

SCIENTIFIC COMMITTEE TWENTIETH REGULAR SESSION

Manila, Philippines 14 – 21 August 2024

Investigating long-term recruitment trends of skipjack tuna in the Western and Central Pacific Ocean and Effort Creep in the Japanese Pole and Line Skipjack Fishery (WCPFC Project: 115)

WCPFC-SC20-2024/SA-WP-06 30 July 2024

Paul Hamer¹, Inna Senina¹, Patrick Lehodey¹, Makoto Nishimoto², Yoshinori Aoki², Naoto Matsubara², Yuichi Tsuda ²

¹ Oceanic Fisheries Programme of the Pacific Community (SPC)

² Japan Fisheries Research and Education Agency (FRA)

Contents

Executive Summary	3
Background	5
Part 1) Exploring evidence of increased recruitment of skipjack tuna in the WCPO	10
Methods	10
Results	10
Summary and Conclusions	26
Part 2) Effort creep in the Japanese pole and line fishery	27
Background	27
Methods	29
Results	31
Summary and Conclusions	34
Supplementary figures from the industry survey results	35
Acknowledgements	38
References	38

Executive Summary

This paper involves two separate but related studies as part of WCPFC project 115. The first part (part 1) explored the increasing trend in skipjack recruitment, particularly from the 1970s to the early 2000s, estimated by successive Multifan-CL (MFCL) skipjack assessments for the Western and Central Pacific Ocean. The second part (part 2) attempts to identify the possible extent and timing of effort creep (catchability increase) over time in the Japanese pole-and-line fishery for skipjack (JPPL).

Part 1 explored various climate and oceanographic data sets and recent preliminary updated skipjack SEAPODYM model estimates of spawning and juvenile habitat area and juvenile biomass trends. These data sets were initially explored in relation to a review of skipjack early life history and conceptual recruitment processes, to assess whether there was evidence that the region of the Western Pacific Warm Pool (WPWP) (where most skipjack spawning occurs) had increased in its suitability and productivity for skipjack spawning and early life stages. We then considered whether the MFCL recruitment trends and interannual dynamics were consistent with the other climate/oceanographic data sources. It was unfortunate that there were no fishery independent data sets on larval or juvenile skipjack abundance over time, or even periodic snap shots, that could provide indications of long-term abundance trends for early life stages. The climate/oceanographic data sets, while supportive of an increase in area of suitable skipjack spawning habitat with a similar long-term increasing trend to the MFCL recruitment estimates, did not show correlation with the interannual dynamics of skipjack recruitment predicted by MFCL. This may be due to the influence of the warm pool dynamics on the fishery dependent data that MFCL fits to being swamped by other fishery dependent processes or observation error. It may also be that skipjack recruitment and warm pool dynamics are not closely related, but we cannot adequately assess this relationship with the data available. The SEAPODYM model, which could be expected to provide a more reliable modelbased indicator of recruitment trends, did not predict a long-term trend in juvenile biomass consistent with the MFCL recruitment trend. However, it did predict a step change to a higher juvenile abundance regime in the early 2000s. We note that the new skipjack SEAPODYM estimates are preliminary. Overall, there are insufficient reliable data to either clearly refute or clearly support the long-term recruitment trend, therefore this trend should be treated as an uncertainty in the skipjack assessment. Modelling approaches should be explored that can moderate the recruitment trend as an alternative to the assumption that the trend is real. Options for such follow-up modelling experiments are recommended below.

Part 2 of the study explored the issue of effort creep in the JPPL fishery through two avenues. Firstly, a survey of Japanese Pole and Line Fishery skippers/crew targeting skipjack (JPPL) fishers was conducted to document the history of technology uptake and obtain their perspectives on the impacts of specific technologies on catches, and also the historic trend in skipjack abundance in their main fishing grounds adjacent to Japan. The survey results provided a qualitative industry perspective on effort creep and data on the timing and trajectory of technology uptake by the fleet. The survey indicated that most of the technological advancements were incorporated by the fleet occurred during the 1980-90s, and that high frequency sonar was considered a very important new technology for improving catches when schools were located. This technology is important once schools have been located to assess the school size and manoeuvre the vessel to intercept and stay with the school, rather than locate a productive fishing ground. Other technologies, notably the availability of satellite data on ocean currents and sea temperatures were important when leaving port for locating fishing grounds.

The second part of this component involved developing a Bayesian state-space model for effort creep (SSM-EC) that explicitly accounts for temporal changes in catchability. The model assumed changes in catchability due to technological innovations in equipment such as high frequency sonar and bird radar and assumed an S-shaped functional form of catchability increase centred around 1990. This was consistent with the pattern of technology uptake from the survey. The model estimated a probable change in catchability from 1972 to 2019 of 1.99 x, equating to approximately 1.5-2% per year catchability increase. The model also showed that assuming a long-term stable catchability scenario, when catchability increases had occurred, can lead to inflated biomass estimates.

Based on the outcomes of the two research components it is recommended that the uncertainty in the MFCL long-term recruitment trend be further explored by:

- 1. Conducting an MFCL modelling experiment using the 2022 diagnostic case that applies incremental (0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0 % per annum) catchability adjustment to the long-term JPPL CPUE time series. This experiment would seek to determine how much CPUE adjustment for catchability increase is required to moderate and/or remove any recruitment trends. The S-shaped scenarios and a linear increase scenario for catchability should be explored to understand sensitivity to the shape of the trend in catchability increase. Each model should be reported with standard model diagnostics to assess how each model preforms in convergence and fits to data.
- 2. From the modelling experiment, compare the results to the plausible levels of catchability creep suggested in the current study, and other literature (e.g. Hoyle, 2024), and provide options for effort creep scenarios to be considered in the 2025 skipjack assessment. These options should be presented and discussed at the 2025 SPC Pre-assessment workshop.

As the free school purse seine indices used in the recent assessment only begin in 2010 it is not expected that effort creep would have had a significant impact on the trend in these indices, however, it could be considered further in future. The above modelling studies should focus initially on the JPPL indices that are the indices available for the period of the MFCL recruitment trend.

We invite the SC20 to note:

- This work has been conducted under WCPFC project 115, but that further modelling work is now required to build on this project. This work would be built into the preparatory work for the 2025 skipjack assessment.
- The results do not provide irrefutable evidence for or against an increasing trend in skipjack recruitment from the 1970s to the early 2000s predicted by successive MFCL skipjack assessments.
- There is a strong need to conduct field studies and regular sampling to improve understanding of the early life history of skipjack tuna in the Western Pacific Warm Pool.
- That industry surveys of JPPL fishers provided information on technology uptake and clear perceptions that key technologies had improved their ability to catch skipjack.
- The increasing recruitment trend should be treated as an uncertainty in the skipjack assessment and alternative models developed that employ plausible effort creep levels to provide alternative recruitment trend scenarios.

Background

Skipjack tuna, *Katsuwonus pelamis*, are a highly abundant and productive epipelagic tuna in the world's tropical and subtropical oceans. They supports the largest commercial catch of all tuna species (approximately 2.8 million mt in 2020) and is a globally significant food resource, ranked third of all global marine fisheries over the last decade (FAO, 2022). By far the largest proportion (approximately 50%) of the global skipjack catch comes from the Western and Central Pacific Ocean (WCPO) (Hare *et al.*, 2023) (**Figure 1**), where commercial fisheries access arrangements support the economies of many Pacific Island countries. Skipjack are also important for domestic fisheries and food security in the region and in southeast Asian counties, including Indonesia, Vietnam and the Philippines, and have long been targeted by Japanese fleets throughout WCPO.

In the early years of the fishery, skipjack were primarily taken by pole and line vessels. Data from the pole and line fisheries provides the longest time series of fisheries data available for assessment of long-term trends (discussed further below in relation to this study). In recent decades, by far the largest catches of skipjack have been taken by purse seine vessels operating in the tropical equatorial region and employing emodernised vessels and sophisticated fishing technology; including, the widespread use of drifting Fish Aggregating Devices (dFADs) (Escalle *et al.*, 2021). dFADs are now almost universally fitted with satellite marker buoys that have sonar technology and the capability to transmit information on both the dFADs position and the size of the associated tuna aggregations. Purse seine fishing on dFADs, as opposed to fishing on free schooling (unassociated) fish, accounts for around half of the purse seine skipjack catches (Hare *et al.*, 2023). However, due to the fact that free school sets often fail due to failure to enclose the moving school, in the recent decade around half as many purse seine sets are required to take the dFAD catch (Hare *et al.*, 2023)

With the introduction of modern purse seine fishing in the 1990's, the annual WCPO skipjack catch has increased to ten times the levels recorded in the early 1960s and 70s when the fishery was primarily a pole and line fishery, peaking in 2019 at just over 2 million metric tonnes (Hare *et al.*, 2023) (**Figure 1**). Management arrangements, most notably the Parties to the Nauru Agreement (PNA) Vessel Days Scheme (VDS) (Parties to the Nauru Agreement, 2010) and high seas effort limits imposed through the Western and Central Pacific Fisheries Commission (WCPFC), have stabilised the WCPO purse seine catch and effort since the late 2000s, with total catches fluctuating between approximately 1.5-2 million metric tonnes (Hare *et al.*, 2023). The consistent high production of the WCPO skipjack fishery over more than a decade is perhaps remarkable and raises questions as to the possibility of hyperstability and or catchability increase due to the nature of the purse seine fishing method and use of modern technologies to locate and target schools, including the use of dFADs with satellite and sonar equipped buoys.

Stock assessments of WCPO skipjack using Multifan-CL (MFCL) (Fournier *et al.*, 1998) have occurred since 2005 (Castillo Jordan *et al.*, 2022; Hoyle *et al.*, 2010, 2011; Langley & Hampton, 2008; Langley *et al.*, 2005; McKechnie *et al.*, 2016; Rice *et al.*, 2014; Vincent *et al.*, 2019). Despite varying approaches, biological assumptions, data inputs and model structures, all have indicated that the skipjack stock in the WCPO is in a healthy state, not overfished or being overfished. A feature of the WCPO skipjack stock assessments, is the estimation of an increasing recruitment trend starting from the 1970s coincident with the increasing catches that have been driven by the expansion of the tropical purse seine fishery (Figure 2).

The 2019 assessment (Vincent *et al.*, 2019) noted the positive correlations of the estimated annual recruitments with the catches and the estimated juvenile fishing mortality. The 2022 assessment

(Castillo Jordan *et al.*, 2022) noted that "the spawning potential, as informed by a number of CPUE indices, has not changed substantially in the face of the notable increases in catches over the last 20–30 years, and that the increased catches have been sustained by increased recruitment levels. The interpretation of stock status based of the $(SB_{recent}/SB_{F=0})$ reference point should bear this in mind".



Figure 1 a) Skipjack tuna catches by gear type in the western and central Pacific Ocean, b) historical spatial distribution of skipjack catches by gear type.

The stability of the estimated biomass is informed by the stability of fishery dependent CPUE abundance indices, the most important being the long-term Japanese pole and line (JPPL) CPUE indices (Figure 3c). The pole and line CPUE indices show no obvious long-term trends, although the new 'free school' purse seine CPUE indices developed for the equatorial regions 6, 7 and 8, in the most recent assessment are showing recent declining trends consistent with the Philippines anchored FAD CPUE for region 5 (Figure 3d). Unfortunately, these later free school purse seine indices use effort based on VMS travel distance between sets and cannot currently be calculated prior to the VMS data becoming available in 2010. However, the increasing trend in recruitment does not continue beyond the early 2000s and the pole and line CPUE indices are the relevant indices over this increasing period.

