate in large numbers in the warm continental shelf waters of the Great Australian Bight (GAB) during the austral summer (Farley et al. 2007). At the end of summer, they migrate to deep oceanic waters spanning from South Africa to New Zealand to spend their winters before a high but unknown proportion return to the GAB for the following summer (Gunn and Block 2001). Archival tag data has shown that the timing of these cyclic migrations can vary greatly between individuals, but for the most part, juveniles enter the GAB between November and January and leave between April and June. They stop returning as they get older, with very few fish above age 5 found in the GAB.

Commercial fishing for SBT began by Australia and Japan in the early 1950s, and the fishery has undergone substantial changes over time. For our purposes here, we are interested in fisheries that caught juvenile SBT during the 1990s and 2000s, since this corresponds to when the tagging data being analysed were collected. The primary fishery that caught SBT of ages 2-4 during these two decades was the Australian purse seine fishery, catching surface schools off South Australia during the summer (December through March). In addition to the surface fishery, juveniles are also caught by various longline fleets operating throughout the southern ocean, mostly during the winter months. The most significant of the longline fisheries in terms of juvenile catches is Japan, followed by Taiwan, Korea and New Zealand.

SBT spatial model

The spatial model for juvenile SBT consists of four regions (Figure 1):

1. Southern Australia (SA), which includes both the Great Australian Bight (GAB) and waters around Western Australia (WA);
2. South Africa;
3. South-East Indian Ocean (SEIO);
4. Tasman Sea

and two seasons:

1. summer (Nov-Apr), corresponding roughly to the summer surface fishery;
2. winter (May-Oct), corresponding roughly to winter longline fisheries.

The model assumes that the surface fishery occurs only in the summer in SA, and that the longline fisheries occur only in the winter in the remaining 3 regions. Tagging, whether conventional or archival, is assumed to occur only in regions and time periods of fishing. Obviously recaptures can occur only in regions and periods of fishing.

At the end of summer, fish in SA migrate to one of the three longline regions. At the end of winter, fish can either stay in their current region or else migrate back to SA (i.e., the model does not allow for direct migration between the longline regions). Movement rates between regions are allowed to vary with age, but are assumed to be the same between years for fish of a given age. Mathematically, these movement dynamics can be described by the following matrices:

End of season 1 (summer) movement probability matrix:

$$\Pi_{a,t} = \begin{bmatrix} 0 & \pi_{a,t,1,2} & \pi_{a,t,1,3} & \pi_{a,t,1,4} \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \quad \text{for odd } t$$

End of season 2 (winter) movement probability matrix:

$$\Pi_{a,t} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ \pi_{a,t,2,1} & \pi_{a,t,2,2} & 0 & 0 \\ \pi_{a,t,3,1} & 0 & \pi_{a,t,3,3} & 0 \\ \pi_{a,t,4,1} & 0 & 0 & \pi_{a,t,4,4} \end{bmatrix} \quad \text{for even } t$$

The subscript in $\pi_{a,t,r,r'}$ refers a fish of age a moving from region r to r' at the end of time period t. Each row must sum to 1, so that $\pi_{a,t,1,4} = 1 - \left(\pi_{a,t,1,2} + \pi_{a,t,1,3}\right)$ for season 1 (odd t) and $\pi_{a,t,r,r} = 1 - \pi_{a,t,r,1}$ for season 2 (even t) and $r = 2,3,4$. The 1's on the diagonal of the season 1 matrix reflect the assumption that any fish in regions

2, 3 and 4 during season 1 remain in the same region at the end of the season. The 1 in the (1,1) position of the season 2 matrix is for completeness, but it is not used because the model assumes there are no fish in SA during winter.

Two-stage approach: 1990s

We estimated the parameters of the movement matrices using archival tag tracks available from fish tagged in 1993 to 2000. In doing so, we assumed that the movement parameters are independent of age. Although this may be too simplistic, the data available are insufficient to provide reliable age-specific estimates. Not all tracks fit unambiguously into the spatial and temporal structure being assumed. Thus, we had to use our best judgement in determining region designations for a number of tags. For example, some fish over-wintered in waters off WA, bordering the division between regions SA and SEIO, and we assigned them SEIO for their winter region. Also, fish that ultimately ended up in waters off South Africa during the winter were assigned South Africa as their winter region regardless of how long they spent migrating through SEIO to get there.

Next we applied the spatial model to the SBT conventional tag and catch data from the 1990s, with the movement parameters fixed at those estimated from the archival tag data. The spatial model was already fit to the conventional tag and catch data as part of FRDC project 2002/015 (see Appendix 16 of Polacheck et al. 2006), however in that case the movement parameters were estimated within the model based on information contained in the conventional tag data. We wanted to see how much the mortality rate and abundance estimates differed when archival tag data were used to determine the movement parameters.

The data sets used as input to the model were:

- Tag release and return data from 1991 to 1997 (we do not include tag returns beyond 1997 because it is the last year for which we have information for estimating reporting rates). Specifically, we included data from fish belonging to cohorts 1990 to 1994 that were tagged at ages 1 to 3 and recaptured up to a maximum of age 5 (beyond age 5 the numbers of recaptures becomes very small). The releases needed to be compiled by year, season, age and region of release, and the returns corresponding to each set of releases (i.e., to each year, season, age and region of release) needed to be compiled by year, season, age and region of recapture.
- Catch data from the commercial fisheries corresponding to the same years and ages of tag recaptures; e.g., for the 1990 cohort, catch data were included for ages 1 to 5 (corresponding to years 1991 to 1995). The catch data needed to be compiled by year, season, age and region of capture.
- Estimates of tag reporting rates by year, season, age and region for years 1991 to 1997. These were calculated by taking the weighted average of fishery-specific reporting rate estimates for fisheries operating in a given season and region using the catch-at-age by fishery as weights. The fishery-specific reporting rates were based on tag seeding experiments for the Australian surface fishery and observer data for the longline fisheries (note that there are a large number of alternative options for the fishery-specific reporting rates, of which only one is considered here). The reporting rate estimates were included as known without error in the model.
- Estimates of immediate and continuous tag shedding rates assumed to be the same across years, seasons, ages and regions, as well as taggers. These were derived from double tagging data from the 1990s conventional tag experiments, and were included as known without error in the model.

Details of each of the data sets and how they were compiled can be found in Appendices 4 and 16 of Polacheck et al. (2006). The tag shedding rates are estimated with good precision since all fish were double-tagged, so including them as known without error is reasonable. On the other hand, the reporting rate estimates are highly uncertain. We have chosen to include them as known for simplicity, since the results presented here are only intended to be illustrative. However, uncertainty in the reporting rates can be included through another likelihood component in applications where it is required.

Although the years of the conventional tag-return data (1991 to 1997) do not overlap exactly with the years of the archival tag data used to estimate the movement parameters (1993 to 2000), data from both tag types suggest that movement dynamics of juvenile SBT remained similar from 1991 through 2000[2]. Thus, it should be reasonable to assume the movement parameters estimated from the archival tag data are applicable to the conventional tag data being included in the model.

The spatial SBT model was developed to include both tag-return data and catch data, although it can be fitted using tag-return data alone. The advantage of including catch data is that it allows for abundance by region to be estimated, whilst

[2] There appears to have been a change in juvenile movement patterns in the early 2000s compared to the 1990s, with fewer fish migrating east to the Tasman Sea after leaving the GAB, as well as some evidence of fewer fish going as far west (Basson et al. 2009).

also contributing information to the fishing mortality estimates. The catch data used here were compiled prior to the independent reviews conducted in 2006 that found evidence of substantial unreported catches of SBT dating back to the 1980s (see Anon. 2006). A number of alternative scenarios for taking into account the unreported catches are being considered by the CCSBT, but these are simply adjustments to the total annual catch statistics. For inclusion in the spatial SBT model, we need to consider how to attribute the unreported catches to regions, seasons and age classes, which is not a trivial problem. As such, we chose to continue using the catch data as compiled for FRDC project 2002/015. Our main objective here is to illustrate the effect that using archival tag data to inform the movement rates can have on the parameter estimates; the actual values of estimates are likely to be biased and must be interpreted cautiously.

