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Southern Shark Tag Database Project

Terence I. Walker, Bruce L. Taylor & Lauren P. Brown

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Acronyms

AFMA	Australian Fisheries Management Authority
CSIRO	CSIRO Division of Marine Research
MAFRI	Marine and Freshwater Resources Institute
NSWFRI	New South Wales Fisheries Research Institute
RTL	Recapture total length of shark
SARDI	South Australia Research and Development Institute
SharkFAG	Southern Shark Fishery Assessment Group
TDPIF	Tasmanian Department of Primary Industry and Fisheries
TL	Total length of shark
TRR	Tag reporting rate
WAMRL	Western Australian Marine Research Laboratories

96/162 Southern Shark Tag Database Project

Principal Investigator Terence I. Walker
Marine and Freshwater Resources Institute
PO Box 1 14 Queenscliff VIC 3225
Telephone: (03) 5258 0111, Fax: (03) 5258 0270

Objectives

Meeting the objectives of tagging gummy shark (*Mustelus antarcticus*) and school shark (*Galeorhinus galeus*) required undertaking two FRDC projects over 6 years. The first was the 'Southern Shark Tagging Project' (FRDC 93/066), a 3-year project undertaken during 1994–96 to design, implement the tagging of sharks and manage tag recaptures. The second was the 'Southern Shark Tag Database Project' (FRDC 96/162), a 3-year project undertaken during 1997–99 to manage tag recaptures and allow time for sufficient tag recaptures. Sharks were also tagged and released as part of the completed project entitled 'Investigation of school and gummy shark nursery areas in south eastern Australia' (FRDC 93/061).

The Southern Shark Tagging Project and Southern Shark Tag Database Project had three overarching objectives.

1. Determine annual rates of movement and mixing of gummy shark and school shark across southern Australia.
2. Provide current estimates of natural mortality and fishing mortality for gummy shark and school shark.
3. Address specific stock hypotheses and their implications for fishery management.

In addition, the Southern Shark Tag Database Project had three operational objectives.

1. Ensure that data from recaptured sharks tagged and released as part of the previously completed FRDC funded Tagging and Nursery Projects are adequately received, verified, and entered into the 'Southern Shark Fishery Tag Database'.
2. Maintain up-to-date summaries and reports of tag release and recapture data.
3. Ensure that tag release and recapture data are made available for scientific analysis.

All of these objectives have now been met completely.

Non-technical summary

As part of the projects, all available tag release-recapture data available from shark tag releases during 1947–56, 1973–76, and 1990–99 have been validated and consolidated in the Southern Shark Tag Database developed in Microsoft ACCESS. The database is routinely updated and has facility for preparing data summaries and extracting data for analysis. Basic summaries with graphical plots and vector analysis of the tag data available to the end of 1999 are presented in a companion report to the present report. The companion report is designed for distribution to all professional shark fishers and other parts of the fishing industry, and is an update and extension to the report provided to FRDC during 1997 for the Southern Shark Tagging Project (FRDC 93/066).

The companion report demonstrates that the first two objectives of the Southern Shark Tag Database Project (FRDC 96/162) were met completely. The present report demonstrates that the third objective of this project was met. The present report provides the results of modelling with tag and other data and specifically explicitly addresses the three overarching objects of both tagging projects.

By the end of 1999, a total of 28 different shark and ray species had been tagged in southern Australia. Most of the 12442 sharks and rays tagged during 1990–99 were gummy sharks (7047) and school sharks (2686). Tag recapture rates are higher for commercial sized gummy sharks (23% for males and 25% for females) than for commercial sized school sharks (19% for males and 21% for females). About 10% the sharks (1157) were double tagged for estimating tag shedding rates.

Tag shedding rates were addressed through double-tag experiments as part of the tag projects. Rototags and jumbo tags attached to the anterior lower portion of the first dorsal fin of sharks during 1990–99 were highly successful with shedding rates at 8% per year. Similarly, internal tags inserted into the coelomic cavity of sharks during 1947–56 and 1973–76 were successful in that they were not shed; however, they were not always seen by fishers when the sharks were caught. Peterson disc fin tags attached to the first dorsal fins during 1947–56 had very high shedding rates at 66% per annum on school shark. Nylon-headed dart tags inserted into dorsal muscle tissue of sharks during 1990–99 had high shedding rates at 41% per year for school shark and 63% per year for gummy shark. Nylon-headed dart tags inserted into the cartilage at the base of the first dorsal fin during 1990–99 rather than in the dorsal musculature halved the shedding rates. A range of other types of tags were used during 1990–99 in insufficient numbers to estimate shedding rates.

Apart from meeting the three overarching objectives, the data provide a valuable resource that can be subjected to ongoing analyses. Already the data have been used in ways unforeseen at the time of seeking the application for grant from FRDC. Models developed through SharkFAG allow the tag data to be incorporated directly into stock assessments and have markedly reduced uncertainty in the assessments.

The first objective of the projects was to estimate rates of movement between broad regions of the fishery and the second objective was to estimate rates of mortality for gummy shark and school shark. Addressing these two objectives required application of a maximum likelihood model developed by MAFRI. This Integrated Tag Model was

originally written in FORTRAN but was rewritten to run in AD Model Builder for estimating various parameters in the Bayesian framework whereby the Markov Chain Monte Carlo method was applied, with 250,000 iterations for each analysis, for determining the 90% prediction intervals on these parameters.

Movement rates between region, catchability in each region and, to account for several other factors, two additional parameters referred to as the 'tag recovery ratio' and 'tag reduction rate' were estimated. 'Tag recovery ratio' accounts for the confounded factors of 'non-reporting of tags by fishers', 'non-sighting of tags by fishers' (including 'predation mortality', 'dropout mortality' and 'dislodgment of tags after recapture' in the fishing gear), and 'initial tag survival ratio' (including 'initial capture and tag induced mortality' and 'initial tag shedding'). The 'tag reduction rate' accounts for the two confounded additional factors of 'natural mortality rate' and 'tag shedding rate'. Because double tag experiments showed that tag shedding-rates were very different for different types of tag, three separate parameters were adopted to represent 'tag reduction rates'. These were for 'rototags and jumbo rototags attached to first dorsal fin', 'dart tags inserted into dorsal musculature near the first dorsal tissue', and 'dart tags anchored in the basal cartilage of the first dorsal fin'. Parameter estimates for 'catchability', 'tag recovery ratio' and the three 'tag reduction rates' were highly correlated with each other but they were only weakly correlated with the parameters for movement rates.

Initial analysis of the data indicated that distances moved and rates of movement differed between males and females for both large gummy sharks and large school shark. Hence estimates of rates of movement were made for each of three categories for gummy shark and four categories for school shark on the basis of sex and total length (TL) of shark. For gummy shark, the three categories were males and females combined 650–1099 mm TL, males ≥1100 mm TL, and females ≥1100 mm TL. For school shark, the four categories were males and females combined 650–1199 mm TL, males and females combined 1200–1399 mm TL, males ≥1400 mm TL, and females ≥1400 mm TL. The lengths were chosen to relate approximately to lengths at first maturity. From one time step to the next in the model, the number of sharks within each category can change as the sharks grow. Only sharks longer than 650 mm TL at the length of tag release were included in the analyses. This was to ensure the validity of the assumption that natural mortality is constant with TL and age; independent studies have demonstrated that small sharks have a much higher rate of natural mortality than middle-sized and large sharks.

Three separate regions were adopted for each of gummy shark and school shark from the four regions of Western Australia (WA), South Australia (SA), Bass Strait (BS) and Tasmania (Tas). The three regions adopted for gummy shark were WA, SA and the other two regions combined (BS/Tas), whereas the three regions adopted for school shark were WA/SA, BS and Tas.

For gummy shark and school shark, separately, six movement parameters (two directions for each pair among the three regions) were estimated for each of the three sex–TL categories for gummy shark and four sex–TL categories for school shark. Three additional movement parameters for each sex–TL category were adopted to represent the sharks that did not change region; these could be simply calculated from the other six movement parameters and therefore did not need to be estimated. Three catchability parameters (one for each region), one 'tag recovery ratio' and three 'tag reduction rate' parameters were estimated. This gave a total of 25 parameters to estimate and 9 to calculate for gummy shark and 31 parameters to estimate and 12 to calculate for school shark.

Gummy sharks exhibit low inter-regional movement rates. Most gummy sharks did not change region for any of the three sex–TL categories. This is particularly marked for juveniles (650–1100 mm TL) where 96, 98 and 96% y^{-1} remained in WA, SA and BS/Tas, respectively. These rates for remaining in a region are 85, 90 and 99% y^{-1}, respectively, for males ≥1100 mm TL and 97, 86 and 91% y^{-1}, respectively, for females ≥1100 mm TL. The highest between region movement rates are from WA to SA (15% y^{-1}, return 6% y^{-1}) for males ≥1100 mm TL and from SA to WA (9% y^{-1}, return 3% y^{-1}) and from BS/Tas to SA (9% y^{-1}, return 5% y^{-1}) for females ≥1100 mm TL. Movement rates out of BS/Tas are particularly low for males ≥1100 mm TL (1% from BS/Tas to SA). The rates between the most widely separated regions of WA and BS/Tas are zero for all three sex–TL categories. These results are consistent with a weak trend for females to move westwards and for males to move eastwards or not move at all as the animals mature.

School shark movement-rates are much higher than for gummy shark. There is a strong trend for juveniles (650–1199 mm TL) to move out of Tas; 42% moved to WA/SA and 20% moved to BS with no returns to Tas from either of these regions. However, there is a strong trend for animals ≥1200 mm TL to move to Tas, with a tendency to remain in Tas (i.e. 72% of sub-adults, 80% of mature males and 51% of mature females remain in Tas each year). There is also a strong trend for mature females (≥1400 mm TL) to move to WA/SA. These trends are consistent with the trends for industry to catch more females than males in WA/SA and to catch more males than females in Tas. The trends are consistent with the hypothesis that females with mid-term embryos tend to aggregate in the Great Australia Bight and mature females aggregate in southern Tasmania. The trends are also consistent with the distribution patterns of *Galeorhinus galeus* on the eastern coast of South America and the western coast of North America, where at certain times of the year the females aggregate in the warmer waters and the males in the cooler waters.

Gummy shark estimates of gillnet catchability are similar between SA (2.76 $\times 10^{-5}$ y^{-1}) and BS/Tas (3.08 $\times 10^{-5}$ y^{-1}) but are lower than in WA (6.73 $\times 10^{-5}$ y^{-1}). Comparing the tag shedding rate of 0.086 (8%) from double tag experiments with the tag reduction rate of 0.369 y^{-1} for rototags and jumbo rototags gives an estimate of natural mortality rate of 0.283 y^{-1} (25%). This value of natural mortality fits reasonably well with the tag shedding rates for dart tags in fin cartilage and dart tags in muscle tissue. An estimate of 0.52 for 'tag recovery ratio' together with an independent estimate of tag reporting rate by fishers of ~0.70 suggests an 'initial tag survival ratio' of 0.74. This implies that 26% of the tags were lost through initial tag mortality, initial tag shedding or non-sighting of the tags by fishers.

School shark estimates of gillnet catchability vary greatly between SA/WA (1.51 $\times 10^{-5}$ y^{-1}), BS (5.49 $\times 10^{-5}$ y^{-1}) and WA (17.0 $\times 10^{-5}$ y^{-1}). Comparing the tag shedding rate of 0.088 y^{-1} (8%) from double-tag experiments with the 'tag reduction rate' of 0.178 y^{-1} for rototags and jumbo rototags gives an estimate of natural mortality rate of 0.090 y^{-1} (9%). This value of natural mortality generally agrees well with the tag shedding rates for dart tags in fin cartilage and dart tags in muscle tissue. An estimate of 0.39 for 'tag recovery ratio' together with an independent estimate of tag reporting rate by fishers of ~0.70 suggests an 'initial tag survival ratio' of 0.56. This implies that 44% of the tags were lost through initial tag mortality, initial tag shedding or non-sighting of the tags by fishers.

The third objective of the projects to address specific stock hypotheses and their implications for management of the fishery was addressed by simulation modelling of alternative hypotheses. Fine resolution movement matrices produced by simulation of alternative hypotheses were then tested against all of the available data through application of stock assessment models developed by SharkFAG.

Gummy shark over the range of the fishery are from a single genetic stock, but the low rates of movement between the major regions of the fishery allow the stock to be arbitrarily divided into convenient sub-stocks for stock assessment purposes. The separate regions adopted for gummy shark stock assessment purposes are the main regions of WA, SA, BS, Tas and NSW. The rationale for assigning the regions this way is based on the combination of political management arrangements; WA and NSW are managed principally by the States and SA, BS and Tas are managed principally by the Australian Fisheries Management Authority. The main reasons for considering SA, BS and Tas separately are differences in completeness and resolution of the data and differences in fishers' targeting practices between the regions. The stock-structuring hypothesis of 'isolation by distance' is adopted for this species for stock assessment purposes. Apart from incorporating tag data, along with all other data sets, into the gummy shark assessments to reduce uncertainty in the assessments, the data provided a basis for validating the assessments. This was achieved by including tag data while dropping out other data sets such as standardised CPUE. There is now very high confidence in the gummy shark assessments.

School shark stock structuring is much more complex. Competing working hypotheses adopted for conceptual purposes in developing appropriate stock assessment models are 'single panmictic population with components of the stock at different life history stages occupying different localities within the range of its distribution' and 'discrete separate sub-populations with no or very limited interbreeding'. The hypothesis adopted by SharkFAG for its 1999 school shark assessment requires there to be separate breeding sub-populations but there is mixing at other life history stages. This might be referred to as a 'mixing multiple sub-stock hypothesis' and combines features of the earlier working hypotheses. School shark stock assessment has benefited greatly from the FRDC tagging projects. The species has particularly low productivity, has complex stock structuring, and CPUE data used as abundance indices are uninformative. Only through incorporation of tag data directly into the assessment using spatially structured models to embrace specific stock-structuring and movement hypotheses have earlier highly uncertain assessments been turned into assessments in which there is confidence.

Background

Scope of report

Meeting the three objectives of tagging of gummy shark (*Mustelus antarcticus*) and school shark (*Galeorhinus galeus*) required two FRDC projects over 6 years. The first was the Southern Shark Tagging Project (FRDC 93/066), a 3-year project undertaken during 1994–96 to design and implement the tagging of sharks. The second was the Southern Shark Tag Database Project (FRDC 96/162), a 3-year project undertaken during 1997–99 to allow sufficient time for tag recaptures.

A report for the first project (FRDC 93/066) was provided to FRDC during November 1997 (Walker *et al.* 1997). The report consolidated data to the end of 1996 and material presented in earlier project milestone reports as well as presenting other material not previously reported. Implementation of these projects, along with several reports and scientific papers from the projects, is the result of scientific collaboration between several fisheries organisations. The organisations are the Marine and Freshwater Resources Institute (MAFRI), CSIRO Division of Marine Research, Australian Fisheries Management Authority (AFMA), and the State fisheries agencies of Western Australia, South Australia, Tasmania, Victoria and New South Wales (see Acknowledgments).

Implementation of the two tagging projects involved nine tasks.

1. Establish a project steering committee with industry, fishery manager and scientist representation (undertaken by the Shark Industry Research Liaison Committee).
2. Undertake pilot tagging to select appropriate tags.
3. Develop an experimental design to determine the appropriate number of sharks to tag and release for estimating rates of movement between broad regions of southern Australia, within acceptable confidence limits.
4. Undertake field tagging of sharks to implement the experimental design.
5. Develop a database for managing all incoming and historic shark tag release and recapture data (referred to as the Southern Shark Tag Database).
6. Liaise with industry to receive tag recapture data and provide feedback on the data and hold periodic tag lotteries.
7. Routinely verify and enter incoming tag recapture data into the Tag Database.
8. Produce ongoing data summaries and basic analyses of the data.
9. Estimate rates of movement and mortality and provide up-to-date data for the SharkFAG stock assessment process.

All nine tasks formed part of the first project whereas Tasks 6–9 were ongoing as part of the second 3-year to manage the several hundred tagged sharks recaptured during 1997–99. Although tagged sharks will continue to be recaptured well into the Twenty-first Century, there are sufficient data by the end of 1999 to undertake full analysis of the data. Sufficient tagged sharks have now been recaptured to provide estimates of movement and mortality for the populations of gummy shark and school shark, to test alternative hypotheses of movement and to apply the tag data in stock assessment. The population parameters were estimated by MAFRI but testing of alternative movement hypotheses and application of the data for stock assessment was undertaken in collaboration with CSIRO and other members of SharkFAG through the SharkFAG process.

A separate report describes and summarises the actual tag release and recapture data available to 31 December 1999 (i. e. for releases during 1947–56, 1973–76 and 1990–99) (Brown *et al.* 2000). That report consolidates and updates information presented in the final report to FRDC for the Southern Shark Tagging Project during FRDC November 1997 (Walker *et al.* 1997) and in subsequent project milestone reports to FRDC for the Southern Shark Tag Database Project. Analyses of movement of only tag recaptures are presented; no inferences are made about movement or mortality for either the population of all tagged sharks or the entire shark population. Special emphasis is given to presenting data for the most recent tag-release period 1990–99, although several of the tables also cover data from the 1947–56 and 1973–76 tag-release periods.

In addition to the separate report (Brown *et al.* 2000) accompanying the present report, six appendices to the present report provide details of all the outputs from the two tagging projects.

1. Details of the methods adopted for developing the experimental design has been published in the internationally refereed *Canadian Journal of Marine and Freshwater Research* (Xiao 1996) (Appendix 1).

2. A computer package displaying the start and finish positions of recaptured tagged sharks (Taylor 1997a) distributed to SharkFAG members (Appendix 2).

3. A computer package displaying dynamics of alternative hypotheses of movement of sharks (Taylor 1997b) distributed to SharkFAG members (Appendix 3).

4. Analysis of tags for shedding rates has been published in the internationally refereed journal *Fisheries Bulletin* (Xiao *et al.* 1999) (Appendix 4).

5. Analysis of tag data for tag reporting rates has been reported to SharkFAG (Brown and Walker 1999) (Appendix 5).

6. List of publications and reports, which contain data produced as part of the tag projects (Appendix 6).

The tag data have been routinely updated and made available to SharkFAG for stock assessments The results presented in Appendices 3, 4 and 5 are integral to SharkFAG's stock assessments. Inclusion of these data has markedly reduced uncertainty in the assessments (Punt 2000a; Punt 2000b; Punt *et al.* 2000; Punt and Walker 1998a).

Previous research

Biological data were collected on school shark and gummy shark by the CSIRO during the 1940s and early 1950s (Olsen 1953; Olsen 1954; Olsen 1959; Olsen 1962; Stanley 1988) and by the Victorian fisheries agency during the mid-1970s (Walker 1983) and mid-1980s (Kirkwood and Walker 1986; Moulton *et al.* 1992; Walker *et al.* 1991; Walker *et al.* 1989). During the 1990s, MAFRI and CSIRO undertook age-validation (Officer 1995; Officer *et al.* 1996; Walker *et al.* 1995), nursery (Stevens and West 1997), genetic (MacDonald 1988; Ward and Gardner 1997), modelling (Punt 2000a; Punt 2000b; Punt *et al.* 2000; Punt and Walker 1998b; Walker 1992; Walker 1994a; Walker 1994b; Walker 1995; Walker 1998; Xiao 1995), and fishery monitoring projects (Walker *et al.* 2000). In addition, the Western Australian Marine Research Laboratories undertook general biological study of sharks (Simpfendorfer *et al.* 1996).

Stock distribution and structure

School shark and gummy shark are harvested on the continental shelf and continental slope of southern Australia. School sharks also occur well off the continental shelf over the abyssal plain and are known to undertake long movements across southern Australia (Olsen 1953; Olsen 1954; Olsen 1962) and occasionally between southern Australia and New Zealand (Brown *et al.* 2000; Coutin *et al.* 1992; Hurst *et al.* 1999; Walker *et al.* 1997).

It has been confirmed that there is a single, widely distributed species of *Galeorhinus galeus* (school shark) from genetic analysis of samples from Australia, New Zealand, South Africa, Argentina and United Kingdom (Ward and Gardner 1997). Both allozyme and mitochondrial DNA techniques were used, and no evidence was found to indicate more than a single stock of school shark in south-eastern Australian waters. There are some genetic differences between Australian and New Zealand sharks, which suggest they are distinct stocks. However, the differences are small, and not incompatible with low levels of exchange between the two areas.

Three genetic stocks of *Mustelus antarcticus* have been identified. All endemic to Australia, one stock ranges along the southern coast of Australia from Bunbury in the west to Eden in the east, a second is located off New South Wales in the region from Newcastle to Clarence River, and a third is located off Queensland near Townsville (Ward and Gardner 1997).

The populations of both species exhibit complex stock structuring. School sharks have distinct ‘pupping’ grounds referred to as ‘nursery areas’ and, although gummy sharks do not have these distinct areas, the newborn pups tend to inhabit shallow inshore areas. Fishers often describe ‘mating grounds’ in particular areas and there is a tendency for large school sharks to occupy the western region of their range in waters off western South Australia and off Western Australia to about 100 nautical miles west of the South Australia–Western Australia border. School sharks (Olsen 1954) and, to a lesser extent, gummy sharks (Walker 1983) undergo long movements to give birth during spring.

Aggregating behaviour appears to be different between school sharks and gummy sharks. School sharks form large schools when migrating and are often found aggregated when feeding on schooling prey such as pilchards, jack mackerel, snoek and squid. Although gummy sharks often feed on aggregated prey or form moving schools, the species is generally more dispersed as it feeds on demersal crustaceans, cephalopods and fish distributed over wide areas.

These characteristics affect the way shark fishers search for sharks and have important implications for interpretation of their catch and effort data. Most fishers tend to set, haul, and then reset gillnets a short distance from the previous set to catch the dispersed gummy sharks, often with a small non-target catch of young school sharks, particularly in Bass Strait. A small group of fishers specialise in targeting school sharks, most commonly off South Australia. These fishers often take a series of small, with occasional zero, catches while searching for school sharks over a broad region, but then, having located aggregations of school sharks, often take large catches. Prior to the widespread introduction of gillnets during the 1970s, most shark fishers specialised in targeting school sharks with longlines. Hence to better interpret catch per unit effort trends and to improve stock assessment, there is a need to better understand the movement and distribution patterns of school sharks and gummy sharks.

SharkFAG has long recognised that the spatially aggregated fishery models initially applied for stock assessment of these species ignore the complex structuring of these stocks. Consequently, SharkFAG subsequently developed species-specific spatially structured models, which incorporate rates of movement between the major regions of the fishery.

Need

The shark fishery of southern Australia is based on several species of temperate-water sharks inhabiting the continental shelf and slope. The annual catch, mostly gummy and school shark, in recent years has been about 5000 tonnes live weight, valued at more than $15.9 million at the first point of sale in Victoria, Tasmania and South Australia (Walker *et al.* 1999). Most of the catch is consumed in Victoria.

Tagging and releasing school and gummy sharks during 1947–56 and 1973–76 (Olsen 1954; Stanley 1988; Walker 1983; Walker 1989) enhanced our knowledge of their movement patterns. However, there are three reasons why it is not possible to adequately estimate rates of movement between broad regions from these early data. Firstly, most of the tagging was confined to the Eastern Region of the fishery; secondly, fishing effort did not adequately cover the fishery; and, thirdly, facility for fishers to report fishing effort was inadequate. At a time when there was better coverage of the fishery with fishing effort, the FRDC funded Southern Shark Tagging Project (FRDC 93/066) was designed to provide data for estimating rates of movement between the major regions of the fishery. The project also provided current estimates of mortality and a basis for testing various stock hypotheses relevant to the management of the fishery.

In general, stock structures of shark populations are highly complex. The stock structure for school shark is particularly complex and several competing hypotheses have been advanced to explain long tag movements and to explain data indicative of differences in age and size composition and breeding condition between separate regions across southern Australia. The complex structure of school shark and, to a lesser extent, gummy shark stocks accounts for much of the uncertainty produced by spatially aggregated models applied in recent years.

For school shark, to reduce the uncertainty in the assessments, SharkFAG, as a matter of high priority, developed spatially structured models that can handle spatially disaggregated data to explore the population dynamics in seven integrated regions across southern Australia. For gummy shark, stock structuring is less complex and similar models are applied to this species, except the stocks are divided on the basis of separate regions and treated as separate stocks.

The tag data have proved essential to the application of these models for stock assessment. The assessments include the full history of shark tag data from the Southern Shark Tag Database, estimates of rates of shark movement between the major regions of the fishery, current estimates of mortality of sharks, and movement matrices developed from simulating competing hypotheses of movement.

Current assessments of the southern shark fishery indicate that the stocks of gummy shark are sound. However, current assessments of school shark using spatially-structured models indicate that the current mature biomass is 12–18% of the initial mature biomass and that current catches are substantially larger than the estimates of maximum sustainable yield (Punt *et al.* 2000).

Objectives

1. Determine annual rates of movement and mixing of gummy shark and school shark across southern Australia.
2. Provide current estimates of natural mortality and fishing mortality of gummy shark and school shark.
3. Address specific stock hypotheses and their implications for fishery management.

These three objectives—for both the Southern Shark Tagging Project (FRDC 93/066) (1994–96) and the Southern Shark Tag Database Project (FRDC 96/162) (1997–99) — have now all been met completely. The value of the data exceed the original expectation in that modern modelling techniques allow the tag data to be incorporated directly in the assessments and thereby markedly reduce uncertainty in the assessments. The data have been used in ways unforeseen at the time of seeking the application for grant from FRDC.

Methods

Determination of movement and mortality rates

Selection of tags

Following an initial pilot tagging phase, rototags and jumbo rototags (large-sized rototags), attached at the lower anterior region of the first dorsal fin, and nylon-headed dart tags, inserted into dorsal muscle tissue or cartilage at the base of the first dorsal fin, were chosen in preference to the Peterson fin tags used during 1947–56 and internal Nesbit tags used during 1947–56 and 1973–76. Peterson fin tags have been shown to be quickly shed and internal tags are difficult and time consuming to insert and can be discarded when sharks are headed and gutted without being seen by fishers. Rototags and jumbo rototags were selected because they had been used successfully in the northern Australian shark fishery by CSIRO (Stevens *et al.* 1990). Dart tags were selected because they can be quickly attached to a shark by tag specialists and by professional and recreational fishers and because they are the most commonly used tags on sharks worldwide.

Experimental design for tag releases during 1993–96

Quantifying shark movements between broad regions across southern Australia from tag release-recapture data required two steps. The first step required developing a procedure for estimating movement parameters in a prescribed model and estimating confidence intervals associated with those estimates. The second step required an experimental design to collect a sufficient amount of data for applying that procedure to provide reliable estimates of the movement parameters.

The statistical framework adopted for developing the estimation procedure and the experimental design involved extending an existing method (Hilborn 1990) using maximum likelihood estimators. This approach provided a basis for determining the amount of data required for estimating movement rates to a chosen accuracy and precision (Xiao 1996).

An experimental design was developed where 500 school sharks and 800 gummy sharks of commercial size (≥650 mm total length) were to be tagged and released in each of four zones on the continental shelf and slope of southern Australia (Xiao 1996). The four tagging zones are Bass Strait (BS) (defined here as between Victoria and the north coast of Tasmania), Tasmania (Tas) (south of latitude 41° South which runs close to the north coast of Tasmania), South Australia (SA) (off South Australia east of longitude 132° East), and the Great Australia Bight (GAB) (off South Australia west of 132° East together with waters off Western Australia). However as is explained later in this report, for the purpose analysis of the data the boundaries of the zones were altered such that the demarcation of longitude 132° East between SA and GAB was changed to longitude 129° East, which coincides with the South Australia–Western Australia political boundary. The two zones SA and GAB were redesignated as SA (expanded) and WA, respectively (Figure 1).

Development of Southern Shark Tag Database

Tag release-recapture data available from CSIRO for shark tag releases during 1947–56, from MAFRI for releases during 1973–76, and from several sources for release during 1990–99 have been verified and consolidated in a Microsoft ACCESS database referred to as the Southern Shark Tag Database. The database is routinely updated with tag releases and recaptures and has facility for preparing data summaries and extracting data for analysis. All available tag data collected by the various fisheries agencies from the Southern Shark Fishery are now secure and managed in this single database.

Tag shedding rates

It is essential to have estimates of tag shedding rates before reasonable estimates of movement rates and mortality rates can be made when applying the Integrated Tag Model described below or in any other model. Similarly, tag shedding rates are essential when tag release-recapture data are applied directly in stock assessment models for school shark and gummy shark.

A new method was developed for estimation of instantaneous rates of tag shedding from double tagging experiments. The tag-shedding model accounts for tag type (including position of attachment on the shark), time at liberty and sex of shark. Tag shedding rates have been estimated from tag-recapture data available to the end of 1996 for gummy shark and school shark. This includes shedding rates for Nesbit internal tags and Peterson fin disc tags on sharks tagged and released during 1947–56. It also includes shedding rates for rototags and jumbo rototags, for nylon-headed dart tags inserted into the dorsal musculature and for nylon-headed dart tags anchored into the cartilage at the base of the first dorsal fin on sharks tagged and released during 1993–96 (Xiao *et al.* 1999) (see Appendix 4).

Tag reporting rates

Estimates of movement and mortality rates and results from application of tag data in stock assessment are affected by the non-reporting of recaptured tagged-sharks by professional and recreational fishers. Estimates of 'tag reporting rate' (TRR) have been made from summaries of tag recapture data and from annual catch data on a vessel by vessel basis from data available for the periods 1973–78 and 1994–96. The TRR was estimated by two methods, which are referred to as the 'tag reporting rate from catch method' (TRR Catch Method) and the 'tag reporting rate from tags per unit catch method' (TRR Tag Method). For the purpose of these analyses, tag recaptures and catch applies to gummy shark and school shark combined together (Brown and Walker 1999) (see Appendix 5).

Initial tag recapture analyses

It is common in the scientific literature to summarise movement dynamics from tag release-recapture studies by plotting information for only the recaptured animals and ignoring the unrecaptured animals. This tag release-recapture plot method of analysis was the earliest and simplest method adopted for gummy shark and school shark. The approach considers the start and finish positions and time at liberty for each animal plotted on a map to provide a visual representation of the magnitude of displacements and rate at which displacement occurs (i.e. velocity) by individual animals (Coutin *et al.* 1992; Hurst *et al.* 1999; Olsen 1954). Several plots of such data for gummy shark and school shark tagged during the 1990s are presented in the accompanying report (Brown *et al.* 2000).

Another approach is to apply vector analysis. Vector analysis of the gummy shark and school shark tag release-recapture data for movement has been undertaken for the 1973–76 tagging study (Walker 1983) and each of the three separate tagging studies using data available to the end of 1996 (Walker *et al.* 1997) and 1999 (Brown *et al.* 2000). This provides an indication of the overall 'average' magnitude and direction of movement for the recaptured population of tagged sharks. An analysis of recaptured tagged school sharks of ≥1400 mm TL to include data available to April 1999 has been published (Walker *et al.* in press). In that publication separate analyses are presented for male and female sharks and the data are separated on the basis of the position at release into the Western and Eastern Regions (demarcated by longitude of the South Australia–Victoria border).

Vector analysis can provide a basis for comparing populations between separate areas for a species or between species on the basis of quantities such as mean displacement, distance, velocity and speed. Such analyses, however, provide information only on the shortest distance between release and recapture positions rather than on the full distance moved between these positions. A major disadvantage of vector analysis (and simply plotting the data) is that no account is taken of the spatial distribution of fishing effort. Furthermore, the results vary depending on when the analyses are undertaken, if the analyses are undertaken before all tags are recaptured. No inferences can be made from these analyses of movement of the full population of tagged sharks or the full population of sharks.

Application of spatially structured fishery assessment models requires estimates of rates of movement between different regions of a fishery. The tag release-recapture plot method of analysis and vector analysis can provide useful quantitative bases for comparing movement between species or for comparing movement between the sexes or different size-classes within a species. They can also help determine patterns of movement or migration. However, neither of these methods can provide information on the actual rates of movement from one region to another. Determination of these rates of movement require special models that explicitly take account the fishing effort in each region, the selectivity of the fishing gear used to recapture each tagged shark, and the growth of each tagged shark while at liberty.

Integrated Tag Model

A maximum likelihood model with provision for estimating movement, mortality and growth rate parameters from tag release recapture data (Dow 1989; Dow 1992; Dow and Kirkwood 1989; Dow and Walker 1989) was developed by MAFRI as part of an earlier FIRTA funded project (Walker *et al.* 1989). As part of the present study, this model, referred to as the Integrated Tag Model, was used for estimating rates of movement between separate regions of the fishery and rates of mortality.

For the purpose of the model, rate of movement is defined as the proportion (also probability) of animals leaving one region to move to another region within a specified time-step (1 year in this study). The model treats the contribution of each tag independently and makes use of information from both the recaptured and unrecaptured tagged sharks. Data inputs to the model include total fishing effort (from the Southern Shark Fishery Monitoring Database (Gason and Walker 1991; Walker *et al.* 1999) for the purpose of the present study) within discrete time intervals (1 year in the present study) for each type of fishing gear in each region. The model also includes shark length and date at the time of release and the time of recapture (Dow 1989). The model allows the sharks to grow while at liberty using reparametrised von Bertalanffy parameters (Francis 1988) as previously determined (Dow 1992; Dow and Walker 1989). The model also requires the gear selectivity function and parameters of each fishing gear deployed in the fishery for gummy shark (Kirkwood and Walker 1986) and school shark (MAFRI unpublished data). In the computer system developed to apply the model, missing data are catered for without discarding particular tag recaptures and the model can be applied to analyse data before all tagged fish die (Dow 1989). This model is similar to one developed for providing an experimental design for tagging gummy sharks and school sharks during 1993–96 (Xiao 1996) and a general simpler method applied in other fisheries (Hilborn 1990).

The model was originally programmed in the language FORTRAN, but was rewritten for AD Model Builder. This provided a system that gave access to more modern procedures for fitting models to data for maximum likelihood estimation of parameters in the Bayesian framework. In particular, the Markov Chain Monte Carlo (MCMC) method was applied for approximating the posterior distribution for each estimated parameter. The likelihood function of each parameter was used for determining the 90% probability distribution (Fournier 1996).

