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Spatial Dynamics of Swordfish in the South Pacific Ocean Inferred from Tagging Data

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Evans, K[1]., D. Kolody[2], F. Abascal[3], J. Holdsworth[4], P. Maru[5] and T. Sippel[6]

[1] Wealth from Oceans National Research Flagship, CSIRO Marine and Atmospheric Research, GPO Box 1538, Hobart, Tasmania, 7001, Australia
[2] Secretariat of the Pacific Community, BP D5, 98848, Noumea, New Caledonia
[3] Instituto Español de Oceanografía, Centro Oceanográfico de Canarias, Apdo. Correos 1373, 38180 - Santa Cruz de Tenerife, Spain
[4] Blue Water Marine Research, PO Box 402081, Tutukaka 0153, New Zealand
[5] Ministry of Marine Resources, PO Box 85, Avarua, Rarotonga, Cook Islands.
[6] Blue Water Marine Research, PO Box 402081, Tutukaka 0153, New Zealand

Spatial dynamics of swordfish in the south Pacific Ocean inferred from tagging data

KAREN EVANS*

*Corresponding author: Wealth from Oceans National Research Flagship, CSIRO Marine and Atmospheric Research, GPO Box 1538, Hobart, Tasmania, 7001, Australia. Phone: 61 3 62325007 Fax: 61 3 62325000 Email: karen.evans@csiro.au

DALE KOLODY

Secretariat of the Pacific Community, BP D5, 98848, Noumea, New Caledonia. Email: daleK@spc.int

FRANCISCO ABASCAL

Instituto Español de Oceanografía, Centro Oceanográfico de Canarias, Apdo. Correos 1373, 38180 - Santa Cruz de Tenerife, Spain. Email: francisco.abascal@ca.ieo.es

JOHN HOLDSWORTH

Blue Water Marine Research, PO Box 402081, Tutukaka 0153, New Zealand. Email: john@bluewatermarine.co.nz

PAMELA MARU

Ministry of Marine Resources, PO Box 85, Avarua, Rarotonga, Cook Islands. Email: P.Maru@mmr.gov.ck

TIM SIPPEL

Blue Water Marine Research, PO Box 402081, Tutukaka 0153, New Zealand. Email: tsippel@gmail.com

ABSTRACT

The stock structure and movement patterns of broadbill swordfish (*Xiphias gladius*) in the south Pacific Ocean are uncertain and potentially have important implications for assessment and management. The most recent stock assessment for swordfish within the Western and Central Pacific Ocean (WCPO) was conducted in 2008. Since then, an expanded electronic tagging dataset has become available, and although still limited by small sample sizes, short periods at liberty and infrequent location information, provides evidence for revising spatial assumptions used in the 2008 assessment. Temperate eastern parts of the southwest Pacific appear to be linked to the tropical eastern part of the south-central Pacific, indicating that these areas should no longer be considered separately. Other assumptions from the 2008 assessment are supported, including: (i) no mixing between the southern and northern WCPO, (ii) no mixing between the WCPO and the eastern Pacific Ocean, and (iii) limited connectivity between the eastern and western parts of the Tasman and Coral Seas. Approximate movement rate estimates are provided which may be relevant for future stock assessments.

Keywords: swordfish, pop-up satellite archival tag, spatial dynamics, stock assessment

INTRODUCTION

Fisheries inherently contain spatial heterogeneities due to the distribution of fish population characteristics (e.g. age structure, maturity, growth, movement and stock structure) and fleet characteristics (e.g. selectivity and effort; Booth 2000). Spatial heterogeneity is particularly relevant to the assessment and management of many pelagic species (e.g. tunas, billfish, sharks), as these species are highly dispersed and capable of large-scale migrations. Fisheries targeting these species cover large areas, often include multiple gear types, differentially harvest multiple age groups and potentially target a number of stocks or sub-populations whose boundaries and connectivity are poorly understood (Caton 1991; Ward et al. 2000).

Stock assessments for most pelagic species attempt to account for some sources of spatial heterogeneity associated population and fishery components (e.g. Fournier et al. 1998). Few assessments, however, incorporate spatial complexity associated with stock structure (particularly at the sub-population level) and movement (Stephenson 1999; Cadrin and Secor 2009), because data are often insufficient for reliably delineating stock structure or estimating movement rates. Stock assessment model boundaries and any internal partitioning are frequently defined on the basis of fishery data available and the political realities of management (e.g. country and regional management jurisdictions), rather than the spatial characteristics of the fish population. Observations of movement from conventional tag data may not be sufficient for describing and estimating movement at the spatial and temporal scales required, and may be confounded with mortality, tag reporting rates and the distribution of the fishing fleet. Inappropriate assumptions about spatial structure and movement could result in poor advice for fisheries management (Cadrin and Secor 2009).

The development of electronic tagging technologies and associated methods to describe the movement of marine species over extended temporal and spatial scales has been ongoing over the last two decades (Gunn and Block 2001). Studies utilising such technologies have provided important insights into the movements, migratory routes and habitats of importance of pelagic species at increasingly finer resolutions (Lutcavage et al. 1999; Evans et al. 2008; Block et al. 2011; Evans et al. 2012). Yet, despite rapid advances in both the technologies and the methods used to detail the movements of pelagic species, direct application of these data into stock assessments or for estimation of fishing parameters is still rare (Miller and Andersen 2008; Kurota et al. 2009; Eveson et al. 2012).

Broadbill swordfish (*Xiphias gladius*; hereafter named swordfish) have a widespread geographical distribution throughout temperate, subtropical and tropical regions and are important target and by-catch species for domestic coastal and distant water longline fleets (Ward et al. 2000). Distributions of individuals have been observed to vary latitudinally, with the seasonal extension and retraction of warmer waters into higher latitudes and variability in prey distributions (Palko et al. 1981). There appears to be heterogeneity in the movements of individuals, with fewer males occurring in colder, higher latitudes than females (Palko et al. 1981). Investigations of catch data and molecular material suggest that there is some population structure to swordfish stocks across the Pacific, Indian and Atlantic Oceans (Reeb et al. 2000; Alvarado-Bremer et al. 2005). In the Pacific Ocean, gene flow appears to have a ⊃-shaped pattern, suggesting movement of animals east-west in the Northern and Southern Hemispheres, with connections across the equatorial zone along the west coast of the Americas (Reeb et al. 2000; Kasapidis et al. 2008). This is consistent with the hypothesis that there are separate stocks for the north Pacific and southwest Pacific (Sakagawa and Bell 1980). These studies suggest that foraging areas may represent sites of admixture between populations that originate from different spawning areas, as observed in the Atlantic (Alvarado-Bremer et al. 2005).

Because of the potential for widespread dispersive migration and/or seasonal spawning/foraging locations, it is difficult to identify the most appropriate spatial structures for the purposes of population assessment and fishery management. In the Western and Central Pacific Ocean (WCPO), swordfish catches are managed under the auspices of the Western and Central Pacific Fisheries Commission (WCPFC). Spatial boundaries in the most recent stock assessment for the species, conducted in 2008, were defined on the basis of a qualitative synthesis of data from larval surveys, fishery characteristics and preliminary results from a small number of conventional and electronic tagging experiments (Kolody et al. 2008, Kolody and Davies 2008).

The 2008 stock assessment was initially approached with a spatial structure that included the southern hemisphere from 140ºE-130ºW, split into four sub-regions with internal boundaries at 165ºE, 175ºW and 155ºW (Fig. 1). It was assumed that movement within each sub-region was dominated by seasonal north-south migrations between foraging and spawning areas. The partitioning of sub-regions in an east-west direction allowed a range of alternative assumptions to be explored, from an almost homogenous population (rapid mixing) to discrete sub-populations (no mixing). Ultimately, quantitative assessment results were only

provided for the South-West (SW) region (140ºE-175ºW), because: (i) only one tag was observed to move between the SW and the South-Central (SC) region (175ºW-130ºW); (ii) the data in the SC region were judged to be of lower quality that that in the SW; and (iii) standardised Catch per Unit Effort (CPUE) trends in the SW and SC demonstrated opposing trends, suggesting that either the two areas were weakly connected, or at least one CPUE series was a poor indicator of relative abundance. Within the SW model, mixing rates across the 165ºE boundary were estimated by fitting a simple diffusion model to the longitudinal displacements of the tagging data.