Integrated approach: 2000s

Archival tag data can be included directly in the spatial tag model through an additional likelihood component. For each archival tag recovery, the data to be included is the region that the fish was in during each time period it was at liberty. To calculate the probability that a fish will be in a given region at a given time period is relatively simple compared to a conventional tag because all intermediate transitions between release and recapture are known. Thus, under the assumption that fish move between regions at the end of each time period, the probability of a fish released in region r_1 in time period t being recaptured in region r_2 in time period t+3 after having made transitions from r_1 to r_3 to r_1 to r_2 is just Pr(survive r_1 in time period t)*Pr(move from r_1 to r_3)*Pr(survive r_3 in time period t+1)*Pr(move from r_3 to r_1)* Pr(survive r_1 in time period t+2)*Pr(move from r_1 to r_2)*Pr(caught in r_2 in time period t+3). For a conventional tag, all possible intermediate transitions need to be accounted for. The survival probabilities are functions of natural mortality and fishing mortality (which may be age, region and/or time dependent), and the movement probabilities are simply the parameters of the transition matrices (which may be age and/or time dependent). Mathematical details for the archival tag likelihood can be found in Eveson et al. (in prep).

There are a number of complicating factors when applying the integrated spatial model to real data:

1. position estimates from archival tags have large uncertainty;
2. many (most) fish tracks fit do not fit unambiguously into the spatial and temporal structure being assumed;
3. tracks estimated from archival tags often stop before the fish is caught and the tag recovered (due to a number of reasons such as the light sensor failing, the battery dying, etc).

In terms of (1), longitude estimates are generally much more accurate than latitude and should be sufficient to determine the broad regions needed for the model. In terms of (2), the spatial and temporal structure of the model is clearly an oversimplification of the truth, and it can be difficult to accommodate some of the archival tag tracks within this structure. This was an issue in estimating the movement matrices for the two-stage approach as well. Again, we used our best judgement for each archival tag track to determine the most appropriate region designation in each season. In terms of (3), the model can be modified to accommodate incomplete archival tag tracks by treating each one the same as any archival tag up until the track stops, then treating it as a conventional tag that was released in the last observed region/time period (and recaptured in the region/time period where the fish was caught).

There are also issues specific to SBT data from the 2000s that make applying the spatial tag model to these data complicated. First, we do not have any basis for estimating reporting rates for the longline fisheries in the 2000s, thus we need to make guesses based on estimates from the 1990s. We can estimate reporting rates for the Australian surface fishery based on data from tag seeding experiments conducted in 2003 to 2009, but the very low estimates in some seasons has brought into question the reliability of these estimates. Second, as mentioned in the Introduction, previous analyses of the conventional tagging data from the 2000s showed that fishing mortality estimates derived from fish tagged at age 1 off WA are much lower than those derived from fish tagged at ages 2 and 3 (primarily in the GAB, although some age 2 off WA) (Polacheck et al. 2007). This difference was not observed in the 1990s tagging data. Brownie-type models, on which the spatial model is based, integrate releases from all ages to produce estimates of fishing mortality and natural mortality. Thus, the estimates obtained from applying these models to the 2000s data will have an unclear interpretation. While it is not the most satisfactory solution, we dealt with this problem simply by omitting data corresponding to WA releases.

The data sets used as input to the model were:

- Tag release and return data from 2001 to 2007. Specifically, we included data from fish belonging to cohorts 2000 to 2004 that were tagged at ages 1 to 3 and recaptured up to a maximum of age 5 (beyond age 5 the numbers of recaptures becomes very small). The releases needed to be compiled by year, season, age and region of release, and the returns corresponding to each set of releases (i.e., to each year, season, age and region of release) needed to be compiled by year, season, age and region of recapture.

- Catch data from the commercial fisheries corresponding to the same years and ages of tag recaptures; e.g., for the 2000 cohort, catch data were included for ages 1 to 5 (corresponding to years 2001 to 2005). The catch data needed to be compiled by year, season, age and region of capture.
- A constant reporting rate value was assumed for each region (i.e., independent of year and age) due to lack of information. The values used were: 0.50 for SA, 0.10 for South Africa, 0.25 for the SEIO, and 0.65 for the Tasman. The SA value is an average estimate from the tag seeding experiments conducted in the GAB in the 2000s, whereas the values for the longline regions are based on average estimates for the 1990s, which themselves are highly uncertain. The reporting rate estimates were included as known without error in the model.
- Estimates of immediate and continuous tag shedding rates assumed to be the same across years, seasons, ages and regions, as well as taggers. These were derived from double tagging data from the 2000s conventional tag experiments, and were included as known without error in the model.

The tag shedding rates for the 2000s are estimated with good precision since all fish were double-tagged, so including them as known without error is reasonable. Clearly, the reporting rate estimates are highly uncertain. We include them as known for simplicity, since the results presented here are intended to be illustrative only. If our purpose was to obtain reliable mortality and abundance estimates, then we would need to conduct sensitivity analyses using different reporting rate values.

The catch data were compiled from data contained in the CCSBT catch database. As for the 1990s catch data, we have not made any adjustments for potential unreported catches (for the reasons discussed in the previous section 'Two-stage approach: 1990s'). We repeat that our main objective is to investigate the effect that including archival tag data in the spatial model has on the parameter estimates; the actual values are likely to be biased and must be interpreted cautiously.

Comparison with non-spatial results

It is of interest to compare parameter estimates from the spatial model with those obtained from an equivalent non-spatial analysis of the same data (equivalent in the sense that if we assumed fishing mortality varied by year, age and region in the spatial model, then we would assume it varied by year and age in the non-spatial model). Population-wide (non-spatial) estimates of mortality rates and abundance are often of as much, or more, interest than regional estimates; however, we expect them to be biased if spatial heterogeneity in mortality rates exists and full mixing of tagged and untagged fish has not been achieved.

When fitting the non-spatial model for the 1990s and 2000s, we used the same conventional tag and catch data as for the spatial model but summed over regions. We did not include archival tag data since the model does not require estimates of movement between regions. The archival tag data could be included exactly the same way as conventional tag data (release and recaptures numbers by year and age), but the sample sizes are so small compared to the conventional tag data that they would have very little influence in the likelihood. For reporting rates for the 1990s, we used the non-spatial reporting rate estimates used in the current CCSBT operating model (OM). The spatial reporting rates we used for the 1990s were based on the same analyses and assumptions used to calculated the non-spatial estimates in the OM. For the 2000s, we simply used a reporting rate estimate of 0.5, as this was a rough average across regions of the spatial reporting rates that we used for the 2000s.

To compare parameter estimates from the spatial and non-spatial models, it is first necessary to calculate population-wide estimates for the spatial model. Natural mortality is already assumed to be the same across regions in the spatial model, so the M estimates can be compared directly. Population-wide abundance can be calculated simply by summing the regional abundance estimates. To compare the fishing mortality estimates is not as straightforward—we cannot simply sum the F estimates across regions because they need to take into account the number of fish in each region. Thus, we calculate average yearly fishing mortalities for the spatial model as outlined in Appendix 11, section 3.5.1, of Polacheck et al. (2006).

Results

Two-stage approach: 1990s

The movement probability matrices estimated using archival tag data from tags released in 1993 to 2000 are given in Table 2. At the end of summer, the majority of fish (67%) are estimated to migrate from SA to the SEIO, with 12% migrating to S. Africa and 21% to the Tasman. At the end-of winter, all fish from the 3 longline regions are estimated to return to SA. The archival tag data contained no concrete evidence of a fish age 5 or less not returning to SA for the summer (for tags released in 1993-2000). There was one tagged fish recaptured off S. Africa in November, but it may still have returned to SA if it had not been caught (a number of fish did not start their return migration until Dec-Jan).