The parameters estimated in the present study are the annual movement rates ('movement probabilities') each way between separate regions and catchability for each fishing gear in each region. $Z+1$ additional parameters were estimated, which are referred to here as the 'tag recovery ratio', ξ, and Z 'tag reduction rates', ζ_z (z is type of tag for Z tag types). The 'tag recovery ratio' has a value in the range 0–1 and is the proportion of animals in the population of tagged animals recaptured and removed from the population that are actually accounted for in the data. 'Tag recovery ratio' accounts for several confounded factors: 'non-reporting of tags by fishers', 'non-sighting of tags by fishers' (including 'predation mortality', 'dropout mortality' and dislodgment of tags after recapture in the fishing gear), and 'initial tag survival ratio' (including 'initial capture and tag induced mortality' and 'initial tag shedding'). These factors can be logically grouped in the equation $\xi = \varpi\iota$ where ϖ is the 'tag reporting ratio' accounting for non-reporting and non-sighting of tags by fishers, and ι is the 'initial tag survival ratio'. Each 'tag reduction rate' includes the two confounded additional factors of 'natural mortality rate', M, and 'tag shedding rates', ς_z, such that $\zeta_z = M + \varsigma_z$.

For this model the likelihood function associated with a recaptured-tagged shark during period T in region r is given by

$$L = \pi_{Tr} c_{Tr}$$

and the likelihood function associated with an unrecaptured-tagged shark is given by

$$L = 1 - \sum_{r=1}^{R} \sum_{\tau=0}^{T} \pi_{\tau r} c_{\tau r} .$$

The expressions and nomenclature adopted in these likelihood functions are defined in the following by several equations. Initially

$$\pi_{\tau r} = \xi p_{r'r} (t'' - t')$$

where the expression $\pi_{\tau r}$ is the probability of arrival of a tagged fish in region r at the start of period τ after release in region r', t'' is the time at the end of the release period $\tau - 1$ and t' is the time at release and $p_{r'r}$ is the probability of movement from region r' to region r of R regions (Dow 1989).

Hence, the probability of arrival in region r at the start of period τ can be calculated recursively by the equation

$$\pi_{\tau r} = \sum_{r'=1}^{R} \pi_{\tau-1,r'} s_{\tau-1,r'} \xi p_{r'r}$$

where survival during period τ in region r, $s_{\tau r}$, is given by

$$s_{\tau r} = e^{-[M + F_{\tau r}(l_\tau)]} .$$

The predicted length of a fish l'' at time ΔT after its initial length of l' when tagged and released is given by the equation

$$l'' = l' + \left[\frac{\lambda g_\lambda - \gamma g_\gamma}{g_\lambda - g_\gamma} - l' \right] \left\{ 1 - \left[1 + \frac{g_\lambda - g_\gamma}{\lambda - \gamma} \right]^{\Delta T} \right\}$$

where g_λ and g_γ are the mean annual growth increments of fish of arbitrary lengths λ and γ, respectively, where λ and γ are chosen to represent the range of the lengths in the growth tag length-increment data (Dow 1992; Dow and Walker 1989; Francis 1988).

$$c_{\tau r} = \frac{F_{\tau r}(l_\tau) e^{-\{M + F_{\tau r}(l_\tau)\} \Delta t}}{M + F_{\tau r}(l_\tau)}$$

where the expression $c_{\tau r}$ is the probability of recapture of a fish at time Δt after the start of period τ in region r and $F_{\tau r}(l_\tau)$ denotes fishing mortality of an animal of length l_τ during period τ in region r (Dow 1989). This formulation depends on two assumptions that are avoided in the present study; one assumption is that natural mortality is constant for all lengths and the other assumption is that there is no tag shedding. There is now evidence that natural mortality is much higher in newborn and small sharks than in larger sharks for gummy shark (Walker 1994a; Walker 1998) and school shark (Punt *et al.* 2000; Punt and Walker 1998b). Hence, in the present study, to accommodate the constant M assumption, only animals ≥650 mm TL when tagged and released are included in the analyses. Also, in the present study, to allow for tag shedding, which has been demonstrated for gummy shark and school shark (Xiao *et al.* 1999), the last equation above is reformulated by replacing M with the expression ζ_z such that

$$c_{\tau r z} = \frac{F_{\tau r}(l_\tau)e^{-\{\zeta_z + F_{\tau r}(l_\tau)\}\Delta t}}{\zeta_z + F_{\tau r}(l_\tau)}.$$

In this equation, the expression $F_{\tau r}(l_\tau)$ can be expressed in separate equations to demonstrate that length-dependent fishing mortality depends on gillnet catchability, q_n, hook catchability, q_h, fishing effort for gillnets of J separate mesh-sizes, $f_{j\tau r}$, fishing effort for hooks, $f_{h\tau r}$, and the length-selectivity of the gillnets, μ_j, and hooks, μ_h, such that

$$F_{\tau r}(l_\tau) = \sum_{j=1}^{J} q_{nr} f_{j\tau r} \mu_j(l_\tau) + q_{hr} f_{h\tau r} \mu_h(l_\tau).$$

In this equation, the expression $q_{hr} f_{h\tau r} \mu_h$ is altered to $q_{nr} H f_{h\tau r}$ where H is the constant of proportionality between hook catchability and gillnet catchability and selectivity for hooks is assumed to be constant for sharks of length ≥650 mm TL. The assumptions made are $H = 1$ and $\mu_h = 1$.

Gillnet selectivity (Kirkwood and Walker 1986) is given by

$$\mu_j = (l / \alpha_j \beta_j)^{\alpha_j} e^{(\alpha_j - l/\beta_j)},$$

where α_j and β_j are parameters related to mesh-size, m_j, and the length of fish, l, where it is assumed that the length of shark at maximum selectivity for net j is proportional to the mesh-size. Hence

$$\alpha_j \beta_j = \theta_1 m_j$$

where θ_1 is the constant of proportionality and the variance is constant θ_2 for all mesh-sizes. These assumptions lead to the following quadratic equation for positive β_j

$$\beta_j = -0.5\{\theta_1 m_j - (\theta_1^2 m_j^2 + 4\theta_2)^{0.5}\}.$$

As part of the present project, the computer system for the model was enhanced to test for the effects of sex and TL of shark on movement rates. This was considered necessary because the tag release-recapture plot method of analysis and vector analysis showed that sex and TL of shark markedly affected movement (Brown *et al.* 2000). Hence estimates of annual movement rates were made for separate length-classes chosen to approximate to size at maturity. Three sex–length-class categories chosen for gummy shark were males and females combined 650–1099 mm TL, males ≥1100 mm

TL and females ≥1100 mm TL; the categories are referred to as 'juveniles', 'mature males' and 'mature females', respectively. Four sex–length-class categories chosen for school shark were males and females combined 650–1199 mm TL, males and females combined 1200–1399 mm TL, males ≥1400 mm TL and females ≥1400 mm TL; the categories are referred to as 'juveniles', 'sub-adults', 'mature males' and 'mature females', respectively. From one time step to the next in the model, the number of sharks within each category can change as the sharks grow. Not all length-classes were well represented in every region because there is generally a lack of small gummy sharks and small school sharks in WA and SA and a lack of large school sharks in BS.

Another enhancement to the computer system was to allow for separate 'tag reduction rates' for different types of tag because double tag experiments demonstrated that 'tag shedding rate' varied depending on tag type (Xiao *et al.* 1999) (Appendix 4). Hence, three separate parameters were adopted to represent 'tag reduction rate'. These were for 'rototags and jumbo rototags', 'dart tags inserted into the dorsal musculature near the first dorsal tissue', and 'dart tags anchored in the basal cartilage of the first dorsal fin'.

Three separate regions were adopted for each of gummy shark and school shark (i.e. $R = 3$ for each species), although four separate regions were defined for the purpose of the analyses. The four regions are Western Australia (WA), South Australia (SA), Bass Strait (BS) and Tasmania (Tas), which are demarcated by the Western Australia–South Australia border, South Australia–Victoria border and latitude 41° South (close to north coast of Tasmania) to demarcate Tas from BS (Figure 1). WA is the longitude range 116°–129° East on the south coast for gummy shark and the longitude range 127°–129° East for school shark. In WA, most school sharks occur within 2° longitude of the WA–SA border. The three regions adopted for gummy shark were WA, SA and the combined regions of BS and Tas (BS/Tas), whereas the three regions adopted for school shark were the regions of WA and SA combined (WA/SA), BS and Tas. The rationale for combining Tas with BS for gummy shark is the low catch and hence low tag-recaptures of gummy shark from Tas. Similarly, the rationale for combining WA with SA for school shark is the low catch and hence low tag recaptures of school shark from WA.

For gummy shark and school shark, separately, six movement parameters (two directions for each of three regions) were estimated for each of the three sex–TL categories for gummy shark and four sex–TL categories for school shark. Three movement parameters for each of the sex–TL categories, representing the sharks that did not change region, were simply calculated from the other six movement parameters. Three catchability parameters (one for each region), one tag recovery ratio' and three 'tag reduction rate' parameters were estimated. This gave a total of 25 parameters to estimate and 9 to calculate for gummy shark and 31 parameters to estimate and 12 to calculate for school shark.

Addressing movement hypotheses

Development and simulation of movement hypotheses

Apart from application of the Integrated Tag Model described above for parameter estimation purposes, other types of models were also developed and applied. In other models movement was modelled as the probability of a shark of a given age and stock moving from one region to another region in monthly steps. The matrix of movement probabilities is selected to represent a mix of large-scale pupping migrations, feeding migrations and random movement. The values for the parameters that determine movement in the SharkFAG assessment model are obtained using a two-step process. First, alternative movement hypotheses are presented using a special Movement Simulation Model. This model operates on a daily time-step and considers movement of individuals within each age-class in a stock between contiguous cells of 1° latitude by 1° longitude. The movement can be displayed on a map of southern Australia by a computer program where alternative hypotheses can be simulated by specifying values for a small number of behaviour-related parameters (e.g. the probability of randomly leaving a cell). Net movement in one direction is achieved by setting the probability of moving in one direction greater than in the opposite direction (Taylor 1997b). For the second step of the process, the results from the Movement Simulation Model are aggregated to monthly and regional resolution and used as initial estimates for the movement rates in the fully age- and spatially-structured fishery stock assessment model. As part of the actual assessment, the initial guesses for the movement rates are modified based on 36 parameters within a separate stock assessment model to better mimic the available tag and catch rate data within eight separate regions (Punt *et al.* 2000). The eight regions adopted includes WA, the division of each of SA, BS and Tas into two regions and the addition of NSW, which includes the waters off New South Wales.

Application of tag data and movement matrices in stock assessment

Apart from applying the data to determine annual rates of movement between broad regions and estimating mortality using the tag model described above, the tag data have been used directly in the stock assessment models (Punt 2000a; Punt 2000b; Punt *et al.* 2000). These models incorporate estimated tag reporting and tag shedding rates and fit the predicted number of annual tag recaptures to the number of observed annual tag recaptures.

For the purpose of its assessment, SharkFAG defined 'stock' as 'a group of animals that have the same pupping grounds and movement patterns'. The SharkFAG model is fitted simultaneously to data disaggregated in the eight regions, and the assessment is based on the assumption that two stocks of school shark occur off southern Australia. A two-stock model was found to fit the data better than a single-stock model that allows for movement, but the data cannot support estimation of parameters for models based on more than two stocks. Movement patterns differ between the two sub-stocks. The probability of moving between regions is assumed to depend on month and age to better capture the relatively complex movement patterns observed from tagging data. Parturition is assumed to occur only in the eastern region of the fishery.

The SharkFAG model allows school sharks from New Zealand to move to Australia where they can be caught. Only animals aged 6–12 years (evidenced by tag returns) are assumed to move from New Zealand to Australia and it is assumed that there is a 50% probability each year that a New Zealand school shark in Australia returns to New Zealand. The impact of fishing in Australia or New Zealand is assumed to have negligible impact on the population in New Zealand because the level of fishing mortality in New Zealand is much lower than that in Australia. For this reason, movement of Australian school sharks to New Zealand is ignored. A range 0–15% is examined for the percentage of the number of school sharks in Australia (in a pristine state) that originated in New Zealand (Punt *et al.* 2000).

Results and discussion

Movement and mortality rates

Tag shedding rates

Results from a new method developed for estimation of instantaneous rates of tag shedding from double tagging experiments indicate shedding rates vary greatly between tag types. In general, the rototags and jumbo rototags attached to the first dorsal fin have much lower shedding rates than dart tags and Peterson fin disc tags. Internal tags have a zero shedding rate, but there is some 'non-sighting of tags by fishers'.

Instantaneous tag shedding rate estimates for rototags and jumbo rototags are 0.088 (0.062 standard error) y^{-1} (8% annually) from gummy shark and 0.086 (0.038) y^{-1} (8%) from school shark. These are clearly very effective tags for gummy shark and school shark. Shedding rates of nylon-headed dart tags inserted into the dorsal musculature near the base of the first dorsal fin are very high at 0.983 (0.112) y^{-1} (63%) from gummy shark and 0.534 (0.179) y^{-1} (41%) from school shark. These shedding rates are approximately halved when the nylon-headed dart tags are anchored into the cartilage at the base of the first dorsal fin; these estimates are 0.377 y^{-1} (0.189) (31%) from gummy shark and 0.265 (0.153) y^{-1} (23%) from school shark. The shedding rate for Peterson fin disc tags, used during the 1947–56 tagging program, is 1.089 (0.103) y^{-1} (66%) from school shark; there are insufficient data from gummy shark to make these estimates (Xiao *et al.* 1999) (see Appendix 4).

These results are used for interpretation of results of estimating movement rates and mortality rates from the Integrated Tag Model (see below). They are also used as inputs when applying available stock assessment models for school shark and gummy shark.

Tag reporting rates

The tag data and the TRR estimates for 1973–75 and 1994–96 are expected to be more reliable than those for 1976–78 because of the presence of researchers working with industry during the earlier period but not during the later period. For all regions combined, the TRR estimates for the three 3-year periods 1973–75, 1976–78 and 1994–96 were 75–79%, 57–67% and 84–92%, respectively, from the TRR Catch Method. Similarly, the TRR estimates for the three periods were 74–79%, 66–71% and 85–87%, respectively, from the TRR Tag Method. The values of these 3-year estimates are generally higher those of 1-year estimates. The 1995 and 1996 1-year estimates are likely to be the most reliable 1-year estimates because they are based on the greatest amounts of data; these estimates are 69–80% for the TRR Catch Method and 72–79% for the TRR Tag Method (Brown and Walker 1999) (see Appendix 5).

Tag recaptures

Distances moved are compared on the basis of mean distance between release and recapture positions of recaptured tagged individuals. Recaptured tagged school sharks moved further than recaptured tagged gummy sharks, and large sharks tended to move further than small sharks for both species. Male and female sharks <950 mm TL moved similar distances to each other but female sharks moved further than male sharks when larger for both species. Recaptured tagged school sharks moved about five times the distance moved by gummy sharks. For tagged sharks released in the east of the range of the fishery (regions BS and Tas) during 1990–99, school sharks moved a mean distance of 485 km whereas gummy sharks moved a mean distance of 120 km. Similarly, for tagged sharks released in the west of the range of the fishery (regions WA and SA) during 1990–99, school sharks moved a mean distance of 621 km whereas gummy sharks moved a mean distance of 117 km. A much more extensive presentation of tag movements is presented in the companion report (Brown *et al.* 2000).

Integrated Tag Model

In general, the model gives smaller confidence intervals on the results for gummy shark than for school shark. This is likely to be because gummy sharks exhibit much simpler patterns of movement than school shark. The model presently estimates annual rates of movement between regions. School sharks require a more complex model to accommodate seasonally based oscillatory movement. Parameter estimates for ‘catchability’, ‘tag recovery ratio’ and the three ‘tag reduction rates’ were found to be correlated with each other but they are only weakly correlated with the parameters for movement rate.

Gummy shark movement rates are low between regions. Most gummy sharks do not change region for any of the three categories of males and females combined 650–1100 mm TL, males ≥1100 mm TL and females ≥1100 mm TL. This is particularly marked for sharks 650–1100 mm TL where 96, 98 and 96% y^{-1} remained in WA, SA and BS/Tas, respectively. These rates for remaining in a region were 85, 90 and 99% y^{-1}, respectively, for males ≥1100 mm TL and 97, 86 and 91% y^{-1}, respectively, for females ≥1100 mm TL. The highest between region movement rates were from WA to SA (15% y^{-1}, return 6% y^{-1}) for males ≥1100 mm TL and from SA to WA (9% y^{-1}, return 3% y^{-1}) and from BS/Tas to SA (9% y^{-1}, return 5% y^{-1}) for females ≥1100 mm TL. Movement rates out of BS/Tas were particularly low for males ≥1100 mm TL (1% from BS/Tas to SA). The rates between the most widely separated regions of WA and BS/Tas were zero for all three sex–TL categories (Table 1, Figure 2). These results are consistent with a weak trend for females to move westwards and for males to move eastwards or not at all for mature animals (Brown *et al.* 2000; Walker 1983).

School shark movement-rates are much higher than for gummy shark. There is a strong trend for juveniles (650–1199 mm TL) to move out of Tas; 42% moved to WA/SA and 20% moved to BS with no returns to Tas from either of these regions. However, there is a strong trend for all other sex–TL categories to move to Tas, with a tendency to remain in Tas (i.e. 72% of sub-adults, 80% of mature males and 51% of mature females remained in Tas each year). There is also a strong trend for mature females (≥1400 mm

TL) to move to WA/SA (Table 3; Figure 3). These trends are consistent with the trends for industry to catch more females than males in WA/SA and to catch more males than females in Tas. The trends are consistent with the hypothesis that females with mid-term embryos tend to aggregate in the Great Australia Bight and mature females aggregate in southern Tasmania. They are also consistent with the distribution patterns of *Galeorhinus galeus* on the eastern coast of South America and the western coast of North America, where at certain times of the year the females aggregate in the warmer waters and the males in the cooler waters (Walker 1999).

Gummy shark estimates of 'catchability', 'tag reduction rate', and 'tag recovery ratio' (Table 3) are reasonably consistent with other data available for the species. Gillnet catchability estimates are similar between SA (2.76×10^{-5} y^{-1}) and BS/Tas (3.08×10^{-5} y^{-1}) but are lower than in WA (6.73×10^{-5} y^{-1}). The higher catchability estimate for WA might be explained by fishing effort being collected in a different way from in SA and BS/Tas and by targeting practices. The estimates of tag reduction rate are 0.37 y^{-1} for rototags and jumbo rototags, 0.64 y^{-1} for nylon-headed dart tags anchored in the basal cartilage of the first dorsal fin, and 0.92 y^{-1} for nylon-headed dart tags inserted in the muscle tissue near the first dorsal fin. These estimates are reasonably consistent with the estimates of tag shedding rate determined independently from double tag experiments (Xiao *et al.* 1999) and the commonly adopted value of 0.20 y^{-1} for natural mortality. Comparing the tag shedding rate of 0.086 (8%) (Xiao *et al.* 1999) specifically with the tag reduction rate of 0.369 y^{-1} for rototags and jumbo rototags (Table 3) gives an estimate of natural mortality rate of 0.283 y^{-1} (25%). This value of natural mortality also fits well with the tag shedding rate of 0.377 (31%) (Xiao *et al.* 1999) and the tag reduction rate of 0.638 y^{-1} for dart tags in fin cartilage (Table 3). However it does not agree quite so well with the tag shedding rate of 0.983 (63%) (Xiao *et al.* 1999) and the tag reduction rate of 0.929 y^{-1} for dart tags in muscle tissue (Table 3). It is appropriate to make this comparison on the basis of rototags and jumbo rototags because many more gummy sharks were tagged with rototags and jumbo rototags (73%) than with tags in fin cartilage (10%) or dart tags in muscle tissue (17%) (Table 1). An estimated value of 0.52 for 'tag recovery ratio' (Table 3) and the independently determined estimate of tag reporting rate by fishers estimate of about 0.70 (Brown and Walker 1999), which includes non-sighting of tags by fishers, suggests an 'initial tag survival ratio' of 0.74. This implies that 26% of the tags were lost through initial tag mortality and initial tag shedding.

School shark estimates of 'catchability', 'tag reduction rate', and 'tag recovery ratio' (Table 3) are a little less consistent with other data available for the species. Gillnet catchability estimates vary markedly between SA/WA (1.51×10^{-5} y^{-1}), BS (5.49×10^{-5} y^{-1}) and WA (17.0×10^{-5} y^{-1}). It is likely that this variation can be only partly explained by differences in type of fishing effort and targeting practices. Problems with effort data in Tas and a lower tag-reporting rate in Tas than in the other regions are suspected of causing the high catchability estimate for Tas. The estimates of tag reduction rate are 0.18 y^{-1} for rototags and jumbo rototags, 0.43 y^{-1} for dart tags in fin cartilage, and 0.40 y^{-1} for dart tags in muscle tissue. As for gummy shark, these estimates are reasonably consistent with the estimates of tag shedding rate determined independently from double tag experiments (Xiao *et al.* 1999) and the commonly adopted value of 0.10 y^{-1} for natural mortality. Comparing the tag shedding rate of 0.088 (8%) (Xiao *et al.* 1999) with the tag reduction rate of 0.178 y^{-1} for rototags and jumbo rototags (Table 3) gives an estimate of natural mortality rate of 0.090 y^{-1} (9%). This value of natural mortality does not agree well with the tag shedding rate of 0.265 (23%) (Xiao *et al.* 1999) and the tag reduction rate of 0.401 y^{-1} for dart tags in fin cartilage (Table 3). However, it fits better with the tag shedding rate of 0.534 (41%) (Xiao *et al.* 1999) and the tag reduction rate of 0.428 y^{-1} for dart tags in muscle tissue (Table 3). It is appropriate to make the comparison on the basis of rototags and jumbo rototags because many more school sharks were tagged with rototags and jumbo rototags (79%) than with or dart tags in fin cartilage (8%) or dart tags in muscle tissue (14%) (Table 1). An estimated value of 0.39 for 'tag recovery ratio' (Table 3) and the independently determined reporting of tags by fishers estimate of about 0.70 (Brown and Walker 1999), which includes non-sighting of the tags by fishers, suggests an 'initial tag survival ratio' of 0.56. This implies that 44% of the tags were lost through initial tag mortality and initial tag shedding.

Movement hypotheses

Development and simulation of movement hypotheses

Stock structuring for gummy shark appears relatively simple. Gummy shark occurring throughout the range of the fishery form a single genetic stock, but because the annual movement rates between the broad regions of the fishery are comparatively low, it is reasonable to treat the populations in these separate regions as separate stocks for stock assessment purposes. Given that the fishing gears and targeting practices of the fishers vary between the regions, there are advantages in treating them as separate stocks. Separate stock assessments have been undertaken for BS (Punt 2000a; Walker 1994a; Walker 1994b; Walker 1998), SA (Punt 2000b; Walker 1994b) and Tas (Punt 2000b).

Stock structuring is much more complex for school shark than for gummy shark. Two alternative movement hypotheses have been considered by SharkFAG for conceptual purposes but spatially structured stock assessment models best fit the available data for a mix of the two hypotheses. The two alternative conceptual hypotheses can be stated simply as follows.

1. Single panmictic population with components of the stock at different life history stages occupying different localities within the range of its distribution.

2. Discrete separate sub-populations with no or very limited interbreeding.

The first hypothesis—the single stock hypothesis—is consistent with the breeding patterns and large-scale movements described for this species (Olsen 1954; Olsen 1962) and with most data collected subsequently. The second hypothesis—the multiple sub-stock hypothesis—was assumed when the stocks were assessed as separate stocks in eight separate regions as part of an earlier assessment (Prince 1991). These hypotheses were represented by the Movement Simulation Model (Taylor 1997).

The hypothesis adopted by SharkFAG for its 1999 school shark assessment requires there to be separate breeding sub-populations but there is mixing at other life history stages (Punt *et al.* 2000). This might be referred to as a 'mixing multiple sub-stock hypothesis' and combines features of the two hypotheses above. One way of explaining mixing sub-stocks for school shark is to invoke the concept of philopatry ('home loving') effected through 'natal homing' whereby pregnant female sharks return to their birth place (Hueter 1998). However, natal homing has not been demonstrated and genetic differences in neonates or young juveniles between nursery areas have not been detected for school sharks; these uncertainties need to be investigated. There is also the question of whether mating occurs between animals of different sub-populations. A supporting argument for separate sub-stocks is the occurrence of 'localised stock depletion', a concept first described for shark species taken in bathing beach meshing programs designed to reduce risk to humans from shark attack (Holden 1977). This appears to have occurred on a broader scale in southern Australia, as once-productive fishing areas became unproductive (notably in eastern regions) while other areas have remained productive (notably in western regions). In addition, the almost complete loss of a once major nursery area in the Geelong Arm in Port Phillip Bay, Victoria, is consistent with the loss of a sub-population, although habitat degradation cannot be ruled out as a possible cause for the loss (Walker 1996; Walker 1998).

Application of tag data and movement matrices in stock assessment

Incorporation of tag data into spatially-structured models has proved to be the key to successful assessment of school shark. School shark has particularly low productivity; complex stock structuring and CPUE data used as abundance indices are uninformative. Only through incorporation of tag data directly into the assessment using spatially-structured models to embrace specific stock-structuring and movement hypotheses have highly uncertain assessments been turned into assessments for which there is high confidence.

The number of annual tag recaptures predicted by the spatially structured stock assessment models applied in the Southern Shark Fishery through SharkFAG agrees remarkably well with the number of observed annual tag recaptures. Fitting the tag data, in addition to other data sets, to the models this way has markedly reduced uncertainty in the assessments. For example, by allowing for spatial- and stock- structure and using tagging data for estimation purposes, the mature biomass of school shark at the start of 1997 is estimated to be 12–18% of the 1927 level (Punt *et al.* 2000). This is a markedly narrower range of uncertainty than that when using a spatially aggregated model and ignoring the tagging data, which estimated the 1994 mature biomass of school shark to be 15–46% of the 1927 level (Punt and Walker 1998b).

There are much more extensive and varied data sets for gummy shark than for school shark and stock structuring is much simpler to incorporate into the assessments of gummy shark than of school shark. Apart from incorporating tag data, along with all other data sets, into the gummy shark assessments to reduce uncertainty in the assessments, the data provided a basis for validating the assessments. This was achieved by including tag data while dropping out other data sets such as standardised CPUE (Punt 2000a). There is very high confidence in the gummy shark assessments.

Benefits

Estimates of movement rates of school shark and gummy shark between the major regions of southern Australia, current estimates of mortality and direct inclusion of tag release and recapture data into fishery-assessment models have markedly reduced uncertainty in stock assessment of the Southern Shark Fishery. The project has contributed to establishing the Southern Shark Fishery as one managed with high sustainable catches. Assessments of gummy shark stocks indicate the species is managed sustainably, whereas assessments of school shark provide a sound basis for setting clear management goals for ensuring sustainable use or rehabilitation of the resource. This will ensure economic viability of industry for the catching and processing sector participants, and will ensure an ongoing supply of fresh shark meat so highly esteemed by some sections the Australian community.

The flow of benefits are allocated as 60% Commonwealth, 10% Victoria, 10% Tasmania, 10% South Australia and 10% Western Australia.

Intellectual property

No intellectual property has arisen from the research that is likely to lead to significant commercial benefits, patents or licences. Intellectual property associated with information produced from the project will be shared equally by the Fisheries Research and Development Corporation and by the Victorian Department of Natural Resources and Environment. CSIRO Division of Marine Research, Tasmanian Department of Primary Industry and Fisheries, and the New Zealand National Institute of Water and Atmospheric Research Limited will continue to retain their intellectual property rights over the tag release-recapture data they contributed to the Southern Shark Tag Database.

Staff

Organisation, position, period on the project and percentage of time each year on the project are listed for each staff member.

Marine and Freshwater Resources Institute			
Terry Walker	Principal Investigator	1 Jul 93–30 Jun 97	35%
		1 Jul 97–30 Jun 00	10%
Lauren Brown	Marine Scientist	1 Jan 94–30 Jun 97	100%
		1 Jul 97–30 Jun 00	40%
Natalie Bridge	Technical Officer	1 Jan 94–30 Jun 97	25%
Bruce Taylor	Fisheries Modeller	1 Jul 95–30 Jun 00	5%
CSIRO Division of Marine Research			
John Stevens	Senior Research Scientist	1 Jul 93–30 Jun 96	15%
Yongshun Xiao	Senior Research Scientist	1 Jul 95–31 Dec 96	10%

Further development

Tags from sharks will continue to be recaptured and reported for many years to come. The tasks of receiving the tags and updating of the Southern Shark Tag Database will continue through the current Southern Shark Monitoring Project funded by AFMA. The database is a source of essential data for ongoing stock assessments of the resources harvested in the Southern Shark Fishery. The results from further analysis of the data will be published in several additional scientific papers. In particular, further analyses for movement will be undertaken to explore the seasonality of shark movements

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The success of this project can be attributed to the active participation and cooperation of many people in Commonwealth and State fisheries research and management agencies, and in commercial and recreational fishing bodies. We wish to thank all those many individual professional and recreational fishers, too numerous to mention, who tagged sharks, captured sharks for tagging, or returned tags, information, and in some cases vertebrae from recaptured tagged sharks.

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Several people provided important scientific input to the tagging projects. John Stevens and Grant West of CSIRO and Colin Simpfendorfer of WAMRL provided input into selection of tags and the logistics of tagging sharks. Yongshun Xiao, formerly of CSIRO and presently of SARDI, developed the Tag Design Model for calculating the accuracy and precision of estimates of movement rates for different experimental designs. This provided a quantitative basis for deciding on the number of sharks to tag and release in each region across southern Australia during 1993–96. Yongshun Xiao also developed and applied a model for estimating tag shedding rates. André Punt of CSIRO provided important advice for estimating tag reporting rates and tag shedding rates. In addition, André Punt, with assistance from Fred Pribac, also of CSIRO, and

with input from SharkFAG developed appropriate models for incorporating tag release-recapture data directly into spatially-structured and spatially-aggregated models for stock assessment of gummy shark and school shark. Nik Dow, formerly of MAFRI, developed the Integrated Tag Model used for analysis of the data in the computer programming language FORTRAN. Mick Olsen, formerly of CSIRO and the South Australian Department of Fisheries, is acknowledged for the collection of the CSIRO 1947–1956 tag release data and formulation of some of the hypotheses of movement.

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Table 1. Number of sharks tagged by tag type

WA, Western Australia; SA, South Australia; BS, Bass Strait; Tas, Tasmania.

Sex	Recapture region or Uncaptured	Number of tagged sharks for each release region			
Gummy shark		WA	SA	BS/Tas	Total
Male & female	Rototags & jumbo rototags	654	984	2409	4047
	Dart tags (fin cartilage)	45	98	433	576
	Dart tags (muscle)	0	137	818	955
	Total	699	1219	3660	5578
School shark		WA/SA	BS	Tas	Total
Male & female	Rototags & jumbo rototags	636	382	598	1616
	Dart tags (fin cartilage)	40	9	110	159
	Dart tags (muscle)	149	54	76	279
	Total	825	445	784	2054

Table 2. Number of recaptured and unrecaptured tagged sharks

WA, Western Australia; SA, South Australia; BS, Bass Strait; Tas, Tasmania.

Sex	Recapture region or Uncaptured	Number of recaptured or unrecaptured sharks for each release region			
Gummy shark		WA	SA	BS/Tas	Total
Male	WA	52	11	0	63
	SA	7	156	7	170
	BS/Tas	0	8	437	445
	Unrecaptured	96	370	1615	2081
	Total	155	545	2059	2759
Female	WA	173	16	1	190
	SA	9	168	35	212
	BS/Tas	0	9	343	352
	Unrecaptured	362	481	1222	2065
	Total	544	674	1601	2819
Total	WA	225	27	1	253
	SA	16	324	42	382
	BS/Tas	0	17	780	797
	Unrecaptured	458	851	2837	4146
	Total	699	1219	3660	5578
School shark		WA/SA	BS	Tas	Total
Male	WA/SA	51	10	18	79
	BS	11	46	20	77
	Tas	6	7	32	45
	Uncaptured	240	225	321	786
	Total	308	288	391	987
Female	WA/SA	84	15	37	136
	BS	14	27	25	66
	Tas	7	5	19	31
	Uncaptured	412	110	312	834
	Total	517	157	393	1067
Total	WA/SA	135	25	55	215
	BS	25	73	45	143
	Tas	13	12	51	76
	Uncaptured	652	335	633	1620
	Total	825	445	784	2054

Table 3. Estimates of annual movement rates and mortality rates for gummy shark and school shark

WA, Western Australia; SA, South Australia; BS, Bass Strait; Tas, Tasmania. 'Tag reduction rate 1' applies mainly to jumbo tags and rotatags, 'tag reduction rate 2' applies dart tags inserted into muscle tissue, and 'tag reduction rate 3' applies to dart tags inserted into the basal cartilage of the first dorsal fin (other types of tag are included in 'tag reduction rate 1'). Exogenous parameter values adopted in the analysis are relative hook power H = 1.0, selectivity parameters are $\theta_1 = 184.3$ and $\theta_2 = 29739$ for gummy shark and $\theta_1 = 188.0$ and $\theta_2 = 55920$ for school shark, and Francis growth length-increment parameters are $g_\lambda = 122$ and $g_\mu = 59$ mm y^{-1} for male gummy shark, $g_\lambda = 107$ and $g_\mu = 84$ mm y^{-1} for female gummy shark, $g_\lambda = 126$ and $g_\mu = 70$ mm y^{-1} for male school shark, and $g_\lambda = 133$ and $g_\mu = 44$ mm y^{-1} for female school shark, where $\lambda = 800$ mm TL and $\mu = 1200$ mm TL. Parameter values were determined by maximum likelihood and 90% prediction intervals by MCMC based on 250,000 iterations.