It is suggested that the increasing recruitment estimated by the model from the 1970s to early 2000s is necessary to explain the increased catches and the observed stable trends in the CPUE abundance

indices, especially the historical pole and line indices. As noted in the 2019 assessment (Vincent *et al.*, 2019), comparisons of catch and recruitment from the 2022 MFCL assessment show similar long-term trends (although the recruitment is stabilising in the later years compared to the catch), and the residuals of the linear trends in catch and recruitment are moderately correlated (Figure 4). The stock status performance indicator is a dynamic depletion SB/SB_{F=0}, where SB represents the actual estimated spawning biomass and SB_{F=0} represents the estimated dynamic 'unfished' spawning biomass. To estimate SB_{F=0} at each model time step the model is fitted initially with the fishing mortality to estimate the recruitment dynamics and is then rerun without fishing, but with the recruitment that was estimated with fishing (adjusted for the stock recruitment relationship).

In the unusual case of skipjack, the increasing trend in recruitment predicted under the fished scenario results in an increasing trend in the estimated 'unfished' spawning biomass, which is the main driver of the decreased stock status over time (i.e. $SB_{F=0}$ increases rather than SB decreasing) (**Figure 3b**). It could be hypothesised that the increased recruitment trend is due to recruitment compensation (density dependence) as the population size has decreased due to sustained increased fishing (e.g., decreased standing stock). If so, we might expect to see a decrease in the fishery CPUE if it is a reliable abundance indicator. However, this is not obvious in the long-term standardised JPPL CPUE data (Figure 3c). Further, for compensation to be occurring would imply a Ricker type stock recruitment relationship with a notable recruitment reduction/increase at higher/intermediate stock size. Although this is inconsistent with the stock-recruitment estimates of multiple previous skipjack stock assessments that estimate higher recruitment and higher spawning stock size post 2000 compared to pre-2000. If this is the reality it would suggest a regime shift in the productivity of the skipjack stock over the last 20 years.

Interpreting the CPUE trends is however complicated by the potential that catchability has increased over time and has mitigated the impact of a "true' declining abundance on the CPUE trend, and that factors influencing changes in catchability (i.e., 'effort or technology creep' due to improved fishing methods, technology uptake etc.) are not being effectively removed in the CPUE standardisations. Further, the CPUE indices from the pole and line fishery may be inherently hyperstable due to the fishing method of searching for schools, and the redistribution of effort to the best fish grounds and seasons over time. The pole and line indices may also be unreliable indices of abundance of skipjack in the equatorial regions where the majority of the biomass occurs. Hence, understanding fleet dynamics, uptake of new technologies and methods and potential implications for catchability trends is essential to understanding whether; stock abundance has declined and density dependent recruitment compensation has supported the consistent high catches for the last 20 years, or alternatively the equatorial Pacific as moved to higher productivity regime for skipjack.

While the increasing recruitment trend has been hypothesised to be a model artifact influenced by the stable pole and line CPUE abundance indices, an alternative hypothesis is that increases in the quality and area of spawning and larval rearing habitat in the western tropical Pacific have occurred over the past several decades, possibly resulting in an increased/increasing recruitment regime. As skipjack are caught at relatively young ages the overall population 'standing' biomass (and CPUE) has not increased substantially as the purse seine fishery has effectively "mopped" up this increased productivity. It is important to understand the plausibility of this hypotheses, as the current levels of catch and associated biomass stability would be contingent on the continuity of an increased productivity regime.

The 2022 skipjack stock assessment identified the need to conduct further research to:

1. Continue work on abundance indices to explore effort metrics related to travel distance for both the purse seine and pole-and-line fisheries, along with exploration of hyperstability and effort creep, focussing on developing effort creep scenarios for the Japanese pole and line fishery.

2. Conduct a study to explore the plausibility and evidence for the model predicted long-term increasing trend in skipjack recruitment.

This paper focusses on:

Part 1) Exploring the evidence/plausibility for the MFCL predicted increased recruitment of skipjack tuna in the WCPO, and;

Part 2) Exploring the evidence/plausibility for catchability increases in the Japanese pole and line fishery resulting from advancements in fishing technologies and operations, and the temporal dynamics and possible level of catchability change.

The outcomes of the paper will inform the next skipjack stock assessment in addressing the historical recruitment trends predicted by the past assessments.

We note that further work will be required leading up to the next assessment to consider aspects still not covered in this paper, including: a) options for alternative effort metrics for pole and line CPUE indices. While discussions with Japanese collaborators on this topic have occurred, options are limited and the limited staff resources have prevented dedicated work on this topic; b) exploring modelling scenarios with catchability trends, this will follow the current paper and be discussed at the 2025 Pre-assessment workshop.



Figure 2 Total annual skipjack recruitment estimated by previous MFCL skipjack stock assessments, a) all model regions, b) model regions in the tropical/equatorial area. Dotted lines are fitter linear trends. Recruitment is estimated at age 1 quarter (approx. 20-30 cm). 2014 assessment (Rice et al., 2014), 2016 assessment (McKechnie et al., 2016), 2019 assessment (Vincent et al., 2019), 2022 assessment (Castillo Jordan et al., 2022).



Figure 3 a) WCPO skipjack stock assessment model regions, b) trajectories of estimated spawning potential (SB) and the spawning potential in the absence of fishing (SBFO) from the 2022 assessment diagnostic model, c) standardised CPUE indices (quarterly) for the Japanese pole and line fishery, and d) the purse seine fisheries (quarterly) (R5, is Philippines anchored FADs in high seas pocket 1, R6, 7, 8 are industrial purse seine free school sets, (Teears et al., 2022a), TMA – is moving average to display trends).



Figure 4 Comparisons of a) normalised skipjack catches and recruitment from the 2022 MFCL assessment, and b) residuals from the linear models fitted through the catch and recruitment data in a), and c) recruitment residual and the mean annual standardised JPPL CPUE index averaged across model regions 1, 2, 3, 4, and 7. Data are from 1972-2020, the 2021 recruitment data is excluded due to low confidence in final model year recruitment estimates.

Part 1) Exploring evidence of increased recruitment of skipjack tuna in the WCPO

Methods

To approach the question of recruitment trends it is important to understand the early history as a basis for focusing the exploration of potential indicators/proxies of recruitment trends and increased productivity regimes. There are no time series of skipjack larval abundance or fishery independent data on juvenile abundance. This lack of empirical field-based evidence for recruitment trends means that the plausibility of increased skipjack recruitment rests on the use of indirect information such as environmental/climatic/oceanographic observations or model predictions that are consistent with increased planktonic productivity that could support enhanced larval/juvenile survival. The reality is that there will always be doubt in the use of such proxies for recruitment trends when there is no actual independent time series of larval/juvenile abundance against which to validate the model/oceanographic data predictions.

The approach to this exploration was broken down in several components:

- Early life history review: recruitment estimated by the MFCL stock assessment is at age 1 quarter (20-30 cm FL). Thus, we conducted a review on the early life-history of skipjack, separated into several early-life stages: 1. spawning and eggs, 2. larval (hatching - 10 mm/metamorphosis), 3. small juveniles (1-20 cm). The aim of the review was to summarize knowledge on spatialtemporal patterns and factors that could influence enhanced survival, such as growth and feeding.
- 2. Skipjack recruitment process: the second component of the investigation used the information from the early life history review to develop a conceptual description of the skipjack recruitment processes, focussed on the larval and early juvenile stages. This conceptual description would then be used to identify potential ecological factors and environmental/oceanographic variables that could be influential on recruitment success of skipjack tuna, independent of spawning biomass.
- **3. Trends in climate-ocean data:** the third component of the work involved collating time series of climate and oceanographic variables that are identified as potentially influential/indicative of enhance planktonic production and/or skipjack recruitment rates in the WCPO.
- 4. Relationships between climate-ocean data and skipjack recruitment dynamics estimated from the MFCL stock assessment model Finally, we explore relationships between oceanographic/environmental variables and the estimates of skipjack recruitment from the 2022 MFCL stock assessment.

Results

1. Early life history review

Information on the spatio-temporal dynamics of skipjack spawning shows that spawning is mostly observed where water temperatures are >24°C, with spawning observed all year in the tropical equatorial waters, and seasonal spawning in the sub-tropical waters further to the north and south in warmer months (Ashida & Horie, 2015; Ashida *et al.*, 2017; Hunter *et al.*, 1986; Ijima & Jusup, 2023; Nishikawa *et al.*, 1985; Reglero *et al.*, 2014; Schaefer, 2001). While spawning capable skipjack have been observed north of 35°N (Ashida, 2020), the northern limit of the distribution of skipjack larvae was considered to be about 35°N by earlier studies (Nishikawa *et al.*, 1985). Furthermore, fecundity and spawning fraction is thought to decline with higher latitudes, either related to lower temperature and or food availability (Ashida, 2020).

The studies to date indicate that the bulk of the skipjack reproductive output in terms of egg and larval production in the WCPO is in the warmer tropical waters between approximately 20°N - 15°S latitude to about 150°W in longitude. This area is characterised by the western Pacific warm pool (hereafter; WPWP), a large area of warm, lower salinity, surface waters that varies in its spatial and vertical characteristics on seasonal, interannual and decadal time scales (De Deckker, 2016; Forget & Ferreira, 2019; Kidwell *et al.*, 2017; Yan *et al.*, 1992). The WPWP is a large region of the western Pacific, typically greater than >30 × 10⁶ km², where the surface temperature is consistently above 28°C (De Deckker, 2016) and is where most of the skipjack catch is taken by the purse seine fishery in the WCPO.

While skipjack spawning occurs predominantly in temperatures >24°C, recent laboratory studies on rates of development, survival and abnormal hatching of the buoyant eggs indicate that an optimal surface temperature is between about 25 and 31°C, with survival dropping rapidly above 31°C. The duration for hatching was however notably shorter at warmer temperatures (i.e. > 28°C) indicating that overall survival of eggs might be expected to be higher in the wild at temperatures from 28-30°C (Fujioka *et al.*, 2024).

The skipjack SEAPODYM model estimates spawning habitat for skipjack based on various environmental features that consider both the distribution of mature adults and the early life stages, including temperature, dissolved oxygen and primary production (Senina *et al.*, 2016). Recent development work to enhance the SEAPODYM model estimation of optimal spawning and larval habitats has included the historical data sets of larval abundance. While this work has initially focussed on yellowfin and albacore, the preliminary work on skipjack supports the optimal temperature of 28-30°C for spawning (below, Inna Senina, SPC, pers. comm).

