Spatiotemporal variability in bigeye tuna vertical distribution in the Pacific Ocean

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Introduction

Bigeye tuna (Thunnus obesus) is a target species of the tropical longline fishery in the Pacific Ocean, with annual catches of large, mainly adult fish of approximately 100,000 tonnes (t). Longline caught bigeye tuna are highquality and destined for fresh and frozen tuna markets in Asia, North America and elsewhere. Bigeye tuna are also caught in the purse seine fishery in the Pacific Ocean, ranging from <5% of the total catch in the western Pacific region to >10% in the eastern Pacific region. Catches have generally exceeded 120,000 t annually since the mid-1990s, which coincides with a large increase in the use of drifting fish aggregation devices (FADs) in Pacific region purse seine fisheries (Harley et al. 2015; IATTC 2015). Purse seine caught bigeye tuna are mostly smaller, juvenile fish, and are sold for canning along with much larger quantities of skipjack tuna and yellowfin tuna, which are the primary target species of this fishery.

In the Pacific Ocean, highly migratory species are managed separately by the Western and Central Pacific Fisheries Commission (WCPFC) and the Inter-American Tropical Tuna Commission (IATTC). While most Pacific Ocean tuna stocks are not estimated to be overfished or subject to overfishing, the most recent estimate of current spawning biomass for 2015 in the eastern Pacific Ocean (EPO) was 20% of the unexploited level (Aires-da Silva et al. 2016). The 2015 assessment of bigeye tuna in the western and central Pacific Ocean (WCPO) indicated it was overfished, and subject to overfishing. While the results of the latest bigeye tuna stock assessment in the WCPO (McKechnie et al. 2017) are more optimistic, they vary significantly depending on the growth curve and regional structure used, and there is still some probability the stock is overfished or subject to overfishing (Anon. 2017). We refer interested readers to SPC Fisheries Newsletter No. 153 for more information on the recent developments in the WCPO bigeye tuna assessment (Hampton 2017).

These assessments rely primarily on data from the purse seine and longline fisheries. An understanding of the vulnerability of bigeye tuna to these fishing methods, including the environmental drivers of variability, is necessary for interpreting catch rates, size composition and other features of the data. In particular, a key question is the extent to which spatial and temporal variations in catch per unit effort (CPUE) in longline and purse seine fisheries reflect changes in abundance or vulnerability (catchability) to the fishing gear being used. Vulnerability of bigeye tuna to both purse seine and longline gear is likely influenced by their vertical distribution in the water column (Evans et al. 2008; Fuller et al. 2015). Purse seine fish aggregating device (FAD) sets are usually deployed in pre-dawn hours (Harley et al. 2009) with nets hanging from the surface to depths of 100-200 m (Lennert-Cody et al. 2008; Delgado de Molina et al. 2010). Bigeye tuna will therefore tend to be more vulnerable to capture by purse seine at times and in locations where they are associated to the FADs, close to the surface at night. Longline sets that target bigeye tuna are typically deployed during the day at depths of 100-400 m, with most hook fishing in the upper part of this range (Evans et al. 2008; Bigelow et al. 2002). Bigeye tuna will therefore be more vulnerable to capture by longline gear when their daytime swimming depth is <300 m. We summarise here the results of a recent study (Abascal et al. 2018), which explored spatiotemporal variability in vertical distribution of bigeye tuna in the Pacific Ocean using data from internally-implanted archival tags.

Data available from archival tags

A total of 851 bigeye tuna were tagged (Figure 1) and released with archival tags (Figure 2) from 1999 to 2014, with tagging efforts being concentrated in the equatorial central Pacific region (5°N–5°S, 140°W–180°), and in the north-western Coral Sea (10–25°S, 146–150°E). 137 archival tags were recovered (16%), of which 65 (7.6% of the 851 archival tags) had useful information for a period of more than 30 days. The archival tags provide observations of swimming depths, internal and external temperatures, and light intensity readings that can be used to estimate geographical positions.

