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**SPATIAL STRUCTURE IN SOUTH PACIFIC SWORDFISH STOCKS AND
ASSESSMENT MODELS**

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Spatial structure in South Pacific Swordfish Stocks and Assessment Models

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Abstract

This paper describes the evidence used to define the spatial structure of the South-West Pacific swordfish stock assessment in 2006, reviews the arguments used in other swordfish fisheries, and describes a new structure that was proposed to the April 2008 swordfish assessment workshop (WCPFC-SC4-2008/SA-IP-1) and adopted for the 2008 assessment (WCPFC-SC4-2008/SA-WP-6, WCPFC-SC4-2008/SA-WP-7). The 2006 spatial structure was based on observations from larval distributions, genetic connectivity studies, and fishery characteristics, including fleet distributions and seasonal patterns in catch, CPUE, and size composition. Since the 2006 assessment, additional studies have been published on swordfish genetics, and several Pop-up Satellite Archival Tags (PSATs) have been deployed in Australia and New Zealand. The new spatial structure is revised in relation to 1) the qualitative description of movements from individual tagged fish (including a handful of conventional tags), 2) the WCPFC request to encompass the broader South Pacific convention area in the assessment, and 3) simplification of the latitudinal structure that was problematic in 2006. Quantitative methods of using the tagging data are discussed, diffusion rates are estimated, and bulk transfer coefficients are calculated for the new spatial structure.

Introduction

Broadbill swordfish (*Xiphias gladius*) is a highly migratory and broadly distributed pelagic species found throughout most of the tropical and temperate regions of the oceans. Because of the potential for large-scale dispersive migration and/or seasonal spawning/foraging migrations, it is difficult to identify the stock structure that is most appropriate for the purposes of population assessment and fishery management. This paper i) provides a review of the relevant data used in defining the SW Pacific spatial structure used in the 2006 assessment (Kolody et al. 2006, Davies et al. 2006), ii) examines the arguments applied in other swordfish fisheries, and describes a revised spatial structure for the 2008 assessment. This paper was initially prepared for the *Southern WCPO Swordfish Assessment Workshop*, held at the Secretariat of the Pacific Community 16-18 Apr 2008 (Anon. 2008), and has been updated to reflect some new information obtained at the workshop.

The model domain adopted in the 2006 assessment was defined in relation to the need for Australian and New Zealand domestic management advice. The spatial boundary was delineated in consideration of the data available at the time (e.g. qualitatively

described in Kolody et al. 2006), but it was recognized that most of these data provide only indirect evidence for movement and stock structure. That assessment included only the South-West Pacific, whereas the Conservation and Management Measure (CMM2006-3) based on the assessment covered the whole WCPFC convention area, South of 20°S (see Figure 1). This represents a substantial mismatch in area between the scientific advice and management measure (and we cannot find documentation that explains the reasoning).

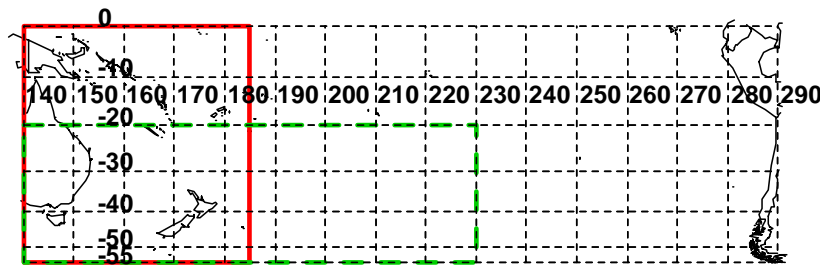


Figure 1. South Pacific map illustrating 2006 swordfish assessment domain (solid red box), and area of application of WCPFC Conservation and Management Measure 2006-3 (broken green box).

The Commission explicitly requested assessment advice in 2008 in relation to the broader South Pacific region. This potentially includes the south-eastern Pacific (outside of the WCPFC convention area) if the request is interpreted literally.

The internal structure of the assessment assumed in 2006 is illustrated in Figure 2 (areas 1-5 only). There is an ongoing debate about how much spatial structure to include in an assessment, and the preference for regional swordfish assessments (eastern Pacific, north Pacific, north Atlantic, and Indian Ocean) has generally been to use a spatially aggregated structure. The motivation for a disaggregated structure in the SW Pacific was largely driven by the perception of serial local depletion, particularly in the Australian Eastern Tuna and Billfish Fishery (ETBF) (e.g. Figure 3), which suggests heterogeneous structure within what is assumed to be a single population. It seems reasonably clear that the fishery has had an effect on the population in this area, but it remains unclear how quickly the stocks mix, and what the appropriate spatial considerations are for effectively managing the stock.

There were a number of problems noted in relation to the internal structure of the 2006 assessment (Kolody et al. 2006), including:

- The spatial split adopted between the southern (SBT-targeting) and northern (all other) longline fisheries did not result in an entirely satisfactory delineation of fleets. i.e. Notably the Australian fleet seemed to show a mix of northern and southern fishery size composition characteristics (the SBT-

targeting fleet tends to catch predominantly very large female swordfish). Furthermore, partitioning the southern region as a fundamentally different fleet did not allow the effective sharing of fishery catchability and selectivity parameters across regions, such that the model had the potential to estimate very high or low southern sub-population abundance that was inconsistent with expectations.

- With only indirect evidence of movement, the migration rates estimated in the model were not expected to be very reliable, and some of the results seemed counter-intuitive.
- The CPUE estimates from different fleets (Japan and Australia) operating in the same area suggested very similar annual trends, but differing patterns of seasonal abundance. This suggests that seasonal fluctuations in CPUE represent a confounding of movement and catchability effects for one or both fleets. As such it is clear that the seasonal CPUE patterns cannot be interpreted directly as movement.

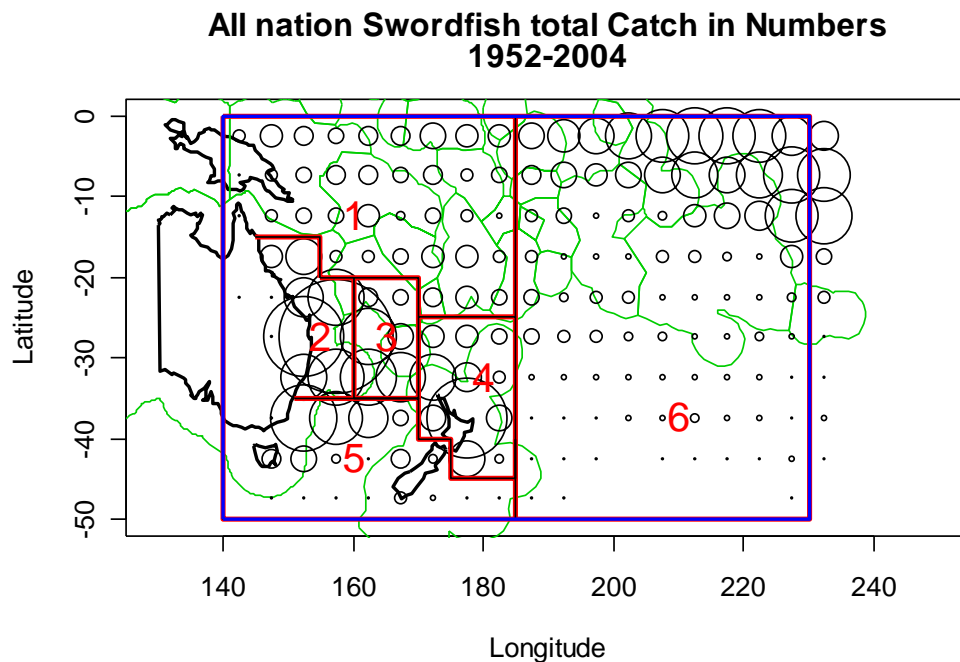


Figure 2. Spatial structure of the SW Pacific swordfish assessment in 2006 (Kolody et al. 2006). Area 6 was initially defined for sensitivity trials but this was not pursued. The area of the black circles represents the relative catch in each $5 \times 5^\circ$ region summed over the period 1952-2004.

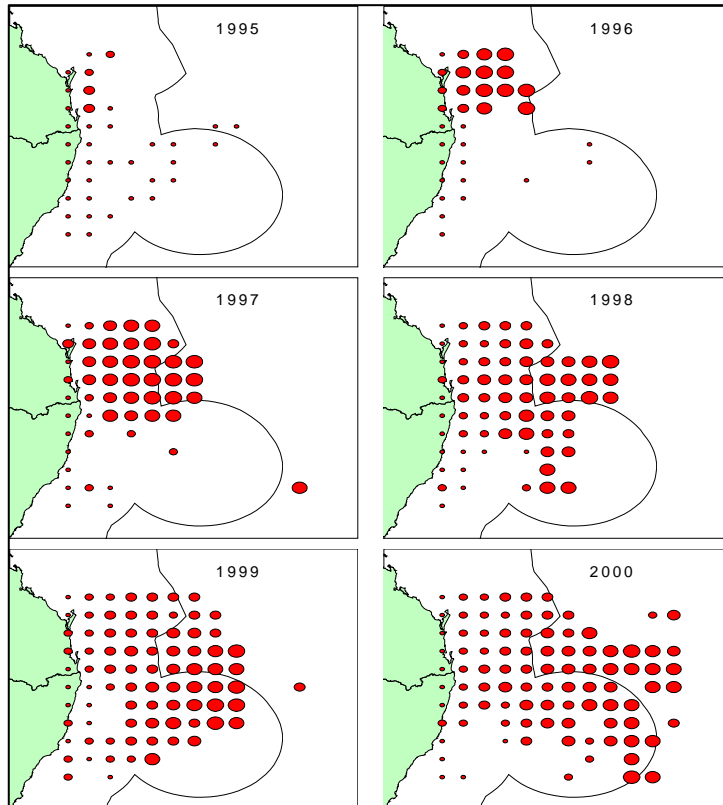


Figure 3. Potential evidence for sequential depletion and spatial heterogeneity observed during the development of the Australian Eastern Tuna and Billfish longline fishery. Circles are proportional to the catch rates. Figure from Campbell and Hobday (2003).

In redefining the spatial boundaries to be applied in the 2008 assessment, we review evidence from the following:

- Population genetics
- Spawning distributions inferred from larval distribution surveys and maturity studies
- Catch demographics (catch rates and size composition)
- PSAT tag tracks and conventional tag release/recoveries

We note that similar lines of evidence were used by Hinton and Alvarado Bremer (2006) to examine spatial structure, particularly in relation to the Eastern Pacific. The tags provide the most substantive new evidence, in that the movements of (a small number of) individual fish have been observed directly.