Sex / Total length range	Estimated parameter	Recapture region	Parameter estimate (with 90% probability interval) for each release region		
Gummy shark			WA	SA	BS/Tas
Juvenile 650–1100 mm TL	Annual movement rate between regions, $p_{r'r}$, (y^{-1})	WA	0.96 (0.85–0.97)	0.00 (0.00–0.04)	0.00 (0.00–0.00)
		SA	0.04 (0.01–0.12)	0.98 (0.96–0.99)	0.04 (0.03–0.05)
		BS/Tas	0.00 (0.00–0.03)	0.02 (0.01–0.04)	0.96 (0.95–0.97)
Male adults ≥1100 mm TL	Annual movement rate between regions, $p_{r'r}$, (y^{-1})	WA	0.85 (0.73–0.90)	0.06 (0.03–0.09)	0.00 (0.00–0.01)
		SA	0.15 (0.08–0.26)	0.90 (0.85–0.93)	0.01 (0.00–0.03)
		BS/Tas	0.00 (0.00–0.02)	0.04 (0.02–0.07)	0.99 (0.96–0.99)
Female adults ≥1100 mm TL	Annual movement rate between regions, $p_{r'r}$, (y^{-1})	WA	0.97 (0.93–0.98)	0.09 (0.06–0.14)	0.00 (0.00–0.02)
		SA	0.03 (0.02–0.07)	0.86 (0.79–0.89)	0.09 (0.05–0.13)
		BS/Tas	0.00 (0.00–0.00)	0.05 (0.03–0.09)	0.91 (0.85–0.93)
Total	Tag recovery ratio, ξ		0.52 (0.44–0.58)	0.52 (0.44–0.58)	0.52 (0.44–0.58)
	Tag reduction rate 1, ζ_1, (y^{-1})		0.37 (0.27–0.44)	0.37 (0.27–0.44)	0.37 (0.27–0.44)
	Tag reduction rate 2, ζ_2, (y^{-1})		0.64 (0.50–0.76)	0.64 (0.50–0.76)	0.64 (0.50–0.76)
	Tag reduction rate 3, ζ_3, (y^{-1})		0.93 (0.79–0.98)	0.93 (0.79–0.98)	0.93 (0.79–0.98)
	Catchability, $q_{r'}$, (x 10^{-5}) (y^{-1})		6.73 (5.53–8.16)	2.76 (2.33–3.24)	3.08 (2.61–3.61)
School shark			WA/SA	BS	Tas
Juvenile 650–1199 mm TL	Annual movement rate between regions, $p_{r'r}$, (y^{-1})	WA/SA	0.97 (0.90–0.98)	0.16 (0.05–0.16)	0.42 (0.31–0.61)
		BS	0.03 (0.01–0.08)	0.84 (0.69–0.90)	0.20 (0.12–0.33)
		Tas	0.00 (0.00–0.03)	0.00 (0.00–0.08)	0.38 (0.14–0.46)
Sub-adults 1200–1399 mm TL	Annual movement rate between regions, $p_{r'r}$, (y^{-1})	WA/SA	0.74 (0.62–0.83)	0.21 (0.06–0.48)	0.18 (0.13–0.31)
		BS	0.09 (0.05–0.16)	0.32 (0.15–0.57)	0.10 (0.06–0.19)
		Tas	0.17 (0.05–0.27)	0.47 (0.10–0.63)	0.72 (0.54–0.75)
Male adults ≥1400 mm TL	Annual movement rate between regions, $p_{r'r}$, (y^{-1})	WA/SA	0.81 (0.31–0.83)	0.24 (0.08–0.58)	0.07 (0.03–0.32)
		BS	0.11 (0.00–0.41)	0.51 (0.05–0.65)	0.13 (0.06–0.48)
		Tas	0.08 (0.01–0.48)	0.25 (0.02–0.69)	0.80 (0.26–0.82)
Female adults ≥1400 mm TL	Annual movement rate between regions, $p_{r'r}$, (y^{-1})	WA/SA	0.71 (0.42–0.82)	0.04 (0.00–0.41)	0.44 (0.27–0.88)
		BS	0.04 (0.01–0.14)	0.52 (0.10–0.82)	0.05 (0.01–0.20)
		Tas	0.25 (0.09–0.48)	0.44 (0.01–0.71)	0.51 (0.00–0.61)
Total	Tag recovery ratio, ξ		0.39 (0.24–0.46)	0.39 (0.24–0.46)	0.39 (0.24–0.46)
	Tag reduction rate 1, ζ_1, (y^{-1})		0.18 (0.01–0.25)	0.18 (0.01–0.25)	0.18 (0.01–0.25)
	Tag reduction rate 2, ζ_2, (y^{-1})		0.43 (0.17–0.61)	0.43 (0.17–0.61)	0.43 (0.17–0.61)
	Tag reduction rate 3, ζ_3, (y^{-1})		0.40 (0.15–0.53)	0.40 (0.15–0.53)	0.40 (0.15–0.53)
	Catchability, $q_{r'}$, (x 10^{-5}) (y^{-1})		1.51 (1.18–2.37)	5.49 (3.82–8.48)	17.0 (12.8–41.5)

Table 4. Correlation coefficients between parameter estimates for gummy shark

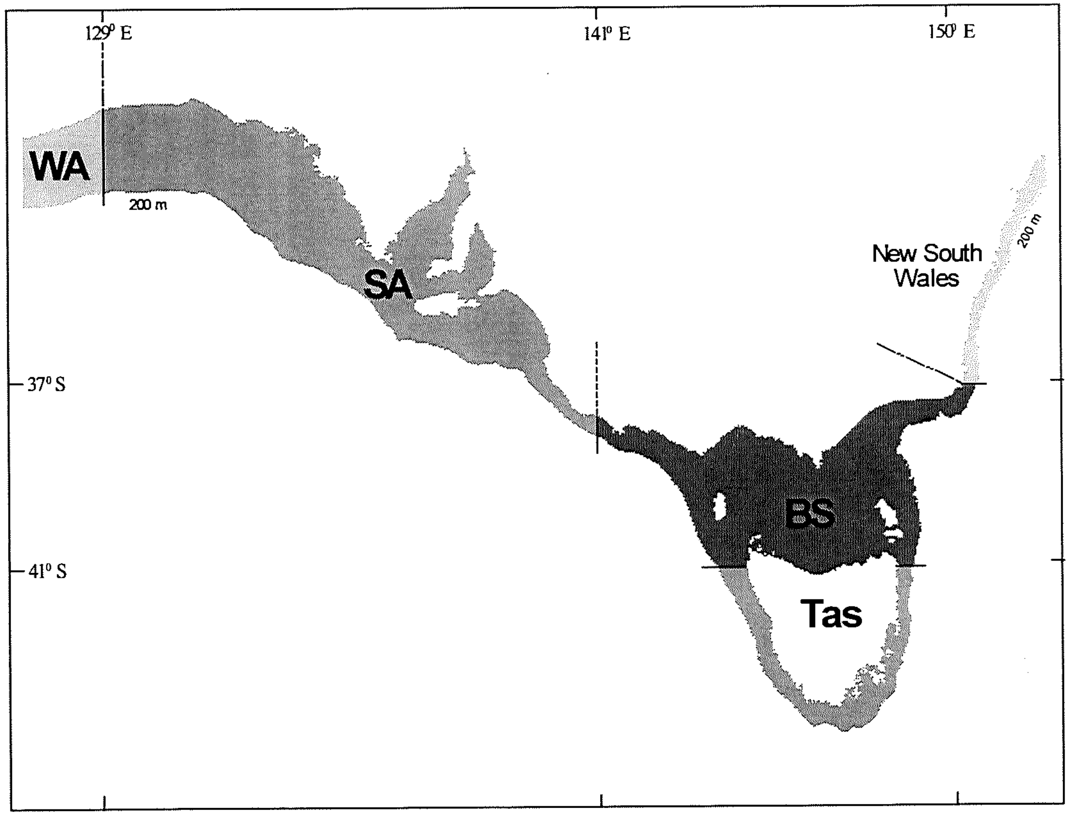
Three sex–length-class categories are males 1100 mm TL (adult male), and females 1100 mm TL (adult female), and males and females combined 650–1099 mm TL (juveniles). The symbol ξ is 'tag recovery ratio', ζ_1 is 'tag reduction rate 1' applying mainly to jumbo tags and rotatags, ζ_2 is 'tag reduction rate 2' applying to dart tags inserted into muscle tissue, and ζ_3 is 'tag reduction rate 3' applying to dart tags inserted into the basal cartilage of the first dorsal fin (other types of tag are included in 'tag reduction rate 1'). The symbol $p_{r'r}$ denotes the probability of movement from region r' to region r where 1 is WA, 2 is SA and 3 is BA/Tas (WA, Western Australia; SA, South Australia; BS, Bass Strait; Tas, Tasmania). The symbol $q_{r'}$ is catchability in region r'.

Parameter index	Sex–TL category	Parameter symbol	Parameter value y^{-1}	Correlation coefficient for each pair of parameters where each parameter is indicated by the parameter index																																	
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
1	Combined	ξ	0.52	1.00																																	
2	Combined	ζ_1	0.37	0.94	1.00																																
3	Combined	ζ_2	0.64	0.47	0.45	1.00																															
4	Combined	ζ_3	0.93	0.47	0.44	0.23	1.00																														
5	Adult male	p_{11}	0.85	-0.02	-0.02	-0.01	-0.01	1.00																													
6	Adult male	p_{12}	0.15	0.02	0.02	0.01	0.01	-1.00	1.00																												
7	Adult male	p_{13}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00																											
8	Adult male	p_{21}	0.06	0.00	0.00	0.00	0.00	-0.10	0.10	0.00	1.00																										
9	Adult male	p_{22}	0.91	-0.01	-0.01	0.00	0.00	0.08	-0.08	0.00	-0.77	1.00																									
10	Adult male	p_{23}	0.04	0.02	0.01	0.00	0.00	0.00	0.00	0.00	-0.04	-0.62	1.00																								
11	Adult male	p_{31}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00																							
12	Adult male	p_{32}	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.01	0.03	0.00	1.00																						
13	Adult male	p_{33}	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	-0.03	-0.01	-1.00	1.00																					
14	Adult female	p_{11}	0.97	0.00	0.00	0.00	0.00	0.01	-0.01	0.00	0.02	-0.02	0.00	0.00	0.00	0.00	1.00																				
15	Adult female	p_{12}	0.03	0.00	0.00	0.00	0.00	-0.01	0.01	0.00	-0.02	0.02	0.00	0.00	0.00	0.00	-1.00	1.00																			
16	Adult female	p_{13}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00																		
17	Adult female	p_{21}	0.09	-0.01	-0.01	0.00	0.00	0.02	-0.02	0.00	0.03	-0.03	0.01	0.00	0.00	0.00	-0.04	0.04	0.00	1.00																	
18	Adult female	p_{22}	0.86	-0.01	-0.01	0.00	-0.01	-0.02	0.02	0.00	-0.03	0.03	-0.01	0.00	0.01	-0.01	0.03	-0.03	0.00	-0.76	1.00																
19	Adult female	p_{23}	0.05	0.03	0.02	0.01	0.01	0.00	0.00	0.00	0.01	-0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	-0.05	-0.61	1.00															
20	Adult female	p_{31}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.01	0.01	0.00	1.00														
21	Adult female	p_{32}	0.09	-0.01	0.00	0.00	0.00	0.00	0.00	0.00	-0.01	0.01	-0.01	0.00	0.00	0.00	-0.01	0.01	0.00	0.00	-0.06	0.09	-0.01	1.00													
22	Adult female	p_{33}	0.91	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	-0.01	0.01	0.00	0.00	0.00	0.01	-0.01	0.00	0.00	0.06	-0.09	0.00	-1.00	1.00												
23	Juvenile	p_{11}	0.96	-0.01	-0.01	0.00	0.00	0.01	-0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	-0.01	0.00	0.01	-0.01	0.00	0.00	0.00	0.00	1.00											
24	Juvenile	p_{12}	0.04	0.01	0.01	0.00	0.00	-0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.01	0.01	0.00	-0.01	0.01	0.00	0.00	0.00	0.00	-1.00	1.00										
25	Juvenile	p_{13}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.01	0.00	1.00									
26	Juvenile	p_{21}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00								
27	Juvenile	p_{22}	0.98	0.01	0.01	0.01	0.01	0.00	0.00	0.00	-0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	-0.01	-0.01	0.03	0.00	0.01	-0.01	0.00	0.00	0.00	-0.01	1.00							
28	Juvenile	p_{23}	0.02	-0.01	-0.01	-0.01	-0.01	0.00	0.00	0.00	0.01	0.00	-0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	-0.03	0.00	-0.01	0.01	0.00	0.00	0.00	0.00	-1.00	1.00						
29	Juvenile	p_{31}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00					
30	Juvenile	p_{32}	0.04	0.04	0.04	0.01	0.01	-0.01	0.01	0.00	-0.02	0.02	0.00	0.00	0.00	0.00	-0.02	0.02	0.00	-0.04	0.05	-0.02	0.00	-0.04	0.04	-0.01	0.01	0.00	0.00	-0.01	0.01	0.00	1.00				
31	Juvenile	p_{33}	0.96	-0.04	-0.04	-0.01	-0.01	0.01	-0.01	0.00	0.02	-0.02	0.00	0.00	0.00	0.00	0.02	-0.02	0.00	0.04	-0.05	0.02	0.00	0.04	-0.04	0.01	-0.01	0.00	0.00	0.01	-0.01	0.00	-1.00	1.00			
32	Combined	q_1	6.73	-0.69	-0.64	-0.32	-0.32	-0.05	0.05	0.00	-0.08	0.07	-0.01	0.00	0.00	0.00	-0.07	0.07	0.00	-0.12	0.10	-0.02	0.00	0.00	0.00	-0.02	0.02	0.00	0.00	-0.01	0.01	0.00	-0.02	0.02	1.00		
33	Combined	q_2	2.76	-0.70	-0.64	-0.31	-0.30	0.06	-0.06	0.00	0.07	-0.07	0.03	0.00	-0.02	0.02	0.06	-0.06	0.00	0.11	-0.11	0.04	0.00	-0.04	0.04	0.03	-0.03	0.00	0.00	-0.04	0.04	0.00	-0.19	0.19	0.46	1.00	
34	Combined	q_3	3.08	-0.87	-0.80	-0.37	-0.34	0.01	-0.01	0.00	0.00	0.02	-0.03	0.00	0.02	-0.02	0.00	0.00	0.00	0.00	0.03	-0.06	0.00	0.03	-0.03	0.01	-0.01	0.00	0.00	0.01	-0.01	0.00	0.06	-0.06	0.60	0.59	1.00

Table 5. Correlation coefficients between parameter estimates for school shark

Four sex–length-class categories are males 1400 mm TL (adult males) and females 1400 mm TL (adult females), males and females combined 1200–1399 mm TL (sub-adults), and males and females combined 650–1199 mm TL (juveniles). The symbol ξ is 'tag recovery ratio', ζ_1 is 'tag reduction rate 1' applying mainly to jumbo tags and rotatags, ζ_2 is 'tag reduction rate 2' applying to dart tags inserted into muscle tissue, and ζ_3 is 'tag reduction rate 3' applying to dart tags inserted into the basal cartilage of the first dorsal fin (other types of tag are included in 'tag reduction rate 1'). The symbol $p_{r'r}$ denotes the probability of movement from region r' to region r where 1 is WA, 2 is SA and 3 is BA/Tas (WA, Western Australia; SA, South Australia; BS, Bass Strait; Tas, Tasmania). The symbol $q_{r'}$ is catchability in region r'.

Parameter	Sex–TL	Parameter	Parameter	Correlation coefficient for each pair of parameters where each parameter is indicated by the parameter index																																								
index	category	symbol	value y^{-1}	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
1	Combined	ξ	0.39	1.00																																										
2	Combined	ζ_1	0.18	0.91	1.00																																									
3	Combined	ζ_2	0.43	0.55	0.52	1.00																																								
4	Combined	ζ_3	0.40	0.71	0.68	0.40	1.00																																							
5	Adult male	p_{11}	0.81	-0.03	-0.01	-0.01	-0.01	1.00																																						
6	Adult male	p_{12}	0.11	-0.05	-0.03	-0.03	-0.02	-0.14	1.00																																					
7	Adult male	p_{13}	0.08	0.06	0.03	0.02	0.03	-0.75	-0.55	1.00																																				
8	Adult male	p_{21}	0.24	0.06	0.06	0.02	0.04	-0.33	0.34	0.05	1.00																																			
9	Adult male	p_{22}	0.51	-0.24	-0.16	-0.12	-0.14	-0.01	-0.24	0.16	-0.30	1.00																																		
10	Adult male	p_{23}	0.25	0.21	0.13	0.11	0.11	0.20	0.04	-0.19	-0.28	-0.83	1.00																																	
11	Adult male	p_{31}	0.07	-0.02	0.03	-0.01	0.01	-0.28	-0.03	0.26	-0.01	0.02	-0.01	1.00																																
12	Adult male	p_{32}	0.13	-0.12	-0.06	-0.05	-0.05	0.00	-0.34	0.22	-0.15	-0.21	0.30	0.07	1.00																															
13	Adult male	p_{33}	0.81	0.11	0.03	0.04	0.03	0.16	0.28	-0.32	0.13	0.15	-0.22	-0.63	-0.82	1.00																														
14	Adult female	p_{11}	0.71	-0.10	-0.05	-0.05	-0.05	0.00	0.01	-0.01	0.05	0.05	-0.07	0.05	0.03	-0.05	1.00																													
15	Adult female	p_{12}	0.04	-0.12	-0.09	-0.06	-0.07	0.00	0.00	0.00	-0.06	0.14	-0.10	0.00	0.03	-0.02	-0.18	1.00																												
16	Adult female	p_{13}	0.25	0.12	0.07	0.07	0.07	0.00	-0.01	0.01	-0.04	-0.08	0.10	-0.05	-0.04	0.06	-0.98	-0.04	1.00																											
17	Adult female	p_{21}	0.04	-0.07	-0.05	-0.03	-0.04	0.00	0.00	0.00	-0.02	0.08	-0.07	0.01	0.02	-0.02	0.02	-0.10	0.00	1.00																										
18	Adult female	p_{22}	0.52	0.02	0.02	0.01	0.02	0.00	0.00	0.00	0.04	-0.02	0.00	0.02	0.00	-0.01	-0.07	-0.05	0.08	-0.19	1.00																									
19	Adult female	p_{23}	0.44	0.01	0.00	0.01	0.00	0.00	0.00	0.00	-0.03	-0.01	0.03	-0.02	-0.01	0.02	0.06	0.09	-0.08	-0.26	-0.90	1.00																								
20	Adult female	p_{31}	0.44	0.00	0.05	0.00	0.02	0.00	0.01	0.00	0.05	0.04	-0.07	0.05	0.02	-0.05	-0.57	0.06	0.56	0.03	-0.05	0.04	1.00																							
21	Adult female	p_{32}	0.05	-0.10	-0.05	-0.05	-0.05	0.00	0.01	0.00	-0.02	0.13	-0.12	0.03	0.03	-0.04	0.14	-0.09	-0.12	-0.02	-0.04	0.05	-0.03	1.00																						
22	Adult female	p_{33}	0.51	0.02	-0.04	0.01	-0.01	0.00	-0.01	0.00	-0.04	-0.07	0.09	-0.06	-0.03	0.05	0.54	-0.04	-0.54	-0.02	0.06	-0.05	-0.98	-0.16	1.00																					
23	Sub-adult	p_{11}	0.74	-0.19	-0.07	-0.10	-0.06	-0.09	-0.07	0.12	0.11	0.15	-0.22	0.17	0.14	-0.21	0.15	0.01	-0.16	0.03	0.04	-0.05	0.13	0.09	-0.15	1.00																				
24	Sub-adult	p_{12}	0.09	-0.43	-0.32	-0.21	-0.25	-0.02	0.01	0.01	-0.07	0.28	-0.24	0.05	0.11	-0.11	0.06	0.12	-0.09	0.07	-0.03	0.00	0.03	0.11	-0.05	0.10	1.00																			
25	Sub-adult	p_{13}	0.17	0.33	0.18	0.16	0.15	0.09	0.06	-0.11	-0.07	-0.24	0.28	-0.17	-0.17	0.23	-0.16	-0.06	0.17	-0.06	-0.02	0.05	-0.13	-0.12	0.15	-0.93	-0.46	1.00																		
26	Sub-adult	p_{21}	0.21	-0.05	-0.02	-0.04	-0.03	0.01	0.13	-0.09	0.10	0.00	-0.06	0.00	-0.06	0.05	0.06	-0.02	-0.06	0.00	0.02	-0.02	0.05	0.02	-0.06	0.07	0.05	-0.08	1.00																	
27	Sub-adult	p_{22}	0.32	-0.35	-0.27	-0.18	-0.22	0.00	0.03	-0.02	-0.06	0.29	-0.26	0.03	0.04	-0.05	0.06	0.11	-0.08	0.06	-0.02	-0.01	0.03	0.11	-0.05	0.15	0.20	-0.21	-0.06	1.00																
28	Sub-adult	p_{23}	0.47	0.30	0.22	0.16	0.18	0.00	-0.11	0.08	-0.03	-0.22	0.23	-0.02	0.01	0.01	-0.08	-0.07	0.10	-0.04	0.00	0.02	-0.06	-0.09	0.08	-0.16	-0.18	0.21	-0.67	-0.70	1.00															
29	Sub-adult	p_{31}	0.18	-0.10	-0.03	-0.05	-0.04	-0.04	0.01	0.03	0.07	0.07	-0.11	0.10	0.06	-0.10	0.08	0.00	-0.08	0.02	0.04	-0.04	0.08	0.05	-0.09	0.02	0.07	-0.04	-0.05	0.08	-0.03	1.00														
30	Sub-adult	p_{32}	0.10	-0.33	-0.24	-0.16	-0.19	0.01	0.02	-0.02	-0.07	0.23	-0.19	0.04	0.08	-0.08	0.05	0.10	-0.07	0.06	-0.01	-0.01	0.03	0.10	-0.05	0.10	0.09	-0.12	0.03	0.09	-0.08	0.05	1.00													
31	Sub-adult	p_{33}	0.72	0.27	0.16	0.13	0.14	0.03	-0.02	-0.01	-0.02	-0.19	0.20	-0.11	-0.09	0.13	-0.09	-0.06	0.10	-0.05	-0.02	0.04	-0.08	-0.09	0.10	-0.07	-0.10	0.10	0.02	-0.11	0.07	-0.83	-0.60	1.00												
32	Juvenile	p_{11}	0.98	0.26	0.23	0.13	0.18	-0.01	-0.02	0.02	-0.01	-0.03	0.03	-0.02	-0.04	0.04	-0.04	-0.02	0.04	-0.01	0.00	0.01	-0.01	-0.02	0.01	-0.08	-0.09	0.11	-0.03	-0.07	0.07	-0.05	-0.07	0.08	1.00											
33	Juvenile	p_{12}	0.02	-0.26	-0.23	-0.13	-0.18	0.01	0.02	-0.02	0.01	0.03	-0.03	0.02	0.04	-0.04	0.04	0.02	-0.04	0.01	0.00	-0.01	0.01	0.02	-0.01	0.08	0.09	-0.11	0.03	0.07	-0.07	0.05	0.07	-0.08	-1.00	1.00										
34	Juvenile	p_{13}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.02	0.00	1.00									
35	Juvenile	p_{21}	0.16	0.29	0.23	0.14	0.17	0.00	-0.01	0.00	0.09	-0.22	0.17	-0.01	-0.06	0.05	-0.02	-0.10	0.04	-0.05	0.03	0.00	0.00	-0.08	0.02	-0.06	-0.21	0.13	0.02	-0.19	0.13	-0.03	-0.20	0.13	-0.06	0.06	0.00	1.00								
36	Juvenile	p_{22}	0.84	-0.29	-0.23	-0.14	-0.17	0.00	0.01	0.00	-0.09	0.22	-0.17	0.01	0.06	-0.05	0.02	0.10	-0.04	0.05	-0.03	0.00	0.00	0.08	-0.02	0.06	0.21	-0.13	-0.02	0.19	-0.13	0.03	0.20	-0.13	0.06	-0.06	0.00	-1.00	1.00							
37	Juvenile	p_{23}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.01	-0.01	1.00						
38	Juvenile	p_{31}	0.42	0.07	0.13	0.03	0.09	0.00	0.02	-0.01	0.10	0.05	-0.11	0.10	0.03	-0.08	0.09	-0.02	-0.09	0.01	0.04	-0.04	0.10	0.05	-0.11	0.22	0.04	-0.21	0.10	0.03	-0.09	0.16	0.03	-0.14	-0.20	0.20	0.00	-0.05	0.05	0.00	1.00					
39	Juvenile	p_{32}	0.20	-0.33	-0.25	-0.15	-0.20	-0.01	0.01	0.00	-0.07	0.30	-0.26	0.05	0.08	-0.09	0.06	0.12	-0.09	0.07	-0.02	-0.01	0.04	0.12	-0.06	0.16	0.29	-0.25	0.01	0.27	-0.21	0.09	0.23	-0.20	0.08	-0.08	0.00	-0.14	0.14	0.00	-0.12	1.00				
40	Juvenile	p_{33}	0.38	0.13	0.03	0.06	0.04	0.00	-0.02	0.01	-0.05	-0.22	0.25	-0.12	-0.07	0.12	-0.12	-0.05	0.13	-0.05	-0.03	0.05	-0.12	-0.11	0.13	-0.29	-0.20	0.33	-0.09	-0.18	0.20	-0.19	-0.16	0.24	0.13	-0.13	0.00	0.13	-0.13	0.00	-0.82	-0.47	1.00			
41	Combined	q_1	1.50	-0.88	-0.79	-0.45	-0.61	0.03	0.04	-0.06	-0.17	0.22	-0.12	-0.06	0.11	-0.05	0.00	0.16	-0.03	0.06	-0.07	0.04	-0.08	0.08	0.07	-0.04	0.40	-0.11	-0.06	0.31	-0.19	-0.02	0.31	-0.16	-0.22	0.22	0.00	-0.31	0.31	0.00	-0.20	0.30	0.00	1.00		
42	Combined	q_2	5.49	-0.61	-0.62	-0.35	-0.47	0.06	0.06	-0.09	0.11	-0.27	0.21	-0.01	0.05	-0.03	0.05	-0.08	-0.03	-0.05	0.02	0.00	-0.04	-0.08	0.05	0.05	0.02	-0.05	0.06	-0.05	-0.01	0.03	-0.01	-0.02	-0.23	0.23	0.00	0.03	-0.03	0.01	-0.08	-0.10	0.12	0.52	1.00	
43	Combined	q_3	17.05	-0.75	-0.55	-0.39	-0.45	0.02	0.06	-0.06	0.03	0.36	-0.38	0.15	0.17	-0.21	0.19	0.13	-0.22	0.09	0.01	-0.05	0.13	0.18	-0.16	0.47	0.47	-0.60	0.15	0.40	-0.40	0.26	0.37	-0.41	-0.23	0.23	0.00	-0.28	0.28	0.00	0.23	0.42	-0.44	0.56	0.31	1.00



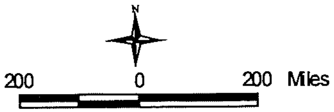
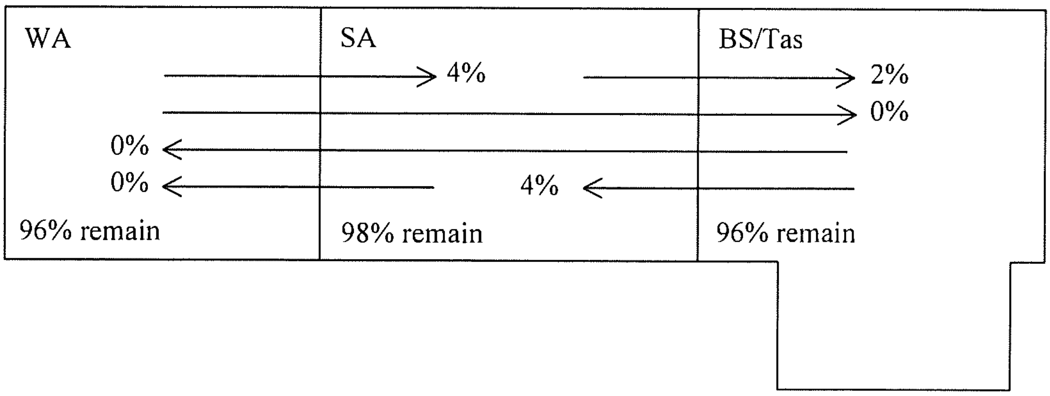


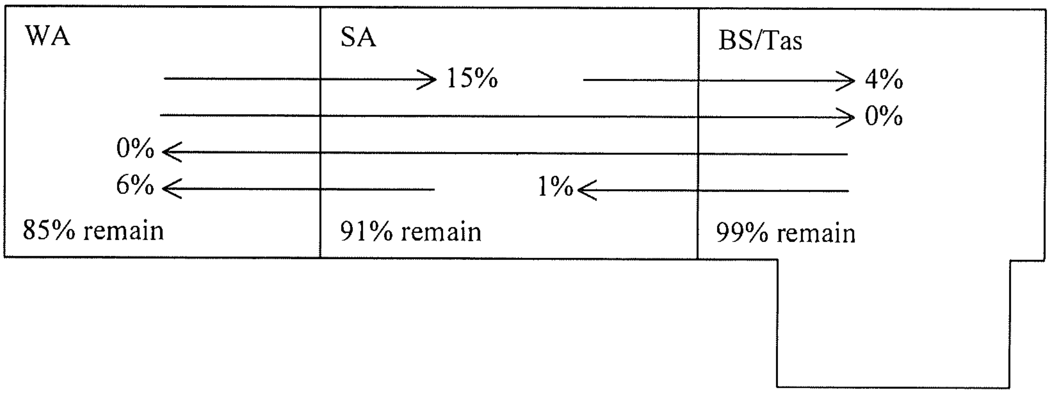
Figure 1. Definition of shark movement regions

Three gummy shark regions are WA (116°–129°E), SA, and BS and Tas combined.
Three school shark regions are WA (127°–129°E) and SA combined, BS and Tas.

Males and females 650–1100 mm



Males ≥1100 mm



Females ≥1100 mm

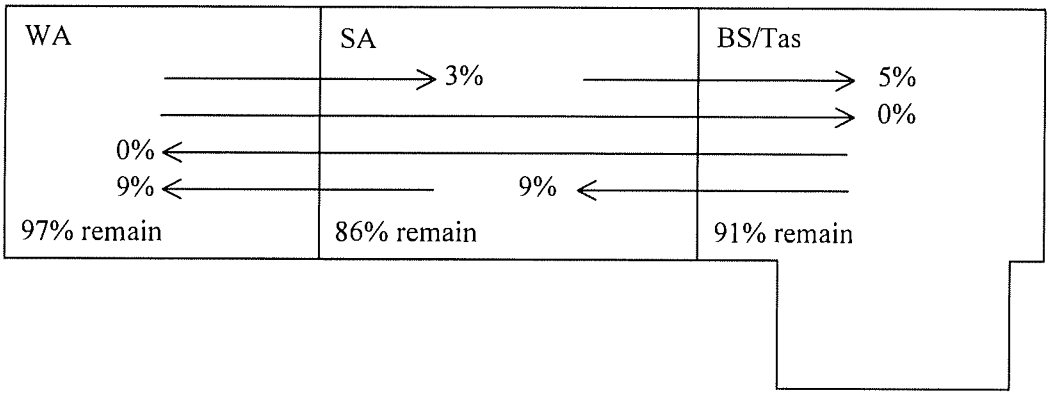
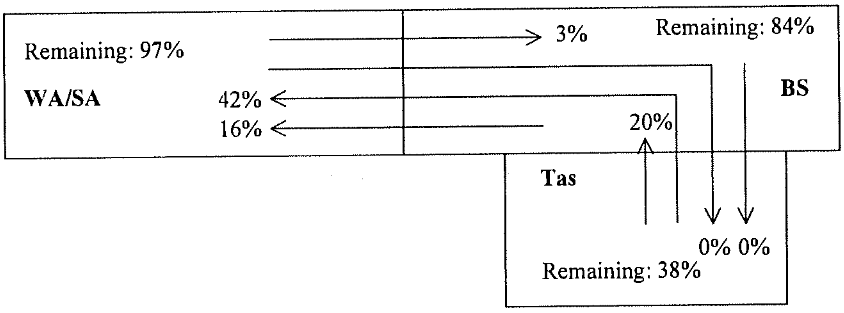


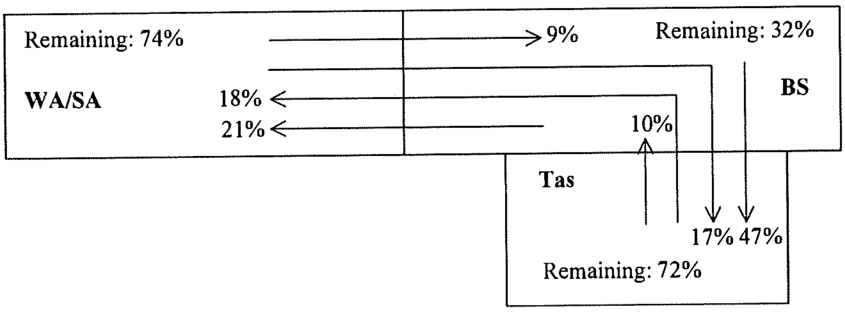
Figure 2. Gummy shark annual movement rates between broad regions

WA, Western Australia; SA, South Australia; BS/Tas, Bass Strait and Tasmania.

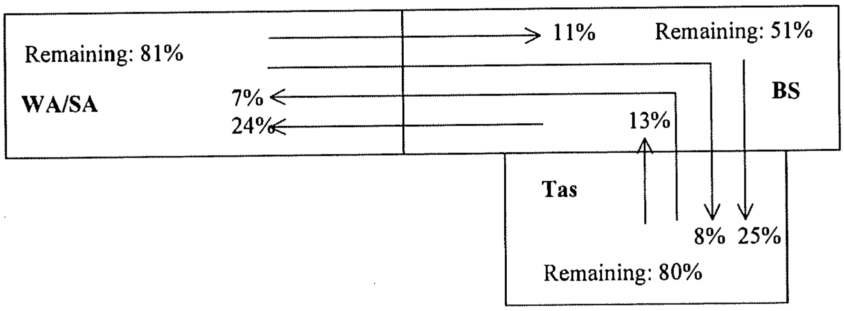
Males and female juveniles 650–1999 mm



Male and Female sub-adults 1200–1399 mm



Males ≥1400 mm



Females ≥1400 mm

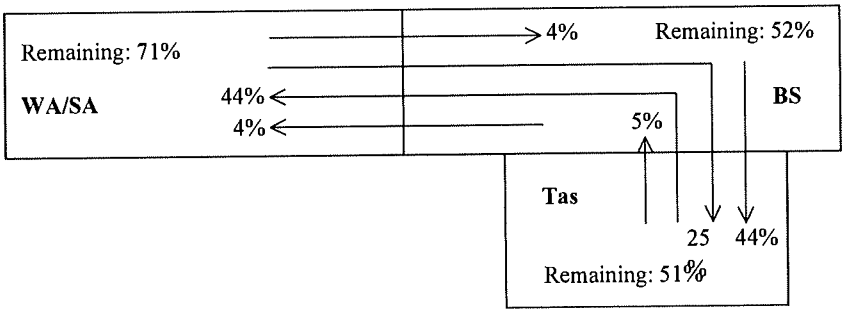


Figure 3. School shark annual movement rates between broad regions

WA/SA, Western Australia and South Australia; BS, Bass Strait; Tas, Tasmania.