Since the 2008 assessment, there have been on-going deployments of pop-up satellite tags (PSATs) on swordfish contributing to an expanded distribution of tagging data across the south Pacific Ocean. Using this larger electronic tagging dataset, in combination with conventional tag returns, here, we reassess the movement patterns of swordfish in light of the spatial domains used in the 2008 stock assessment.

MATERIALS AND METHODS

Tagging data

Conventional tags (Hallprint, Australia) were deployed on swordfish via tagging programs in Australian (AU) and New Zealand (NZ) waters conducted by commercial and recreational (NZ only) fishing industries during the 1990s and 2000s, resulting in small numbers (AU: n = 7; NZ: n = 2) of recaptures from each region (Table 1). Full details of programs and deployments of conventional tags (CTs) are detailed in Stanley (2006) and Holdsworth and Saul (2011).

Pop-up satellite archival tags (PAT4: n = 26, Mk10: n = 69, Wildlife Computers, USA) were deployed on large swordfish in waters off eastern AU (PAT4: n = 26; Mk10: n = 28), northern NZ (Mk10: n = 19), south of the area between Fiji and French Polynesia in the western Pacific Ocean (SWPO; Mk10: n = 13), the Cook Islands (CI; Mk10: n = 9) and the northern coast of Chile in the eastern Pacific Ocean (EPO; n = 21) across 2004 – 2009. Methods associated with deployments of pop-up satellite archival tags (PSATs) employed in AU, SWPO and CI are detailed in Evans et al. (2011a). Those employed in NZ waters are detailed in Holdsworth et al. (2007) and those employed in the EPO are detailed in Abascal et al. (2010). Briefly, fish were caught during commercial longline operations with those

considered in good condition (hooked in the lip or upper mouth, lively and not bleeding) and of a large size and mass (>150cm OFL and >50kg wet mass so that the tag constituted ~0.2% or less of additional mass to the animal) lead alongside the vessel to a position near the sea door. A custom made stainless steel floy-type anchor (AU, SWPO and CI), either a stainless steel or medical grade nylon dart (EPO) or a medical grade nylon dart (NZ) was inserted into the dorsal musculature of the fish in a position just ventral to the primary dorsal fin using a customised tagging pole similar to that described in Chaprales et al. (1998). Once tagged, the fish was cut from the line and allowed to swim away from the vessel. Deployment positions of tag releases were recorded using the vessels' onboard GPS system. Sea surface temperatures recorded by vessels at the time of tagging ranged 16.4ºC – 26.0ºC. All personnel involved in tagging were experienced in the estimation of swordfish mass, selection of suitable tagging candidates (i.e. those of suitable size and condition) and tagging methods and all efforts were made to ensure tagging was conducted as efficiently as possible while minimizing potential impacts on the fish. Tags were programmed to release from fish and transmit summarised depth, temperature and light data after periods of time ranging from 60 days to the limit of the tags, which was 365 days post-release. Failure of tags to report to the Argos system occurred in 14 of the 95 tags deployed. Further details of tag set-up and proposed and achieved deployment periods for AU, NZ and EPO deployments are detailed in Holdsworth et al. (2007); Abascal et al. (2010) and Evans (2010).

Only those data derived from tag deployments > 30 days were included here to ensure that biases associated with any short-term impacts of tagging were minimised (Table 2; n = 54). Daily positions derived from each tag were calculated using the state-space model described in Nielsen and Sibert (2007) implemented in the R software package "trackit" (downloaded from: www.soest.hawaii.edu/tag-data/trackit).

Models for distinguishing random diffusion from directed migration

We used simple statistical models aimed at emphasising population level characteristics, similar to those used in the 2008 stock assessment (Kolody and Davies 2008), to examine migration characteristics in relation to three broad categories of movement.

1. Unbounded Diffusion (UD): which assumes that each individual engages in a permanent random walk and that the variance of the distribution continues to increase linearly over the time period of interest.

2. Bounded Diffusion (BD): which assumes that each swordfish engages in an independent random walk, but is bounded by a home range or habitat constraints, and that the variance of the distribution increases to an asymptote and stabilises.

3. Seasonal migration with Site Fidelity (SF): which assumes that each individual engages in a consistent annual migration. Each individual is predicted to be near the same place at the same time each year, but different individuals can have very different migratory paths from each other. Within this model the variance of the distribution expands and contracts in an annual cycle.

These models are not intended to make explicit predictions about the position or movement of individuals, but were only used in an attempt to classify movement characteristics at a level that is relevant to the formulation of coarse resolution stock assessment models.

Models were derived from simple extensions to Sibert and Fournier (2001), in turn based on Feller (1968), which note that a discrete-time unbiased random walk movement models result in spatial distributions that are equivalent to a continuous diffusive process. In this case, we were only concerned with one-dimensional movement, because latitudinal and longitudinal movements have different implications (and different observation error characteristics). The probability density function for future 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:

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

There is also a position error associated with each estimate $x_{observed,t} = x_t + \varepsilon_t$, and we assume $\varepsilon_t \sim Normal(\mu = 0, \sigma)$.

Within the UD model, parameters were estimated using a negative log-likelihood function (with constants removed):

$$(2) \qquad L(x_{observed} \mid D, \sigma) = \sum_i \log\left(\sqrt{2Dt_i + \sigma^2}\right) + \frac{x^2_{observed,i}}{2(2Dt_i + \sigma^2)}$$

Within the BD model, the variance term $2Dt$ is replaced by $\alpha t/(\beta + t)$. This was adopted from a Beverton-Holt stock-recruit function (i.e. the function describes displacement variance as a function of time, instead of recruitment as a function of biomass) and is not intended to

accurately represent the physics of particle diffusion in a container. At one extreme the model degenerates to the case of unbounded diffusion (within the lifespan of an individual fish) and at the other, the variance rapidly reaches an asymptote, consistent with the idea that individuals are constrained to a home range. Substituting this variance term into (2) results in:

$$(3) \qquad L(x_{observed} \mid \alpha, \beta, \sigma) = \sum_i \log\left(\sqrt{\frac{\alpha t_i}{\beta + t_i} + \sigma^2}\right) + \frac{x^2_{observed,i}}{2\left(\frac{\alpha t_i}{\beta + t_i} + \sigma^2\right)}$$

Similarly, displacement variance for the SF model is described by a wave function $(A + A\sin(t\omega + \phi))$. The wavelength ($\omega$ =2π/365.25), and phase angle (ϕ = -0.5π) were fixed to represent annual periodicity with a minimum on the calendar day of tag release, thereby providing a convenient first approximation for a system that expands and contracts in an annual cycle. The corresponding likelihood function is:

$$(4) \qquad L(x_{observed} \mid A, \omega, \phi, \sigma) = \sum_i \log\left(\sqrt{A + A\sin(t_i\omega + \phi) + \sigma^2}\right) + \frac{x^2_{observed,i}}{2(A + A\sin(t_i\omega + \phi) + \sigma^2)}$$

We fit the three models to four different datasets, three of which included only the release and recovery or first transmission position information. The four datasets comprised:

A. release and recapture or first transmission positions from all CTs and PSATs;

B. release and recapture or first transmission positions from CTs and PSATs deployed in the WCPO only;

C. release and first transmission positions from PSATs deployed in the WCPO only;

D. release and first transmission positions and light-based geopositions from PSATs deployed in the WCPO only. The time and displacement between each geoposition and the corresponding release point was considered to be an independent observation (such that each tag implicitly had a different weight in the likelihood, depending on the number of geopositions).

Each model was fit independently to latitude and longitude estimates and fit with a fixed value of σ = 1.0. While this value can be considered as reasonable for release and first transmission positions for electronic tags, it is likely to be an underestimate for light-based geopositions, particularly for latitude (see Evans and Arnold 2009 for an overview of

geolocation methods and uncertainties). Accordingly, all models for dataset D were also fit with σ estimated. We also fit the SF model with σ estimated for each dataset, as it was plausible that the model might require additional freedom associated with variability in timing and/or homing accuracy.