Bigeye tuna exhibit a variety of vertical movement profiles that were previously classified into three broad behavioural types: characteristic, associative, and 'other' (see Fuller et

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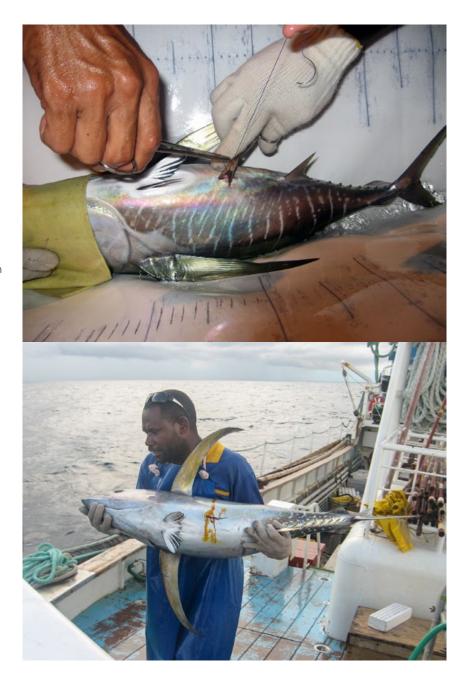


Figure 1. An archival tag has been inserted in a bigeye tuna; the incision is closed with a few stitches (image: Bruno Leroy).

Figure 2. A bigeye tuna fitted with an electronic tag ready to be released (image: Bruno Leroy).

al. 2015). Bigeye tuna generally stay close to the surface at night. At dawn, bigeye tuna that are displaying characteristic behaviour descend well below the thermocline where they generally remain throughout the day and feed on prey. They briefly return to warmer waters above the thermocline during this period to increase their internal temperature, before returning to deeper and colder waters. Bigeye tuna displaying associative behaviour generally remain within the mixed layers throughout the day. The 'other' behaviour type covers all depth profiles that do not fall under characteristic behaviour or associated behaviour. For each day of tag data, we assigned 'associative', 'characteristic' or 'other' behaviour, using the classification method of Fuller et al. (2015). The median depths for each day and night were calculated from the tags' depth measurements, removing data recorded within one hour of dawn and dusk. Depths of the 18°C and 20°C isotherms were

calculated for each 24 h period using the depth and temperature information recorded by the tags.

Vertical distributions of bigeye tuna

Median recorded depths displayed strong spatial trends for all combinations of behaviour type and daytime/night-time, with the shallowest average depths generally at the most easterly range of observations, and increasing average depths moving westwards (Figures 3 and 4). The spatial trends in average depths displayed a positive relationship with the thermal structure of the water column. Average depths were generally deeper in areas with deeper thermoclines (i.e. the western equatorial Pacific region and in the Coral Sea, and vice versa for the eastern Pacific region). Additionally, the

strength of thermal stratification displayed an association with average depths. For example, average night-time depths were shallower in the Coral Sea than in the western equatorial Pacific region; both regions have similar thermocline depths but thermal stratification is generally stronger in the Coral Sea with lower sea surface temperatures.

Models of median vertical depths

Exploratory analyses of swimming depths recorded by the archival tags demonstrated strong spatial and temporal

variation in swimming depths (see above). Statistical models are simplified representation of reality, and provide a way to disentangle the effects of different variables on swimming depths (e.g. what is the effect of fish size on swimming depths, if all else is equal?). We used additive mixed models to estimate the effects on average depths of the thermal structure of the water column, of fish size, and for models of night-time depths, of lunar illumination. The depth of the 20°C isotherm was included as a proxy for thermocline depth, with the difference in depth between the 18°C and 20°C isotherms being included as a metric of thermal stratification. Tag identification was

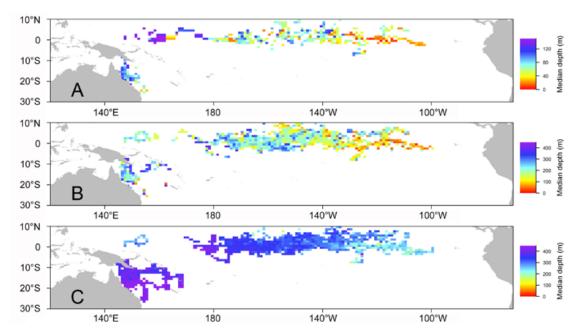


Figure 3. Daytime median depths averaged for spatial cells of one degree of longitude and latitude for fish showing associative (A), other (B) and characteristic (C) behaviours.

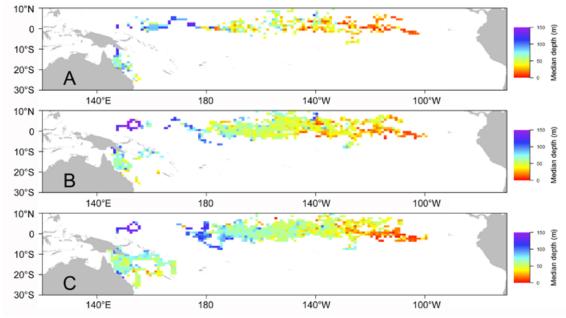


Figure 4. Night-time median depths averaged for spatial cells of one degree of longitude and latitude for fish showing associative (A), other (B) and characteristic (C) behaviours.

included as a random intercept to account for variations in depths between individuals. Separate models were used for each day/night-behavioural type combination.

