

SCIENTIFIC COMMITTEE ELEVENTH REGULAR SESSION Pohnpei, Federated States of Micronesia 5–13 August 2015

Examination of trends in abundance of skipjack tuna with an emphasis on temperate waters

WCPFC-SC11-2015/SA-WP-05

Graham M. Pilling¹, Laura Tremblay-Boyer¹, Keith Bigelow², Shelton J. Harley¹, Hidetada Kiyofuji³, Simon Nicol¹, Joel Rice⁴ and Inna Senina⁵

¹Oceanic Fisheries Programme, Secretariat of the Pacific Community

²NOAA Fisheries Pacific Islands Fisheries Science Center, Honolulu, Hawaii, USA

³National Research Institute of Far Seas Fisheries, Japan

⁴Joel Rice Consulting Ltd., Saint Paul, USA

 $^{^5\}mathrm{CLS},$ Toulouse, France

Contents

1	Introduction	5
	1.1 Concerns raised within Scientific Committee and Commission meetings	5
	1.2 Aims of the paper	7
2	Theory on the biogeography of exploited fish populations and range contraction	ı 9
3	Insights from existing data	12
	3.1 CPUE trends in SPC-held longline observer data	13
	3.2 Skipjack catch rates within the French Polynesian artisanal fishery	15
	3.3 Analysis of US island state and territories fisheries' CPUE	16
	3.4 Catch and CPUE data from Japanese fisheries	21
	3.5 Analysis of length frequency data	22
	3.6 Tagging	24
	3.7 Molecular and biochemical signatures	25
	3.8 Synthesis from existing data	26
4	Insights from integrated models	30
	4.1 MULTIFAN-CL	30
	4.2 Seapodym	31
	4.3 Synthesis from integrated models	33
5	Development of a spatial model for investigating hypotheses	35
	5.1 Local population dynamics	35
	5.2 Defining habitat quality by cell	36
	5.3 Movement of individuals between cells	36
	5.4 Spatial patterns in fishing mortality	37
6	Overall discussion and recommendations for future research	39
	6.1 Recommendations for future research	40
7	Acknowledgements	41
8	Tables	46
9	Figures	47
10) Appendix 1 - South Pacific longline CPUE standardisation diagnostics	74

Executive Summary

How a fish population responds to exploitation is a critical question, particularly for tuna stocks found across a wide geographic range and exploited by many fleets. This paper responds to concerns of several CCMs over the potential impact of increases in fishing pressure on skipjack in tropical waters on those parts of the stock found in temperate waters, and the fisheries – often coastal – that depend on them for food security and livelihoods. It represents an output of Project 67.

The purpose of the analysis presented here is three-fold:

- Assemble available indicators on trends in abundance of skipjack tuna from catch, effort, CPUE, size, tagging, and integrated models (MULTIFAN-CL and SEAPODYM) – focusing on temperate waters. We also assess the magnitude of skipjack mixing between tropical and temperate waters;
- 2. Develop a spatially-structured population dynamics model that could be used to examine different hypotheses about how skipjack spatial distribution might respond to increased fishing pressure in tropical waters, as described in the third part of the Project 67 scope of work;
- 3. Provide advice to the SC on whether the data assembled in (1) above is likely to be sufficient to support a detailed modelling exercise using the model described in (2).

Two potential mechanisms that might drive range contraction are highlighted, being:

- 1. Direct effects of fishing at the edge of the species' range being too high resulting in localized depletion in those regions, where abundance is naturally low; and
- 2. Fishing mortality at the core of the range being too high, reducing density at and movement from the optimal conditions at the core to the edges. This is 'density dependent habitat selection' and is explained in more detail within Section 2 of the paper.

Analyses based upon a wide range of available data sources are presented in Section 3:

- Analyses of trends in skipjack CPUE data from twelve industrial or coastal longline, troll, and pole and line fisheries distributed across much of the WCPFC-CA latitudinal range showed no spatial or temporal consistency. This was also true within EEZs where data from multiple fisheries were available (e.g. French Polynesia, Hawaii and Japan). There was no clear indication that skipjack range contraction was occurring, nor which of the two potential 'causal' mechanisms might drive it. Analyses were necessarily disjointed, as data were only available from within specific EEZs. Use of standardised CPUE time series was important to limit the influence of factors other than stock abundance on trends.
- As longliners tend to catch larger skipjack than other gears, trends in their length frequency data may offer an early indication of regional or local abundance changes. However, length

distributions from the five longline fisheries examined were relatively consistent over time, showing no clear trends and little insight into population-level impacts.

- Skipjack RTTP/PTTP tagging information suggested limited connectivity between tropical and temperate regions. However, the design of recent tagging programmes, given their focus on tropical waters and the distribution of fishing effort that influences recaptures, affected their ability to address the question.
- Integrated models (MULTIFAN-CL and SEAPODYM) link available data, underlying stock biology and the characteristics of exploiting fleets. The models provided slightly different views of regional connectivity. MULTIFAN-CL indicated limited connectivity between the tropical and northern temperate model regions, and that exploitation in the northern temperate region was comparatively limited. SEAPODYM results indicated localised effects in the coastal Japan area from overall (tropical and temperate) WCPO fishing impacts, which was consistent with Japanese CPUE data. The outputs also indicated a higher level of connectivity between tropical and temperate regions than MULTIFAN-CL or the tagging data. Whether those levels of connectivity were sufficient to lead to range contraction effects through density dependent habitat selection or local depletion, could not be identified.

Overall, the data were considered of insufficient quality to support a detailed modelling exercise using the simulation model developed under Project 67. The work has, however, identified several potential areas of further research. The following recommendations are aimed at improving the quality of the information sufficiently to warrant fuller examination, and to examine the assumptions underpinning the analysis of movement by integrated models:

- A key constraint to understanding skipjack stock connectivity was limitation in the latitudinal range of existing tagging programmes. If work on range contraction is considered a priority, we recommend investigating the feasibility of expanding skipjack tagging programme activities within temperate regions.
- Continued collection of biological marker samples under Project 35 and application of new approaches to better understand stock spatial connectivity is recommended.
- Investigation of the use of operational longline data from across the WCPO to improve the spatial and temporal coverage of CPUE data and allow its standardisation, is recommended.
- Improved collection and availability of economic information is recommended to better understand its potential influence on fleet behaviour and hence CPUE.
- Further examination of the ability of available integrated models to describe range contractionstyle dynamics, if they were occurring, is recommended.

We invite the WCPFC-SC to consider the results described here, and determine and prioritise areas of future work to be undertaken within the work plan of the WCPFC-SC to support the Commission's consideration of range contraction within WCPO fishery management.

1 Introduction

Species are limited in their geographic range due to physiological and ecological constraints. Within the resulting range, there is clear evidence that organisms are more common in particular areas than others. This is thought to reflect the fact that habitat quality varies within a range, and this variation impacts population rates like growth, fecundity and survival over that space (Sibly and Hone, 2002; Benton et al., 2006).

Harvested marine fish move over their geographic range using cues that are distinct from those used by fishing fleets to exploit them. Mobile pelagics migrate long distances for food and reproduction, using information from their biotic and abiotic environment to direct that movement (Block et al., 2005). In contrast, fishing vessels target areas to maximize catch rates, minimize fishing costs, and follow management regulations. In the Pacific, for example, industrial and artisanal fisheries harvest shared stocks of highly-mobile tuna over both the tropical and temperate parts of these species' range. Fleets may be limited in the range they can exploit based on the location of their EEZs within the stock range, as well as fishing agreements negotiated bilaterally or multilaterally between countries. These socio-economic factors are independent of the target species' biology and result in an uneven spatial pattern of fishing mortality. Taken together with the harvested species own dispersal over the range, these patterns make it challenging to interpret fisheries-derived indices of abundance and identify spatial trends in stock status.

In this section we summarise concerns raised within WCPFC meetings on the potential impacts of fishing for skipjack tuna within the tropical region on those fisheries at the margins of the WCPFC Convention Area. We then describe the aims of this paper.

1.1 Concerns raised within Scientific Committee and Commission meetings

In recent years, concerns have been raised by some WCPFC coastal states, whose waters lie outside the core equatorial fishery, that declines in the local biomass of target tropical tuna species that occur [often seasonally] in their waters at the margins of the stock range have been significant, and potentially greater than that of the regional stock. The concerns over this 'range contraction', which have been suggested due to low catch rates on the stock range margin, have focused on skipjack and yellowfin tuna (see also Figure 1). While we cover the concerns raised over both species here, we concentrate on skipjack tuna throughout the remainder of the document.

SC advice in various years

The potential for range contraction of skipjack was noted within the summary report of the 6th Scientific Committee in Nuku'alofa, Tonga (WCPFC, 2010). The report noted that "There is concern, yet to be substantiated, that high catches [of skipjack] in the equatorial region could result

in range contractions of the stock, thus reducing skipjack availability to higher latitude (e.g. Japan, Australia, New Zealand) fisheries" (para 38). This comment was repeated in the management advice for skipjack within the summary report of the 7th Scientific Committee meeting in Pohnpei (2011), and again stated in 2014 within the SC10 report where SC "advised the WCPFC that there is concern that high catches in the equatorial region could result in range contractions of the stocks, thus reducing skipjack availability to high latitude fisheries." (paras 54 and 315).

The concerns over the potential for range contraction led to the development in 2012 of a nocost proposal to investigate range contraction for tropical tunas in the WCPO (Harley, 2012). This project was formalised within the Scientific Committee workplan as Project 67 ("Range contraction of tropical tunas, sharks, and billfish"). Analyses from this research were presented within working paper SC10-MI-WP-06. SC10 recommended further research for range contraction of skipjack should be conducted in the framework of Project 67 (para 313).

Concerns over range contraction were also raised during discussions at the Management Objectives Workshop 3 on skipjack target reference points, and the implications of different target levels for fisheries at the margins of the stock range.

CCMs stating particular concern over range contraction at WCPFC meetings have been Japan, the USA, and New Zealand. Information provided by these countries are now detailed.

Japanese concerns

The Japanese delegation made a statement at WCPFC8 that noted "concern regarding the pole and line skipjack fishery in its waters which is diminishing substantially year by year. Although range contraction has been suggested as an explanation, Japan believes the stock is being depleted and asked the Commission to take measures in tropical waters to prevent further depletion." At SC10, Japan presented a working paper (Kiyofuji et al., 2014) outlining the abundance of skipjack tuna migrating to the Pacific coastal waters of Japan, as indicated by standardised Japanese coastal troll and pole-and-line CPUE. The results of that analysis were felt by Japan to "suggest that migration of skipjack stock to coastal area around Japan has been diminished since around 2006 possibly due to range contraction of this species in the WCPO." (para 297 of the SC10 report). During the subsequent discussion, Japan stated that: "one of the reasons for the small catch in the edge area (high latitudinal region) was the range contraction of the stock as presented in the CPUE standardization analysis, and proposed that the investigation of the range contraction should be continued at SC. The Commission should consider developing measures to reduce skipjack catch in order to limit the declines in catch rate associated with further declines in biomass with consideration for the possibility of range contraction and take into account the state and structure of regional fisheries." (para 299 of the SC10 report; WCPFC (2014); see also para 49).

Concerns of the United States of America

Further concerns over range contraction of skipjack were raised by the United States of America, at SC10. USA noted that they had "several small fisheries for skipjack in high latitudes (e.g., the Hawaii pole-and-line fishery which has 3 vessels and annual catches of only 200-400 mt per year). The limited nature of those fisheries, and hence the data from them, meant that it was difficult to identify statistical evidence for range contraction. However, the USA stated that these localized fisheries may have reduced availability of skipjack and hence they shared Japan's concern about range contraction." (para 302 of the SC10 report; WCPFC (2014)).

New Zealand concerns

New Zealand raised concerns over potential range contraction of yellowfin within its country statement at SC7. This CCM noted that their domestic yellowfin fishery catches had declined "since 2001 and are at historic lows" (SC7 report; WCPFC (2011), para 121). New Zealand hypothesised the decline might be due to "potential range contraction of the yellowfin stock or due to the high level of regional fishing effort to the north and east of New Zealand".

1.2 Aims of the paper

This paper arises from work under Scientific Committee Project 67 (Review of the impacts of recent high catches of skipjack tuna on fisheries on the margin of the WCPFC Convention Area), in response to the concerns raised by SC10, as detailed above. The project objective is to analyse available fisheries data from the northern and southern margins of the convention area, with a view to determining the cause(s) of a reduced abundance of skipjack tuna and to facilitate the provision of appropriate management advice. This paper represents the annual project progress report for presentation at SC11, as detailed in the outputs and schedule of the project Terms of Reference.

The paper aims to identify whether there may be a biological or fisheries mechanism underlying changes in the abundance patterns of key tuna species at the margins of their range within the WCPFC-CA. We review the range of data and analytical tools available to provide insights on the potential underlying mechanisms, discuss their usefulness in their current form and highlight areas of research that could be further explored.