The skipjack larval period is a critical stage for determining cohort strength. Skipjack, larvae (3 – 10 mm) are commonly found in the epipelagic zone from near the surface to around 60 m depth, and smaller juveniles from 10-200 mm length may be found down to 200 m (Boehlert & Mundy, 1994; Llopiz *et al.*, 2010; Llopiz & Hobday, 2015; Strasburg, 1960; Tanabe *et al.*, 2017). However, the depth range over which juveniles may occur is suggested to vary depending on water temperature, with a range of occurrence from 20-30°C, and they may be more abundant below 20 m depth compared to closer to the surface (Tanabe *et al.*, 2017). There is no strong evidence for diel vertical migration in either larvae or juveniles (Boehlert & Mundy, 1994; Tanabe *et al.*, 2017). For yellowfin tuna laboratory experiments identified an optimal range of 26–31 °C for rapid growth and moderate to high survival in first feeding larvae (Wexler *et al.*, 2011). This study also indicated total mortality of yellowfin larvae where dissolved oxygen concentrations were < 2.2 mg O₂ L⁻¹ (34% saturation). Similar information is lacking for skipjack, but the observations for yellowfin are thought to be indicative for skipjack.

Feeding behaviour of larval skipjack has received surprisingly little study, with no studies in the WCPO region, and in particular, the key WPWP area. Studies in the eastern Indian Ocean showed that skipjack larvae (from 3.5-10 mm SL) fed mainly on appendicularians (larvaceans or 'pelagic tunicates') and to a lesser degree on fish larvae, along with calanoid copepods and their nauplii stages (Davis & Young, 1990). Skipjack larval diets composed of appendicularians and cladocerans were also observed in earlier studies off northeast Australia (Uotani *et al.*, 1981). A more recent study in the Gulf of Mexico further indicated the high importance of appendicularians, along with fish larvae (Llopiz *et al.*, 2010). Skipjack larvae feed predominantly in daylight hours (Davis & Young, 1990).

Appendicularians are clearly an important prey item for skipjack larvae throughout larval development and are amongst the most abundant components in marine mesozooplankton (Purcell

et al., 2005). Unlike other gelatinous zooplankton the calorific content and percentages of nitrogen and carbon in appendicularians is similar to copepods, and their lack of exoskeleton and slow swimming speed may make them easier to catch and ingest by skipjack larvae (see Purcell et al. 2005 and refs therein).



From Ijima and Jusup 2023, https://arxiv.org/abs/2304.09442

Figure 5 a) Indicative global map of sea surface temperatures indicating the region of the Western Pacific Warm Pool, b) quarterly larval skipjack distributions based on modelling of historical skipjack larval sampling data sets, adapted from (Ijima & Jusup, 2023).

Appendicularians are also highly productive, with faster generation times than copepods and have been reported to show biomass increases of 1000% day⁻¹ in tropical waters (Hopcroft & Roff, 1995). Further, appendicularians are efficient consumers of small nano- and picoplankton size particles as well as colloidal organic matter and can respond rapidly to increases in primary production. The high dependence of skipjack larvae on appendicularians, compared to other tuna larvae (Davis & Young, 1990), is likely a critical factor in their high productivity, and continual spawning in the tropical Pacific.

Larval tunas generally have fast growth rates and selective feeding habits, adapted for survival in warm, oligotrophic seas (Davis & Young, 1990). Fast growth and accelerated ontogeny during the larval stages requires high energy intake and utilisation, and the impacts of starvation and low growth rate are considered critical to reduced survival rates in the larval and early juveniles stages of tunas and other pelagic species (Anderson, 1988; Aoki *et al.*, 2020; Jenkins *et al.*, 1991; Llopiz &

Hobday, 2015; Reglero *et al.*, 2011; Satoh *et al.*, 2013; Takasuka *et al.*, 2003). Food availability and temperature are considered the two main external influences on individual larval growth for tunas. In bluefin tuna, studies have shown that both increased temperature and food density can positively influence larval growth rate (Jenkins *et al.*, 1991; Satoh *et al.*, 2013). Higher growth rates are hypothesised to generally lead to higher individual survival due to shorter duration at more vulnerable smaller sizes and faster progression to ontogenetic stages/sizes that are less vulnerable to starvation and predation (i.e. growth-mortality hypotheses). There are various other theories on drivers of enhanced larval survival, including the 'critical period', wherebye, feeding success of first feeding larvae, that are highly vulnerable to starvation mortality, is critical to survival and cohort strength (Anderson, 1988). Ultimately multiple process will be at play, but food availability and predation are important factors for all of them.

Surprisingly, there are few studies describing the early life-development of skipjack in the wild. Laboratory rearing studies show that skipjack eggs hatch after around 15-35 hrs depending on temperature (Fujioka *et al.*, 2024), the yolk sac is absorbed by around 40-50 hrs post hatch, first feeding is at about 3.5-4 mm SL and around 3-4 days post hatch (Ueyanagi, 1973; Ueyanagi *et al.*, 1974). It has been difficult to rear skipjack larvae beyond about 4 mm SL and 5 days post-hatch, with mass mortality of larvae due to failure to feed, indicating that starvation in the wild will likely kill skipjack larvae within 5 days post hatching. Based on development of yellowfin tuna, flexion is likely at 4.5-6 mm and around 10 days post hatch, and post-flexion is 6-12 mm and 10-15 days post hatch (Ueyanagi, 1973; Ueyanagi *et al.*, 1974).

Skipjack larval growth accelerates after flexion, when other fish larvae become important in the diet (Aoki *et al.*, 2020; Ashida *et al.*, 2018; Tanabe *et al.*, 2017). The appearance of this rapid growth period in the early life history of scombroid fishes is common and corresponds to the timing of digestive system development and switch to piscivory (Tanaka *et al.*, 1996). Tanabe *et al.*, (2017) noted for small juveniles the percentage of stomachs containing food was 73.3% for skipjack tuna and 70.0% for other tunas. They also observed the main prey taxa found in the stomachs of skipjack tuna juveniles were fish larvae, Euphausiacea, Copepoda, Amphipoda, and Cephalopoda, and the dominance of fish larvae in the stomach contents was remarkable.

Cannibalism has been suggested to be important in tuna species, and is likely important in skipjack, along with predation by larvae and juveniles of other co-occurring tuna species (Reglero et al., 2011; Uriarte et al., 2019). Reglero et al., (2014) in a study of larval feeding and energetics for several tuna species, indicated that feeding on zooplankton alone may be insufficient to sustain individual growth, particularly at densities of zooplankton found in oligotrophic waters. They suggest that early piscivory is a necessary adaptation for tuna larvae to obtain the required energy for their fast growth. Furthermore, cannibalism by larger individuals from earlier spawning cohorts or faster growing individuals from spawning at similar times could play a role in regulation of skipjack larval survival rates and recruitment. This introduces a cannibalism related density dependent compensation influence on skipjack larval cohort strength. However, it would be expected the level of cohort regulation/recruitment compensation due to larval/juvenile cannibalism will still depend to an extent on the availability of other food sources, including both zooplankton and other species of fish larvae. In situations of higher food availability overall cohort feeding success, including first feeding, and overall survival should still increase, as per-capita probability of death by cannibalism and starvation should be reduced for any particular larval density. Thus, in a regime change (productivity increase) situation, irrespective of cannibalism, larval abundance would be predicted to increase. Alternatively, in situations where other food sources are low or become depleted as a cohort develops the occurrence of cannibalism may support enhanced survival of the faster growing individuals. This along with the continuous spawning of skipjack in the topical waters may provide a conspecific food source to moderate or 'buffer' against the implications of variable zooplankton prey abundance on

larval survival, and moderate juvenile recruitment variation.

2. Skipjack recruitment process

Based on the review of early life history (above, and summarised in Table 1), a conceptual diagram of skipjack tuna early life history survival/juvenile recruitment in the WPWP is proposed (Figure 6). This provides the basis for hypotheses of climate/environmental or oceanographic drivers of long-term trends and interannual variations in productivity of the WPWP that could be driving recruitment trends and dynamics. Such hypothesis can then be explored further through analysis of specific climate and or oceanographic time series (Table 1).

 Table 1
 Skipjack tuna early life history summary information.

Stage	Region	Timing	Environmental features	Prey	Predators	Other
Spawning/eggs	Main spawning	All year in tropical	Water temperature	NA	Zooplankton, other fish	Skipjack eggs are
	region is equatorial	equatorial region,	>24°C, optimal range for		larvae and small pelagic	buoyant,
	20°N-15°S	season in the	higher successful hatch		fishes.	approximately 1
	throughout WCPO,	warmer months	and shorter hatch time			mm in diameter,
	highest spawning	when temperature	28-30°C. Other factors			hatching after 10-
	region between 10°N	increases to >24°C	include feeding			30 hrs, faster
	-10°S, spawning also	to north and south	conditions and			hatch times in
	occurs in the South	of the equatorial	dissolved oxygen levels			warmer water.
	China Sea, and	band. Batch	(>2.5 mL.L ⁻¹) for adults,			
	Indonesian -	spawners,	which influence suitable			
	Philippines region.	frequency every 1-2	adult habitat, and egg			
		days.	production/quality.			
Larvae	Widely distributed	All year in the	Optimal temps ~25-	Small yolk sac,	Other	Hatched larvae
	throughout the	equatorial region,	30°C	rapid transition to	tuna/scombrid/istiophorid	2.5-3 mm,
	equatorial Pacific,	warmer months to	Yellowfin tuna larvae	first feeding on	larvae and juveniles.	metamorphosis
	distribution expands	north and south.	hatchlings have high	copepod nauplii,		to juvenile occurs
	to northern latitudes		mortality at < 21 °C and	and		at about 12 mm
	during boreal warm		> 33 °C, and dissolved	appendicularians.		SL and 10-15
	months and		oxygen concentrations	Larger copepods		days age. Tuna
	southward shift		of < 2.2 mg $O_2 L^{-1}$, likely	stages, then mixed		larvae are
	during austral warm		that skipjack larvae	prey, with		suggested to be
	months.		have similar tolerances.	transition to high		highly vulnerable
				levels of piscivory		to starvation, and
				(feeding on other		have a high
				fish larvae) from		metabolic
				about 5 mm length.		demand to
				Cannibalism likely		support fast
				to be high.		growth.

Small juveniles 2-20	Wide distribution –	All year in warmer	Expect similar tolerance	Largely piscivores	Other tuna would be the	No swim bladder
cm	consistent with larval	equatorial waters.	to larvae, but able to	feeding on fish	dominant predators.	by around 2 cm,
	stages.		have more control on	larvae but also		effectively
			water column positions,	euphausiids, more		swimming.
			have been sampled	diverse diet that		
			from near the surface to	other small tropical		
			200 m.	tunas.		



Figure 6 Simple conceptual description of skipjack recruitment process and potential environmental indicators.

3. Exploring trends in climate/ocean data

Area of the Western Pacific Warm Pool (WPWP)

The WPWP shows considerable temporal variability in the spatial extent of its warm surface waters, thought to be influenced by both long-term (decadal) and short-term (interannual) climate phenomena, including the Pacific Decadal Oscillation and the ENSO. However, global warming is thought be influencing a gradual sustained increase in the area of the WPWP (Roxy *et al.*, 2019). Roxy *et al.*, (2019) indicated that the "warm pool has been expanding on average by 2.3×10^5 km² (*the size of Washington State*) per year during 1900–2018 and at an accelerated average rate of 4×10^5 km² (*the size of California*) per year during 1981–2018". The Hadley Centre sea ice and sea surface temperature (SST) data set version 1 (HadISST1) (Rayner et al., 2003) provides estimates of the long-term variability in the WPWP area. Figure 7 shows the variability and long-term trends in the WPWP, based on the area of surface water temperatures $\geq 29^{\circ}$ C (WP29) in the region; longitude 125°E - 90°W and latitude 45°N - 40°S.