There are also additional considerations in the formulation of assessment boundaries that are not driven by swordfish biology, including:

- Fishery structure
- Data quality, quantity and accessibility
- Tractable limits of assessment model representation and parameter estimation
- Commission convention boundaries

After a largely qualitative discussion and synthesis of these factors, some new boundaries were proposed as a basis for discussion at the *Southern WCPO swordfish assessment workshop* (Anon. 2008). A quantitative analysis of the tagging data is described in which diffusion parameters were estimated, and these parameters were translated into bulk transfer coefficients that were used directly in the stock assessment (Kolody et al. 2008, Davies et al. 2008).

Population Genetics

Genetic differences among regions can provide strong evidence for distinct populations, however, the absence of genetic differences does not provide sufficient evidence to conclude that there is a single spawning stock, or a justification for assuming a homogenous population structure in an assessment model. In some cases, the genetic markers examined might not be sufficiently informative, or sample sizes too small, for population differences to be detected. Relatively few dispersers (of any age), could result in substantive genetic mixing. However, whether or not there are genetically identifiable sub-populations, the mixing rates might be relatively slow, and there may be important implications for fishery management.

Reeb et al. (2000), suggests a broad “ \supset ”-shaped genetic connectivity pattern for swordfish in the Pacific Ocean, such that the SW and NW Pacific populations seem to be the most distinct from each other (Figure 4), with central and eastern populations intermediate between the two (and the SW Pacific indistinguishable from the eastern Indian Ocean). Alvarado Bremer et al. (2006) were able to conclude that the South-East Pacific stock was genetically distinct from the North-East and South-West. They collected additional evidence to suggest that the South-Central Pacific might represent a population intermediate between the SW and SE, (and North-Central and NE), but it was recognized that sample sizes in the South-Central region were not sufficient to be conclusive (Michael Hinton, IATTC, pers. comm.).

There is currently not much evidence to indicate that swordfish stocks from the Eastern Indian Ocean and SW Pacific are separate, (e.g. Reeb et al. 2000 pooled samples from these regions because sample sizes were small from both regions). However, the potential migration corridors around the north and south of Australia are thought to have relatively low swordfish densities. Given the distances involved, it seems unlikely that the Indo-Pacific mixing would be substantive (though larval drift through the northern route might not be trivial).

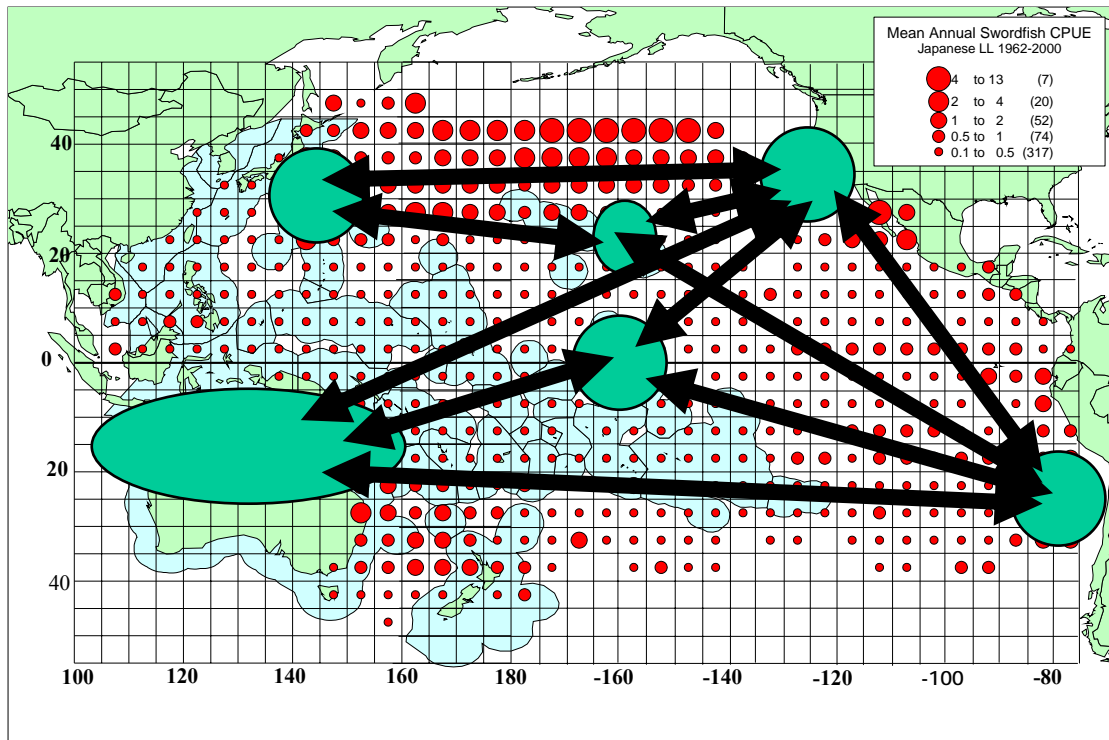


Figure 4. Schematic representation of swordfish genetic connectivity in the Pacific Ocean (after Reeb et al. 2000). Green circles indicate sample locations. Samples linked by arrows are more closely related than those that are not linked. Red circles indicate mean annual swordfish catch rates from the Japanese longline fleet (1962-2000), as an approximation of swordfish density.

Larval Distribution Surveys and Maturity Studies

Japanese studies of larval distributions from the 1950s-80s (Nishikawa et al. 1985) provide some indication of likely spawning locations in the Pacific, although spatial and temporal coverage in the South Pacific is patchy. In the South Pacific, substantive larvae concentrations were identified in the tropical/subtropical waters near the North-east coast of Australia, and lesser concentrations are found in more Eastern regions of the South Pacific (Figure 5). These data suggest a major spawning ground off NE Australia, and a maximal latitudinal bound for spawning activity. In the 2006 assessment, it was assumed that the area off NE Australia was the main spawning area in the SW Pacific (however, this assumption was only relevant for the site-fidelity models, and did not affect the final assessment results which were based on a homogenous mixing assumption that assumed that all spawners contributed to recruitment irrespective of location). The PSAT tag tracks (see below) suggest that SW Pacific swordfish might be migrating from southern foraging grounds toward Northern spawning grounds (which meet warm temperature characteristics typical of billfish spawning), without any obvious longitudinal preference. If the NE coast of Australia actually is a particularly dense spawning region, it might reflect a larger population in the Western-most region of the South Pacific, rather than any substantive longitudinal spawning migration. However, it is equally plausible that the aggregate larval survey results might reflect spatial and temporal sampling biases.

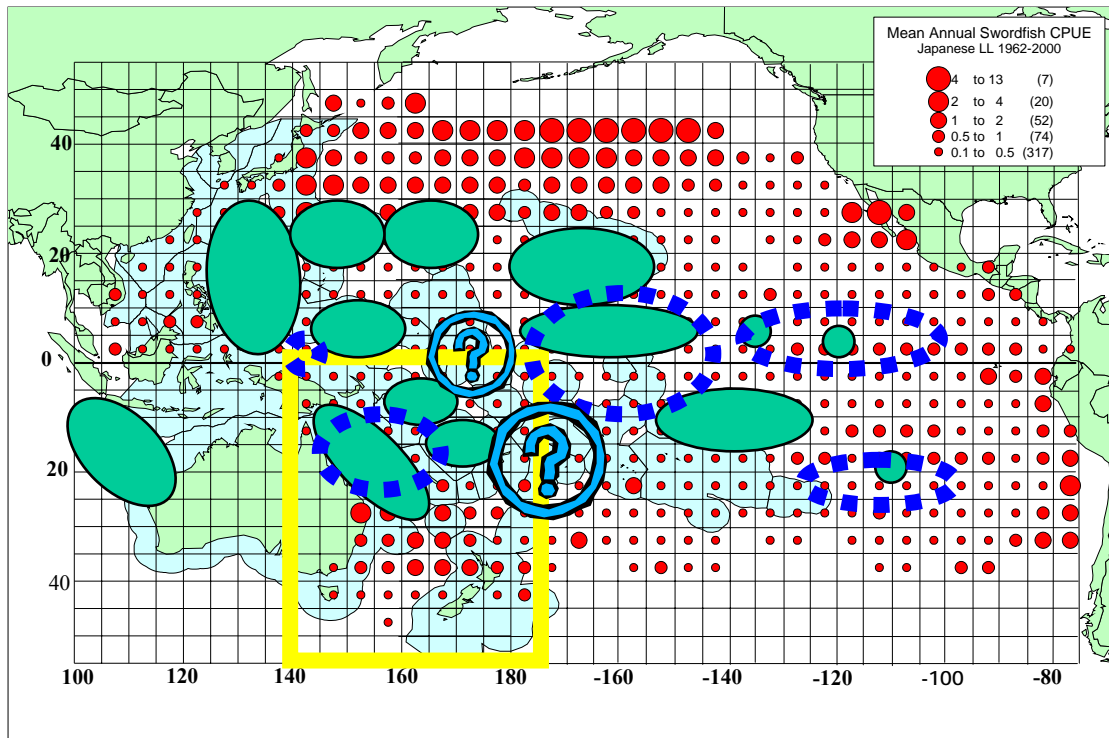


Figure 5. Cartoon of likely swordfish spawning regions in the Pacific. Larval distributions observed in Japanese surveys are approximated by (solid) green ovals. Areas with substantial numbers of mature females estimated from Spanish and Australian catch sampling are approximated by (broken) blue ovals. Yellow box indicates SW Pacific region defined for stock assessment in 2006. Question marks indicate regions in the South-West/South-Central Pacific that are particularly poorly sampled by maturity studies.

Anecdotal evidence presented at the swordfish workshop (Anon. 2008) revealed that substantial numbers of very small swordfish were observed recently in the Cook Islands, and this was considered unusual.

Regions with likely active spawning as inferred from maturity studies suggest broad areas of overlap with the larval distributions (Figure 5). Young and Drake (2002) describe the spatial distribution of mature spawners observed in the Australian Eastern Tuna and Billfish Fishery (ETBF). They estimate that spawning occurs in waters warmer than 24°C, with higher proportions of active spawners observed north of 27°N in the SW Pacific spawning season. This study did not include any samples from the region East of 168°E and north of 35°S. Mejuto et al. (2008) describe spawning activity from collections made by the Spanish longline fleet operating throughout the Pacific. They observed relatively few mature (active) female spawners south of 10°S in the SW Pacific, but very few samples were taken from the region 10-25°S. However, they did find a high proportion of active spawners in the equatorial region 10°N-10°S east of 180°. It is unclear to what extent the central equatorial spawners contribute to northern or southern hemisphere populations. This study had very little equatorial sampling west of 180°. If there are substantial numbers of spawners in this region, then they presumably contribute to the populations of either the northern or southern hemisphere (i.e. because Reeb et al. 2000 suggest that the northern and southern populations in the western Pacific are genetically distinct).

