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The horizontal and vertical dynamics of swordfish in the South Pacific Ocean

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ABSTRACT

The movement patterns of broadbill swordfish (*Xiphias gladius*) in the South Pacific Ocean are largely unknown. Understanding the connectivity of the species across the Pacific and any variability in diving behaviour as it relates to fisheries availability/catchability are of particular relevance. Here, we present an electronic tagging dataset spanning the western and eastern South Pacific Ocean regions. Movements observed suggest a lack of connectivity between the southern and northern regions of the western and central Pacific Ocean (WCPO) and limited connectivity between the eastern and western parts of the Tasman and Coral Seas in the south-western Pacific Ocean. At least some swordfish appear to undertake movements between tropical waters extending from around Vanuatu to French Polynesia to waters around New Zealand, indicating greater connectivity than previously thought. Observations indicate no movement between the WCPO and the eastern Pacific Ocean (EPO), although data from boundary areas are lacking. Swordfish demonstrated a mixture of diel vertical distributions and daytime surface behaviour, spending time mostly in waters <100 m during the night and >400 m during the day. Diel vertical movements resulted in movement through water temperatures that varied on the order of 15–20° C with temperatures at depth as low as 2.4° C and those at the surface as high as 31.4° C. Vertical distributions of swordfish varied both spatially and temporally with swordfish in the Tasman/Coral Seas demonstrating the least variability. Spatio-temporal variability in vertical distributions is likely driven by variability in environmental conditions and associated prey distributions. Swordfish tagged in the Tasman/Coral Seas and in the EPO interrupted deeper daytime distributions with two distinct types of surfacing behaviour: temporally associated and temporally isolated. Temporally isolated surface behaviour occurred throughout the year and in association with on average lower sea surface temperatures. Temporally associated surface behaviour was restricted to austral summer months only and in association with on average higher sea surface temperatures. Our results represent a major step towards reducing uncertainty about the spatial dynamics of swordfish in the South Pacific Ocean. At the same time, questions as to the extent of connectivity of swordfish throughout the south Pacific and the linkages between spawning ground and foraging ground locations are raised. Further investigation of the movements of swordfish from the central southern Pacific Ocean is required to determine what linkages there may be between the WCPO and the EPO and whether connectivity suggested by genetic studies is supported.

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1. Introduction

The geographic distribution of fisheries inherently contain spatial heterogeneities due to the distribution of fish population characteristics (e.g. age structure, sex, growth and movement) and fleet characteristics

(e.g. selectivity and effort; Booth, 2000). Spatial heterogeneity is particularly relevant to the assessment and management of many large pelagic species (e.g. tunas, billfish, sharks), as these species are highly dispersed and capable of extensive migrations. Fisheries targeting these species cover large areas and can 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 by partitioning the population and fishery into multiple geographic components (e.g. Fournier et al., 1998). Few assessments, however, incorporate spatial structure (particularly at the sub-population level) and movement (Cadrian and Secor, 2009; Stephenson, 1999) of populations, because data are often

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insufficient for reliably delineating spatial structure, estimating movement rates and assessing vulnerability to fishing gear. Additionally, many stock assessment approaches lack the quantitative framework allowing incorporation of spatial structure and movement. Stock assessment model boundaries and any internal partitioning are frequently defined on the basis of available fishery data and the political realities of management (e.g. country and regional management jurisdictions), rather than the spatial characteristics of the fish population. Not taking into account the spatial characteristics of a population may lead to inappropriate assumptions made in regard to population dynamics, movement and vulnerability to fishing, resulting in poor advice for fisheries management (Cadrian and Secor, 2009).

Broadbill swordfish (*Xiphias gladius*; hereafter referred to as swordfish) are globally distributed throughout temperate, subtropical and tropical waters and are important target and by-catch species for domestic coastal and distant water longline fleets (Ward et al., 2000). Distributions of catches across basins suggest that populations range with the seasonal extension and retraction of warmer waters into higher latitudes and seasonal shifts in productivity (Neilson et al., 2009, 2013; Palko et al., 1981). There appears to be some heterogeneity in the movements of males and females, with more males caught by fisheries in warmer, lower latitudes and females dominating catches in cooler, higher latitudes (DeMartini et al., 2000; Palko et al., 1981). Investigations of catches and molecular data have suggested some ocean basin scale population structure of swordfish stocks across the Pacific, Indian and Atlantic Oceans (Alvarado-Bremer et al., 2005; Reeb et al., 2000), but finer-scale structure within basins is less certain.

Genetic studies on swordfish in the Pacific Ocean have found both little evidence of genetic differentiation in samples collected across the basin (Kasapidis et al., 2008; Rosel and Block, 1995; Ward et al., 2001) and some evidence of population subdivision (Reeb et al., 2000). Subdivisions that has been observed suggest low levels of mitochondrial gene flow which appears to have a \cap -shaped pattern, with connectivity of animals east–west in the Northern and Southern Hemispheres and connections across the equatorial zone along the west coast of the Americas (Reeb et al., 2000). This is consistent with the hypothesis of separate stocks in the north and southwest Pacific Ocean (Sakagawa and Bell, 1980). Larval distributions, reflecting areas of spawning across the Pacific Ocean, also suggest some evidence for separation of stocks in the western Pacific Ocean (Grall et al., 1983; Nishikawa et al., 1985). Although both spatially and temporally patchy, these surveys suggest that spawning occurs in the Northern Hemisphere during the boreal summer in waters 0–30° N in the western and central Pacific Ocean (WCPO) and in the Southern Hemisphere during the austral summer in waters to the north east of Australia.