Figure 7 Temporal dynamics of the Western Pacific Warm Pool (WPWP) area based on the area with SST \ge 29°C (WP29), a) quarterly mean ± SD, b) annual average. (Data is form HadISST monthly data file from <u>http://www.metoffice.gov.uk/hadobs/hadisst</u>; (Rayner et al., 2003)). Linear trend in b) y=220,184x + 1E+07, r²=0.645.

The striking feature of the WPWP time series is the increasing trend since the early 1970s (approximate doubling in the area of surface water $\geq 29^{\circ}$ C). Roxy et al. (2019) show a similar

doubling in the WPWP area for SST >28°C. The increasing trend and decadal dynamics in the area of the WPWP are thought to be driven by anthropogenic forcings (greenhouse gas driven global warming), and linked to the Pacific Decadal Oscillation (Weller *et al.*, 2016), while shorter term spatial dynamics in warm pool surface area and depth is interrelated with ENSO (Kidwell *et al.*, 2017).

The increase in the size of the WPWP has provided a greater viable thermal habitat area for skipjack spawning, which could have contributed to an increase in stock productivity (regime change) that is offsetting the impacts of the increased fishing effort and catches since the early 1970s. However, there is no fishery independent information to test this hypothesis. Analysis of the relationship between the WPWP trend and variability with the recruitment estimates from the MFCL skipjack stock assessment are presented below.

Tropical Pacific Primary and Secondary Production

While the expansion of the WPWP has increased the area of optimal thermal habitat for skipjack, increased production of recruits would also require suitable productivity of planktonic food for skipjack larvae under the expanded WPWP. The benefits of an expanded thermal habitat for skipjack recruitment could be offset by a reduced planktonic productivity (phytoplankton and zooplankton), and therefore have limited overall impact on increased skipjack productivity. There are no historic time series that can provide a reliable indication of the trends in primary/secondary production in the WPWP, and in general there is a lack of information on the zooplankton dynamics of the WPWP (Long *et al.*, 2021).

The equatorial Pacific has two distinct regions, the WPWP region and the central and eastern Pacific, that are separated by a distinct salinity frontal zone (Picault *et al.*, 1996). The frontal zone, and the region of warmer, lower salinity surface water that characterise the WPWP, moves to the east and west at interannual time scales in phase with the El Niño/Southern Oscillation (ENSO) (i.e. WPWP expansion in El Niño/contraction to west in La Niña). The Interdecadal Pacific Oscillation (IPO) (closely related to the Pacific Decadal Oscillation (PDO)(Mantua *et al.*, 1997)) (Henley *et al.*, 2015; Power *et al.*, 1999) also influences longer term trends in the physical and chemical characteristics of these regions and interacts with the ENSO related dynamics (Hasegawa & Hanawa, 2003; Zhang & McPhaden, 2006).

Under normal/ENSO neutral conditions, the WPWP skipjack spawning region, has a deeper thermocline and nitricline, with very low nutrient (oligotrophic) concentrations in the surface mixed layer. In contrast, the central/eastern equatorial Pacific region has a shallower thermocline, and higher macronutrient concentration in the surface waters (Wang *et al.*, 2010). However, primary production in the eastern and central region can be limited by low Fe and Si concentrations and it is often referred to as a High-Nutrient-Low-Chlorophyll (HNLC) region (Barber & Chavez, 1991; Wang *et al.*, 2010).

In relation to skipjack recruitment trends, the dynamics and trends of primary and secondary production in the WPWP are of most interest. Primary production in the WPWP is thought to be higher when El Niño conditions occur (Turk & Lewis, 2001). This occurs due to the eastward expansion and shoaling (shallowing) of the warm pool which results in a shallower nitracline, thinner barrier layer and subsequent increased nutrient supply to the well lit surface layer, which may also be enhanced by the increased strength of westerly wind inducing turbulent upwelling (Turk *et al.*, 2001; Turk & Lewis, 2001). In contrast productivity in the central and eastern Pacific is known to decline under El Niño conditions due the deepening of the thermocline and suppression of upwelling (Park *et al.*, 2011). Thus, the El Niño/Southern Oscillation (ENSO) is hypothesised to provide a proxy

indicator of short-term dynamics in skipjack recruitment dynamics, with higher recruitment predicted during stronger El Niño phases.

Longer-term trends in primary production of the WPWP are however difficult to assess from satellite remote sensing/ocean colour data because the Chla maximum generally occurs at depth (50-100 m) (Turk & Lewis, 2001). Recent studies have suggested an increasing trend in primary production at basin scale for data from 1997-2010 globally, and that the percent of large phytoplankton has increased (Sharma *et al.*, 2019). They link the increasing phytoplankton biomass trends to increased winds and relevant mixing length scale. These trends are consistent with another recent study showing significant positive trends in phytoplankton populations attributed to climate warming for 56% of the global surface ocean, mainly in regions around the equator to 40° of latitude (Cael *et al.*, 2023). Based on these studies it has been suggested that the tropical oceans have become warmer and possibly "greener" in the past 20 years. However, while these studies suggest a general increase in planktonic productivity over the time scale of the MFCL skipjack recruitment trend, these observations are too broad in scale and the time series are insufficient to relate directly to the skipjack recruitment trends.

The oceanographic station ALOHA in the North Pacific oligotrophic subtropical gyre (22°45′N, 158°W), north of Hawaii, provides the longest time series of in situ ocean physical and biogeochemical observations in the tropical Pacific. Data from this station can be accessed at <u>https://hahana.soest.hawaii.edu/hot/hot-dogs/</u>. Figure 8 a and b show the long-term dynamics and trends of the Chla and the integrated primary production, respectively for this station from 1991-2021. Both time series show increasing trends, consistent with the above cited global and basin scale studies. Mesozooplankton data (0.2-5 mm) is also available from the ALOHA station and shows an increase from 1994 to 2001 but a stable trend after that, with an overall low long-term increasing trend (Figure 9).



Figure 8 a) Annual mean Chla measured by HPLC for the ALOHA station, b) annual mean depth (0-200 m) integrated primary production at the ALOHA station (error bars are SD of quarterly measurements, R² is linear correlation with year).



Figure 9 Mean annual (error bars are SD of monthly measurements) zooplankton dry weight integrated over vertical net hauls 0-200 m at the ALOHA station. R² is linear correlation with year.

While the ALOHA station data lends support to the published studies suggesting a 'greening' trend for the tropical Pacific, the location of this station is very remote from the skipjack spawning region, and it is not appropriate to directly relate this data to the MFCL skipjack recruitment data or consider it a potential indicator for increased larval survival in the WPWP. It is provided in this paper as the closest long-term data set on primary and secondary production in the Pacific.

ENSO

The key climate/oceanographic feature of the tropical Pacific is the El Niño/Southern Oscillation (ENSO). As discussed previously El Niño conditions are predicted to be indicative of increased primary productivity in the WPWP and diminished productivity in the central and eastern Pacific (Gierach *et al.*, 2012). The ENSO dynamics would be expected to have some influence on skipjack recruitment dynamics. There are various indices that can indicate ENSO dynamics. The Oceanic Niño Index (ONI) is perhaps the most relevant in this case because it is a measure of ocean temperature conditions in the equatorial band (SST anomalies in the Niño 3.4 region (5°N-5°S, 120°-170°W)). Figure 10 shows the ONI index from 1970 to 2023, there are 8 relatively strong El Niño and about 8 relatively strong La Niña periods since 1970. There is no obvious increasing predominance of strong El Niño events since the 1970s.



Figure 10 The Oceanic Niño Index (quarterly averages) for the time period 1970-2023. Data from: https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php

SEAPODYM

SEAPODYM is another modelling framework that can provide predictions of spatial and temporal recruitment dynamics of skipjack in the WCPO (Lehodey *et al.*, 2008, 2013; Lehodey & Senina, 2009; Senina *et al.*, 2020, 2016). While the model does incorporate some of the same fisheries data as the MFCL assessments, it has fundamental differences in the modelling in that it includes, i) environmental forcing such as temperature, currents, euphotic depth, primary production and dissolved oxygen concentration, ii) prediction of the temporal and spatial distributions of functional groups of prey, iii) prediction of the spatial dynamics of the age-structured skipjack (predator) population, iv) prediction of the total catch and the size-frequency of catch by fleet, and v) parameter optimization based on fishing data assimilation techniques. SEAPODYM's estimates of abundances of different life stages in space and time are strongly influenced by the dynamics of the environmental forcing can be argued to provide a more informed modelling approach for estimating skipjack recruitment trends.

The skipjack SEAPODYM model is currently undergoing enhancements to improve the environmental forcings, as those previously used (Senina et al., 2020) were computed from the NEMO model with ERA-INTERIM atmosphere, which appears to have some bias in its SST. The new model will include the HadlSST – observations (ERA5 and JRA55). In SEAPODYM, the function minimizer can estimate a persistent recruitment trend due to environment only if there is a signal in the model forcing information. The most recent published skipjack SEAPODYM study (Senina et al., 2020), did not indicate an increasing trend in recruitment across the entire Pacific domain of the model (estimates were not provided for just the WCPO/WPWP region), however, as mentioned that model has concerns around the bias of forcings from the NEMO model, particularly in relation to SST and the expansion of the WPWP (the model does not show the WPWP expansion to the extent of the observations) (Inna Senina, pers. comm). The supplementary material for Senina et al., (2020) includes information on catchability estimates for fisheries where catchability was allowed to vary linearly with time to account for the change in the gear/strategy efficiency and/or model biases. With the above caveat regarding the potential bias in the SST forcing, in seven of eight fisheries/time periods with time varying catchability, catchability increases were estimated (see Senina et al. 2020 supplementary materials).

Preliminary results for the updated SEAPODYM model with the JRA55 forcings suggest an increasing trend in skipjack spawning habitat since the mid-1980s, but a decreasing trend from the 1960s to the mid-1980s (Figure 11Figure 11a). Note that spawning habitat in SEAPODYM is defined by the ensemble of environmental conditions, that are favourable for spawning and optimal for larvae survival; including, sea surface temperature, primary production as a proxy for prey of larvae (it can also be zooplankton density, if available), and surface micronekton as predators of larvae. The recent results also suggest increased area of feeding habitat (driven by suitable temperature, dissolved oxygen and micronekton) for juveniles (skipjack prior to fishery recruitment) since the 1990s (Figure 11b), and a step up in biomass of juveniles from the late 1990s, although the estimates for very recent years are similar to estimates for the 1990s (Figure 11c). The juvenile biomass trend tends to follow the primary production (Figure 11c).

While the updated skipjack SEAPODYM model is a work in progress and the results presented should be treated as preliminary, it does not predict the long-term increasing trend in recruitment from the 1970s to the early 2000s that is estimated by the MFCL models, although it does suggest a shift to a high recruitment regime during the 2000s and an increase in juvenile habitat from the early 1990s. While difference between estimates from SEAPDOYM and MFCL are partly related to the modelling

approaches, SEAPODYM's use of environmental forcing, would suggest the potential trends in skipjack habitat area and quality have led to moderate increased recruitment since 2000, but not to the extent suggest by the MFCL models which do not have any environmental data to inform recruitment estimates.