For all models, thermocline depth had the strongest effect on median depths, with median depths increasing with thermocline depth (Figures 5 and 6). Median depths decreased with stronger thermal stratification for daytime-characteristic behaviour, and average depths increased with fish length for fish smaller than 80 cm. Median fish length and thermal stratification had no detectable effect on median depths for daytime-associated behaviour. It was not possible to fit robust models to median depths for the daytime-other category.

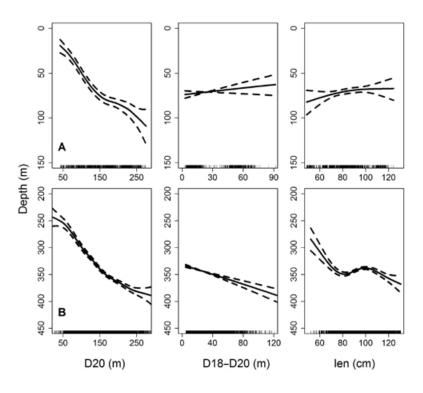


Figure 5. Modelled effects of depth of the 20°C isocline (D20), water column stratification (D18–D20) and fish size (len) on median depth during daytime. A- Associated; B- Characteristic.

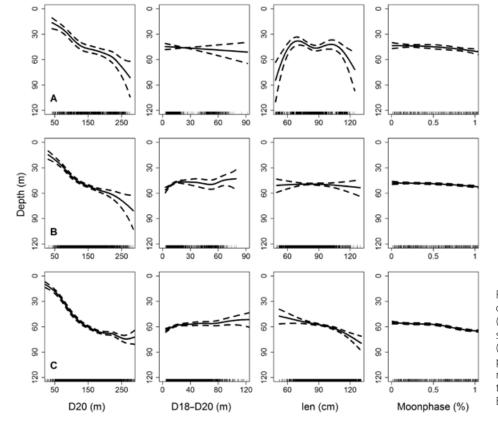


Figure 6. Modelled effects of depth of the 20°C isocline (D20), water column stratification (D18–D20), fish size and phase of the moon on median depth during night-time. A- Associated; B- Other; C- Characteristic.

For night-time-associated behaviour, there was no detectable effect of thermal stratification on median depths. Median depths for night-time-other and night-time-characteristic behaviours were generally insensitive to thermal stratification, with the exception of a slight decrease in median depths as thermal stratification weakened from the highest observed levels (i.e. when the 18°C and 20°C isotherms were less than 15 m apart). Median depths increased with fish length for night-time-characteristic behaviours, with a non-linear relationship between median depths and fish length for night-time-associated and no detectable effect of fish length on median depths for night-time-other. Night-time median depths increased weakly with moonillumination for all three behaviour types, particularly for bigeye tuna displaying characteristic behaviour.

Predicted median depths and potential effects on standardised CPUEs

Thermocline depth had the strongest effect of the modelled explanatory variables on median depths for bigeye tuna during both daytime and night-time, regardless of behaviour type. Thermal stratification of the water column was also influential on daytime median depths for bigeye tuna displaying characteristic behaviours. Thermocline depth and thermal stratification display substantial spatial and temporal variation in the Pacific Ocean, which is reflected in strong spatial and temporal variation in predicted median depths throughout the Pacific Ocean (Figure 7). For example, longitudinal trends in predicted depths of daytime-characteristic

and night-time-associated behaviours strengthen in La Niña conditions and weaken El Niño conditions.

We tested for a potential relationship between estimated median depths and fish catchability by modelling standardised catch per unit effort (CPUE) from region 4 of the 2017 bigeye tuna assessment (i.e. 170°E to 150°W, 10°S to 20°N; McKechnie et al. 2017) as a function of estimated daytime median depths for bigeye tuna displaying characteristic behaviour. A clear negative relationship between standardised catch rates and median fish depth was identified (Figure 8). This suggests that standardised catch rates – used as indices of relative abundance in stock assessments – also reflect changes in vulnerability of bigeye tuna to longline gear due to varying swimming depths.

Discussion

The analysis summarised here represents the first basin-wide analysis of archival tagging data within a statistical framework to identify the main drivers of swimming depths in bigeye tuna.