Appendix 1. Experimental design for tag releases

A framework for evaluating experimental designs for estimating rates of fish movement from tag recoveries

Yongshun Xiao

Abstract: Reliable estimates of fish movement rates from tag recoveries require an experimental design for collecting sufficient data and a procedure for estimating quantities of interest from the data. Although many such procedures have been developed, suitable experimental designs have not been. In this paper, I present a framework for calculating the accuracy and precision of estimates of movement rates for different experimental designs combined with an estimator, thereby providing a basis for collecting sufficient data to estimate movement rates to a chosen accuracy and precision. The framework is used to evaluate a set of experimental designs for a tagging program for school shark, *Galeorhinus galeus*, when Hilborn's (R. Hilborn. 1990. Can. J. Fish. Aquat. Sci. 47: 635–643) maximum likelihood method is used to estimate movement rates. In this application, the minimum, mean, maximum, and three common norms of both relative bias and relative standard error of estimates of all movement rates were each regressed on the total number of fish released as a power function. From these regression equations, one can calculate the number of releases to achieve a certain level of precision and accuracy in estimates of movement rates or vice versa. Extensions of Hilborn's (1990) model and other statistical movement models can be examined similarly.

Résumé : Il faut un plan d'expérience pour recueillir suffisamment de données et une méthode pour déduire les résultats chiffrés qu'on cherche à extraire de ces données si l'on veut obtenir des estimations fiables des taux de déplacement de poissons à partir de la recapture de sujets marqués. Il existe un grand nombre de méthodes pour cela, mais pas de plans d'expérience bien adaptés à cette tâche. Dans cet article, l'auteur présente un cadre pour le calcul de l'exactitude et de la précision des estimations des taux de déplacement des poissons en fonction de différents plans d'expérience combinés à l'utilisation d'un estimateur, ce qui constitue une base pour la cueillette d'une quantité suffisante de données pour estimer les taux de déplacement avec l'exactitude et la précision choisies. Ce cadre est appliqué à l'estimation d'un ensemble de plans d'expérience à utiliser dans le cadre d'un programme de marquage de chiens de mer (*Galeorhinus galeus*) lorsque la méthode de la probabilité maximale de Hilborn (R. Hilborn. 1990. J. can. sci. halieut. aquat. 47: 635–643) est employée pour estimer les taux de déplacement. Dans cette application, on effectue une régression de fonction de puissance entre le nombre total de poissons libérés et le minimum, la moyenne, le maximum et trois normalisations courantes des estimations de biais relatif et d'écart-type relatif de tous les taux de déplacement des poissons. À partir de ces équations de régression, on peut calculer le nombre de lâchers requis pour obtenir un niveau cherché de précision et d'exactitude dans les estimations des taux de déplacement, et l'inverse. On peut, de la même manière, examiner des extensions du modèle de Hilborn (1990) et d'autres modèles statistiques de déplacements.

Introduction

Many fish move long distances to complete their life cycles; understanding these movements is essential to studies of their population dynamics. Estimates of rates of fish movement between spatial strata from tag recoveries rely on (*i*) an experimental design for collecting sufficient data and (*ii*) a procedure for estimating quantities of interest from the data. Many such procedures are available. The simplest is to draw arrows from the sites of release to the sites of recapture and to calculate proportions of recaptures to total releases as a function of time for all sites (e.g., Schaefer et al. 1961). This analysis can, however, be substantially biased, because it does not allow for spatiotemporal variations in fishing effort, which also affects the number of recaptures. Several statistical methods for estimating movement rates from tag recoveries have also been developed (e.g., Ishii 1979; Cormack 1981; Sibert 1984; Hilborn 1990; Schwarz et al. 1993; Schweigert and Schwarz 1993; Anganuzzi et al. 1994).

By contrast, the problem of selecting an experimental design, such as allocation of the number of fish releases by area and time, remains unsolved. This lack of systematic designs can have major implications for previous and, if not addressed, future estimates of movement rates. Obviously, if fewer recaptures than are needed to estimate movement rates reliably are made from a tagging experiment, then both the accuracy (measured, say, by relative bias) and the precision (measured, say, by relative standard error) of the resulting estimates are compromised, and the experiment can be considered a failure. In this case, caution must be exercised, in ensuing applications, about poor accuracy and precision in existing estimates of parameters. On the other hand, if more than the required number of recaptures is made, more resources than necessary have been consumed for unnecessarily accurate and precise estimates; such resources might have otherwise been used for wiser purposes. Thus, an experiment must be designed to avoid

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Y. Xiao. CSIRO Division of Fisheries, GPO Box 1538,
Hobart, Tasmania 7001, Australia. e-mail: xiao@ml.csiro.au

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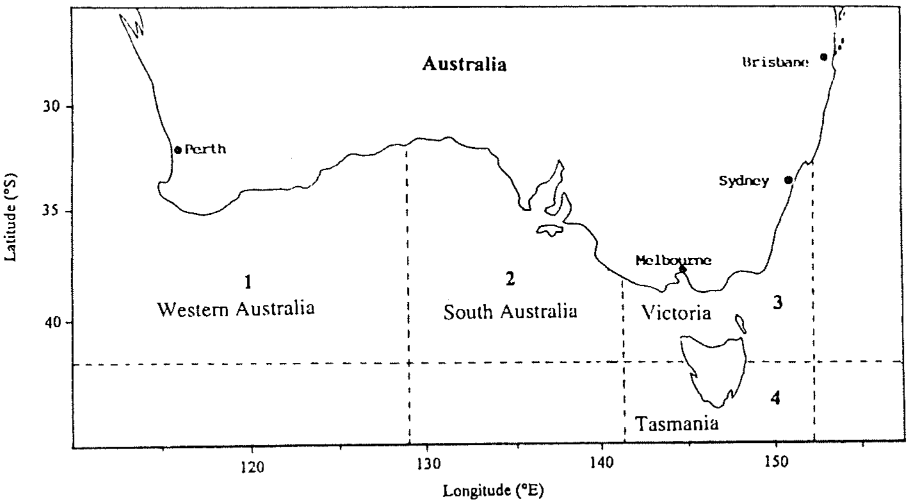
Fig. 1. Management areas in the Australian southern shark fishery. Area 1, Western Australia; area 2, South Australia; area 3, Victoria; area 4, Tasmania.



either too few or too many recaptures. In other words, the design must determine how many fish should be released, when and where, to achieve a chosen level of precision and accuracy in estimates of movement rates.

School shark, *Galeorhinus galeus* (Linnaeus) (Last and Stevens 1994), is a major species in the Australian southern shark fishery. The fishery extends from Western Australia in the west through South Australia to Bass Strait and Tasmania in the east (Fig. 1) and has an annual landed value of $A 15.6 million (Walker et al. 1994). Tagging programs were undertaken to study its growth and natural mortality (Grant et al. 1979) and local movements in Victoria and off southern Tasmania (T.I. Walker, Victorian Fisheries Research Institute, P.O. Box 114, Queenscliff, Victoria 3225, Australia, unpublished data). Both studies suggest that school shark are highly migratory, but they provide little information about the sharks' movement rates beyond these areas, where most sharks were tagged and released. Also, fishing effort was poorly documented at the time of Grant et al.'s (1979) tagging program (1940s and 1950s) and the data are inadequate for quantifying movement rates. Finally, predominant use of gill nets with large mesh sizes (8 in.; 1 in. = 25.4 mm) off the southern coast of Western Australia and off South Australia at the time of T.I. Walker's tagging program (1970s) led to a low level of fishing effort and a small number of recaptures.

The implications of fish movements for stock assessment and management are poorly understood. It seems, however, that assuming that the fish are not moving while they are leads to a loss in potential yields (e.g., Tuck and Possingham 1994), whereas assuming that they are moving while they are not can result in a depletion of the most accessible stocks (Hilborn and Walters 1992). The lack of quantitative information on the movement rates of school shark has precluded a quantitative analysis of the implications of an often-made assumption that its regional stocks do not mix. A large-scale tagging program is essential for quantifying its movement rates so that they can be incorporated in management decisions. Such a program was initiated recently by the Victorian Fisheries Research Institute (VFRI) in collaboration with the CSIRO Division of Fisheries.

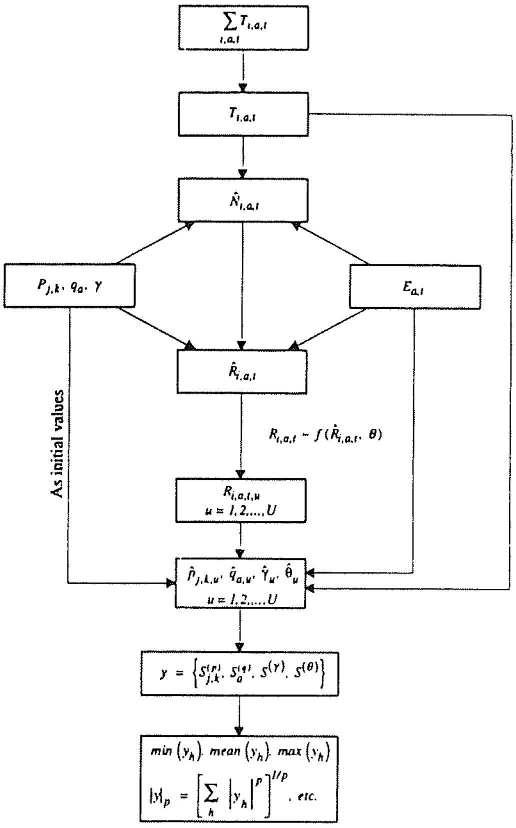
In this report, I present a framework for calculating the accuracy and precision of estimates of fish movement rates that can be expected from different experimental designs combined with an appropriate estimation procedure, thereby providing a basis for collecting sufficient data to achieve a chosen accuracy and precision in estimates of movement rates. The framework is used to evaluate a set of experimental designs for the tagging program for school shark, when Hilborn's (1990) maximum likelihood method is used to estimate movement rates. This estimation procedure is chosen because it is simple and widely applicable. Extensions of Hilborn's (1990) model and other statistical models can be examined similarly.

Framework

In this framework (Fig. 2), different experimental designs for determining rates of fish movement from tag recoveries can theoretically be developed by varying the number and patterns of fish released by area and time, controlling the levels of fishing effort, and varying the values of model parameters including movement rates. In reality, it is unusual to control fishing effort for this purpose because of the difficulties in doing so (Hilborn and Walters 1992).

The variant of the framework described below assumes constant, but can readily be expanded to handle time-varying, values of natural and fishing mortalities, tag shedding rate, and movement rates. For consistency, Hilborn's (1990) notation will be used below with minimal modifications. Let $T_{i,a,t}$ = number of tags released from tag group i in area a at time t, $\hat{N}_{i,a,t}$ = expected number of tagged fish in tag group i in area a at time t, $R_{i,a,t}$ = number of tags recovered from tag group i in area a at time t, $\hat{R}_{i,a,t}$ = expected number of tags recovered from tag group i in area a at time t, $p_{j,k}$ = probability of movement from area j to k, $E_{a,t}$ = fishing effort in area a at time t, q_a = catchability coefficient in area a, M = constant instantaneous

Fig. 2. Flow chart of simulation.



natural mortality rate, and λ = constant instantaneous tag shedding rate. Other notations will be introduced as they arise.

The tag group must be defined properly to get the desired results. Generally, a tag group is a group of fish tagged in a spatiotemporal stratum but this could be extended to include size groups, sex, or whatever criteria thought to be important in movement, survival, and probability of recapture. At the least, fish released in each area must be treated as a tag group. The framework involves 13 steps.

(1) Specify a population dynamics and movement model, an observation model, and a procedure for parameter estimation. In the example below, I will use Hilborn's (1990) models and procedure.

(2) Select a set of input fish movement rates $p_{j,k}$, catchability coefficients q_a, and other parameters γ in the estimation procedure.

(3) Select projected levels of future fishing effort $E_{a,t}$.

(4) Specify the total number of fish releases $x = \sum_{i,a,t} T_{i,a,t}$ and a procedure for allocating releases to spatiotemporal strata, $T_{i,a,t}$.

(5) Calculate the expected number of tags recovered from tag group i in area a at time t, $\hat{N}_{i,a,t}$, from $T_{i,a,t}$, $p_{j,k}$, q_a, γ, and $E_{a,t}$ using the population dynamics and movement model.

(6) Calculate the expected number of tags recovered from tag group i in area a at time t, $\hat{R}_{i,a,t}$, from $\hat{N}_{i,a,t}$, q_a, and $E_{a,t}$ using the observation model.

(7) Specify a statistical distribution for the recapture process $R_{i,a,t} \sim f(\hat{R}_{i,a,t}, \theta)$ with a mean of $\hat{R}_{i,a,t}$ and a vector of parameters (other than those in population dynamics and movement model and observation model) θ, and simulate a sufficiently large number U of data sets of recaptures $R_{i,a,t,u}$, with $u = 1, 2, \ldots, U$.

(8) Estimate, for the uth set of simulated data, movement rates $p_{j,k,u}$, catchability coefficients $q_{a,u}$, γ_u, and θ_u from $R_{i,a,t,u}$, $T_{i,a,t}$, and $E_{a,t}$, with $u = 1, 2, \ldots, U$ and with the input values of $p_{j,k}$, q_a, γ, and θ as the initial values of parameters.

(9) Calculate statistics (e.g., relative bias and relative standard error) that summarize the estimates of movement rates $S^{(p)}_{j,k}$, catchability coefficient $S^{(q)}_a$, $S^{(\gamma)}$, and $S^{(\theta)}$. In the example below, I will calculate the relative bias of estimates of movement rates

$$B^{(p)}_{j,k} = 1 - \frac{1}{p_{j,k}U}\sum_u \hat{p}_{j,k,u}$$

and relative standard error of estimates of movement rates

$$RSD^{(p)}_{j,k} = \frac{1}{p_{j,k}}\left(\frac{1}{U}\sum_u\left(\hat{p}_{j,k,u} - \frac{1}{U}\sum_u \hat{p}_{j,k,u}\right)^2\right)^{1/2}.$$

(10) Form vector $\mathbf{y} = \{S^{(p)}_{j,k}, S^{(q)}_a, S^{(\gamma)}, S^{(\theta)}\}$ and calculate the minimum, mean, and maximum of all elements of vector $\mathbf{y}$, i.e., $\min_h(y_h)$, $\text{mean}_h(y_h)$, and $\max_h(y_h)$, and various norms of vector $\mathbf{y}$, i.e.,

$$|y|_p = \left[\sum_h |y_h|^p\right]^{1/p}.$$

(11) Repeat above steps for different values of $\sum_{i,a,t} T_{i,a,t}$, $T_{i,a,t}$, $P_{j,k}$, q_a, γ, θ, and $E_{a,t}$ to get corresponding minimum, mean and maximum of all elements, and various vector norms, of vector $\mathbf{y}$.

(12) Determine the empirical relationships of minimum, mean, and maximum of all elements, and various norms, of vector $\mathbf{y}$, with $\sum_{i,a,t} T_{i,a,t}$, $T_{i,a,t}$, $P_{j,k}$, q_a, γ, θ, and $E_{a,t}$. In this study, I regress each of them, S, on the total number of releases x using the power function $S = ax^{-b}$, where a and b are regression parameters to be estimated.

(13) Evaluate those empirical relationships and decide, for a tagging experiment, appropriate values of $\sum_{i,a,t} T_{i,a,t}$, $T_{i,a,t}$, $p_{j,k}$, q_a, γ, θ, and $E_{a,t}$ to achieve a chosen level of accuracy and precision in terms of minimum, mean, and maximum of all elements, and various norms, of vector $\mathbf{y}$.

Design of a tagging experiment for school shark: an application

Of a few statistical models, I choose to illustrate my framework using Hilborn's (1990) model and maximum likelihood estimator because of their simplicity and wide applicability. His population dynamics and movement model is rewritten as

Table 1. Summary of inputs to the model.

	j/a	1	2	3	4
$a_{j,a}(p_{j,a})$	1	0.50 (0.985777)	0.10 (0.001110)	0.20 (0.005564)	0.20 (0.007549)
	2	0.10 (0.002990)	0.70 (0.992280)	0.10 (0.002052)	0.10 (0.002677)
	3	0.05 (0.001235)	0.10 (0.002276)	0.80 (0.995374)	0.05 (0.001115)
	4	0.10 (0.002990)	0.30 (0.009688)	0.10 (0.002052)	0.50 (0.985270)
q_a	—	2.43×10^{-9}	1.31×10^{-9}	2.78×10^{-9}	3.21×10^{-9}
M	—	0.193×10^{-2}	0.193×10^{-2}	0.193×10^{-2}	0.193×10^{-2}
λ	—	0.914×10^{-3}	0.914×10^{-3}	0.914×10^{-3}	0.914×10^{-3}
$E_{a,t}$	—	64 986	217 002	150 397	29 200
$T_{i,a,0}$	—	140	0	0	0
$T_{i,a,1}$	—	0	140	0	0
$T_{i,a,2}$	—	0	0	140	0
$T_{i,a,3}$	—	0	0	0	140
$T_{i,a,4}$	—	140	0	0	0
...	—	...	...	...	...

Note: (1) conversion of annual movement rates $a_{j,a}$ to weekly movement rates $p_{j,a}$ by taking the 7/365.25th = 28/1461th power of square matrix $\{a_{j,a}\}$ using Mathematica (Wolfram 1991), with 1 = Western Australia, 2 = South Australia, 3 = Victoria, 4 = Tasmania; (2) catchability coefficient q_a ((m·hook lifts·week^{-1})$^{-1}$); (3) instantaneous natural mortality M (week^{-1}); (4) instantaneous tag shedding rate λ (week^{-1}); (5) fishing effort $E_{a,t}$ (m·hook lifts·week^{-1}); (6) number and pattern of fish releases $T_{i,a,t}$ (individuals) that are continued until the total number of releases is reached. Subscripts: $a,i,j,k = 1, 2, \ldots, n = 4$; $t = 1, 2, \ldots, \max(t) = 157$ weeks; $u = 1, 2, \ldots, U = 500$ trials. —, not applicable. Fish released in each area are considered a tag group. The release protocol is repeated for a total number of release of 560 to 10 640 by 560.

$$\hat{N}_{i,a,t+1} = \sum_{j=1}^{n} \hat{N}_{i,j,t}\,(1 - q_j E_{j,t})\,\mathrm{e}^{-(M+\lambda)}\,p_{j,a} + T_{i,a,t},$$

and his observation model as

$$\hat{R}_{i,a,t} = \hat{N}_{i,a,t}\,q_a E_{a,t},$$

with $\hat{N}_{i,a,0} = 0$ and a maximum of $n(n+1)$ parameters (assuming that both M and λ are known constants), of which n^2 are movement rates and n catchability coefficients. The number of movement parameters is reduced to $n(n-1)$ under the constraint $\sum_k p_{j,k} = 1$. Note that $T_{i,a,t}$ in his population dynamics and movement model must be multiplied by a term to correct for its associated mortality over the period $[t, t+1]$, unless releases are made at the very end of each period. In this application, then, $\gamma = \{M,\lambda\}$ and $\theta = 0$. Gear selectivity, initial tag loss, underreporting of fish recaptures, and emigration can also be incorporated into this model, but are ignored below because of a lack of quantitative information. These models can be implemented for any time intervals (e.g., day, week, month, or year) after conversion of movement rates (see Table 1 for a proper conversion). Since recaptures are recorded as date of recapture, one may as well be as prepared to convert annual movement rates and fishing effort to daily movement rates and effort as to convert daily to annual recaptures. In this work, t is measured in weeks. Also, for most tagging programs, it should be reasonable to expect sufficient tag recoveries within not too long a period (e.g., 3–6 years). For this application, I set $\max(t) = 157$ weeks, and considered fish released in each area as a tag group.

To estimate various model parameters, I assume that $R_{i,a,t}$ follows a Poisson distribution with a mean (and also variance) of $\hat{R}_{i,a,t}$, i.e., $R_{i,a,t} \sim \mathrm{Poisson}(\hat{R}_{i,a,t})$, and simulate a sufficiently large number ($U = 500$) of data sets of recaptures $R_{i,a,t,u}$, with $u = 1, 2, \ldots, U$. For the uth simulated data set, the Poisson distribution for fish from tag group i in area a at time t can be written as

$$L\,(R_{i,a,t,u}|\hat{R}_{i,a,t}) = \frac{e^{-\hat{R}_{i,a,t}}\,\hat{R}_{i,a,t}^{R_{i,a,t,u}}}{R_{i,a,t,u}!},$$

and the total likelihood function as

$$\prod_{i,a,t} \frac{\mathrm{e}^{-\hat{R}_{i,a,t}}\,\hat{R}_{i,a,t}^{R_{i,a,t,u}}}{R_{i,a,t,u}!}$$

(Hilborn 1990). Model parameters can then be estimated by minimizing

$$\sum_{i,a,t} [\hat{R}_{i,a,t} - R_{i,a,t,u} \log\,(\hat{R}_{i,a,t})].$$

A summary of inputs to the model is given in Table 1. $T_{i,a,t}$ is determined mainly by the availability of fish to be tagged and by logistics, although it is desirable and sometimes essential to examine a variety of release patterns. Releases should at least cover all of the spatiotemporal strata concerned to provide contrast in the data. In the case of school shark, I examined only one release pattern. Initial trials from a pilot tagging program during 1994 by staff from the VFRI indicated that personnel available for that tagging program could go to the field weekly. Because it is a small team, as in most tagging programs, various spatial strata would have to be visited consecutively. Existing data suggested that for tagging purposes, school shark would be equally available in all spatial strata and at all times; approximately 140 sharks can be tagged during a weekly trip to a single area, and releases are assumed to be made at the very end of each period. In this application, I assume, therefore, that the four areas are visited consecutively; each area is visited in turn for a week to tag 140 sharks. This tag and release protocol is maintained until the total number of releases specified is reached. Finally, I repeat steps 4–10 of the general framework by varying the total number of releases from 560 to 10 640 by 560, while holding constant $p_{j,k}$, q_a, γ, θ, and $E_{a,t}$, all for Hilborn's (1990) population dynamics and movement model, observation model, and estimation procedure.

It is difficult to determine $E_{a,t}$ reliably, although fishing effort in the near future should be adequately approximated by averaging the fishing effort over the past few (say 4) years. In the case of school shark, I estimated fishing effort for 1990–1993 from the VFRI's data (T.I. Walker, personal communication). Since several types of gear (gill nets of various mesh sizes, and hooks) are used in the fishery, all effort for South Australia, Victoria, and Tasmania was converted to m·hook lifts·week^{-1} through a regression of catch on fishing effort and types of gear (see below). Note that this method for standardizing catch and effort uses catches as the dependent variable, and effort and all other factors that contribute to catch variations as independent variables. Thus, provided that catches are given in the same unit, it suits effort even of entirely different kinds. The effort for Western Australia (C. Simpfendorfer, Western Australia Marine Research Laboratories, P.O. Box 20, North Beach, Western Australia 6020, Australia, personal communication) also used several types of gear. It was calculated from information from the VFRI, as associated catch data were not available at the time of standardization. In this application, fishing effort $E_{a,t}$ in the future is assumed to be constant over time for a particular area: 64 986, 217 002, 150 397, and 29 200 m·hook lifts·week^{-1} for Western Australia, South Australia, Victoria, and Tasmania, respectively.

For this application, I had planned to estimate $p_{j,k}$ from three sets of tagging data: one from Grant et al. (1979), one from a pilot tagging program as part of this experimental design, and the third from a tagging study by the VFRI. As mentioned earlier, the first source of data was limited in release site to the coasts of Tasmania, Victoria, and South Australia. When fitted into Hilborn's (1990) model and estimation procedure under various hypothetical patterns of fishing effort (as a result of a lack of detailed data on fishing effort), these data gave unrealistic estimates of $p_{j,k}$ and q_a, which were therefore not used below. The pilot tagging program has, as of February 1995, resulted in about 200 recaptures mainly from the sites of release, which are insufficient for estimating annual movement rates even roughly. The VFRI's data, which were collected mainly from Victoria and Tasmania, are still being analysed to determine local movement rates. Data from all three sources and analysis of the length frequency distribution of school shark (T.I. Walker, personal communication) indicate, however, that the annual movement rates in Table 1 are possible for South Australia, Victoria, and Tasmania. Since there were no releases, relatively little fishing effort in, and almost no recaptures from, Western Australia, $p_{1,k}$s and $p_{j,1}$s cannot be determined but are assumed to take the values in Table 1. These annual movement rates were converted by appropriate matrix manipulations (see Table 1 for details) to weekly movement rates, which were then used as input movement rates.

For school shark, q_as can be estimated in many ways. Previous estimation attempts by multiple linear regression did not meet with much success, probably because some process error estimators, which may behave badly (Punt 1989), had been used in almost all cases. For this application, they were estimated from the VFRI's catch and effort data (T.I. Walker, unpublished data) through an observational error estimator conditional on catch, by minimizing

$$\sum_{a,t,j} (\log(C_{a,t,j}) - \log(q_{a,j} B_t E_{a,t,j}))^2,$$

where $C_{a,t,j}$ is observed catch in area a at time t for gear type j, $q_{a,j}$ is catchability coefficient for area a and gear type j, $E_{a,t,j}$ is observed fishing effort in area a at time t for gear type j, and B_t is fish biomass at time t as calculated from the Schaefer (1954) production model, $B_{t+1} = B_t + rB_t(1 - B_t/K) - \sum_{a,t,j} C_{a,t,j}$, with rate of population natural increase r and environmental carrying capacity K. $q_{a,j}$, r, K, and B_0 are parameters to be estimated. Thus, fish in all areas are assumed to be in a unit stock and errors in $C_{a,t,j}$ are assumed to be independent, identical lognormal variates. The standardized (in reference to gear type 1, i.e., hooks) total fishing effort, as used above, is calculated as

$$E_{a,t} = \frac{1}{q_{a,1}} \sum_j q_{a,j} E_{a,t,j}.$$

Let $q_{a,1} = q_a$. The estimates of catchability coefficient thus obtained are $q_1 = 2.43 \times 10^{-9}$, $q_2 = 1.31 \times 10^{-9}$, $q_3 = 2.78 \times 10^{-9}$, and $q_4 = 3.21 \times 10^{-9}$ (m·hook lifts·week^{-1})$^{-1}$. These catchability coefficients correspond to weekly exploitation rates of 0.016, 0.028, 0.042, and 0.009%, respectively, or annual exploitation rates of 0.821, 1.483, 2.182, and 0.489%.

The instantaneous natural mortality of school shark M is 0.193×10^{-2}·week^{-1} (Grant et al. 1979), and the instantaneous tag shedding rate is assumed to be the same ($\lambda = 0.914 \times 10^{-3}$·week^{-1}) as that of a similarly sized and shaped species of shark *Carcharhinus tilstoni* (G. West, CSIRO Division of Fisheries, GPO Box 1538, Hobart, Tasmania 7001, Australia, personal communication).

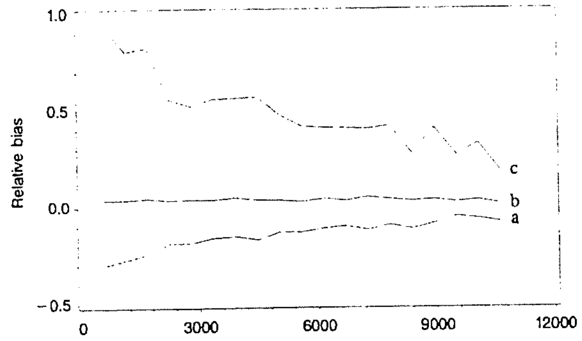
There are many criteria for determining the number of fish releases by area and time, other than relative bias and relative standard error of, and various norms derived from, estimates of all parameters. Two of these are time averages of relative biases of $\hat{N}_{i,a,t}$, which is the expected number of tagged fish in area a at time t, and $\hat{R}_{i,a,t}$, which is the expected number of tags recovered in area a at time t. Also, since the purpose of determining movement rates is usually to improve fisheries management, apart from increasing our knowledge, various summary statistics might be given by such management variables as quotas. Finally, one can examine the absolute bias and absolute standard error of estimates of each parameter and then devise a common criterion for an experimental design. As required, in this application, I used relative bias and relative standard error of estimates of all parameters as measures of their accuracy and precision.

The model parameters are estimated by Nelder and Mead's (1965) simplex method. Only the movement parameters were estimated; catchability coefficients, instantaneous natural mortality, and instantaneous tag shedding rate were fixed and hence not estimated, to save computer time. Regression analyses of the minimum, mean, and maximum of all elements of vector y, i.e., $\min_h (y_h)$, $\operatorname{mean}_h (y_h)$, and $\max_h (y_h)$, and various norms of vector y, i.e.,

$$\|y\|_p = \left(\sum_h |y_h|^p \right)^{1/p},$$

as functions of the number of releases were made, using non-

Fig. 3. Minimum (a), mean (b), and maximum (c) relative bias of estimates of all parameters as functions of the total number of fish releases. ind, individuals.



linear least squares method assuming identically, independently, and normally distributed errors in the dependent variables. Estimates of each parameter were also related, as a first approximation, to its input values and fishing effort in an area through a stepwise regression analysis to examine the interactions between fishing effort and values of input movement rates.

Results

For a max(t) of 157 weeks (i.e., 3 years), the minimum, mean, and maximum relative bias of estimates of all parameters increased, decreased, and decreased towards zero, respectively, with increased number of fish released, each following a power function of the form $S = ax^{-b}$, with a and b being regression parameters estimated by the nonlinear least squares method under the assumption that errors in S follow an independent, identical normal distribution (Fig. 3, Table 2). Three common norms, i.e., absolute norm $|v|_1 = \sum_h |v_h|$, Euclidean norm $|v|_2 = (\sum_h |v_h|^2)^{1/2}$ and maximum norm $|v|_\infty = \max_h |v_h|$, of the relative bias of estimates of all parameters also decreased towards zero as the number of fish released increased, each following a power function (Fig. 4, Table 2). Note that in this case the maximum norm is equivalent to the above maximum relative bias.

Similarly, minimum, mean, and maximum relative standard error of estimates of all parameters all decreased with an increased number of fish released (Fig. 5, Table 2). Absolute, Euclidean, and maximum norms of relative standard error all decreased with an increased number of fish released, again each following a power function (Fig. 6, Table 2). Again, the maximum norm is also equivalent to the above maximum relative standard error.

The relative bias and relative standard error of the estimate of each parameter $\hat{p}_{j,k}$ were related, separately, to input movement rate $p_{j,k}$ and fishing effort $E_{a,t}$ (million m·hook lifts·week^{-1}) through a stepwise multiple linear regression, with the full model of the form $Y = \beta_0 + \beta_1 p_{j,k} + \beta_2 E_{a,t}$, where βs are parameters to be estimated, under the assumption that errors in Y are normally distributed with a mean of $\hat{Y}$ and a (constant) variance of σ^2. For relative bias, the regression analysis yielded $\hat{\beta}_0 = 0.0761$, SE($\hat{\beta}_0$) = 0.0173, $t = 4.393$, $P = 0.0001$; $\hat{\beta}_1 = -0.0521$, SE($\hat{\beta}_1$) = 0.0208, $t = -2.501$, $P = 0.0129$; $\hat{\beta}_2 = -0.2210$, SE($\hat{\beta}_2$) = 0.1209; $t = -1.828$, $P = 0.0685$; $F_{[2,301]} = 4.798$, $P = 0.0089$, $R^2 = 0.0309$, $n = 304$. Although the linear regression model is formally significant (because of the large number of degrees of freedom, 304), from the practical viewpoint, inclusion of both variables is inconsequential ($R^2 = 0.0309$).

For the relative standard error, the stepwise multiple linear regression gave an R^2 value of 0.4465 for $p_{j,k}$ alone, of 0.0041 for $E_{a,t}$ alone, and of 0.4505 for $p_{j,k}$ and $E_{a,t}$ jointly. Thus, the model with $p_{j,k}$ only is appropriate: $\hat{\beta}_0 = 0.8109$, SE($\hat{\beta}_0$) = 0.0260, $t = 31.225$, $P = 0.0001$; $\hat{\beta}_1 = -0.8213$, SE($\hat{\beta}_1$) = 0.0526, $t = -15.607$, $P = 0.0001$; $F_{[1,302]} = 243.590$, $P = 0.0001$, $R^2 = 0.4465$, $n = 304$. Then, the relative standard error of the estimate of each parameter decreased with input movement rate but was not related statistically significantly to fishing effort. In other words, if the movement rate is small, then that parameter is difficult to estimate.

Discussion

The framework developed above for evaluating different experimental designs, combined with an appropriate estimation procedure, provides a systematic basis for selecting the total number of fish released to estimate their movement rates and other model parameters of interest to a chosen accuracy and precision. For example, one can now readily calculate the number of releases for school shark to achieve a chosen level of accuracy and precision. Since the minimum, mean, and maximum of all elements, and various norms, of vector **y** is a power function of the number of releases, of the form $S = ax^{-b}$, there is not an objective criterion for choosing a particular total number of releases that will give a level of accuracy and precision in estimates of various parameters. Thus, one has to decide the value of S first, and then calculate $x = (a/S)^{1/b}$ by substituting appropriate estimates of a and b in Table 2. For a maximum relative standard error of 1.6079, $x = (12.2741/1.6079)^{1/0.2386} = 5000$, which corresponds to a maximum relative bias of $10.7145 \times 5000^{-0.3718} = 0.4516$.

This work also provides information on the performance of Hilborn's (1990) model and estimation procedure. Generally, the degree of relative bias of an estimator depends on the input values of model parameters, the structures of the population dynamics and movement model and the observational model, max(t), error structures of the recapture process, and the definition of a tag group. For this application, the first two possibilities can be excluded because the data used were simulated from specific models. My limited trials suggest that the performance of Hilborn's model and estimation procedure improves as max(t) increases. As shown above, his model and estimation procedure are robust for Poisson-distributed recaptures, whose variance equals their mean. Finally, definition of a tag group will greatly affect the bias: those that reduce data contrast increase relative bias and vice versa. More studies are needed to understand this problem. The mean relative bias was only about 0.0376 (SD = 0.0084) over the range of fish releases tested (560 – 10 640 individuals). Thus, Hilborn's (1990) model and estimation procedure are unbiased, at least for the

Table 2. Minimum, mean, maximum, and three common norms of relative bias (RB) and relative standard error (RSD) of estimates of all parameters as a power function of the number of fish releases of the form $S = a\left(\sum_{i,a,t} T_{i,a,t}\right)^{-b}$, where parameters a and b are estimated by the nonlinear least squares method under the assumption that errors in S are normally distributed with a mean of $\hat{S}$ and a (constant) variance of σ^2.