Results from fitting the spatial model to the conventional tag and catch data: (a) fixing the movement parameters at those estimated from the archival tag data (above); and (b) estimating the movement parameters within the spatial model (using only conventional tag data) are compared in Tables 2 and 3 and Figure 2. A number of different model parameterizations were considered, but the results presented here are based on the following:

- Natural mortality (*M*) is assumed to vary by age only (i.e., independent of year and region), and *M* at ages 2 and above is assumed to stay constant (this is because when fish are tagged at $n=3$ consecutive ages, only $n-1=2$ *M* parameters can be estimated).
- Fishing mortality (*F*) is assumed to vary by year, age and region.
- To account for non-mixing directly following tagging, fishing mortality is allowed to differ between tagged fish in the time period of tagging and untagged fish in that same time period; i.e., for fish tagged at age *a* in time period *t* in region *r*, we replace $F(a,t,r)$ with $F^*(a,t,r)$. There are identifiability issues with this model that we overcome by assuming $F^*(a,t,r) = k * F(a,t,r)$, where *k* is a parameter estimated in the model.
- Movement parameters are assumed to be independent of year and age (since this was the assumption made in estimating the movement parameters from the archival tag data).
- Age 1 abundance (P_1) is allowed to vary between years, but the distribution of age 1 fish amongst the 4 regions at the start of season 1 is assumed to be the same each year.

The end-of-summer movement estimates from the model are reasonably similar to those from the archival tag data (Table 2). However, the end-of-winter estimates suggest very different movement dynamics than those suggested by the archival tag data. For instance, the archival tag data suggest that essentially 100% of juvenile SBT return to SA at the end of winter, whereas the model estimates suggest the majority of fish remain in their winter longline region for the summer. This is most likely because the model has difficulty separating fishing mortality from movement with conventional tag data alone.

The natural mortality rate estimates are higher, especially for age 2+, when the movement probabilities are fixed at those estimated from the archival tag data rather than estimated in the model (Table 3). The fishing mortality estimates are also significantly affected (Table 3, Figure 2). Most noticeable is that the *F* estimates for SA are generally quite a bit smaller with the fixed archival-tag based movement parameters than the model-estimated movement parameters (Figure 2). This is because when the movement probabilities are fixed, the resulting abundance estimates suggest significantly more fish are in SA in the summer than when the movement probabilities are estimated within the model (Figure 3); when abundance is higher, a smaller *F* achieves the same number of recaptures. Some of the *F* estimates for S. Africa are very large, and even more so with the fixed archival-tag based movement parameters (Figure 2); however, the abundance estimates for S. Africa are very small (Figure 3) so these large *F*'s do not translate to huge catch numbers.

The total age 1 abundance estimates are quite similar using the fixed versus model-estimated movement probabilities, but the breakdown into regions at age 1 is very different (Table 3). When the movement probabilities are fixed, essentially all age 1 fish are estimated to be in SA in the summer season, whereas when the movement probabilities are estimated in the model, a greater percentage of age 1 fish are estimated to be in SEIO than SA in the summer.

The effect of the different movement probability options on the regional abundance estimates over time is apparent in Figure 3, which shows that significant numbers of juvenile fish are estimated to remain in the SEIO and Tasman regions in the winter when the movement parameters are estimated within the model whereas essentially no juveniles remain in these regions when the archival tag-based movement estimates are used.

Integrated approach: 2000s

The spatial model was fitted to the SBT data from the 2000s first using only conventional tag and catch data, and second including archival tag data. A number of different model parameterizations were considered, but the results presented here were based on the following:

- Natural mortality (*M*) is assumed to vary by age only (i.e., independent of year and region), and *M* at ages 2 and above is assumed to stay constant (this is because when fish are tagged at $n=3$ consecutive ages, only $n-1=2$ *M* parameters can be estimated).
- Fishing mortality (*F*) is assumed to vary by year, age and region.
- To account for non-mixing directly following tagging, fishing mortality is allowed to differ between tagged fish in the time period of tagging and untagged fish in that same time period; i.e., for fish tagged at age *a* in time period *t*

in region *r*, we replace $F(a,t,r)$ with $F^*(a,t,r)$. There are identifiability issues with this model that we overcome by assuming $F^*(a,t,r) = k * F(a,t,r)$, where *k* is a parameter estimated in the model.

- The end-of-summer movement probabilities are assumed to be independent of age and cohort (i.e., year). In other words, the proportion of fish leaving SA and going to each of the 3 longline regions is the same for all ages and years.
- The end-of-winter movement probabilities are assumed to be separable into multiplicative age and region effects, meaning that the proportion of fish returning to SA at the end of winter can vary with age, but the *relative* proportion coming from each of the longline regions is the same for all ages. For example, the relative proportion of fish that return from each of the longline regions may be 0.2 from S. Africa, 0.5 from SEIO and 0.3 from the Tasman. If the total proportion of age *a* fish returning to SA is α_a, then the proportion of age *a* fish returning from S. Africa is $0.2\alpha_a$, from SEIO is $0.5\alpha_a$ and from the Tasman is $0.3\alpha_a$.
- Age 1 abundance (P_1) is allowed to vary between years, but the distribution of age 1 fish amongst the 4 regions at the start of season 1 is assumed to be the same each year.

The parameter estimates are summarized in Table 4 and Figure 4. When archival tag data are included in the model, the movement probability estimates at the end of summer suggest most fish (91%) migrate from SA to the SEIO, whereas without archival tag data, 75% of fish are estimated to migrate to S. Africa and 24% to the SEIO. At the end of winter, the movement estimates obtained with archival tag data suggest that almost all fish return from the SEIO to SA at age 1 and about 30% return from S. Africa and the Tasman. These percentages decline with age. Without archival tag data, almost all fish are estimated to return from S. Africa at age 1, 85% from the SEIO and none from the Tasman. Again, these percentages decline with age.

The *M* estimates are slightly larger at age 1 and smaller at ages 2+ when archival tag data are included, but in both cases suggest *M* at age 1 is much higher than at ages 2-5 (Table 4). The *F* estimates tend to be smaller in all regions except S. Africa when archival tag data are included; however, the *F* estimates for ages 3 and 4 in SA are still very high (>0.6 for all cohorts except 2004) (Table 4; Figure 4). Some of the *F* estimates for S. Africa obtained when including archival tag data were very high, particularly for the 2001 cohort, but they do not translate to huge catch numbers because the abundance estimates for this region are very small (Figure 5).

The total age 1 abundance estimates are consistently higher when archival tag data are included (by roughly 0.2 million), but the breakdown amongst regions at age 1 is very similar (Table 3). However, if we use the mortality and movement parameters to calculate the regional abundance estimates over time (age), we see they are quite different for S. Africa and the SEIO when archival tag data are included (Figure 5). In particular, the model without archival tag data has substantial numbers of fish off S. Africa at ages 2-5, and relatively few fish in the SEIO.

Comparison with non-spatial results

We first consider the 1990s results. Figure 6 compares the *F* estimates obtained for the 1990s using the non-spatial model with those obtained by averaging the region-specific *F* estimates from the spatial model, both when the movement parameters were estimated within the model using the conventional tag data and when the movement parameters were fixed at those determined from the archival tag data. For the 1990-1992 cohorts, the non-spatial estimates tend to be slightly larger than the spatially-derived estimates, but this is not the case for the 1993-1994 cohorts. Generally speaking, however, there is fairly good agreement between the *F* estimates. The age 1 *M* estimate obtained from the non-spatial model (0.462) is similar to the estimate obtained from both applications of the spatial model (see Table 3); however, the age 2+ estimate (0.395) is substantially higher. The total age 1 abundance estimates from the non-spatial model (2.8, 2.5, 1.8 1.4 and 1.3 million for cohorts 1990-1994 respectively) are lower than the estimates from the spatial models for cohorts 1990-1992 but higher for cohorts 1993-1994.

We now consider the 2000s results. Figure 7 compares the *F* estimates obtained for the 2000s using the non-spatial model with those obtained by averaging the region-specific *F* estimates from the spatial model, both when archival tag data were and were not included. In this case, there is a consistent tendency for average *F* estimates derived from the spatial model that included archival tag data to be smaller than the non-spatial estimates (as well as smaller than the average *F* estimates derived from the spatial model without archival tag data). The differences for ages 3 and 4 of cohorts 2001-2003 ranged from 0.09 to 0.22. The age 1 *M* estimate obtained from the non-spatial model (0.482) is very similar to the estimates obtained from the spatial model with and without archival tag data (see Table 4); however, the age 2+ estimate (0.207) is somewhat higher than the estimate obtained from the spatial model with archival tag data. The total age 1 abundance estimates from the non-spatial model (0.99, 0.80, 0.66, 1.37 and 1.48 million for cohorts 2000-2004 respectively) are consistently smaller than those from the spatial model, both with and without archival tag data but particularly with.