Catch Demographics

Commercial fisheries data in the South Pacific are described in more detail in Campbell et al. (2008), and Campbell (2008). We only mention summary points below in reference to figures in those documents.

Catch and CPUE Distributions

Figure 2 illustrates the distribution of total swordfish catches in the South Pacific WCPFC convention area (summed over time). There are two major concentrations of catch: the northern Tasman Sea to southern Coral Sea area (~20-40° S), and the South-Central equatorial region. In contrast, the mean CPUE estimates from the Japanese fleet suggest only one major concentration (the Tasman-Coral Sea region, Figure 4). The difference between the catch and CPUE distributions reflects the enormous amount of longline effort targeted at the tropical tunas in the equatorial region. CPUE is generally considered to be the more appropriate measure of fish density, and on this basis alone, it is easy to recognize 3-4 large-scale swordfish concentrations in the Pacific: North-West, South-West, and Eastern. Further scrutiny, and other lines of evidence suggest a northern and southern delineation in the Eastern Pacific (e.g. Hinton and Bremer 2006).

Size Composition

Unfortunately, size composition sampling in the South-West Pacific has been limited for most fleets. However, a couple important size trends are evident:

- In the SW Pacific, there seems to be a seasonal cycle of larger fish tending to be relatively more abundant in the tropical spawning regions (off Central-Northern Australia) in quarters 1 and 4, and conversely more abundant in the southern waters (e.g. New Zealand) during quarters 2 and 3. This is strongly suggestive of spawning migrations.
- The southern SBT-targeting fisheries in the SW Pacific tend to catch predominantly very large, (mostly female) swordfish (though in relatively small numbers) as by-catch.
- Declining size trends have been observed in the western part of the Australian fishery for the last few years, which is suggestive of a depletion effect. However, due to the poor size sampling, it is unclear whether these trends are occurring in the other fisheries.

Spatial inferences from tagging studies

At the time of this analysis, we were aware of 21 successful swordfish PSAT tags that had reported positions from the SW Pacific (14 Australian and 7 New Zealand). The tags we consider here were at liberty for at least 60 days, and have position fixes for release and pop-off (Argos positioning), plus several intermediate point estimates for positions from SST- and light-based geo-positioning.

Only six conventional swordfish tags have been recovered in the South Pacific that we know of, four with release durations longer than 60 days. These tags are less informative than the PSAT tags in that only release and recovery positions are available, and recoveries are restricted to commercial fishing operations (and the

associated non-random effort distributions). However, the conventional tags are more informative than the PSAT tags in terms of the long release durations (3 of 1-2 years, and one of 6 years). There is also one unconfirmed tag that suggests a movement across the Tasman Sea (from New Zealand to the Australian inshore fishery) (Clive Stanley, CSIRO, pers. comm.).

South Pacific-Indian Ocean tagging studies are ongoing, with several more releases expected over the next year. As such, there has not yet been a concerted effort to analyse the existing tag tracks to form a general synthesis, and this is expected to occur over the next 1-2 years (Chris Wilcox, CSIRO, pers. comm.). This descriptive work undertaken in support of the assessment represents a first attempt to make some qualitative and quantitative inferences. Three possible approaches for using PSAT tagging tracks (and conventional tag recapture data) in the swordfish assessment context were considered:

1. Qualitative summary. Given the small number of tags, it is not clear that anything conclusive will come out of a quantitative analysis at this time, while a visual depiction of movements can be interpreted in the context of the other qualitative work described in this paper.
2. PSAT tag tracks can be modelled in a spatially-disaggregated assessment model in a fashion analogous to conventional tags. This approach involves simply breaking up a continuous track into a series of consecutive release/recapture events according to the spatial structure and time-step of the assessment model, and defining special fisheries that catch 100% of PSAT tagged fish and 0% of untagged fish. While there are caveats associated with this approach, it may be feasible to attempt with the data available.
3. One can attempt to formulate and estimate parameters for advection-diffusion models (e.g., Sibert et al. 1999). Quantitative estimates from these models can be translated into bulk transfer coefficients (or priors) that are compatible with spatially-disaggregated assessment models. We did attempt to estimate the parameters for a diffusion model and discuss the appropriateness of this model in the context of the swordfish assessment.

Each of these is discussed under separate headings below. We note the following caveats in relation to our description and interpretation of the tagging data:

- Tag releases are not seasonally representative, as they tend to be released during the peak of the swordfish fishing season. Tag release durations have typically been short, with only 3 PSAT tags out for longer than 6 months, so evidence regarding cyclic migrations and site fidelity would be expected to be weak. Conventional tag releases are longer (up to 6 years), but recoveries are dependent on fishery operations, and potentially biased by non-reporting.
- Size and sex of the released fish are uncertain (though visual size approximations are recorded)
- All swordfish tag tracks to date are based on the limited data that are available from Argos satellite transmissions (as opposed to the full archival data that would be available if a tag was returned). The algorithms used to select which data are transmitted to the satellite are not well described, and there may be issues with data transmission reliability.

- In general, the light-based geo-positioning estimates are expected to be more accurate and precise for longitude than latitude (and this is especially true near the equinoxes, when day length is constant with latitude).
- The PSAT track descriptions feeding into these analyses were not estimated using identical methods:
 - The Australian tag tracks use the Wildlife Computer longitude estimates, which are proprietary and poorly described. Latitude estimates were based on an SST matching algorithm (Toby Patterson, CSIRO, pers. comm.). Position errors are sometimes sufficiently large that they can be recognized as implausible on the basis of physiological limits to migration rates. In this presentation, an arbitrary limit was adopted to reject all points with estimated migration rates faster than 400km/d (this removed two conspicuous back and forth longitudinal movements).
 - The NZ tag position estimates are based on light (longitude) and SST-based (latitude) position estimates using the SST-Kalman filtering algorithm (Nielsen et al. 2006). Statistical constraints on position estimates link consecutive position estimates in such a way that the few large and questionable movements estimated for the Australian tags are presumably less likely to be estimated with this algorithm. However, there are suspicious characteristics in the NZ latitude estimates, in that all of the positions from all tags were estimated to be north (often substantially) from the release and pop-off points.
- SST-based estimates of latitude are generally considered to be better than the light-based latitude estimates, however, it is unclear that the errors in the SST position estimates are properly understood, given the low level of ground-truthing for the SST fields in relation to PSAT near-surface temperature measurements. e.g. In using the Kalman filter – SST algorithm, on the New Zealand PSAT tags, latitude estimates were very sensitive to the smoothing assumptions assumed for the SST fields (Tim Sippel, Auckland University, pers. comm.).

Qualitative summary of tag tracks

Australian and New Zealand PSAT tag tracks are shown in Figure 6. Figure 7 illustrates a rectangle for each of these tag tracks, which encapsulates the maximum NS and WE region of the point estimates. The rectangular box exaggerates the perception of spatial movement of each tagged fish, but facilitates a useful visualization of multiple overlapping tracks. One New Zealand tag exhibits unique behaviour in that there is a large East-West displacement (~3000km), that seems to be reliably supported on the basis of multiple proximal position fixes. There appears to be a 20°S northern boundary for the Aus and NZ tags, and it would be interesting to know if this is a real bound (i.e. perhaps spawners need only migrate to a region of sufficiently high SST, and have no reason to go further). But this may be a coincidence of a small number of tags, or an artefact of the SST-based latitude position estimation algorithms used. Two of the NZ PSAT tagged fish overlapped with the Australian tagged fish. Figure 8 illustrates only the release and pop-off locations of the PSAT tags, along with conventional tag recoveries.

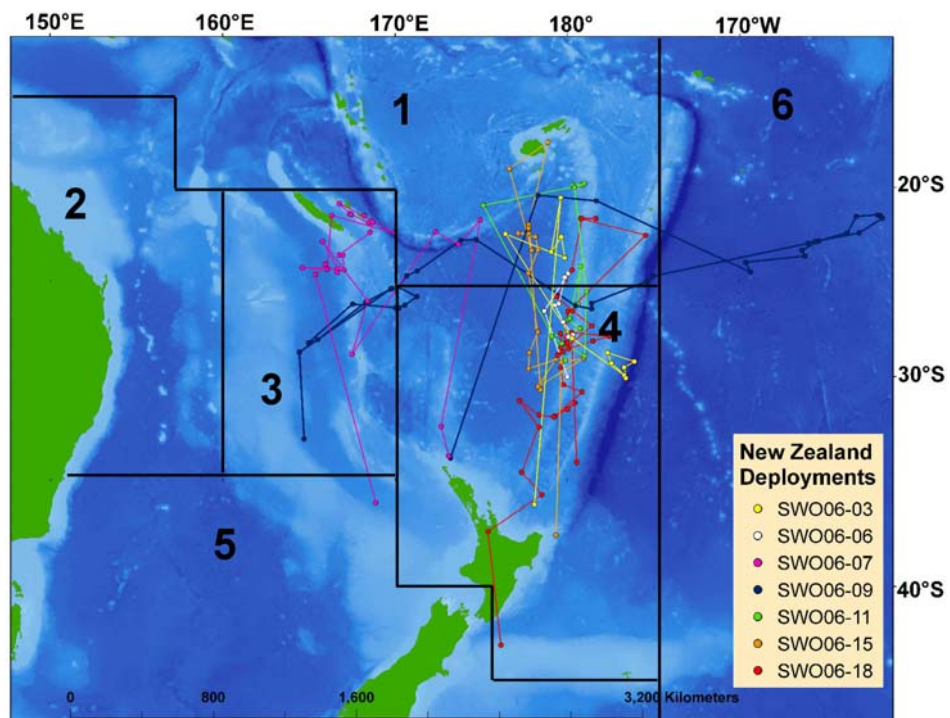
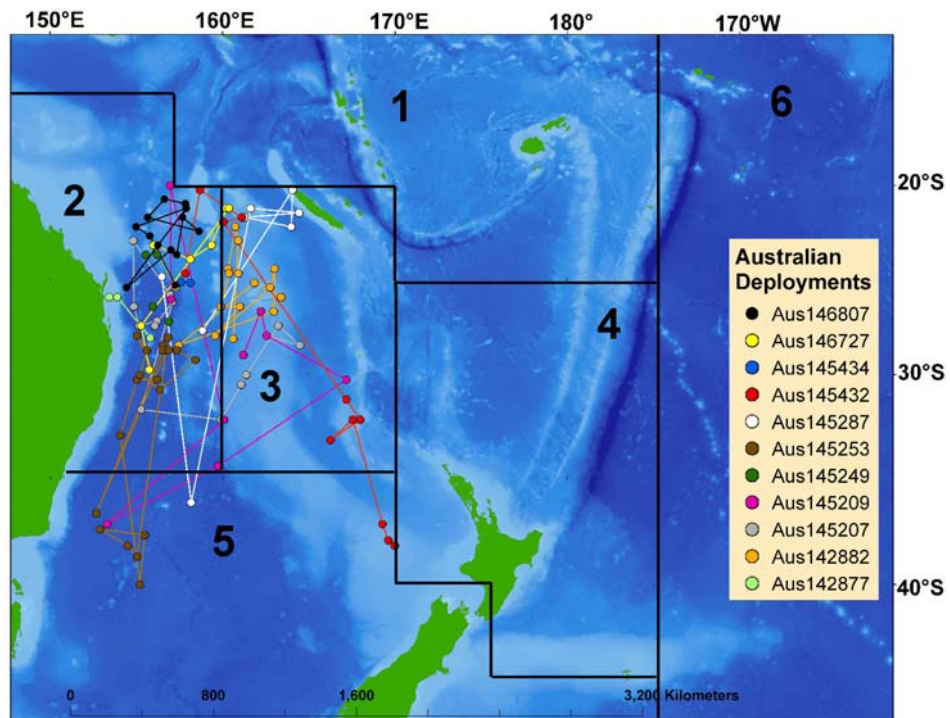