RESULTS

Observed movements

Conventional tags were at liberty for 85 – 3538 days (Table 1) and PSATs at liberty for 43 – 364 days (Table 2). Displacements observed between release and recapture points ranged 92 – 3046 km for CTs and 92 – 2988 km for PSATs, with displacements greater than 2000 km achieved in as little as 49 days. All AU swordfish remained within the Coral/Tasman Sea, with only one individual observed to move east of 170ºW and into the eastern Tasman Sea and (Figs. 1 and 2). Latitudinal movements were also limited, with the majority of individuals moving < 10 degrees. Swordfish tagged elsewhere across the WCPO demonstrated varying latitudinal and longitudinal movements with individuals distributing across the WCPO. Two NZ swordfish were observed to undertake circular movements to the New Caledonia/Vanuatu region before returning to waters around NZ (Fig. 2). Sea surface temperatures collected by the tags (not shown) reflected latitudinal gradients associated with such circular movements. The remaining NZ swordfish moved to the west, north and to the northeast (NE) towards CI (Fig. 2). Tags on SWPO swordfish predominantly moved to the north with only one tag moving to the south, while CI swordfish moved to the southwest (SW), with one entering NZ waters (Fig 2).

Only three tags released east of 170ºW were subsequently observed west of 170ºW and only one of those released west of 170ºW moved east of 170ºW (Figs. 2 and 3). Longitudinal movement also did not appear to be biased by tags at liberty for short durations, as a similar pattern was observed when data were restricted to only those deployments longer than 180 days (not shown). Maximum displacements of all tags were less than 25° latitude and 30° longitude and movements and displacement positions did not appear to be related to size of individuals, with individuals of 50 – 120kg observed to travel distances of greater than 1,000 km (Fig. 4).

Four of the six swordfish tagged in the EPO undertook directed movements in a NW direction. One individual moved west before heading south and then NE, while another moved NW before heading in a westerly direction. All movement was restricted to the EPO, with no tagged swordfish moving west of 110ºW (Figs. 1 and 2).

The aggregate WCPO swordfish geoposition data did not demonstrate clear seasonal patterns in latitudinal or longitudinal movements. However, when partitioned according to release longitude (west and east of 165ºE), a seasonal signal in latitudinal movement was evident in swordfish tagged to the east of 165ºE (Fig. 4). Individuals were distributed to the south during the second and third quarters of the year (April – September) and to the north in the first and fourth quarters of the year (October – March). Swordfish tagged to the east of 165ºE appeared to have a narrow distribution between 165 – 180ºW throughout the second quarter of the year (April – June), and a much broader longitudinal distribution during the rest of the year, although low numbers of observations during April – June are likely to influence this. In contrast, little seasonal variability in latitude or longitude was evident in swordfish tagged to the west of 165ºE (Fig. 4).

Latitudinal movements of swordfish tagged in the EPO occurred during the second and third quarters of the year (May – September). Determining seasonality in movements is somewhat restricted however by lengths of deployments, with observations only available across the months of April – September.

Movement models

Of the three models, the BD model fit latitude data best in terms of likelihood and Akaike Information Criterion (AIC ; Table 3, Fig. 5). The UD model provided an intermediate fit and the SF model produced the worst fit. When the SF model was allowed to estimate σ, it fit best with high values of σ for datasets A-C, degenerating to a form with negligible seasonality. In this case, the SF model became largely indistinguishable from the BD model, except possibly in the first few days to weeks (not shown). The SF model estimated a substantial seasonal cycle with dataset D however, it was still a much poorer fit than the other models. Differences between datasets A-C and D were largely driven the large number of position observations immediately after PSAT release, at a time when the displacement variance tends to be increasing. These initial observations influenced the SF model in such a way to prevent the variance from expanding too rapidly.

The best longitude model fit varied between datasets (Table 4; Fig. 6). The BD model had the lowest likelihood (or equal lowest), while the UD model had the lowest AIC for datasets B, C and D. The BD model took on a degenerate form identical to UD for dataset D. The SF longitude model was similar to the SF latitude model, providing the worst fit and degenerating to a form with negligible seasonality when σ was estimated for datasets A-C. The predictions of the UD and BD models were very similar for tags in the first year at liberty (Fig. 6). After the first year the two models diverged, with the more flexible BD model able to better describe both the rapid initial increase in displacement variance, and the asymptote of the variance. Performance differences between UD and BD however, were subtle across all datasets and non-existent in the case of dataset D. Values of AIC suggest that the BD model provided a marginally better fit than the UD model for dataset A, however, the extra parameter in the BD model does not appear to be justified for datasets A-C.

Noting the apparent differences in migration characteristics by release location (Fig. 4), datasets C and D were disaggregated into tag releases west and east of 165ºE and the three models refit separately to the data (not shown). Similarly to the aggregated data, the BD model provided the best fit for latitude displacement and the UD model for longitude (on the basis of AIC). Displacement parameters were estimated to be considerably larger in the east than west for both latitude and longitude. When the likelihoods for the disaggregated models were summed, however, the AIC was similar or only marginally better than that of the aggregate models.

DISCUSSION

Tagging data provide the most direct information on fish movement and are potentially useful stock assessment and other population dynamics models. Although CTs can provide valuable information for fisheries biology and stock assessment (including estimation of growth rates, mortality and abundance), electronic tags can provide substantially more information on the movement dynamics of individuals. Conventional tagging is a fishery-dependent mark-recapture technique that depends almost entirely on animal recaptures within fisheries. Because fishing effort is not equally distributed through time and space, information from CT returns tends to be biased in these aspects. Reporting rates for CT returns are often low and may be inconsistent across fleets, which can further bias the perception of movement (Hoenig et al. 1998; Pollock et al. 2001; Polacheck et al. 2006). Even with large numbers of

deployments, it is often logistically impossible to release tags in a manner that is representative of the distribution of the population, particularly for widespread species such as tunas and billfishes. In contrast, electronic tags, and in particular PSATs, can provide position information from times and places that may be beyond fishery boundaries and without relying on recapture and return from fisheries. Deployment of a relatively small number of electronic tags within carefully selected regions across a species distribution allows for dispersal and the observation of movement throughout the wider region.

Observed movements

Observations of movement derived from tags released on swordfish in the SW Pacific presented here suggest some heterogeneity in movements that may indicate population sub-structure. Movements observed suggest that the probability of undertaking long distance movements in regards to both latitude and longitude is higher for fish tagged east of 165ºE compared with those tagged to the west of 165ºE. Mixing of swordfish in the area east of 165ºE could be potentially substantial, and greater than that between AU and NZ. It seems likely that fish moving between NZ and CI represent one population with seasonal migration between foraging and spawning areas, while fish in the AU region probably represent a somewhat distinct population that has access to spawning and foraging areas within the Coral and Tasman Seas.

Observations of movement from limited numbers of tag deployments however, have the potential to be misleading. Observed movements do not appear to reflect the seemingly continuous distribution of catch across tropical regions of the WCPO and observations of spawning areas in the tropical region directly north of NZ (Nishikawa et al. 1985), both of which suggest that it should not be necessary for fish that forage near NZ to migrate all the way to CI to spawn.

Investigations into the reproductive dynamics of swordfish across the Tasman/Coral Sea region have reported reproductively active females off the east coast of Australia and around New Caledonia (Young et al. 2003). Examination of maturity in gonads suggests that spawning occurs across an extended season from September to March. In Australian waters, mature females have been predominantly observed west of 158ºE and in waters above 24ºC, suggesting spawning occurs in the warm waters of the Coral Sea and the East Australian Current (EAC). Gonads sampled from NZ waters suggest no active spawning of females in this region across the same period.

The somewhat restricted longitudinal and latitudinal movement of swordfish tagged in AU waters may be related to oceanographic conditions in the region. The EAC is a boundary current that carries warm water from tropical regions southward and into the Tasman Sea and dominates waters off the east coast of AU from approximately 18 – 35ºS (Ridgway and Dunn 2003). As the EAC moves south, eddies separate from the main body of the EAC which migrate south in the Tasman Sea forming a region of intense upwelling and downwelling, which results in enhanced seasonal productivity (Tilburg et al. 2002). Regional circulation of the EAC is limited by the bathymetry of the Tasman basin, which is bounded by AU to the west, NZ to the southeast and the island archipelago of New Caledonia, Vanuatu and Fiji to the northeast. A series of seamounts are also found off the east coast of Australia around which potential forage sources for swordfish are enhanced (Young et al. 2011).