	Summary statistic	a	b	R^2
RB	Minimum	−5.3967 (1.4202)	0.4394 (0.0340)	0.9708
	Mean	0.0710 (0.0357)	0.0758 (0.0604)	0.9587
	Maximum	10.7145 (2.8164)	0.3718 (0.0334)	0.9786
	$\lvert y\rvert_1$	24.7859 (5.4263)	0.3581 (0.0278)	0.9835
	$\lvert y\rvert_2$	9.3622 (2.4009)	0.3294 (0.0323)	0.9800
	$\lvert y\rvert_\infty$	10.7145 (2.8164)	0.3718 (0.0334)	0.9786
RSD	Minimum	0.0031 (0.0004)	0.0662 (0.0145)	0.9975
	Mean	3.0288 (0.1405)	0.1930 (0.0057)	0.9995
	Maximum	12.2741 (0.9127)	0.2386 (0.0092)	0.9987
	$\lvert y\rvert_1$	48.4611 (2.2473)	0.1930 (0.0057)	0.9995
	$\lvert y\rvert_2$	15.6667 (0.8317)	0.1921 (0.0065)	0.9994
	$\lvert y\rvert_\infty$	12.2741 (0.9127)	0.2386 (0.0092)	0.9987

Note: Values in parentheses are asymptotic standard error. Absolute norm $\lvert y\rvert_1 = \sum_h \lvert y_h\rvert$; Euclidean norm $\lvert y\rvert_2 = \left(\sum_h \lvert y_h\rvert^2\right)^{1/2}$; maximum norm $\lvert y\rvert_\infty = \max_h \lvert y_h\rvert$; $560 \le \sum_{i,a,t} T_{i,a,t} \le 10\,640$; $n = 19$ in all cases. All regressions were significant at $P < 0.0001$.

Fig. 4. Maximum (a), absolute (b), and Euclidean (c) norm of relative bias of estimates of all parameters as functions of the total number of fish releases. ind, individuals.

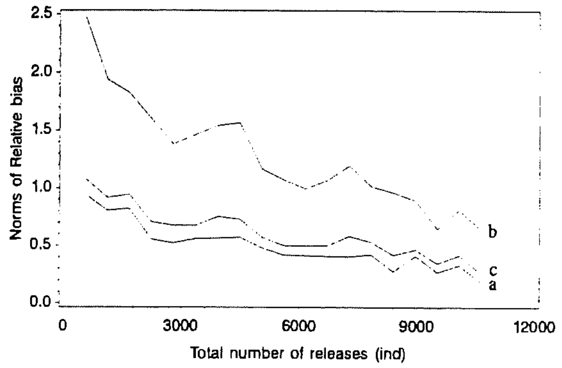


Fig. 5. Minimum (a), mean (b), and maximum (c) relative standard error of estimates of all parameters as functions of the total number of fish releases. ind, individuals.

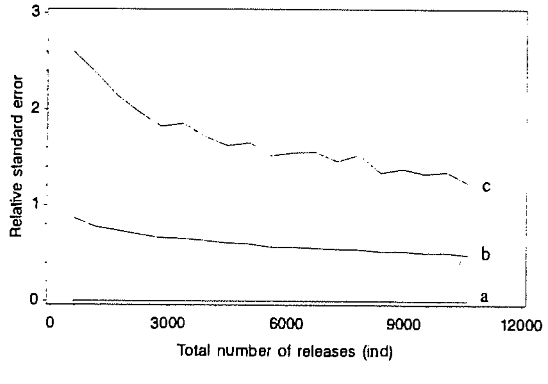
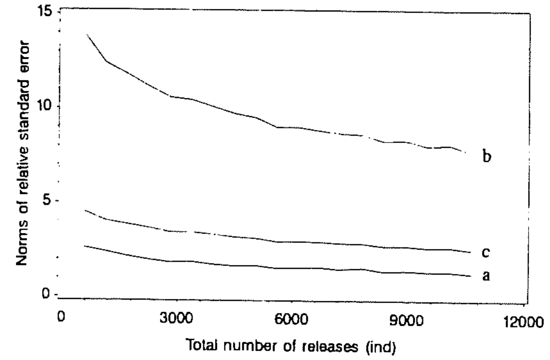


Fig. 6. Maximum (a), absolute (b), and Euclidean (c) norm of relative standard error of estimates of all parameters as functions of the total number of fish releases. ind, individuals.



above application. They are not very precise, however, because the minimum, mean, maximum, and three common norms of relative standard error of estimates of all parameters all do not tend to zero reasonably quickly with an increase in the number of fish releases (Figs. 5 and 6, Table 2). For example, the mean relative standard error varied from about 87% at a release of 560 fish to about 48% at a release of 10 640 fish.

In applying the results from that application and in discussing the merits and problems of Hilborn's (1990) model and estimation procedure, one must realize that the present study has examined only one set of input movement rates, catchability coefficients, and other parameters. Major departures from this set may result in quantitative changes in the conclusions, but qualitative conclusions, such as a decrease in relative standard error with an increase in the number of fish released, should not change. Ideally, one should examine a reasonable range of movement rates and catchability coefficients to determine the sensitivity of those conclusions to their changes. Finally, I have assumed values of catchability coefficients, instantaneous natural mortality rate, instantaneous tag shedding rate, and fishing effort to be known without error, and population dynamics, movement, and observation models to be correct. The results from that application may be overly optimistic.

The value of this work also lies in its insight into experimental designs of tagging experiments for estimating fish movement rates. Hilborn (1990) hypothesized that the best experimental design needs tagging and release to be done in each area, and fishing effort data to be available by time for each area. As shown above, the estimate of each parameter was related to its input value, such that the smaller a movement rate, the more difficult it was to estimate. Thus, to achieve the same or similar relative bias for each movement rate, more fish should be released in areas with low rates of inward and outward movement. Although the above application considered one release pattern only, regression equations may be established between the relative bias and relative standard error of estimates of each parameter Y and its input movement rate $p_{j,k}$, fishing effort $E_{a,t}$, and fish release $T_{i,a,t}$ of the form, say, $Y = \beta_0 + \beta_1 p_{j,k} + \beta_2 E_{a,t} + \beta_3 T_{i,a,t}$, where βs are again parameters to be estimated, under the assumption that errors in Y are identically, independently, and normally distributed with a mean of $\hat{Y}$ and a (constant) variance of σ^2. One may then allocate the total number of fish releases and, if practical, regulate levels of fishing effort to achieve a given level of accuracy and precision of estimates of movement rates. Thus, Hilborn's (1990) hypothesis can be refined as follows: a good experimental design not only needs tagging and release to be done in each area, and fishing effort data to be available by time for each area, but also is a function of the values of input fish movement rates and possibly input fishing effort.

The application can be extended in several ways. Although simple and deterministic patterns of fish release and distribution of fishing effort have been assumed in it, complex patterns can be readily tested with my framework. Thus, one can try a range of values of $p_{j,k}$, $T_{i,a,t}$, $E_{a,t}$, q_a, and γ, but this would usually require a prohibitively large number of trials. Let n be the number of parameters in the model and m the number of values to be evaluated for each parameter, then there are m^n trials to run, for each release pattern. If $n = 16$, then one has $\geq 2^{16} = 65\,536$ trials to do, for a range of values of each parameter (i.e., $m \geq 2$). If one trial needs 1 min to complete, then one would require 45.5 days to evaluate all trials.

A computationally less intensive alternative is to limit the number of trials by assuming a joint distribution for all model parameters. Thus, fishing effort can be treated as a random variable with its errors following certain statistical distributions (e.g., $E_{a,t} \sim \Gamma\,(\bar{E}_{a,t}, \sigma^2_{E_{a,t}})$); movement rates can be assigned appropriate statistical distributions, say, $p_{j,k} \sim \Gamma\,(\bar{p}_{j,k}, \sigma^2_{p_{j,k}})$. Even this would require a substantial amount of computer time. The computation for that application takes about 12 days of central processor unit time to complete on an IBM PC (with a 66-MHz Pentium processor and Lahey FORTRAN 90), when Nelder and Mead's (1965) simplex method is used as a maximizer in the general framework. Therefore, before attempting a simulation, one should assess one's computing capacity.

One can also examine the effects of absence of fishing in one or more areas on, say, the relative bias and relative standard error of parameter estimates. Such effects are clearly important for design of a tagging experiment: if absence of fishing in one area would grossly bias estimated parameters in others, then there is little hope of unbiased estimates from real fisheries, where fishing may be absent in some areas; if it does not have any appreciable effects, one would expect that estimates of parameters are not biased by an absence of fishing in one or more areas. A related problem is to examine the effects of emigration. Failure to consider the whole fish population in a tagging study may affect the reliability of estimates of movement rates, if these estimates are biased by this process. Intuitively, the fewer data one has about a whole picture, the more prone one is to chance events. It might well be that the more areas considered, the less the bias. If so, certain estimates of movement rates would be biased. To avoid such bias, a tagging program should cover as wide an area as possible, should not be undertaken lightly, and must be based on sufficient information about fish distribution. Therefore, the effects of fish emigration should be examined.

Finally, experimental designs to estimate size- or sex-dependent movement rates can be realized by following my framework. One can obtain a separate set of estimates of movement rates for each sex or size group, from which differences in movement rates between sexes and sizes can be examined. One can also estimate each movement rate as an explicit function of fish size or sex. The second approach is preferred for three reasons. First, division into, say, fish larvae, juveniles, and adults involves arbitrary decisions. Within each group, there may also be considerable size variations. Treatment of a movement rate as an explicit function of fish size gives an objective decision, where size is seen as a continuous variable. Second, it is statistically desirable, because size- and (or) sex-dependent movement rates are estimated in a single framework, with movement rates as functions of size and (or) sex. If well determined, they allow predictions to be made for all sizes within the size range studied. Third, it does not require as many data as the first approach. Obviously, the requirement for more releases and hence recaptures is relatively large for estimating size- and (or) sex-mediated movement rates. If reliable estimation of movement rates for males requires a release of 1000 fish, then a release of roughly 2000 is required for both males and females if their movement rates are different from those of males. Thus, twice as many fish must be released to estimate movement rates by sex. The same argument applies to fish sizes. To be able to detect size-related differences, one has to recognize at least two size groups and to estimate two sets of movement rates; again, one needs at least twice as many releases as for one size group only. As the number of size groups increases, the increase in the requirement for the number of releases follows arithmetic progression, if the first approach is adopted. However, use of the second approach will usually substantially reduce the number of releases if many size groups are involved. This is because a couple of parameters may well describe some of those differences.

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Appendix 2. Tag display package SHARKTAG

Computer Software Tool for Displaying Tag Release–Recapture Data from the Australian Southern Shark Fishery.

Bruce Taylor

Marine and Freshwater Resources Institute
P.O. Box 114, Queenscliff, Victoria 3225 Australia

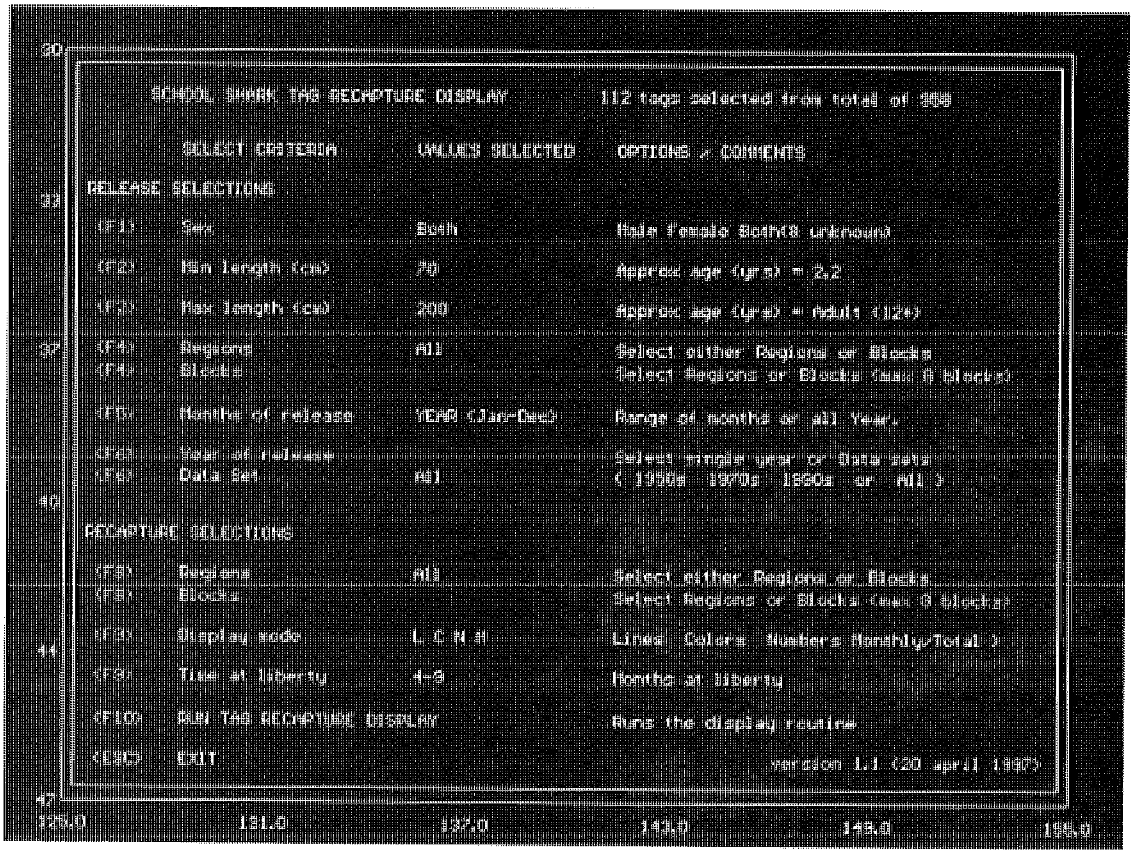
A computer software package SHARKTAG is used for displaying selected subsets of shark tag release–recapture data available in the Southern Shark Tag Database for the period 1947–96. The package is used for selecting subsets of data from files produced from the Tag Database and then displaying release and recapture fishing blocks, time at liberty and distance travelled.

The tag release-recapture data for display can be selected by:

sex
a range of length on release (minimum and maximum lengths)
region(s) or block(s) of release
month(s) of release
year(s) or period of release
region(s) or block(s) of release
region(s) or block(s) of recapture
a range of time at liberty (first and last months)

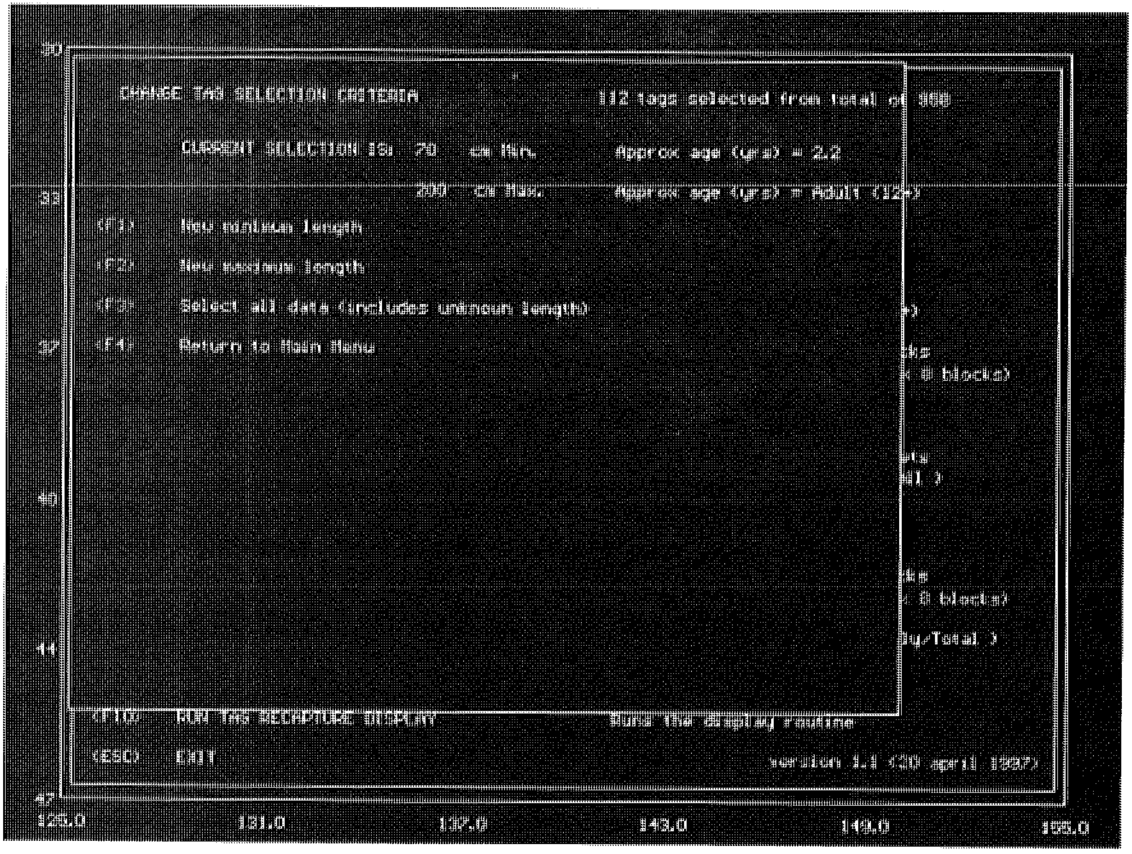
The selected options are clearly documented on the screen (Figure A2.1) as are the values of the selection criteria. These options can be readily changed interactively (Figure A2.2).

Coloured tag lines join the tag-release cell and the tag-recapture cell and can be shown growing by month to give an impression of relative movement. In addition, the number of recaptured tagged sharks in each cell can be displayed by colour code or number. These can be displayed by month (Figure A2.3) or as the final result (Figures A2.4 and A2.5).



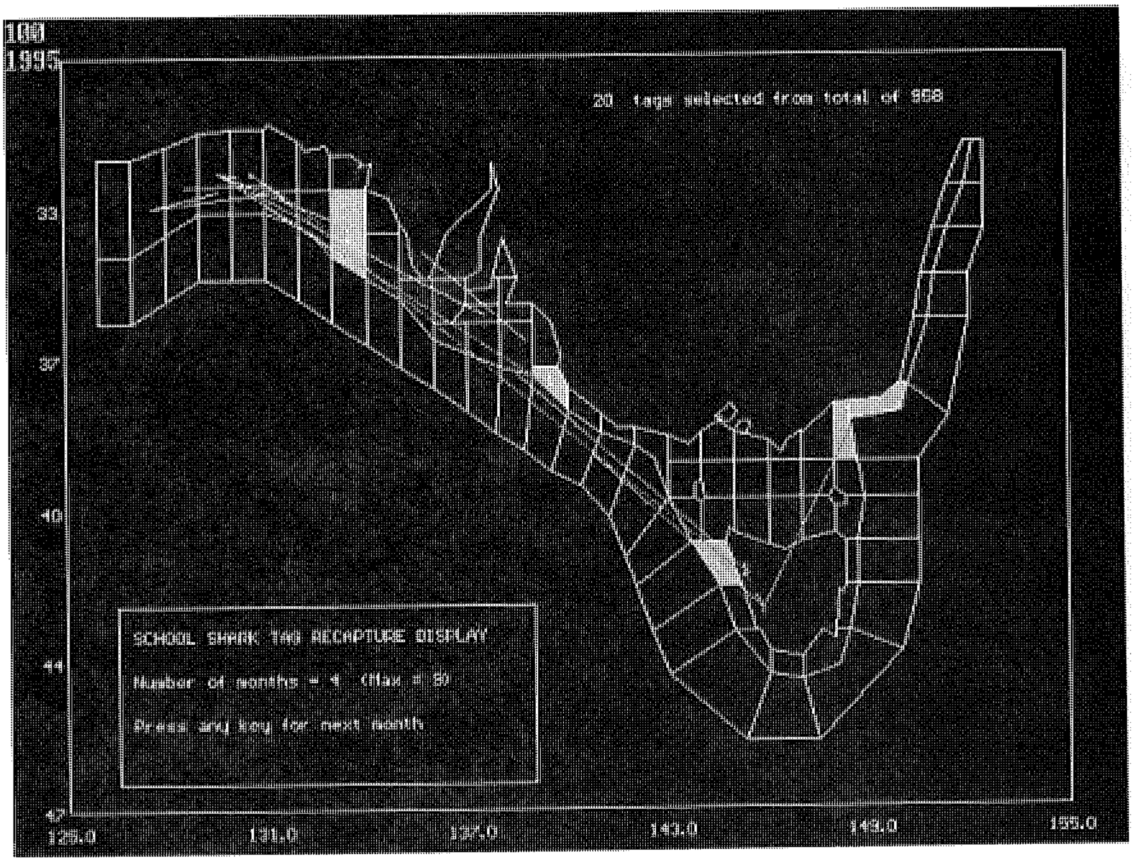
```
      SCHOOL SHARK TAG RECAPTURE DISPLAY        112 tags selected from total of 388

          SELECT CRITERIA       VALUES SELECTED   OPTIONS / COMMENTS
RELEASE SELECTIONS
 (F1)     Sex                   Both              Male Female Both(8 unknown)

 (F2)     Min length (cm)       70                Approx age (yrs) = 2.2

 (F3)     Max length (cm)       200               Approx age (yrs) = Adult (12+)

 (F4)     Regions               All               Select either Regions or Blocks
 (F4)     Blocks                                  Select Regions or Blocks (max 8 blocks)

 (F5)     Months of release     YEAR (Jan-Dec)    Range of months or all Year.

 (F6)     Year of release                         Select single year or Data sets
 (F6)     Data Set              All               ( 1950s  1970s  1990s  or  All )

RECAPTURE SELECTIONS

 (F8)     Regions               All               Select either Regions or Blocks
 (F8)     Blocks                                  Select Regions or Blocks (max 8 blocks)

 (F8)     Display mode          L C N M           Lines  Colors  Numbers Monthly/Total )

 (F9)     Time at liberty       4-9               Months at liberty

 (F10)    RUN TAG RECAPTURE DISPLAY               Runs the display routine

 (ESC)    EXIT                                          version 1.1 (20 april 1997)
```

Figure A2.1. Main menu and selection options



```
   CHANGE TAG SELECTION CRITERIA               112 tags selected from total of 388

          CURRENT SELECTION IS:  70   cm Min.     Approx age (yrs) = 2.2
                                 200  cm Max.     Approx age (yrs) = Adult (12+)
 (F1)     New minimum length

 (F2)     New maximum length

 (F3)     Select all data (includes unknown length)

 (F4)     Return to Main Menu

 (F10)    RUN TAG RECAPTURE DISPLAY               Runs the display routine

 (ESC)    EXIT                                          version 1.1 (20 april 1997)
```

Figure B2. Change menu for length at release



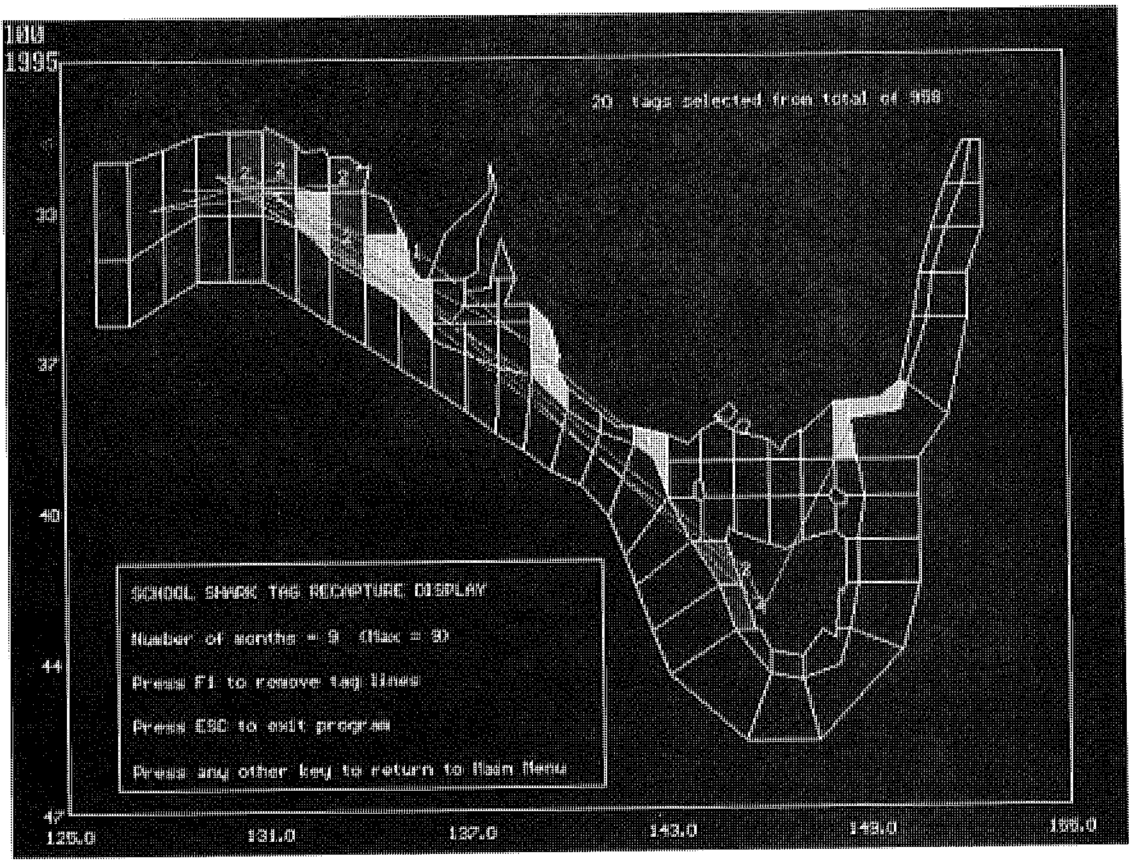
20 tags selected from total of 988

SCHOOL SHARK TAG RECAPTURE DISPLAY

Number of months = 4 (Max = 9)

Press any key for next month

Figure A2.3. Display screen showing early recaptures



20 tags selected from total of 988

SCHOOL SHARK TAG RECAPTURE DISPLAY

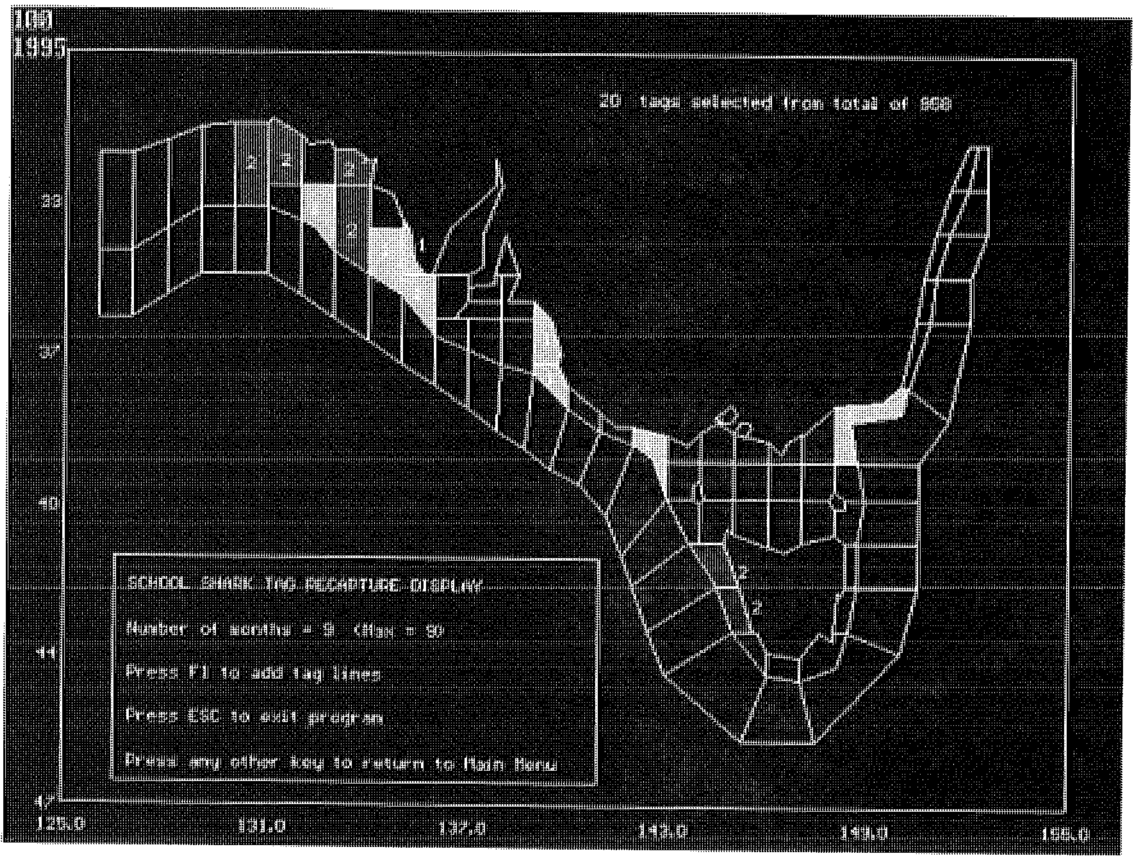
Number of months = 9 (Max = 9)

Press F1 to remove tag lines

Press ESC to exit program

Press any other key to return to Main Menu

Figure A2.4. Display screen showing tag release-recapture patterns



20 tags selected from total of 808

SCHOOL SHARK TAG RECAPTURE DISPLAY

Number of months = 9 (Max = 90)

Press F1 to add tag lines

Press ESC to exit program

Press any other key to return to Main Menu

Figure A2.5. Display screen showing recapture patterns only

Appendix 3. Movement Modelling Shell SSMOVE

Movement Modelling Shell for School Shark (Galeorhinus galeus) in the Australian Southern Shark Fishery:

A users guide to SSMOVE (Version 1)

Bruce Taylor

Marine and Freshwater Resources Institute
P.O. Box 114, Queenscliff, Victoria 3225 Australia

Introduction

SSMOVE is a computer program for displaying changing distribution patterns of a shark population for any assumed movement parameters within the basic framework of a movement model. The user can represent alternative hypotheses of movement and explore the implications of varying the movement parameters. These in turn can be used for determining alternative movement rates for spatially disaggregated stock assessment models. These rates will be eventually compared with broad level rates estimated from analysis of the tagging data.

The underlying model

The movement parameters driving the model are the relative numbers of sharks remaining in each fishing block or moving in each direction to an adjoining block each day. Overall movement of a population is achieved by setting movement greater in one direction than in the opposite direction.

Version 1 of the computer program is currently set up to display two basic movement patterns—one for juveniles and the other for adults. The juvenile model investigates the movement of juvenile school shark from east to west. It assumes that 0–2 year old sharks remain near the nursery grounds of Bass Strait and eastern Tasmania. The 3–9 year olds move westward, slowly at first and, then more rapidly, to western South Australia. The model allows two different movement rates to be considered jointly (a 'slow' rate and a 'fast' rate)

The adult model has two 'adult' areas—one in western SA (west of Port Lincoln) and the other in Bass Strait. The proportion of the population in each area can be altered. The breeding adults move from western South Australia east to Bass Strait during spring and then move back to western South Australia during autumn.

Running the program

The program and data files are supplied on floppy disk. The files ssmove.exe, au_cell1.dat and au_cell2.dat are needed to run the program. The documentation (without the figures) is in ssmove.doc in Word6 format. SSMOVE was developed on a 486DX–33 computer where its speed is acceptable. It runs faster on a Pentium-75. It may run slowly on earlier computers.

SSMOVE runs directly under DOS. To install SSMOVE on a hard disk from a floppy disk, type **a:setup**. It can also be run from the floppy disk. Type **ssmove** to begin the program.

From the first menu (Figure A3.1), either a model can be run or another menu chosen. The juvenile models run a year at a time and then pause until any key is pressed before running the following year. The model can be exited at this stage by pressing the Esc key. The adult model runs for one year. The adult migration display is every 6 days while all other models display every month where there are 30 'days' in each month.

When the models are run, the colour scale is shown in the lower box, while the movement parameters for the slower group (juveniles) or circulating group (adults) are shown in the upper box. The behaviour of the model is altered by changing the movement values using the Change Movement Values menu (Figure A3.2).

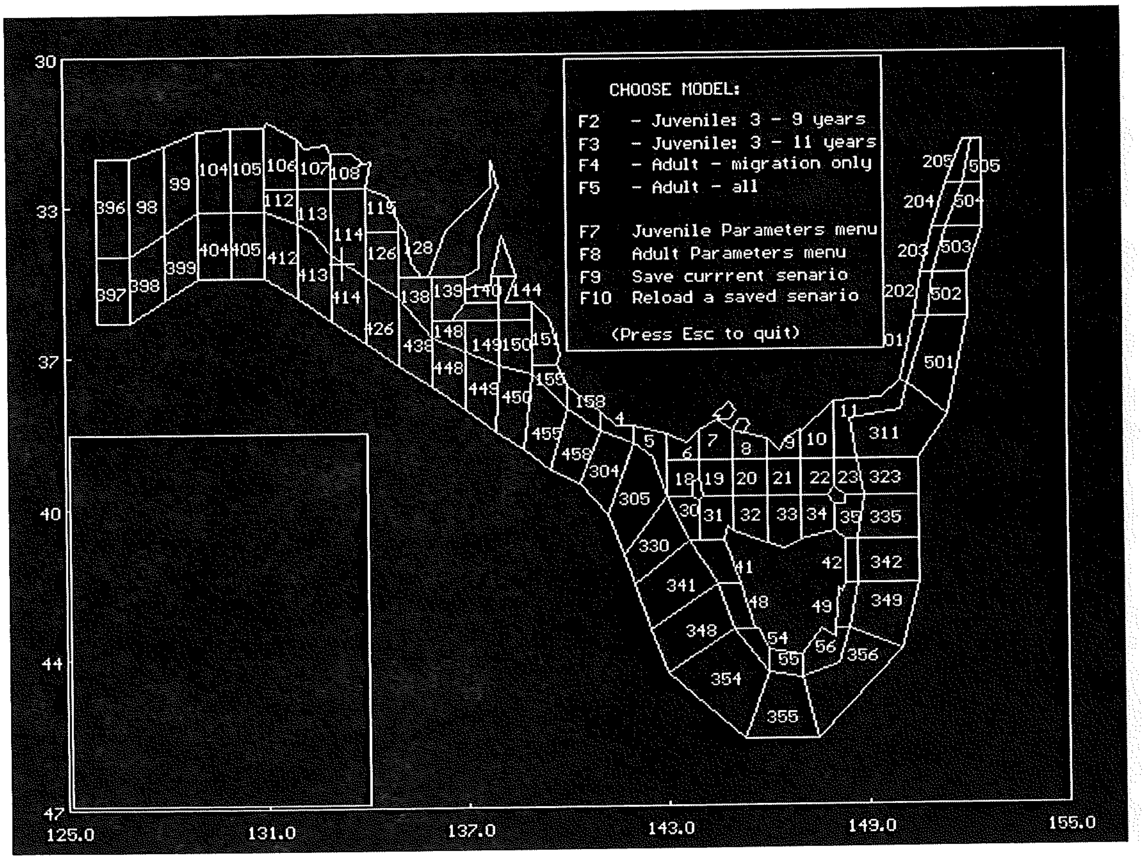
User defined parameters

The Change Movement Values menus (Figures A3.3 and A3.4) display the current movement values for the juvenile or adult models and allow them to be changed, saved or recalled. The values displayed in yellow can be changed. The initial values are also displayed as a reference point.

