Spatial and temporal effects on albacore growth and reproduction

February 2025

Simon Hoyle
Hoyle Consulting

Spatial and temporal effects on albacore growth and reproduction

Simon Hoyle[1]

Hoyle Consulting

Indian Ocean Tuna Commission, FAO

Executive Summary

Biological parameters for Indian Ocean albacore are relatively poorly understood. Better estimates of these parameters are required, because they are influential for the stock assessment. In this report, literature on albacore growth and reproductive parameters in all oceans is reviewed. Representative estimates of growth require the sampling of fish from a range of sizes, and across potential sources of variation such as longitude. Similarly, representative estimates of reproductive parameters require sampling across potential sources of variation, which include latitude and seasons, and may also include longitude.

Availability at size is reviewed. The best potential source of small fish appears to be longline fisheries south 35 °S between April and August.

Analysts should consider dropping the Taiwanese logbook length frequency data from the stock assessment, given the inconsistencies in its pattern though time, while retaining Taiwanese observer data, as in the tropical tuna assessments. Stock assessments need to fit well to their input data, and the model cannot fit well to size data that conflict either with other sizes or with CPUE data.

Both the Japanese and the Taiwanese size data show increasing mean sizes through time. These trends will be influential if used uncritically in the stock assessment, to the extent that they conflict with increasing fishing pressure. Analysts should consider the hypothesis that the increasing sizes are caused by increasing growth rates due to lower predator densities. The alternative explanation is trends in sampling bias in both datasets. In either case, the model should prioritize fitting the CPUE data over fitting the composition data.

1. Introduction

A simulation study conducted in 2019 (Moore et al., 2019) indicated that bias in the estimates of biological parameters could substantially affect the results of albacore tuna stock assessments. A coordinated age and growth sampling program was considered useful to address the bias on juvenile growth and quantify the variance of length at age.

This paper conducts a desktop review of the spatiotemporal patterns in growth and reproductive variability of albacore tuna in the Indian Ocean and other oceans, to provide a better understanding of the population structure and dynamics of the species, as well as to pinpoint knowledge gaps and future research needs.

---

[1] Email: simon.hoyle@gmail.com

First, I review the literature on albacore growth and reproductive parameters, to report patterns observed in other oceans, and to identify gaps in data and knowledge for the Indian Ocean. In addition, I analyse available data on spatial patterns in the sizes of Indian Ocean albacore sizes.

Life history: Young albacore (up to 3 years old) in the Indian Ocean primarily inhabit cooler temperate waters (15-18°C), often found south of the subtropical convergence zone. Their distribution seems continuous with Atlantic juveniles, suggesting that transoceanic movement may occur. As they mature, albacore shift towards warmer waters (17-26°C). The spawning season occurs between October and March, primarily in tropical and subtropical waters between 10 and 30S where temperatures exceed 24°C (Dhurmeea et al., 2016; Schaefer, 2001).

Albacore grow to around 80-90 cm fork length by age 5 and may reach up to 140 cm. Age is typically estimated through otolith analysis (Farley et al., 2019; Farley et al., 2013a), but uncertainties exist due to variable growth patterns and challenges in interpreting seasonal marks.

There is ongoing debate regarding the existence of multiple albacore stocks within the Indian Ocean, which has implications for management strategies (Labonne et al., 2024; Nikolic et al., 2020).

2. Background

WPTMT08.01 (para 71) noted the absence of small albacore (<75 cm fork length) in the sample used for estimating the current growth curve (Farley et al., 2019) and the fact that most otoliths in the sample were collected in the southwestern Indian Ocean (Figure 1) . Given that spatial variability in growth has been observed in albacore in the Pacific Ocean (Williams et al., 2012), the WPTmT recommended to the SC that the collection and analysis of otolith samples is expanded to cover the whole Indian Ocean, with a particular focus on obtaining a broad range of sizes and locations, including fish from the eastern part of the ocean.

3. Growth

Growth estimates are a fundamental component of age-structured length-based stock assessments, and the growth curve used is highly influential for assessment outcomes. This is particularly true for models that fit to length data, as in most tuna assessments. Assumed distributions of length at age are used by the model to translate size structure observations into age structure. Both the mean and the variation of length at age are important and influential for model outcomes. Growth is also a key determinant of stock productivity.

Fish growth often varies spatially and through time (Gertseva et al., 2017; Williams et al., 2012). However, growth curves in fish stock assessments are almost always assumed to be uniform in space and time, due to limitations of the assessment software. Explicitly modeling spatiotemporal growth variation in assessments can be prohibitively expensive in terms of both model complexity and computing resources.

Nevertheless, omitting these sources of variation from the assessment will introduce bias (Correa et al., 2021). It is therefore important to understand the sources of variability and the consequences for assessment outcomes of ignoring variation, and to use methods that nevertheless produce good outcomes.

Issues associated with estimating growth of fishes are summarized by Lee et al. (2024), and studies of tuna growth are reviewed by Murua et al. (2017).

3.1. Sources of variation in growth estimates

One of the key components of growth estimation for stock assessment is identifying factors associated with growth variation.

Natural variation occurs among individuals, due to factors such as individual quality and local habitat variation. This source of variability may be lower for tunas than for many other species.

Growth differences between sexes have been clearly identified for albacore tuna in multiple oceans (Chen et al., 2012; Farley et al., 2019; Megalofonou, 2000; Williams et al., 2012). It may be relatively strong for albacore compared to other species of tuna (Farley et al., 2021b; Farley et al., 2021c; Pacicco et al., 2021).

Temporal growth variation will occur for species to some degree, given changes in ocean productivity and population densities, but the degree of variation has not been estimated for albacore due to the lack of long-term data series. Statistically significant variation has identified for several tuna species where long-term studies have been undertaken, including southern bluefin tuna (Farley and Gunn, 2007) and eastern Atlantic bluefin tuna (Andrews et al., 2023).

Similarly, spatial growth variation is likely to occur due to nutrient availability, temperature, and other factors that may affect metabolic rates (Lee et al., 2024). Mediterranean albacore have consistently been found to grow to smaller sizes than in the Atlantic and elsewhere (Murua et al., 2017), but it is unclear whether this is due to lower nutrients of a local adaptation. Bergmann's rule states that, across taxa, body sizes tend to increase with distance from the equator. However, their seasonal north-south movement pattern may preclude this from being a factor for albacore.

Relatively large discrepancies in estimates of albacore growth rate have been observed both within and between geographic areas (Murua et al., 2017). Some variation is likely due to differences between study methods. For example, there are different estimates of length at age one, one at 20–30 cm and a second at 40–55 cm FL (Murua et al., 2017) (though the estimate of 40-55 cm appears more likely based on counts of daily micro-increments (Farley et al., 2013a)).

Growth comparisons within a single study are more reliable, given consistent methods for sampling, ageing, and modeling, and the availability of statistical tests for genuine differences. Spatial variation has been identified in South Pacific albacore (Farley et al., 2021a; Williams et al., 2012), with slightly larger lengths at age further east. No latitudinal variation in length at age was found, with similar estimates for north, central, and southern areas. In the eastern North Pacific, juvenile length-at-age was larger for fish caught south of 40°S relative to fish caught north of 40°S (Renck et al. 2014), although again this may be due to faster growing fish moving to spawning grounds at younger ages, rather than growth differences in those areas.

Prior to 2019, Indian Ocean growth studies used scales, spines, and length frequency analysis, and provided growth parameters that were different other oceans. Estimates of asymptotic length were larger and growth coefficients were smaller (Murua et al., 2017). However, growth curves based on otolith data (Farley et al., 2019) provided asymptotic lengths that were smaller than previous Indian Ocean estimates, and consistent with North and South Pacific estimates. Growth coefficients, however, were much larger than previous estimates and higher than most Pacific estimates. These new Indian Ocean estimates were probably affected by the lack of small fish in the samples, with positively biased lengths at age in younger age classes due to preferential sampling of faster growing fish in the longline fishery (Farley et al., 2019). Similarly, mean lengths at age estimated for young fish were larger than estimates for the Pacific but older fish were similar to the Pacific.

3.2. Sampling effects

The size selectivity associated with fishing gear can affect estimates of length at age. This effect is commonly seen in albacore sampling, with longline fisheries dominated by large fish and small fish taken in troll, pole-and line, and driftnet fisheries (Langley and Hoyle, 2016; Moore et al., 2020).

Spatial variation in numbers at length also affects estimation of length at age. Albacore sizes vary with latitude in all oceans, with smaller immature fish found at higher latitudes, and larger mature albacore found in the subtropics and tropics (Nikolic et al., 2017). Although the smallest albacore caught at higher latitudes are taken in fisheries that select small fish, such as troll, pole and line, and net fisheries (Castillo-Jordan et al., 2021; ISC Albacore Working Group, 2023; Rice, 2022), longline fisheries also tend to catch progressively smaller albacore at higher latitudes (Bromhead et al., 2009).

Gear selectivity and ontogenetic movement can affect estimates of length at age, since the young fish that move first to lower latitudes, like the young fish that are caught first in longline fisheries, tend to be those with faster growth. This is why sampling only at lower latitudes or with longline gear tends to overestimate length at age for young fish. In the South Pacific, otolith sampling for ageing has occurred across a range of latitudes, including in New Zealand troll fisheries in temperate waters (Williams et al., 2012). Although sampling of the NZ troll fishery was necessary to compensate for biases associated with subtropical longline sampling, it remains difficult to achieve a precisely balanced, representative sample of numbers at length and age across the population.