In contrast, waters off northern NZ rarely reach temperatures of 24ºC and bathymetric structures in the region are largely located to the north and far west and beyond the southern limits of waters of 24ºC. Around the NZ region, the Tasman Front (TF), into which the EAC feeds, moves eastward across the Tasman basin and attaches to the continental slope north of New Zealand. It then becomes established as a boundary current, part of which becomes the west Auckland current (Ridgway and Dunn 2003). Four large warm core eddies are associated with the flow of the TF around the northern and eastern coasts of NZ and have important biological implications for the region by increasing vertical mixing and enhancing productivity (Bradford et al. 1982; Tilburg et al. 2002). Enhanced productivity in this region may support important seasonal foraging opportunities for large marine predators such as swordfish.

It is notable that electronic tagging of striped marlin (*Kajikia audax*) in eastern Tasman Sea waters showed no movement of individuals across Tasman Sea over multiple seasons (Sippel et al. 2011). Electronic tagging of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*) in the western Coral Sea also showed movements of individuals were largely restricted to the Coral Sea, with only a small number of individuals moving further east and into the greater western Pacific Ocean (Evans et al. 2008; Evans et al. 2011b). It may be that oceanographic mechanisms are linked to regional population sub-structure across multiple species in the WCPO region.

Movement models

Inclusion of a larger tag dataset did not improve parameter estimates of movement dynamics within the simple movement models investigated. Of the options examined, simple diffusion provided the best description of longitudinal movement, and associated diffusion parameters can be conveniently translated into bulk transfer coefficients for stock assessment models. The BD model provided the best fit to latitudinal movements observed, which is consistent with our expectations of a bounded home range, but did not demonstrate any seasonality in movements, which might be expected on the basis of catch data available and current hypotheses of seasonal movements. Observed variability in sex ratios (Palko et al. 1981, Grall et al. 1983, Taylor and Murphy 1992, De Martini et al. 2000, Young et al. 2003; Poisson and Fauvel 2009), has predominantly been associated with the hypothesis that smaller, male swordfish reside lower latitude waters where spawning occurs and larger, female swordfish undertake extensive feeding migrations into higher latitude waters, returning to lower latitudes to spawn (De Martini et al. 2000). Without sex-specific information however, the potential importance of this fundamental biological trait on movement dynamics cannot be investigated.

There was little difference in fits to longitudinal movements between the UD and BD models in the short-term, with the BD model preferred for dataset A. Across the longer-term (>1y, for which there are few observations), the two models tend to diverge and UD estimates dispersion rates that would be expected to result in gene flow that is too high to maintain current understanding of genetic structure across the South Pacific (Reeb et al. 2000). The lowest estimate of D predicts that 2.5% of swordfish from CI would be located east of 120°E in the EPO after five years. Given the model fits observed, we would predict that larger numbers of longer duration tag observations would result in either the BD model providing a better fit to the data (as is currently the case if conventional tags and PSATs deployed in the EPO are included), or the UD model would estimate lower diffusion rates as a result of seasonal migration being interpreted more appropriately as structured noise around the true random movement. Because of this, the current estimates of dispersion might be more reasonably interpreted as an upper bound on movement, and the possibility of relatively discrete sub-populations should not be dismissed.

The SF models did not describe potential directed seasonal migrations very well at the population level. While there may be good reasons for individuals from the same region to

share migration patterns, there is no reason to think that these patterns would be consistent. It may be that relatively few individuals that are observed to undertake movement into high latitudes exaggerate our perceptions of migration in the general population. Large portions of the population might undertake relatively undirected foraging migrations of similar or greater magnitude and duration to directed spawning migrations, thereby confounding the ability to discern migrations associated with spawning. There may also be considerable variability in the timing of migrations within and among individuals depending on age, sex or individual condition. Given that spawning occurs across a broad season (Young et al. 2003), migrations between foraging and spawning regions might be initiated anytime within the season, possibly more than once within a year and not necessarily every year.

We recognise that all three models investigated here are extreme simplifications of complex behaviour, which is influenced by the size/age and sex of the individual, and inter-annual variability introduced through density dependent processes and local oceanographic conditions. Differences observed in the movement characteristics of swordfish west and east of 165ºE suggests that there is additional information that might be gained by more detailed, disaggregated analyses. However, with the small number of tags, and relatively short periods of liberty, it is not clear how more detailed spatial modelling would improve any short-term advice for formulating stock assessment models.

Recommendations for the next stock assessment

From the results presented here, it seems reasonable to assume that there is substantial latitudinal mixing of swordfish within the south Pacific Ocean, and that there is still no direct evidence of movement across the equator. The decision made in the 2008 assessment to treat the SW and SC regions (west and east of 175ºW) independently is no longer defensible on biological grounds. It remains unclear whether the WCPFC eastern boundary of 130ºE (south of 3ºS) is biologically ideal, but at present there is no evidence to indicate that it is biologically inappropriate. Movement patterns across the Tasman and Coral Seas are suggestive of limited mixing or the partial overlap of sub-populations that may not mix strongly on the spawning grounds.

We suggest that the next stock assessment for swordfish in the WCPFC management area should consider two regions bounded at the equator in the Southern Hemisphere. The western region should extend from the AU coast to 165ºE, and the eastern region should extend from 165ºE - 130ºW. The eastern WCPFC convention boundary (130ºW) is suggested in the

absence of other information (movements east of 150ºW were not observed in this study, but we recognize that other fisheries information might provide a basis for revising this suggestion). We consider diffusive mixing across the boundary at 165ºE (diffusion rate, D = 0.11 calculated from the UD model fit to dataset C) as the best estimate of movement between regions at this time. However, we strongly recommend examining the sensitivity of this assumption, including alternative interpretations at the extremes (i.e. very high and zero mixing), in recognition that this estimate is highly uncertain (and qualitatively wrong if spawning populations really are isolated).

Directions for future research

While inclusion of an expanded tagging dataset has proved to be informative in better understanding the spatial dynamics of swordfish in the south Pacific Ocean, there are still many uncertainties regarding swordfish movement. Extension of tag releases across the region would improve our understanding of movement patterns, particularly if fish from particular size-classes, sexes and regions could be selected. In particular, deployments in tropical regions, directly north of NZ (~180ºE) and in the temperate region south of 140 – 160ºW would fill important gaps. Releases from the southeastern WCPFC boundary area, would help in establishing how well this management boundary agrees with the population structure and what linkages there may be between the WCPO and the EPO. Because the majority of movement data were derived from deployments of PSATs and deployments were often affected by premature detachment of tags, information on seasonality and inter-annual variability in movements is somewhat restricted. Further longer-term (i.e. multi-year) deployments of tags, such as internally implanted archival tags or recently developed PSATs utilising solar power sources (and therefore capable of extending battery life of tags) may provide longer-term data required in order to address this.

Position data derived from PSATs enable a range of alternative modelling approaches to be pursued to describe movement at various spatial scales, potentially at the level of the individuals and/or in relation to oceanographic variability (e.g. by using Hidden Markov Models or Individual-Based Models). Under such modelling frameworks, parameters from individuals could be combined to estimate parameters for the population as a whole. Development of such models would allow for an improved treatment of errors associated with geolocation methods, and potentially allow for more detailed investigations of the influence of individual sizes or release locations on movements. Further development of stock

assessment methods (potentially including multiple discrete populations that overlap on fishing grounds) and management strategy evaluation (e.g. Smith et al. 1999), will help determine if different stock structure and movement assumptions are likely to have an important effect on management options and outcomes. This would, in turn, be of use in determining if additional tagging and analyses are justified, and could be used to inform tagging experiment design.

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Table 1. Recaptures of conventional tags on broadbill swordfish in the western Pacific Ocean.