To date, little information has been available on the movements of swordfish across the Pacific Ocean. Tagging studies from which movements have been recorded have largely been restricted to small numbers of conventional tag deployments in the south-west Pacific Ocean (Holdsworth and Saul, 2011; Stanley, 2006), and in the central and eastern North Pacific Ocean (Ito and Coan, 2005; Wraith and Kohin, 2011), limited deployments of electronic tags off the east coasts of North and South America and one archival tag deployed off the east coast of Japan (Abascal et al., 2010; Carey and Robison, 1981; Dewar et al., 2011; Takahashi et al., 2003). Conventional tag returns have been limited to very low return rates and electronic tag deployments have largely been limited by short deployment periods. Certainty of the extent of connectivity of populations between eastern and western parts and the lack of connectivity between the northern and southern parts of the Pacific Ocean as suggested by genetic data are still largely unknown.

Deployments of pop-up satellite tags (PSATs) on swordfish in the southern Pacific Ocean by a number of research programmes (Abascal et al., 2010; Evans, 2010; Holdsworth et al., 2007) have provided an opportunity to investigate the spatial dynamics of swordfish and connectivity, particularly in the south-western and south-central Pacific Ocean. Elements of these tagging data have been used to investigate

the suitability of spatial partitioning used in stock assessments for the swordfish in the WCPO and to provide recommendations for on-going stock assessments by the Western and Central Pacific Fisheries Commission (WCPFC; Evans et al., 2012a). In this paper, we provide a detailed summary of the combined data, including a synthesis of horizontal and vertical movements and a qualitative description of potential environmental influences and physiological traits that might contribute to variability in the movements and behaviour observed. Considerations on current hypotheses on connectivity of swordfish in the Pacific Ocean and for future quantitative analyses including stock assessment are discussed.

2. Materials and methods

2.1. Tagging data

Pop-up satellite archival tags (PAT4: $n = 26$, Mk10: $n = 91$, Wildlife Computers, U.S.A.) were deployed on large swordfish in waters off eastern Australia (AU; PAT4: $n = 26$; Mk10: $n = 29$), northern New Zealand (NZ; Mk10: $n = 19$), south of the area between Fiji and French Polynesia in the western Pacific Ocean (SFFP; Mk10: $n = 13$), the Cook Islands (CI; Mk10: $n = 9$) and the northern coast of Chile in the eastern Pacific Ocean (EPO; Mk10: $n = 21$; Abascal et al., 2010) during 2004–2009. Methods associated with deployments of pop-up satellite archival tags (PSATs) in AU, SFFP and CI are detailed in Evans et al. (2011). Methods used in NZ waters are detailed in Holdsworth et al. (2007) and those in the EPO 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 (>150 cm OFL and >50 kg wet mass so that the tag contributed $\sim 0.2\%$ or less of additional mass to the animal) lead alongside the vessel to a position near the sea door. To attach PSATs to swordfish a custom made stainless steel floy-type anchor (AU, SFFP and CI), a stainless steel or medical grade nylon dart (EPO) or a medical grade nylon dart (NZ) was inserted into the musculature just ventral to the primary dorsal fin of the fish using a customised tagging pole similar to that described in Chaprales et al. (1998). Once tagged, the fish was cut from the fishing line and allowed to swim away from the vessel. Deployment positions of tag releases were recorded using the vessels' onboard GPS system. All personnel involved in tagging were experienced in the selection of candidates (i.e. those of suitable size and condition) and methods used. All efforts were made to ensure that potential impacts associated with handling and time taken to lead in and tag individuals were minimised.

Tags were programmed to release from fish and transmit summarised depth, temperature and light data after periods of time ranging from 60 days to 365 days post-release. Data summarisation varied both within and between tagging programmes with data binned into 1, 4, 6 or 12 hour time periods and varying depth and temperature ranges. Further details of tag set-up and proposed and achieved deployment periods for AU, NZ and EPO deployments are detailed in Abascal et al. (2010), Evans (2010) and Holdsworth et al. (2007).

2.2. Horizontal movement

To ensure that the potential for movement, particularly the potential for seasonal movement, and connectivity between deployment regions was captured, we included only those data returned from tags at liberty for greater than 30 days (Table 1; $n = 53$). Intermediate positions between deployment and transmission locations were estimated by fitting the state-space model “trackit” described in Nielsen and Sibert (2007; downloaded from: www.soest.hawaii.edu/tag-data/trackit) to time series of light data. The model was run both with and without the incorporation of sea surface temperature (SST) data, however because convergence was rarely achieved when SST was incorporated in the model (83.7% model runs failed to achieve convergence), final model fits were estimated from trackit without SST. All model runs of trackit

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