The purpose of the analysis presented here is three-fold:

1. Assemble available data on trends in abundance of skipjack tuna – from catch, effort, CPUE, size, tagging, and integrated models (MULTIFAN-CL and SEAPODYM), with an emphasis on indicators of abundance in temperate waters. We also examine this information to assess the magnitude of mixing between tropical and temperate waters for skipjack;

- 2. Develop a spatially-structured population dynamics model that could be used to examine different hypotheses about how the spatial distribution of skipjack tuna in the WCPO might respond to increased fishing pressure in tropical waters, as described in the third part of the Project 67 scope of work;
- 3. Provide advice to the SC on whether the data assembled in (1) above was likely to be sufficient to support a detailed modelling exercise using the model described in (2).

This paper represents a collaborative attempt by the Scientific Service Provider and CCM Departments, across disciplines, to examine and evaluate the available information for Project 67. In the following sections, we first describe the biogeographical theory behind range contraction. We then examine available skipjack CPUE time series and other data available from fisheries across the WCPO and investigate whether they can provide indications of trends in abundance or fishery impacts in temperate regions. We review information from available integrated models, describe the development of a specific simulation model to examine this issue further under Project 67, and finally summarise findings and develop recommendations for consideration by WCPFC-SC.

2 Theory on the biogeography of exploited fish populations and range contraction

According to the latest skipjack stock assessment, this species is exploited at a sustainable level (Rice et al., 2014). However, concern over declines indicated by countries located at the edges of these tuna's range might suggest a spatial contraction of the areas of high catch rates towards the tropical Western Pacific, considered optimal habitat for these species because they prefer warmer waters. Spatial trends were identified in Tremblay-Boyer et al. (2014) for yellowfin tuna (see also Figure 1), however data for skipjack were not examined during that analysis. Given that these stocks have been exploited, the changes in range might reflect concurrent changes in the distribution of biomass. However, the processes underlying the patterns identified may be complex.

Two key mechanisms could explain patterns consistent with 'range contraction' (see also Figure 1). These are:

- the direct effects of fishing at the edge of the species' range being too high, resulting in localized depletion in those regions where abundance is naturally low. The result would be 'range contraction' with the stock range reducing due to fishing at the margins removing available individuals; and
- Fishing mortality at the core of the range (e.g. the equatorial region for tropical tuna species) could be too high, reducing density at and movement from those optimal conditions at the core to the edges. The mechanism underlying this cause of 'range contraction' is 'density dependent habitat selection' (DDHS) and is explained in detail below, due to its potential novelty to the Scientific Committee and its importance for this paper.

It is important to attempt to understand the mechanisms underlying the changes in range, as they imply opposite management recommendations: in the first instance, fishing in the edges may need to be reduced, while in the second instance, fishing in the core may need to be reduced. Understanding the ecological drivers of movement within the range is thus highly relevant to the management of exploited stocks, which relies on cooperation between countries located both in the core and the edges of the species' range.

Density dependent habitat selection

This mechanism is based upon the theory of 'Ideal Free Distribution' (Fretwell and Lucas, 1969), where the fitness of an individual is dependent on the density of other individuals in their location or 'patch'. Where individual density is higher, competition for resources is higher. While a patch may be highly productive, when individual density and hence competition increases to a certain level, an individual is better moving to an area of lower density that may be slightly less productive, in order to maximise their individual fitness. Under the theory, individuals distribute themselves in the environment to balance patch quality with the density of other individuals. The resulting distribution of individuals at equilibrium is called the Ideal Free Distribution (IFD). Underlying the theory lie a number of strong assumptions, primarily:

- 1. Individuals are free to move between patches;
- 2. Individuals have perfect knowledge of patch quality;
- 3. There is no cost to individual movement.

While Ideal Free Distribution is often critiqued based on the challenges of finding a relevant measure of individual fitness (e.g. Kennedy and Gray, 1993), both empirical and theoretical studies show that informed dispersal, whereby some form of environmental or social cue (e.g. the density of individuals) is used to make a decision about movement, tends to be a better strategy for individuals than random dispersal to maximise fitness (reviewed in Bowler and Benton, 2005; see also Clobert et al., 2009).

Density-dependent habitat selection (DDHS) occurs when individuals preferentially move to the most suitable sites, with suitability being a positive function of habitat quality and a negative function of the local density of individuals (MacCall, 1990). Under this theory, individuals occupy the part of the range that has the highest habitat quality. As local density increases, competition with other individuals lowers the effective suitability of the core site, such that sites of formerly inferior habitat now become suitable and receive increased immigration. This results in an expansion of the range as population size increases. Conversely, if fishing intensity within the 'core' habitat region reduces the density in that region, the core becomes a more attractive habitat than the extremes of the range, and individuals from those extremes 're-colonise' the core region. This leads to 'range contraction'.

Identifying the theoretical relationship between individual density and range is challenging, as external factors will affect it. Changes in environmental variables that affect growth rates (e.g. SST) could increase the area suitable to species and result in an increase in both population and distributional area. In turn, the suitability of a habitat and its effect on fitness is not always practical to measure in nature. Metrics selected to model it (e.g. sea surface temperature as a proxy for prey availability) may not be directly related, while there is generally an underlying assumption that habitats of better quality can sustain a higher density of individuals. Van Horne (1983) outlines instances in which this assumption is not respected.

The extent of individual movement compared to the size of its range will also influence the relationship. A more mobile species may be able to better 'predict' habitat quality in unobserved patches (see assumption 2 above).

The extent of individual movement would also affect the ability to identify localised depletion, the alternative cause of 'range contraction'. If individuals are highly-mobile and move large distances within their range, the high turn-over of individuals will redistribute the impacts of local fishing

mortalities over the range. On the opposite end of the spectrum, local mortality will be directly related to local fishing if individuals are sedentary and constrained to limited areas over their lifetime. In the intermediate case when individuals are highly-mobile but do not move over the entirety of their range, a lack of knowledge on the extent to which individuals move within the range hinders predictions of local and regional impacts of spatial patterns in fishing mortality.

The level of movement will therefore affect the potential causes for range contraction, and gaps in our knowledge will affect our ability to understand it.

3 Insights from existing data

A common approach to attempt to identify potential range contraction is through the use of catchper-unit-effort (CPUE) data. CPUE has been used in fisheries science for decades as an index of species abundance in the management of fish stocks, based on the assumption that changing catches over the same level of fishing effort should reflect changes in abundance (Maunder and Punt, 2004).

Fishing trips can be considered as surveys as they do, in effect, collect species occurrence data, but since they were not especially designed as such there are multiple confounding factors that can affect CPUE, beyond that of the species' abundance itself (Harley et al., 2001). In turn, fishing trips are not spatially independent as, for example, they will be influenced by minimizing costs such as the distance travelled from the base port, and bias may occur as fishing vessels will preferentially travel to areas where they expect high catch rates.

In this section we examine two primary groups of information within this section

- Fishery data, focusing on CPUE data and length frequency distributions;
- Other biological data sources, focusing on tagging information.

First, we examine a range of skipjack CPUE data within the WCPO region for trends consistent with range contraction, for example reductions in the abundance of skipjack at the margins of the stock range. CPUE data from the primary fishery exploiting skipjack - the tropical purse seine fishery - are generally considered unrepresentative of regional abundance due to increased vessel productivity (Tidd et al., 2015) and non-linear relationships between stock abundance and CPUE ('hyperstability'; Scott et al., 2015). This reduces not only the quantity of data that can be analysed, but the spatial extent of that data.

In an attempt to identify spatial trends in existing skipjack CPUE series that may provide insights, analyses examined data from coastal/nearshore fisheries and offshore/industrial fisheries in temperate and sub-tropical regions. These fisheries were primarily longline, pole and line and troll fisheries. While these may vary in their targeting of skipjack, trends in the time series are felt better related to skipjack abundance.

We then examine available skipjack length frequency distributions from longline observer programme data, to identify patterns that might provide alternative, or supporting, signs of exploitation to the CPUE series; for example, declines in size over time consistent with decreasing CPUE trends.

Beyond fishery data time series, there are other sources of information that can be used to identify connectivity between tropical and temperate regions, and hence support discussions on range contraction. These include information from tagging programmes within the WCPO, and novel developing techniques in the field of biochemical signatures.

3.1 CPUE trends in SPC-held longline observer data

While not the target species for the industrial longline fishery, as these fisheries generally catch larger skipjack individuals than other gears, trends in longline skipjack CPUE may offer an early indication of changes within regional or local skipjack abundance.

Spatial/temporal coverage of the reported skipjack catches within longline logsheet data could provide a useful data source to illustrate general population trends (in space and time) via catch rate for skipjack, as the longline fishery has one of the largest geographic ranges within the WCPO. However, initial analysis of logsheet information highlighted constraints in the availability of operational longline logsheet data across the WCPO. Combined with the fact that skipjack are rarely encountered in the fishery, available logsheet data was felt deficient in reporting of skipjack catches.

As a result, this analysis concentrated on available observer information from the WCPO longline fleet operating within the southern hemisphere, where the majority of consistent longline observer data holdings were found (we note that Hawaiian longline observer data are available from the late 2000s, and that this region is covered through analyses described below). Although observer coverage of the fleet has generally been comparatively low, and the reporting of skipjack varies by observer program even in adjacent waters, the improved species composition information provided a better data set compared to logsheet information.

The SPC longline observer database contains records from the early 1980's to recent years. However skipjack were not continually present in the dataset, while historically coverage of the overall activity was so low that results were seriously unreliable. This analysis therefore covered the years 1995 to 2014 on the region-wide scale, and for shorter time periods for the individual observer programme components.

The data were validated and filtered (records with missing values for key explanatory variables removed) to include only relevant data from the species' primary habitat in the south Pacific. First, data were filtered by observer program code with only those programs having greater than 1% of the sets with non-zero (positive) skipjack catch being kept. The second step to trimming was designed to limit data to a geographic area where skipjack were most often seen. The observer dataset indicated that 95% of the positive catch came from the region 5°S to 37°S; data outside this range were excluded. Further national areas ("GL", "HB", "NF", "PX") and flags that never reported positive catch were filtered from the dataset. This left data from observer programs dominated by New Caledonia, Fiji, Australia and French Polynesia (Figure 2b). Analyses were carried out at the regional, and sub-regional scales based on the trimmed data.

Population dynamics models for skipjack (e.g. Rice et al., 2014) in the Pacific usually use a quarterly time-step, due to the short-lived nature of this species. However there were insufficient data to conduct analyses on such a fine time scale, and hence a yearly time-step was used. CPUE was calculated as the number of individuals caught per 1,000 hooks.

CPUE standardization methodology

CPUE is commonly used as an index of abundance for marine species. However, it is important that raw nominal catch rates be standardized to remove the effects of factors other than abundance (e.g. fishing technique, season, bait type). Further, catch data for non-target species often contain large numbers of observed zeros as well as large catch values where areas of higher densities are encountered; this needs to be explicitly modelled (Bigelow et al., 2002; Campbell, 2004; Ward and Myers, 2005; Minami et al., 2007). The filtered datasets were standardized using generalized linear models (McCullagh and Nelder, 1989) using the software package R (www.r-project.org). The negative binomial family of GLMs (Lawless, 1987) was used in the standardization because it is suitable for count data and is typically more robust to issues of overdispersion than the Poisson family (overdispersion can arise due to excess zeros or from correlations between observations. Multiple methods of calculating the indices of abundance and confidence intervals exist depending on the model type (Shono, 2008; Maunder and Punt, 2004). In this study estimates were calculated by predicting results based on the fitted model for the year effects with each covariate set at its mean value (Zuur et al., 2009). Confidence intervals were calculated as $\pm 1.96 \times SE$; where SE is the standard error associated with the predicted year effect term.

Results

Although observer data on longline vessels are collected throughout the south Pacific, data collection varies by observer program, and reporting of skipjack tuna catch has fluctuated greatly between 1995 and 2014. The percentage of sets with positive counts of skipjack during the study period varied between 10% and 55% over the time period, and if targeting were similar throughout the equatorial south Pacific we would expect to see similar levels of positive catch (Figure 3b). However, the fact that prior and subsequent low levels of catch occur within the time series from the study area (mainly NC, FJ, AU and PF; see Figure 3a) suggest that some trends may be due to changes in reporting practices.

Consequently, analyses were first conducted on the region-wide scale (Figure 4). Results show a slightly increasing trend, with perodic large decreases in the CPUE (Figure 5). Given the indication of changes in reporting by program over the years we fit the regional model with a program code and year interaction (PCODE:YY in Appendix 1, Table 1). This proved to be significant and led to additional analysis based on individual observer programs. Diagnostics for the various standardisations are presented in Appendix 1.