Figure 6. Estimated trajectories for Australian and New Zealand PSAT tagged swordfish in the SW Pacific. Figures from Holdsworth et al. (2007), Karen Evans and Chris Wilcox, CSIRO, unpublished data.

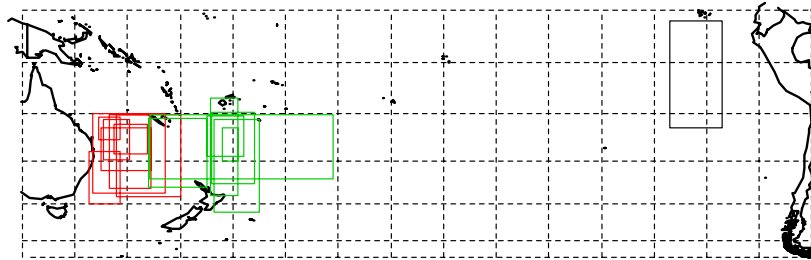


Figure 7. Boxes illustrating the maximum North-South and West-East extent of swordfish PSAT tag track releases from Australia (red), New Zealand (green) and Spain (black) for tags with pop-off times of 60+ days (the latter inferred from Abascal et al 2007).

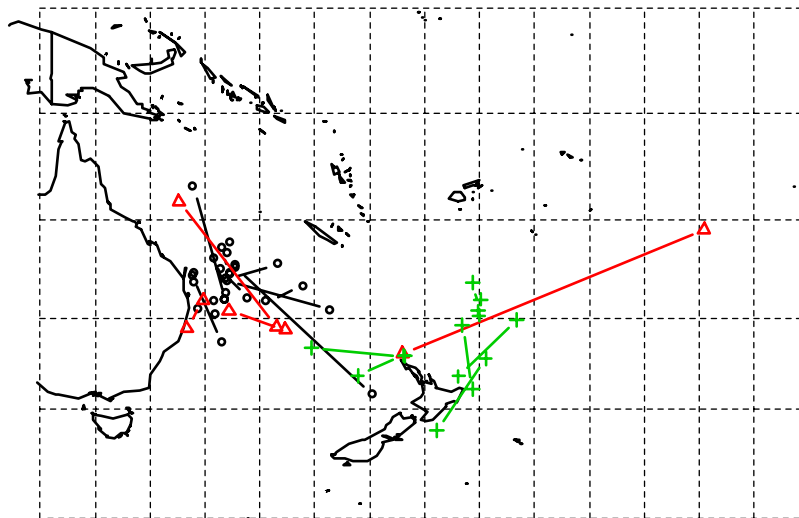


Figure 8. Release and pop-off points for Australian (black circles) and New Zealand (green "+") PSAT tags and convention tags (red triangles), for tags at liberty between 60 days and 6 years.

The PSAT tracks do not suggest much longitudinal migration in relation to spawning (as had been considered likely in 2006). While the tags are plausibly consistent with south-north spawning migrations, the Coral Sea does not seem to hold any special significance. This does not support the site-fidelity models as defined in the 2006 assessment (i.e. represented schematically in Figure 9), though site fidelity could still be important in different ways.

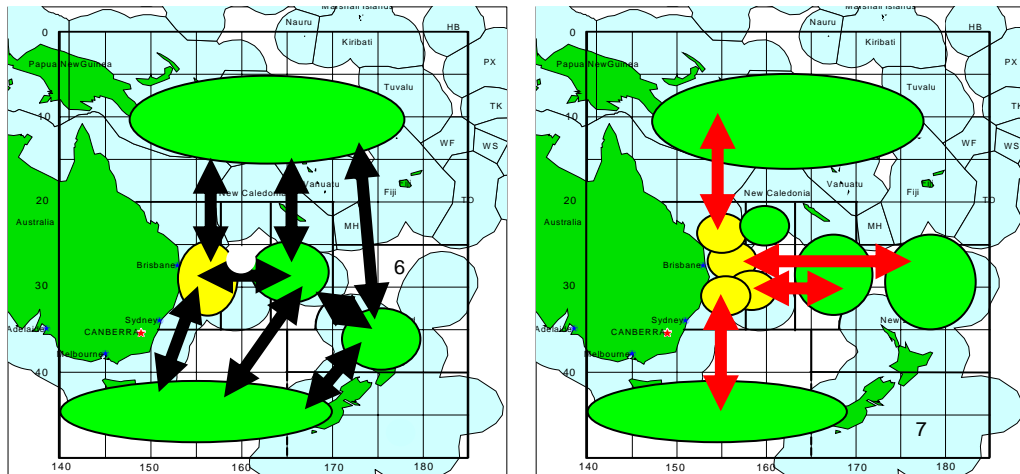


Figure 9. Migration hypotheses and stock structure explored in the 2006 assessment. Left panel illustrates a conventional homogenous mixing structure, while the right panel illustrates a site fidelity model with migration to shared spawning grounds.

In light of the new evidence, we consider the conceptual idea of homogenous mixing vs site fidelity to be more relevant on a broader scale (e.g. Figure 10), and note that the two mechanisms could work simultaneously and across a range of scales.

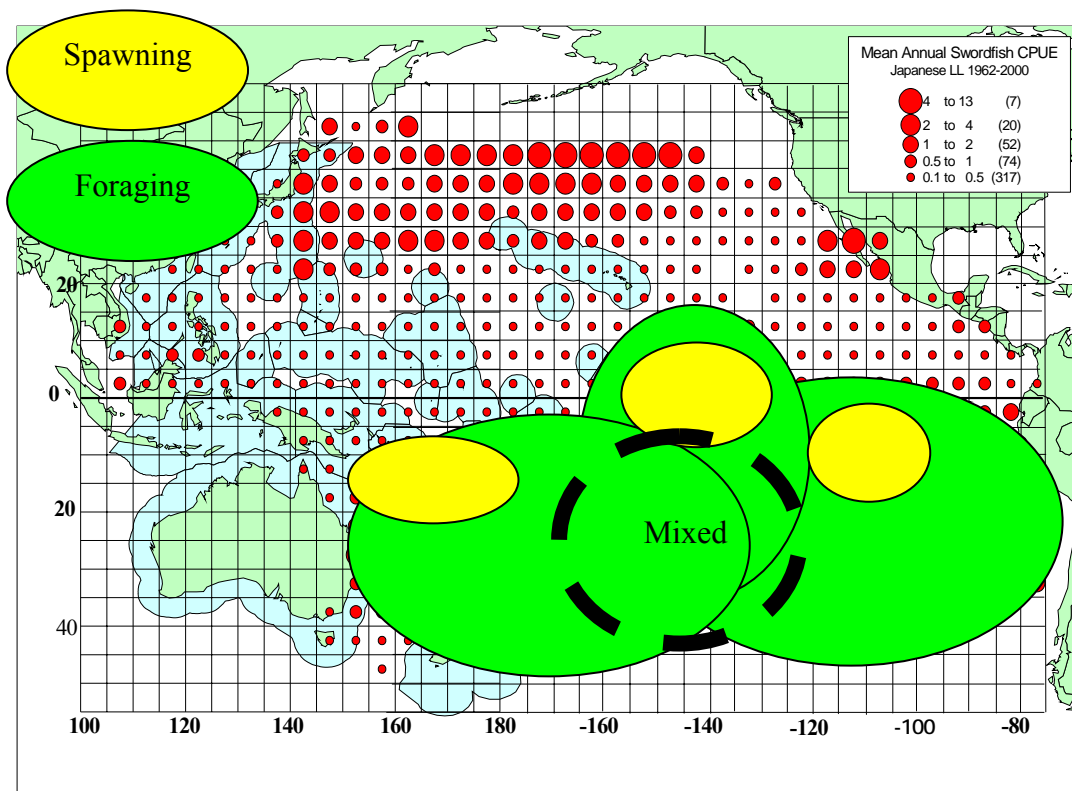
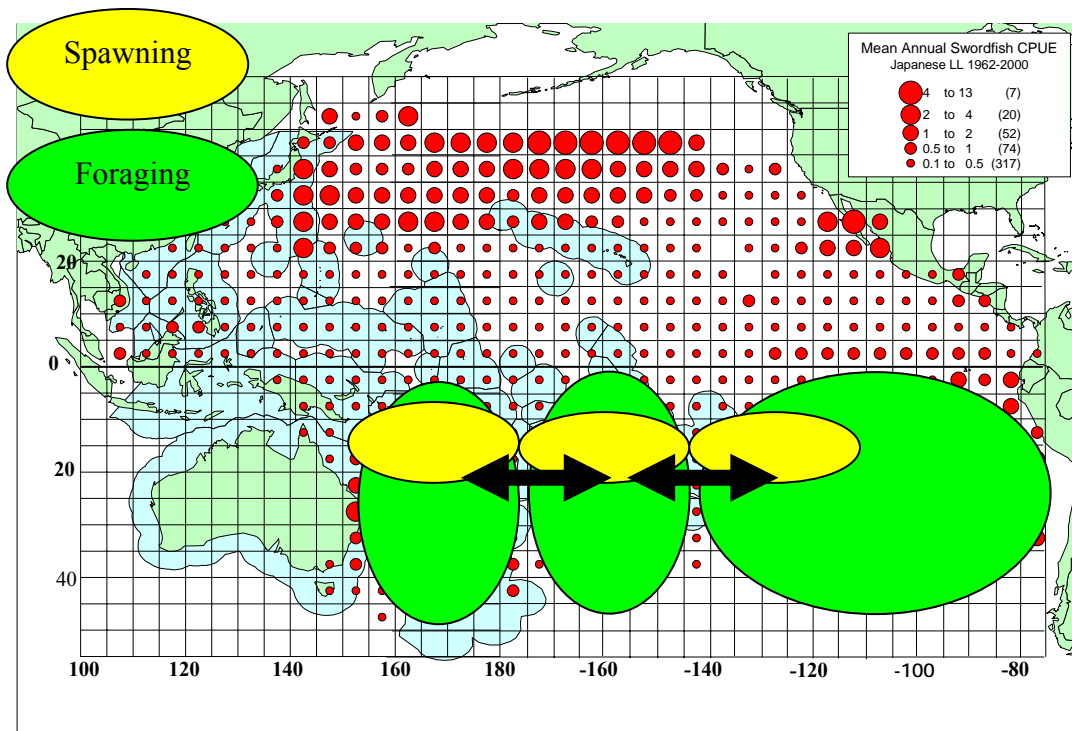