Discussion

In this study we demonstrated how archival tag data can be used, either indirectly through a two-stage approach or directly through an integrated likelihood, to inform a spatial model for estimating mortality rates, movement and abundance.

We applied the two-stage approach to SBT data from the 1990s (since the data were insufficient to apply the integrated approach), and found that the movement probabilities suggested by the archival tag data were substantially different than those estimated in the spatial model with only conventional tag and catch data as inputs. In particular, archival tag data suggest that essentially 100% of juvenile SBT return to SA at the end of winter, whereas the model estimates suggest the majority of fish remain in their winter longline region for the summer. When the movement parameters were fixed in the spatial model at those estimated from the archival tags, many of the other parameter estimates were notably affected. For instance, the fishing mortality estimates for the SA region (where the Australian purse seine fishery operates) were substantially lower across most cohorts and ages. Based on previous information and inferences about juvenile SBT migration, we expect the majority of juveniles to return to SA but that the proportion is likely to differ with age (since fish stop showing up, at least in the catches, beyond age 5). Unfortunately, we have very few archival tag tracks for fish at ages 4 and 5 in the 1990s so our oversimplified model did not allow for movement to differ with age.

The archival tag data and conventional tag data for SBT cohorts in the 2000s overlapped considerably, so we were able to apply the integrated spatial model to these data. Including archival tag data in the model had a significant affect on many of the parameter estimates. For instance, the F estimates tended to be smaller in all regions except S. Africa. Also, when archival tag data were included, the resulting estimates of abundance by age and region showed many more fish in the SEIO and SA regions, and less fish off S. Africa.

Population-wide estimates derived from the spatial model results for the 1990s and 2000s gave similar overall trends in fishing mortality and abundance compared to estimates derived directly from a non-spatial model; however, there were some notable differences in the magnitude of the estimates. This was particularly true for the fishing mortality estimates for the 2000s: the average estimates calculated from the spatial model results that included archival tag data were consistently smaller (by as much as 0.22) than the estimates obtained from the non-spatial model.

Although we have illustrated the benefits from incorporating archival tag data into the spatial model, we need to keep in mind that the parameter estimates obtained are intended to be illustrative of the potential usefulness of archival tag data. The actual parameter values presented are subject to biases due to a number of issues with the data, including: lack of information on reporting rates (particularly for the 2000s, but also for the 1990s); biased catch data due to under-reported catches (affecting both the 1990s and 2000s data), and the inexplicable lack of returns of age 1 fish tagged off WA in the 2000s (which we dealt with simply by omitting WA releases for the 2000s).

In our application of the two-stage approach to SBT data from the 1990s, we treated the movement parameters that we estimated from the archival tag data as known when we input them to the spatial model. In a more rigorous application, the movement estimates could be treated as priors in the model (assuming, for example, that they are normally distributed with means and variances estimated from the archival tag data). This would allow for them to be updated with information about movement from the conventional tag data, and also for their uncertainty to be propagated through to the other parameter estimates. The integrated approach, which we applied to SBT data from the 2000s, is the preferable approach when sufficient overlapping archival and conventional tag data exist. In this case, all sources of data (archival tag, conventional tag and catch) contribute to the estimation of all parameters (both the point estimates and their uncertainty).

The SBT spatial model as presented here assumes that all fish migrate out of SA at the end of summer. This appears to be roughly true for the GAB, but not for WA (recall that SA encompasses the GAB as well as waters south of WA). The accumulation of more archival tag tracks has shown that, in fact, quite a few fish spend winter in waters off WA. We altered the spatial model to have an alternative movement structure that allows for fish to over-winter in SA but still assumes no fishing takes place in SA during the winter. We applied this alternative model to the data from the 2000s (including archival tag data). A significant percent of fish (27%) were estimated to remain in SA for the winter, but the fishing mortality estimates were largely unaffected. Further investigation of this model was not considered warranted (especially since the age 2+ natural mortality rate estimate went to zero, which is not very plausible). A better alternative may be to split SA into two regions, WA and GAB, where the movement dynamics for WA would be similar to the longline regions (i.e., fish could migrate from the GAB to WA at the end of summer, and fish could either remain in WA or return to the GAB at the end of winter) but fish remaining in WA in the winter would not be subject to fishing.

In terms of the season definitions in the model, the archival tag data suggest they are reasonable, but perhaps oversimplified. The general notion that juvenile SBT migrate to SA for the summer and out of SA for the winter is clearly supported, but the exact timing of these migrations is more variable than might have been expected. Furthermore, the assumption that fish move directly between regions is obviously unrealistic, particularly in the case of a fish migrating between SA and S. Africa, as it must move through the SEIO in getting there. If fish migrate rapidly from SA to their winter region then this assumption is not seriously violated, but the archival tag tracks show that many fish took more than a month to migrate to their ultimate winter region and did not always take a direct route (e.g., some fish headed eastward out of the GAB before turning west towards to the SEIO). There is also the issue of site-fidelity (i.e., fish returning to the same longline region each winter), which would be a violation of the Markov movement model assumption. Site-fidelity is difficult to assess since not many of the archival tags have tracks spanning two winters, however the few tracks that are available show that not all fish return to the same winter region. There may be a tendency towards site-fidelity but, if so, it is not absolute. These are all potential areas for further investigation in future.

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Table 1. Numbers of a) conventional and b) archival tag releases by age and year of release. Corresponding numbers of recaptures up to and including age 5 are given in italics (age 5 is the maximum recapture age used in the model). Conventional tag releases from WA are omitted for years 2000-2008 for reasons discussed in the text.

a) Conventional tags

RELEASE YEAR	RELEASE AGE					
	1		2		3	
1991	3301	*145*	3209	*361*	811	*87*
1992	2147	*127*	4715	*392*	1110	*88*
1993	4898	*402*	3161	*260*	2909	*197*
1994	9003	*914*	3177	*331*	3737	*264*
1995	8594	*1010*	5968	*897*	2728	*240*
1996	82	*16*	2524	*601*	1516	*349*
1997	884	*109*	593	*131*	553	*143*
1998	-		-		-	
1999	-		-		-	
2000	-		-		-	
2001	-		-		-	
2002	334	*67*	158	*34*	21	*2*
2003	60	*16*	2484	*657*	3251	*617*
2004	622	*78*	3247	*787*	1009	*380*
2005	144	*20*	7856	*1852*	705	*170*
2006	126	*12*	6486	*870*	3124	*581*
2007	22	*2*	7443	*815*	478	*84*
2008	-		-		-	

b) Archival tags

RELEASE YEAR	RELEASE AGE					
	1		2		3	
1991	-		-		-	
1992	-		-		-	
1993	-		29	*2*	1	*0*
1994	-		1	*0*	142	*12*
1995	-		88	*30*	52	*11*
1996	-		-		-	
1997	-		-		-	
1998	-		3	*1*	99	*27*
1999	-		-		30	*8*
2000	-		-		21	*6*
2001	1	*0*	4	*3*	-	
2002	-		14	*3*	8	*0*
2003	29	*3*	-		-	
2004	14	*3*	52	*15*	17	*2*
2005	-		59	*10*	25	*4*
2006	10	*2*	52	*5*	51	*11*
2007	45	*0*	64	*3*	22	*0*
2008	-		54	*0*	33	*0*

Table 2. Movement probability estimates for SBT cohorts from the 1990s: (i) obtained from the spatial model applied to conventional tag and catch data; (ii) based on an independent analysis of the archival tag data.