The region wide CPUE results (Figure 5) are quite similar to the results from only the New Caledonia observer program (Figure 6a) suggesting that the results are biased towards the New Caledonia data. The results based on the Fiji observer program (Figure 6b) indicate the opposite trend to that estimated for the nearby waters of New Caledonia, over the same time frame. The

last individual observer program that had sufficient data to analyze independently was of French Polynesia. Data exists from 2002 to 2014, and showed a general decreasing trend, with some peaks (e.g. in 2009; Figure 6c). The region wide analysis that excludes NC, FJ, and PF observer data (i.e. all other observer records in the trimmed data set) shows a relatively flat trend, with large inter-annual fluctuations (Figure 6d). Indeed, standardisation resulted in a much flatter trend than seen in the nominal data.

In general there is little in any of the longline observer data analysis to indicate that the models are representative of the relative abundance of skipjack specifically, rather than resulting from changes in reporting and catchability due to a longline fleet that is targeting billfish, other tunas and sharks.

3.2 Skipjack catch rates within the French Polynesian artisanal fishery

The artisanal fleet of French Polynesia is primarily comprised of two types of vessel: "bonitiers", and "poti marara". Bonitiers are typically made of wood and are between 10 to 13 meters in length. They are used to target skipjack tuna ("bonite") and can fish further from the coast than the second type: poti marara. Poti marara are made of fiberglass or wood, are smaller (6 to 8 meters) but strong boats made to resist harsher ocean conditions. They were traditionally used to target marara (flying fish) but in recent years have shifted to a diversified catch of fast-moving species like mahi mahi and marlins. Detailed operational data were available since 1997 for the artisanal fleet (collected through logsheets and observations at landing points), though the coverage rate varies between the archipelagos of French Polynesia and there is some uncertainty in the values within the artisanal data set.

Skipjack tuna comprise the bulk of the artisanal catch, followed by a group of fishes including flying fish and reef fishes, and yellowfin tuna and mahi mahi. Figure 7 shows annual trends in effort (in number of trips and hours) and catch (in individuals and hundred tonnes) for Archipel de la Société (the French Polynesian archipelago, which includes Tahiti), split by boat type. Effort has fluctuated over the extent of the time-series but has steadily increased since 2005. Total catches in weight have increased since 1997, with poti marara making a progressively higher contribution to the annual catch, becoming the dominant boat type in the fleet both in terms of vessel numbers and contribution to the catch (Figure 8). Total catch in numbers has been increasing since 2006 but has not, unlike effort in both number of trips and hours, surpassed pre-2000s levels.

Catch composition differs between bonitiers and poti marara fleets, and for trips made within and outside the Archipel de la Société (Figure 9). Bonitiers overwhelmingly catch skipjack (82.8% of the catch composition, on average) and the proportion of this species in their catch has remained generally constant between years within the Archipel de la Société (minimum: 69% in 2012; maximum: 88.8% in 2004) (Figure 9, left). Bonitiers fishing outside of the Archipel de la Société have a much more variable catch pattern, in part due to the proportions of skipjack and other fish species ("OTH2") strongly varying between years. Other fish species make up a more substantial portion

of the catch compared to bonitiers in Archipel de la Société.

Catches by poti marara are much more diverse, divided between mahi mahi, reef fishes, skipjack and yellowfin tuna (Figure 9, right). Skipjack was the most frequently reported species for Archipel de la Société boats, but still to a lesser extent than for bonitiers in that same region. Outside of Archipel de la Société, skipjack comprised a relatively small portion of the catch: reef fish, flying fish and, lately, paru (a deep-water snapper), made an increasingly higher contribution to the catch in numbers over time.

To calculate nominal CPUE, catch in number of individuals was used, since data for catch weight are considered to be less reliable (C. Ponsonnet, pers. comm). Skipjack catch and CPUE have declined over time: higher CPUEs were generally observed earlier in the time-series (see Figure 10) and the number of high CPUE events has also declined over time, together with the number of trips where skipjack was reported. However, skipjack used to be caught primarily by pole and line (canne) whereas most of the catch now is by troll (traine), for which skipjack catch rates are on average lower (Figure 10 c).

Standardizing skipjack CPUE for Iles du Vent (the southeastern part of the western isles, including Tahiti) and Iles Sous-le-Vent (the northwestern part fo the western isles, including Bora Bora) were calculated to account for differences in gear type within each region. The trend in the nominal CPUE was similar to the standardized CPUE in Iles du Vent, but declines faster in Iles Sous-le-Vent. This can be explained by the changing trends in gear type in both archipelagos. The relative change in frequency between troll and pole and line is much more pronounced in Iles Sous-le-Vent than Iles du Vent: in the former pole and line went from being very common to rare and was effectively replaced by troll, while in Iles du Vent troll was already quite frequent by the beginning of the time-series, such that the shift in prevalence from troll to pole and line does not bias the interpretation of CPUE trends as much for this region (Figure 10 d). Therefore, CPUE trends appear driven by changes in fleet composition, which has contributed to the declines seen in catch.

3.3 Analysis of US island state and territories fisheries' CPUE

Data were analysed by NOAA Fisheries from US states and territories, covering fisheries in the main Hawaiian Island, Guam, and the Commonwealth of the Northern Mariana Islands (CNMI). Throughout, time strata where there are less than 3 fishery participants were removed, to ensure confidentiality was maintained.

Main Hawaiian Island (MHI) troll fishery

Data from this fishery were available for the period 1980-2014. Estimates of the number of MHI troll fishers was based on the number of unique State of Hawaii, Division of Aquatic Resources (HDAR) issued Commercial Marine Licenses (CMLs) submitting Fishing Reports. The number of

days fished by the MHI troll fishery was calculated using that Fishing Report data (Figure 11a). A MHI troll day fished is defined as a unique CML number fishing on a unique day for the gear types and fishing in areas defined for the MHI troll fishery at the beginning of this model. The number of days fished includes days that fishers did not catch anything or days that fish were caught but not sold (Figure 11b).

Effort, in terms of both number of vessels and number of troll days fished, increased between 1980 and the mid-1990s, before stabilising for the remainder of the time period. There is notable seasonality in both the vessels fishing and hence days fished, that remains relatively consistent throughout the period; the second and third quarters of the year showing higher effort.

Skipjack tuna landings for the MHI troll fishery were derived from HDAR Commercial Fishing and Marine Dealer Report data. As necessary, weights in pounds (lb) were converted into kilograms. The resulting time series is presented in Figure 12. Retained catch (mt) again showed seasonality, and followed the increasing trend in effort from the 1980s to mid-1990s. However, catch subsequently declined slightly, although large quarterly peaks are seen.

The MHI troll nominal (unstandardised) CPUE values were calculated using HDAR Commercial Fishing Report data (Figure 13a). The catch landed of yellowfin tuna and skipjack tuna was divided by the number of MHI troll Days Fished. Prior to 1994, each fisher was assigned a different CML in each year, such that a unique fisher and CML could not be followed from 1980 to 1994. Fishers were assigned unique and consistent Commercial Marine Licenses (CMLs) starting in 1994. To standardise the CPUE series, two GLMs with an assumed negative binomial distribution were therefore fit for the two time periods to take into consideration the fisher effect post 1994, and these two series spliced together.

From 1980 to 1996 (4th quarter of 1995), the GLM was:

 $glm.nb(lbs_kept \sim as.factor(yr_qr) + offset(log(effort)))$

where lbs_kept is the skipjack catch, yr_qr is the Year and Quarter of catch, and effort is the days of trolling effort per Year and Quarter for each CML. The time period was from 1980 to 1996 to have an 8 quarter overlap (1994-1996) for splicing onto a 2nd GLM from 1994 to 2014.

From 1994.25 (1st quarter of 1994) to 2014 (4th quarter of 2013), the GLM was:

 $glm.nb(lbs_kept \sim as.factor(yr_qr) + as.factor(cml.F) + offset(log(effort)))$

where the additional cml.F term is the unique and consistent CML per fisher.

For each GLM, the covariates (cml.F and/or effort) were set to their mean values and the R predict function was used to estimate yr_qr effects. To splice the resulting two series together, the predicted values for the overlapping 8 quarters (1994.25-1996) in the 1st GLM were divided by the predicted values in the 2nd GLM. The mean was estimated for these 8 quarters and the predicted values from 1980 to 1996 in the 1st GLM were divided by the mean to ensure the scales were comparable. The standardized and spliced CPUE time-series values were taken from the 1st (1980.25-1994) and 2nd GLM (1994.25-2014) (Figure 13b).

Nominal CPUE increased with effort to the mid 1990s, before declining over the remaining time series, with a potential recovery in recent years (Figure 13a). These trends were also seen in the standardised CPUE time series, although the decline in CPUE was lower (Figure 13b).

Hawaii aku boat (pole and line) fishery

Data for this fishery were available from 1980 to 2013, while the number of vessels were available up to 2014. The number of fishers was based on the number of unique State of Hawaii, Division of Aquatic Resources (HDAR) issued Commercial Marine Licenses (CMLs) submitting Fishing Reports (Figure 14a). The number of aku boat vessels was determined by counting the number of unique vessel names. A unique combination of HDAR Commercial Marine License numbers, landing month and day was used to calculate an aku boat trip (Figure 14b). The total number of aku boat trips included zero landing trips. Due to confidentiality rules (less than 3 vessels operating), data summaries were not available for some quarters.

The vessel and trip activity of the aku boat fishery has been in decline over the last 30 years. The steep decline occurred in the 1980s and was attributed primarily to the closure of the tuna cannery. Attrition of vessels, many of which were built in the 1940s, and poor skipjack tuna landings also contributed to the long-term decline in this fishery.

Skipjack tuna landings for the aku boat fishery were derived from HDAR Commercial Fishing and Marine Dealer Report data (Figure 15). Catch levels have followed the trends in effort, showing notable declines over time.

The aku boat CPUE values originate from HDAR Commercial Fishing Report data. CPUE based on catch per day fished was calculated from Pounds Landed of skipjack tuna divided by the number of Aku Boat Days Fished (Figure 16a). The number of Days Fished includes days that fishers did not catch anything or days that fish were caught but not sold. Nominal CPUE showed a decline over the early years of the fishery (1980 - 1985), but then a recovery and stabilisation, with considerable variability, until the mid-2000s.

For CPUE standardisation, prior to 1994, each fisher was assigned a different CML in each year, such that a unique fisher and CML could not be followed from 1980 to 1994. Fishers were assigned unique and consistent Commercial Marine Licenses (CMLs) starting in 1994. Two GLMs with an assumed negative binomial distribution were fit. GLM CPUE standardization was the same as for the MHI troll fishery (above) (Figure 16b). Standardised CPUE also exhibited declines in the early time series to 1986, followed by a slight recovery and stabilisation to the mid-2000s. However, standardised CPUE appears to have fallen in recent years, with considerable seasonal variability. We note that given effort has dropped sharply in recent years, the significance of this decline is

unclear.

Guam troll fishery

Data were available from the 2014 Pelagic Team Report for Guam (Draft May 2015, Western Pacific Regional Fisheries Management Council), and sourced from The Division of Aquatic and Wildlife Resources (DAWR) offshore creel sampling program and its associated computerized data expansion system files, expanded with the assistance of NMFS.

This data source permitted the development of three effort time series, based on the number of active vessels, the number of trips undertaken, and the number of hours fished.

Estimates of the number of troll vessels were developed for the period 1982 - 2014, based upon the creel survey data. Since only a fraction of the days of the year are sampled, it is not possible to know the exact number of boats participating in the fishery. The 2013 trolling boat log was converted and processed through a boat estimator model 1,000 times, providing estimates of uncertainty.

Since 1982, the general trend on Guam has been an increase in the number of boats participating in the pelagic fishery, especially since the addition of two marinas to be covered within the offshore sampling program (Figure 17a). There appears to be a general increase in the number of small boats participating in Guam's pelagic fishery, particularly between 1982 and 1995, while the number of charter vessels has remained fairly constant for several years.

In terms of number of trolling trips and number of hours spent trolling, the creel survey allowed the development of estimates for the period 1982-2014. To do this, the data expansion system is run on a calendar year's worth of survey data to produce catch and effort estimates for each fishing method surveyed. Figures 17b and 17c present the estimated number of trips and estimated boat hours spent fishing for the trolling method, as taken directly from creel survey expansion system printouts. While the number of vessels within the fishery has tended to increase, the number of trips and number of hours fishing has plateaued after a peak in 1990 and shown some decline since the late 1990s.

Skipjack tuna catch within the Guam troll fishery has fluctuated over the reporting period (Figure 18). A drop in skipjack tuna during 2002 may be due to direct hits by two super typhoons. An increasing catch in skipjack tuna since 2007 reflects an increase in small boats targeting this species. These boats are primarily crewed by Micronesian fishermen.