Figure 10. Schematic representation of two possible stock structure representations for South Pacific swordfish: top panel = homogenous mixing, bottom panel = foraging site fidelity.

Modelling PSAT tracks as conventional tags

This is intended to be a simple approach for allowing PSAT tracks to be informative with respect to movement parameters in a stock assessment model. It does, however, require some model modifications relative to the conventional assessment model assumptions (i.e. a theoretical fishery with 100% tag recovery every time-step, and 0% exploitation of non-tagged fish)(Figure 11). The approach has the additional advantage of jointly estimating migration with the other population parameters. Given the non-representative pattern of PSAT releases, other data (i.e. seasonal CPUE and size distribution patterns), might provide additional constraints that prevent the estimation of dispersive migration estimates that might otherwise result if only half of the migration pattern is well observed. Problems with this approach include:

- Sequential PSAT track locations are not independent, and this would be expected to under-estimate the variance relative to the equivalent pattern that might be observed with truly independent release/recovery events.
- The short release durations available to date cannot fully describe seasonal movements.
- Multiple movements may occur within time-steps.

The conventional tag analogue model was not pursued in the 2008 assessment.

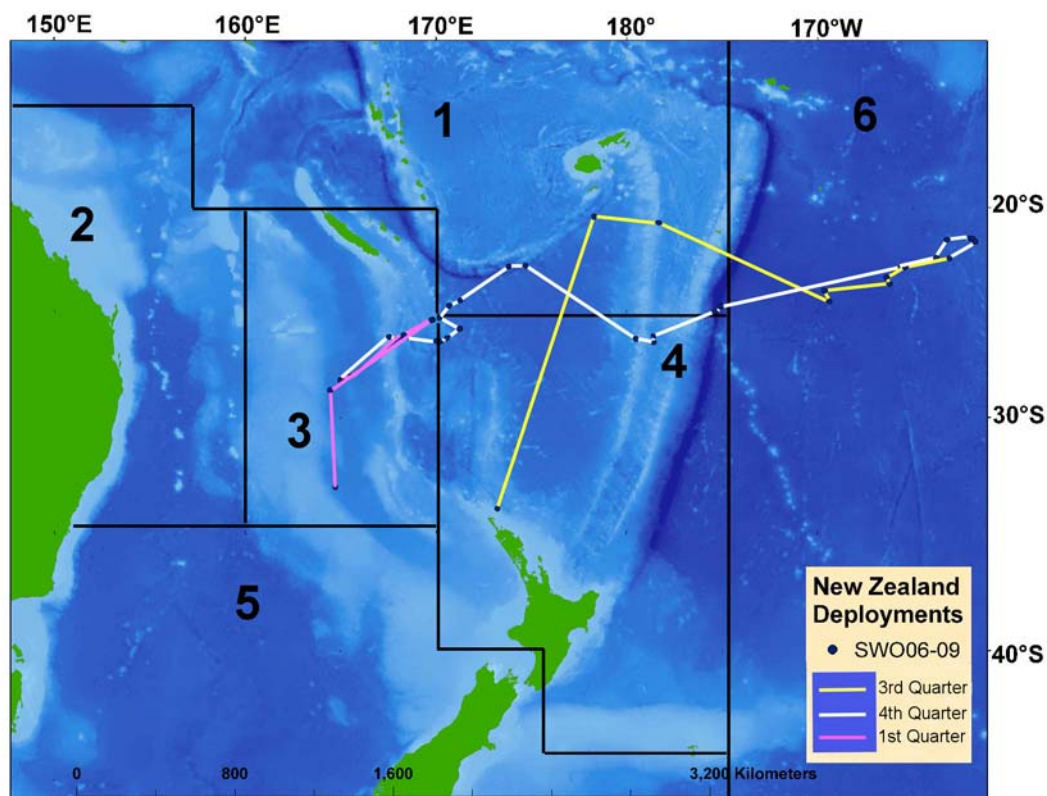


Figure 11. PSAT tag track split into 3 consecutive observations, analogous to conventional tag releases and recaptures.

Parameterization of Advection-Diffusion Models

There are a number of possible approaches for using tagging data to parameterize movement (e.g. Kleiber and Hampton 1994, Sibert et al. 1999) in population models. There is also speculation about the diverse migration characteristics that swordfish stocks are likely to have, including:

- Size/age-based migration/distribution
- Sex-based migration/distribution
- Homogenous mixing vs: site fidelity (with directed seasonal migrations)

We do not consider it feasible to attempt to estimate a full description of the migration dynamics, (i.e. including the potential ontogenic and sex-specific variability) from the available data. However, it is feasible to analyse the available data in the context of purely diffusive mixing. In the following, we attempt to estimate a diffusion rate for the SW Pacific swordfish population, purely in a longitudinal direction. Swordfish likely undertake substantive latitudinal migrations in the SW Pacific (e.g. very large, spawning age fish are found in the extreme south of the distribution, but spawning only occurs in the north; there are seasonal patterns in CPUE and size composition consistent with seasonal migration). However, there are two justifications for ignoring the north-south movements in the assessment at this time: 1) The latitudinal position estimates of the PSAT tags are not thought to be very reliable, and 2) the revised spatial structure of the assessment is being designed to integrate over North-South seasonal migration effects (i.e. assuming that seasonal catchability and selectivity can effectively represent the implications of migration on the population). We feel that it is reasonable to assume that individuals from the north and south in the same longitudinal band (within the SW Pacific) are more likely to be closely related than individuals located in the same latitudinal band an equivalent distance apart in a west-east direction.

A few summaries of Australian PSAT migration rates and migration distances as a function of time are illustrated in Figure 12 and Figure 13. From these plots it is evident that rapid migration appears to occur in the first few days, and then the rate decreases. There may be different mechanisms contributing to this effect, but we would consider the most parsimonious explanation to be the effect of position estimation error. The position estimation error would be expected to have a greater effect on the migration rate near the time at release. This error will be constant in magnitude over time, and hence larger in proportion to the actual displacement when the tagged fish has not had time to move very far.

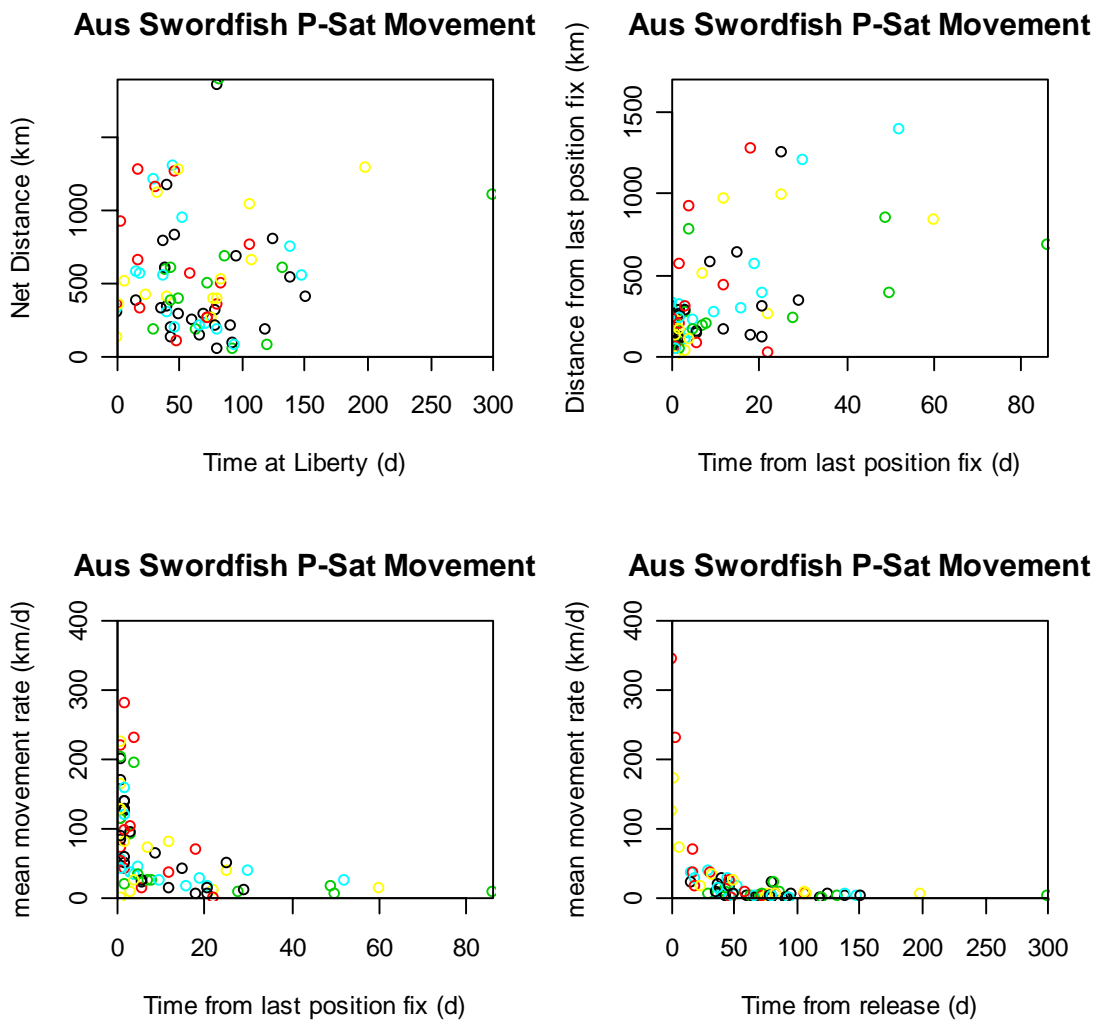


Figure 12. Australian swordfish PSAT tag displacements and movement rates over time (relative to the release point). All Australian PSAT tags are included (each circle represents an individual position fix and time interval since the previous position fix). Different colours represent different tags