Tag	Release				Recapture			
	Date	**Latitude**	**Longitude**	**Estimated mass (kg)**	**Date**	**Latitude**	**Longitude**	**TAL (days)**
Australia								
431	24 Jul 2000	-25.83	153.88	15	09 Nov 2001	-32.52	156.52	473
9	12 Oct 2000	-26.30	154.03	20	05 Jan 2001	-25.25	154.07	85
20	20 Oct 2000	-26.05	155.33	15	06 Jul 2004	-34.18	154.03	1355
534	09 Jan 2001	-28.03	154.88	4	12 Jul 2002	-31.02	153.35	549
882	23 Jul 2001	-33.77	173.00	20	24 Jul 2007	-21.00	-159.58	2192
646	11 Sep 2002	-30.80	161.52	15	12 Dec 2003	-18.30	153.60	457
311	22 Sep 2002	-29.12	157.18	15	17 Jul 2003	-31.17	162.30	298
New Zealand								
20862	18 Jun 1992	-32.33	172.25	12	24 Feb 2002	-32.83	167.33	3538
26600	05 Feb 1996	-37.17	-178.17	20	09 Jun 2004	-38.80	178.98	3047

^ Estimated mass is an estimate of gilled and gutted mass; TAL: time at liberty.

Table 2. Deployments of pop-up satellite archival tags on broadbill swordfish in the Pacific Ocean at liberty for >30 days.

Tag	Release				Pop-up transmission			
	Date	Latitude	Longitude	Estimated mass (kg)^	Date	Latitude	Longitude	TAL (days)
Australia								
03P0463	20 Sep 2004	-28.12	155.82	n/a	18 Dec 2004	-28.95	154.40	89
03P0466	24 Sep 2004	-28.17	160.63	n/a	20 Dec 2004	-26.68	163.92	87
04P0574	07 Oct 2006	-25.88	156.96	50	06 Mar 2007	-24.40	161.61	150
04P0443	08 Oct 2006	-26.11	157.02	50	06 Aug 2007	-29.12	166.44	302
04P0577	03 Nov 2006	-28.09	156.84	100	17 Mar 2007	-29.56	155.99	134
04P0578	03 Nov 2006	-28.07	156.81	90	16 Dec 2006	-16.87	153.92	43
04P0576	28 Nov 2006	-24.93	156.49	55	24 Feb 2007	-27.84	158.87	88
04P0588	30 Jan 2007	-24.75	157.84	50	07 Jun 2007	-38.25	170.24	128
04P0474	07 Feb 2007	-24.84	156.34	90	07 Aug 2007	-32.01	157.29	181
04P0472	04 Mar 2007	-25.46	157.30	70	01 Jun 2007	-22.80	156.53	89
04P0564	04 Mar 2007	-25.37	157.28	80	30 Aug 2007	-23.42	157.06	179
04P0473	28 Nov 2007	-27.30	157.42	140	25 Feb 2008	-30.41	153.61	89
04P0338	19 Jan 2008	-28.37	157.38	150	17 Apr 2008	-31.42	156.13	89
06A0718	28 Jan 2007	-25.61	157.22	80	28 Mar 2007	-14.30	152.07	59
06A1162	25 Feb 2008	-29.36	159.60	60	23 Feb 2009	-28.12	160.42	364
06A1161	20 Mar 2008	-25.68	156.68	120	11 Dec 2008	-33.28	157.22	266
06A1165	21 Mar 2008	-25.95	156.57	200	14 Dec 2008	-23.26	155.67	268
06A1140	24 Mar 2008	-25.87	156.57	80	22 Dec 2008	-36.10	151.27	273
06A1160	24 Mar 2008	-25.73	156.28	140	12 Oct 2008	-24.70	155.69	202
06A1130	26 Mar 2008	-26.02	156.98	140	09 Dec 2008	-22.86	158.25	258

Tag	Release				Pop-up transmission			
	Date	Latitude	Longitude	Estimated mass (kg)^	Date	Latitude	Longitude	TAL (days)
06A1133	22 Apr 2008	-25.75	156.19	65	15 Aug 2008	-23.40	154.88	115
06A1137	22 Apr 2008	-25.97	156.62	130	20 Jan 2009	-29.61	158.98	273
06A1151	24 April 2008	-26.11	156.76	140	22 Jan 2009	-23.99	161.61	273
06A1156	13 Jan 2009	-26.97	156.68	170	14 May 2009	-21.84	163.36	121
06A1135	15 Jan 2009	-26.73	156.62	175	13 Jul 2009	-24.87	158.24	179
06A1139	11 Feb 2009	-23.93	155.91	100	14 Jul 2009	-40.88	153.64	153
08A0098	19 Jun 2008	-28.71	154.04	100	17 Aug 2008	-21.83	159.06	59
08A0101	12 Dec 2008	-25.73	156.09	145	09 Feb 2009	-33.24	156.45	59
08A0096	13 Dec 2008	-25.73	156.24	165	10 Feb 2009	-32.82	159.24	59
08A0100	15 Dec 2008	-25.89	155.36	170	12 Feb 2009	-34.77	153.94	59
New Zealand								
06A0358	09 Jul 2006	-36.24	178.10	56	29 Oct 2006	-30.077	-176.602	113
06A0366	10 Sep 2006	-29.63	179.94	56	15 Nov 2006	-27.97	-179.918	67
06A0367	23 Jul 2006	-33.93	173.12	130	15 Jan 2007	-36.155	168.908	177
06A0368	03 Jul 2008	-36.52	179.26	120	29 Jan 2009	-29.249	-160.524	210
06A0369	23 Jul 2006	-34.03	173.22	90	15 Mar 2007	-33.1	164.732	236
06A0504	07 Sep 2006	-29.18	179.89	56	14 Feb 2007	-26.259	-179.396	161
06A0538	01 Nov 2006	-30.66	178.43	80	14 Feb 2007	-37.678	179.344	106
06A0539	10 Jul 2008	-36.44	178.10	75	05 Feb 2009	-41.985	-178.465	210
06A0540	25 Jul 2007	-33.74	174.23	130	14 Feb 2008	-33.872	171.66	204
06A0541	07 Nov 2006	-34.25	-179.47	80	15 Mar 2007	-42.65	176.08	128
Western Pacific								
07A0859	10 Jun 2008	-31.317	-171.133	108	04 Aug 2008	-27.71	-170.38	55

Tag	Release				Pop-up transmission			
	Date	**Latitude**	**Longitude**	**Estimated mass (kg)^**	**Date**	**Latitude**	**Longitude**	**TAL (days)**
07A0865	18 Jul 2008	-33.733	-174.0167	64	26 May 2009	-39.506	-172.052	312
07A0866	29 Jul 2008	-27.633	-172.283	77	11 Sep 2008	-15.751	-170.954	44
07A0867	15 Aug 2008	-32.35	-169.467	53	01 Oct 2008	-15.97	-172.55	47
07A0954	15 Sep 2008	-32.22	-162.73	91	21 Nov 2008	-14.18	-155.44	70
Cook Islands								
08A0756	08 Nov 2009	-20.81	-159.82	65	10 Oct 2010	-32.03	-171.8	336
08A0744	27 Nov 2009	-20.723	-159.935	130	13 Nov 2010	-26.59	-166.37	351
08A0743	05 Dec 2009	-21.186	-160.193	65	14 Mar 2010	-42.314	-178.821	99
Eastern Pacific#								
06A0931	31 Mar 2007	-22.78	-87.17	n/a	30 May 2007	-02.45	-97.68	60
06A0957	26 May 2007	-22.17	-81.82	76	14 Jul 2007	-09.52	-99.20	49
06A0947	30 May 2007	-22.05	-84.45	n/a	09 Aug 2007	-14.40	-101.43	71
06A0956	11 June 2007	-18.58	-84.62	n/a	24 Nov 2007	-14.72	-91.32	166
06A0950	17 June 2007	-19.20	-83.35	n/a	21 Sep 2007	-06.08	-96.62	96
06A0966	30 June 2007	-19.82	-80.72	76	12 Oct 2007	-07.65	-105.42	104

^ estimated mass is an estimate of gilled and gutted mass; # estimated lengths of swordfish: 150 – 180 cm length to caudal fork; TAL: time at liberty. Note tags first transmit 48 hours after pop-up.

Table 3. Parameter estimates for movement models in relation to latitude. Parameters are defined in terms of days and degrees of latitude.