Nominal CPUE time series for the fishery is developed from two sources:

- 1. from the total annual landings of skipjack divided by the total number of hours spent fishing (gear in use) (Figure 19a); and
- 2. direct from the offshore creel sampling program with Non-charter and Charter aggregated (Figure 19b).

The wide fluctuations in CPUE for skipjack tuna are probably due to the high variability in the year-to-year abundance and availability of the stocks, although skipjack tuna is caught year round. However, it is not possible to allocate species-specific effort, since effort used to target other species can result in an artificially high or low catch rate for a given species. Since 2007, a fleet of small boats targeting skipjack has resulted in increasing catch rates. No standardisation of the time series was possible.

CNMI troll fishery

Data were available from the 2014 Pelagic Team Report for Commonwealth of the Northern Mariana Islands (Draft May 2015, Western Pacific Regional Fisheries Management Council), and sourced from the Division of Fish and Wildlife (DFW) boat-based creel survey.

Effort within the fishery was estimated as the number of trolling trips, and the number of trolling hours, based upon the DFW boat-based creel survey, and taken from the creel survey expansion outputs (Figures 20a and 20b). The data expansion system is run on a calendar year's worth of survey data to produce catch and effort estimates for each fishing method surveyed.

Skipjack landings within the fishery were developed from the annual boat-based creel survey (Figure 21a). A 365-day (366 days during leap years) annual expansion is run for each calendar year of survey data to produce catch and effort estimates for the pelagic fishery to avoid over-estimating seasonal pelagic species. Percent species composition is calculated by weight for the sampled catch for each method to produce species catch estimates for the period 2000-2014. A second source of landings data was from commercial receipt invoices, which spanned the period 1983-2014 (Figure 21b).

The two sources of landings information show different trends over the comparable time period. That from the boat-based creel survey suggests a general decline in catches between 2000 and 2014. That from the commercial receipt invoices suggests generally lower catch levels, but catches appeared to peak in the period 2005-2006.

Nominal CPUE within the fishery was calculated in four ways:

- 1. from the annual boat-based creel survey estimates of total annual landings of skipjack divided by the total number of hours spent fishing (gear in use) (Figure 22a);
- 2. from the Commercial Purchase Database, which provides average pounds caught per trip. Annual catch rates were obtained by calculating the average weight per trip for each year. Trips were assumed to be one day in length and each commercial invoice represents one trip (Figure 22b);
- 3. from the annual boat-based creel survey estimates, but to make these comparable to the CPUE estimates from the Commercial Purchase Database, as the sum of skipjack weight

from all trolling trip interviews divided by the number of trolling trips interviewed (also Figure 22b);

4. from the annual boat-based creel survey estimates, but with non-charter and charter fleet data aggregated. Note: CPUE represents Number of fish per hour fished in this instance (Figure 22c).

These nominal CPUE time series indicated variable trends. The total CNMI boat-based creel trolling skipjack catch rates (Figure 22a) showed a relatively stable CPUE for the period 2000-2006, followed by a reduction to around 15 lb/hr for the remainder of the time series.

Comparing CPUE in terms of lb/trip (Figure 22b), commercial receipt data indicated high and increasing CPUE between 1983 and 1989, followed by over a 50% reduction in CPUE for the period 1992 to 2004, and subsequent fluctuations with peaks in 2007 and 2014. CPUE estimates from the creel survey follow a different trend, with evidence of an increasing trend between the late 1980s and 2006, followed by reductions to levels comparable to that calculated from the Commercial data source.

Estimates of number of fish per hour fished from the creel interviews (Figure 22c) indicates a slight increase in CPUE between 2000 and 2007, and a decline since that time. However, there is considerable variability in the time series. Standardised CPUE time series could not be developed for this fishery.

3.4 Catch and CPUE data from Japanese fisheries

The coastal troll fishery of Japan is comprised primarily of small vessels (less than 10 GRT), and targets skipjack tuna and yellowtail (*Seriola quinqueradiata*). The structure of fishing gear is quite simple and consists of a rod, main line, trolling depressor, leader line and lure. The trolling depressor can be used to submerge the lure when it is being towed. Their fishing grounds are mainly within approximately 60 n.m. from the landing port, because their trip is usually one day.

Time series of catch data were available for fishing fleets, including the coastal troll fishery, within the Japanese EEZ and region 1 of the 2014 skipjack stock assessment:

- Japanese coastal troll and pole-and-line catches from MAFF : Gyogyou yousyokugyou seisan toukei nenpou (Yearbook of fisheries and aquaculture production statistics of Japan, Statistics Department, Minister's Secretariat, Ministry of Agriculture, Forestry and Fishery).
- Catches from offshore and distant water pole-and-line fleets and purse seine fleets were compiled from the logbook data used within Multifan-CL skipjack assessment area 1.

While effort data were not directly available, standardised CPUE time series data were supplied for three fishery groups:

- Standardised CPUE for two coastal troll fisheries (Wakayama prefecture and Tokyo Hachijyo Islands, separately) from SC documents (Kiyofuji et al., 2013, 2014; Okamoto et al., 2014).
- Standardised CPUE for offshore pole and line from the 2014 skipjack stock assessment. Note that the pole and line CPUE in region 1 was only from offshore PL (Kiyofuji and Okamoto, 2014).

Annual catch data from the pole and line, troll and purse seine fleets showed considerable interannual variability (Figure 23a). Therefore, a lowess smoother was used to examine the general temporal trends in each time series (Figure 23b). Catches within the offshore pole and line fishery, the fishery with the largest annual catches of skipjack throughout the time series, peaked in the 1984, but the general smoothed trend was a decline from the late 1970s over the next 30 years. A shallow declining smoothed trend was seen in the distant water pole and line fishery over the period. Catches of small, and subsequently large, purse seiners increased to the late 2000s, and subsequently declined. Coastal pole and line catches showed little trend through the time series, while coastal troll catches declined from the mid-1990s.

Standardised CPUE time series for the offshore pole and line fishery (as used within the 2014 skipjack stock assessment) and coastal troll fisheries (Wakayama prefecture and Tokyo Hachijyo Islands) were plotted on the same relative scale (Figure 24a). The reader is pointed to the references for the standardisation procedures.

The quarterly standardised CPUE series and smoothed trend for the offshore pole and line fishery (Figure 24b) indicate an increase in CPUE between 1972 and the late 1990s, followed by a decline to the mid 2000s and subsequent recovery in recent years. In contrast, CPUE for the standardised coastal troll fishery CPUE series have tended to decline across the shorter, more recent period, in part influenced by notably high relative CPUEs in the late 1990s/early 2000s.

Trends in the coastal fishery therefore appear quite different in recent years to those in the offshore pole and line fishery. Both catches and CPUE have declined in the coastal fishery in recent years (compare Figure 23b and Figure 24b), and while that of the offshore pole and line fishery has fallen from a peak in the late 1990s, there is some evidence of a recent recovery.

3.5 Analysis of length frequency data

Size shifts in the length frequency data collected by observers can be used to identify changes in the population that may relate to fishing (e.g. a reduction in size) or movement between regions. However, length data are confounded by the selectivity pattern of the gear used. To examine the utility of available observer length frequency data, we looked at data collected from the longline fishery, representing a potentially greater latitudinal range than that from purse seiners, for example. We note that - in general - longliners tend to catch larger individuals than other gears. If consistent across regions, and as noted above for the longline observer data CPUE analysis, a focus on larger fish may offer an early indication of changes within the regional or local skipjack population.

Consistent with geographic areas examined within the CPUE analyses described earlier, skipjack length frequency data were examined for the Hawaii-based longline fishery (as noted, not used within the CPUE analysis), the New Caledonia, Fiji and French Polynesian EEZs, and a combined collection of other EEZs for which observer length frequency data were available.

Hawaii-based longline fishery skipjack size data

Skipjack size (fork length; FL) as measured by observers (2001-2014) was extracted from the observer database. Measurements were from the deep-set (tuna) sector (n=31,738) as there were less measurements from the shallow-set (swordfish) sector. Data were plotted for the period 2003-2014 (Figure 25).

There was no clear trend in skipjack size over the recent period within this data. The mean of the distribution was relatively stable at between 67.4 and 72.2 cm, and only slight evidence of modal progression was visible.

New Caledonia longline observer skipjack size data

Available length frequency data (fork length or measurements converted as necessary to fork length) from the New Caledonian EEZ for the period 2003-2014 were extracted from the observer database (Figure 26). Throughout the period, the number of samples in each 5cm length band each year was relatively low, the exceptions being in 2009-2011, a period where skipjack availability (or observer coverage) may have been greater. Despite the fluctuating sample sizes, mean size appeared to increase slightly over time, from 68.8 cm in 2003 to 71 cm in 2013 (noting that the mean of 74.2cm in 2014 is developed from <60 individuals).

Fiji longline observer skipjack size data

Available length frequency data (fork length or converted as necessary to fork length) from the Fiji EEZ for the period 2003-2014 were extracted from the observer database (Figure 27). Sample sizes were relatively large, with the exception of the period 2010-2012. While the mean size varied slightly more than seen in Hawaii and New Caledonia samples, it ranged between 61.6 cm and 70.6 cm across the period, but exhibited no clear overall trend.

French Polynesia longline observer skipjack size data

Available length frequency data (fork length or converted as necessary to fork length) from the French Polynesian EEZ for the period 2003-2014 were extracted from the observer database (Figure

28). Similar to New Caledonia, annual samples from the longline fishery were comparatively low. The range of sizes were also greater than seen in the other fisheries, from 35 cm to 102 cm. Despite this greater range, the mean size was comparable to that seen in the other fisheries, although the annual variability was slightly greater (60.1 cm to 75 cm). There was no clear overall trend in mean size, nor in the presence of the larger fish seen in this fishery.

Combined other longline observer skipjack size data

Available length frequency data (fork length or converted as necessary to fork length) for the period 2003-2014 were extracted from the observer database and combined for the following EEZs: Australia, Cook Islands, Kiribati, New Zealand, RMI, Papua New Guinea, Solomon Islands, Tonga, Tuvalu and Vanuatu, as well as the high seas. This pooling led to greater sample sizes, but also slightly greater variability in the distribution (Figure 29). The annual mean size varied from 63.4 cm to 71.5 cm. There was no clear overall trend in mean size. In turn, where sufficient data were available there seemed little consistent difference in mean size across EEZs.

3.6 Tagging

Tagging information provides a direct indication of movement, at least between the locations of tagging and capture. These data might help answer whether movement is sufficient to lead to density dependent habitat selection, and hence the potential to result in Ocean-wide range contraction and the causes for it. For example, if individuals are highly-mobile and move large distances within their range, there is greater associated knowledge of habitat suitability and opportunity for range contraction through density dependent habitat selection. If individuals are less mobile and constrained to limited areas over their lifetime, local mortality will be directly related to local fishing, and hence range contraction through depletion at the range margins may be more likely. In the intermediate case when individuals are highly-mobile but do not move over the entirety of their range, a lack of knowledge on the extent to which individuals move within the range hinders predictions of local and regional impacts of spatial patterns in fishing mortality.

However, the ability of the tagging data set to answer questions on tropical/temperate connectivity is somewhat weakened as currently, conventional tagging studies implemented within the WCPO over the recent period have generally focused on tropical regions, and only limited tagging of bigeye, yellowfin and skipjack has occurred in locations north of $10^{\circ}N$ and south of $10^{\circ}S$. The difficulties of tagging large numbers of fish over each species' size range in these regions and the recent focus on estimating the fishing mortalities associated with purse-seine fisheries has been a key reason for the limited tagging in these regions. This means that the chances of detecting tagged tuna that move towards the equator is lower (Figure 30; Tables 1, 2 and 3). Indeed, the overwhelming majority of Pacific Tuna Tagging Programme (PTTP; 2006-present) tags, for example, have been released in the equatorial region (Table 1), and the returns are also focused in this area (Table 2). Even in the earlier Regional Tuna Tagging Programme (RTTP; 1989-1992 and earlier SSAP) data, where more fish were tagged outside the latitudial range of $\langle -15^{\circ}S \text{ to } \rangle 15^{\circ}N$, returns suggested relatively high residency in those regions, and little movement from the equatorial band to those more temperate zones (Table 3), noting that only 303 tags were released in the northern region and 60 recovered there. However, we note the Japanese tagging programme, which has been included within the skipjack stock assessment model and which could provide further information for the current study.

Tagging is also hampered by the lower potential for tag recovery in areas outside of the $15^{\circ}N - 15^{\circ}S$ regions due to the lower and more dispersed fishing effort from industrial fisheries in these regions (Figure 30). Tuna tagged in equatorial waters that subsequently move to higher latitudes consequently have a lower probability of recapture by industrial fisheries, reducing knowledge of movement from the equator to the 'margins'. Most are longline fisheries and this gear typically only selects larger size classes. Consequently information on smaller size classes is even more difficult to obtain.