When developing a growth curve for the north Pacific, Chen et al. (2012) sampled 244 albacore from longline vessels, and 49 smaller fish from pole and line vessels. Wells et al. (2013) sampled larger fish from longline vessels in the western and central north Pacific, and smaller fish from troll and recreational fishers in the eastern Pacific.

To develop a growth curve for the Indian Ocean, Farley et al. (2019) sampled fish east of Madagascar by longline and off South Africa by pole and line, with a small number collected from purse seine fishing between 0-10° S (Figure 1). There was difficulty obtaining small fish, with the smallest measuring 66 cm, and the next smallest 74 cm (Figure 2). Size data from South Africa's pole and line port sampling programme suggest that fish as small at 60 cm are likely to be available in most years (Figure 3). However, there is uncertainty about whether the fish caught in the pole and line fishery on the west (Atlantic) coast of South Africa are part of the Indian Ocean stock (Labonne et al., 2024; Nikolic et al., 2020).

Considering other options for obtaining small fish from the Indian Ocean as a whole, fish less than 60cm are recorded in reasonable proportions in the gillnet, offshore gillnet, offshore ringnet and troll fisheries (Figure 4). However, the troll size data reported from Indonesia near the equator (Figure 5), where small albacore are generally considered unlikely, may actually be misreported skipjack or another small tuna species (IOTC Secretariat, 2013) . Similarly, the offshore ring net and offshore gillnet data are reported from Sri Lanka near the equator where small albacore are unlikely.

Size-selective sampling is usually used to obtain samples across a broad range of sizes for ageing, although this affects estimates of length at age in a similar way to gear selectivity and spatial patterns of availability. Potential otolith sampling strategies include random (ROS), fixed (FOS), and proportional (POS) otolith sampling (Chang et al., 2019; Goodyear, 2019; Schemmel et al., 2022).

Random sampling (Kimura, 1977) is associated with modeling growth as length at age, but this type of sampling tends to be inefficient, and estimates are affected by the sources of size-based selectivity discussed above (Schemmel et al., 2022). Supplementing the least abundant size strata with additional samples can lead to biased estimates of growth parameters. Targeted sampling of small fish from a fishery with size-dependent selectivity will compensate for the size selection to some extent but not in a systematic way. Results will not be statistically robust. Targeted sampling of large fish will lead to overestimation of lengths at age for large fish (Chang et al., 2019).

There is a need to adjust the modeling method used to estimate lengths at age so that it is consistent with the sampling method.

Albacore stocks generally have large datasets of catch at length. Sampling is commonly size-dependent

Analysis of the growth of albacore tuna in the Atlantic has used a wide range of methods, including ageing from the hard parts scales, vertebrae, and spines (first dorsal fin ray), growth increments from mark-recapture experiments, and analysis of length frequency data (Nikolic et al., 2017; Santiago and Arrizabalaga, 2005). No otolith work has yet been published which makes comparisons difficult. Some spatial variation in growth has been inferred (Bard, 1981).

3.3. Indian Ocean estimates

The Indian Ocean albacore stock assessment (Langley, 2019; Rice, 2022) now uses growth from sampling in the Indian Ocean (Farley et al., 2019). However, samples used to develop this growth curve come from a relatively limited area, with the majority taken between latitudes 23°S to 15°S, and longitudes 48°E to 62°E (Figure 1). There was a lack of small fish in the samples: only one fish was less than 74 cm FL, and the majority were over 90 cm. Fish tend to be relatively large in the areas sampled (Figures 11 and 12).

The small spatial coverage is likely to have affected estimation of the growth curve. Size-dependence in availability is likely to have positively biased the growth curve estimates of length at age for younger age classes. In future, more sampling in latitudes south of 30 °S, and preferably south of 35 °S, is needed to increase the number of small fish and provided better estimates of length at age. Availability in longline fisheries of small fish by latitude is shown in Figure 6. Length frequencies by month and flag for fish sampled since 2000 south of 35 °S (Figure 7) suggest that, when there is sampling within a latitude band, similar proportions of fish < 70 cm are found across months. However, most of the size sampling south of 30 °S occurs during between April and August (Figure 8). Comparing these length frequency data with the drift gillnet fisheries (Figure 4 and Figure 9) and the South African pole and line fishery (Figure 3) suggest that the sizes are comparable. If we accept that the small fish from the northern IO are not albacore, no Indian Ocean fishery can provide consistent access to as small as those caught in South Pacific troll fisheries (Figure 10).

In addition, coverage across more longitudes will be needed to permit analysts to investigate spatial variation in growth.

4. Reproductive potential

Reproductive potential is a fundamental component of the albacore stock assessment, representing the adult stock size in terms of its potential reproductive output. Stock assessments generally use the term spawning stock biomass (SSB) to represent the size of the reproductive population, with SSB included in the stock recruitment relationship. SSB can be seen as a generic term for reproductive output, which is not necessarily based on biomass alone. In its simplest form it is the summed product of numbers at age, weight at age, and maturity at age. However, other factors can affect the reproductive output of a population. For example, the spawning stock biomass per recruit (SSBR), which represents the expected lifetime reproductive potential of an average recruit, also allows for the sex ratio and fecundity at age (Goodyear, 1993). Total egg production (TEP) has been included in stock assessments as a substitute for SSB, calculated as

$$TEP = \sum_{a-1}^{m} n_a Q_a w_a f_a$$

where n_a is the number of females at age, Q_a proportion mature, w_a mean weight, f_a fecundity, and m is the maximum age (Kell et al., 2016). The proportion of active females and the daily spawning fraction at age may also be considered, when they are likely to improve the representation of reproductive output. Egg viability can also vary substantially with age and affect reproductive output, though this relationship is uncertain and little-studied for tunas (Medina, 2020).

Each of these factors can affect the pattern of SSB through time and its relationship with recruitment, and thereby change MSY-related parameters (Hoyle, 2008; Minte-Vera et al., 2019).

Stock assessments for Indian Ocean albacore since 2014 (Hoyle et al., 2014; Langley and Hoyle, 2016; Rice, 2022) have used estimates of SSB based on the product of female numbers, weight, and reproductive potential. In these cases, reproductive potential is calculated at length as the product of maturity, fecundity, and spawning fraction. Given the limitations of available data from the Indian Ocean, the ogives used in these assessments are based on calculations for South Pacific albacore (Hoyle et al., 2012).

Developing ogives of reproductive potential for a stock assessment can be complex and data intensive. A representative ogive for the entire stock requires broadly-based sampling and appropriate statistical analysis. Albacore tunas, like many fish species, show considerable spatial and seasonal variability in the length of 50% maturity. During the spawning season mature fish tend to be found in spawning areas, where the proportion mature at every length is therefore higher than elsewhere and in other seasons. Raising the proportion mature also reduces the length at 50% maturity. Conversely, length at 50% maturity is higher in non-spawning areas and seasons. Samples from different areas and seasons will therefore provide different ogives.

To develop reproductive potential ogives for the whole population, the analyst needs to account for this spatial and seasonal variation. Farley et al. (2014) analysed data for South Pacific albacore to estimate spatial and seasonal patterns of maturity at length and used these models to predict maturity across the whole population, with relative abundances based on CPUE indices. The resulting ogives indicated 50% maturity at 3 cm larger than estimates based on the raw data.

Similarly reweighting should be applied to estimates of spawning fraction and fecundity at length, since they too have potential to vary within the population. Analyses for South Pacific albacore (Farley et al., 2013b) found that the best models for activity, spawning fraction (which included activity), and fecundity all included both fork length and month. There was also some support for spatial variables, but more statistical power (data) would be needed to estimate them reliably.

These parameters were integrated into an ogive used in the 2012 stock assessment for South Pacific albacore tuna (Hoyle et al., 2012). The aggregation method has not previously been documented. Fecundity and spawning fraction by length and month were predicted across all combinations of months and lengths from models fitted to the South Pacific albacore dataset (Farley et al., 2013b). The spatially and seasonally integrated ogive of maturity at length was multiplied by these two ogives at month and length, and the product was then aggregated across the year to produce relative reproductive potential at length for females. This approach would have introduced a small bias by aggregating across the seasonality in the maturity ogive before multiplying by the other two components.

5. Maturity

Estimates of length at 50% maturity (L_{50}) for females are available for most oceans, albeit affected by the difficulty of obtaining population-level estimates as discussed above. Estimates at age are also available for some oceans but are less reliable due to both smaller datasets and ageing uncertainties. A review of data suggests L_{50} of about 90cm in all oceans except the Mediterranean where, although the L_{50} is not available, estimates appear to be smaller (Nikolic et al., 2017). The different reproductive strategy of Mediterranean albacore (shorter spawning season and higher relative batch fecundity) may represent adaptation to local environmental conditions (Saber et al., 2015). In that case, information from Mediterranean albacore may not be relevant to studies in Indian Ocean.

Sampling in the western Indian Ocean carried out from 2013 to 2015 provided data to inform an estimated L_{50} of 85.3 cm (Dhurmeea et al., 2016). One difficulty with this study was that only 4% (24 or 27 depending on the method) of the 665 sampled and staged females were immature, which was too few to explore spatial and seasonal patterns in the L50. The proportions mature at length by region were not reported, but females less than 82 cm were all sampled in region D south of 30S, and most of the immature fish were likely to have been sampled from here. Dhurmeea et al. (2016) note that “latitudes south of 30S are inhabited mainly by immature fish while the regions north of 30S are mostly occupied by mature fish”. If there was a spatial effect on length at maturity as observed in the South Pacific, increasing the proportion of samples from region D may have increased the estimated L_{50}.