	From spatial model (no archival tag data)	Based on archival tag data
End-of-summer		
SA to S. Africa	0.09	0.12
SA to SEIO	0.77	0.67
SA to Tasman	0.14	0.21
End-of-winter		
S. Africa to SA	0.00	1.0
SEIO to SA	0.40	1.0
Tasman to SA	0.41	1.0

Table 3. Parameter estimates obtained from applying the spatial model to the 1990s conventional tag and catch data for SBT with the movement parameters: (left) estimated within the model; (right) fixed at those estimated from the archival tag data.

				Movement parameters estimated in model					**Movement parameters fixed based on archival tags**				
M				Age1	Age2+				Age1	Age2+			
				0.474	0.213				0.503	0.276			
F	Cohort	Season	Region	Age1	Age2	Age3	Age4	Age5	Age1	Age2	Age3	Age4	Age5
	1990	1	SA	0.037	0.053	0.084	0.067	0.018	0.014	0.019	0.032	0.027	0.008
	1990	2	S.Africa	0.003	0.006	0.187	0.280	0.176	0.001	0.004	0.223	0.437	0.294
	1990	2	SEIO	0.000	0.004	0.011	0.015	0.019	0.000	0.005	0.014	0.019	0.026
	1990	2	Tasman	0.000	0.137	0.197	0.151	0.340	0.000	0.090	0.122	0.097	0.214
	1991	1	SA	0.019	0.052	0.096	0.124	0.018	0.008	0.019	0.036	0.049	0.008
	1991	2	S.Africa	0.000	0.016	0.106	0.355	0.263	0.000	0.010	0.110	0.559	0.444
	1991	2	SEIO	0.000	0.002	0.020	0.031	0.015	0.000	0.002	0.024	0.040	0.022
	1991	2	Tasman	0.000	0.084	0.060	0.311	0.113	0.000	0.052	0.041	0.222	0.073
	1992	1	SA	0.002	0.038	0.224	0.223	0.125	0.001	0.014	0.083	0.085	0.053
	1992	2	S.Africa	0.000	0.009	0.060	0.296	0.178	0.000	0.007	0.066	0.564	0.359
	1992	2	SEIO	0.000	0.006	0.055	0.045	0.016	0.000	0.007	0.069	0.059	0.023
	1992	2	Tasman	0.001	0.007	0.089	0.079	0.169	0.001	0.005	0.059	0.055	0.123
	1993	1	SA	0.000	0.059	0.626	0.766		0.000	0.022	0.206	0.288	
	1993	2	S.Africa	0.000	0.015	1.511	5.000		0.000	0.010	5.000	1.604	
	1993	2	SEIO	0.000	0.033	0.199	0.064		0.000	0.040	0.254	0.100	
	1993	2	Tasman	0.000	0.005	0.026	0.140		0.000	0.004	0.018	0.132	
	1994	1	SA	0.001	0.112	0.962			0.000	0.041	0.280		
	1994	2	S.Africa	0.000	0.017	1.136			0.000	0.011	5.000		
	1994	2	SEIO	0.000	0.042	0.188			0.000	0.050	0.240		
	1994	2	Tasman	0.000	0.003	0.062			0.000	0.002	0.043		
Proportion age 1				SA	S.Afr	SEIO	Tas		SA	S.Afr	SEIO	Tas	
abundance by region				0.39	0.00	0.48	0.13		0.91	0.00	0.00	0.09	

	Cohort	SA	S.Afr	SEIO	Tas	Total	SA	S.Afr	SEIO	Tas	Total
Age 1 abundance (millions)	1990	1.17	0.00	1.43	0.38	2.98	2.88	0.00	0.00	0.27	3.16
	1991	1.19	0.00	1.44	0.39	3.02	2.94	0.00	0.00	0.28	3.23
	1992	0.87	0.00	1.05	0.28	2.20	2.02	0.00	0.00	0.19	2.22
	1993	0.45	0.00	0.55	0.15	1.14	1.10	0.00	0.00	0.10	1.20
	1994	0.39	0.00	0.48	0.13	1.00	1.00	0.00	0.00	0.09	1.09

Table 4. Parameter estimates obtained from applying the spatial model to SBT data from the 2000s: (left) results when only conventional tag and catch data are used; (right) results when archival tag data are integrated into the model.

				Results WITHOUT archival tag data					**Results INCLUDING archival tag data**				
M				Age1	Age2+				Age1	Age2+			
				0.462	0.187				0.490	0.132			
F	Cohort	Season	Region	Age1	Age2	Age3	Age4	Age5	Age1	Age2	Age3	Age4	Age5
	2000	1	SA	0.000	0.029	1.281	1.155	0.732	0.000	0.022	1.063	0.468	0.971
	2000	2	S.Africa	0.000	0.002	0.008	0.053	0.078	0.003	0.019	0.049	0.306	0.483
	2000	2	SEIO	0.000	0.012	0.040	0.164	0.186	0.000	0.004	0.012	0.042	0.041
	2000	2	Tasman	0.000	0.024	0.044	0.085	0.349	0.000	0.006	0.011	0.020	0.071
	2001	1	SA	0.000	0.082	3.885	5.000	5.000	0.000	0.067	3.114	0.727	5.000
	2001	2	S.Africa	0.004	0.001	0.055	0.162	0.140	0.046	0.013	0.369	1.028	5.000
	2001	2	SEIO	0.000	0.019	0.509	0.636	5.000	0.000	0.006	0.105	0.105	0.125
	2001	2	Tasman	0.000	0.021	0.090	0.573	0.417	0.000	0.005	0.022	0.114	0.055
	2002	1	SA	0.006	0.337	1.132	2.780	5.000	0.005	0.266	0.922	0.623	2.799
	2002	2	S.Africa	0.000	0.004	0.028	0.087	0.073	0.000	0.035	0.158	0.366	0.304
	2002	2	SEIO	0.000	0.021	0.160	0.541	0.645	0.000	0.006	0.037	0.087	0.063
	2002	2	Tasman	0.000	0.029	0.186	0.246	0.416	0.000	0.006	0.039	0.044	0.056
	2003	1	SA	0.000	0.150	1.108	4.827	0.320	0.000	0.125	0.947	0.727	0.342
	2003	2	S.Africa	0.000	0.002	0.044	0.034	0.034	0.003	0.019	0.358	0.183	0.235
	2003	2	SEIO	0.000	0.028	0.198	0.142	0.207	0.000	0.008	0.045	0.032	0.036
	2003	2	Tasman	0.000	0.017	0.116	0.166	0.276	0.000	0.004	0.028	0.036	0.051
	2004	1	SA	0.407	0.129	0.440	0.980	0.374	0.357	0.107	0.392	0.383	0.418
	2004	2	S.Africa	0.000	0.007	0.030	0.018	0.030	0.004	0.071	0.255	0.108	0.176
	2004	2	SEIO	0.000	0.009	0.039	0.089	0.067	0.000	0.003	0.011	0.022	0.015
	2004	2	Tasman	0.001	0.211	0.450	0.591	5.000	0.000	0.046	0.085	0.072	0.107
End-of-summer movement				SA to SAfr	SA to SEIO	SA to Tas			SA to SAfr	SA to SEIO	SA to Tas		
				0.00	0.75	0.24			0.05	0.91	0.04		

End-of-winter movement		SAfr	SEIO	Tas			SAfr	SEIO	Tas		
	Age	to SA	to SA	to SA			to SA	to SA	to SA		
	1	0.99	0.85	0.00			0.30	0.99	0.28		
	2	0.57	0.49	0.00			0.18	0.59	0.17		
	3	0.36	0.31	0.00			0.19	0.63	0.18		
	4	0.22	0.19	0.00			0.05	0.16	0.05		
Proportion age 1		SA	S.Afr	SEIO	Tas		SA	S.Afr	SEIO	Tas	
abundance by region		0.03	0.00	0.96	0.01		0.03	0.00	0.92	0.05	
Age 1 abundance	Cohort	SA	S.Afr	SEIO	Tas	Total	SA	S.Afr	SEIO	Tas	Total
(millions)	2000	0.03	0.00	1.11	0.01	1.15	0.04	0.00	1.23	0.07	1.34
	2001	0.02	0.00	0.76	0.01	0.79	0.03	0.00	0.87	0.05	0.94
	2002	0.02	0.00	0.75	0.01	0.78	0.03	0.00	0.95	0.05	1.03
	2003	0.04	0.00	1.40	0.02	1.46	0.05	0.00	1.54	0.08	1.67
	2004	0.05	0.00	1.55	0.02	1.62	0.05	0.00	1.72	0.09	1.86