Electronic tags with capacity for satellite linkage for download of recorded information provide a method to overcome many of these obstacles. Information these tags record can be analysed to estimate a continuous movement track since the individual was tagged. The tags are preset to transmit this information to satellites which means that the tag does not need to be recovered to obtain the information necessary for track estimation. A limitation to this technology is the individual typically needs to be 15-20 kg or larger for the tag not to interfere with its normal behaviour and this typically prevents tagging of juvenile size classes and skipjack. Nevertheless in higher latitudes regions this technology provides a viable option for monitoring tuna movements.

3.7 Molecular and biochemical signatures

The physical, chemical and biological properties of the ocean vary spatially. These regional differences can be either temporally or permanently stored as signatures in the soft and hard tissue of tuna. If an individual moves from one sub-region to another the subsequent analyses of these signatures in the tissue can provide a record of this movement (i.e. provide a natural electronic tag).

Analyses of stable isotopes from bone, muscle tissue, organs, blood, scales and otoliths enable retrospective analyses of movement. Nitrogen and oxygen isotope signatures can be used as tracers of geographical movements. Similarly, carbon isotope signatures which are strongly driven by ocean temperature can be used to infer feeding locations. The difference in isotope turnover rates (e.g. between muscle and liver) can be used to infer short term movement if the liver and muscle have different isotope signatures (i.e. movement is the more probable explanation to explain the differences). Similar to stable isotopes, fatty acids tracers can be used to infer short-term movement. The composition of fatty acid differs over the ocean landscapes and if the fatty acid signature in the

fish tissue differs from that of its capture location movement can be inferred. Analyses of hard parts offer a record of longer term movement as the chemical composition of the ecosystem is captured in the hard part as it grows with time (e.g. otoliths). If the animal moves into different chemical environments then this is recorded in the deposition of new material. Evidence for movement can be further established by the analysis of trace elements and metals that accumulate in hard and soft tissues as the multivariate signature of trace elements also varies spatially. Analyses of this material from hard parts have the advantage that the history of movement can be correlated with time if the age of material deposition can be reliably estimated.

Operationalising the use of these technologies for analysing range contraction requires investment in describing the oceanscapes for isotopes, fatty acids and trace elements. At small scales these oceanscapes are likely to also be temporally variable. WCPFC's investment through Project 35, which has established a tuna tissue bank for the WCPO, provides a basis for these oceanscapes to be estimated with observers attempting to collect biological samples for all species and size classes across the WCPO on a continuous basis. Not only does this provide the material to estimate the oceanscapes but it also allows for fish size dependent differences to be evaluated.

Molecular methods offer an alternative for rapid identification of species stock structure. A benefit of the improving genome profiling for each tuna species is the capacity to develop genome wide markers for analyses at fine scale resolution. An examination of the degree of genetic structuring across the range of the species using markers that represent recent time periods would allow inference on movement. The absence of sub-regional differences in structure would indicate a higher rate of mixing within the population. The tuna tissue bank provides a source of genetic material for these types of analyses.

3.8 Synthesis from existing data

In this section we attempt to synthesise the trends and information identified in the available data sources.

Many different CPUE time series were developed, spanning an approximate latitudinal range of $-20^{\circ}S$ to $30^{\circ}N$. In Figure 31 we attempt to present some of these time series over a consistent timescale and relative to their geographic location. Note that not all the CPUE trends were standardised, and unstandardised series are presented within grey boxes.

There was little spatial and temporal consistency in the pattern of CPUE trends across the region. In the southern hemisphere, the New Caledonia series is closest to what might be called the 'core' skipjack region of the western equatorial zone. This series showed a positive trend in standardised skipjack longline CPUE. This contrasted with the declining pattern found in the observer data in neighbouring Fiji, comparable with that seen further east in the data from French Polynesia. Within French Polynesian waters, however, standardised time series from the artisanal fisheries were relatively constant or (slightly) increasing. We note that in this artisanal fishery, there was a sharp decline in the nominal CPUE that disappeared when the data were standardized for gear, but there was also a decline in catch.

In the northern hemisphere, unstandardised Guam troll CPUE increased in the last 10 or so years. However, this was felt to result from the increase in more targeted fishing by small vessels within that fishery, rather than changes in abundance. Just to the north of Guam, the unstandardised CPUE series from CNMI showed either a decline and recent recovery, or a recovery and then slight decline, dependent upon the source of data used. This highlights the challenges in available data, and the need to obtain standardised indices to assist the analyses.

On a similar latitude, the Hawaiian fisheries examined showed different trends within their standardised CPUE series. The CPUE from the troll fishery remained relatively stable, with some slight decline over the long term and a slight recovery in recent years. By contrast, Aku vessel CPUE declined in recent years. As for French Polynesia, this difference in trends within similar locations between fisheries is notable.

Finally, the most northerly data sets from Japan, like those of Hawaii and French Polynesia, showed different trends between fisheries. The offshore pole and line standardised CPUE appeared relatively stable, noting declines and recovery in recent years. By contrast, that of the coastal troll showed a general decline over a similar recent period.

There appears no consistent spatial trends, therefore, within the CPUE data analysed here. The information is insufficient to say whether abundance has declined, to identify if range contraction is occurring within skipjack, or which mechanisms (localised depletion at the extremes of the range or density-dependent habitat selection), if any, could be driving it.

In turn, the fact that different fisheries within the same region (e.g. Japan, French Polynesia, Hawaii) show different trends suggests that localised effects of fishing, and/or small-scale oceanographic effects, which both impact upon the local availability of fish to gears with potentially different selectivities, will influence trends and must be considered within analyses.

As is clear from the example of the Guam troll fishery, where the increase in unstandardised CPUE is likely a result of a change in fleet composition, further analyses should be based upon standardised CPUE time series. In turn, the analysis of localised individual fisheries represents a 'piecemeal' approach and does not allow a comprehensive examination by latitudinal band, for example. The analysis was limited to longline observer data, which generally falls within the EEZs of CCMs, and hence limits the latitudinal range. Noting that the issue of species catch recording within logsheets needs to be examined further, the provision of operational data from the high seas, as well as EEZs, would facilitate further investigation of standardised indices.

Brouwer et al. (2015) note that the economics of fisheries can drive trends within CPUE time series. Incorporation of knowledge of local economics into these analyses is an important component to identify trends driven by factors other than underlying abundance.

We note that oceanographic conditions affect the location of purse seine fishing activity (e.g. Williams and Terawasi, 2014). Whether a similar influence occurs for non-target skipjack in longline fisheries is not clear. However, the potential influence on local abundance and hence local CPUE time series, is noted. We also note that the CPUE standardisations of e.g. Okamoto et al. (2014) contained a significant sea surface temperature term. Whether this would extend to longline fisheries cannot yet be determined.

Ultimately, analysis of CPUE data is hampered when analysing longline observer data, due to limited fleet and spatial coverage and the uncertainty on whether standardised trends are indicative of the relative abundance of skipjack specifically, rather than resulting from changes in reporting and catchability due to a longline fleet that is targeting billfish, other tunas or sharks. The potential absence of a direct relationship between purse seine CPUE and underlying abundance (see Scott et al., 2015) restricts the use of the more numerous, but also more geographically limited, data for further investigation. The generally local nature of troll fisheries and pole and line fisheries, along with the decline of the latter over time due to economic factors and technological advances in the purse seine fishery (Williams and Terawasi, 2014) again frustrates regional-scale analyses. Ultimately, if species composition issues can be overcome, the use of operational longline data to allow standardisation of time series, may offer the greatest geographic range of information to pursue these analyses further.

Examination of longline length frequency data for signals that may be related to abundance did not provide a clear signal of fishery impacts in any of the fisheries examined, and hence no patterns across the latitudinal range of the data. Generally the length frequency distributions were stable. A wider analysis combining data from other fisheries may offer further insights. However, the challenge of identifying signals while disentangling gear selectivity issues, the rapid growth of skipjack, sampling issues, movement and any population abundance changes remains.

From the available tagging information, movement was generally assessed as limited, with the majority of skipjack appearing to remain resident within the region in which they were tagged. This might reduce the likelihood of large-scale range contraction through density dependent habitat selection. However, as noted earlier, the constraints and limitations of the tagging programmes (focussing on particular areas, limited range of tuna sizes that can be tagged) and of the operations of the fisheries that might recover the tags (their size selectivity, lower and more dispersed fishing effort in higher latitudes) hamper the use of tagging data to detect range contraction.

The developing science area of biomarkers offers future potential for improved knowledge of spatial connectivity, and as noted, the WCPFC's investment in a tuna tissue bank (Project 35) provides a basis for the estimation of oceanscapes for isotopes, fatty acids and trace elements.

The data available for analysis within this work struggle to identify range contraction or its potential causal mechanisms on their own. For instance, range contraction due to DDHS should incur a

steeper decline in abundance at the edges of the range than at the core. However, in situations where fishing effort is much higher at the core than the edges, this signal is confounded with abundance declines at the core resulting from the directed fishing in that area. Trends seen in biological data cannot therefore be separated from the biology of the exploited stock and the characteristics of fisheries exploiting them. There is therefore benefit in examining the outputs from models that use these data to provide an integrated assessment.

4 Insights from integrated models

Integrated models represent modelling frameworks that can utilise multiple data sources in order to best describe population dynamics. The two primary integrated models used within the WCPO are MULTIFAN-CL (Fournier et al., 1990) and SEAPODYM (Lehodey et al., 2012). We examine outputs from both these models to inform the current study:

- MULTIFAN -CL
 - Estimated patterns of movement
 - Estimated trends in regional biomass
- SEAPODYM
 - Basic results of changes in biomass and fishery impacts over the period of the SEAPODYM model (fishery impact)
 - Specific simulations examining connectivity between tropical and temperate regions

4.1 MULTIFAN-CL

The MULTIFAN-CL assessment for skipjack tuna (Rice et al., 2014) assimilates the available biological and fishery data sources, including some of those data sets discussed above, for a WCPOwide assessment of the status of this stock. That assessment covers the geographic range of the western and central Pacific Ocean from $50^{\circ}N$ to $20^{\circ}S$ and from oceanic waters adjacent to the east Asian coast ($110^{\circ}E$ between $20^{\circ}N$ and $20^{\circ}S$; $120^{\circ}E$ north of $20^{\circ}N$) to $150^{\circ}W$ (Figure 32). It should be noted therefore that the assessment only covers the northern temperate region, and examination of model results will therefore concentrate on estimates of the tropical regions compared to that northern temperate region.

It should be noted that regional movement and regional recruitment are parameters that MULTIFAN-CL can adjust to achieve a best fit to all the input data by distributing fish between regions. Hence estimates may also reflect patterns seen within regional fishery size frequency data, catch levels, etc. Care must therefore be taken when examining the trends shown.

Estimated patterns of movement

The information on skipjack movement available from tagging programmes, including the Japanese tagging programme, contributes to the estimation of regional movement (along with other data sources). Skipjack movement estimated within the assessment was assumed to be time invariant and to occur instantaneously at the beginning of each quarter between regions sharing a common boundary. Note however that fish can move between non-contiguous regions in a single time step

due to the "implicit transition" computational algorithm employed. Movement was parameterised as the proportion of fish in a given region that move to the adjacent region. Across each interregional boundary in the model, movement was possible in both directions for the four quarters, each with their own movement coefficients. The seasonal pattern of movement persists from year to year with no allowance for longer-term variation in movement. Usually there are limited data available to estimate age-specific movement and the movement coefficients are normally invariant with respect to age. A prior of 0.1 is assumed for all movement coefficients, inferring a relatively high mixing rate between regions.

Under the assumption that regional movement estimated within MULTIFAN-CL reflects the actual movement within the regions of the WCPO, the distribution of regional biomass by source region derived from a simulation using the movement coefficients is presented in Figure 33. For regions 1, 3 and 4, a relatively high proportion of the total biomass is predicted to be sourced from within those regions. For region 1, less than 10% of the estimated recruits were 'sourced' from the tropical region of the model, suggesting this region would be less influenced by fishing impacts in other regions. In the opposite direction, Region 1 supplies limited biomass to all other regions of the model (less than 20% of Region 2-4 biomass comes from Region 1). We note that this assessment is of total biomass, and will include a high proportion of juvenile fish whose opportunity for movement may be lower, thereby reducing estimated regional movement.

Estimated trends in regional biomass

MULTIFAN-CL provides estimates of stock biomass broken down into model regions. From the 2014 assessment, the eastern equatorial region (region 3) was the region with the greatest spawning potential; the central equatorial region (region 2) the second largest; the single northern region (Region 1) was the third largest (Figure 34).