6. Reproductive activity, spawning fraction, and fecundity

Albacore spawning occurs generally in tropical and subtropical waters in summer when sea surface temperatures (SST) exceed 24 °C (Schaefer, 2001). Albacore are batch spawners with asynchronous oocyte development and indeterminate annual fecundity. Annual fecundity can be estimated from batch fecundity and spawning frequency (Nikolic et al., 2017).

There have been few studies of reproductive activity in the Atlantic. Some information on spawning locations has come from larval surveys (Ueyanagi, 1971), which suggested two spawning areas. In 2021 a project commenced to study reproductive biology for the northern Atlantic stock, including maturity schedules (L_{50}) and egg production (size/age related fecundity), and to clearly identify spawning areas and seasons (Ortiz de Zárate et al., 2024). This work is ongoing.

The spawning area for South Pacific albacore is located between 10-25°S, and spawning occurs primarily between November and January (Mondal and Lee, 2023). Mean spawning frequency during peak spawning months (1.7 and 1.3 days) and mean relative batch fecundity (50.5 and 64.4 oocytes per gram) were estimated to be similar in the North Pacific and South Pacific respectively (Chen et al., 2010; Farley et al., 2013b). In the South Pacific spawning fraction (the inverse of spawning frequency) was found to increase with fish size and vary by month, with peak spawning fraction from October to December. Batch fecundity was found to increase with fish length and vary by month, with peak fecundity at the start of the season in October.

In the Indian Ocean, spawning was observed only between 10°S and 30°S, from October to January with a peak in November and December. The mean spawning frequency in the spawning region between November and January was estimated to be 2.2 days, which is a longer interval than in the

Pacific. Batch fecundity was estimated to be 53 ± 23 oocytes per gram of body weight, which is consistent with the Pacific.

7. Methods

I applied several approaches to explore spatial patterns of size distribution in the longline size data.

The size database reports the number of fish in each length bin per time-area-fleet stratum. The lengths are in columns and each row represents a time (year + month) x location x fleet x gear type stratum. I extracted the longline data (gear code LL, ELL, ELLOB or LLOB) for Taiwan and Japan, at all spatial stratification levels (5 x 5 - TW and JP, and 10 x 20 – JP only).

For the length analyses, the data were processed to provide a row for each length bin in each stratum.

First, I applied a simple standardization model to size data by location and year-quarter, with the formula: size ~ year-quarter + location, implemented as follows using the R package mgcv (Wood, 2011). These models were applied separately to the Taiwanese and Japanese length data.

```
mod <- gam(len ~ yrqtr + te(lon, lat, k = c(10,10)), data=dat, weights = dat$nfish).
```

Analyses to explore quarterly size distributions employed the same model but restricted the input data to samples obtained during a single quarter. These models were applied to the Taiwanese length data only.

```
datq <- filter(dat, qtr = q)
```

```
mod_qtr <- gam(len ~ yrqtr + te(lon, lat, k = c(10,10)), data=datq, weights=datq$nfish).
```

Similar models were applied to standardize the means weights reported in the size database, though these weights may have been calculated from the length frequency data rather than collected independently.

```
mod <- gam(meanwt ~ yrqtr + te(lon, lat, k = c(10,10)), data=dat, weights=sqrt(datq$tnofish)).
```

Different stratifications and flags were standardized separately. Taiwanese data were also standardized separately by quarter. Expected sizes through time were predicted for the median location in each dataset. Expected spatial sizes were predicted for the median year-quarter in each dataset.

8. Results

Standardization of Japanese and Taiwanese longline data consistently showed trends by latitude, with smaller fish found further south, particularly beyond about 25 °S (Figures 11 and 12). Smaller fish tended to be found further north in the eastern Indian Ocean then in the west. There was some seasonal variation in distribution, though issues with data quality in the Taiwanese dataset made this difficult to characterize (Figures 13 and 14).

Analyses of temporal size indices after adjusting for location showed different patterns in the Japanese and Taiwanese data, and by sampling stratification level in the Japanese data. Note that the different stratifications and flags were standardized separately, and mean lengths through time were predicted for the median location in each dataset. Quarterly plots were also based on separate standardization by quarter. Thus, groups may differ due to changes in average fishing location, rather than due to selectivity, sampling bias, or changes in fish size.

Japanese data sampled at 10x20 resolution showed an increase in mean size from an average of about 95cm in 1970 to almost 100 cm in 1985. This was followed by stable sizes at about 100 cm through to 2000 (Figure 15). Subsequently there was a large reduction in sample sizes at this spatial resolution and estimates became noisy, but the mean sizes appeared to drop considerably to average around 96 cm. Japanese 5x5 sampling was available from 2009 to 2020, and they showed relatively stable mean weights through this period.

In contrast, the standardized Taiwanese size data showed a large increase in standardized mean sizes between 1980 and 2022, by almost 10cm or 5kg (Figure 16). There were also periods of large variation, with a spike of large mean sizes over 105 cm around 1990 soon followed by a dip as low as 80cm. Seasonal estimates suggest similar variation through time in each season, but with different average sizes. Fish caught in the austral spring and summer of quarters 1 and 4 tended to be larger than those caught in quarters 2 and 3 (Figures 17 and 18).

9. Conclusions

This working paper provides support for efforts to develop representative biological parameters for the Indian Ocean albacore assessment, including a growth curve and reproductive parameters. Estimating biological parameters will require broadly-based sampling across the major sources of variation. For the growth curve the main requirement is to obtain enough small fish, which is affected by latitude and season. The data show some consistent seasonal size variation at the same latitude (gam analysis not presented here), most of the increase in availability of small fish during the austral winter is due to increased sampling further south.

If growth rate varies spatially with longitude as seen in south Pacific albacore (Williams et al., 2012), it would be useful to distribute sampling across longitudes. The current analyses indicate that small fish are available further north in the eastern Indian Ocean.

For reproductive parameters, the main sources of variation are latitude and season. Like sampling for growth, sampling for reproductive parameters should be broadly based. In particular, it should cover both spawning and non-spawning areas and seasons.

Two notable features of the standardized size data are a) the high variability of the estimates from the Taiwanese data, and b) the increasing trends in mean size through time in both the Japanese and Taiwanese data.

Analysts should seriously consider dropping the Taiwanese logbook length frequency data from the albacore stock assessment. Fitting observed size data is important for stock assessment outcomes, and the model cannot fit conflicting patterns in size data, or size trends that conflict with CPUE data. Recent assessments of tropical tuna species have dropped logbook length measurement data but included logbook weight measurement data and length data sampled by observers, as recommended by a review of tropical tuna size data (Hoyle et al., 2021).

An increasing trend is observed in the standardized size estimates in both the Japanese data from 1970 to 2000 and in the Taiwanese data from 1980 to 2022. These trends will be influential if used uncritically in the stock assessment, to the extent that they conflict with increasing fishing pressure on the stock. Analysts should consider the hypothesis that the increasing sizes are caused by increasing growth rates due to lower predator densities. The alternative explanation is trends in sampling bias in both datasets. In either case, the model should prioritize fitting the CPUE data over fitting the composition data, as recommended by Francis (2011).

10. Acknowledgements

This project was funded by the Indian Ocean Tuna Commission. Thanks to ISC albacore working group for providing access to files from the North Pacific albacore stock assessment.

11. Bibliography

Andrews, A.J.; Di Natale, A.; Addis, P.; Piattoni, F.; Onar, V.; Bernal-Casasola, D.; Aniceti, V.; Carenti, G.; Gómez-Fernández, V.; Garibaldi, F. Vertebrae reveal industrial-era increases in Atlantic bluefin tuna catch-at-size and juvenile growth. ICES Journal of Marine Science. 80:836-847; 2023.

Bard, F.X. Le thon germon Thunnus alalunga (Bonaterre 1788) de lÆocqan atlantique. De la dynamique des populations a la strategie demographiqueFrance, Universite de Paris. 333; 1981.

Bromhead, D., B.; Williams, A.; Hoyle, S.D. Factors affecting size composition data from South Pacific albacore longline fisheries. 2009

Castillo-Jordan, C.; Hampton, J.; Ducharme-Barth, N.; Xu, H.; Vidal, T.; Williams, P.; Scott, F.; Pilling, G.; Hamer, P. Stock assessment of South Pacific albacore, WCPFC-SC-2017/SA-WP-02. Western and Central Pacific Fisheries Commission Scientific Committee, Seventeenth Regular Session. Online meeting; 2021

Chang, Y.-J.; Hsu, J.; Shiao, J.-C.; Chang, S.-K. Evaluation of the effects of otolith sampling strategies and ageing error on estimation of the age composition and growth curve for Pacific bluefin tuna Thunnus orientalis. Marine and Freshwater Research. 70:1838-1849; 2019.

Chen, K.S.; Crone, P.R.; Hsu, C.C. Reproductive biology of albacore Thunnus alalunga. J Fish Biol. 77:119-136; 2010. 10.1111/j.1095-8649.2010.02662.x

Chen, K.S.; Shimose, T.; Tanabe, T.; Chen, C.Y.; Hsu, C.C. Age and growth of albacore Thunnus alalunga in the North Pacific Ocean. Journal of fish biology. 80:2328-2344; 2012.