Observations of swimming depths from the archival tags clearly demonstrated strong spatial variation in swimming depths, with deeper swimming depths in the western Pacific region compared to the eastern Pacific region. The statistical modelling of median depths indicated that the local oceanographic environment had the strongest effect on swimming depths – in particular the depth of the thermocline,

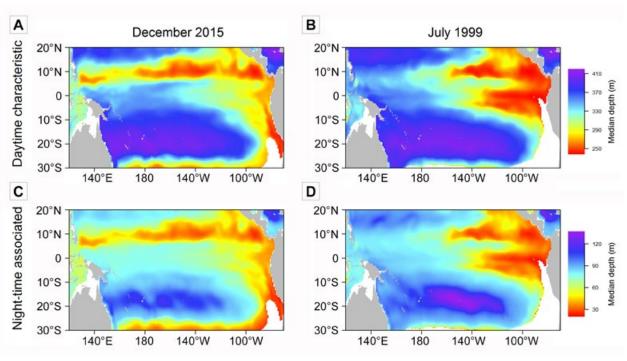


Figure 7. Predicted daytime depth distribution for a 115 cm fish showing characteristic behaviour (A, B) and night-time depth for a 50 cm fish displaying associated behaviour (C, D), under strong El Niño (A, C) and La Niña (B, D) conditions.

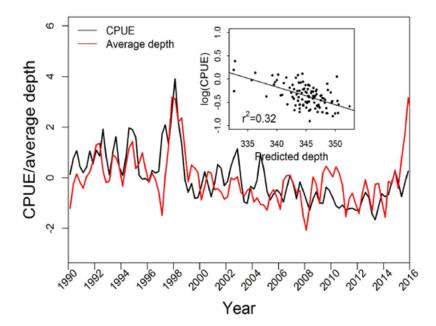


Figure 8. Time series of standardised longline CPUE in region 4 and predicted average depth in the region. Values are provided as z-scores, and the axis for predicted average depth has been reversed for illustrative purposes.

regardless of the time of day (day/night) or behaviour type. We used thermocline depth and thermal stratification as explanatory variables in the statistical models because they gave superior fits to observed swimming depths, and because these variables were based directly on data from temperature and depth sensors on the archival tags. However, it seems likely that bigeye tuna depth distributions are strongly linked to diurnal vertical migration of prey, but are constrained by the thermal layer and the oxygen concentration tolerance of bigeye tuna (e.g. Evans et al. 2008; Schaefer and Fuller 2010). We also fitted statistical models with oxygen concentration, and deep scattering layer depths, which rely on linking to external datasets using estimates of tag geolocations. The inclusion of these alternative environmental variables, at the expense of thermocline depth and thermal stratification, worsened fits to observed swimming depths. Light-based estimates of geolocations can be uncertain (e.g. see Basson et al. 2016) and as such we might expect tag-sensor derived environmental variables to better explain observed variation in swimming depths.

Predicted swimming depths of bigeye tuna throughout the Pacific Ocean demonstrated strong temporal and spatial variability, in part driven by the El Niño Southern Oscillation (ENSO) cycle. Furthermore, the detected relationship between predicted swimming depths and standardised CPUE suggests that indices of relative abundance used in the assessment models also reflect varying vulnerability of bigeye tuna to longline gear due to varying swimming depths.

This is problematic as the indices of relative abundance are assumed to reflect only changes in abundance, not vulnerability. Work is ongoing on including the effects of environmental variables on catchability within models used to standardise catch rates of tropical tuna (Tremblay-Boyer et al. 2017). This should improve the assessment models, through the use of more appropriate CPUE series as indices of abundance, and better estimates when scaling the biomass between regions.

There were limited data available from instrumented bigeye tuna in the western equatorial region - in fact all observations in the equatorial region west of 160°E came from just two tags. There was some suggestion that the swimming depths of these two tagged fish were inconsistent with expected depths based on the local oceanography and estimated fish length; this difference can be attributed to variation in swimming depths between individuals. Data from additional archival tagged bigeye tuna in the area would allow this to be explored in more detail. We note that few bigeye tuna were released with archival tags on the skipjack-focussed 2017 WP4 tagging cruise in the western equatorial region, due to the low numbers of large bigeye fish caught. Additional tag releases in the western equatorial region would improve the spatial coverage of the archival tagging dataset, which would crucially increase the amount of information available from an area with extensive purse seine and longline fishing efforts.

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