Figure 11 Times series of estimated, a) area of skipjack spawning habitat, b) area of juvenile feeding habitat (prior to fishery recruitment, <11 months age), c) juvenile skipjack biomass (SKJ) and primary production (PP), from preliminary runs of the skipjack SEAPODYM with the updated JRA55 forcings. Dark lines are annual the averages.

4. Relationships between recruitment predictions from MFCL stock assessment models and WPWP and ONI time series

MFCL skipjack recruitment and the area of the WPWP (WP29)

For these analyses we explored the relationship between the WP29 time series and the MFCL recruitment time series. Initially we compared the recruitment time series across the last four WCPFC skipjack stock assessments to confirm the recruitment patterns and trends are consistent across the assessments, and not just peculiar to the 2022 assessment (Castillo Jordan *et al.*, 2022). Figure 2 shows the comparison of total annual recruitment predictions for the 2014, 2016, 2019 and 2022 assessment diagnostic models, for both the entire model area a) and the equatorial model regions b). The general patterns of recruitment variation are consistent among the assessments despite the many changes that have occurred in conducting each of these assessments, although the absolute magnitudes are higher, and the increasing recruitment trend is steeper for the 2014 and 2016 assessments compared to 2019 and 2022. The recruitment dynamics are, as expected, very similar between the combined all model regions and the equatorial model regions. However, as

the estimated distribution of recruitment across model regions by MFCL can use a combination of movement and regional recruitment to distribute fish, the region-specific recruitment estimates should be interpreted with some caution. For the subsequent analysis we have therefore used the 'all model' regions and the 2022 assessment recruitment data with the longest time series. Furthermore, the last year of recruitment estimates is highly uncertain and/or are typically set to the average recruitment in MFCL, so the last year of the recruitment data is excluded.

For the comparison of the 2022 MFCL assessment recruitment and the WP29 data, we considered the annual and longer-term relationships. If recruitment and the WP29 are showing a similar long-term trend, and there is a causal relationship between the WP29 and MFCL recruitment, we might predict that there will also be a relationship for the annual dynamics. Although quarterly recruitment estimates and quarterly WP29 data are available, data at this resolution can have substantial noise/error, so we have focussed on the annual dynamics. For the WP29 data we have used the annual average area, and for the recruitment, the total annual recruitment summed across model regions (Figure 12). The data are different scales and metrics and to directly compare the dynamics the data were normalised (min-max=0-1) before analysis.



Figure 12 Comparison of the time series of annual average WP29 area and total skipjack recruitment estimated from the 2022 assessment diagnostic model.



Figure 13 Normalised data linear model trends with time with residuals for the WP29 annual average and estimated total annual recruitment from the 2022 assessment diagnostic model (1972-2020). Linear model equations in figure 12.



Figure 14 Comparison of the of time series of residuals from the linear models of WP29 annual average and total annual recruitment from the 2022 assessment diagnostic model. (**1972-2020**: R = 0.049, 95% CI -0.235 to 0.326, P= 0.738. **1972-2002**: R=0.291, 95% CI -0.070 to 0.585, P=0.111).

ENSO

The ONI was used as the ENSO indicator for comparison with the MFCL 2022 recruitment estimates. We again used annual data as there is correlation between quarters in both ONI and recruitment data. The annual average ONI index was compared to the annual recruitment residuals from the linear model with year (Figure 15b). We also compared the ONI and the annual WP29 residuals from the linear model with year (Figure 15a). The ONI is highly correlated with the WP29, which is consistent with the expected expansion of the WPWP under El Niño conditions. It was therefore as expected that the MFCL recruitment residuals from the linear model with time were not correlated with the ONI.



Figure 15 a) Comparison (1972-2021) of the annual average ONI (Oceanic Nino Index) with WP29 residuals for the average annual data linear model with year (R=0.605, 0.393 to 0.756, P< 0.001), and b) comparison (1972-2020) annual average ONI (Oceanic Nino Index) compared to the MFCL recruitment residuals for the average annual data linear model with year (R=0.093, 95% CI -0.194 to 0.364, P= 0.527).

Summary and Conclusions

It is difficult to confirm or reject the possibility of a long-term increasing trend in skipjack recruitment in the Western and Central Pacific Ocean from the data available. While there is evidence of increased spawning area and possibly juvenile habitat, there are no fishery independent data to provide reliable time series, or even periodic snap shots of larval or juvenile abundance in the WPWP. Based on the available information it is possible to construct plausible hypotheses for increased recruitment. However, while the long-term increasing recruitment trend predicted by MFCL was consistent with the trend in the long-term expansion of the WPWP, the annual variability of the MFCL recruitment estimates was not correlated with WPWP (or the ONI) (Figure 14, Figure 15). If the warm pool size is a key driver of skipjack recruitment variation, we might expect that both the long-term trend in MFCL recruitment and the interannual variability would correlate with the warm pool size. This is not the case, but this might be due the MFCL model estimates of recruitment not adequately representing 'true' recruitment dynamics.

On the other hand while the long-term trend in MFCL recruitment was not as closely matched with the catch trend as it was with the WPWP trend (Figure 4, Figure 14), the annual recruitment dynamics were correlated, to the annual catch dynamics one year later, and similarly to the JPPL CPUE (Figure 4). These correlations are expected since the MFCL model estimates the recruitment numbers that account for the catch and CPUE indices (along with the other data in the model, such as size composition). For the MFCL recruitment estimates to show correlation with an environment/oceanographic driver, that driver needs to have a prevalent influence on the fishery dependent catch, CPUE and size composition dynamics. As there are many other processes and observation error that influence the catch, CPUE and size compositions, it is likely that only strong environmental drivers would be expected to dominate the fishery dependent data to the extent that MFCL recruitment estimates correlate with the environmental/oceanographic data. The lack of correlation between the MFCL recruitment and the environmental indices explored in this study, at the annual scale, would suggest that these indices are not having an overwhelming influence on the fishery dependent data generation processes. It may be that the environmental signals are being swamped by other influences on the data or that the environmental-recruitment relationships are indeed weak.

It is clear that lack of field collected fishery independent information on spatial and temporal dynamics of skipjack early life stages is a major gap in our understanding of recruitment dynamics and processes for skipjack tuna in the Pacific. In the absence of fishery independent field data, our best estimation of skipjack recruitment dynamics would be from the SEAPODYM model, because of its enhanced biological/ecological realism. The recent improvements to the skipjack SEAPODYM model and the preliminary model runs discussed in this paper are supportive of a recent step up in recruitment from the late 1990s (Figure 11), but not a long-term increasing trend to the extent estimated by the MFCL assessments. While more work is required on the updated skipjack SEAPODYM model, it does cast some doubt on the long-term MFCL recruitment trend.

In conclusion, given the lack of irrefutable evidence for or against the increasing recruitment trend, the trend should be considered as an uncertainty in the stock assessment. Under the hypothesis that the recruitment trend is at least partly a model estimation artifact related to stable JPPL CPUE abundance trends due to effort creep, alternative CPUE indices adjusted for plausible changes in catchability should be modelled. As the free school purse seine indices used in the recent assessment only begin in 2010 it is not expected that effort creep would be significantly influencing the trends in these indices, and much of the technological advancements in purse fishing have occurred prior to the start of the new indices. The above modelling studies should initially focus on

the JPPL indices that are the data component informing the model about trends in vulnerable biomass over the period of the MFCL recruitment trend. Modelling scenarios could involve incremental increases in catchability trends to explore what level is required to eliminate the MFCL recruitment trend. The results of these analysis can then be compared against the indicators of catchability increase in part 2) of this paper for the JPPL, and consideration of the information provided for purse seine fisheries in Hoyle (2024), to assess whether the levels of catchability increase required to remove the recruitment trends are plausible.

Part 2) Effort creep in the Japanese pole and line fishery

Background

Skipjack pole-and-line fishery data from the Japanese fleet is used in stock assessments in the WCPO to construct CPUE abundance indices. The Japanese pole and line (JPPL) data provide the longest available CPUE time series and are the only abundance indices used for the recent skipjack stock assessment for the period prior to 2005 (see Part 1, Figure 3). JPPL CPUE indices are therefore influential in providing the assessment model with information on the historical abundance trend. The pole and line fishery data has been the subject of significant previous studies and detailed modelling work using geostatistical models (VAST, sdmTMB) and simulation of the implications of spatial contraction of pole and line effort (Ducharme-Barth et al., 2019; Kinoshita et al., 2019; Teears et al., 2022b). While the pole and line fishery has contracted and is now of limited value for indexing abundance in the equatorial region, a feature of the indices developed for previous stock assessments is their stable long-term trends. This stability is apparently not consistent with anecdotal reports from Japanese industry, that the skipjack abundance has declined, particularly in regions north of 10°N and closer off Japan. The Japanese pole and line fleets are categorized by vessel size with vessels between 20 and 199 GRT defined as OS, fishing closer to Japan on shorter trips, and vessels greater than or equal to 200 GRT defined as DW, fishing further afield and on the high seas with longer trips. The paper by Matsubara et al. (2022) provides a good description of the operational features of JPPL fishing.

The pole and line effort metric is the vessel day (i.e., catch in kilograms per daily logsheet record). Previous standardizations have included year-quarter, vessel ID, spatial and spatiotemporal random effects, vessel class (OS, DW), number of poles, GRT, and sea surface temperature, however, standardisations have had not resulted in downward adjustments to the CPUE over time. It is possible that the effort metric and the variables used in the standardisation models are not capturing the improvements in efficiency due to technology and other operational changes over time. The likely impact of 'effort creep' and associated increasing catchability over time may not be accounted for in CPUE indices, leading to biased stable CPUE trends when the true abundance or local availability has declined.

Catchability trends for CPUE indices are often assumed to be removed via standardisations and catchability is often assumed invariant over time to simplify modelling. However, various studies have shown that catchability can clearly change with the developments of fishing gear and uptake of technology. Such temporal changes in catchability due to technological developments in fishing equipment such as sonar and bird radar are referred to as technological creep. Previous research indicates that long-term fisheries assessments that ignore the implications of technological creep on catchability can lead to overestimation of stock abundance (Thurstan et al. 2010; Eigaard et al. 2014; Rousseau et al. 2019). Technological developments in the JPPL vessels fishing for skipjack have been previously reported to the SC by Matsubara et al. (2022) for the DW vessels. That study attempted to

account for effort creep in standardisation models (delta-GLM model) that included factors for uptake of technology; chilled bait tanks, high frequency sonar, NOAA satellite data, bird radar 1, and bird radar 2. However, the analysis indicated that fishing effort effectiveness was only increased by about 0.2% after installing the five fishing devices, with around 10% increase in CPUE due to the devices after 1990. Despite this result, the presence and magnitude of effort creep in the JPPL fishery CPUE remains uncertain, and there was a need for more work including consider the OS fishery component and alternative approaches to explore the effort creep issue. Furthermore, given the contraction of the DW JPPL fleet, it is likely that the OS fleet will provide the ongoing abundance index for the northern regions of the skipjack assessment.