Correa, G.M.; McGilliard, C.R.; Ciannelli, L.; Fuentes, C. Spatial and temporal variability in somatic growth in fisheries stock assessment models: evaluating the consequences of misspecification. ICES Journal of Marine Science. 78:1900-1908; 2021.

Dhurmeea, Z.; Zudaire, I.; Chassot, E.; Cedras, M.; Nikolic, N.; Bourjea, J.; West, W.; Appadoo, C.; Bodin, N. Reproductive biology of albacore tuna (Thunnus alalunga) in the Western Indian Ocean. PLoS One. 11:e0168605; 2016.

Farley, J.; Eveson, P.; Bonhommeau, S.; Dhurmeea, Z.; West, W.; Bodin, N. Growth of albacore tuna (*Thunnus alalunga*) in the western Indian Ocean using direct age estimates. IOTC-2019-WPTmT07(DP)-21_Rev1. Indian Ocean Tuna Commission Working Party on Temperate Tunas (Data Preparation). Online; 2019

Farley, J.; Gunn, J. Historical changes in juvenile southern bluefin tuna Thunnus maccoyii growth rates based on otolith measurements. Journal of Fish Biology. 71:852-867; 2007.

Farley, J.; Krusic-Golub, K.; Eveson, P. Updating age and growth parameters for South Pacific albacore (Project 106). WCPFC-SC17-2021/SA-IP-10; 2021a

Farley, J.; Krusic-Golub, K.; Eveson, P.; Clear, N.; Luque, P.L.; Artetxe-Arrate, I.; Fraile, I.; Zudaire, I.; Vidot, A.; Govinden, R.; Ebrahim, A.; Romanov, E.; Chassot, E.; Bodin, N.; Parker, D.; Murua, H.; Marsac, F.; Merino, G. Estimating the age and growth of bigeye tuna (*Thunnus obesus*) in the Indian Ocean from counts of daily and annual increments in otoliths. IOTC-2021-WPTT23-18_Rev1. Indian Ocean Tuna Commission Working Party on Tropical Tunas. online; 2021b

Farley, J.; Krusic-Golub, K.; Eveson, P.; Luque, P.L.; Clear, N.; Fraile, I.; Artetxe-Arrate, I.; Zudaire, I.; Vidot, A.; Govinden, R.; Ebrahim, A.; Ahusan, M.; Romanov, E.; Shahid, U.; Chassot, E.; Bodin, N.; Parker, D.; Murua, H.; Marsac, F.; Merino, G. Estimating the age and growth of yellowfin tuna (*Thunnus albacares*) in the Indian Ocean from counts of daily and annual increments in otoliths. IOTC-2021-WPTT23-05. Indian Ocean Tuna Commission Working Party on Tropical Tunas. online; 2021c

Farley, J.; Williams, A.; Clear, N.; Davies, C.; Nicol, S. Age estimation and validation for South Pacific albacore Thunnus alalunga. Journal of fish biology. 82:1523-1544; 2013a.

Farley, J.H.; Hoyle, S.D.; Eveson, J.P.; Williams, A.J.; Davies, C.R.; Nicol, S.J. Maturity Ogives for South Pacific Albacore Tuna (Thunnus alalunga) That Account for Spatial and Seasonal Variation in the Distributions of Mature and Immature Fish. PloS one. 9:e83017; 2014.

Farley, J.H.; Williams, A.J.; Hoyle, S.D.; Davies, C.R.; Nicol, S.J. Reproductive dynamics and potential annual fecundity of South Pacific albacore tuna (Thunnus alalunga). PloS one. 8:e60577; 2013b.

Francis, R.I.C.C. Data weighting in statistical fisheries stock assessment models. Canadian Journal of Fisheries and Aquatic Sciences. 68:1124-1138; 2011.

Gertseva, V.; Matson, S.E.; Cope, J. Spatial growth variability in marine fish: example from Northeast Pacific groundfish. ICES Journal of Marine Science. 74:1602-1613; 2017.

Goodyear, C.P. Spawning stock biomass per recruit in fisheries management: Foundation and current use. Canadian Special Publication of Fisheries and Aquatic Sciences. 120:67-81; 1993.

Goodyear, C.P. Modeling growth: consequences from selecting samples by size. Transactions of the American Fisheries Society. 148:528-551; 2019.

Hoyle, S.; Hampton, J.; Davies, N. Stock assessment of albacore tuna in the South Pacific ocean. Scientific Committee, Eighth Regular Session, 7-15 August 2012, Busan, Republic of Korea; 2012

Hoyle, S.D. Adjusted biological parameters and spawning biomass calculations for South Pacific albacore tuna, and their implications for stock assessments. WCPFC-SC4-ME-WP-2. 4th Scientific Committee. Nouméa, New Caledonia: Western and Central Pacific Fisheries Commission; 2008

Hoyle, S.D.; Chang, S.-T.; Fu, D.; Itoh, T.; Lee, S.I.; Lucas, J.; Matsumoto, T.; Yeh, Y.-M.; Wu, R.-F.; Lee, M.K. Review of size data from Indian Ocean longline fleets, and its utility for stock assessment. IOTC-2021-WPTT23-07. Working Party on Tropical Tunas. Online: Indian Ocean Tuna Commission; 2021

Hoyle, S.D.; Sharma, R.; Herrera, M. Stock assessment of albacore tuna in the Indian Ocean for 2014 using Stock Synthesis, IOTC–2014–WPTmT05–24. IOTC Working Party on Temperate Tunas. Busan, Rep. of Korea; 2014

IOTC Secretariat. Report and documentation of the Indian Ocean Tuna Fisheries of Indonesia Albacore Catch Estimation Workshop: Review of Issues and Considerations. IOTC Technical Report. No. 2013/01. Bogor-Jakarta: Indian Ocean Tuna Commission; 2013

ISC Albacore Working Group. Stock assessment of albacore tuna in the North Pacific Ocean in 2023. 23rd Meeting of the International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific Ocean. Kanazawa, Japan; 2023

Kell, L.T.; Nash, R.D.; Dickey-Collas, M.; Mosqueira, I.; Szuwalski, C. Is spawning stock biomass a robust proxy for reproductive potential? Fish and Fisheries. 17:596-616; 2016.

Kimura, D.K. Statistical assessment of the age-length key. Journal of the Fisheries Research Board of Canada. 34:317-324; 1977.

Labonne, M.; Darnaude, A.M.; Fily, T.; Petit, C.; Nikolic, N.; Parker, D.; Norman, S.J.; Clear, N.; Farley, J.; Eveson, J.P. New Insights in Lifetime Migrations of Albacore Tuna (Thunnus alalunga, Bonnaterre, 1788) between the Southwest Indian and the Southeast Atlantic Oceans Using Otolith Microchemistry. Fishes. 9:38; 2024.

Langley, A. Stock assessment of albacore tuna in the Indian Ocean using Stock Synthesis for 2019. IOTC–2019–WPTmT07 (AS)–11; 2019.

Langley, A.; Hoyle, S. Stock assessment of albacore tuna in the Indian Ocean using Stock Synthesis, IOTC–2016–WPTmT06–25. IOTC Working Party on Temperate Tunas. Shanghai, China; 2016

Lee, H.; Maunder, M.N.; Piner, K.R. Good Practices for estimating and using length-at-age in integrated stock assessments. Fisheries Research. 270:106883; 2024.

Medina, A. Reproduction of Atlantic bluefin tuna. Fish and Fisheries. 21:1109-1119; 2020.

Megalofonou, P. Age and growth of Mediterranean albacore. Journal of Fish Biology. 57:700-715; 2000.

Minte-Vera, C.V.; Maunder, M.N.; Schaefer, K.M.; Aires-da-Silva, A.M. The influence of metrics for spawning output on stock assessment results and evaluation of reference points: an illustration with yellowfin tuna in the eastern Pacific ocean. Fisheries Research. 217:35-45; 2019.

Mondal, S.; Lee, M.-A. Habitat modeling of mature albacore (Thunnus alalunga) tuna in the Indian Ocean. Frontiers in Marine Science; 2023.

Moore, B.; Langley, A.; Farley, J.; Hoyle, S. Improving biological knowledge of albacore tuna, Thunnus alalunga, in the Indian Ocean: a scoping study. IOTC–2019–WPTmT07(AS)–04. IOTC Working Party on Temperate Tunas. Kuala Lumpur, Malaysia: Indian Ocean Tuna Commission,; 2019

Moore, B.; Langley, A.; Farley, J.H.; Hoyle, S. Improving biological knowledge of albacore tuna, Thunnus alalunga, in the Indian Ocean: a scoping study. The Food and Agriculture Organization of the United Nations (Indian Ocean Tuna Commission); 2020

Murua, H.; Rodriguez-Marin, E.; Neilson, J.D.; Farley, J.H.; Juan-Jordá, M.J. Fast versus slow growing tuna species: age, growth, and implications for population dynamics and fisheries management. Reviews in Fish Biology and Fisheries. 27:733-773; 2017.

Nikolic, N.; Montes, I.; Lalire, M.; Puech, A.; Bodin, N.; Arnaud-Haond, S.; Kerwath, S.; Corse, E.; Gaspar, P.; Hollanda, S. Connectivity and population structure of albacore tuna across southeast Atlantic and southwest Indian Oceans inferred from multidisciplinary methodology. Scientific reports. 10:15657; 2020.