Enhancements

Some of the possible extensions that can be added are outlined below. This list needs to be amended then sorted into priorities for implementation.

Output of movement rates from a given cell after a month (Version 1a).
Off continental shelf (cryptic) population added.
Juveniles remaining in Bass Strait, just as some adults remain.
NSW population added.
Output or display of movement probabilities from a given cell after a several months.
Ability to redefine the initial distribution at 3 years of age.
Include provision for habitat effects, which need to be defined.
Display regional population (on a subscreen).
Total numbers of all age-classes on a single display.
Subscreen for numbers by age when total number of all ages is on main screen.



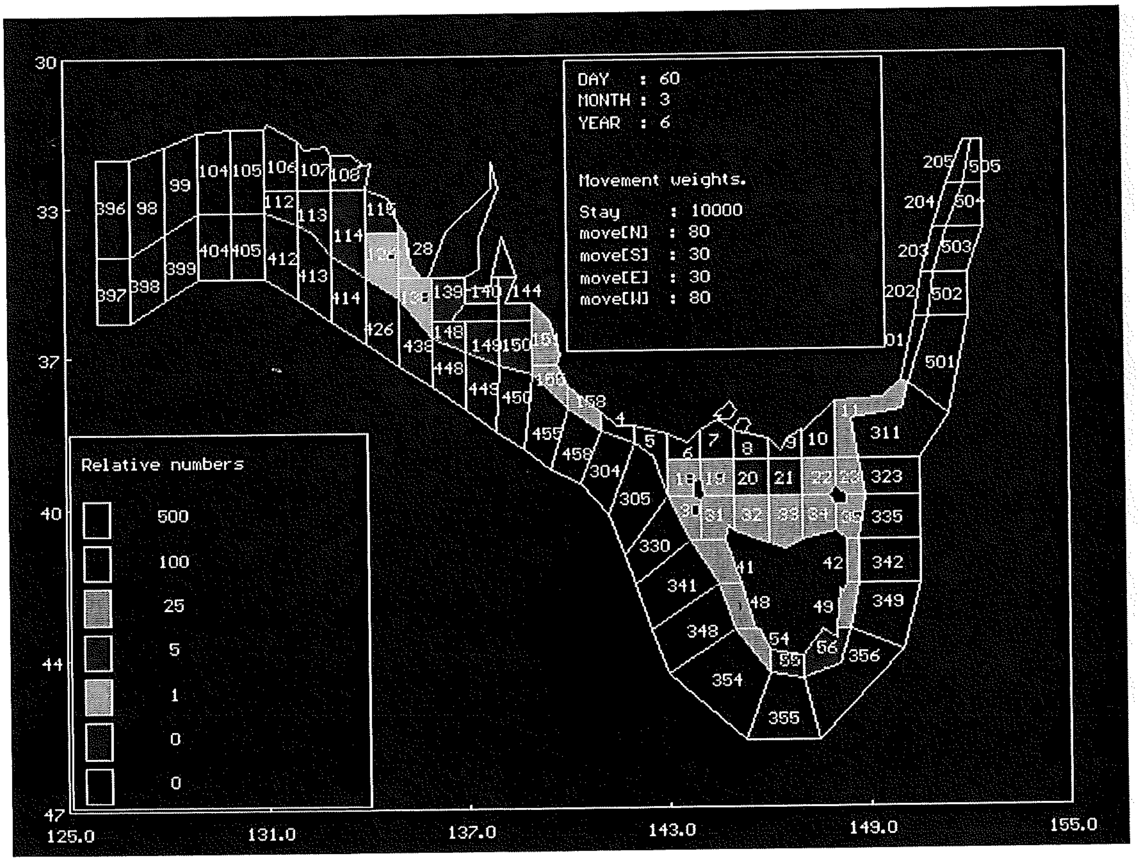
CHOOSE MODEL:

F2 - Juvenile: 3 - 9 years
F3 - Juvenile: 3 - 11 years
F4 - Adult - migration only
F5 - Adult - all

F7 Juvenile Parameters menu
F8 Adult Parameters menu
F9 Save currrent senario
F10 Reload a saved senario

(Press Esc to quit)

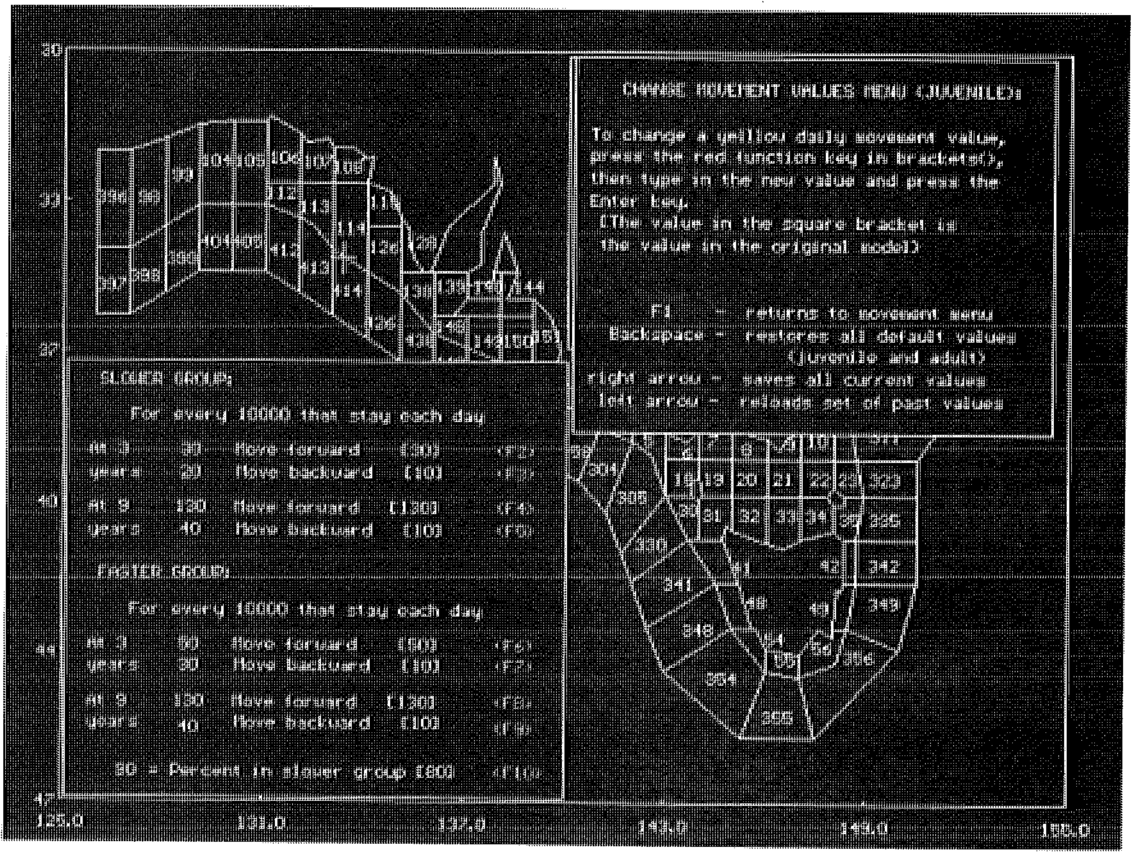
Figure A3.1. Initial menu



DAY : 60
MONTH : 3
YEAR : 6

Movement weights.
Stay : 10000
move[N] : 80
move[S] : 30
move[E] : 30
move[W] : 80

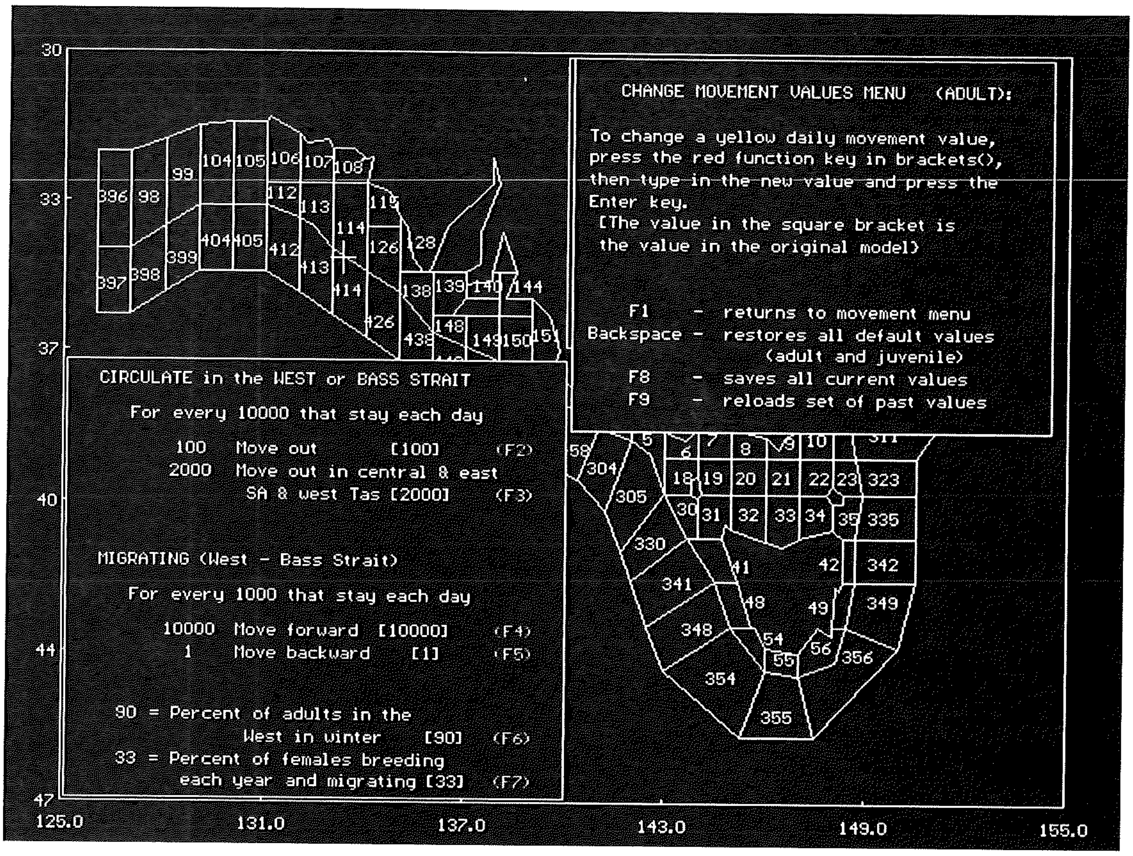
Figure A3.2. Juvenile model running



```
CHANGE MOVEMENT VALUES MENU (JUVENILE):

To change a yellow daily movement value,
press the red function key in brackets(),
then type in the new value and press the
Enter key.
 [The value in the square bracket is
 the value in the original model)


     F1     -  returns to movement menu
 Backspace  -  restores all default values
                  (juvenile and adult)
right arrow -  saves all current values
 left arrow -  reloads set of past values
```

```
SLOWER GROUP:

     For every 10000 that stay each day

At 3     30   Move forward    [30]     (F2)
years    20   Move backward   [10]     (F3)

At 9     130  Move forward   [130]     (F4)
years    40   Move backward   [10]     (F5)

FASTER GROUP:

     For every 10000 that stay each day

At 3     90   Move forward    [90]     (F6)
years    30   Move backward   [10]     (F7)

At 9     130  Move forward   [130]     (F8)
years    40   Move backward   [10]     (F9)

   80 = Percent in slower group [80]   (F10)
```

Figure A3.3. Menu for changing juvenile parameters



```
CHANGE MOVEMENT VALUES MENU   (ADULT):

To change a yellow daily movement value,
press the red function key in brackets(),
then type in the new value and press the
Enter key.
 [The value in the square bracket is
 the value in the original model)


     F1     -  returns to movement menu
 Backspace  -  restores all default values
                  (adult and juvenile)
     F8     -  saves all current values
     F9     -  reloads set of past values
```

```
CIRCULATE in the WEST or BASS STRAIT

   For every 10000 that stay each day

     100   Move out          [100]      (F2)
    2000   Move out in central & east
              SA & west Tas [2000]      (F3)

MIGRATING (West - Bass Strait)

   For every 1000 that stay each day

   10000   Move forward  [10000]        (F4)
       1   Move backward     [1]        (F5)

  90 = Percent of adults in the
              West in winter     [90]   (F6)
  33 = Percent of females breeding
       each year and migrating [33]     (F7)
```

Figure A3.4. Menu for changing adult parameters

Initial parameters

Juveniles

These values are linearly interpolated for ages from 4 to 8 years (e.g. at age 6 years, the value is midway between the 3 and 9 years values)

'Slower' group
For every 10000 sharks remaining in a block each day,
at 3 years, 30 move forward in each direction (north or west)
at 9 years, 130 move forward (north or west)
at 3 years, 20 move backward (south or east)
at 9 years, 130 move backward (south or east)
'Faster' group
For every 10000 sharks remaining in a block each day,
at 3 years, 50 move forward in each direction (north or west)
at 9 years, 130 move forward (north or west)
at 3 years, 30 move backward (south or east)
at 9 years, 130 move backward (south or east)

Adults

Circulating in western SA or in Bass Strait
For every 10000 sharks remaining in a block each day,
100 move out in each direction

Circulating in eastern central SA, eastern SA or western Tas
For every 10000 sharks remaining in a block each day,
2000 move out in each direction

The adults in western SA during winter are 80 per cent of the total.

Adult Migration

Migrating between western SA and Bass Strait
For every 1000 sharks remaining in a block each day,
10000 move forward
1 moves backward

The percentage of females breeding each year (and migrating) is 33 per cent.

Migration dates are fixed in Version 1 but will be changeable in Version 2.

16 August	Beginning of migration eastward
1 October	Peak of migration eastward
1 November	End of migration eastward
1 March	Beginning of migration westward
16 April	Peak of migration westward
30 May	End of migration westward

Appendix 4. Estimation of tag shedding rates

Abstract.–Fish and other animals are often tagged to estimate their abundance as well as rates of growth, fishing mortality, natural mortality, and movement. Results of these studies are biased if tags are not retained permanently and if tag loss is not taken into account. In this paper, we develop a simple tag shedding model to account for the effects of time at liberty, sex, and other factors and use one of its special cases to estimate the instantaneous tag shedding rate from data based on two double-tagging experiments on the school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, off southern Australia. For either species, tag shedding rate could vary with tag type, position of tag on fish, and sex of fish, but not with length at release or time at liberty. The shedding rate of Petersen disc fin tags was well above 50%/yr. Dart tags were shed at a higher rate (41%/yr for school shark; 63%/yr for gummy shark) than either "Roto" or "Jumbo" fin tags (8%/yr for school shark; 6%/yr for gummy shark). For either species of shark, the shedding rate of dart tags anchored in the basal cartilage of the dorsal fin was about half that of dart tags anchored in the dorsal musculature.

Estimation of instantaneous rates of tag shedding for school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, by conditional likelihood

Yongshun Xiao
CSIRO Division of Marine Research
GPO Box 1538, Hobart, Tasmania 7001, Australia
Present address: South Australian Aquatic Sciences Centre
SARDI, 2 Hamra Avenue, West Beach, South Australia 5024, Australia
E-mail address: xiao.yongshun@pi.sa.gov.au

Lauren P. Brown
Terence I. Walker
Marine and Freshwater Resources Institute
PO Box 114, Queenscliff, Victoria 3225, Australia

André E. Punt
CSIRO Division of Marine Research
GPO Box 1538, Hobart, Tasmania 7001, Australia

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Tags are markers placed on or in animals to identify an individual. Animals are tagged to estimate their abundance as well as rates of growth, fishing mortality, natural mortality, and movement. In many studies, a tagged animal is assumed to retain its tag permanently. This assumption, however, is not valid for certain types of tags. Consequently, many attempts have been made to estimate tag shedding rates (e.g. Davis and Reid, 1982; Francis, 1989; Faragher and Gordon, 1992; Treble et al., 1993; Hampton, 1996; Xiao, 1996a).

Tag shedding models are of three main types; all are based on Beverton and Holt's (1957, p. 205, equations 14.32–14.37) model for a double-tagging experiment. Some models are conditional on the number of recaptured fish with a single tag, as well as the number of recaptured fish with both tags as a function of time at liberty, and use the least squares method (Gulland, 1955, 1963; Chapman, 1961; Paulik, 1963; Chapman et al., 1965; Bayliff and Mobrand, 1972; Russell, 1980; Kirkwood, 1981; Alt et al., 1985) or more generally the maximum likelihood method (Robson and Regier, 1966; Seber, 1973; Seber and Felton, 1981; Wetherall, 1982; Kremers, 1988; Fabrizio et al., 1996) for estimation of parameters. Other models are conditional on the number of recaptured fish retaining at least one tag as a function of time at liberty and on the exact times at liberty (Wetherall, 1982). Use of these types of models in data analysis requires grouping recaptured fish by time at liberty because of an insufficient number of recaptures for a particular (exact) time at liberty, especially in small-scale tagging experiments. Still other models are conditional only on the exact times at liberty (Kirkwood and Walker, 1984; Hampton and Kirkwood, 1989; Hearn et al., 1991; Xiao, 1996a). These models 1) use the exact times at liberty in model fitting, 2) use probabilities of tag retention directly rather than using the often statistically undesirable ratios as the dependent variable in regression analysis, 3) apply to both small (but see below) and large numbers of recaptures, and 4) yield estimates of tag shedding rates independent of instantaneous fishing mortality, natural mortality, and mortalities due to all other causes. Almost all previous tag shedding models have considered only the effects of fish time at liberty on shedding rates, ignoring effects of other equally or potentially more important factors, such as fish sex and size.

School shark *Galeorhinus galeus* (Linnaeus) and gummy shark *Mustelus antarcticus* (*sensu* Last and Stevens, 1994) are major species in the Australian southern shark fishery—a commercial fishery that extends from Western Australia through South Australia to Bass Strait and Tasmania in the east and that has an annual landed value of $A15.6 million (Walker et al., 1996). Two tagging studies were undertaken to study the growth (Moulton et al., 1992), natural mortality (Grant et al., 1979), and local movements of these two species within Bass Strait and off eastern Tasmania (T. I. Walker, Marine and Freshwater Resources Institute, PO Box 114, Queenscliff, Vic 3225 Australia, unpubl. data). These studies suggest that school shark are highly migratory, compared with gummy shark, but they provide little quantitative information about their rates of movements beyond these areas, where most sharks were tagged and released. Also, fishing effort was too poorly documented at the time of Grant et al.'s (1979) tagging program (1940s and 1950s) to be adequate for quantifying the rates of movement for these two species. Finally, predominant use of gill nets with large mesh sizes (8 inches) off the southern coast of Western Australia and off South Australia at the time of T.I. Walker's tagging study (1970s) led to a low level of fishing effort and a small number of recaptures. Such a lack of quantitative information on rates of movement hampered stock assessment. Consequently, a large-scale tagging experiment was designed (Xiao, 1996b) and implemented to fill in this gap. In that study, thousands of individuals were released; each individual was tagged with an easily attachable and highly visible external tag (a Roto tag or a dart tag), the shedding rate of which was to be determined through an accompanying double-tagging experiment (see below).

In this paper, we develop a simple tag shedding model to account for the effects of fish sex, size, and factors other than time at liberty and use a special case to estimate the instantaneous tag shedding rate for the two species of sharks.

Materials and methods

Tagging experiments

Two double-tagging experiments were performed on *G. galeus* and *M. antarcticus*. In the first experiment (Olsen, 1953; Walker, 1989; Table 1), a total of 2597 school and 363 gummy sharks with a respective total length range of 31–164 (85 ±43, n=2586) cm and 32–179 (102 ±24, n=362) cm were captured by longline hooks, measured to the nearest centimeter, tagged with an internal and external tag, and released in inshore waters off Victoria, South Australia, and Tasmania, Australia, from 22 May 1949 to 10 July 1954. Internal tags were either 50 mm long and 23 mm wide (J-tag), or 50 mm long and 22 mm wide (L-tag), or 35 mm long and 10 mm wide (S-tag) and were inserted into the body cavity through an incision on the left flank parallel to the muscles in the lower half of the body immediately below the posterior half of the first dorsal fin. External tags were a white (W-tag) or gray Petersen disc (G-tag); both were 16 mm in diameter and 1 mm thick and were placed in the midcentral part of the first dorsal fin. Of those released, 417 school and 20 gummy sharks were recaptured within 42.5 years. Their respective total length at recapture ranged from 43 to 175 (127 ±35, n=267) cm and from 83 to 152 (125 ±19, n=12) cm; their respective times at liberty ranged from 31 to 15,510 (2761 ±2758, n=417) d, and from 52 to 3900 (1771 ±1159, n=20) d.

In the second double-tagging experiment (Table 2), as part of a major tagging experiment (see above), 291 school and 731 gummy sharks with a respective total length range of 38–168 (134 ±17, n=291) cm and 40–176 (108 ±20, n=729) cm were captured in gill nets, measured to the nearest millimeter, tagged with two external tags (a Roto tag and a dart tag) either in the lower half or basal cartilage of the first dorsal fin, and released off southern Australia, from 15 December 1993 to 24 April 1996. Two types of Roto tags were used: either a 45-mm-long and 18-mm-wide Jumbo (Roto) tag, or a 36-mm-long and 9-mm-wide Roto tag (Daltons of New South Wales, Australia). The dart tag was 95 mm long and 2 mm in diameter (Hallprint of South Australia, Australia). As of 1 May 1997, 48 school and 207 gummy sharks were recaptured. Their respective total length at recapture ranged from 85 to 179 (135 ±18, n=38) cm and from 66 to 167 (115 ±17, n=150) cm; their respective times at liberty ranged from 31 to 633 (269 ±163, n=48) d, and from 1 to 1138 (275 ±244, n=207) d.

Table 1

Description of the first double-tagging experiment for gummy and school sharks. The number of recaptures includes, consecutively and in parentheses, that with two tags, with tag A only, and with tag B only; "—" indicates unknown or not computable.

Row	Species	Tag A	Tag B	Sex	Number released	Mean length at release (cm)	Length range at release (cm)	Number recaptured	Mean length at recapture (cm)	Length range at recapture (cm)	Mean time at liberty (d)	Range of time at liberty (d)
1	gummy	L-tag	W-tag	M	11	110 ±07	99–122	—	—	—	—	—
2	gummy	L-tag	W-tag	F	1	90 ± –	90–090	—	—	—	—	—
3	gummy	L-tag	G-tag	M	128	108 ±12	79–144	6(0,6,0)	131 ±16	114–145	2224 ±1154	1209–3900
4	gummy	L-tag	G-tag	F	129	112 ±20	77–179	13(0,13,0)	128 ±15	106–152	1698 ±1104	80–3531
5	gummy	S-tag	W-tag	M	32	86 ±28	33–136	—	—	—	—	—
6	gummy	S-tag	W-tag	F	14	65 ±20	38–102	—	—	—	—	—
7	gummy	S-tag	G-tag	M	27	88 ±22	39–119	1(0,1,0)	83 ±–	83–083	52 ± –	52–52
8	gummy	S-tag	G-tag	F	21	63 ±25	32–117	—	—	—	—	—
9	school	J-tag	W-tag	M	59	127 ±26	62–154	18(2,15,1)	146 ±11	125–155	5039 ±4369	705–15251
10	school	J-tag	W-tag	F	41	128 ±33	60–164	14(1,13,0)	152 ±15	113–167	3260 ±2333	319–8380
11	school	L-tag	W-tag	M	32	145 ±07	116–160	7(1,6,0)	155 ±14	143–174	4382 ±3142	841–9539
12	school	L-tag	W-tag	F	15	148 ±15	106–160	4(0,4,0)	161 ±08	155–167	3809 ±5548	546–12114
13	school	L-tag	G-tag	—	4	137 ±18	112–155	2(0,2,0)	152 ±–	152–152	2971 ±0769	2427–3515
14	school	L-tag	G-tag	M	521	141 ±12	71–163	127(4,123,0)	147 ±12	114–175	3858 ±3100	82–15510
15	school	L-tag	G-tag	F	292	137 ±17	73–164	71(6,65,0)	149 ±12	112–167	3142 ±2341	89–9107
16	school	S-tag	W-tag	—	2	67 ±09	60–073	—	—	—	—	—
17	school	S-tag	W-tag	M	14	48 ±06	40–057	2(0,2,0)	83 ±–	83–083	2652 ±2456	915–4389
18	school	S-tag	W-tag	F	14	54 ±06	43–065	5(0,5,0)	107 ±40	57–141	2566 ±1944	260–5262
19	school	S-tag	G-tag	—	15	57 ±12	32–067	2(1,1,0)	—	—	377 ±0434	70–684
20	school	S-tag	G-tag	M	781	54 ±13	31–148	86(7,79,0)	97 ±35	43–159	1568 ±1604	31–7555
21	school	S-tag	G-tag	F	807	53 ±12	31–148	79(13,64,2)	95 ±33	51–159	1221 ±1512	35–6200

Table 2

Description of the second double-tagging experiment for gummy and school sharks. The number of recaptures includes, consecutively and in parentheses, that with two tags, with tag A only, and with tag B only. "—" indicates unknown or not computable; tagging position refers to tag B's position.

Row	Species	Tag A	Tag B	Tagging position	Sex	Number released	Mean length at release (cm)	Length range at release (cm)	Number recaptured	Mean length at recapture (cm)	Length range at recapture (cm)	Mean time at liberty (d)	Range of time at liberty (d)
1	gummy	Jumbo	dart	fin	M	68	115 ±08	97–140	13(9,3,1)	117 ±08	107–130	192 ±119	64–386
2	gummy	Jumbo	dart	fin	F	66	125 ±21	80–176	19(17,1,1)	122 ±10	108–145	119 ±083	13–309
3	gummy	Jumbo	dart	muscle	M	101	109 ±14	87–144	41(22,19,0)	112 ±14	86–148	278 ±232	5–818
4	gummy	Jumbo	dart	muscle	F	164	119 ±21	68–175	43(19,24,0)	123 ±20	91–167	340 ±273	6–1138
5	gummy	Roto	dart	muscle	—	1	106 ± –	106–106	1(0,1,0)	—	—	83 ± –	83–83
6	gummy	Roto	dart	muscle	M	151	96 ±18	45–135	37(20,15,2)	106 ±17	66–148	309 ±262	2–1059
7	gummy	Roto	dart	muscle	F	180	99 ±18	40–136	53(26,26,1)	112 ±14	78–138	278 ±256	1–886
8	school	Jumbo	dart	fin	M	46	135 ±14	108–168	3(3,0,0)	136 ±13	123–149	136 ±089	34–202
9	school	Jumbo	dart	fin	F	81	139 ±12	108–167	15(11,3,1)	141 ±12	110–157	306 ±130	123–546
10	school	Jumbo	dart	muscle	M	77	134 ±11	100–158	12(9,2,1)	140 ±20	107–179	263 ±201	33–633
11	school	Jumbo	dart	muscle	F	53	140 ±14	100–164	9(6,3,0)	142 ±10	122–155	272 ±179	31–551
12	school	Roto	dart	muscle	M	13	108 ±23	71–152	3(3,0,0)	110 ±22	85–124	317 ±164	146–474
13	school	Roto	dart	muscle	F	21	110 ±29	38–160	6(2,4,0)	115 ±15	100–136	229 ±172	34–468

Model

Consider a (single) fish i that is captured, double tagged, and released at time $t_0(i)$. The index i can be used to examine the effects of any factor on the instantaneous tag shedding rate. Let A and B indicate the two types of tags and

$P(i,A,B,t(i))$ = probability of retaining both tags at time $t(i)$;
$P(i,A,0,t(i))$ = probability of retaining only tag A at time $t(i)$;
$P(i,0,B,t(i))$ = probability of retaining only tag B at time $t(i)$;
$P(i,0,0,t(i))$ = probability of retaining neither tag at time $t(i)$;
$\dot{C}(i,A,B,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained both tags;
$\dot{C}(i,A,0,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained only tag A;
$\dot{C}(i,0,B,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained only tag B;
$\dot{C}(i,0,0,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained neither tag;
$\dot{U}(i,A,B,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained both tags;
$\dot{U}(i,A,0,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained only tag A;
$\dot{U}(i,0,B,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained only tag B;
$\dot{U}(i,0,0,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained neither tag;
$\dot{D}(i,A,B,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained both tags;
$\dot{D}(i,A,0,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained only tag A;
$\dot{D}(i,0,B,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained only tag B;
$\dot{D}(i,0,0,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained neither tag;
$\pi(i)$ = probability that it remains alive after type-I mortality (i.e. mortality due to the immediate effects of tagging and handling);
$\rho(i,j)$ = probability that it retains tag j ($j=A,B$) after type-I shedding (i.e. tag shedding due to the immediate effects of tagging and handling);
$F(i,t(i))$ = instantaneous rate of fishing mortality at time $t(i)$;
$M(i,t(i))$ = instantaneous rate of natural mortality at time $t(i)$;
$R(i,A,B,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained both tags;
$R(i,A,0,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained only tag A;
$R(i,0,B,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained only tag B;
$R(i,0,0,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained neither tag;
$\lambda(i,A,t(i))$ = instantaneous shedding rate of tag A at time $t(i)$; and
$\lambda(i,B,t(i))$ = instantaneous shedding rate of tag B at time $t(i)$.

We assume that, in the time interval $[t(i),t(i)+\Delta t]$, the probability that fish i retaining both tags is caught is $F(i,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, the probability that it is dead is $M(i,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, the probability that it sheds tag A is $\lambda(i,A,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, and the probability that it sheds tag B is $\lambda(i,B,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, where $O(\Delta t)\to 0$ as $\Delta t\to 0$. It is also assumed that these events are independent with no more than one event occurring in the time interval. Under these assumptions, the probability that fish i retains both tags at time $t(i)+\Delta t$ given that it has retained both tags at time $t(i)$ is given by

$$P(i,A,B,t(i)+\Delta t)=[1-F(i,t(i))\Delta t-M(i,t(i))\Delta t-\lambda(i,A,t(i))\Delta t-\lambda(i,B,t(i))\Delta t]\,P(i,A,B,t(i))+O(\Delta t).$$

Taking the limit $\Delta t\to 0$ and letting the dot above a quantity denote the first derivative of that quantity with respect to $t(i)$ yields

$$\dot{P}(i,A,B,t(i))=-[F(i,t(i))+M(i,t(i))+\lambda(i,A,t(i))+\lambda(i,B,t(i))]\,P(i,A,B,t(i)).$$

This and similar arguments yield a tag shedding model of the form

$$\left\{\begin{array}{l} \dot{P}(i,A,B,t(i))=-\left[F(i,t(i))+M(i,t(i))+\lambda(i,A,t(i))+\lambda(i,B,t(i))\right]P(i,A,B,t(i)) \\ \dot{P}(i,A,0,t(i))=-\left[F(i,t(i))+M(i,t(i))+\lambda(i,A,t(i))\right]P(i,A,0,t(i))+\lambda(i,B,t(i))P(i,A,B,t(i)) \end{array}\right. \quad (1)$$

$$
\left\{
\begin{array}{l}
\dot{P}(i,0,B,t(i)) = -\left[F(i,t(i)) + M(i,t(i)) + \lambda(i,B,t(i))\right]P(i,0,B,t(i)) + \lambda(i,A,t(i))P(i,A,B,t(i)) \\
\dot{P}(i,0,0,t(i)) = -\left[F(i,t(i)) + M(i,t(i))\right]P(i,0,0,t(i)) + \lambda(i,A,t(i))P(i,A,0,t(i)) + \lambda(i,B,t(i))P(i,0,B,t(i)) \\
\dot{C}(i,A,B,t(i)) = F(i,t(i))R(i,A,B,t(i))P(i,A,B,t(i)) \\
\dot{C}(i,A,0,t(i)) = F(i,t(i))R(i,A,0,t(i))P(i,A,0,t(i)) \\
\dot{C}(i,0,B,t(i)) = F(i,t(i))R(i,0,B,t(i))P(i,0,B,t(i)) \\
\dot{C}(i,0,0,t(i)) = F(i,t(i)) = R(i,0,0,t(i))P(i,0,0,t(i)) \\
\dot{U}(i,A,B,t(i)) = F(i,t(i))\left[1 - R(i,A,B,t(i))\right]P(i,A,B,t(i)) \\
\dot{U}(i,A,0,t(i)) = F(i,t(i))\left[1 - R(i,A,0,t(i))\right]P(i,A,0,t(i)) \\
\dot{U}(i,0,B,t(i)) = F(i,t(i))\left[1 - R(i,0,B,t(i))\right]P(i,0,B,t(i)) \\
\dot{U}(i,0,0,t(i)) = F(i,t(i))\left[1 - R(i,0,0,t(i))\right]P(i,0,0,t(i)) \\
\dot{D}(i,A,B,t(i)) = M(i,t(i))P(i,A,B,t(i)) \\
\dot{D}(i,A,0,t(i)) = M(i,t(i))P(i,A,0,t(i)) \\
\dot{D}(i,0,B,t(i)) = M(i,t(i))P(i,0,B,t(i)) \\
\dot{D}(i,0,0,t(i)) = M(i,t(i))P(i,0,0,t(i))
\end{array}
\right.
\qquad \left[t_0(i) \le t(i)\right]
$$

(1)
continued

with initial conditions

$$
\left\{
\begin{array}{l}
P(i,A,B,t_0(i)) = \pi(i)\rho(i,A)\rho(i,B) \\
P(i,A,0,t_0(i)) = \pi(i)\rho(i,A)\left[1 - \rho(i,B)\right] \\
P(i,0,B,t_0(i)) = \pi(i)\left[1 - \rho(i,A)\right]\rho(i,B) \\
P(i,0,0,t_0(i)) = \pi(i)\left[1 - \rho(i,A)\right]\left[1 - \rho(i,B)\right] \\
C(i,A,B,t_0(i)) = 0 \\
C(i,A,0,t_0(i)) = 0 \\
C(i,0,B,t_0(i)) = 0 \\
C(i,0,0,t_0(i)) = 0 \\
U(i,A,B,t_0(i)) = 0 \\
U(i,A,0,t_0(i)) = 0 \\
U(i,0,B,t_0(i)) = 0 \\
U(i,0,0,t_0(i)) = 0 \\
D(i,A,B,t_0(i)) = 0 \\
D(i,A,0,t_0(i)) = 0 \\
D(i,0,B,t_0(i)) = 0 \\
D(i,0,0,t_0(i)) = 0
\end{array}
\right.
$$

Solution of this system of ordinary differential equations as an initial value problem gives

$$
\begin{cases}
P(i,A,B,t(i)) = \pi(i)e^{-\int_{t_0(i)}^{t(i)}[F(i,s)-M(i,s)]ds}\rho(i,A)\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}[\lambda(i,A,s)+\lambda(i,B,s)]ds} \\
P(i,A,0,t(i)) = \pi(i)e^{-\int_{t_0(i)}^{t(i)}[F(i,s)+M(i,s)]ds}\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\left[1-\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right] \\
P(i,0,B,t(i)) = \pi(i)e^{-\int_{t_0(i)}^{t(i)}[F(i,s)+M(i,s)]ds}\left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds} \\
P(i,0,0,t(i)) = \pi(i)e^{-\int_{t_0(i)}^{t(i)}[F(i,s)+M(i,s)]ds}\left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\left[1-\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right] \\
C(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)R(i,A,B,s)P(i,A,B,s)ds \\
C(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)R(i,A,0,s)P(i,A,0,s)ds \\
C(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)R(i,0,B,s)P(i,0,B,s)ds \\
C(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)R(i,0,0,s)P(i,0,0,s)ds \\
U(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)[1-R(i,A,B,s)]P(i,A,B,s)ds \\
U(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)[1-R(i,A,0,s)]P(i,A,0,s)ds \\
U(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)[1-R(i,0,B,s)]P(i,0,B,s)ds \\
U(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)} F(i,s)[1-R(i,0,0,s)]P(i,0,0,s)ds \\
D(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)} M(i,s)P(i,A,B,s)ds \\
D(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)} M(i,s)P(i,A,0,s)ds \\
D(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)} M(i,s)P(i,0,B,s)ds \\
D(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)} M(i,s)P(i,0,0,s)ds
\end{cases}
\tag{2}
$$

This tag shedding model follows essentially the same line of thought as Xiao's (1996a) and can be readily phrased in the standard terminology of competing risks in survival analysis (David and Moeschberger, 1978). Also, notice that the left-hand side of Equation 1 sums to zero; the left-hand side of Equation 2 sums to $\pi(i)$.