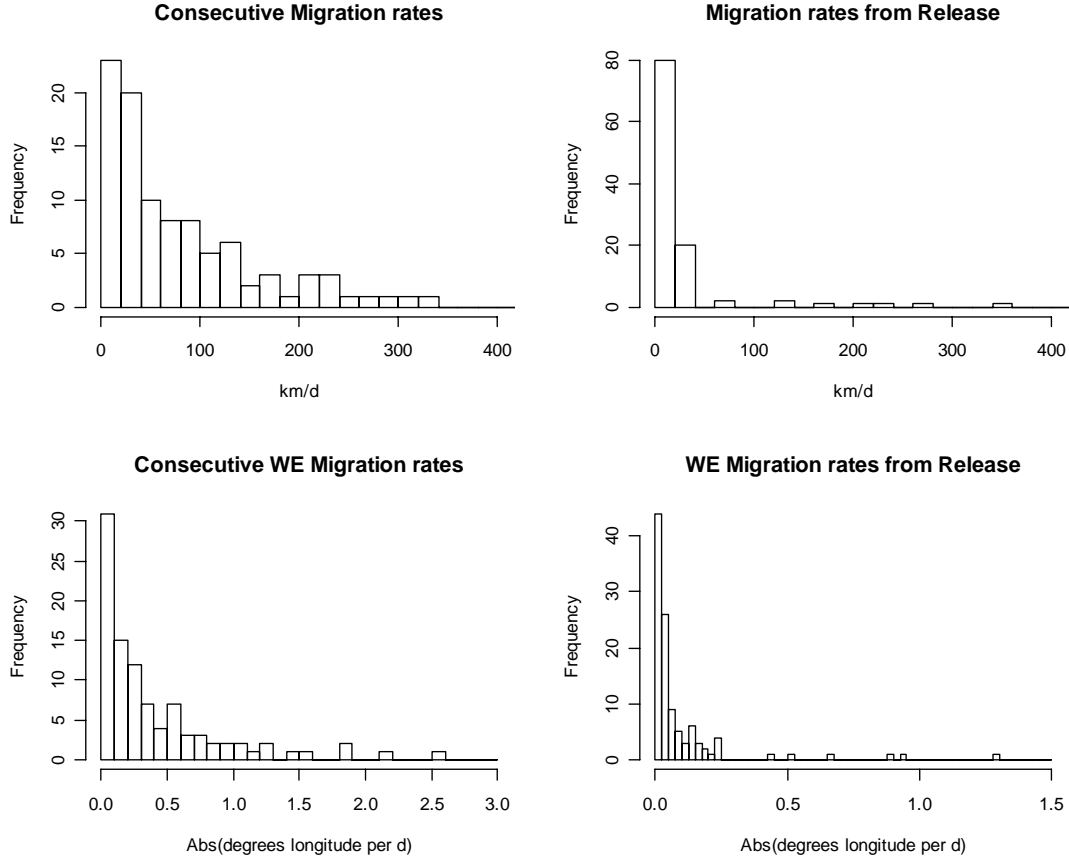


Figure 13. Estimated migration rates, between consecutive position estimates (left panels), and net from point of release (right) in absolute distance (top) and absolute longitude only (bottom).

In the following, we attempt to estimate a diffusive longitudinal mixing rate from the PSAT tracks, assuming that swordfish populations can be adequately described by diffusion. Sibert and Fournier (2001, based on Feller 1968), illustrate that a discrete-time random walk model results in distributions that are equivalent to continuous diffusive processes. In this case, we are only concerned with a one dimensional (unbiased) random walk. The probability density function for longitudinal positions, x , can be described by a normal distribution with variance $2Dt$, where t is the time elapsed since release and D is the diffusion rate:

$$P(t, x) = \frac{1}{\sqrt{4\pi Dt}} \exp\left(-\frac{x^2}{4Dt}\right)$$

There is also a position error associated with each longitude estimate for the PSAT locations. This is large for the geo-positioning estimates, but expected to be much smaller for the release point and the final Argos position fix:

$$x_{observed,t} = x_t + \varepsilon_t,$$

where $\varepsilon_t \sim Normal(\mu = 0, \sigma)$.

Assuming that the fish follow an unbiased random walk process, we can estimate the diffusion parameter D , and the longitudinal geo-positioning error, σ , using the (negative log-)likelihood function:

$$L(x_{observed} | D, \sigma) = \sum_i \log\left(\sqrt{2\Delta t_i D + \sigma^2}\right) + \frac{x_{observed,i}^2}{2\Delta t_i D + \sigma^2}.$$

Where every position estimate, $x(i)$, represents the longitudinal distance (degrees) from release and Δt_i is the elapsed time since release, corresponding to that position.

Two different datasets were fit:

- A) Only the Australian PSAT tag data were included. All sequential light-based geo-position estimates (relative to the initial release time/location) from each tag were considered as independent observations. NZ track positions were not included because they were estimated using a different geo-positioning algorithm. One obvious problem with this model is the faulty assumption that every sequential track location is an independent observation, which would be expected to under-estimate the variance of the estimated parameters.
- B) Australian and New Zealand PSAT tags were combined with conventional releases/recaptures. Only release and final Argos position estimates were included from the PSAT tracks. This uses all of the most reliable position data and ignores the light- and SST-based geo-positioning estimates.

The likelihood surface for the parameter estimates of the two datasets are shown in Figure 14, and seem plausibly consistent with one another. Model A is estimated to have a substantially higher observation error than model B (as expected, i.e. Argos and conventional tag recapture position errors would be expected to be smaller than light-based geo-positioning). Model B also has smaller diffusion rate point estimates than A. If migration is not a random diffusive process (e.g. if there are habitat constraints on the movements, or cyclic seasonal migrations), then we would expect diffusion rates estimated from the longer release durations (i.e. particularly the conventional tags) to be lower than the short releases.

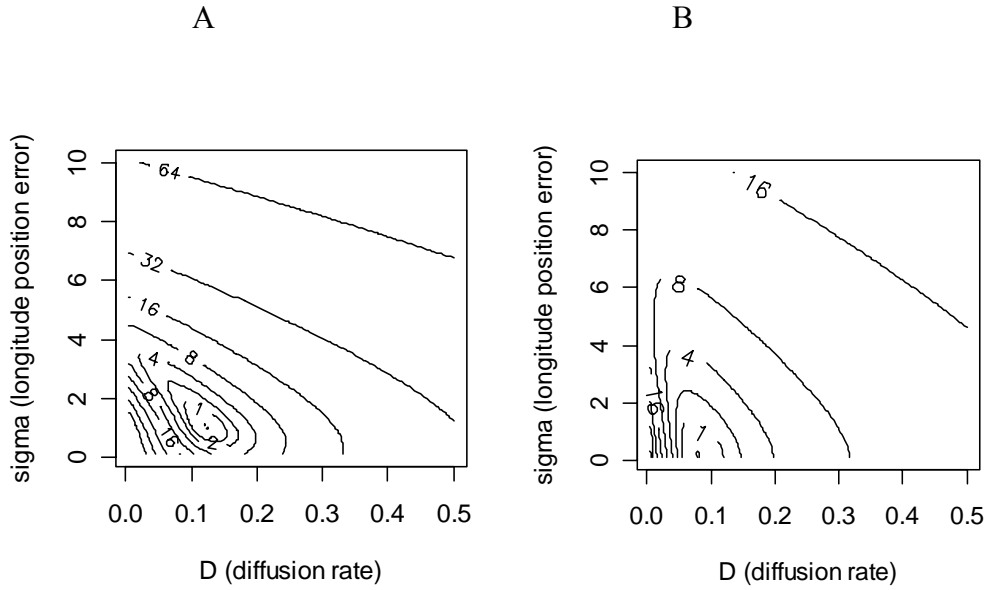


Figure 14. Negative Log-Likelihood surface for the longitudinal diffusion rate and longitudinal geo-positioning error estimated from the pure diffusion model, using A) the Australian swordfish PSAT tag data with all (sensible) geo-position estimates from each track, B) Combined Australian and NZ PSAT tags (Release and Argos pop-off locations only), plus the conventional tags.

Diffusion models rely on the important assumption that swordfish are actually swimming with an unbiased random walk behaviour. However, the conventional wisdom suggests that swordfish have habitat preferences, directed migrations (at least North-South), and potentially site fidelity in spawning/foraging migrations. Thus, a diffusion model would be expected to over-estimate movement rates if short-term tracks are extrapolated over the lifetime of a fish.

Two additional models were briefly explored to examine the appropriateness of the diffusion assumption. The second, more flexible model (“Flex”) has pure diffusion (linear increase in longitudinal variance over time) as a special case, but a non-linear parameter allows the longitudinal variance to decrease, stabilize or increase over time, relative to what pure diffusion would predict. We used a Ricker (stock-recruitment) function to describe this situation. This is a convenient function for our purposes, but we do not intend to imply any specific mechanistic justification for it.