Nikolic, N.; Morandeau, G.; Hoarau, L.; West, W.; Arrizabalaga, H.; Hoyle, S.; Nicol, S.J.; Bourjea, J.; Puech, A.; Farley, J.H. Review of albacore tuna, Thunnus alalunga, biology, fisheries and management. Reviews in fish biology and fisheries. 27:775-810; 2017.

Ortiz de Zárate, V.; Macías, D.; Arocha, F.; Su, N.-J.; Dheeraj, B.; Hanke, A.; Puerto, M.; Gómez, M.; Quelle, P.; Chapela, I.; Jaranay, M. Albacore (*Thunnus alalunga*) reproductive biology study for the North Atlantic stock: Years 2023 and 2024. SCRS/2024/033. Collect Vol Sci Pap ICCAT. 81:1-17; 2024.

Pacicco, A.E.; Allman, R.J.; Lang, E.T.; Murie, D.J.; Falterman, B.J.; Ahrens, R.; Walter III, J.F. Age and Growth of Yellowfin Tuna in the US Gulf of Mexico and Western Atlantic. Marine and Coastal Fisheries. 13:345-361; 2021.

Rice, J. Stock assessment of albacore tuna (Thunnus alalunga) in the Indian Ocean using Stock Synthesis. IOTC-2022-WPTmT_8 (Virtual meeting July-11-22 2022); 2022

Saber, S.; de Urbina, J.O.; Gómez-Vives, M.J.; Macías, D. Some aspects of the reproductive biology of albacore Thunnus alalunga from the western Mediterranean Sea. Journal of the Marine Biological Association of the United Kingdom. 95:1705-1715; 2015.

Santiago, J.; Arrizabalaga, H. An integrated growth study for North Atlantic albacore (*Thunnus alalunga*, Bonn. 1788). ICES Journal of Marine Science. 62:740-749; 2005. 10.1016/j.icesjms.2005.01.015

Schaefer, K.M. Reproductive biology of tunas. in: Block B.A., Stevens E.D., eds. Tuna physiology, ecology, and evolution: Academic Press; 2001

Schemmel, E.; Bohaboy, E.C.; Kinney, M.J.; O'Malley, J.M. An assessment of sampling approaches for estimating growth from fishery-dependent biological samples. ICES Journal of Marine Science. 79:1497-1514; 2022.

Ueyanagi, S. Larval distribution of tunas and billfishes in the Atlantic Ocean. FAO Fishery Report: UN-FAO; 1971

Wells, R.J.D.; Kohin, S.; Teo, S.L.H.; Snodgrass, O.E.; Uosaki, K. Age and growth of North Pacific albacore (Thunnus alalunga): Implications for stock assessment. Fisheries Research. 147:55-62; 2013. 10.1016/j.fishres.2013.05.001

Williams, A.J.; Farley, J.H.; Hoyle, S.D.; Davies, C.R.; Nicol, S.J. Spatial and sex-specific variation in growth of albacore tuna (Thunnus alalunga) across the South Pacific Ocean. PLoS One. 7:e39318; 2012. 10.1371/journal.pone.0039318

Wood, S.N. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Series B (Statistical Methodology). 73:3-36; 2011.

12. Tables

Table 1: Number of albacore lengths measured per year by flag, held in the IOTC size database.

	CHN	JPN	KOR	SYC	TWN	ZAF
1965	0	29131	0	0	0	0
1966	0	24641	0	0	0	0
1967	0	10117	0	0	0	0
1968	0	6885	0	0	0	0
1969	0	8310	0	0	0	0
1970	0	7004	0	0	0	0
1971	0	8783	0	0	0	0
1972	0	4569	0	0	0	0
1973	0	7336	0	0	0	0
1974	0	7377	0	0	0	0
1975	0	4122	0	0	0	0
1976	0	8569	0	0	0	0
1977	0	5564	0	0	0	0
1978	0	5067	0	0	0	0
1979	0	4810	0	0	0	0
1980	0	6033	0	0	21178	0
1981	0	13696	0	0	117347	0
1982	0	12879	0	0	198040	0
1983	0	10740	0	0	158930	0
1984	0	11977	0	0	151661	0
1985	0	18319	0	0	45833	0
1986	0	15340	0	0	43826	0
1987	0	13269	0	0	39540	0
1988	0	7441	0	0	26188	0
1989	0	9218	0	0	7977	0
1990	0	9660	0	0	7331	0
1991	0	4083	0	0	9226	0
1992	0	6282	0	0	12157	0
1993	0	2325	0	0	16082	0
1994	0	856	0	0	42038	0
1995	0	927	0	0	38122	0
1996	0	581	0	0	68541	0
1997	0	2849	0	0	33976	0
1998	0	2479	0	0	41362	0
1999	0	1575	0	0	22734	0
2000	0	2326	0	0	46905	0
2001	0	4236	0	0	69761	0
2002	0	2457	0	0	84823	257
2003	0	1656	0	0	146642	183
2004	0	2407	0	0	155769	209
2005	0	6293	0	0	210183	39
2006	0	9921	0	0	83034	118
2007	0	7008	437	2701	74868	1
2008	0	516	0	12259	88789	48
2009	822	2240	12	3244	122637	127
2010	730	1933	1166	351	183474	50
2011	0	4962	0	5518	76912	0
2012	101	3287	6901	89	46480	0
2013	354	3522	12054	3587	141602	0
2014	616	16101	120	1374	225331	0

	CHN	JPN	KOR	SYC	TWN	ZAF
2015	3	6147	609	7	174906	0
2016	1291	3861	16	90	140327	0
2017	4	3086	163	4105	139052	655
2018	6612	10119	1596	99	356215	1780
2019	2550	15580	5	363	399115	1695
2020	16	234	55	5116	314815	0
2021	10227	0	26	18356	205821	0
2022	502	0	0	10344	330510	0

13. Figures

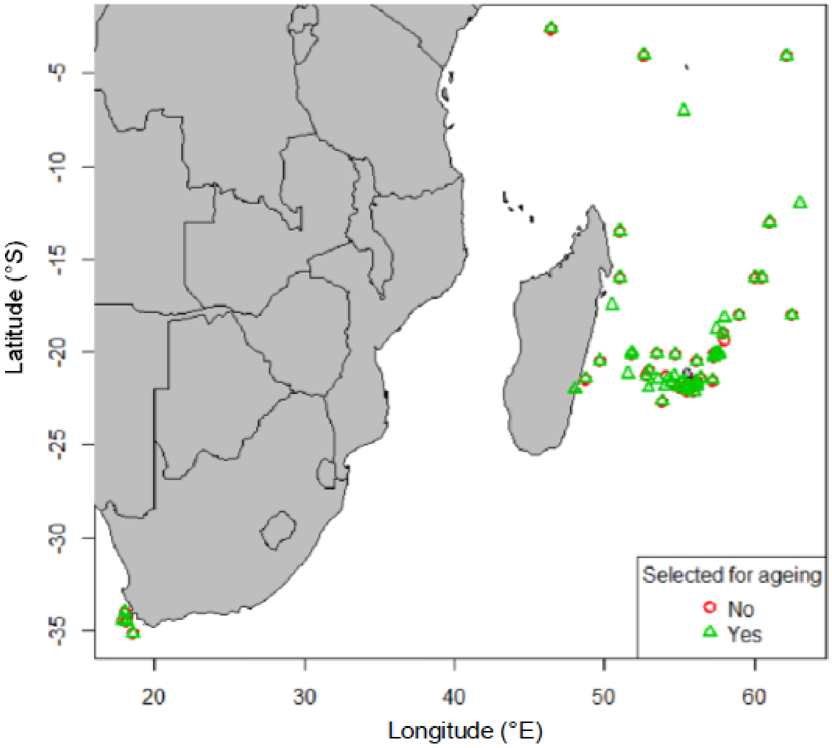

Figure 1: Map of albacore otolith sampling locations in the Indian Ocean (Farley et al., 2019). Green triangles indicate samples that were selected for ageing.

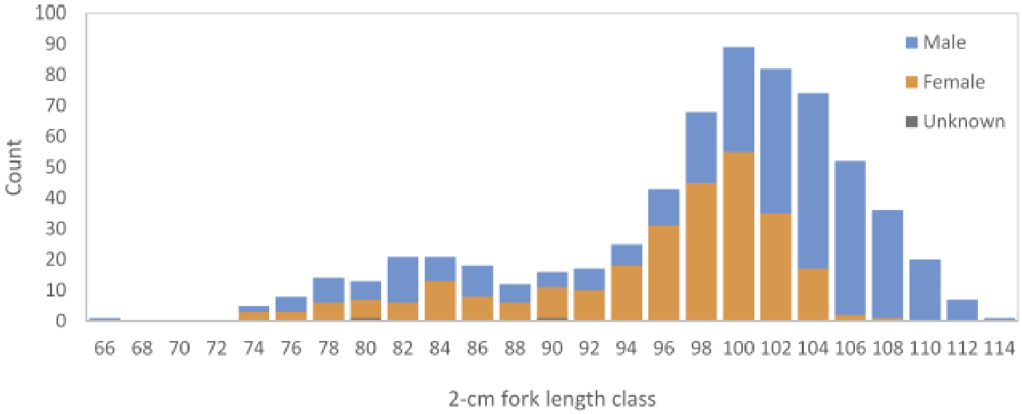

Figure 2: Length frequencies (2-cm) of Indian Ocean albacore selected for age estimation by sex.