Figure 1. The 4 regions defined in the spatial tagging model for juvenile SBT. (SA = Southern Australia; SEIO = South-East Indian Ocean)

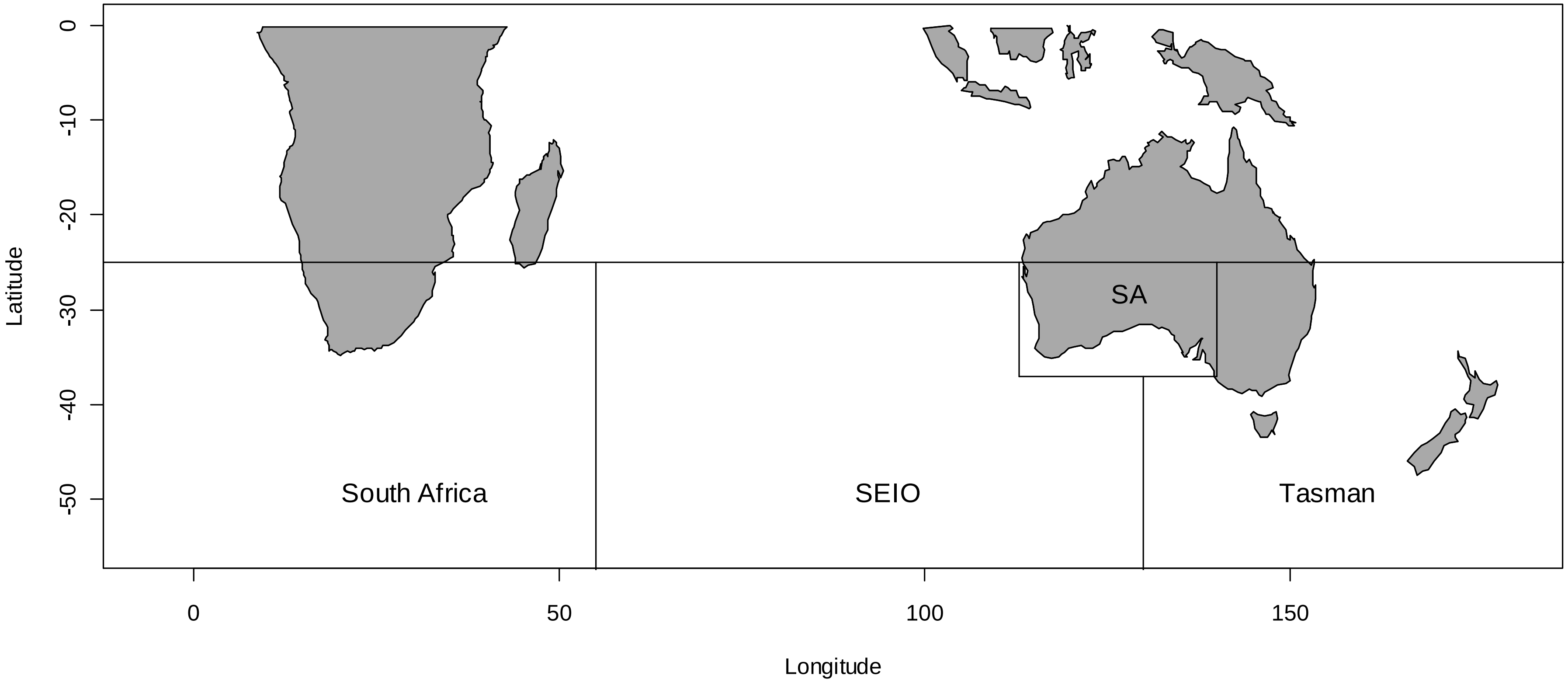

Figure 2. Fishing mortality rate estimates obtained from applying the spatial model to the 1990s conventional tag and catch data for SBT with the movement parameters: (left) estimated within the model; (right) fixed at those estimated from the archival tag data.

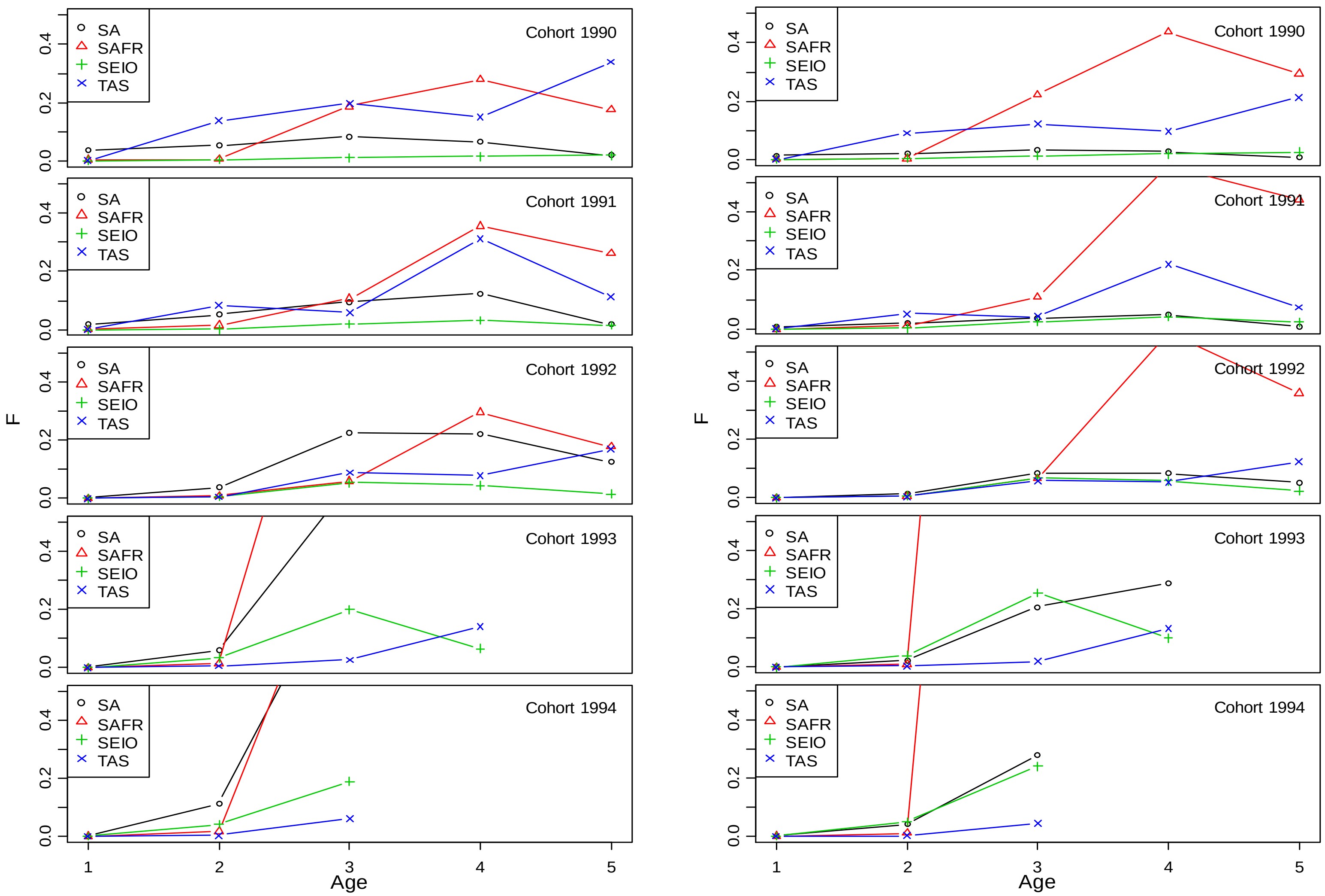

Figure 3. Abundance over time (age) by region for cohorts 1990-1994, as calculated using parameter estimates obtained from the spatial model with movement parameters: (left) estimated within the model; (right) fixed at those estimated from the archival tag data.