In Flex, the variance term $2\Delta t_i D$ is replaced by $2\Delta t_i D \exp(-k\Delta t_i)$, and the likelihood function becomes:

$$L(x_{observed} | D, \sigma) = \sum_i \log\left(\sqrt{2\Delta t_i D \exp(-k\Delta t_i) + \sigma^2}\right) + \frac{x_{observed,i}^2}{2\Delta t_i D \exp(-k\Delta t_i) + \sigma^2}$$

The additional parameter k is estimated. A third model, (SF for Site Fidelity) was examined, in which it was assumed that there was an explicit annual migration cycle, such that the variance in longitudinal position was described by a sine wave ($A*\sin(t*\omega + \phi)$). The corresponding likelihood function is:

$$L(x_{observed} | D, \sigma) = \sum_i \log\left(\sqrt{A + A \sin(\Delta t_i \omega + \phi) + \sigma^2}\right) + \frac{x_{observed,i}^2}{2(A + A \sin(\Delta t_i \omega + \phi) + \sigma^2)}$$

In this case, the wavelength, ω , and phase angle, ϕ , were fixed ($\omega = \pi/365$, $\phi = 0$), and only the amplitude, A , and observation error σ were estimated. There is no reason why we would expect this particular waveform to be the most appropriate for describing the positional variance over time, however, it is a convenient caricature for describing possible annual migration pattern with perfect site fidelity (i.e. the key feature of the model is the oscillating expansion and contraction of the variance every 12 months).

When applied to only the Australian PSAT tags (dataset A), the three models all fit the data almost equivalently. The maximum likelihood parameter estimates and objective function values of the three models are listed in Table 1. The difference in likelihood is trivial and not statistically significant among the three. This is not surprising given that the estimated functions are very similar for tag release intervals of less than 100 days, and only 2 tag observations are of duration longer than 150d. On the basis of the Australian PSAT tags alone, we cannot conclude that continuous diffusion is more likely than seasonal migration with site fidelity, or something intermediate in character.

Longer duration tag releases are required to discriminate the differences (i.e. a minimum of one year would be expected to provide information on the seasonal patterns that we normally assume to be occurring). Furthermore, we note that even with a large number of quality observations, the Flex model would not actually disprove diffusion or seasonal migration. If swordfish move at random, but subject to habitat constraints (which of course they are), this will eventually provide a limit to the diffusive mixing that would otherwise be possible in an infinite habitat, so we would expect the pure diffusion assumption to break down eventually if movement rates are high. Similarly, swordfish could have seasonal migrations with perfect site fidelity, but this might be difficult to identify in this simplified analysis if the sine wave is grossly inappropriate for describing the seasonal movement (i.e. there could be short, rapid and asynchronous movements between foraging and feeding grounds).

The three models were refit with dataset B (Australian, New Zealand and conventional tags). Adding the conventional tags provides 4 observations of release duration greater than one year (including the single tag that was out for 6 years). The additional data also suggest that pure diffusion is a reasonable description of the longitudinal tag displacement, though removal of the longest time-at-liberty tag weakens the argument (Figure 15). Parameter values and likelihood estimates are provided in Table 1.

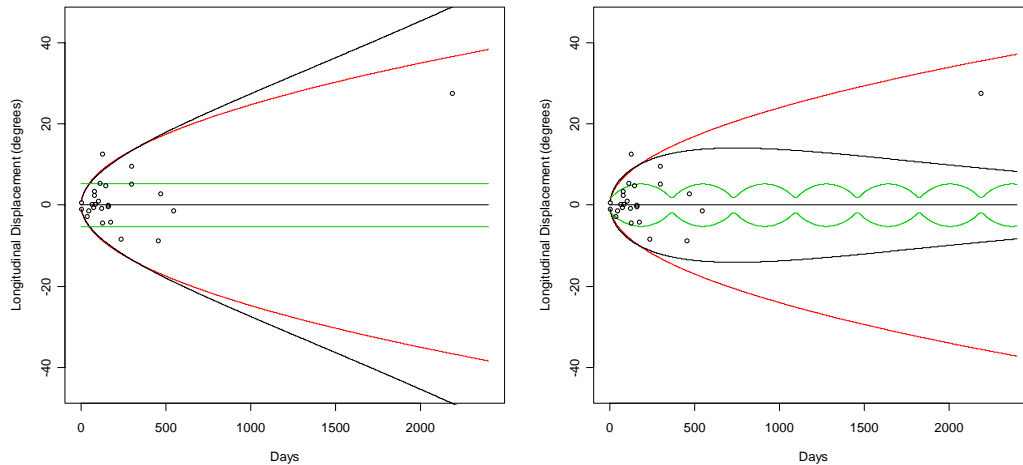


Figure 15. Models of swordfish diffusion based on the combined Australian (n=14) and New Zealand (n=6) PSAT (using only the final Argos position estimate) and conventional (n=5) tags (dataset A). Red bounds are the 95% confidence limits for longitudinal displacement based on the pure diffusion model, black bounds represent the “Flex” model, and green bounds represent the “Site Fidelity” sine wave model. Left panel models include all points, right panel omits the single conventional tag observation that was at liberty for more than 2000 days from the model fitting.

We would tentatively conclude that the tagging evidence provides a reasonable justification for bounding longitudinal migration assumptions using diffusion rates as upper bounds on mixing. This is worth revisiting in light of additional tagging results and analyses, however, it seems as though more long duration release events will be required to provide convincing evidence. And toward this goal, we should not underestimate the importance of conventional tags relative to the sophisticated electronic tags.

Figure 16 illustrates how pure diffusion translates into longitudinal bulk transfer coefficients in an assessment context (i.e. the proportion of fish expected to move from one region to an adjacent region in a given time-step), relative to different spatial dimensions:

$$m = \int_{l=0}^L \frac{1}{\sqrt{4\pi DT}} \exp\left(-\frac{l^2}{4DT}\right),$$

where: m is the migration rate coefficient, T is the time interval (time-step used in the assessment model difference equations), l is longitude, and L is the longitudinal block size. Note that for relatively large values of D or T , or small values of L , a substantial number of fish would actually pass through the adjacent region into neighbouring regions.

Table 1. Parameter estimates for the swordfish movement models.

Model	DataSet	D	sigma	other	-ln(likelihood)
Diffusion	A	0.123	1.04		196.4
Flex	A	0.179	0.834	k=0.0051	194.9
Site Fidelity	A		0.947	A=32.3	196.6
Diffusion	B	0.0792	0.196		49.05
Flex	B	0.0714	0.334	k=-0.00031	48.91
Site Fidelity	B		(xxx)	A = 0.00	61.89
Diffusion	B*	0.0746	0.292		45.02
Flex	B*	0.0941	0.000	k=0.00135	44.89
Site Fidelity	B*		0.847	A=24.3	47.49

*excludes the single tag that was at liberty for six years

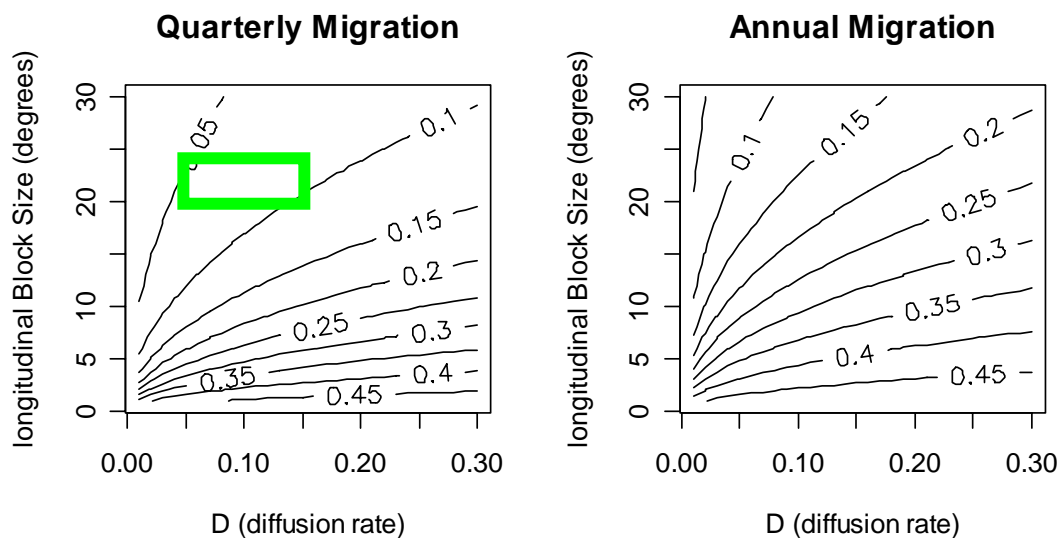


Figure 16. Contour plots of bulk transfer coefficients (i.e. proportion of net movement of fish expected to move from one region through to an adjacent region, at the end of the indicated time interval) corresponding to a range of diffusion rates, D , and spatial structures with longitudinal width of 0-30 degrees. Left panel corresponds to a quarterly time-step and right panel corresponds to annual. The green box roughly outlines the parameter space corresponding to the assessment model assumptions in Kolody et al. (2008) and Davies et al. (2008).

From this analysis, we adopted bounds on the diffusion rate of $D = 0.05-0.15$ for the assessment models. These values roughly correspond to the upper and lower bounds of the 2 likelihood unit contour in dataset B, (Figure 14) (the 1.92 likelihood unit contour would represent the 95% confidence limit). Model mis-specification is likely to lead to an overestimation bias in D (i.e. short duration tag releases, combined with habitat constraints and site fidelity would tend to over-estimate D and hence the mixing rates). However, given the small number of tags, uneven distribution of tag releases, and short durations at liberty, we would expect these values to be revisited in

time. The bulk transfer coefficients corresponding to these diffusion rates, and the spatial structure assumed in the assessment model (Figure 17) are outlined in Figure 16.

We are aware of additional recent or planned PSAT tag deployments from French Polynesia, the Cook Islands, Australia, NZ, and Spain, which are not available for this analysis, and which should help to further refine our understanding of Pacific swordfish migration. Additionally, more substantive analyses of the individual tracks using updated geo-positioning algorithms, and in relation to environmental covariates is expected in the latter part of 2008-9 (Chris Wilcox, CSIRO, pers. comm.).

Review of spatial structure considerations in other swordfish populations and assessments

The following section provides a brief (and incomplete) overview of some spatial considerations in the biology and assessment of swordfish stocks in the Atlantic, Eastern Pacific, Northern Pacific and Indian Oceans.

Atlantic Ocean

A long time series of Atlantic swordfish sex ratios and maturity stages have been collected since 1990. Spatio-temporal variation in length-specific sex ratios indicate seasonal spawning migrations (Arocha et al. 1994). Certain parts of the Atlantic were identified as being important spawning areas. A range of studies of spatio-temporal sex-ratio at size in Atlantic swordfish and a 10 year time series were subsequently reviewed with the aim of identifying consistent patterns in sex ratios (Mejuto et al. 1998). Differences in the migrations of males and females were inferred from sex-specific CPUE, with females estimated to be more wide-ranging and associated with colder areas. From this it was hypothesised that preferential areas exist for reproduction and feeding, with migration corridors linking the two.