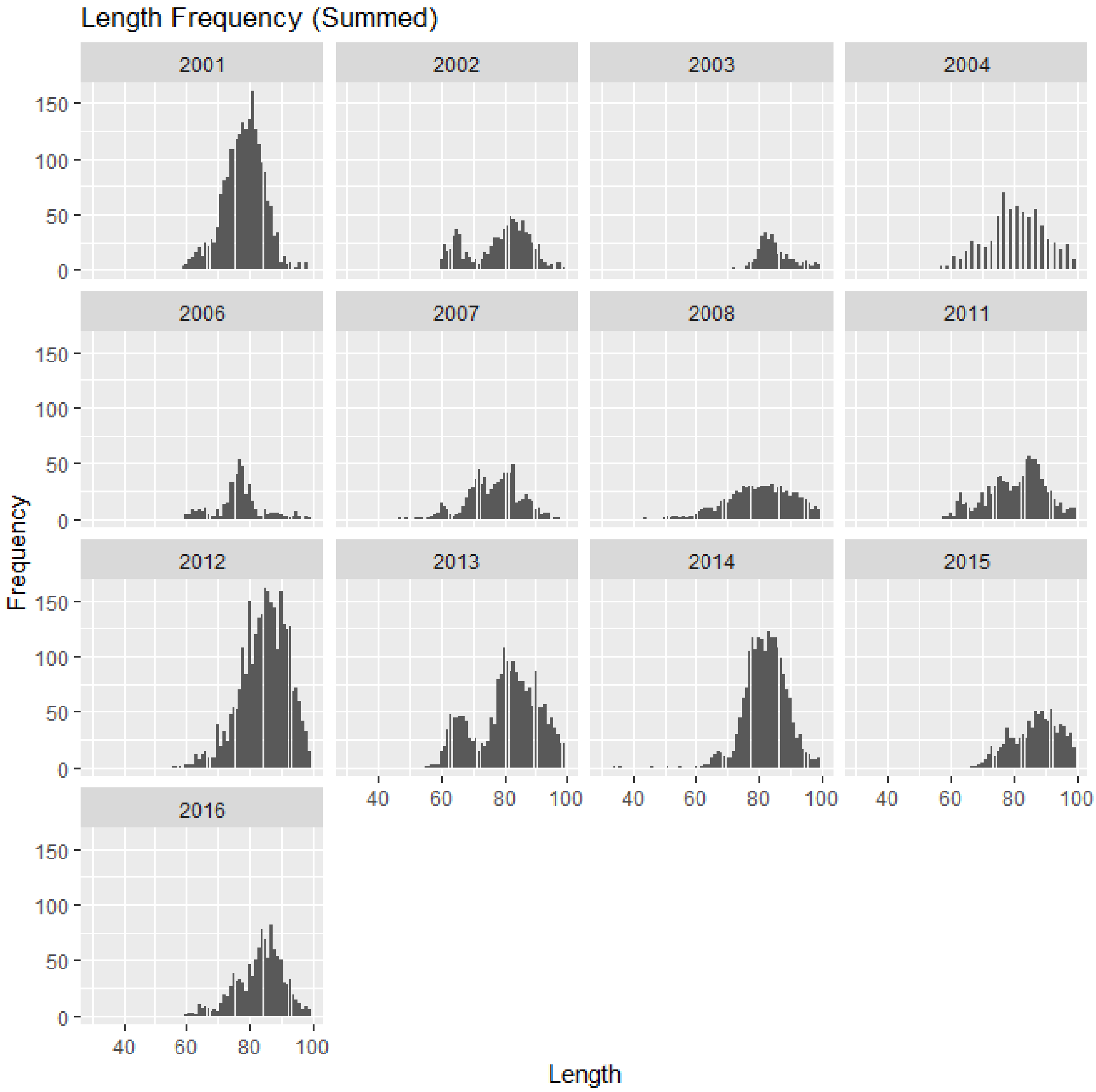

Figure 3: Length frequencies by year of albacore sampled from the South African pole and line fishery, which mostly operates on the Atlantic coast.

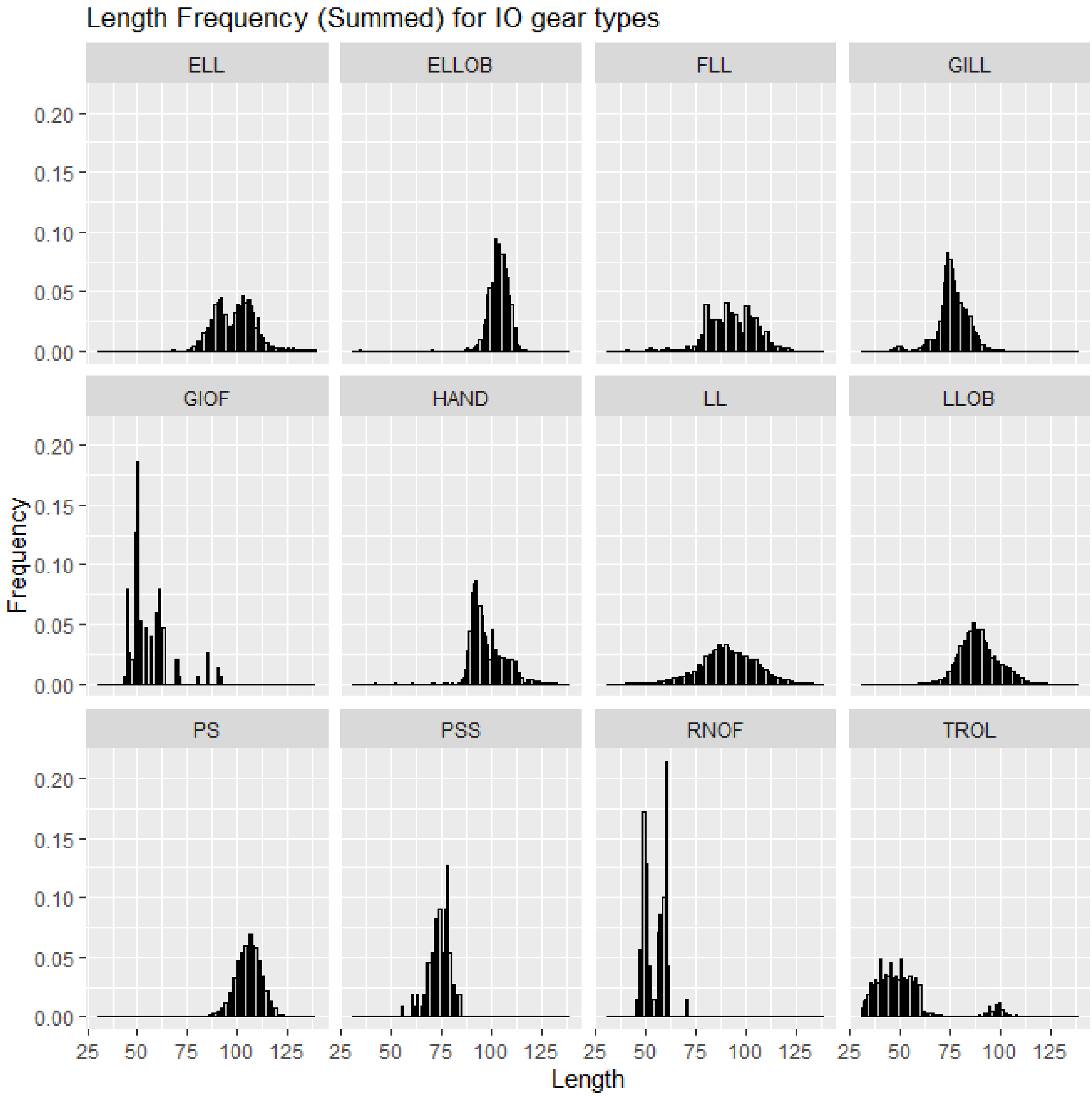

Figure 4: Length frequencies by gear type for albacore size data held in the IOTC databases. ELL: longline targeting swordfish; ELLOB: observer longline targeting swordfish; FLL: longline fresh; GILL: driftnet; GIOF: offshore gill net; HAND: hand line; LL: longline; LLOB: longline with observer; PS: purse seine; PSS: small purse seine; RNOF: offshore ring net; TROL: troll.