Interviews and survey questionnaires of industry members can provide both qualitative and semiquantitative information on changes in vessel/fishing operational conditions and features and fisher perspectives on stock trends. Incorporating such information into quantitative data analysis can be effective in better defining technology creep timing and potential implications for catchability (Marriott et al. 2011). There is also a need to build statistical models for resource assessment that can take advantage of the results of fisher surveys, as discussed at SC19 (Nishimoto et al. 2023).

The purpose of this study is to present a statistical framework for exploring the effort creep problem (Figure 16) and to apply the proposed method to the case of the JPPL skipjack fishery in the waters around Japan to clarify the temporal trends in catchability and biomass. First, we present data on the perspectives of fishers (from industry survey questionnaires) regarding the timing of equipment installation on fishing vessels, impacts on catches, and abundance trends. We focus on the JPPL OS component to complement the previous work that focussed on the DW component (Matsubara et al., 2022). We developed a Bayesian state-space model for exploring effort creep (SSM-EC), which can explicitly incorporate information on the timing of technological innovation from the industry survey. We constructed and applied this model to pole-and-line fishery data from the OS JPPL skipjack fishery. We applied an S-shaped change scenario for the hypothesised true functional form of catchability increase, consistent with the progressive uptake of technologies in the 1980-90s indicated from the industry surveys, and a constant scenario (time-invariant) as the null hypothesis (representing the status-quo assumption). We also assumed two process models for the state-space model: the Ricker model and the Gomperz model. Finally, the estimation results are discussed in relation to an appropriate consideration of catchability change to consider for the JPPL skipjack CPUE indices in the stock assessment.



Figure 16 Statistical framework for solving the problem of effort creep. The functional form of catchability is considered through interviews or questionnaires, and the timing information of technology adoption is explicitly integrated into the population model. The use of a Bayesian state-space model that can account for observational error allows us to deal with uncertainty in the observational data.

Methods

Questionary survey for JPPL skippers

The survey of OS JPPL skipjack fishermen was conducted in November 2023 and involved the industry representatives communicating the survey questionaries to shipowners and boat captains in liaison with the Japanese (FRA) scientist (refer to SC19 IP for the survey content (Nishimoto et al. 2023)). The survey questions aimed to document the fishers' perspectives on the status of skipjack resources, convert fishers' knowledge from the field into data, and to identify the period when the technological and operational innovations occurred. The fishermen were asked to complete the survey and fax or mail it within 4 weeks. The exact number of skipjack pole-and-line fishermen in Japan is unknown, but it is estimated to be 60 to 80. The number of responses received from this survey was 37. Respondents ranged in age from approximately 30 to 70 years, and almost all had been on board pole and line vessels for more than 10 years.

Japanese longline logbook

JPPL fisheries are primarily conducted in the northern western Pacific Ocean, predominately within the Japan exclusive economic zone. The data period for the JPLL fishery logbook is from 1972 to 2023. The logbooks contain daily operational information such as date of catch, location of catch, catch (tons), number of fish caught by species, vessel tonnage, and number of poles. Focusing on skipjack in the waters around Japan (Figure 17Figure 17), we analyzed pole-and-line data on total annual catch and total annual fishing effort (vessel days). Due to the large vessels covering the equatorial Pacific Ocean and the spatial sparsity and bias in sampling the target population off Japan, data from small and medium vessels in OS fleet were used in this analysis. Data from May to November, representing the season when skipjack are predominantly caught in the nearshore JPPL fishery in the study area, were included in the analysis.



Figure 17 The study area: the main area of Japan's OS pole-and-line fishery in the Northwest Pacific Ocean. The colored areas indicated by the 2.5-degree grid represent the relative catch. Areas with zero catch data are shown in gray.

Statistical model

The state-space model for effort creep (SSM-EC) assumes changes in catchability due to technological innovations in equipment such as sonar and bird radar. This assumption of catchability change is supported by the survey. An S-shaped functional form of catchability change is applied, consistent with the pattern of technology uptake near Japan (Figure 19) (Matsubara et al. 2022).

The relationship between catch (tonnes) and population abundance over a 48-year period, from 1972 to 2019, was expressed as an observational process. In year t (t=1,2,3,...,T), the expected value of catch E[C[t]] can be represented by the following equation, where q[t] is the time-varying catchability parameter, E[t] is the fishing effort (product of days and number of vessels), and N[t] is the population density (e.g., Eigaard et al., 2014):

$$\mathbb{E}[C[t]] = q[t]E[t]N[t].$$

Because skipjack catches are recorded in the logbooks in tonnage, which is a continuous value, the observed catch is assumed to follow the below normal distribution with variance σ^2 for the observation error:

 $C[t] \sim \operatorname{Normal}(q[t]E[t]N[t], \sigma^2).$

We assumed that q[t] is represented by two models: a constant scenario (q=const) and an S-shaped change scenario (q[t]=a+b/(1+e^(-X[t])), where X[t] is discrete-time data (1972,1973,...2019) standardized to continuous values. We hypothesize, based on industry surveys, that the S-shaped scenario is the most likely scenario. We constructed a prior distribution where the S-shaped inflection point, i.e. where the catchability curve changes significantly from the start year to the end year, is around 1990.

It is recommended to examine both the Gompertz and Ricker population models, depending on the species and the assumed functional form of catchability. Hence, in the process model, following Hostetler and Chandler (2015), we applied the stochastic Ricker model and the stochastic Gompertz model (hereafter referred to as the Gompertz model), which accounted for the density dependence of population dynamics in the state process. In this study, we assumed the harvest-based Ricker model that estimates biomass and catchability by considering the annual catch amount C[t], and the dynamics of fish biomass N[t] is described as follows:

$$N[t+1] = N[t] \left(\exp\left(r \left(1 - \frac{N[t]}{K} \right) \right) \right) - C[t] + \omega[t],$$

where r is the population growth rate and K is the carrying capacity, and $\omega[t]$ indicates the annual variation in the population growth rate for the stock state.

In the Gompertz model, the dynamics of fish species biomass, N[t], are described as follows (see Hostetler and Chandler (2015) for details):

$$N[t+1] = N[t] \left(\exp\left(r \left(1 - \frac{\log \left(N[t] + 1 \right)}{\log \left(K + 1 \right)} \right) \right) - C[t] + \omega[t] \right)$$

For the prior distribution of the initial state, the population density in the first year follows a normal distribution with mean 0 and variance ε^2 :

$N[1] \sim \text{Normal}(0, \varepsilon^2)$

We sampled from the posterior distribution using Markov Chain Monte Carlo (MCMC) with Stan. To improve the stability of sampling using MCMC, scaled-effort data (E /10000) were used in the calculations. The MCMC convergence was evaluated using R-hat with R-hat < 1.1, which is the convergence criterion. The MCMC method was implemented in Stan using the R package cmdstanr ver. 0.5.3.

Results

Questionnaire survey

For the survey of mid-sized vessel skipjack pole-and-line fishermen the response to the "Question: Do you feel that you are not catching as many skipjack as when you first got on the boat and if so why?" almost all of the 37 respondents (36 of the 37 respondents (36) felt that skipjack had decreased (Figure 18). Regarding the timing of the introduction of various types of equipment, the median values for V-radar, NOAA satellite information, high frequency-sonar, and bird radar were clustered around 1990 (Figure 19). Fishermen felt that the addition of most of this equipment to the skipjack pole-and-line fishery improved both catch and ease of finding fish (Table 2). The response to which of the various equipment was most important to the success of skipjack pole-and-line fishing fishery, of 16 votes, excluding multiple responses, the majority of the fishers (9) indicated that the high-frequency sonar (Figure 20a) was most important. This is likely due to the fact that high-frequency sonar is the only way to gain a visual understanding of the specific size and direction of the school, and assists the vessel to intercept and stay on the school. In addition, the question was followed up by asking, if high-frequency sonar were to be eliminated, by what percentage would the amount of fish caught per day change? Seven of the nine respondents answered that the amount of fish caught per day would decrease by 50% (Figure 20b).







Figure 19 Timing of the introductions of equipment on Japanese skipjack pole-and-line fishing boats, survey question 6) Please indicate the decade when the ship's equipment from the 1970s to the present day was first introduced. NOAA refers to satellite SST and current maps, BR refers to vessel radar.



Figure 20 Fishermen's perception of (a) the most important gear in the skipjack pole-and-line fishery and (b) the degree of decline in daily catch expected if High -frequency sonar was no longer available. Of the 37 responses, those with more than one checked are excluded here. This refers to the question 12) Which equipment is most important for the skipjack pole-fishing fishery? And question 13) Without the equipment in Q12, how much will your catch decrease per day?

Table 2 Impressions of fishermen on the impact of each piece of equipment on their vessels on the catch and ease of finding skipjack. Answer items were rated on a 5-point scale (increased a lot, increased, stayed the same, decreased, decreased a lot), and the top two responses are summarized here. Note that the questionnaire results consisted of responses from 37 respondents. This relates to survey questions 7-11.

Equipment	Q. How has the introduction of fishing	Q. How has the introduction of fishing			
	equipment influence the amount of fish	equipment influence the ease of finding			
	caught?	fish?			
Bird radar	increased (n=24), increased a lot (n=9)	increased (n=22), increased a lot (n=11)			
Sonar	increased (n=26), increased a lot (n=10)	increased (n=25), increased a lot (n=11)			
Satellite imagery	increased (n=27), increased a lot (n=6)	increased (n=28), increased a lot (n=6)			
Bait tank	stayed the same (n=24), increased (n=11)	Not applicable			
Smartphone and LINE app.	stayed the same (n=26), increased (n=18)	stayed the same (n=20), increased (n=14)			
Notes for some of the equipment did respondents chooses degreesed, or degreesed a lat					

Note: for none of the equipment did respondents choose; decreased, or decreased a lot

Application of the proposed method to Japanese skipjack pole-fishing fishery data

Application of the statistical model to Japanese skipjack pole-and-line data confirmed MCMC convergence in both the constant and S-shaped scenarios for the Gompertz model but not the Ricker model (Figure 21). Thus, the Gompertz model was supported as the population model that better represented the skipjack dynamics. The median values of the estimated catchability as of 1972 for the constant and S-shaped scenarios for catchability are almost the same, while the median value of the posteriori distribution for the S-shaped scenario, and the S-shaped scenario showed a decreasing trend in biomass estimates from around 1990 to more recent years, the constant scenario predicts a much higher biomass from the mid 1980's onwards. The difference in median biomass between the constant and S-shaped scenarios was 325,355 tons in the most recent year, 2019 (Figure 22). This suggests the risk of overestimating stock abundance when ignoring increased catchability due to technological progress (creep).



Figure 21 Changes over time in catchability and biomass estimated using data from the Japan skipjack poleand-line fishery. The upper panel shows the constant scenario, and the lower panel shows the S-shaped change scenario; the figure is blank because MCMC did not converge in the case of the Ricker model for the S-shaped change scenario. The blue solid line in the figures indicates the median, dark gray shading indicates the 80% CI, light gray shading indicates the 95% CI. Based on the previous studies on technological innovation in the JPPL fleet, and the results of the questionnaire, the S-shaped scenario seems to be appropriate for catchability; the change in catchability in the S-shaped scenario is likely due to the introduction of high frequency sonar, satellite imagery, and V-radar around 1990, based on the results of the questionnaire survey. The questionnaire survey results suggest that the S-shaped scenario is largely influenced by high-frequency sonar, satellite imagery, and V-radar introduced around 1990. In the S-shaped scenario, the estimated biomass decreased as the year approached recent years, which was supported by the results of the questionnaire survey, which indicated that skipjack have been decreasing in recent years, according to the fishermen's opinion. The method presented here can be applied to different fish species and fishing methods by improving the observation and process models and is expected to be useful in the future as a basic statistical model.