When a single fish is double tagged and released at time $t_0(i)$, one of 16 mutually exclusive events can happen at time $t(i)$ (Equation 1 or 2). However, only three events are actually observable: the fish has, upon recapture, retained both tags, retained tag A and lost tag B, or lost tag A and retained tag B, with respective probabilities of $\dot{C}(i,A,B,t(i))$, $\dot{C}(i,A,0,t(i))$ and $\dot{C}(i,0,B,t(i))$. The event that it has shed both tags upon recapture, with a probability of $\dot{C}(i,0,0,t(i))$, cannot be observed, for when both tags are shed, a fish cannot be reliably distinguished from one that was never tagged. A likelihood function can be constructed to estimate parameters in Equation 1 or 2 by following arguments in standard competing risk analysis, but these estimates are substantially biased. To overcome this problem, we estimated model parameters by conditioning on observations of three events only, i.e. by maximizing the conditional likelihood function for all reported recaptures with at least one tag retained

$$L=L_1 \cdot L_2 \cdot L_3,$$

with

$$L_1=\prod_{h=1}^{n}\frac{\dot{C}(h,A,B,t(h))}{\dot{C}(h,A,B,t(h))+\dot{C}(h,A,0,t,(h))+\dot{C}(h,0,B,t(h))}$$

$$=\prod_{h=1}^{n}\frac{R(h,A,B,t(h))\theta(h,A,B,t(h))}{R(h,A,B,t(h))\theta(h,A,B,t(h))+R(h,A,0,t(h))\theta(h,A,0,t(h))+R(h,0,B,t(h))\theta(h,0,B,t(h))}$$

$$L_2=\prod_{j=1}^{m}\frac{\dot{C}(j,A,0,t(j))}{\dot{C}(j,A,B,t(j))+\dot{C}(j,A,0,t(j))+\dot{C}(j,0,B,t(j))}$$

$$=\prod_{j=1}^{n}\frac{R(j,A,0,t(j))\theta(j,A,0,t(j))}{R(j,A,B,t,(j))\theta(j,A,B,t(j))+R(j,A,0,t(j))\theta(j,A,0,t(j))+R(j,0,B,t(j))\theta(j,0,B,t(j))} \tag{3}$$

$$L_3=\prod_{k=1}^{p}\frac{\dot{C}(k,0,B,t(k))}{\dot{C}(k,A,B,t(k))+\dot{C}(k,A,0,t(k))+\dot{C}(k,0,B,t(k))}$$

$$=\prod_{k=1}^{n}\frac{R(k,0,B,t(k))\theta(k,0,B,t(k))}{R(k,A,B,t(k))\theta(k,A,B,t(k))+R(k,A,0,t(k))\theta(k,A,0,t(k))+R(k,0,B,t(k))\theta(k,0,B,t(k))}$$

$$\left\{\begin{array}{l}\theta(i,A,B,t(i))=\rho(i,A)\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}[\lambda(i,A,s)+\lambda(i,B,s)]ds} \\ \\ \theta(i,A,0,t(i))=\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\left[1-\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right]\end{array}\right.$$

$$\begin{cases} \theta(i,0,B,t(i)) = \left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds} \\ \theta(i,0,0,t(i)) = \left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\left[1-\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right], \end{cases} \quad (3)\ \text{continued}$$

where *h*, *j*, and *k* index fish recaptures with both tags retained, with tag A only, and with tag B only; *n*, *m* , and *p* are the total numbers of fish recaptures with both tags retained, with tag A only, and with tag B only.

In the estimation, we assumed that $t_0(i)=0$, there was no type-I tag shedding (i.e. $\rho(i,A)=\rho(i,B)=1$), and $R(i,A,B,t(i))=R(i,A,0,t(i))=R(i,0,B,t(i))$. The latter assumption makes Equation 3 independent of probability of reporting at time $t(i)$. We also set the instantaneous shedding rate of tag *j* (j=A,B) as a function of fish total length at release $L(i)$ and time at liberty $t(i)$ of the form $\lambda(i,j,t(i))=\beta_0(j)+\beta_1(j)L(i)+\beta_2(j)t(i)$, where $\beta_0(j)$, $\beta_1(j)$ and $\beta_2(j)$ are parameters to be estimated. Thus, $\lambda(i,j,t(i))$ has three terms and seven (2^3-1) nested models, since each term can be included or excluded in a nested model and a nested model has at least one term. Under these assumptions, Equation 3 becomes

$$L=L_1 \cdot L_2 \cdot L_3, \quad (4)$$

with

$$L_1 = \prod_{h=1}^{n} \frac{\theta(h,A,B,t(h))}{\theta(h,A,B,t(h))+\theta(h,A,0,t(h))+\theta(h,0,B,t(h))}$$

$$L_2 = \prod_{j=1}^{n} \frac{\theta(j,A,0,t(j))}{\theta(j,A,B,t(j))+\theta(j,A,0,t(j))+(\theta(j,0,B,t(j))}$$

$$L_3 = \prod_{k=1}^{n} \frac{\theta(k,0,B,t(k))}{\theta(k,A,B,t(k))+\theta(k,A,0,t(k))+\theta(k,0,B,t(k))}$$

$$\begin{cases} \theta(i,A,B,t(i)) = e^{-[\beta_0(A)+\beta_1(A)L(i)+\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}[\beta_2(A)+\beta_2(B)]t(i)^2} \\ \theta(i,A,0,t(i)) = e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\left[1-e^{-[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2}\right] \\ \theta(i,0,B,t(i)) = \left[1-e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\right]e^{-[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2} \\ \theta(i,0,0,t(i)) = \left[1-e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\right]\left[1-e^{-[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2}\right] \end{cases}$$

For the first experiment, $\lambda(i,A,t(i))=0$ because internal tags (tag A) were inserted into the shark's body cavity and were not shed, except under very unusual circumstances. For the same reason, although three recaptured school sharks appeared to have shed their internal tags (rows 9 and 21, Table 1), these events were actually due to failure to detect the tag upon recapture. Consequently, both tags were assumed to be present for these recaptures. Also, tag shedding rates of white and gray Petersen discs were estimated, singly or in combination, to examine their possible differences (Table 3). Data on $\lambda(i,A,t(i))$(Roto tags)

Table 3

Instantaneous rate of tag shedding for school shark estimated from data based on the first double-tagging experiment assuming that the shedding rates of internal tags (tag A) are zero, i.e., $\lambda(i,A,t(i))=\beta_0(A)=0$, and those of external tags (tag B) depend only on their types, i.e., $\lambda(i,B,t(i))=\beta_0(B)$; n is the number of recaptures. $-\log(L)$ gives values of the negative of the logarithm of the likelihood function; "—" indicates not applicable or not computable. J = J-tag; L = L-tag; S = S-tag; W = W-tag; G = G-tag. The word "and" indicates pooling of data: J and L for pooling data from J-tag and L-tag; M and F for pooling data from males and females. Estimates for tag A of J and L and tag B of G are the same as those for tag A of L and tag B of G; estimates for tag A of J and S and tag B of G are the same as those for tag A of S and tag B of G.

Row	Tag A	Tag B	Sex	n	$\beta_0(B)$ (SE)/yr	$-\log(L)$
1	J	W	M and F	32	0.3718(0.1089)	9.4439
2	J	W	M	18	0.2829(0.1104)	5.4509
3	J	W	F	14	0.5816(0.2946)	3.3332
4	L	W	M and F	11	0.6446(0.3609)	2.3503
5	L	W	M	7	0.3617(0.2605)	1.3295
6	L	W	F	4	—	—
7	L	G	M and F	200	0.7347(0.1012)	45.4817
8	L	G	—	2	—	—
9	L	G	M	127	1.1439(0.2534)	14.3301
10	L	G	F	71	0.5202(0.1016)	27.4639
11	S	W	M and F	7	—	—
12	S	W	—	0	—	—
13	S	W	M	2	—	—
14	S	W	F	5	—	—
15	S	G	M and F	167	3.0653(0.4739)	47.9105
16	S	G	—	2	1.2692(1.5899)	0.3407
17	S	G	M	86	4.5992(1.0705)	18.1029
18	S	G	F	79	2.3509(0.4955)	26.9553
19	L	W and G	M and F	211	0.7291(0.0974)	47.8580
20	L	W and G	—	2	—	—
21	L	W and G	M	134	1.0272(0.2119)	16.8622
22	L	W and G	F	75	0.5466(0.1040)	28.3971
23	S	W and G	M and F	174	3.0857(0.4735)	48.0298
24	S	W and G	—	2	1.2692(1.5899)	0.3407
25	S	W and G	M	88	4.5993(1.0702)	18.1029
26	S	W and G	F	84	2.3912(0.4975)	27.1604
27	J and L	W	M and F	43	0.4165(0.1084)	12.1642
28	J and L	W	M	25	0.2993(0.1016)	6.8258
29	J and L	W	F	18	0.7464(0.3367)	4.0018
30	J and L	W and G	M and F	243	0.6460(0.0780)	59.5387
31	J and L	W and G	—	2	—	—
32	J and L	W and G	M	152	0.7457(0.1255)	27.0143
33	J and L	W and G	F	89	0.5508(0.0979)	31.7369
34	J and S	W	M and F	39	0.4434(0.1207)	11.6709
35	J and S	W	—	0	—	—
36	J and S	W	M	20	0.3162(0.1168)	6.1176
37	J and S	W	F	19	0.7587(0.3557)	4.4422
38	J and S	W and G	M and F	206	1.6579(0.2133)	80.2783
39	J and S	W and G	—	2	1.2692(1.5899)	0.3407
40	J and S	W and G	M	106	1.5043(0.2682)	45.5600
41	J and S	W and G	F	98	1.8729(0.3550)	34.0001

continued

were too limited from the second experiment (Table 2) to estimate two or more parameters. We estimated $\beta_0(A)$ only, which can, however, be scaled to $\beta_1(A)$ or $\beta_2(A)$ given $L(i)$ and $t(i)$. For tag B (Petersen discs or dart tags), all seven nested models of $\lambda(i,B,t(i))$ were fitted, where possible, to data from each tagging experiment. The final and most parsimonious model was decided by the χ^2 statistic (Seber and Wild, 1989, p.196–197). All parameters were estimated by minimizing $-\log(L)$ by using the simplex algorithm by a FORTRAN 77 program (available on request).

Results

Maximization of Equation 4 for both sets of tagging data yielded estimates of shedding rate for various (independent) combinations of fish sex, tag type, and tag position, and their (asymptotic) standard errors (Tables 3 and 4). If a tag was retained in all recaptured fish, we assumed that its shedding rate was zero in order to estimate other parameters of the model. Because shedding rates must be nonnegative, the assumption of zero shedding rate will lead to an underestimate of the parameter concerned and introduce a positive bias into the estimates of other parameters. The extent of such bias could be assessed by simulation studies but is beyond the scope of this work.

Fish length at release or time at liberty, or both, entered certain final models for $\lambda(i,B,t(i))$, only when the number of fish recaptured was small. By contrast, whenever there were many fish recaptures (e.g. rows 14–15 and 20–21, Table 1), neither factor entered the final model. Therefore, we conclude that fish length at release or time at liberty, or both, did not significantly affect tag shedding rates; and their inclusion in certain models was a result of too few recaptures.

Fish sex affected tag shedding rates of Petersen discs for some combinations of tag type and tag position. For a combination of a 50-mm-long and 23-mm-wide internal tag (J-tag) with a white Petersen disc (external) tag (W-tag) (rows 1–3, Table 3), $\lambda(i,B,t(i))$=0.3718 (±0.1089)/yr if data are pooled for both sexes of school shark, with a –log-likelihood of 9.4439. For the sex-specific model, $\lambda(i,B,t(i))$=0.2829 (±0.1104)/yr for males; $\lambda(i,B,t(i))$=0.5816 (±0.2946)/yr for females, with a (male and female) combined –log-likelihood of 8.7841 (=5.4509+3.3332). The increase in value of the –log-likelihood function for an extra parameter is, in this case, negligible ($\chi^2_{1,0.2507}$=2×(9.4439–8.7841)=1.3196), suggesting no statistically significant differences in tag shedding rates between sexes for white Petersen discs.

Table 3 (continued)

Row	Tag A	Tag B	Sex	n	$\beta_0(B)$ (SE)/yr	$-\log(L)$
42	L and S	W	M and F	18	0.9094(0.4251)	3.4541
43	L and S	W	—	0	—	—
44	L and S	W	M	9	0.4791(0.3116)	1.7664
45	L and S	W	F	9	—	—
46	L and S	G	M and F	367	1.2892(0.1331)	116.1464
47	L and S	G	—	4	1.2729(1.5769)	0.3409
48	L and S	G	M	213	2.1071(0.3520)	41.2981
49	L and S	G	F	150	0.9537(0.1327)	67.8985
50	L and S	W and G	M and F	385	1.2679(0.1274)	119.8703
51	L and S	W and G	—	4	1.2729(1.5769)	0.3409
52	L and S	W and G	M	222	1.8674(0.2992)	45.8682
53	L and S	W and G	F	159	0.9818(0.1336)	68.9822
54	J and L and S	W	M and F	50	0.4753(0.1168)	14.1985
55	J and L and S	W	—	0	—	—
56	J and L and S	W	M	27	0.3252(0.1063)	7.4610
57	J and L and S	W	F	23	0.8956(0.3763)	4.8981
58	J and L and S	G	M and F	367	1.2892(0.1331)	116.1464
59	J and L and S	G	—	4	1.2729(1.5769)	0.3409
60	J and L and S	G	M	213	2.1071(0.3520)	41.2981
61	J and L and S	G	F	150	0.9537(0.1327)	67.8985
62	J and L and S	W and G	M and F	417	1.0891(0.1026)	137.7412
63	J and L and S	W and G	—	4	1.2729(1.5769)	0.3409
64	J and L and S	W and G	M	240	1.2738(0.1761)	63.3863
65	J and L and S	W and G	F	173	0.9478(0.1251)	72.8067

Table 4

Instantaneous rate of tag shedding for gummy and school sharks estimated from data based on the second double-tagging experiment assuming that $\lambda(i,A,t(i))=\beta_0(A)$ and $\lambda(i,B,t(i))=\beta_0(B)$. Tagging position refers to tag B's position; n is the number of recaptures; $-\log(L)$ gives values of the negative of the logarithm of the likelihood function; "—" indicates not applicable or not computable. The word "and" indicates pooling of data: Jumbo and Roto for pooling data from Jumbo tag and Roto tag; M and F for pooling data from males and females.

Row	Species	Tag A	Tag B	Position of tag	Sex	n	$\beta_0(A)$ (SE)/yr	$\beta_0(B)$ (SE)/yr	$-\log(L)$
1	gummy	Jumbo	dart	fin	M and F	32	0.1912(0.1349)	0.3770(0.1886)	19.5193
2	gummy	Jumbo	dart	fin	M	13	0.2133(0.2125)	0.5642(0.3260)	10.98
3	gummy	Jumbo	dart	fin	F	19	0.1771(0.1770)	0.1890(0.1890)	8.0212
4	gummy	Jumbo	dart	muscle	M and F	84	—	0.9239(-)	67.5957
5	gummy	Jumbo	dart	muscle	M	41	—	0.8550(0.2021)	34.5527
6	gummy	Jumbo	dart	muscle	F	43	—	0.9902(-)	32.9376
7	gummy	Roto	dart	muscle	M and F	91	0.1304(0.0747)	1.0502(0.1712)	71.5838
8	gummy	Roto	dart	muscle	—	1	—	—	—
9	gummy	Roto	dart	muscle	M	37	0.1581(0.1110)	0.8183(0.2187)	31.8327
10	gummy	Roto	dart	muscle	F	53	0.0918(0.0913)	1.2111(0.2563)	37.1817
11	gummy	Jumbo	dart	fin and muscle	M and F	116	0.0569(0.0402)	0.8278(0.1243)	91.8731
12	gummy	Jumbo	dart	fin and muscle	M	54	0.0586(0.0584)	0.8042(0.1749)	47.2285
13	gummy	Jumbo	dart	fin and muscle	F	62	0.0555(0.0553)	0.8503(0.1766)	44.6251
14	gummy	Jumbo and Roto	dart	muscle	M and F	175	0.0641(0.0369)	0.9828(0.1121)	141.3449
15	gummy	Jumbo and Roto	dart	muscle	—	1	—	—	—
16	gummy	Jumbo and Roto	dart	muscle	M	78	0.0809(0.0570)	0.8379(0.1484)	67.8238
17	gummy	Jumbo and Roto	dart	muscle	F	96	0.0447(0.0446)	1.0948(0.1656)	70.9707
18	gummy	Jumbo and Roto	dart	fin and muscle	M and F	207	0.0857(0.0381)	0.9172(0.1012)	164.2892
19	gummy	Jumbo and Roto	dart	fin and muscle	—	1	—	—	—
20	gummy	Jumbo and Roto	dart	fin and muscle	M	91	0.1011(0.0580)	0.8083(0.1361)	79.4274
21	gummy	Jumbo and Roto	dart	fin and muscle	F	115	0.0692(0.0487)	0.9989(0.1474)	82.5257
22	school	Jumbo	dart	fin	M and F	18	0.0973(0.0972)	0.2646(0.1530)	11.0858
23	school	Jumbo	dart	fin	M	3	—	—	—
24	school	Jumbo	dart	fin	F	15	0.1104(0.1103)	0.2948(0.1706)	10.6735
25	school	Jumbo	dart	muscle	M and F	21	0.1041(0.1038)	0.4262(0.1917)	14.7690
26	school	Jumbo	dart	muscle	M	12	0.1727(0.1725)	0.3219(0.2282)	6.6030
27	school	Jumbo	dart	muscle	F	9	—	0.5484(0.3201)	7.3704
28	school	Roto	dart	muscle	M and F	9	—	0.7845(0.3967)	8.5426
29	school	Roto	dart	muscle	M	3	—	—	—
30	school	Roto	dart	muscle	F	6	—	1.6867(0.8865)	5.6360
31	school	Jumbo	dart	fin and muscle	M and F	39	0.1003(0.0708)	0.3466(0.1230)	26.0748
32	school	Jumbo	dart	fin and muscle	M	15	0.1421(0.1419)	0.2700(0.1912)	7.0831
33	school	Jumbo	dart	fin and muscle	F	24	0.0773(0.0772)	0.3831(0.1571)	18.7670
34	school	Jumbo and Roto	dart	muscle	M and F	30	0.0798(0.0796)	0.5339(0.1793)	24.0789
35	school	Jumbo and Roto	dart	muscle	M	15	0.1188(0.1188)	0.2263(0.1602)	7.5881
36	school	Jumbo and Roto	dart	muscle	F	15	—	0.8882(0.3425)	14.0341
37	school	Jumbo and Roto	dart	fin and muscle	M and F	48	0.0876(0.0619)	0.4254(0.1233)	35.8236
38	school	Jumbo and Roto	dart	fin and muscle	M	18	0.1038(0.1037)	0.1997(0.1414)	7.9368
39	school	Jumbo and Roto	dart	fin and muscle	F	30	0.0746(0.0745)	0.5510(0.1755)	26.7306

However, for a combination of a 50-mm-long and 22-mm-wide internal tag (L-tag) with a gray Petersen disc (external) tag (G-tag) (rows 7–10, Table 3), $\lambda(i,B,t(i))=0.7347$ (± 0.1012)/yr if data are pooled for both sexes, with a –log-likelihood of 45.4817. For the sex-specific model, $\lambda(i,B,t(i))=1.1439$ (± 0.2534)/yr for males; $\lambda(i,B,t(i))=0.5202$ (± 0.1016)/yr for females, with a (male and female) combined –log-likelihood of 41.7940 (=14.3301+27.4639). The increase in value of the –log-likelihood function for an extra parameter is statistically significant ($\chi^2_{1,0.0066}=2\times(45.4817-41.7940)=7.3754$), suggesting significant differences in tag shedding rates between sexes for gray Petersen discs. Similarly, for a combination of a 35-mm-long and 10-mm-wide internal tag (S-tag) with a gray Petersen disc (external) tag (rows 15–18, Table 3), $\lambda(i,B,t(i))=3.0653$ (± 0.4739)/yr if data are pooled for both sexes, with a –log-likelihood of 47.9105. For the sex-specific model, $\lambda(i,B,t(i))=4.5992$ (± 1.0705)/yr for males; $\lambda(i,B,t(i))=2.3509$ (± 0.4955)/yr for females, with a (male and female) combined –log-likelihood of 45.0582 (=18.1029+26.9553). The increase in value of the –log-likelihood function for an extra parameter is, again, statistically significant ($\chi^2_{1,0.0169}=2\times(47.9105-45.0582)=5.7046$), again suggesting significant differences in tag shedding rates between sexes for gray Petersen discs. Notice, in these cases, that tag shedding rates for males nearly doubled those for females. For the second tagging experiment, no differences in tag shedding rates were found among sexes for either species of shark (Table 4).

The shedding rate of Petersen discs for the school shark was very high. When combined with a 50-mm-long and 23-mm-wide internal tag (J-tag), white Petersen disc (W-tag) had a shedding rate of $\lambda(i,B,t(i))=0.2829(\pm0.1104)$/yr or $100\times(1-e^{-0.2829}) \approx 24.64\%$/yr for males, and $\lambda(i,B,t(i))=0.5816(\pm0.2946)$/yr or 44.10%/yr for females (rows 1–3, Table 3). When combined with a 50-mm-long and 22-mm-wide internal tag (L-tag), gray Petersen disc (G-tag) had a shedding rate of $\lambda(i,B,t(i))=1.1439$ (±0.2534)/yr or 68.14%/yr for males and $\lambda(i,B,t(i))=0.5202$ (±0.1016)/yr or 40.56%/yr for females (rows 7–10, Table 3). When combined with a 35-mm-long and 10-mm-wide internal tag (S-tag), gray Petersen disc (G-tag) had a shedding rate of $\lambda(i,B,t(i))=4.5992$ (±1.0705)/yr or 98.99%/yr for males and $\lambda(i,B,t(i))=2.3509$ (±0.4955)/yr or 90.47%/yr for females (rows 15–18, Table 3). Other combinations of tag type and tagging position for the first tagging experiment did not yield reliable (in accuracy and precision) estimates of tag shedding rate because of insufficient data.

For the second tagging experiment, tag shedding rates varied considerably for both species of sharks (rows 1–10 and 22–30, Table 4). However, dart tags had a higher shedding rate than either Roto or Jumbo tags. For example, for male gummy shark tagged in the fin, dart tags had an instantaneous shedding rate of 0.5642 (±0.3260)/yr and Jumbo tags 0.2133 (±0.2125)/yr (row 2, Table 4). For either gummy or school shark, the shedding rate of dart tags placed in the fin was about half that of dart tags placed in the muscle (rows 1–10 and 22–30, Table 4).

Discussion

We developed a simple tag shedding model (Equations 1–4) to account for the effects of time at liberty, sex, size, tag position, and other factors and used a special case to estimate the instantaneous shedding rates of Petersen discs, Roto tags, and dart tags in two species of sharks. It can be used to estimate the shedding rates of two tags, singly or in combination, and has two interesting features. In Equation 1, both $F(i,t(i))$ and $M(i,t(i))$ are independent of the 16 state variables. This independence ensures that $P(i,A,B,t(i))$, $P(i,A,0,t(i))$, $P(i,0,B,t(i))$ and $P(i,0,0,t(i))$ are all expressible as a product (Equation 2), which in turn ensures that terms involving $F(i,t(i))$ and $M(i,t(i))$ in the likelihood function (Equation 3 or 4) are cancelled out. Thus, as in Xiao (1996a), our tag shedding model applies, even when $F(i,t(i))$ and $M(i,t(i))$ are arbitrary functions of time $t(i)$. On the other hand, if fishing and natural mortalities depend on the state variables of tags A and B, then terms in $P(i,A,B,t(i))$, $P(i,A,0,t(i))$, $P(i,0,B,t(i))$ and $P(i,0,0,t(i))$ involving four fishing mortalities $F(i,A,B,t(i))$, $F(i,A,0,t(i))$, $F(i,0,B,t(i))$ and $F(i,0,0,t(i))$ and four natural mortalities $M(i,A,B,t(i))$, $M(i,A,0,t(i))$, $M(i,0,B,t(i))$ and $M(i,0,0,t(i))$ cannot be factored out. Then, for estimation of parameters by maximizing Equation 3, particular functional forms of all the eight mortalities must be hypothesized. This tag shedding model is more general but more data-demanding. The other interesting feature of our tag shedding model is that Equation 3 is independent of probabilities of reporting $R(i,A,B,t(i))$, $R(i,A,0,t(i))$, $R(i,0,B,t(i))$ and $R(i,0,0,t(i))$ if these probabilities are identical, arbitrary functions of time $t(i)$ because of the way they enter Equation 3.

Statistically significant differences in shedding rates of Petersen discs between male and female school sharks were detected when many fish were recaptured. We do not know why such differences existed but we postulate that male sharks have a higher tag shedding rate because they are more active and would tend to rub off the tags and that female sharks have a lower tag shedding rate because they are larger and have thicker fins. An external fin tag, such as a Petersen disc, is shed only after its pin or locking mechanism has cut through the fin. The larger the tagged fish, the thicker is its fin and hence the farther the distance its pin or locking mechanism has to cut through to the posterior edge of the fin. Consequently, larger animals have lower shedding rates. Thus, sex is confounded in its effects with size. That is probably why the length at release of school sharks did not affect the shedding rates of Petersen discs within a wide size range examined, although the loss of anchor tags (Floy tags) was size-dependent for striped bass *Morone saxatilis* (Waldman et al., 1990) but size-independent for lake trout *Salvelinus namaycush* (Fabrizio et al., 1996). We could not detect differences between sexes with fewer recaptures, however, because the use of Equation 1 or 2 to resolve sexual differences in tag shedding rate requires many recaptures (see below).

Shedding rates of Petersen discs, Roto tags, and dart tags did not change with time at liberty. Some tagged fish have higher shedding rates than others, because tags that are less securely attached are shed earlier. The proportion of less securely attached tags decreases with increasing time at liberty. This will yield an apparent decrease in tag shedding rate with time at liberty. A similar argument applies when tag shedding rates vary among individuals. The lack of a trend may indicate negligible tag losses from improper attachment, insignificant individual variability in tag shedding rate, or insufficient data (see below).

Estimates of tag shedding rates in Tables 3 and 4 must be used cautiously because only those that are based on many recaptures are reliable, whereas those that are based on few recaptures are unreliable. For example, the estimates of tag shedding rates for a combination of a 50-mm-long and 22-mm-wide internal tag (L-tag) with a white Petersen disc (W-tag, external) (rows 4–6, Table 3) were based on only 11 recaptures (rows 11 and 12, Table 1), only one of which had retained both tags (row 11, Table 1), and hence are unreliable. No estimates could even be obtained for a combination of a 35-mm-long and 10-mm-wide (S-tag) internal tag with a white Petersen disc (W-tag, external) (rows 11–14, Table 3), despite seven recaptures, none of which had retained both tags (rows 16–18, Table 1). Similarly, no estimates could be obtained, for any tag combinations, from data on gummy sharks from the first double-tagging experiment, despite 20 recaptures, none of which had retained both tags (rows 1–8, Table 1). Equally unreliable estimates of tag shedding rates could also result from pooling of information while ignoring differences in its sources. For example, estimates from pooling all three internal tags (i.e. J-tag, L-tag and S-tag) (rows 54–65, Table 3) should be treated cautiously because of sexual differences inferred above. By contrast, for both sexes of school sharks, the estimates of shedding rates of gray Petersen discs are reliable for its combination with a 50-mm-long and 22-mm-wide internal tag (L-tag) (rows 9 and 10, Table 3) or with a 35-mm-long and 10-mm-wide (S-tag) internal tag (rows 17 and 18, Table 3) because information from many fish recaptures was used in their estimation. Much less reliable estimates were obtained for dart tags on gummy sharks (rows 5, 6, 9, and 10, Table 4). Although rather high in all cases, all these shedding rates are actually underestimated, as will be shown and published elsewhere.

Although we have examined only the effects of tag type, sex, length at release, and time at liberty on tag shedding, many other factors, such as tagging operator (Hampton, 1996), can also affect tag shedding rate. However, hundreds or even thousands of fish need to be recaptured (many more need to be released) to estimate effects of tagging operators reliably. Such a great demand of data is well expected of Equation 1 or 2, which is a compartmental model. The solution of a compartmental model can be given by a linear combination of exponentials and is known to yield bad ill-conditioning (Seber and Wild, 1989, p. 118–119). Indeed, for some compartmental models, no amount of data is sufficient for identifying model parameters. Similarly, the "best" model of all possible models of a general model is identifiable only by a sufficient volume of data. As mentioned above, fish length at release or time at liberty, or both, entered certain "best" models for $\lambda(i,B,t(i))$, when the number of fish recaptured was small, but did not, when there were many fish recaptures. This finding suggests that fewer data than sufficient cannot identify the "best" model. To detect and address problems with parameter and model identifiability for a particular general model (e.g. Equation 1 or 2), one might generate as large a set of data as necessary, for example, by duplicating each record of an existing set of data from a double-tagging experiment a necessary number of times, analyse it, and design one's tagging experiment accordingly (e.g. to determine the number of fish to be released and the expected number of fish to be recaptured).

Results of our study have major implications for future double-tagging experiments for estimating instantaneous tag shedding rate and for analysis of tagging data. Because estimation of a single parameter requires many fish recaptures and hence incurs considerable financial resources, use of an easily detected and permanent tag eliminates a need for considering tag loss and is preferred in any tagging experiment. However, with a commercially or recreationally harvested species, problems of tag reporting remain. Use of two readily detectable, identical tags with a moderate shedding rate in a double-tagging experiment reduces the number of parameters to be estimated by one half. A moderate shedding rate is necessary because too low a shedding rate requires some recaptures after a long time at liberty for reliable estimation of parameters; too high a shedding rate renders the tag useless for some applications.

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Appendix 5. Estimation of tag reporting rates

SharkFAG/99/D11 (8–10 April 1999)

Tag Reporting Rates for Gummy Shark and School Shark Estimated from Catch and from Tags per Unit Catch

Lauren P. Brown and Terence I. Walker

Marine and Freshwater Resources Institute
PO Box 114, Queenscliff, Vic. 3225

Abstract

Estimates of 'tag reporting rates' (TRR) from two slightly different methods using reported tag recaptures and annual catch data provided similar results. Estimates for the three 3-year periods 1973–75, 1976–78 and 1994–96 were 75–79%, 57–67% and 84–92%, respectively, from the TRR Catch Method. The estimates were 74–79%, 66–71% and 85–87% for the three periods, respectively, from the TRR Tag Method.

Introduction

Estimates of movement and mortality rates are affected by the non-reporting of recaptured tagged-sharks. In this report we endeavour to produce estimates of 'tag reporting rate' (TRR) from summaries of tag recapture data and from annual catch data on a vessel by vessel basis. These estimates are made from data available for the periods 1973–78 and 1994–96.