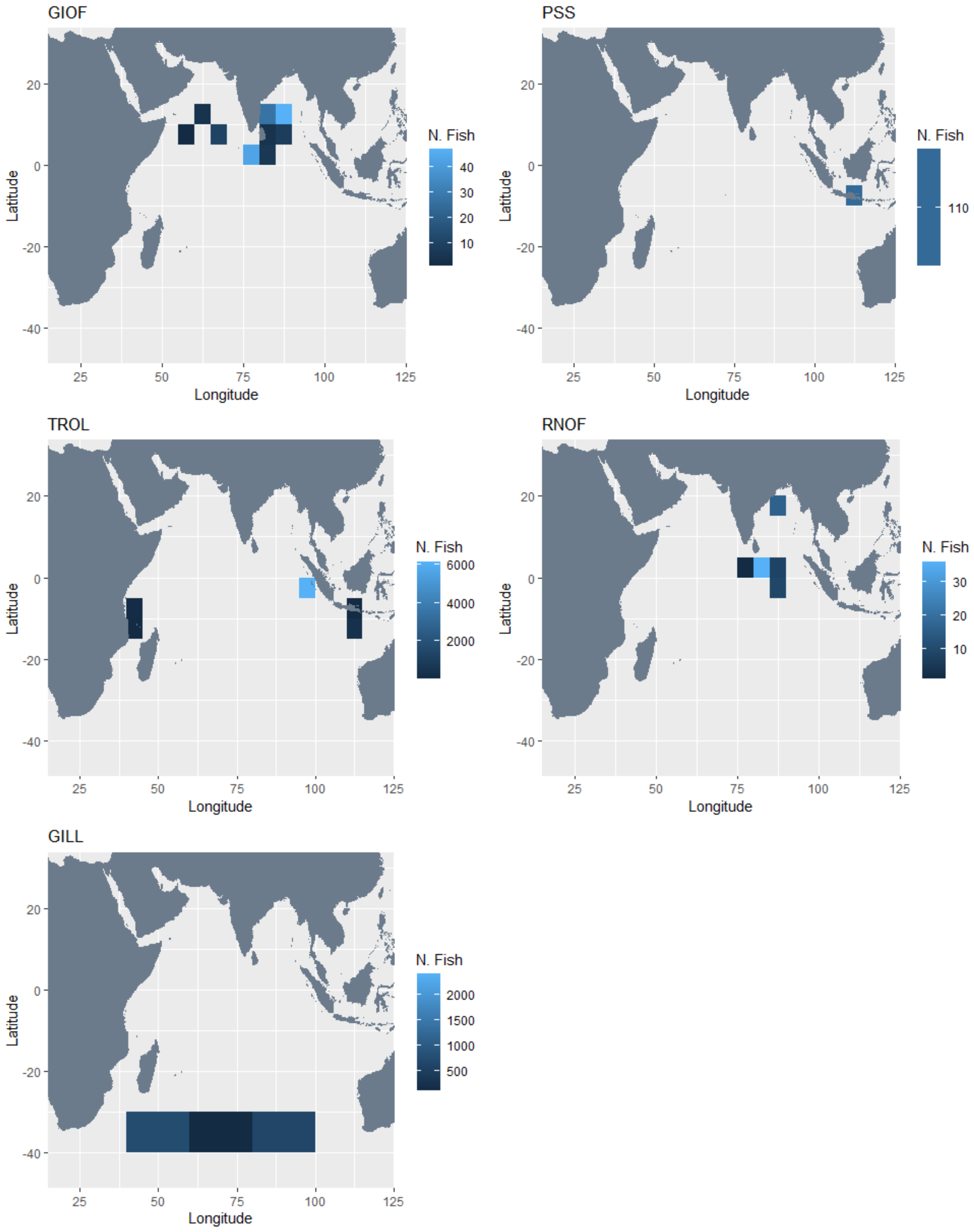

Figure 5: Reported catch locations from all fisheries catching smaller fish than those caught in the longline fishery. These are the offshore gillnet fishery (GIOF), the Indonesian small purse seine fishery (PSS), several troll line fisheries (TROL), offshore ringnet fisheries (RNOF), and the drift gillnet fishery (GILL).

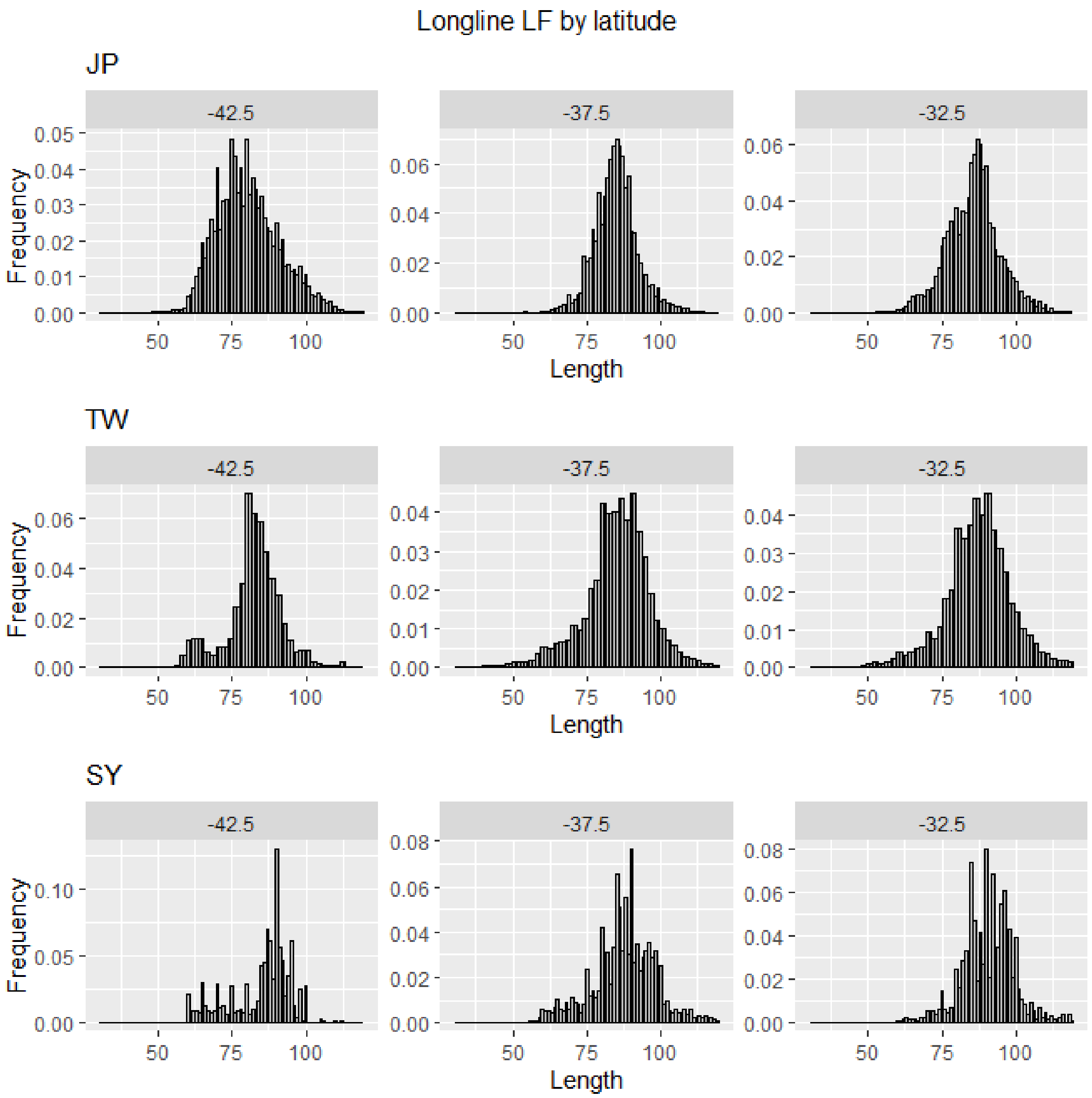

Figure 6: Length frequency distribution south of 30 °S by fleet and latitude, aggregated across years, for the 3 longline fleets with the most data.