Model	σ	Other parameters	LLH	AIC
Dataset A (n = 63)				
UD (σ fixed)	1.00	D = 0.37	18.76	20.76
BD (σ fixed)	1.00	α = 67.00; β <0.01	0.00	4.00
SF (σ fixed)	1.00	A = 130.00	81.22	83.22
SF (σ estimated)	8.20		0.01	4.00
Dataset B (n = 57)				
UD	1.00	D = 0.29	16.69	18.69
BD	1.00	α = 56.70; β <0.01	0.00	4.00
SF (σ fixed)	1.00	A = 110.00	81.22	83.22
SF (σ estimated)	6.74	A <0.01	<0.01	4.00
Dataset C (n = 48)				
UD (σ fixed)	1.00	D = 0.34	10.53	12.53
BD (σ fixed)	1.00	α = 58.20; β <0.01	0.00	4.00
SF (σ fixed)	1.00	A = 130.00	14.63	16.63
SF (σ estimated)	4.75	A = 11.20	0.01	4.00
Dataset D (n = 1535)				
UD (σ fixed)	1.00	D = 0.26	10.48	12.48
UD (σ estimated)	<0.01		10.20	14.20
BD (σ fixed)	1.00	α = 250.00; β = 380.00	0.94	4.94
BD (σ estimated)	<0.01		0.00	6.00
SF (σ fixed)	1.00	A = 97.80	218.25	220.25
SF (σ estimated)	2.69		99.06	103.06

LLH: -log likelihood (minus the lowest LLH for each dataset); AIC: Akaike Information Criterion. Note: likelihoods are not comparable between datasets.

Table 4. Parameter estimates for movement models in relation to longitude. Parameters are defined in terms of days and degrees of longitude.

Model	σ	Other parameters	LLH	AIC
Dataset A (n = 63)				
UD (σ fixed)	1.00	D = 0.24	7.19	9.19
BD (σ fixed)	1.00	α = 64.30; β = 0.01	0.00	4.00
SF (σ fixed)	1.00	A = 87.90	317.12	319.12
SF (σ estimated)	8.02	A <0.01	0.33	4.33
Dataset B (n = 57)				
UD (σ fixed)	1.00	D = 0.11	1.52	3.52
BD (σ fixed)	1.00	α = 170.00; β = 570.00	0.00	4.00
SF (σ fixed)	1.00	A = 55.00	322.37	324.37
SF (σ estimated)	6.74	A <0.01	5.46	9.46
Dataset C (n = 48)				
UD (σ fixed)	1.00	D = 0.12	0.67	2.67
BD (σ fixed)	1.00	α = 84.40; β = 200.00	0.00	4.00
SF (σ fixed)	1.00	A = 61.80	14.99	16.99
SF (σ estimated)	4.75	A = 11.20	0.86	4.86
Dataset D (n = 1535)				
UD (σ fixed)	1.00	D = 0.19	14.07	16.07
UD (σ estimated)	<0.01	D = 0.19	0.00	4.00
BD (σ fixed)	1.00	α = 6.76e+8; β = 1.81e+9	14.07	18.07
BD (σ estimated)	<0.01	α = 1.65e+7; β = 2.20e+4	0.00	6.00
SF (σ fixed)	1.00	A = 76.10	253.46	255.46
SF (σ estimated)	2.69	A = 49.50	200.82	204.82

LLH: -log likelihood (minus the lowest LLH for each dataset); AIC: Akaike Information Criterion. Note: likelihoods are not comparable between datasets

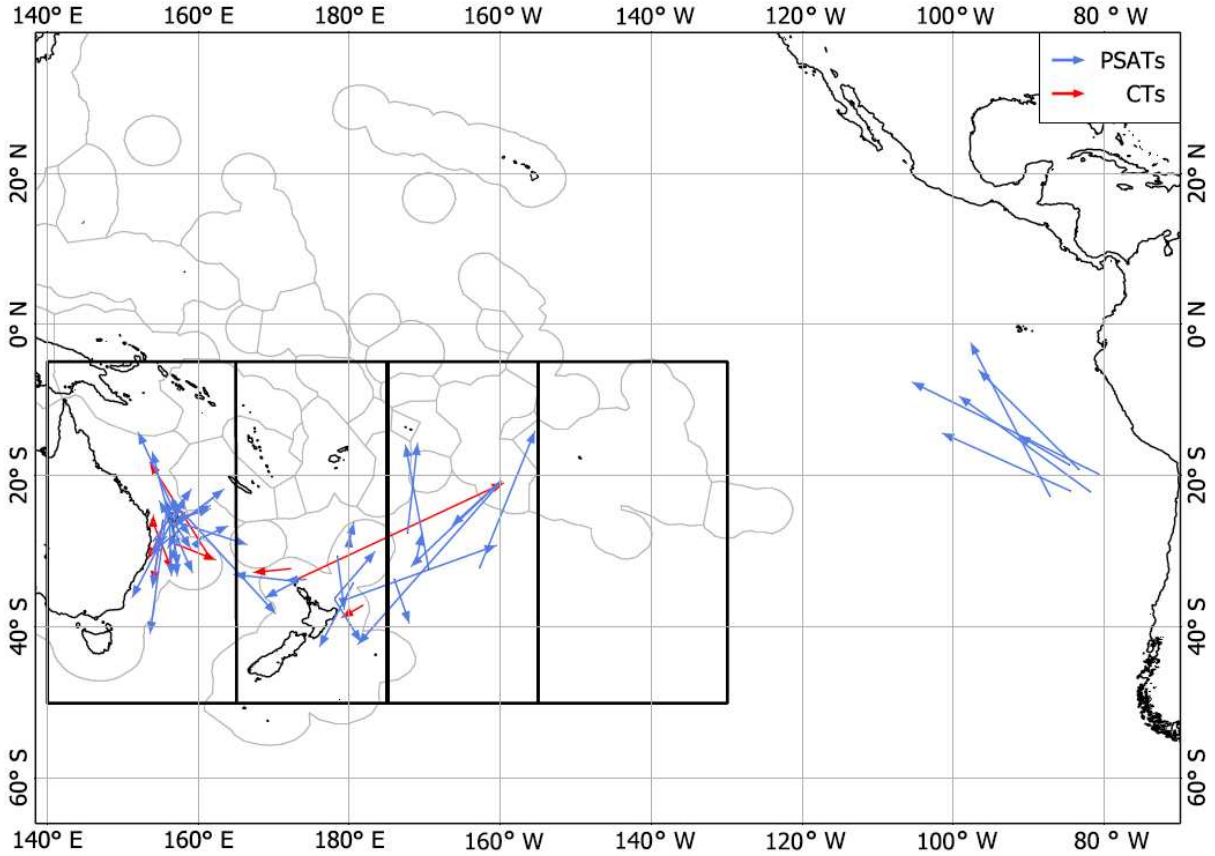

Fig. 1. Release and recapture (conventional tags) or first transmission points (pop-up satellite archival tags) of tags deployed on swordfish at liberty >30 days in the south Pacific Ocean between 1992 and 2010. Spatial boundaries used in the 2008 stock assessment are given (taken from Kolody et al. 2008).