The assessment also examined fishery impact by region, relative to estimated levels of biomass that would have been present in the absence of fishing. That analysis suggested that declines in spawning potential in regions 1 (northern temperate) and 3 (eastern equatorial) were driven primarily by the estimated recruitment, while fishery impacts are greatest in regions 4, 5 and to a certain extent in region 2 (western equatorial region). Indeed, the northern region 1 was assessed to be the least impacted region, with recent biomass levels around 73% of unexploited levels. Declines in the tropical region were larger (e.g. Region 2: 43%, Region 3: 63%).

4.2 Seapodym

SEAPODYM is a model developed for investigating spatial tuna population dynamics, under the influence of both fishing and environmental effects. The model is based on advection-diffusionreaction equations, and population dynamics (spawning, movement, mortality) are constrained by environmental data (temperature, currents, primary production and dissolved oxygen concentration) and simulated distribution of mid-trophic (micronektonic tuna forage) functional groups. The model simulates tuna age-structured populations with length and weight relationships obtained from independent studies. Different life stages are considered: larvae, juveniles and (immature and mature) adults. After juvenile phase, fish become autonomous, i.e., they have their own movement (linked to their size and habitat) in addition to be transported by oceanic currents. Fish are considered immature until pre-defined age at first maturity and mature after this age, i.e., contributing to the spawning biomass and with their displacements controlled by a seasonal switch between feeding and spawning habitat, effective outside of the equatorial region where changes in the gradient of day length is marked enough and above a threshold value. The last age class is a plus class where all oldest individuals are accumulated. The model includes a representation of fisheries and predicts total catch and size frequency of catch by fleet when fishing data (catch and effort) are available. A Maximum Likelihood Estimation approach is used to optimize the model parameters. Conventional tagging data is integrated into the estimation of movement parameters. A full description of the seapodym model for skipjack used in the analyses is provided in Lehodey et al. (2014).

Five simulations of the skipjack model were performed. The first simulated the population from 2003 to 2012 with the historical fishing included in the simulation. The second simulation repeated the first but with no history of fishing. The difference between these simulations can then be used to infer what the impact fishing has had on the distribution and abundance of the skipjack population. At the range extremes of skipjack, such as the Japan EEZ, the CPUE of the coastal troll fishery has been generally declining for the last decade whereas the offshore CPUEs have been stable or increasing (see Section 3.4). We examined the fishery impact on skipjack across the EEZ to assess whether the pattern of impact was consistent with these trends.

The next set of simulations excluded the historical fishing and turned recruitment off from the equatorial waters, essentially mimicking the total removal of fish from those regions. The first turned recruitment off in area 1 (see Figure 35), the second turned recruitment off in area 2 (see Figure 35) and the third turned recruitment off in area 1 and 2. We then chose two range extremes, the Japan and New Zealand EEZs and calculated the change in adult biomass under each of these scenarios. This change represents a measure of the connectivity between these EEZs and each equatorial region (ie how much of the population in each EEZ originates from the equatorial region).

The first set of simulations indicated that the impact of fishing is higher in the regions of the coastal troll fisheries of the Japanese EEZ than elsewhere in EEZ. Fishery impacts were as high as 9% over the simulation period but decreased in the later years of the simulation (Figure 36). This observation was consistent with the CPUE trends reported for the Japan EEZ (see coastal troll CPUE trends compared to the offshore fishery, Figure 24), suggesting that the coastal region may be impacted to a greater extent by fishing than offshore areas.

The second set of simulations estimated a decrease in adult skipjack biomass within the Japanese EEZ of between 12.8% and 33.3% when recruitment was turned off in particular equatorial regions (Table 4). A similar result was observed for the New Zealand EEZ (Table 4). Some differences were observed between Japan and New Zealand EEZs, with the New Zealand demonstrating more connectivity with area 2 of the simulation than with area 1 (Table 4). We note that the impacts of turning off recruitment were greater in the 'rest of the WCPO' region than in the Japanese and New Zealand EEZs, suggesting that those EEZs still rely on temperate waters for the majority of their recruitment. SEAPODYM assumes recruitment will occur within regions that have appropriate oceanographic conditions; these results suggest that those conditions in the temperate region are sufficient to allow recruitment under model assumptions.

4.3 Synthesis from integrated models

The two integrated models commonly used within the WCPO (MULTIFAN-CL and SEAPODYM) provide different insights into potential interactions between tropical and temperate regions.

MULTIFAN-CL's primary role is to assess status at the stock level. While it integrates information from a wide range of different data sources, and estimates spatial patterns in movement and biomass from which insights can be gained, care must be taken when doing so as conflicting input data can lead to unexpected outcomes. Indeed, as noted earlier, regional movement is one of the parameters that MULTIFAN-CL can adjust to achieve a best fit to all the input data by distributing fish between regions; regional recruitment levels are another variable that can be adjusted and hence estimates may also reflect patterns seen within regional fishery size frequency data, catch levels, etc. In turn, geographic regions within the model are relatively coarse, and hence fine-scale evaluations of stock status are difficult to make. This noted, the 2014 assessment of skipjack suggests that the northern temperate region is relatively 'stand alone' in terms of its reliance on other regions for recruitment to maintain the population, with some limited reliance of other regions on recruitment from Region 1. This result was consistent with the results seen from tagging data (noting the caveats that were detailed above for those data). In turn, the impact on the stock in the northern region have been relatively low, compared to that in the tropical region.

In contrast, SEAPODYM attempts to assess fishing and climate influences on stocks at a much finer spatial scale. Results of fishing simulations presented here were consistent with trends seen within the Japanese CPUE time series. Inshore areas were assessed to be more affected by fishing in other areas (the Japanese EEZ and beyond) than the offshore region. In turn, the results of further SEAPODYM simulations suggested greater connectivity between tropical and temperate regions than indicated by either MULTIFAN-CL or the available tagging data. SEAPODYM modelling incorporates available tagging programme information during the model fitting process (Lehodey et al., 2014). Incorporation of these data in the likelihood estimation produced antagonistic effects, especially through the estimation of movement parameters. In previous experiments without tagging data, the model had a tendency to increase diffusion and decrease advection parameters estimates while with tagging data the model has an opposite tendency. There is reasonable agreement between final observed and predicted distributions of tagged fish in the WCPO from where all tags were released (Lehodey et al., 2014). However, predicted recaptures are therefore slightly greater at higher latitudes than seen within the tagging data set, which increases estimated connectivity between tropical and temperate regions.

5 Development of a spatial model for investigating hypotheses

In this section we describe a spatially structured model that allows different patterns of dispersal / movement / mixing to be parameterised. Combined with alternative patterns of exploitation in relation to the distribution of abundance, different hypotheses can be examined to investigate the relationship between catches and trends in abundance. This model represents the completion of Step 3 of Project 67's scope of work.

Spatial patterns in the use of habitats by marine organisms and fishers are driven by different mechanisms. Our goal here is to explore how interactions between these patterns can impact population dynamics over space. We start by defining a spatially-explicit model for the geographic range of a mobile harvested species, with individual movement between cells dictated by different strategies. We represent heterogeneity in habitat quality by defining 'core', high quality areas where individuals experience fast growth, and 'edge', low quality habitats where individuals experience slow growth. Note that the 'core' and 'edge' labels do not necessarily reflect their actual geographic position within the range, but are used instead as general labels to refer to good and marginal habitats, respectively (see also Sagarin and Gaines, 2002). Four scenarios are used to represent spatial patterns in fishing mortality: (1) even fishing mortality throughout the range (baseline); (2) fishing mortality proportional to cell biomass (ideal-free-distribution); (3) fishing effort in core, high-productivity areas only; (4) fishing effort in edge, low-productivity areas only. These are simplified but representative versions of the key types of complex fleet behaviour existing in modern fisheries. Lastly, we incorporate individual movement decisions by allowing individuals to either move randomly between cells (baseline), or show preferential movement towards 'better' cells (the second assumption behind Ideal Free Distribution theory, of perfect knowledge of patch quality). This last quantity is defined either based on habitat quality alone or based on the balance of habitat quality and conspecific density, following density-dependent habitat selection. The next sections detail the practical implementation of each model component.

5.1 Local population dynamics

The geographic range of the harvested species is defined under a grid layout, with each cell having 8 neighbours as well as periodic boundaries when the cell occurs at the edge of the grid⁶. Local, cell-wise, populations dynamics follow a logistic model. For each cell, two main parameters are defined: (1) the carrying capacity K and (2) the *per capita* growth rate r. Local abundance at the next time step $(N_{-t} + 1)$ is then a function of abundance at the previous timestep, the expected population growth given how close abundance is to the carrying capacity $r \times (1 - \frac{N_{-t}}{K})$, fishery catches (C_{-t}) , and the balance of immigration and emigration from neighbour cells $(I_{-t} - E_{-t})$.

⁶When boundaries are periodic, cells at one edge of the grid send individuals to cells at opposite edges. This allows for a continuous distribution of neighbours versus reflecting boundaries where cells at the edge send back individuals to themselves.

$$N_{t} + 1 = N_{t} + N_{t} \times r \times (1 - \frac{N_{t}}{K}) - C_{t} + I_{t} - E_{t}$$
(1)

Because we do not model weight explicitly, we use abundance and biomass interchangeably to refer to population numbers. Abundance at each time-step is calculated under the following order of operations: individuals move between cells, local growth occurs, and then fishing is applied to the cell. Qualitative results were not affected by inverting the order of fishing and reproduction.

5.2 Defining habitat quality by cell

Growth and mortality rates vary over the geographic range of species, but this variation is not necessarily correlated since separate factors can affect these rates independently. For instance, reproduction by mobile animals could only occur in certain parts of the range, while mortality would be expected to occur throughout the range. This can be represented by breaking down the logistic part of equation 1 to highlight the two roles it performs: adding individuals (growth, reproduction, r_G thereafter) and removing individuals (natural mortality, r_M thereafter):

$$N_{-t} \times r \times (1 - \frac{N_{-t}}{K}) = \underbrace{N_{-t} \times r_{-G}}_{-growth} - \underbrace{N_{-t} \times r_{-M} \times \frac{N_{-t}}{K}}_{-mortality} \quad (2)$$

In order to introduce heterogeneity in habitat quality, we decided to define habitat quality to be directly related to growth (r_G) , such that 'core', high quality, habitats and 'edge', low quality, habitats can be introduced by setting r_G to higher values in designated core cells. Since r_M is set to the same value throughout the range, the lower r_G in edge cells results in slower growth for individuals in those cells, as well as a lower equilibrium abundance, K_eff :

$$K_eff = \frac{r_G}{r_M} \times K \tag{3}$$

This is representative of many highly-mobile pelagics which are only found in the edges of their range during the warmer months of the year.

5.3 Movement of individuals between cells

Individuals move between cells in three stages: emigration from the natal cell, movement between cells, and immigration to a destination cell. Cues from the biotic or abiotic environment can be used to inform the direction of movement at any of these stages. In the current model we implemented individual decision at the immigration step only to focus on dispersal strategies at that level (see diagram in Figure 37). At each time-step a constant proportion of individuals (ϵ) emigrate from their natal cell. They then move to cells adjacent to their natal cell, possibly informed by some
feature of their environment - e.g. better habitat quality. We defined three scenarios to account for different types of movement:

- 1. *No dispersal:* Individuals do not move between cells. This is unlikely for large pelagics but it serves as a useful baseline scenario to investigate whether and how within-stock mobility can change the predicted effects of fishing;
- 2. Constant dispersal, no choice: Individuals emigrating from their natal cell are distributed evenly between neighbour cells $(D_pref$ is set to 0 in equation 4 below);
- Constant dispersal, preferential movement: Individuals preferentially move to neighbour cells where their effective growth is maximized. Effective growth is a function of habitat quality as represented by r_G, and density in the target cell N/K_eff (see the growth part of equation 2). The proportion of emigrating individuals from a cell that goes to a given neighbour i Pn_i is defined as:

$$Wn_{-i} = \left[r_{-G}, i \times exp(1 - \frac{N_{-i}}{K_{-e} f f, i})\right]^{D_{-pref}}$$

$$\tag{4}$$

$$Pn_{-i} = \frac{Wn_{-i}}{\sum_{-i} = 1^{N=8} Wn_{-i}}$$
(5)

where Wn_i is the metric of effective habitat quality that is then standardized based on Wn_i for all cells. The value of D_pref controls the strength of dispersal preference: as $D_pref \to 0$, dispersal becomes increasingly uniform. When $N = K_eff$, the direction of movement is informed by the value of r_G only.