Figure 22 Comparison plot of change over time in biomass for the constant catchability scenario (black) and the S-shaped change scenario (red). Solid lines indicate medians; colored areas indicate 95% CIs.

Summary and Conclusions

The industry survey suggests that technology uptake by the JPPL vessels was particularly prevalent during the 1980s to early 1990s. The industry perspectives were that skipjack abundance had declined in the waters around Japan. It was notable that the introduction of high-frequency sonar was perceived to have been valuable in increasing pole-and-line fishing success. This technology is most useful when schools have been located in the vicinity of the vessel, rather than locating fishing grounds where schools are more abundant. Other advances were noted to have improved catches such as use of NOAA satellite imagery of ocean currents and temperatures and interfleet communications (LINE), that help to locate fishing grounds. The effort creep Bayesian state-space model estimated the probable (median of posterior) change in catchability from 1972 to 2019 was 1.99, or approximately 2% per year. Pole-and-line catchability may therefore have plausibly doubled since the 1970s and this could be considered as a basis for pole-and-line CPUE effort creep scenarios

in the next assessment. An s-shaped effort creep scenario seems most consistent with the timing and trajectory of technology uptake across about 10 years by the JPPL vessels, cantered around 1990. In this study of the skipjack pole-and-line fishery off Japan, not accounting for catchability changes would overestimate stock biomass, emphasizing the importance of considering effort creep implications for catchability in long-term stock assessment analyses.



Supplementary figures from the industry survey results

Question 2: What is important when leaving the port and deciding on the first fishing ground?

- a Overseas operating permit,
- b past experience,
- c temperature and ocean current charts,
- d weather maps,
- e vessel size,
- f vessel horsepower and speed,
- g fuel charges,

h satellite buoys,

i wireless communications – (sharing fishing information, catch, locations) (usually shared 4 times a day – all offshore vessels and coastal?, most vessels report – if they can join, in the past this was not openly reported) DW have different frequency.,

j LINE, etc.

K Other

Question 3: What is important when looking for skipjack after arriving at the fishing grounds?

a bird radar,

b low-frequency sonar,

- c high-frequency sonar,
- d binoculars,
- e temperature and current charts,
- f weather maps,

g vessel radar,

h ship size,

i horsepower and speed of the ship,

j fuel charges,

k wireless communication (sharing fishing information over radio – regular reports),

I LINE,

m foreign crew,

Others()





Question 4. What is important when fishing for skipjack? a gear type (pole and line) – lure/jig types etc..... b how to manoeuvre the vessel, c the state of the fish school, d water spray and throwing bait, e bait (type, freshness, size, quantity), f power of foreign crew, g experience of crew, h presence of other vessels, Others()

Question 6 - in main text





Question 8. How has the in introduction of sonar changed the amount of fish caught (left) and the ease of finding them (right)?



Question 9. How has the introduction of satellite imagery changed the amount of fish caught (left) and the ease of finding them (right)?



Question 10. How has the amount of fish caught changed since the bait tanks (tank for storing live bait) were introduced?





Question 11. How has the introduction of smart phones and LINE changed the amount of fish you catch (left) and the ease of finding them (right)?

Acknowledgements

We thank the WCPFC for their support of this work under Project 115. We thank the Japanese pole and line fishing industry for their support of this work through completing the survey questionnaire and the Japanese Fisheries Research and Education Agency for allowing staff time to conduct the work in part 2.

References

- Anderson, J. T. (1988). A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fisheries Science*, *8*, 55–66.
- Aoki, Y., Jusup, M., Nieblas, A.E., Bonhommeau, S., Kiyofuji, H., & Kitagawa, T. (2020). Early-life ontogenetic developments drive tuna ecology and evolution. *Journal of Marine Systems*, 206, 103307.
- Ashida, H. (2020). Spatial and temporal differences in the reproductive traits of skipjack tuna *Katsuwonus pelamis* between the subtropical and temperate western Pacific Ocean. *Fisheries Research*, *221*, 105352.
- Ashida, H., & Horie, M. (2015). Reproductive condition, spawning season, batch fecundity and spawning fraction of skipjack tuna *Katsuwonus pelamis* caught around Amami-Oshima, Kagoshima, Japan. *Fisheries Science*, *81*, 861–869.
- Ashida, H., Tanabe, T., & Suzuki, N. (2017). Difference on reproductive trait of skipjack tuna *Katsuwonus pelamis* female between schools (free vs FAD school) in the tropical western and central Pacific Ocean. *Environ Biol Fish*, *100*, 935–945.
- Ashida, H., Watanabe, K., & Tanabe, T. (2018). Growth variability of juvenile skipjack tuna (*Katsuwonus pelamis*) in the western and central Pacific Ocean. *Environmental Biology of Fishes*, 101, 429–439.
- Barber, R. T., & Chavez, F. P. (1991). Regulation of primary productivity rate in the equatorial Pacific. *Limnology and Oceanography*, *36*, 1803–1815.
- Boehlert, G. W., & Mundy, B. C. (1994). Vertical and onshore-offshore distributional patterns of tuna larvae in relation to physical habitat features. *Marine Ecology Progress Series*, 107, 1–13.
- Cael, B. B., Bisson, K., Boss, E., Dutkiewicz, S., & Henson, S. (2023). Global climate-change trends detected in indicators of ocean ecology. *Nature*, *619*, 551–554.

- Castillo Jordan, C., Teears, T., Hampton, J., Davies, N., Scutt Phillips, J., McKechnie, S., ... Hamer, P. (2022). Stock assessment of skipjack tuna in the western and central Pacific Ocean: 2022. WCPFC-SC18-SA-WP-01.
- Davis, T. L. O., & Young, J. (1990). Feeding ecology of larvae of southern bluefin, albacore and skipjack tunas (Pisces: Scombridae) in the eastern Indian Ocean. *Marine Ecology Progress Series*, 61, 17–29.
- De Deckker, P. (2016). The Indo-Pacific Warm Pool: critical to world oceanography and world climate. *Geoscience Letters*, *3*, 20.
- Ducharme-Barth, N., Vincent, M., Pilling, G., & Hampton, J. (2019). Simulation analysis of pole and line CPUE standardization approaches for skipjack tuna in the WCPO. WCPFC-SC15-2019/SA-WP-04. Pohnpei, Federated States of Micronesia 12-20 August 2019.
- Eigaard O. R., Marchal P., Gislason H., & Rijnsdorp A. D. (2014). Technological Development and Fisheries Management. *Reviews in Fisheries Science and Aquaculture*, 22: 156–174.
- Escalle, L., Hare, S. R., Vidal, T., Brownjohn, M., Hamer, P., & Pilling, G. (2021). Quantifying drifting Fish Aggregating Device use by the world's largest tuna fishery. *ICES Journal of Marine Science*, *78*, 2432–2447.
- FAO. (2022). The State of World Fisheries and Aquaculture 2022. FAO.
- Forget, G., & Ferreira, D. (2019). Global ocean heat transport dominated by heat export from the tropical Pacific. *Nature Geoscience*, *12*, 351–354.
- Fournier, D. A., Hampton, J., & Sibert, J. R. (1998). MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 2105–2116.
- Fujioka, K., Aoki, Y., Tsuda, Y., Okamoto, K., Tsuchida, H., Sasaki, A., & Kiyofuji, H. (2024). Influence of temperature on hatching success of skipjack tuna, *Katsuwonus pelamis*: Implications for spawning availability of warm habitats. *Journal of Fish Biology*, jfb.15767.
- Gierach, M. M., Lee, T., Turk, D., & McPhaden, M. J. (2012). Biological response to the 1997–98 and 2009–10 El Niño events in the equatorial Pacific Ocean. *Geophysical Research Letters*, *39*, 2012GL051103.
- Hamer, P. (2022). Report from the SPC Pre-assessment Workshop (PAW), March 2022, WCPFC-SC18-2022/SA-IP-02, Online meeting. July 2022.
- Hare, S. R., Williams, P. G., Castillo Jordan, C., Day, J., Hamer, P., Hampton, J., ... Pilling, G. M. (2023).
 The western and central Pacific tuna fishery: 2022 overview of stock status. Tuna Fisheries
 Assessment Report no. 23. Pacific Community.
- Hasegawa, T., & Hanawa, K. (2003). Decadal-scale variability of upper ocean heat content in the tropical Pacific. *Geophysical Research Letters*, *30*, 2002GL016843.
- Henley, B. J., Gergis, J., Karoly, D. J., Power, S., Kennedy, J., & Folland, C. K. (2015). A Tripole Index for the Interdecadal Pacific Oscillation. *Climate Dynamics*, *45*, 3077–3090.
- Hopcroft, R. R., & Roff, J. C. (1995). Zooplankton growth rates: extraordinary production by the larvacean *Oikopleura dioica* in tropical waters. *Journal of Plankton Research*, *17*, 205–220.
- Hostetler, J. A., and R. B. Chandler. (2015). Improved state-space models for inference about spatial and temporal variation in abundance from count data. *Ecology*, 96, 1713-1723. doi:10.1890/14-1487.1.
- Hoyle, S. (2024). Effort creep in longline and purse seine CPUE and its application in tropical tuna assessments. WCPFC-SC20-2024/SA-IP-09.
- Hoyle, S., Kleiber, P., Davies, N., Harley, S., & Hampton, J. (2010). Stock assessment of skipjack tuna in the western and central Pacific Ocean. WCPFC-SC6-2010/ST-IP-02. Nuku'alofa, Tonga, 10–19 August 2010.
- Hoyle, S., Kleiber, P., Davies, N., Langley, A., & Hampton, J. (2011). Stock assessment of skipjack tuna in the western and central Pacific Ocean. WCPFC-SC7-2011/SA-WP-04. Western and Central Pacific Fisheries Commission.