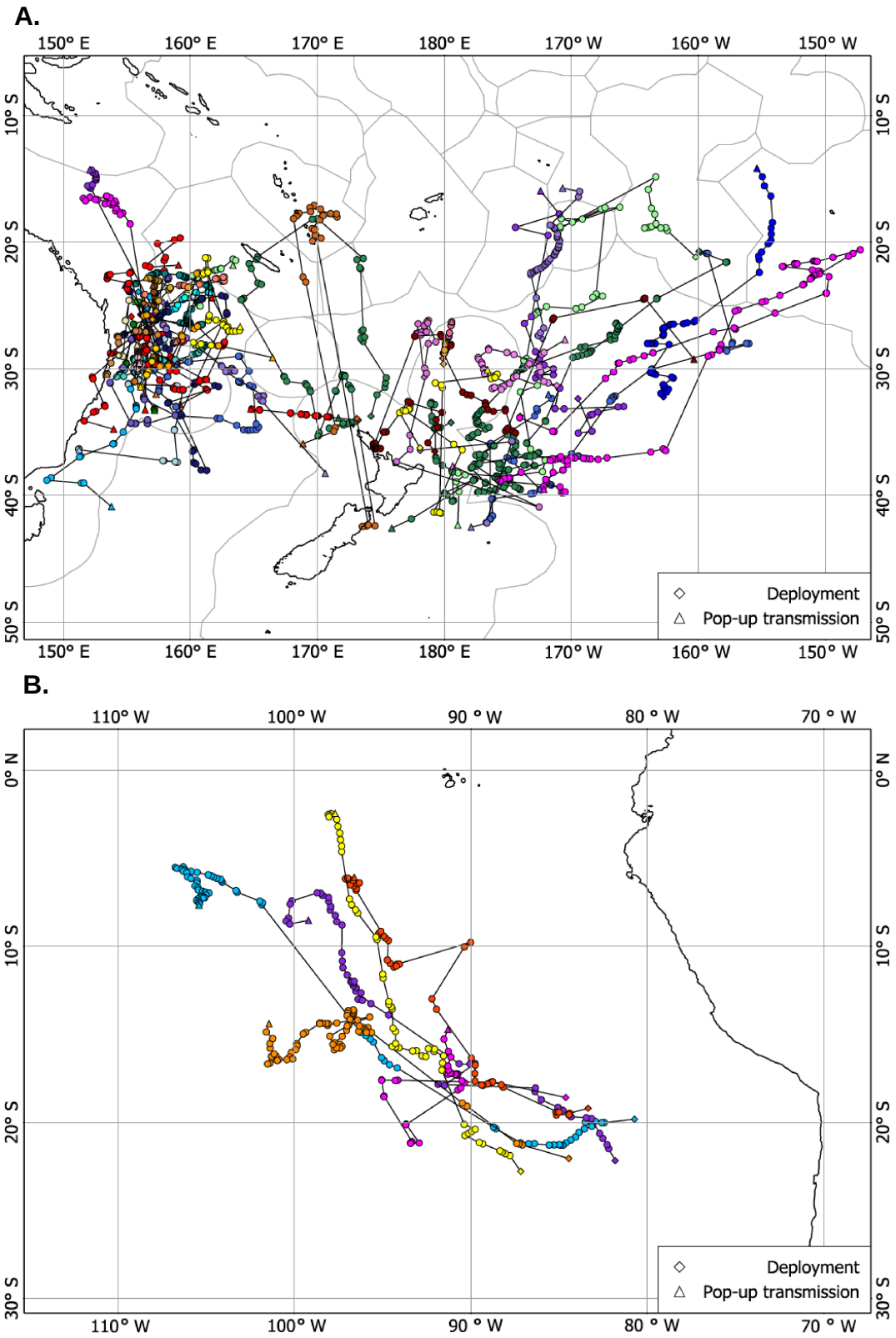

Fig. 2. Position estimates of swordfish from pop-up satellite archival tags at liberty >30 days in the south Pacific Ocean between 2006 and 2010 in (a) the WCPO and (b) the EPO.

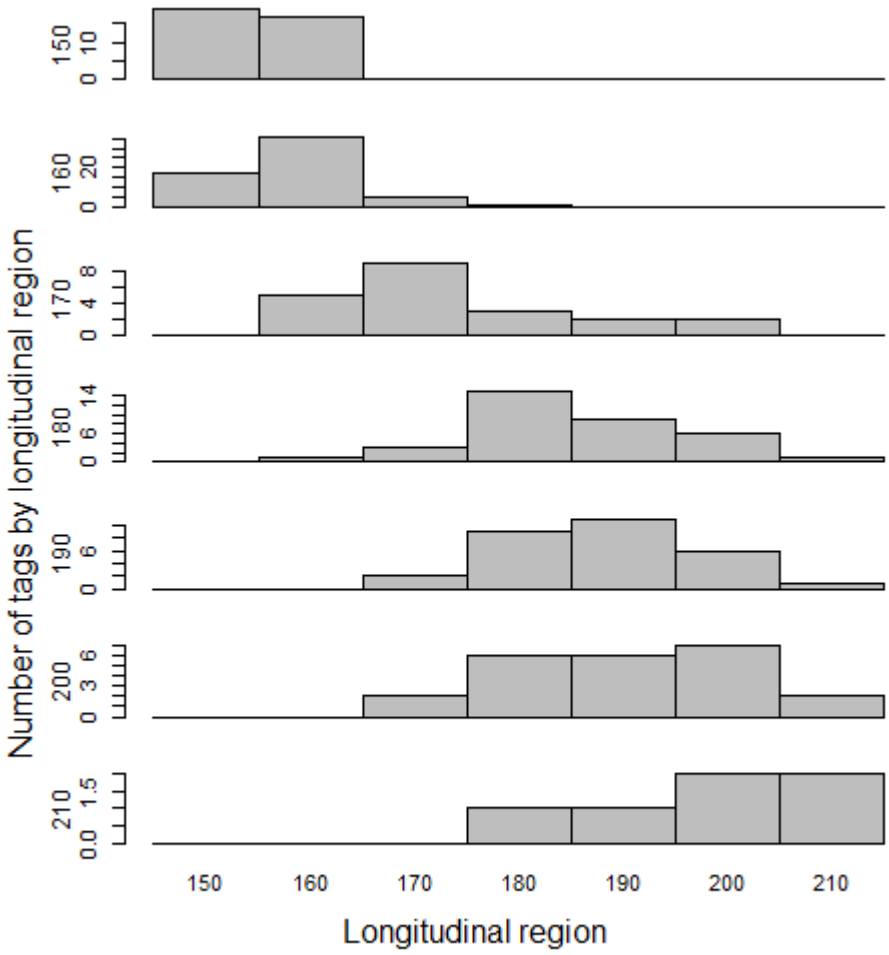

Fig. 3. Longitudinal overlap in the distribution of tagged swordfish among 10° regions in the southern WCPFC convention area. Each panel represents the number of tags that entered the longitudinal block indicated on the Y-axis that also entered the longitudinal block indicated on the X-axis.

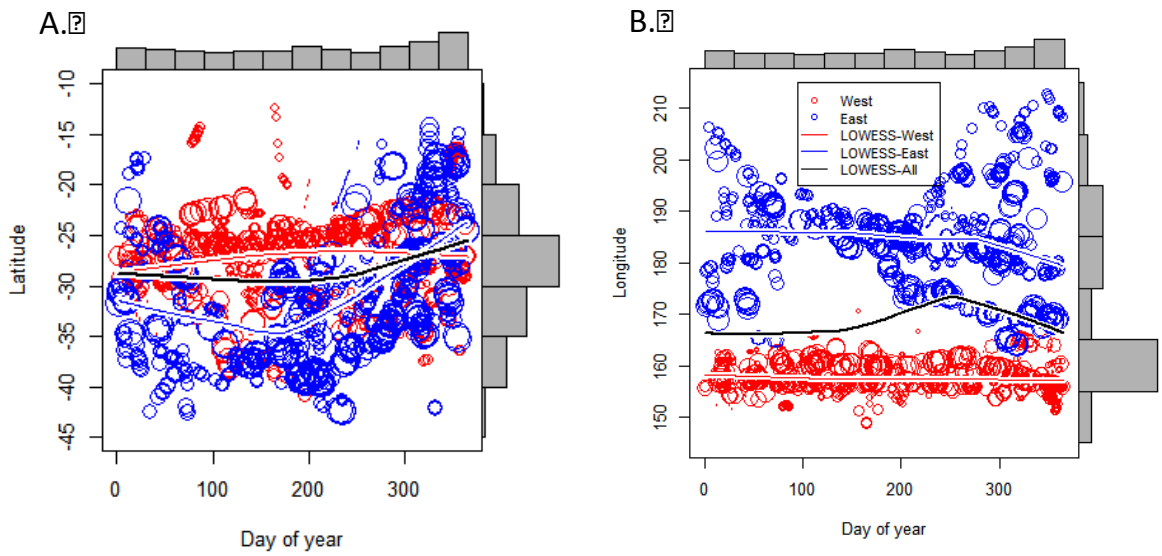

Fig. 4. Seasonal distribution of (a) latitude and (b) longitude estimates of swordfish from pop-up satellite archival tags at liberty >30 days in the southern WCPFC convention area (partitioned by release locations east and west of 165°E). Circle diameter is proportional to the estimated release mass (50 – 200 kg, points indicate missing size values). Frequency distributions of observations are shown along the top and right borders (n = 1583).