5.4 Spatial patterns in fishing mortality

Fishing mortality is the proportion of individuals removed by fishing at a given point in time. To easily relate fishing mortality F to traditional management metrics, we define F as a function of the cell's $r_{-}G$ since, in logistic population models, the fishing mortality required to achieve maximum sustainable yield $(F_{-}MSY)$ occurs at 0.5r. Low, medium and high fishing mortalities are then defined as below, equal to and greater than $F_{-}MSY$, respectively. When there is habitat heterogeneity, the value of $r_{-}G$ in the core is being used to set the fishing mortality throughout the range. In this case, a fishing mortality equal to $F_{-}MSY$ in the core will be comparatively high for edge cells as their $F_{-}MSY$ is lower than that of core cells (since $r_{-}G$, edge $< r_{-}G$, core). Catches are calculated from fishing mortality as:

$$C_{-t} = F_{-t} \times N_{-t} \tag{6}$$

We use four scenarios that encompass a range of spatial patterns in fishing mortality:

1. *Ideal-free-distributed*: total F is spread amongst cells to be proportional to cell abundance – this is representative of what naturally happens in many fisheries;

- 2. Even fishing: F is set at the same proportion of r_G for each cell;
- 3. Core fishing only: F is set at the same proportion of r_G for cells in core regions only, F is set to 0 otherwise;
- 4. Edge fishing only: F is set at the same proportion of r_G for cells in edge regions only, F is set to 0 otherwise.

6 Overall discussion and recommendations for future research

We have analysed a wide range of available data sources to assess whether they offer insights into trends in abundance and fishery impacts in the temperate regions of the WCPO, and hence range contraction. We have also examined whether that information can support further modelling work on the issue. We briefly summarise the findings (see also the earlier synthesis sections), discuss their usefulness for evaluating range contraction, and provide WCPFC-SC with recommendations highlighting potential areas of future research.

Analysis of trends in skipjack CPUE data showed little spatial or temporal consistency across the latitudinal range examined. There were no clear signals to indicate whether range contraction was occurring in skipjack, nor which of the two potential 'causal' mechanisms put forward within Section 2 of this paper might be driving it. The analysis was by necessity a 'piecemeal' exercise, with data only available from specific EEZs as a result of the reliance on longline observer data. If further work in this area is to be pursued, and noting that longline fleet information offers the data set with the greatest spatial range, longline operational data (rather than observer information with its low operational coverage and more limited spatial distribution) may offer the best data set for further investigation of potential trends across the stock range. In turn, standardisation of CPUE time series proved a key requirement for the analysis, in order to remove the influence of fleet composition changes seen in three examined regions, and to take changes in species targeting into account. Operational data are therefore necessary to allow standardisation of the CPUE series. We note that there is concern over longline logsheet species composition information for skipjack, including variable reporting of non-target species. This would first need to be investigated before undertaking any further analyses.

The skipjack longline length frequency data appeared to offer little insight into population-level impacts. There is the potential to widen the analysis to incorporate data from other fisheries in order to gain further insights and support analyses of other data. However, this area of further work may be considered of lower priority.

Existing tagging data suggested limited connectivity between tropical and temperate regions, and may influence outputs from the integrated models on regional connectivity. However, challenges in assessing tropical/temperate connectivity arose due to the design of recent tagging programmes, given their focus on tropical waters and the distribution of fishing effort that influences recaptures. If work on range contraction is considered a priority, and the cost implications permit it, expansion of tagging programme activities into the temperate region should be considered.

The results of integrated models (MULTIFAN-CL and SEAPODYM) offer a link between the examination of individual biological data components and the underlying biology of the stock and the characteristics of those fleets exploiting it. The two models provided slightly different evaluations of regional connectivity. MULTIFAN-CL indicated that the reliance of the northern temperate region on the tropical area for recruitment was low, and exploitation in the northern temperate region to be comparatively limited. SEAPODYM outputs indicated localised effects in the northern temperate area due to overall (combined tropical and temperate) WCPO fishing impacts, which mirrored those seen in the coastal Japanese fishery CPUE data. This model also indicated a higher level of connectivity between tropical and temperate regions than both MULTIFAN-CL or the tagging data examined. Whether those levels of connectivity were sufficient to lead to range contraction effects through density dependent habitat selection, rather than local depletion, could not be acertained.

Ultimately, the results of data analyses and integrated modelling have not shown conclusive evidence of range contraction in WCPO skipjack tuna. We note the issues raised above with respect to the data available, and the potential uncertainties within the integrated models examined, and raise recommendations for future research to address these.

6.1 Recommendations for future research

The investigations described within this paper and summarised above have identified several potential areas for further research. We invite the WCPFC-SC to consider and prioritise these, and suggest any other specific analyses which they feel would be of value to the Commission's consideration of range contraction within WCPO, and in particular skipjack, stock management.

The analyses were challenged by different data issues, and appear unlikely to identify range contraction or its potential causal mechanisms in their current form. We recommend that they first be improved by work in the following research areas, which may then increase their quality to warrant fuller examination within the simulation model described earlier:

- A key constraint to understanding the regional connectivity of the skipjack stock was limitations in the latitudinal range of recent tagging programmes. We recommend investigation of the feasibility of expanding skipjack tagging programme activities within temperate regions to better understand connectivity and movement levels. Improved knowledge from such a programme would help inform current modelling. Further analysis of the Japanese tagging data set would also be useful.
- The developing field of biological markers to assess stock spatial connectivity offers potential for an alternative source of information to tagging programmes. Continued collection of biological marker samples under Project 35 and research into the application of these new approaches is recommended.
- CPUE data analyses were constrained geographically, due to available data. To improve the latitudinal analysis of CPUE time series, the quantity of available data, and to allow necessary standardisation of time series, investigation of the use of operational longline data from across the WCPO is recommended.
- Further to CPUE standardisation, the potential implications of economic conditions were noted, which are particularly important factors in small scale mixed fisheries such as many of

those examined here. Improved collection and availability of economic information to better understand the fleet behaviours underlying CPUE time series is also recommended (see also Brouwer et al. 2015).

While offering some insights, the integrated models currently used within the WCPO have not been developed to study the particular dynamics of range contraction and are somewhat constrained by the assumptions underpinning the analysis of movement:

• Further examination of the ability of available integrated models to describe range contractionstyle dynamics, if they were occurring, is recommended.

7 Acknowledgements

We acknowledge with thanks the assistance of staff within the departments of each of the authors, the observers and data collection officers the information from whom the analyses described rely, and their respective national fishery departments.

We also thank Tom Peatman for the tagging information and excellent plot, and Valerie Allain, Sam McKechnie and John Hampton for detailed reviews of earlier drafts of this document. You too, dear reader, should be thankful.

This work was funded under Project 67 of the WCPFC Scientific Committee.

References

- Benton, T., Plaistow, S., and Coulson, T. (2006). Complex population dynamics and complex causation: devils, details and demography. *Philosophical Transactions of the Royal Society of London B*, 273(1591):1173–1181.
- Bigelow, K., Hampton, J., and Miyabe, N. (2002). Application of a habitat-based model to estimate effective longline fishing effort and relative abundance of Pacific bigeye tuna (*Thunnus obesus*). *Fisheries*, 11(3):143–155.
- Block, B., Teo, S., Walli, A., Boustany, A., Stokesbury, M., Farwell, C., Weng, K., Dewar, H., and Williams, T. (2005). Electronic tagging and population structure of Atlantic bluefin tuna. *Nature*, 434:1121–1127.
- Bowler, D. and Benton, T. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological reviews*, 80(2):205–225.
- Brouwer, S., Harley, S. J., and Pilling, G. (2015). The influence of catch rate on fishing effort
 an investigation using south Pacific albacore as an example. WCPFC-SC11-2015/SA-IP-04,
 Pohnpei, Federated States of Micronesia, 5–13 August 2015.
- Campbell, R. A. (2004). CPUE standardisation and the construction of indices of stock abundance in a spatially varying fishery using general linear models. *Fisheries Research*, 70:209–227.
- Clobert, J., Le Galliard, J.-F., Cote, J., and Meylan, S. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, 12(3):197–209.
- Fournier, D. A., Sibert, J., Majkowski, J., and Hampton, J. (1990). MULTIFAN a likelihood based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern blufin tuna (*Thunnus maccoyii*). Canadian Journal of Fisheries and Aquatic Sciences, 47:301–317.
- Fretwell, S. and Lucas, H. L. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, 19(1):16–36.
- Harley, S., Myers, R., and Dunn, A. (2001). Is catch per unit effort proportional to abundance? Canadian Journal of Fisheries and Aquatic Sciences, 58:1760–1772.
- Harley, S. J. (2012). A proposal to investigate range contraction for tropical tunas in the WCPO. WCPFC-SC8-2012/SA-IP-03, Busan, Republic of Korea. 7-15 August 2012.
- Kennedy, M. and Gray, R. (1993). Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments in the ideal free distribution. *Oikos*, 68:158–166.

- Kiyofuji, H., Ashida, H., Sugimoto, M., Horii, Y., and Okamoto, H. (2014). Abundance of skipjack migrating to the Pacific coastal water of Japan indicated by the Japanese coastal troll and pole-and-line CPUE. WCPFC-SC10-2014/SA-WP-10 Rev 1, Majuro, Republic of the Marshall Islands. 6-14 August 2014.
- Kiyofuji, H. and Okamoto, H. (2014). An update of the standardized abundance index of skipjack by the Japanese pole-and-line fisheries in the WCPO. WCPFC-SC10-2014/SA-IP-16, Majuro, Republic of the Marshall Islands. 6-14 August 2014.
- Kiyofuji, H., Okamoto, H., Ashida, H., Horii, Y., and Hoshikawa, A. (2013). Comparison of CPUE trends for skipjack tuna between two coastal troll fisheries around Hachijo-Island and south off Wakayama prefecture. WCPFC-SC9-2013/SA-WP-13, Pohnpei, Federated States of Micronesia. 6-14 August 2013.
- Lawless, J. (1987). Negative binomial and mixed Poisson regression. The Canadian Journal of Statistics, 15(3):209–225.
- Lehodey, P., Senina, I., Titaud, O., Calmettes, B., Conchon, S., Dragon, A., Nicol, S., Caillot, S., Hampton, J., and Williams, P. (2014). Project 62: SEAPODYM applications in the WCPO. WCPFC-SC10-2014/EB-WP-02. Revision 1, 23 July 2014, Majuro, Republic of the Marshall Islands. 6-14 August 2014.
- Lehodey, P., Senina, I., Titaud, O., Calmettes, B., Nicol, S., Hampton, J., Caillot, S., and Williams, P. (2012). Project 62: SEAPODYM applications in the WCPO. . WCPFC-SC9-2012/EB-WP-03, Busan, Republic of Korea, 7–15 August 2012.
- MacCall, A. (1990). Dynamic geography of marine fish populations. Univ. Washington Press., Seattle, US.
- Maunder, M. N. and Punt, A. E. (2004). Standardizing catch and effort data: a review of recent approaches. *Fisheries Research*, 70(2):141–159.
- McCullagh, P. and Nelder, J. (1989). Generalized Linear Models. Chapman and Hall, London.
- Minami, M., Lennert-Cody, C., Gaoc, W., and Roman-Verdesoto, M. (2007). Modeling shark bycatch: The zero-inflated negative binomial regression model with smoothing. *Fisheries Research*, 84:210–221.
- Okamoto, H., Kiyofuji, H., Horii, Y., and Ashida, H. (2014). Standardized skipjack CPUE of coastal troll fishery around Hachijo-Island from 1996 to 2013. WCPFC-SC10-2014/SA-IP-12, Majuro, Republic of the Marshall Islands. 6-14 August 2014.
- Rice, J., Hampton, J., Davies, N., and McKechnie, S. (2014). Stock assessment of skipjack tuna in the western and Central Pacific Ocean. WCPFC-SC10-2014/SA-WP-05, Majuro, Republic of the Marshall Islands, 6–14 August 2014.