Methods and Results

'Tag reporting rate' was estimated by two methods, which are referred to as the 'tag reporting rate from catch method' (TRR Catch Method) and the 'tag reporting rate from tags per unit catch method' (TRR Tag Method). For the purpose of these analyses, tag recaptures and catch applies to gummy shark and school shark combined together.

Both methods depend on the same set of simplifying assumptions.

1. Vessels reporting one or more tags reported all tags caught and are referred to as 'reporter' vessels.
2. Vessels reporting no tags did catch tagged sharks but failed to report them and are referred to as 'non-reporter' vessels.
3. All of the catch is reported for all vessels.
4. The probability of capture of a tagged shark per tonne of shark landed is equal between 'non-reporter' vessels and 'reporter' vessels.

For the TRR Catch Method, the TRR is calculated as the catch summed over all vessels reporting >0 tag recaptures divided by the catch summed over all vessels. For the TRR Tag Method, TRR is calculated as the number of tag recaptures observed from the 'reporter' vessels divided by the number of tag recaptures expected from all vessels. For this second method, the number of tag recaptures expected from the all vessels is determined by assuming the number of tag recaptures per unit catch for the 'non-reporter' vessels equals that for the 'reporter' vessels.

The analyses were undertaken for the SharkFAG Regions WBS and EBS during 1973–78 and all seven SharkFAG regions during 1994–96. Within each of these regions separately, an analysis was undertaken for each calendar year separately and then for each of the 3-year periods 1973–75, 1976–78 and 1994–96. Too few tagged sharks were recaptured outside Regions WBS and EBS to include other SharkFAG regions in the 1973–78 analyses.

Plots of the annual number of tags reported against annual catch by vessel within SharkFAG Regions WBS and EBS during 1973–78 (Fig. 1.1) and all seven SharkFAG Regions during 1994–1996 (Fig. 1.2) indicate the 'non-reporters' (on x-axis) and 'reporters' (above x-axis). Data for the variables number of tags released, number of recaptured tags reported, catches summed over 'non-reporter' vessels (i.e. 0 tags) and catches summed over 'reporter' vessels (i.e. >0 tags) by SharkFAG region each year during 1973–78 (Table 1.1) and during 1994–1996 (Table 1.2) are presented for each of the three annual catch-classes >5 t, >10t and >15t. Data for these variables are also presented for each of the 3-year periods 1973–75, 1976–78 and 1994–96 (Table 1.3), but the sizes of the three catch-classes are tripled to >15t, >30t and >45t. Adopting the same pattern of breakdown in terms of region, period (i.e. 1 year and 3 years) and catch-classes, the variables mean number of recaptured tags reported per 10 tonne of catch, number of 'non-reporter' vessels, number of 'reporter' vessels, and estimates of TRR are tabulated for the TRR Catch Method (Tables 2.1–2.3). Similarly, the variables number of vessels, catch, mean number of recaptured tags reported per 10 tonne of catch, number of observed recaptures from 'reporter' vessels, estimates of expected recaptures from all vessels, and estimates of TRR are tabulated for the TRR Tag Method (Tables 3.1–3.3).

The tag data and the TRR estimates for 1973–75 are expected to be more reliable than those for 1976–78 because of the presence of researchers working with industry during the earlier period but not during the later period. For all regions combined, the TRR estimates for the three 3-year periods 1973–75, 1976–78 and 1994–96 were 75–79%, 57–67% and 84–92%, respectively, from the TRR Catch Method (Table 2.3). Similarly, the TRR estimates for the three periods were 74–79%, 66–71% and 85–87%, respectively, from the TRR Tag Method (Table 3.3). The values of these 3-year estimates are generally higher those of 1-year estimates. The 1995 and 1996 1-year estimates are likely to be the most reliable 1-year estimates because they are based on the greatest amounts of data; these estimates are 69–80% for the TRR Catch Method and 72–79% for the TRR Tag Method.

There are several patterns in the estimates.

1. TRR is highly variable between SharkFAG region, year and 3-year period.
2. TRR tends to drop marginally as annual catch increases from > 5t to >10 t to >15 t.
3. TRR values are higher for 3-year estimates than for 1-year estimates.
4. TRR estimates for 1994–96 tend to be higher than those for 1973–78.
5. TRR estimates from the two methods agree closely.

Discussion

The validity of the estimates of the two methods depends on how well the assumptions hold and for the present analyses Assumptions 2 and 4 are most likely to be violated, particularly for 1973–78, because of the low numbers of tags available to be caught. Violation of Assumptions 2 and 4 biases TRR towards under-estimation by incorrectly classifying vessels not catching tags as 'non-reporters'. Assumption 4 is likely to be important because the tags are not distributed throughout a region such that they are available to all vessels operating within that region. The high variability in the estimates is also largely a result of making estimates from small numbers. The tendency for tag reporting rate to increase marginally as annual catch increases from >5 t to >10 t to >15 t is consistent with a reduced probability of violating Assumption 2.

Violation of Assumptions 2 and 4 is likely to be particularly important when comparing the 1973–78 estimates with the 1994–96 estimates. Far fewer tags were released during 1973–78 than during 1994–96 and given the stock biomass was much larger during 1973–78 than during 1994–96, it is expected that the number of tags captured per 10 tonne is much lower for 1973–78 than for 1994–96. Other potential biases are over-estimation of tag reporting rate caused by violation of Assumption 1 where 'reporters' fail to report all tag recaptured and by violation of Assumption 3 where 'non-reporters' under report a greater proportion of the catch than do the 'reporters'.

Table 1.1 Number of shark tags reported and the combined catch of gummy and school shark by non-reporters and reporters for three different minimum levels of annual catch within two of the seven school shark SharkFAG regions for the years 1973–78.

Year	SharkFAG region	Annual catch >5t				Annual catch >10t				Annual catch >15t			
		No. of tags		Catch (tonne)		No. of tags		Catch (tonne)		No. of tags		Catch (tonne)	
		Released	Recaptured	0 tags	>0 tags	Released	Recaptured	0 tags	>0 tags	Released	Recaptured	0 tags	>0 tags
1973	WBS	145	3	305	83	145	3	232	83	145	3	193	83
	EBS	367	19	493	563	367	19	452	563	367	19	402	563
	ALL	512	22	798	646	512	22	684	646	512	22	595	646
1974	WBS	31	8	220	117	31	6	186	102	31	5	174	90
	EBS	38	25	400	474	38	25	350	474	38	24	269	461
	ALL	69	33	620	591	69	31	536	576	69	29	443	551
1975	WBS	745	13	221	221	745	11	198	204	745	9	145	180
	EBS	159	26	350	498	159	25	298	488	159	25	226	488
	ALL	904	39	572	719	904	36	496	693	904	34	370	668
1976	WBS	220	13	163	206	220	11	140	191	220	10	95	180
	EBS	59	23	494	314	59	19	454	298	59	16	403	276
	ALL	279	36	658	520	279	30	594	489	279	26	497	457
1977	WBS	0	19	170	281	0	18	102	272	0	12	78	229
	EBS	0	11	516	226	0	10	483	218	0	10	457	218
	ALL	0	30	686	507	0	28	585	489	0	22	535	447
1978	WBS	0	20	230	198	0	15	185	173	0	12	158	145
	EBS	0	6	502	123	0	6	424	123	0	5	310	109
	ALL	0	26	732	321	0	21	609	296	0	17	468	253

Table 1.2 Number of shark tags reported and the combined catch of gummy and school shark by non-reporters and reporters for three different minimum levels of annual catch within each of the seven school shark SharkFAG regions for the years 1994, 1995 and 1996.

Year	SharkFAG region	Annual catch >5t				Annual catch >10t				Annual catch >15t			
		No. of tags		Catch (tonne)		No. of tags		Catch (tonne)		No. of tags		Catch (tonne)	
		Released	Recaptured	0 tags	>0 tags	Released	Recaptured	0 tags	>0 tags	Released	Recaptured	0 tags	>0 tags
1994	WSA	456	14	61	162	456	14	49	162	456	6	28	136
	CSA	132	18	312	228	132	15	249	220	132	14	197	205
	SAV	142	11	55	76	142	5	36	51	142	2	23	25
	WBS	651	15	292	240	651	15	209	240	651	15	175	240
	EBS	1209	122	94	570	1209	93	47	493	1209	85	32	458
	WT	4	0	137	0	4	0	119	0	4	0	82	0
	ET	253	0	133	0	253	0	117	0	253	0	92	0
	ALL	2847	180	1083	1276	2847	142	826	1166	2847	122	629	1064
1995	WSA	611	33	40	191	611	32	28	185	611	27	0	158
	CSA	571	98	248	261	571	97	207	252	571	85	165	227
	SAV	160	20	31	108	160	20	31	108	160	12	31	70
	WBS	646	76	132	463	646	75	103	457	646	73	69	433
	EBS	555	145	66	635	555	130	25	601	555	124	25	576
	WT	493	7	28	56	493	7	0	56	493	7	0	56
	ET	176	0	124	0	176	0	112	0	176	0	89	0
	ALL	3212	379	668	1714	3212	361	506	1660	3212	328	378	1520
1996	WSA	3	55	36	238	3	55	28	238	3	47	16	211
	CSA	33	100	224	410	33	93	169	382	33	81	134	358
	SAV	19	31	14	79	19	28	0	64	19	8	0	17
	WBS	506	56	123	225	506	51	96	204	506	46	45	169
	EBS	288	53	181	457	288	43	134	414	288	39	98	390
	WT	60	2	11	11	60	2	11	11	60	0	0	0
	ET	502	14	79	81	502	14	57	81	502	8	45	70
	ALL	1411	311	668	1501	1411	286	495	1395	1411	229	338	1214

Table 1.3 Number of shark tags reported and the combined catch of gummy and school shark by non-reporters and reporters for three different minimum levels of combined catch within two of the seven school shark SharkFAG regions for the periods 1973–75, 1976–78 and 1994–96.

Period	SharkFAG region	Combined catch >15t				Combined catch >30t				Combined catch >45t			
		No. of tags		Catch (tonne)		No. of tags		Catch (tonne)		No. of tags		Catch (tonne)	
		Released	ecaptured	0 tags	>0 tags	Released	ecaptured	0 tags	>0 tags	Released	ecaptured	0 tags	>0 tags
1973–75	WBS	921	21	400	619	921	13	340	489	921	12	306	449
	EBS	564	70	523	2141	564	65	423	2026	564	62	315	1950
	ALL	1485	91	923	2760	1485	78	763	2515	1485	74	621	2399
1976–78	WBS	220	45	359	762	220	37	324	671	220	33	189	601
	EBS	59	34	969	988	59	33	745	966	59	32	579	935
	ALL	279	79	1328	1750	279	70	1069	1637	279	65	768	1536
1994–96	WBS	1803	134	289	843	1803	72	116	500	1803	41	50	219
	EBS	2052	248	155	1423	2052	118	31	832	2052	65	0	375
	ALL	3855	382	444	2266	3855	190	147	1332	3855	106	50	594

Table 2.1 Tag reporting rate from catch method' for three different levels of annual catch within two of the seven school shark SharkFAG regions for the years 1973–1978.

Tag reporting rate from catch is defined as sum of catches from 'reporters' / total catch.

Year	SharkFAG region	Annual catch >5t				Annual catch >10t				Annual catch >15t			
		Tag/10t	No. Vessels		Reporting rate	Tag/10t	No. Vessels		Reporting rate	Tag10/t	No. Vessels		Reporting rate
			0 tag	>0 tag			0 tag	>0 tag			0 tag	>0 tag	
1973	WBS	0.08	20	3	0.21	0.10	12	7	0.26	0.11	13	9	0.26
	EBS	0.18	21	14	0.53	0.19	23	13	0.55	0.20	20	15	0.55
	ALL	0.15	41	17	0.45	0.17	35	20	0.49	0.18	33	24	0.49
1974	WBS	0.24	10	3	0.35	0.21	8	5	0.35	0.19	9	7	0.35
	EBS	0.29	15	14	0.54	0.30	16	13	0.58	0.33	13	14	0.58
	ALL	0.27	25	17	0.49	0.28	24	18	0.52	0.29	22	21	0.52
1975	WBS	0.29	7	3	0.50	0.27	7	4	0.51	0.28	5	5	0.51
	EBS	0.31	11	14	0.59	0.32	10	12	0.62	0.35	7	14	0.62
	ALL	0.30	18	17	0.56	0.30	17	16	0.58	0.33	12	19	0.58
1976	WBS	0.35	11	8	0.56	0.33	15	10	0.58	0.36	14	12	0.58
	EBS	0.28	24	12	0.39	0.25	24	8	0.40	0.24	31	5	0.40
	ALL	0.31	35	20	0.44	0.28	39	18	0.45	0.27	45	17	0.45
1977	WBS	0.42	8	6	0.62	0.48	5	9	0.73	0.39	8	8	0.73
	EBS	0.15	19	10	0.30	0.14	19	7	0.31	0.15	20	5	0.31
	ALL	0.25	27	16	0.42	0.26	24	16	0.46	0.22	28	13	0.46
1978	WBS	0.47	4	5	0.46	0.42	3	6	0.48	0.40	6	6	0.48
	EBS	0.10	15	8	0.20	0.11	17	7	0.23	0.12	11	4	0.23
	ALL	0.25	19	13	0.31	0.23	20	13	0.33	0.24	17	10	0.33

Table 2.2 Tag reporting rate from catch method' for three different levels of annual catch within each of the seven school shark SharkFAG regions for the years 1994, 1995 and 1996.

Tag reporting rate is defined as sum of catches from 'reporters' / total catch.

Year	SharkFAG region	Annual catch >5t				Annual catch >10t				Annual catch >15t			
		Tag/10t	No. Vessels		Reporting	Tag/10t	No. Vessels		Reporting	Tag10/t	No. Vessels		Reporting
			0 tag	>0 tag	rate		0 tag	>0 tag	rate		0 tag	>0 tag	rate
1994	WSA	0.63	5	5	0.73	0.67	4	7	0.77	0.37	3	9	0.83
	CSA	0.33	22	8	0.42	0.32	15	9	0.47	0.35	14	16	0.51
	SAV	0.84	5	6	0.58	0.58	1	6	0.59	0.42	2	7	0.51
	WBS	0.28	22	9	0.45	0.33	9	15	0.53	0.36	10	13	0.58
	EBS	1.84	10	28	0.86	1.72	6	26	0.91	1.74	13	20	0.93
	WT	0.00	9	0	0.00	0.00	4	1	0.00	0.00	1	1	0.00
	ET	0.00	6	0	0.00	0.00	7	0	0.00	0.00	6	3	0.00
	ALL	0.76	79	56	0.54	0.71	46	64	0.59	0.72	49	69	0.63
1995	WSA	1.43	3	5	0.83	1.50	2	6	0.87	1.71	2	9	1.00
	CSA	1.92	13	7	0.51	2.11	10	8	0.55	2.17	6	12	0.58
	SAV	1.44	2	3	0.78	1.44	1	6	0.78	1.19	0	5	0.69
	WBS	1.28	10	9	0.78	1.34	5	14	0.82	1.45	6	10	0.86
	EBS	2.07	3	18	0.91	2.08	1	21	0.96	2.06	7	15	0.96
	WT	0.83	6	0	0.67	1.25	0	1	1.00	1.25	1	1	1.00
	ET	0.00	4	0	0.00	0.00	5	0	0.00	0.00	3	3	0.00
	ALL	1.59	41	42	0.72	1.67	24	56	0.77	1.73	25	55	0.80
1996	WSA	2.00	1	3	0.87	2.06	0	4	0.89	2.07	1	7	0.93
	CSA	1.58	9	6	0.65	1.69	6	6	0.69	1.65	3	10	0.73
	SAV	3.34	1	1	0.85	4.37	1	3	1.00	4.78	0	1	1.00
	WBS	1.61	7	9	0.65	1.70	2	12	0.68	2.14	2	7	0.79
	EBS	0.83	2	15	0.72	0.78	1	19	0.76	0.80	4	13	0.80
	WT	0.92	3	0	0.50	0.92	0	1	0.50	na[A]	na[A]	na[A]	na[A]
	ET	0.88	2	0	0.51	1.01	3	0	0.59	0.70	2	2	0.61
	ALL	1.43	25	34	0.69	1.51	13	45	0.74	1.48	12	40	0.78

[A] not applicable

Table 2.3 Tag reporting rate from catch method' for three different levels of combined catch within two of the seven school shark SharkFAG regions for the periods 1973–75, 1976–78 and 1994–96.

Tag reporting rate is defined as sum of catches from 'reporters' / total catch.

Period	SharkFAG region	Combined catch >15t				Combined catch >30t				Combined catch >45t			
		Tag/10t	No. Vessels		Reporting rate	Tag/10t	No. Vessels		Reporting rate	Tag10/t	No. Vessels		Reporting rate
			0 tag	>0 tag			0 tag	>0 tag			0 tag	>0 tag	
1973–75	WBS	0.21	8	13	0.61	0.16	5	7	0.59	0.16	4	6	0.59
	EBS	0.26	13	25	0.80	0.27	8	20	0.83	0.27	5	18	0.86
	ALL	0.25	21	38	0.75	0.24	13	27	0.77	0.25	9	24	0.79
1976–78	WBS	0.40	3	7	0.68	0.37	7	9	0.67	0.42	9	14	0.76
	EBS	0.17	8	11	0.50	0.19	13	12	0.56	0.21	23	13	0.62
	ALL	0.26	11	18	0.57	0.26	20	21	0.60	0.28	32	27	0.67
1994–96	WBS	1.18	11	28	0.74	1.17	3	12	0.81	1.52	1	4	0.81
	EBS	1.57	7	47	0.90	1.37	1	20	0.96	1.73	0	7	1.00
	ALL	1.41	18	75	0.84	1.28	4	32	0.90	1.65	1	11	0.92

Table 3.1 'Tag reporting rate from tags per unit catch method' for three different levels of annual catch within two of the seven school shark SharkFAG regions for the years 1973–1978.

Tag recaptures expected is defined as the number of tags recaptured divided by 10 tonne multiplied by the total catch. Tag reporting rate is defined as number of tag recaptures observed divided by number of tag recaptures expected.

Year	SharkFAG region	All vessels					Reporter vessel annual catch > 5t			Reporter vessel annual catch > 10t			Reporter vessel annual catch > 15t		
		No. vessel	Total Catch (t)	Recaptures			Tag/10t	Recaptures expected	Reporting rate	Tag/10t	Recaptures expected	Reporting rate	Tag/10t	Recaptures expected	Reporting rate
				No. vessel	Observed	Tag/10t									
1973	WBS	62	427	3	3	0.07	0.36	15	0.19	0.36	15	0.19	0.36	15	0.19
	EBS	76	1107	14	19	0.17	0.34	37	0.51	0.34	37	0.51	0.34	37	0.51
	ALL	138	1534	17	22	0.14	0.34	52	0.42	0.34	52	0.42	0.34	52	0.42
1974	WBS	66	419	12	13	0.31	0.68	29	0.45	0.59	25	0.53	0.55	23	0.56
	EBS	93	950	15	27	0.28	0.53	50	0.54	0.53	50	0.54	0.52	50	0.55
	ALL	159	1369	27	40	0.29	0.56	76	0.52	0.54	74	0.54	0.53	72	0.56
1975	WBS	57	483	9	13	0.27	0.59	28	0.46	0.54	26	0.50	0.50	24	0.54
	EBS	67	880	17	29	0.33	0.52	46	0.63	0.51	45	0.64	0.51	45	0.64
	ALL	124	1363	26	42	0.31	0.54	74	0.57	0.52	71	0.59	0.51	69	0.61
1976	WBS	60	439	10	17	0.39	0.63	28	0.61	0.58	25	0.67	0.55	24	0.70
	EBS	65	842	13	24	0.29	0.73	62	0.39	0.64	54	0.45	0.58	49	0.49
	ALL	125	1281	23	41	0.32	0.69	89	0.46	0.61	79	0.52	0.57	73	0.56
1977	WBS	68	504	12	22	0.44	0.68	34	0.64	0.66	33	0.66	0.52	26	0.83
	EBS	74	797	11	15	0.19	0.49	39	0.39	0.46	37	0.41	0.46	37	0.41
	ALL	142	1301	23	37	0.28	0.59	77	0.48	0.57	74	0.50	0.49	64	0.58
1978	WBS	78	484	17	28	0.58	1.01	49	0.57	0.87	42	0.67	0.83	40	0.70
	EBS	98	687	5	6	0.09	0.49	33	0.18	0.49	33	0.18	0.46	32	0.19
	ALL	176	1171	22	34	0.29	0.81	95	0.36	0.71	83	0.41	0.67	79	0.43

Table 3.2 'Tag reporting rate from tags per unit catch method' for three different levels of annual catch within each of the seven school shark SharkFAG regions for the years 1994, 1995 and 1996.

Tag recaptures expected is defined as the number of tags recaptured divided by 10 tonne multiplied by the total catch. Tag reporting rate is defined as number of tag recaptures observed divided by number of tag recaptures expected.

Year	SharkFAG region	All vessels					Reporter vessel annual catch > 5t			Reporter vessel annual catch > 10t			Reporter vessel annual catch > 15t		
		No. vessel	Total Catch (t)	Recaptures			Tag/10t	Recaptures expected	Reporting rate	Tag/10t	Recaptures expected	Reporting rate	Tag/10t	Recaptures expected	Reporting rate
				No. vessel	Observed	Tag/10t									
1994	WSA	43	249	5	14	0.56	0.87	22	0.65	0.87	22	0.65	0.44	11	1.28
	CSA	173	614	8	18	0.29	0.79	48	0.37	0.68	42	0.43	0.68	42	0.43
	SAV	58	177	11	20	1.13	1.45	26	0.78	0.98	17	1.15	0.81	14	1.39
	WBS	88	567	12	20	0.35	0.62	35	0.57	0.62	35	0.57	0.62	35	0.57
	EBS	110	723	32	128	1.77	2.14	155	0.83	1.89	137	0.94	1.86	135	0.95
	WT	55	163	1	1	0.06	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00
	ET	93	181	3	9	0.50	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00
	ALL	620	2673	72	210	0.79	1.41	377	0.56	1.22	326	0.64	1.15	307	0.68
1995	WSA	53	246	8	35	1.42	1.73	43	0.82	1.73	43	0.82	1.71	42	0.83
	CSA	280	585	11	100	1.71	3.75	219	0.46	3.84	225	0.45	3.74	219	0.46
	SAV	75	191	13	28	1.47	1.85	35	0.79	1.85	35	0.79	1.71	33	0.86
	WBS	64	638	21	82	1.28	1.64	105	0.78	1.64	105	0.78	1.69	108	0.76
	EBS	84	746	29	153	2.05	2.28	170	0.90	2.16	161	0.95	2.15	160	0.95
	WT	33	105	4	16	1.52	1.25	13	1.22	1.25	13	1.22	1.25	13	1.22
	ET	56	162	4	24	1.48	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00
	ALL	645	2673	90	438	1.64	2.21	591	0.74	2.17	580	0.76	2.16	577	0.76
1996	WSA	50	295	12	61	2.07	2.31	68	0.90	2.31	68	0.90	2.22	65	0.93
	CSA	283	691	17	101	1.46	2.44	169	0.60	2.44	169	0.60	2.27	157	0.64
	SAV	80	140	13	40	2.85	3.95	55	0.72	4.37	61	0.65	4.78	67	0.60
	WBS	75	394	18	79	2.01	2.49	98	0.81	2.50	98	0.80	2.71	107	0.74
	EBS	111	680	22	55	0.81	1.16	79	0.70	1.04	71	0.78	1.00	68	0.81
	WT	73	51	5	15	2.92	1.84	9	1.59	1.84	9	1.59	na[A]	na[A]	na[A]
	ET	103	194	5	16	0.82	1.72	33	0.48	1.72	33	0.48	1.15	22	0.72
	ALL	775	2446	92	367	1.50	2.07	506	0.72	2.05	501	0.73	1.89	462	0.79

[A] not applicable

Table 3.3 'Tag reporting rate from tags per unit catch method' for three different levels of combined catch within each of the seven school shark SharkFAG regions for the periods 1973–75, 1976–78 and 1994–

Tag recaptures expected is defined as the number of tags recaptured divided by 10 tonne multiplied by the total catch. Tag reporting rate is defined as number of tag recaptures observed divided by number of tag recaptures expected.

Period	SharkFAG	All vessels					Reporter vessel combined catch > 15t			Reporter vessel combined catch > 30t			Reporter vessel combined catch > 45t		
	region	No. vessel	Total	Recaptures			Tag/10t	Recaptures	Reporting	Tag/10t	Recaptures	Reporting	Tag/10t	Recaptures	Reporting
			Catch (t)	No. vessel	Observed	Tag/10t		expected	rate		expected	rate		expected	rate
1973–75	WBS	185	1328	24	29	0.22	0.34	45	0.64	0.27	35	0.82	0.27	35	0.82
	EBS	236	2937	46	75	0.26	0.33	96	0.78	0.32	94	0.80	0.32	93	0.80
	ALL	421	4265	70	104	0.24	0.33	141	0.74	0.31	132	0.79	0.31	132	0.79
1976–78	WBS	206	1427	39	67	0.47	0.59	84	0.80	0.55	79	0.85	0.55	78	0.86
	EBS	237	2326	29	45	0.19	0.34	80	0.56	0.34	79	0.57	0.34	80	0.57
	ALL	443	3753	68	112	0.30	0.45	169	0.66	0.43	160	0.70	0.42	159	0.71
1994–96	WSA	146	791	25	110	1.39	1.46	115	0.95	1.45	115	0.96	1.66	131	0.84
	CSA	736	1890	36	219	1.16	1.63	308	0.71	1.61	304	0.72	1.69	319	0.69
	SAV	213	508	37	88	1.73	2.08	106	0.83	2.09	106	0.83	2.40	122	0.72
	WBS	227	1598	51	181	1.13	1.28	205	0.88	1.30	208	0.87	1.35	216	0.84
	EBS	305	2149	83	336	1.56	1.65	355	0.95	1.67	359	0.94	1.62	348	0.97
	WT	161	319	10	32	1.00	0.79	25	1.27	0.79	25	1.27	0.79	25	1.27
	ET	252	537	12	49	0.91	0.43	23	2.12	0.30	16	3.04	0.30	16	3.04
	ALL	2040	7792	254	1015	1.30	1.51	1177	0.86	1.50	1169	0.87	1.54	1200	0.85

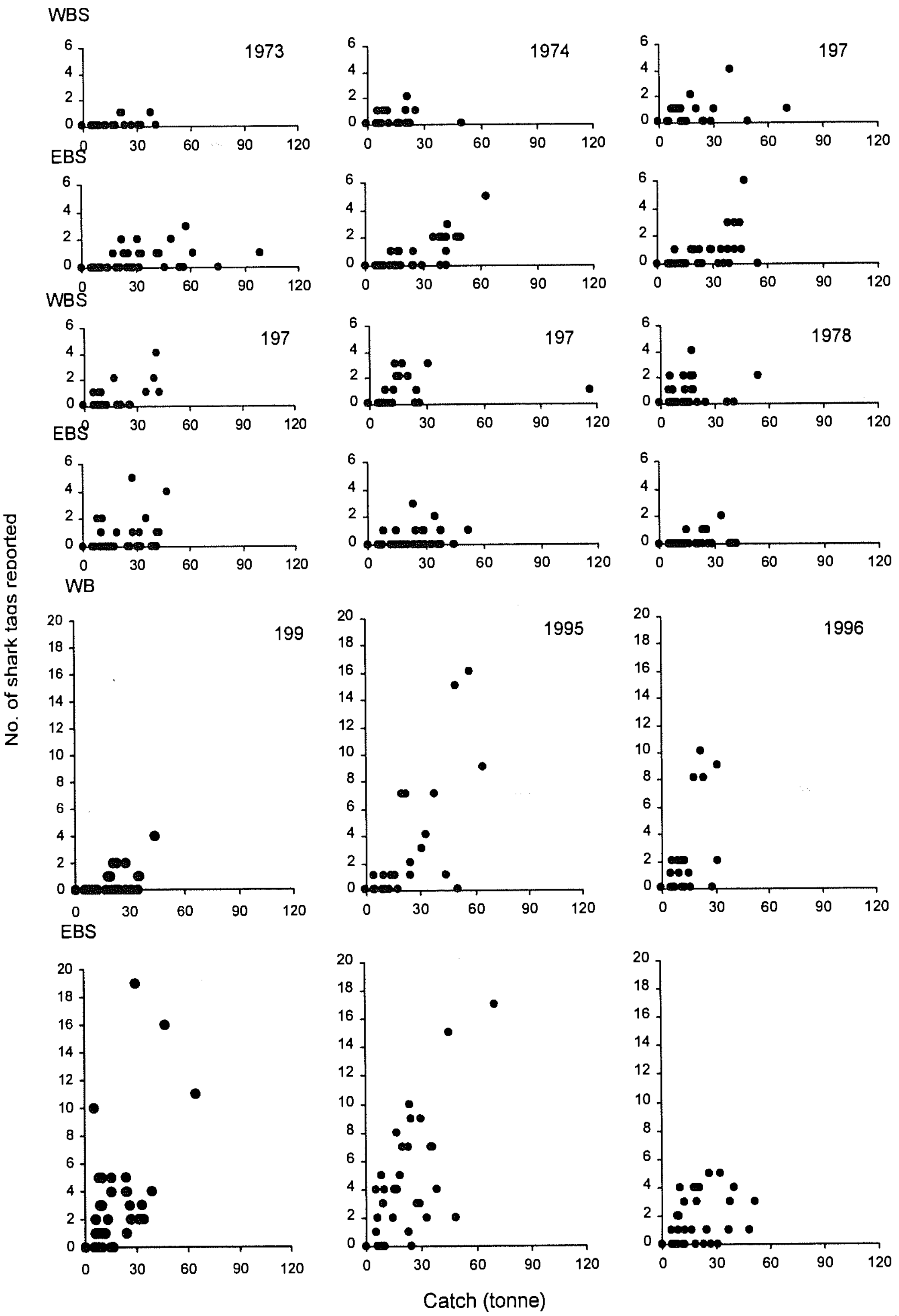

Fig. 1.1 Number of shark tags reported against the annual catch of each vessel operating within two of the seven school shark SharkFAG regions for the years 1973–1978 and 1994–96.

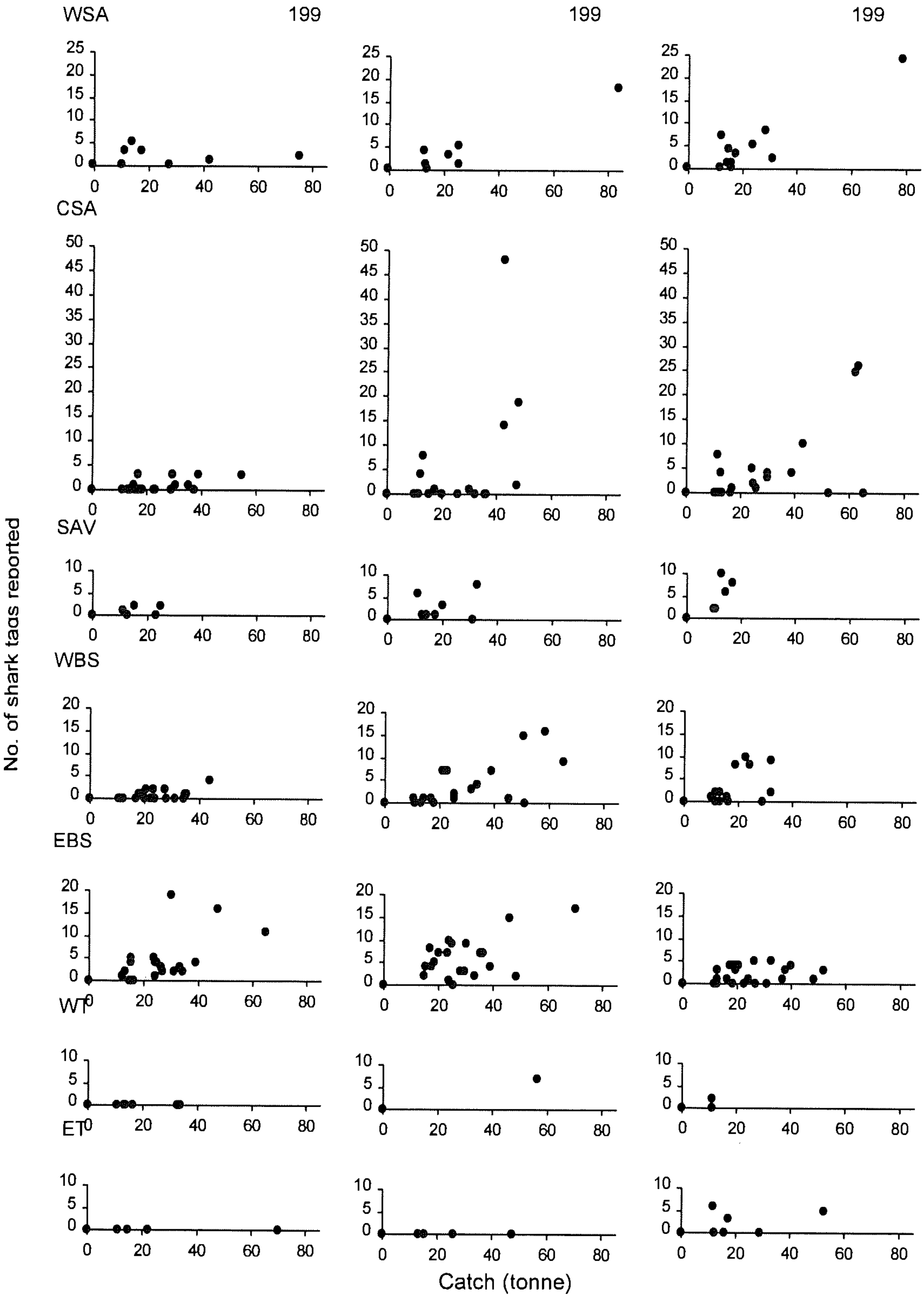

Fig. 1.2 Number of shark tags reported against the annual catch of each vessel operating within each of the seven school shark SharkFAG regions for the years 1994, 1995 and 1996.

Appendix 6. Publications & reports about the project or using data from project

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MARINE & FRESHWATER RESOURCES INSTITUTE

QUEENSCLIFF OFFICE Weeroona Parade Queenscliff Victoria PO Box 114 Queenscliff Victoria 3225 Australia
MAIN SWITCH Ph: (03) 5258 0111 Fax: (03) 5258 0270 MARINE DISCOVERY CENTRE Ph: (03) 5258 3344 Fax: (03) 5258 1435

BM 3833