- Hunter, J. R., Macewicz, B. J., & Sibert, J. R. (1986). The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the south Pacific. *Fishery Bulletin*, *84*, 895–903.
- Ijima, H., & Jusup, M. (2023). Tuna and billfish larval distributions in a warming ocean, 2023. https://arxiv.org/abs/2304.09442
- Jenkins, G. P., Young, J. W., & Davis, T. L. O. (1991). Density Dependence of Larval Growth of a Marine Fish, the Southern Bluefin Tuna, *Thunnus maccoyii*. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 1358–1363.
- Kidwell, A., Han, L., Jo, Y.-H., & Yan, X.-H. (2017). Decadal Western Pacific Warm Pool Variability: A Centroid and Heat Content Study. *Scientific Reports*, *7*, 13141.
- Kinoshita, J., Aoki, Y., Ducharme-Barth, N., & Kiyofuji, H. (2019). Standardized catch per unit effort (CPUE) of skipjack tuna of the Japanese pole-and-line fisheries in the WCPO from 1972 to 2018. WCPFC-SC15-2019/SA-WP-14. Pohnpei, Federated States of Micronesia.
- Langley, A., & Hampton, J. (2008). Stock assessment of skipjack tuna in the western and central Pacific Ocean. WCPFC-SC4-2008/SA-WP-4. Western and Central Pacific Fisheries Commission.
- Langley, A., Hampton, J., & Ogura, M. (2005). Stock assessment of skipjack tuna in the western and central Pacific Ocean. WCPFC-SC1-SA_WP-4. Western and Central Pacific Fisheries Commission.
- Lehodey, P., Senina, I., & Murtugudde, R. (2008). A spatial ecosystem and populations dynamics model (SEAPODYM) – Modeling of tuna and tuna-like populations. *Progress in Oceanography*, 78, 304–318.
- Lehodey, P., Senina, I., Calmettes, B., Hampton, J., & Nicol, S. (2013). Modelling the impact of climate change on Pacific skipjack tuna population and fisheries. *Climatic Change*, *119*, 95–109.
- Lehodey, P., & Senina, I. (2009). A user manual for SESEAPODYM version 2.0: application with data assimilation (draft version). WCPFC-SC5-2009/EB-IP-13. Port Villa, Vanuatu. 10-21 August 2009.
- Llopiz, J. K., Richardson, D. E., Shiroza, A., Smith, S. L., & Cowen, R. K. (2010). Distinctions in the diets and distributions of larval tunas and the important role of appendicularians. *Limnology and Oceanography*, 55, 983–996.
- Llopiz, J. K., & Hobday, A. J. (2015). A global comparative analysis of the feeding dynamics and environmental conditions of larval tunas, mackerels, and billfishes. *Deep Sea Research Part II: Topical Studies in Oceanography*, 113, 113–124.
- Long, Y., Noman, M. A., Chen, D., Wang, S., Yu, H., Chen, H., ... Sun, J. (2021). Western Pacific Zooplankton Community along Latitudinal and Equatorial Transects in Autumn 2017 (Northern Hemisphere). *Diversity*, 13, 58.
- Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production. *Bulletin of the American Meteorological Society*, *78*, 1069–1079.
- Marriott, R. J., Wise, B., & St John, J. (2010). Historical changes in fishing efficiency in the west coast demersal scalefish fishery, Western Australia: Implications for assessment and management. ICES Journal of Marine Science, 68, 76–86.
- Matsubara, N., Aoki, Y., & Tsuda, Y. (2022). Historical development of fishing devices in Japanese pole-and-line fishery. WCPFC-SC18-2022/SA-IP-16.
- McKechnie, S., Hampton, J., Pilling, G. M., & Davies, N. (2016). Stock assessment of skipjack tuna in the western and central Pacific Ocean. WCPFC-SC12-2016/SA-WP-04. Bali, Indonesia, 3–11 August 2016.
- Nishikawa, Y., Honma, M., Ueyanagi, S., & Kikawa, S. (1985). Average distribution of larvae of oceanic species of scombroid fishes, 1956–1981. *Far Seas Fish.Res.Lab., 99 p.*
- Nishimoto, M., Aoki, Y., Matsubara, N., & Tsuda, Y. (2023). Technological developments of the fishing devices in the Japanese pole-and-line vessel identified in past surveys. WCPFC-SC19-2023/SA-IP-14

- Park, J.-Y., Kug, J.-S., Park, J., Yeh, S.-W., & Jang, C. J. (2011). Variability of chlorophyll associated with El Niño–Southern Oscillation and its possible biological feedback in the equatorial Pacific. *Journal of Geophysical Research*, *116*, C10001.
- Parties to the Nauru Agreement. (2010). A THIRD ARRANGEMENT IMPLEMENTING THE NAURU AGREEMENT SETTING FORTH ADDITIONAL TERMS AND CONDITIONS OF ACCESS TO THE FISHERIES ZONES OF THE PARTIES. As amended 11th September 2010. Parties to the Nauru Agreement.
- Picault, J., Ioualalen, M., Menkes, C., Delcroix, T., & McPhaden, M. J. (1996). Mechanism of the Zonal Displacements of the Pacific Warm Pool: Implications for ENSO. *Science*, *274*, 1486–1489.
- Power, S., Casey, T., Folland, C., Colman, A., & Mehta, V. (1999). Inter-decadal modulation of the impact of ENSO on Australia. *Climate Dynamics*, *15*, 319–324.
- Purcell, J. E., Sturdevant, M., & Galt, C. P. (2005). A review of appendicularians as prey of fish and invertebrate predators. *Response of Marine Ecosystems to Global Change: Ecological Impact of Appendicularians* (pp. 359–435).
- Rayner, N. A., Parker, D. E., Horton, E. B., Folland, C. K., Alexander, L. V., Rowell, D. P., ... Kaplan, A. (2003). Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *Journal of Geophysical Research: Atmospheres*, *108*, 2002JD002670.
- Reglero, P., Urtizberea, A., Torres, A., Alemany, F., & Fiksen, Ÿ. (2011). Cannibalism among size classes of larvae may be a substantial mortality component in tuna. *Marine Ecology Progress Series*, *433*, 205–219.
- Reglero, P., Ortega, A., Blanco, E., Fiksen, Ø., Viguri, F. J., De La Gándara, F., ... Folkvord, A. (2014).
 Size-related differences in growth and survival in piscivorous fish larvae fed different prey types. *Aquaculture*, 433, 94–101.
- Rice, J., Harley, S., Davies, N., & Hampton, J. (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.
- Roxy, M. K., Dasgupta, P., McPhaden, M. J., Suematsu, T., Zhang, C., & Kim, D. (2019). Twofold expansion of the Indo-Pacific warm pool warps the MJO life cycle. *Nature*, *575*, 647–651.
- Rousseau, Y., R. A. Watson, J. L. Blanchard, E. A. Fulton, (2019). Evolution of global marine fishing fleets and the response of fished resources. Proc. Natl. Acad. Sci. U.S.A. 116, 12238–12243.
- Satoh, K., Tanaka, Y., Masujima, M., Okazaki, M., Kato, Y., Shono, H., & Suzuki, K. (2013). Relationship between the growth and survival of larval Pacific bluefin tuna, Thunnus orientalis. *Marine Biology*, *160*, 691–702.
- Schaefer, K. (2001). Reproductive biology of tunas. Fish Physiology, 19, 225–270.
- Senina, I., Lehodey, P., Sibert, J., & Hampton, J. (2020). Integrating tagging and fisheries data into a spatial population dynamics model to improve its predictive skills. *Can. J. Fish. Aquat. Sci.*, 77, 576–593.
- Senina, I., Lehodey, P., Calmettes, B., Nichol, S. J., Caillot, S., J, H., & P, W. (2016). *Predicting skipjack tuna dynamics and effects of climate change using SEAPODYM with fishing and tagging data*. WCPFC-SC12-2016/EB WP01.
- Sharma, P., Marinov, I., Cabre, A., Kostadinov, T., & Singh, A. (2019). Increasing Biomass in the Warm Oceans: Unexpected New Insights From SeaWiFS. *Geophysical Research Letters*, *46*, 3900–3910.
- Strasburg, D. W. (1960). Estimation of larval tuna abundance in the central Pacific. *Fisheries Bulletin*, 60, 231–255.
- Takasuka, A., Aoki, I., & Mitani, I. (2003). Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. *Marine Ecology Progress Series*, 252, 223–238.
- Tanabe, T., Kiyofuji, H., Shimizu, Y., & Ogura, M. (2017). Vertical distribution of juvenile skipjack tuna *Katsuwonus pelamis* in the tropical western Pacific Ocean. *JARQ*, *51*, 181–189.

- Tanaka, M., Kaji, T., Nakamura, Y., & Takahashi, Y. (1996). Developmental strategy of scombrid larvae: high growth potential related to food habits and precocious digestive system development. In: Watanabe Y, Yamashita Y, Oozeki (eds)AA Balkema, Rotterdam, p 125–139. Survival strategies in early life stages of marine resources. Watanabe Y, Yamashita Y, Oozeki (eds) (pp. 125–139).
- Teears, T., Aoki, Y., Matsubura, N., Tsuda, Y., Castillo Jordon, C., Hampton, J., ... Hamer, P. (2022a). Background analyses and data inputs for the 2022 skipjack tuna stock assessment in and central Pacific Ocean. WCPFC-SC18-2022/SA-IP-05.
- Thurstan, R. H., Brockington, S. & Roberts, C. M. (2010). The effects of 118 years of industrial fishing on UK bottom trawl fisheries. Nat. Commun. 1, 15.
- Turk, D., & Lewis, M. R. (2001). Geographical distribution of new production in the western/central equatorial Pacific during El Niño and non-El Niño conditions. *Journal of Geophysical Research*, 106, 4501–4515.
- Turk, D., McPhaden, M. J., Busalacchi, A. J., & Lewis, M. R. (2001). Remotely sensed biological production in the equatorial Pacific. *Science*, *283*, 471–474.
- Ueyanagi, S. (1973). Report on experiments on the development of tuna culturing techniques (April, 1970 March, 1973). Far Seas Fisheries Research Laboratory. S Series 8. Shimizu 424, Japan.
- Ueyanagi, S., Nishikawa, Y., & Matsuoka, T. (1974). Artificial fertilization and larval development of skipjack tuna, Katsuwonus pelamis. *Bulletin of Far Seas Fisheries Research Laboratory*, *10*, 179–188.
- Uotani, I., Matsusaki, K., Makino, Y., Noda, K., Inamura, O., & Horikawa, M. (1981). Food habits of larvae of tunas and their related species in the area northeast of Australia. *Bulletin of Japansese Society of Scientific Fisheries*, *47*, 1165–1172.
- Uriarte, A., Johnstone, C., Laiz-Carrión, R., García, A., Llopiz, J. K., Shiroza, A., ... Alemany, F. (2019). Evidence of density-dependent cannibalism in the diet of wild Atlantic bluefin tuna larvae (*Thunnus thynnus*) of the Balearic Sea (NW-Mediterranean). *Fisheries Research*, 212, 63–71.
- Vincent, M., Pilling, G., & Hampton, J. (2019). *Stock assessment of skipjack tuna in the WCPO*. WCPFC-SC15-2019/SA-WP-05. Pohnpei, Federated States of Micronesia.
- Wang, X. J., Murtugudde, R., & Le Borgne, R. (2010). Climate driven decadal variations of biological production and plankton biomass in the equatorial Pacific Ocean: is this a regime shift? March 26, 2010, doi:10.5194/bgd-7-2169-2010.
- Weller, E., Min, S.-K., Cai, W., Zwiers, F. W., Kim, Y.-H., & Lee, D. (2016). Human-caused Indo-Pacific warm pool expansion. *Science Advances*, *2*, e1501719.
- Wexler, J. B., Margulies, D., & Scholey, V. P. (2011). Temperature and dissolved oxygen requirements for survival of yellowfin tuna, *Thunnus albacares*, larvae. *Journal of Experimental Marine Biology and Ecology*, 404, 63–72.
- Yan, X.-H., Ho, C.-R., Zheng, Q., & Klemas, V. (1992). Temperature and Size Variabilities of the Western Pacific Warm Pool. *Science*, *258*, 1643–1645.
- Zhang, D., & McPhaden, M. J. (2006). Decadal variability of the shallow Pacific meridional overturning circulation: Relation to tropical sea surface temperatures in observations and climate change models. Ocean Modelling, 15, 250–273.