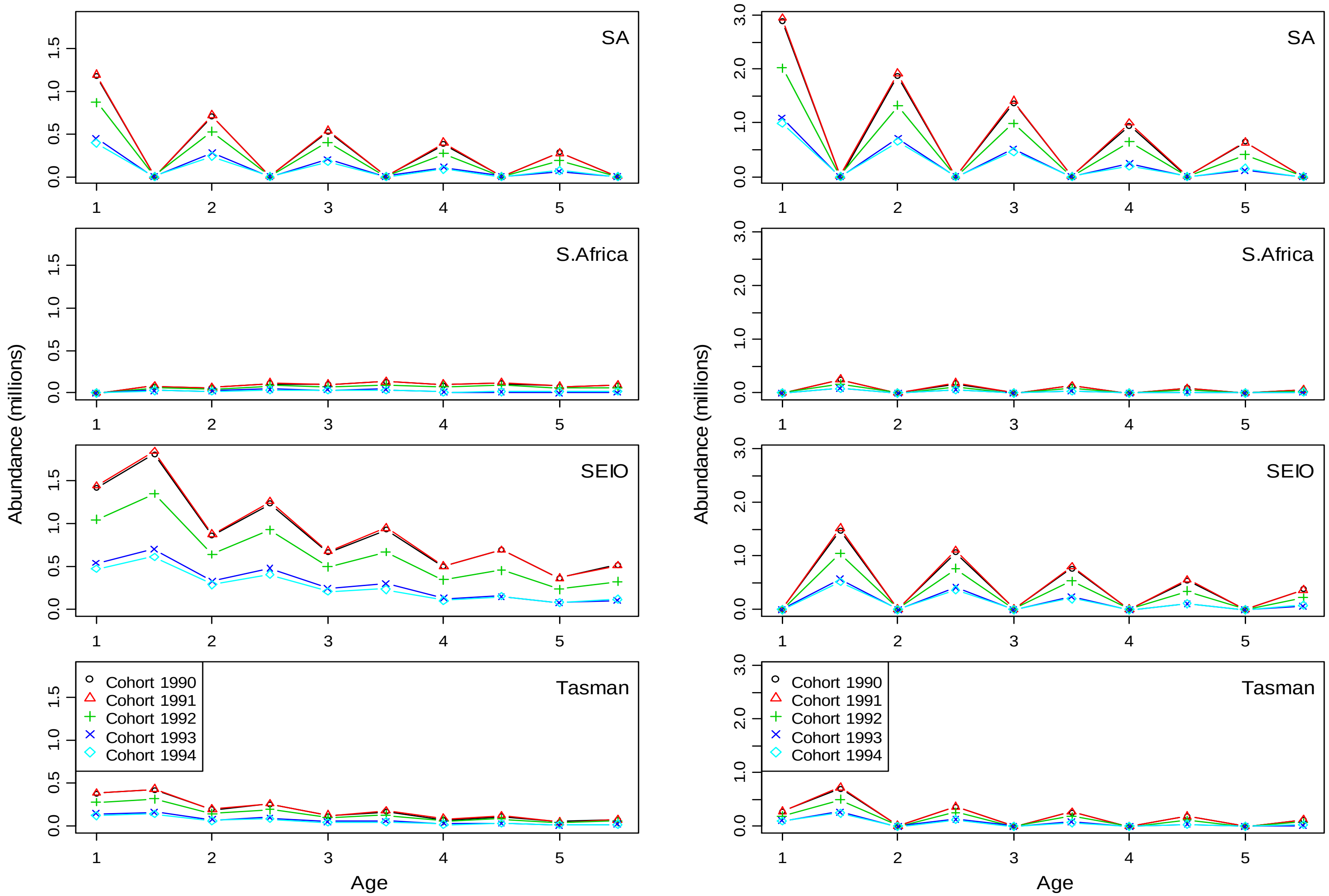

Figure 4. Fishing mortality rate estimates obtained from applying the spatial model to SBT data from the 2000s: (left) when only conventional tag and catch data are used; (right) when archival tag data are integrated into the model.

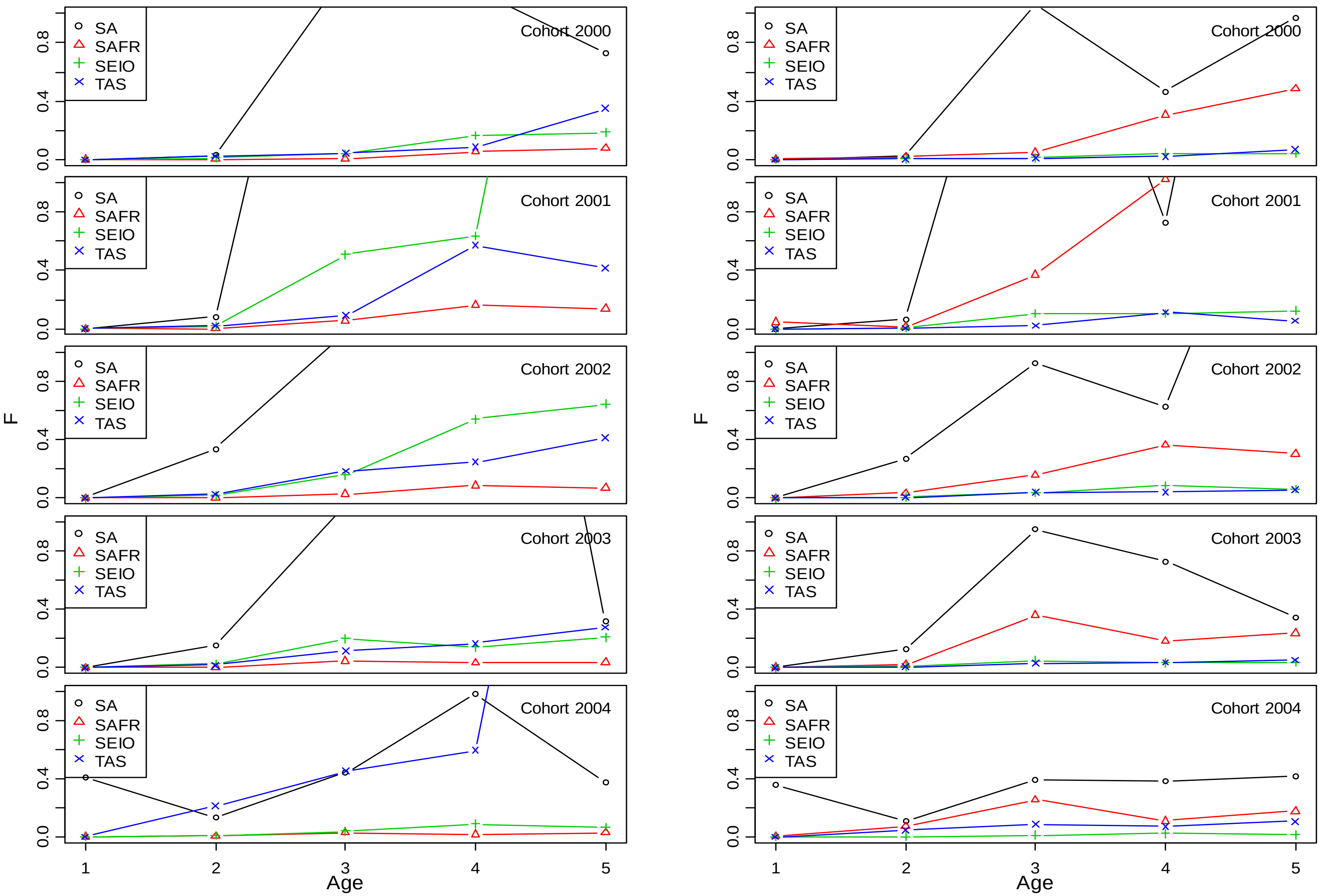

Figure 5. Abundance over time (age) by region for cohorts 2000-2004, as calculated using parameter estimates obtained from the spatial model (left) when only conventional tag and catch data are used; (right) when archival tag data are integrated into the model.