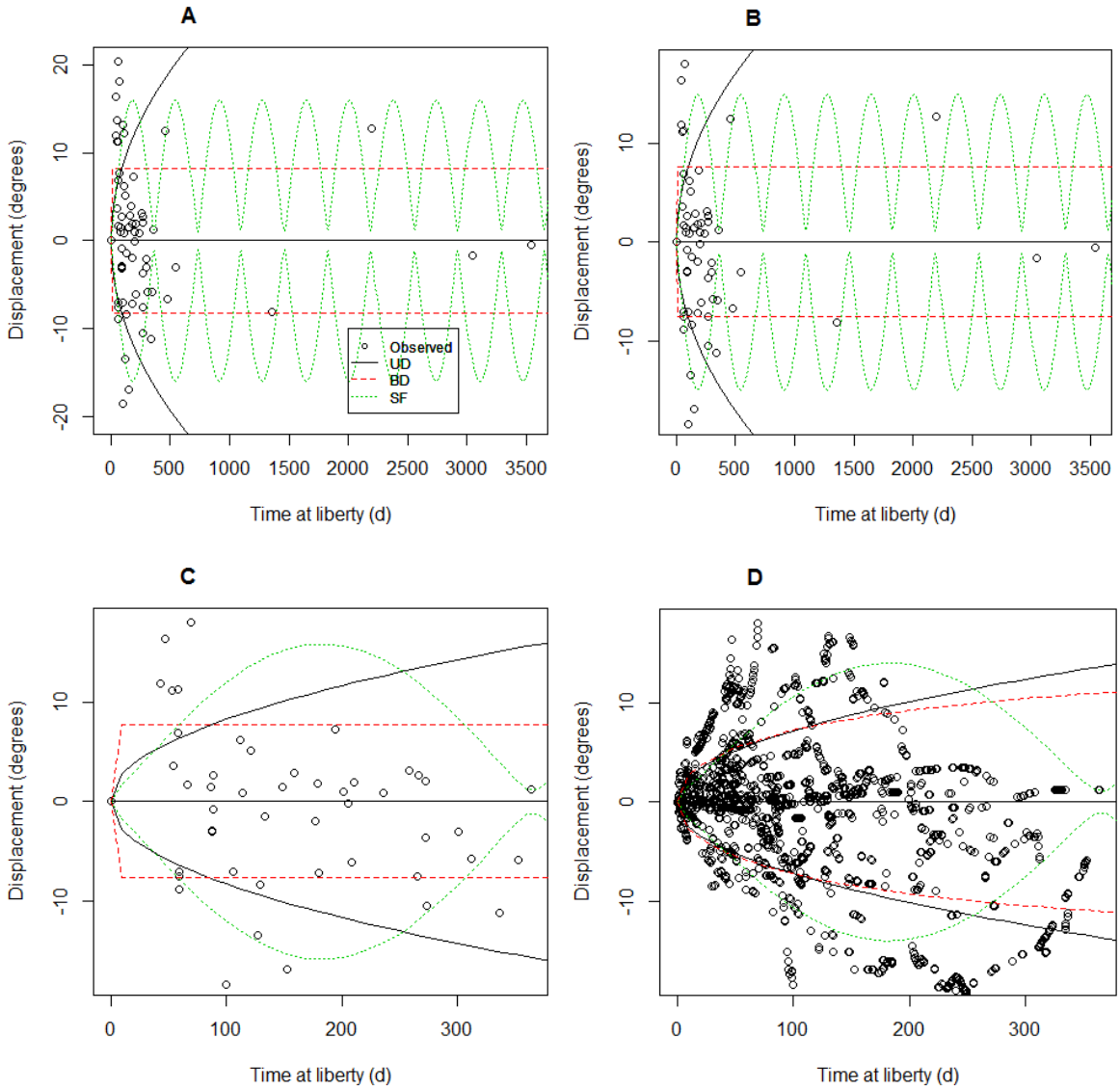

Fig. 5. Comparison of the models UD, BD and SF (fixed σ = 1.0) used to describe latitudinal displacement of swordfish in the south Pacific Ocean for datasets A-D. Lines indicate the estimated SD of the displacement distribution.

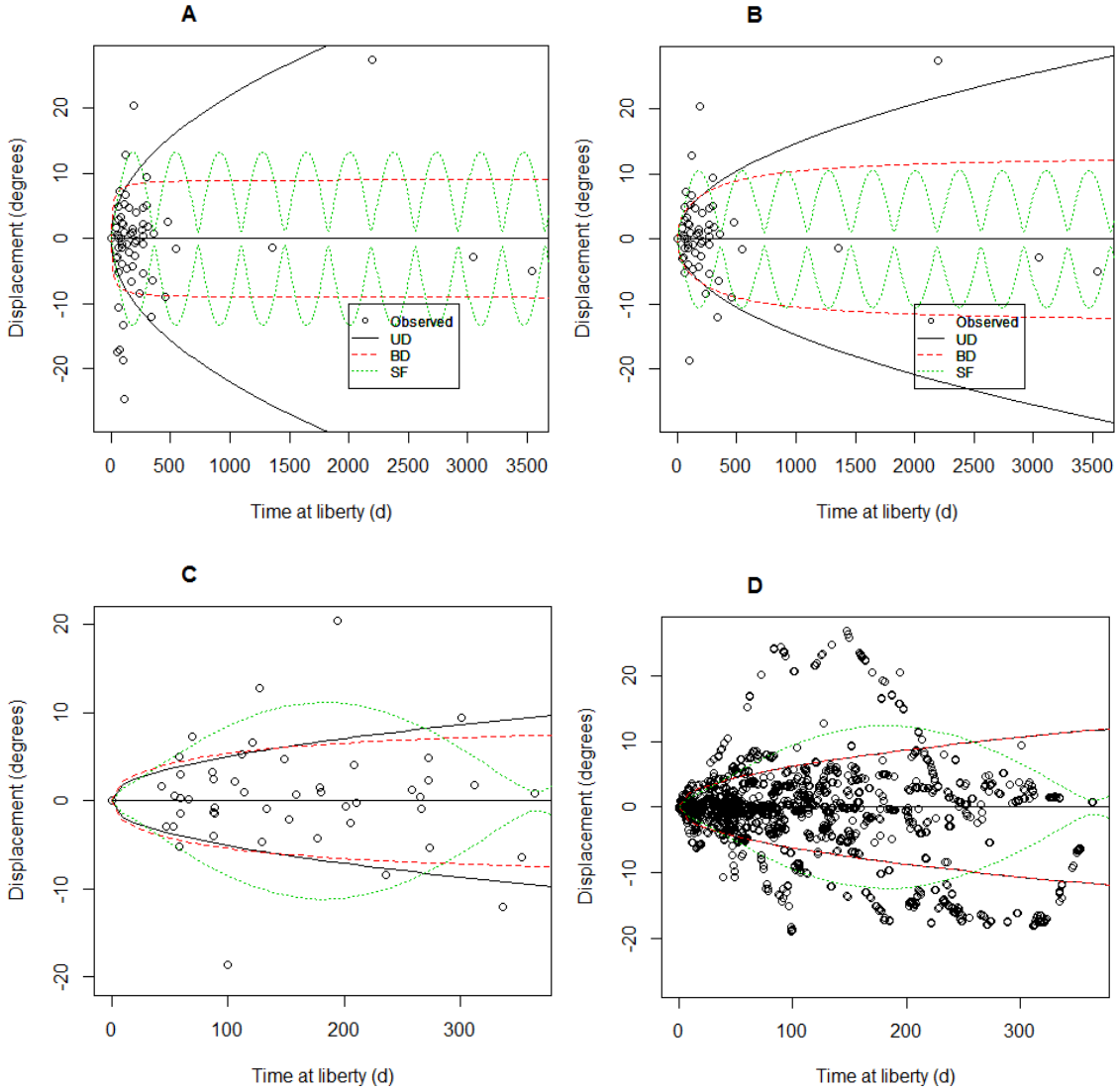

Fig. 6. Comparison of the models UD, BD and SF (fixed σ = 1.0) used to describe longitudinal displacement of swordfish in the south Pacific Ocean for datasets A-D. Lines indicate the estimated SD of the displacement distribution.