The complete time series of sex-specific observations was recently examined to describe spatio-temporal patterns in female swordfish reproductive activity in the Atlantic based on a large sample (~ 18 000) of gonads (i.e., gonad index, Mejuto & García-Cortés, 2007). Reproductive activity was found to be related to swordfish length and sea surface temperature, with distinct areas of intense reproductive activity being identified. A high proportion of males from 125 to 165 cm LJFL were associated with areas of intense reproductive activity. The results support the concept of a complex population structure segregated by sex and reproductive behaviour, with migration corridors linking areas of intense seasonal reproductive activity.

Given this population structural complexity, it therefore seems reasonable that a GLM used to estimate standardised CPUE indices for North Atlantic swordfish, 1963 to 2005, included area as a categorical variable (Ortiz et al. 2007). There are 14 relatively large zones in this analysis.

Despite the apparent spatial heterogeneity in the North Atlantic swordfish population, assessments have assumed a single homogeneous uni-sex stock. A length-based separable sequential population analysis (LSSVPA) was applied to Atlantic swordfish

that fits to observations at length (Kimura & Scott 1994). The population estimates were similar to those of the VPA (age-based) used to routinely assess the population. No spatial disaggregation was assumed in either model.

After a 2006 workshop that reviewed available research on Atlantic swordfish stock structure, the existing stock structure assumed for Atlantic swordfish assessments, i.e. three separate stocks (Mediterranean, North Atlantic and South Atlantic), was not altered (Anon. 2007). The information reviewed is summarised in the Table below. The assessment models for the North and South Atlantic stocks assume discrete stocks, with no mixing and no spatial disaggregation. For the 2006 assessment, a Schaefer stock-production model was used, with a sensitivity test using a Fox model shape parameter. Additionally a VPA model was fitted (5 age classes) to 17 separate age-specific single sex CPUE indices (Anon 2007).

Results from recent tagging studies in the North Atlantic raise questions about the spatial assumptions made in the assessment model. A PSAT tagging study goes some way to addressing the possibility of a division between eastern and western Atlantic stocks (Nielsen et al. 2007). Data have been collected from 23 PSAT units. The movement estimated from the PSAT data was generally North-South, with no trans-Atlantic migration despite long periods at liberty (> 1 year). There were indications of migrations toward and away from spawning areas (as identified from larval distribution studies), and foraging site fidelity for some tagged fish (i.e. returned to the same southern location after an apparent northward migration).

Table extracted from Anon. (2007):

Table 1. Summary of available information on the Atlantic and Mediterranean swordfish stock structure. The text in parenthesis indicates the conclusions reached by SCRS in 1994. (Source: SCRS/2006/010).

Στοιχ. Η υπόθεση	ΧΠΥ Ε βγ α γ ε	Χατζη Δ ιατριβ οτι ο ν (Μ α σ κ ρ Φ έ σ τ ο)	Μ α σ κ ρ/ Ρ ε γ α π τ ο ρ ε	Λ ε ν γ η/ Ω σ τ η ρ	Σ π α ω ν ι ν γ Α ρ ε α σ	Γ ε ν ε τ ι ζ ο	Β ι ο λ ο γ ι κ ή Μ α σ κ ρ ο
Mediterranean Single Stock (different from Atlantic)	Inconclusive	Inconclusive	Yes	Inconclusive	Yes	(Yes) Yes ⁴	Yes
North Atlantic single stock	(Yes) Yes ¹	(Yes) Yes	²	(Yes) Yes	(?) Yes	(⁵) ?	
North (E + W) separate stocks	(No) No ¹	(No) No	²	(No) No	(?) No	(⁵) ?	
North + South single stock	No info	(Yes) ?	No ³	No info	Inconclusive	(?) No ⁶	

¹ Based on trends in CPUE reported by country (2002 stock assessment).

² Interpretation of the conventional mark/recapture studies are complicated by variable reporting rates among fleets, and distribution of releases and recapture effort.

³ Three tags have shown evidence of movement from the North to the northern limit of the southern stock, but need to be verified.

⁴ Papers presented dealing with this hypothesis were unanimous. Some evidence of population heterogeneity within the Mediterranean also presented. There is evidence of mixed zones in the area off the west coast of Gibraltar and along the northern coast of Morocco.

⁵ SCRS earlier failed to reject either the null or alternate hypotheses of homogeneity/heterogeneity. New evidence indicates possibility of overlapping stocks, but the extent of overlap is uncertain.

⁶ Several independent studies now support the conclusion, but the location of the management boundary remains uncertain.

Eastern Pacific Ocean (EPO)

Standardised CPUE, biological and genetic data were reviewed for describing the structure of EPO swordfish to be used for structuring a stock assessment in 1998 (Hinton & Deriso 1998). Temporal shifts in relative abundance with respect to spatial zones (2° × 5° squares), and gonad condition were identified. It was concluded that a

stock was centred in the Southern EPO. The population model was fitted to the relative mean annual CPUE weighted over all spatial zones making up the southern EPO and therefore assumed a single stock with no spatial disaggregation.

A 2006 assessment of southern EPO swordfish using SS2 repeated this stock structure assumption, such that EPO swordfish are assumed to have distinct stocks separated at 5°S (Hinton & Maunder 2006). The western limit of the southern EPO stock was assumed to be 150°W. Fisheries were defined with coastal and offshore subareas (separated at 90°W). The 2006 assessment ignored the subarea structure used in the previous (2005) assessment, but rather defined six (or seven) fisheries in respect of unique selectivities and spatial structure.

In 2007, the results from analyses of standardised catch rates on a fine spatial scale, spatio-temporal size compositions and gonad condition for Pacific swordfish were reviewed (Hinton & Alvarado Bremer 2007). The review also included all Pacific swordfish genetic studies, including a recent study with a larger sample size, (Alvarado Bremer et al. 2006). This provided a basis for identifying stock separation in the Pacific. An hypothesis consistent with both sets of analyses points to four separate stocks in the Pacific Ocean: northwest (of the equator, 150W), northeast (of 5S, 150W), southwest (of the equator, 150W) and southeast (of 5S, 150W). It was recommended that separate assessments be conducted for the eastern and western stocks.

North Pacific

Kleiber & Yokawa (2002) described a preliminary swordfish assessment in the North Pacific (north of 10°N), with 4 regions in respect of 30°N, 160°E: NW, NE, SW and SE. They found the estimated migration rates to be implausible (i.e. showing strong source-sink dynamics), and therefore fixed the migration rates in the model at a constant level of 10% per year.

Wang et al. (2006) describe a sex disaggregated model for the north Pacific. This model is spatially aggregated, although fleets were disaggregated on the basis of the 4 spatial units assumed by Kleiber & Yokawa (2002), with the equator forming the southern boundary.

Indian Ocean

Anon. (2006) describes a preliminary stock assessment for swordfish based on deterministic surplus production models for the whole of the Indian Ocean. While these aggregate models seemed plausible, it was noted that there is evidence for depletion in the area around La Reunion. It was recognized that these localized fishery effects should be examined more closely.

Proposed Alternative Spatial Structures

There is always a debate in any model formulation process about the optimal level of complexity. In this assessment, the debate is particularly formulated around stock structure and spatial structure (and to a lesser extent sex structure). If the model is not suitably disaggregated, there is a risk of statistical biases from the aggregation of non-

homogenous units. If the model has too much disaggregation, the parameter estimation uncertainty is likely to be very high (and the problem becomes more technically and computationally demanding).

Depending on the biology of the populations, the available data, how the fishery operates, and the management objectives, there might be no reason to disaggregate the assessment. On balance, we think it is worth maintaining spatial disaggregation for the SW Pacific swordfish assessment at this time. The primary justification is the (potential at least for) non-homogenous units as a result of differential harvesting within the SW Pacific. If there are real conflicting trends in CPUE and size composition between two areas due to differential fisheries exploitation, this might not be describable on the basis of an aggregate population with two different selectivity assumptions. A two area model that fits all the data provides a much more satisfying description of the system than a compromise solution in which none of the data fits. We are proposing a spatial structure consisting of four longitudinal regions across the South Pacific convention area (Figure 17), for the following reasons:

- Genetics and fishery demographics suggest that 1) the Northern and Southern hemisphere swordfish stocks are reasonably isolated in the Western Pacific Ocean, and 2) the South-Eastern swordfish stocks are relatively isolated from the northern and south-western stocks.
- North-South migration within the Southern hemisphere cannot be well estimated at the moment, and the main fisheries tend to follow the seasonal swordfish concentrations.
- PSAT and conventional tags do provide a means for estimating East-West diffusive movement. While preliminary, these estimates are likely to represent an upper bound of mixing rates (i.e. if site fidelity and habitat constraints are important).
- The longitudinal stratification facilitates a direct comparison between the aggregate assessment results from the 2006 assessment and the 2008 assessment. Depending upon considerations of data quality and stock structure, it is easy to remove one or both of the more eastward extensions of the model domain.
- The revised spatial structure and tagging data downplays the importance of site fidelity models within the SW Pacific, such that the relatively small migration rates observed in West-East directions can probably be assumed to come from homogenous mixing.
- Four regions represents a tractable estimation problem.

Disadvantages of this spatial structure relative to 2006 include:

- The coarser spatial structure means that the model will have less capacity to describe localized depletion, and will potentially introduce biases by aggregating non-homogenous regions.
- The catch rate and size composition data in the South-Central Pacific is more sparse and poorly understood than the South-West Pacific. It may prove unreasonable to attempt an assessment in the South-Central region.

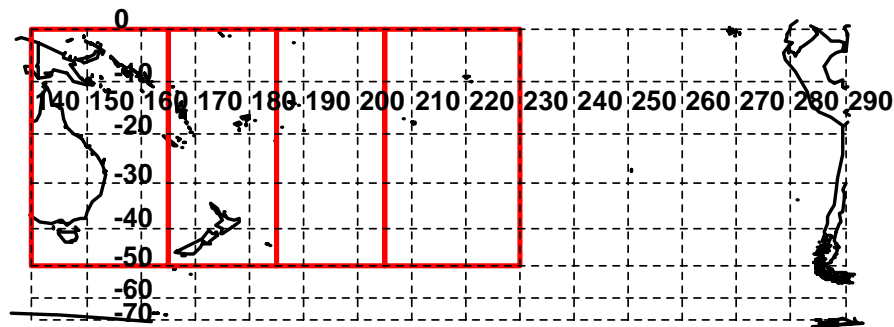


Figure 17. Proposed spatial structure for the 2008 South-West/South-Central Pacific swordfish assessment.

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