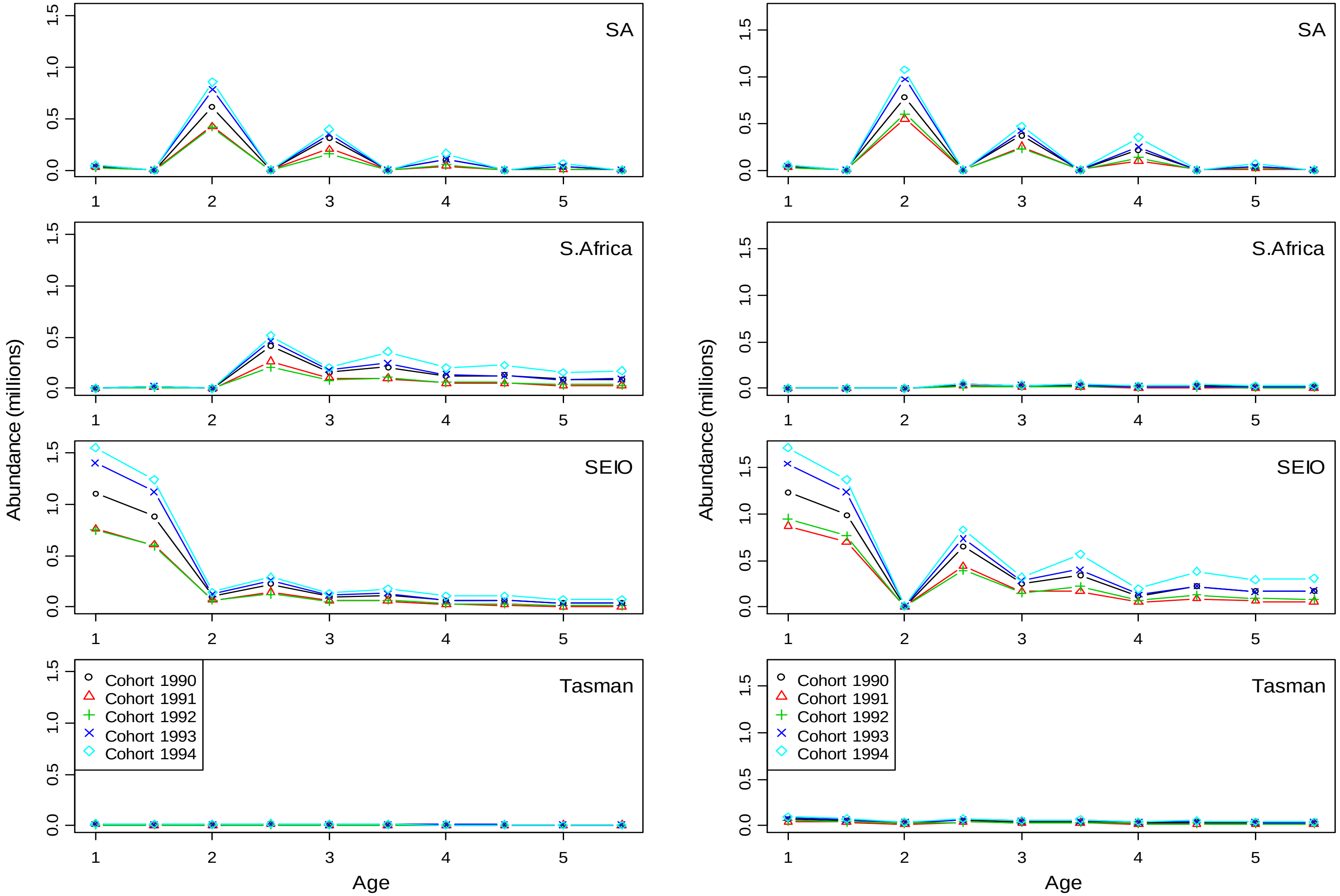

Figure 6. Comparison fishing mortality rate (F) estimates obtained for the 1990s using the non-spatial model with those obtained by averaging the region-specific F estimates from the spatial model when the movement parameters were estimated within the model (without archival tag data) and when the movement parameters were fixed at those determined from the archival tag data.

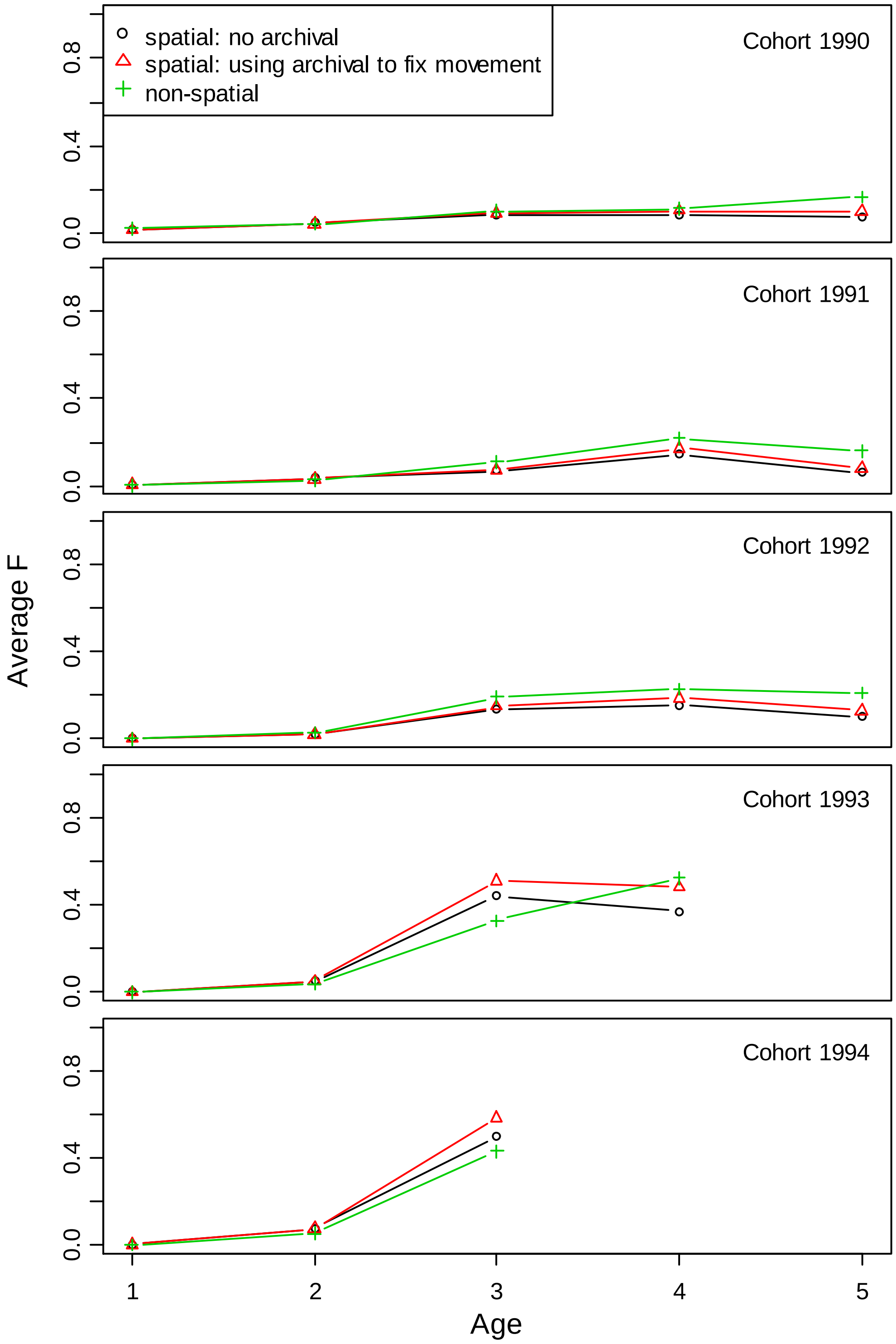

Figure 7. Comparison fishing mortality rate (F) estimates obtained for the 2000s using the non-spatial model with those obtained by averaging the region-specific F estimates from the spatial model when archival tag data were and were not included.