- Sagarin, R. and Gaines, S. (2002). The 'abundance centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters*, 5(1):137–147.
- Scott, R. D., Tidd, A., Davies, N., Pilling, G., and Harley, S. (2015). Implementation of alternative CPUE/abundance dynamics for purse seine fisheries within MULTIFAN-CL with application to eort-based projections for skipjack tuna. WCPFC-SC11-2015/SA-IP-02, Pohnpei, Federated States of Micronesia, 5–13 August 2015.
- Shono, H. (2008). Application of the Tweedie distribution to zero-catch data in CPUE analysis. Fisheries Research, 93:154–162. doi:10.1016/j.fishres.2008.03.006.
- Sibly, R. and Hone, J. (2002). Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society of London B*, 357(1425):11531170.
- Tidd, A., Pilling, G., and Harley, S. J. (2015). Examining productivity changes within the tropical wcpo purse seine fishery. WCPFC-SC11-2015/MI-WP-06, Pohnpei, Federated States of Micronesia, 5–13 August 2015.
- Tremblay-Boyer, L., Harley, S. J., and Pilling, G. M. (2014). Relationship between abundance and range size in longline target species. WCPFC-SC10-2014/MI-WP-06, Majuro, Republic of the Marshall Islands, 6–14 August 2014.
- Van Horne, B. (1983). Density as a misleading indicator of habitat quality. Journal of Wildlife Management, 47(4):893–901.
- Ward, P. and Myers, R. (2005). A method for inferring the depth distribution of catchability for pelagic fishes and correcting for variations in the depth of longline fishing gear. *Canadian Journal* of Fisheries and Aquatic Sciences, 62(5):1130–1142.
- WCPFC (2010). Report of the Scientific Committee sixth regular session. Summary report, Commission for the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean., Nukualofa, Tonga. 1019 August 2010.
- WCPFC (2011). Report of the Scientific Committee seventh regular session. Summary report, Commission for the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean., Pohnpei, Federated States of Micronesia. 917 August 2011.
- WCPFC (2014). Report of the Scientific Committee tenth regular session. Summary report, Commission for the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean., Majuro, Republic of the Marshall Islands, 6–14 August 2014.
- Williams, P. and Terawasi, P. (2014). Overview of tuna fisheries in the western and central Pacific Ocean, including economic conditions - 2013. WCPFC-SC10-2014/GN-WP-01, Majuro, Republic of the Marshall Islands, 6–14 August 2014.

Zuur, A., Ieno, E., Walker, N., Saveliev, A., and Smith, G. (2009). Mixed Effects Models and Extensions in Ecology with R. Springer.

8 Tables

		$<-15^{\circ}S$	Equatorial	$> 15^{\circ}N$
PTTP	Releases	0	246767	0
	Recoveries	3	30055	14
RTTP	Releases	81411	167302	303
	Recoveries	4099	14190	60

Table 1: Geographical pattern of release and recoveries in the PTTP and RTTP (+SSAP).

Table 2: Proportion of tags released in the PTTP within one geographical region (left) being caught in each geographic region (top).

		Return		
		$< -15^{\circ}S$	Equatorial	$> 15^{\circ}N$
Release	$< -15^{\circ}S$	0.00	0.00	0.00
	Equatorial	0.00	1.00	0.00
	$> 15^{\circ}N$	0.00	0.00	0.00

Table 3: Proportion of tags released in the RTTP within one geographical region (left) being caught in each geographic region (top).

		Return		
		$< -15^{\circ}S$	Equatorial	$> 15^{\circ}N$
Release	$< -15^{\circ}S$	0.95	0.05	0.00
	Equatorial	0.00	0.99	0.00
	$> 15^{\circ}N$	0.00	0.46	0.54

Table 4: Connectivity table for skipjack predicted by SEAPODYM with ECCO-VGPM 1deg x 30d forcing (Lehodey et al., 2014). Table shows the percentage of decrease (with respect to reference) in virgin adult skipjack biomass in the Japanese and New Zealand EEZs and the rest of WCPO when the recruitment in the donor zone (see the tropical regions on Figure 35) is set to zero. Note, all connectivity simulations were run without fishing.

	Japan	New Zealand	Rest of WCPO
Average adult biomass	133656	36764	9269488
Skipjack recruitment = zero in donor region:	The % decrease of skipjack adult biomass		
Region 1	12.8	0.2	12.1
Region 2	23.4	34.1	64.1
Region $1 + $ Region 2	33.3	34.2	72.6

9 Figures

1990 1970 2010 High (90th quantile) Mechanism #1: Mechanism #2: Medium (50th quantile) overfishing in the edges overfishing in the core Low (10th quantile) Fishing edge core edge edge core edge

Relative abundance for Pacific yellowfin tuna, 1970-2010

Figure 1: Top: Changes in the relative abundance of yellowfin tuna over space and time, based on catch-per-unit-effort indices of abundance. We defined high, medium and low regions of abundance from the 90th, 50th and 10th quantiles of observed density by 5 degree cell over the range between 1970-2010. Bottom: Mechanisms that could explain abundance declines in the edge, and the result-ing predictions on the distribution of abundance over core and edge habitats (green arrows indicate movement of tuna from the edge toward the core habitat. Grey lines indicate pre-exploitation stock abundance, and the blue lines the resulting distribution resulting from each of the two mechanisms.) See also Tremblay-Boyer et al. (2014).



(a) Observed effort (grey dots) & catch (orange)(b) Observer data by program code.Figure 2: Map of observed effort and catch in the longline fishery of the south Pacific.



(a) Nominal longline skipjack CPUE by year

(b) Proportion of positive skipjack sets

Figure 3: Nominal CPUE (SKJ/1000 hooks) over time, and proportion of positive sets for skipjack in the south Pacific from observer programs reporting more than 1% of observed sets encountering a skipjack and from national waters (EEZ) reporting skipjack catch during the study period.



Figure 4: Observer data by program code from the available trimmed dataset.



Figure 5: Standardized CPUE for skipjack in the south Pacific, all observer data.





2005

Year

2010

andardized CPUE %CI

2000

0.0

1995

(d) All other observer programmes

2005

Year

2010

2000

Figure 6: Standardized CPUE for skipjack in the south Pacific, by observer programme. Values scaled to the maximum estimate.

0.0

1995



Figure 7: Effort (top two panels, thousands of trips and hours (100,000s)) and catch in 100,000s of individuals (middle) and weight 100,000s of kilogrammes (bottom) by year for bonitiers (BON) and poti marara (PM). Note that the data for catch in individuals is considered more accurate than that of weight.



Figure 8: Percentage of vessels by boat type by year between 1997 and 2012 (based on vessels that submitted logsheets for that year)



Figure 9: Species composition of the catch (in individuals) for bonitiers (left) and poti marara (right), split for catches within and outside the Archipel de la Société region. MAH - dolphinfish; THA - wahoo, OTH1 and OTH2 are two grouped 'other' species.



Figure 10: Interpretation of skipjack CPUE for Archipel de la Société. Nominal (blue) and standardized (red) CPUE for the Iles du Vent (a) and the Iles Sous-le-Vent (b). Observed CPUE values (individuals per hour) are shows as grey circles. Median catch rates in individuals per hour for the two main fishing techniques used to target skipjack (pole and line (canne) and troll (traine)) (c). Annual proportion of trips that used traine and canne in Iles du Vent (blue) vs. Iles Sous-le-Vent (green) (d).







Figure 12: Retained quarterly skipjack catch (mt).



Figure 13: Quarterly time series of nominal and standardised MHI troll skipjack CPUE



Figure 14: Effort time series for Hawaii aku boat (pole and line) by year and quarter



Figure 15: Retained quarterly skipjack catch from Hawaii aku boats (pole and line).



Figure 16: Quarterly time series of Hawaii aku boat skipjack CPUE



Figure 17: Estimated effort time series (number of boats, trips and thousands of hours) for Guam troll vessels by year and quarter. The line is the estimated linear trend in vessel numbers over time. Non-charter data is shown in green, charter data in blue.



Figure 18: Estimated skipjack landings from the Guam troll fleet, 1982-2014. The line is the estimated linear trend in total landings over time.



Figure 19: Estimated skipjack quarterly CPUE from the Guam troll fleets (non-charter in green, charter in blue, total in red).



Figure 20: CNMI boat-based creel estimated effort



Figure 21: Alternative CNMI annual estimated skipjack landings ('000 lb)



(c) CPUE (no./hr fished) fleets aggregated.

Figure 22: Alternative CNMI annual CPUE estimates



(a) Annual catches by fleet.

(b) Smoothed catches by fleet.

Figure 23: Annual skipjack catches ('00 tons) by fishing fleet. Small purse seiners = 30-200 GRT; large purse seiners = 200-500 GRT.



(a) Standardised CPUE series

(b) Smoothed standardised CPUE series

Figure 24: Annual and smoothed standardised CPUE time series for offshore Region 1 pole and line fishery (blue line) and two coastal troll fisheries (Wakayama prefecture and Tokyo Hachijyo Islands; orange lines).



Figure 25: Skipjack size (FL) as measured by observers (2003-2014) from the Hawaiian deep-set (tuna) sector. n is the number of samples, mean is the average fork length in a given year



Figure 26: Probability density distribution of annual skipjack size (FL, cm) as measured by observers (2003-2014) in the New Caledonian EEZ.



Figure 27: Probability density distribution of annual skipjack size (FL, cm) as measured by observers (2003-2014) in the Fiji EEZ.



Figure 28: Probability density distribution of annual skipjack size (FL, cm) as measured by observers (2003-2014) in the French Polynesian EEZ.



Figure 29: Probability density distribution of annual skipjack size (FL, cm) as measured by observers (2003-2014) in all other EEZs (see main text for details).



Figure 30: Plots of information for the Regional Tuna Tagging Programme (left) and Pacific Tuna Tagging Programme (right). From top to bottom: Distribution and level of tag releases, recoveries, and the relative distribution of skipjack catch by combined gears (RTTP: pole and line, purse seine, longline; PTTP: purse seine and longline).



Figure 31: Skipjack CPUE time series by fishery (unstandardised series shown in grey boxes), relative to its general geographic location.



Figure 32: Regional structure of the skipjack reference case stock assessment model.



Figure 33: Proportional distribution of total biomass (by weight) in each region apportioned by the source region of the fish for the reference case. The colour of the home region is presented below the corresponding label on the x-axis. The biomass distributions are calculated based on the long-term average distribution of recruitment between regions, estimated movement parameters, and natural mortality. Fishing mortality is not taken into account.



Figure 34: Comparison of the estimated spawning potential trajectories (lower solid black lines) with those trajectories that would have occurred in the absence of fishing (upper dashed red lines) for each region and for the WCPO for the reference case.



Figure 35: Geographical areas of the WCPO manipulated within SEAPODYM simulations. Red zone is the approximation of the Japanese EEZ; blue zone is the approximation of the New Zealand EEZ.



Figure 36: Plot of the relative impact of fishing on the distribution and abundance of the skipjack population in the northern WCPO. Red indicates greater relative impact (max 9%; see contours), blue lower relative impact.


Figure 37: Sample cell layout with core-edge habitat structure (core cells in reds have higher habitat quality, edge cells in blues have lower habitat quality). Under the no preference dispersal scenario (bottom right), emigrating individuals move to all 8 neighbour cells in equal proportions. Under the prefered dispersal scenario (top left), emigrating individuals move to the 8 neighbour cells with a heavier proportion towards high quality cells (here the 'quality' depends on the cell habitat type only (colour), but in the model it is a function of cell quality and conspecific density).

10 Appendix 1 - South Pacific longline CPUE standardisation diagnostics



Figure 38: Diagnostic plots for model fits from region-wide analysis.



(c) French Polynesia observer programme.



Figure 39: Diagnostic plots for model fits from each observer programme.



Figure 40: Step-plot showing the piecewise addition of the explanatory variables to the region wide analysis.



Figure 41: Step-plot showing the stepwise addition of explanatory variables to the analysis by data set.

Diagnostic Tables

	DF	Deviance Explained	Resid. DF	Resid. Dev	AIC
NULL			20508	119706	
+YY	19	7541	20489	112165	435081
+MM	30	13817	20478	113065	429615
$+ program_code$	40	28312	20468	113993	418165
+PCODE:YY	120	51037	20388	113442	402505

Table 5: Deviance table for region wide analysis

Table 6: Deviance table for analysis from New Caledonia observer program

	DF	Deviance Explained	Resid. DF	Resid. Dev	AIC
NULL			1211	9634	
+YY	13	1168	1198	8466	33210
+MM	24	2866	1187	8604	31952
$+HK_bt_ft$	35	3272	1176	8575	31689
$+hook_type$	35	3029	1108	8177	30022

Table 7: Deviance table for analysis from Fiji Islands observer program

	DF	Deviance Explained	Resid. DF	Resid. Dev	AIC
NULL			3144	26606	
+YY	11	3190	3133	23416	100659
+MM	22	5857	3122	23493	98565
$+HK_bt_ft$	60	8209	3084	23492	96954
$+ hook_type$	62	8238	3082	23484	96936

Table 8: Deviance table for analysis from French Polynesia observer program

	DF	Deviance Explained	Resid. DF	Resid. Dev	AIC
NULL			2960	2950	
+YY	12	270	2948	2680	8997
+MM	23	455	2937	2695	8865
$+hk_bt_ft$	53	791	2907	2689	8668
+ EEZ	56	833	2904	2691	8645
+ HookType	58	847	2902	2692	8639

	DF	Deviance Explained	Resid. DF	Resid. Dev	AIC
NULL			13147	64848	
+YY	19	6980	13128	57867	212224
+MM	30	9285	13117	58242	210360
$+hk_bt_flt$	78	22204	13069	58441	200890
+ EEZ	90	24556	13057	58042	199217
+HookType	58	847	2902	2692	8639

Table 9: Deviance table for analysis from observer programs (not NC, FJ, PF)