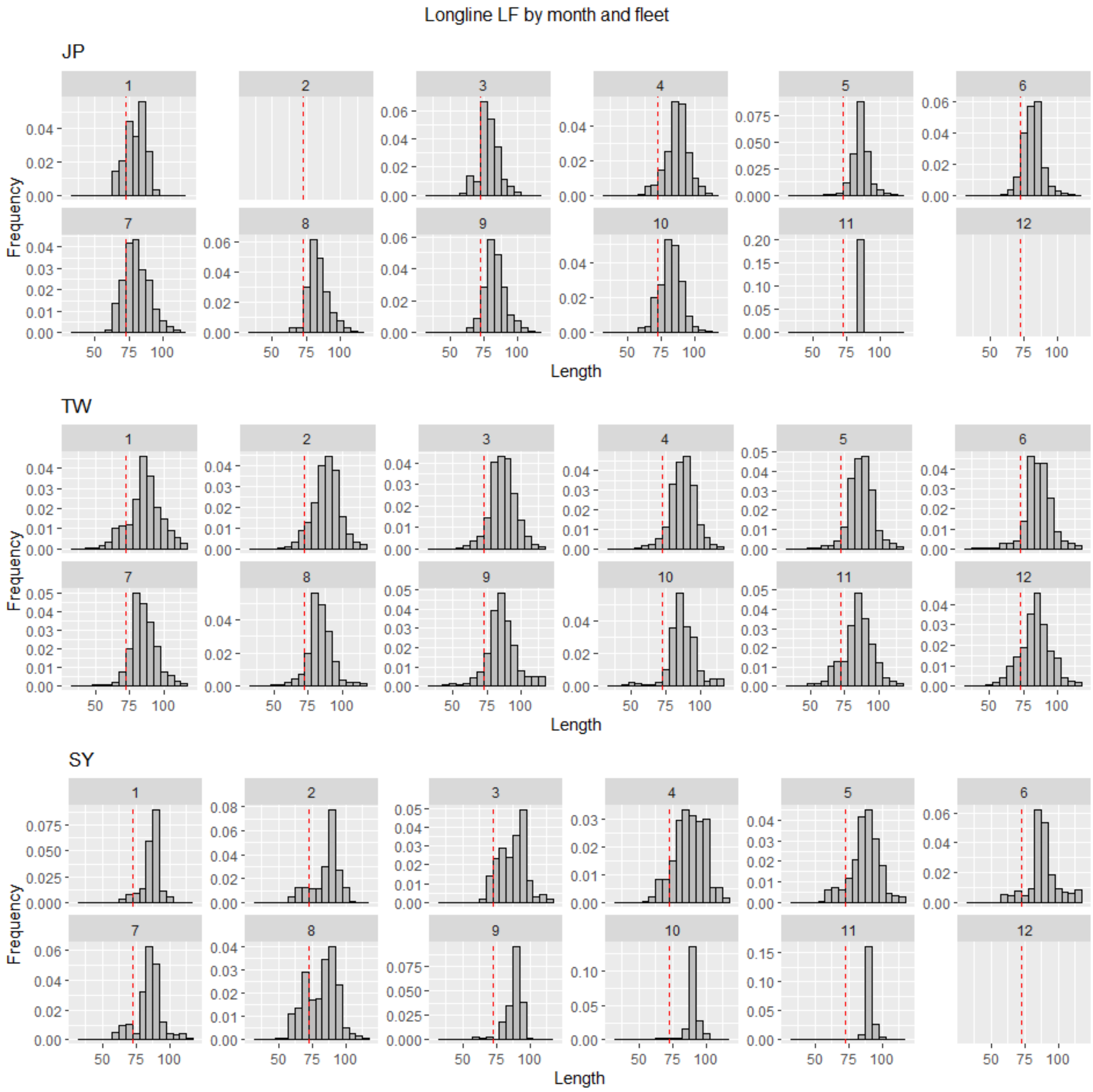

Figure 7: Length frequency distributions of fish sampled since 2000 and south of 35 °S, by month and flag. The red dashed line is at 70cm in each plot.

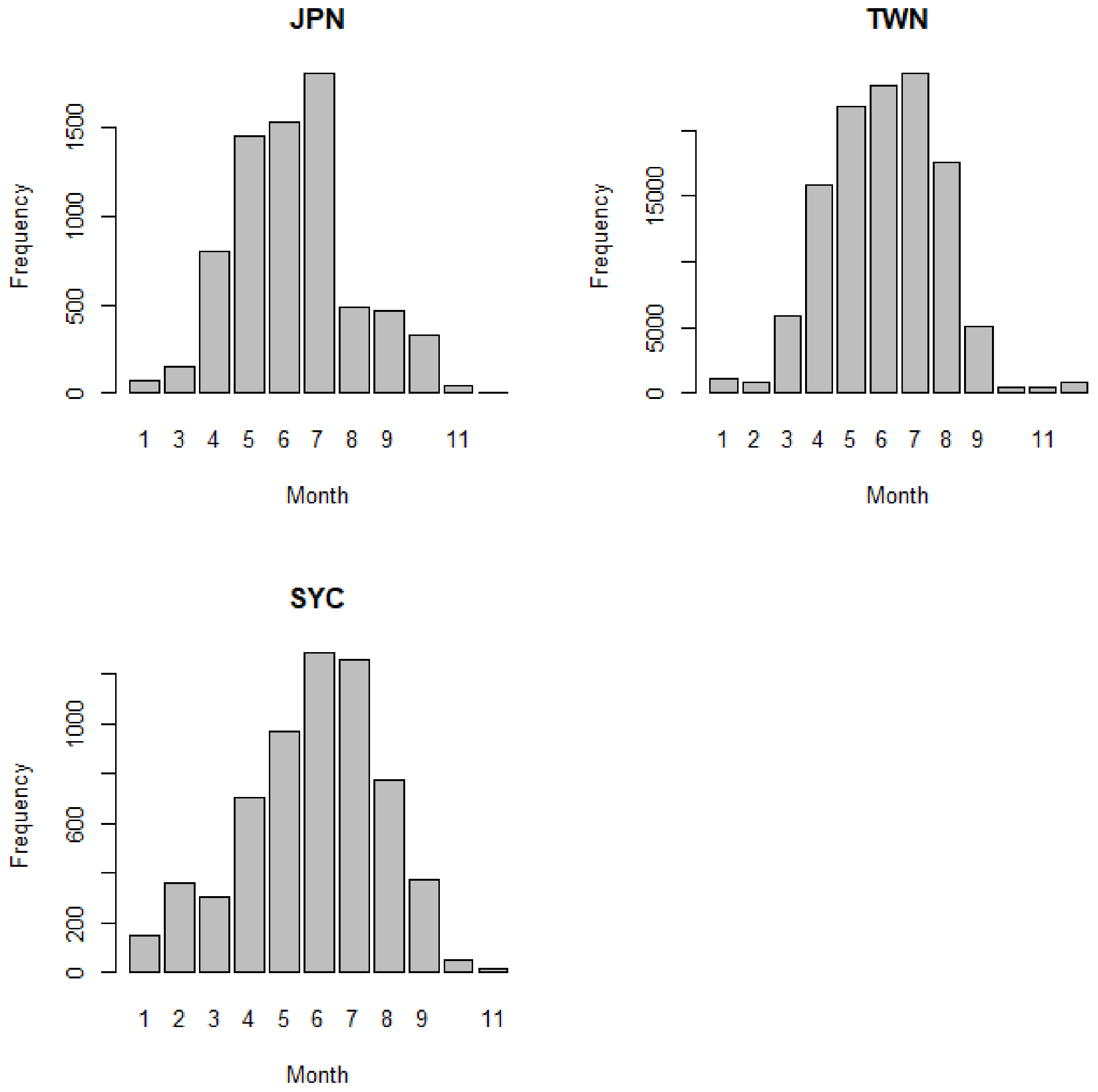

Figure 8: Mean number of samples per month and year by fleet for the period since 2000.

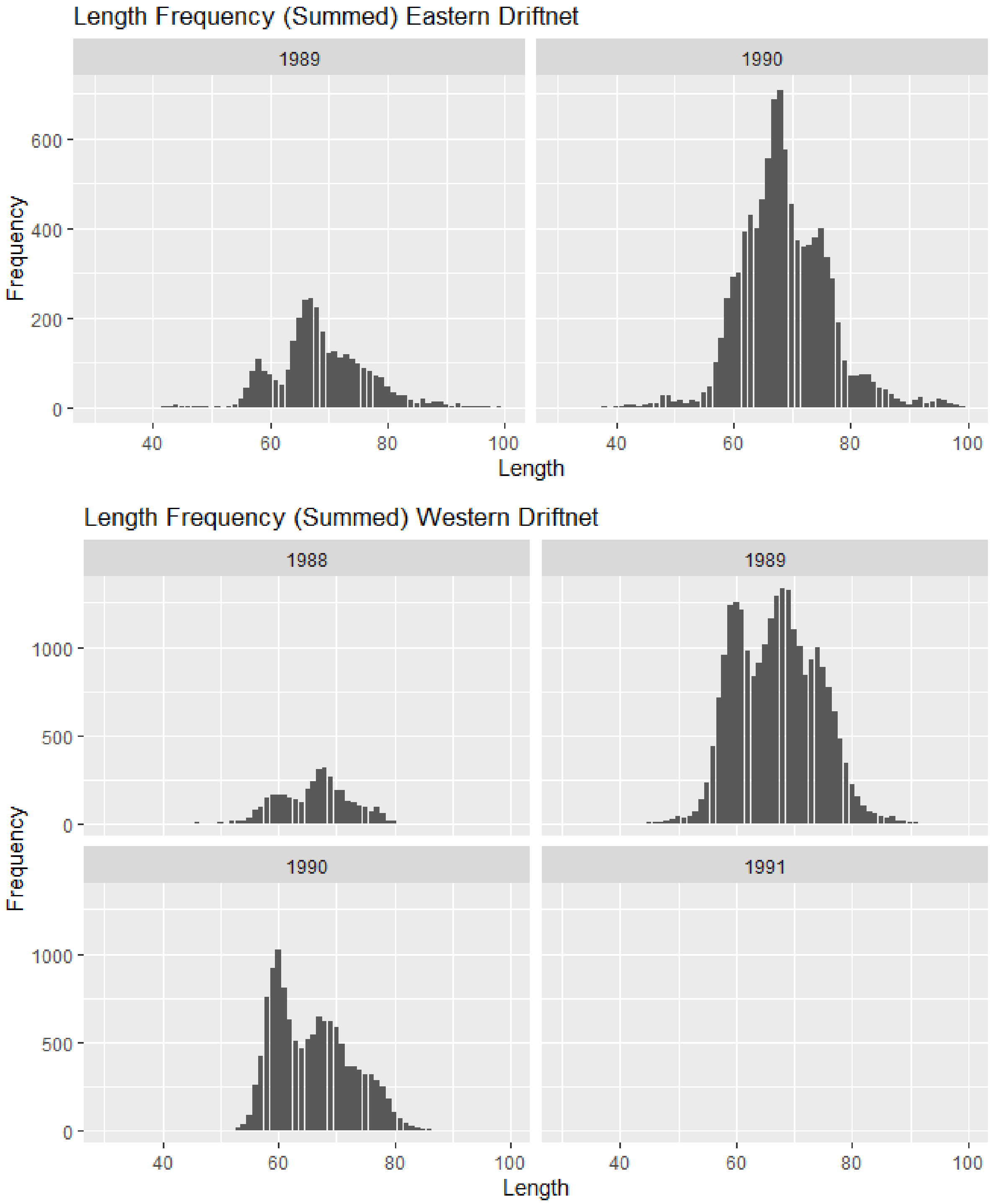

Figure 9: Length frequencies by year of albacore sampled from the driftnet fishery in the South Pacific Ocean, to the east (above) and the west (below) of 180° longitude.

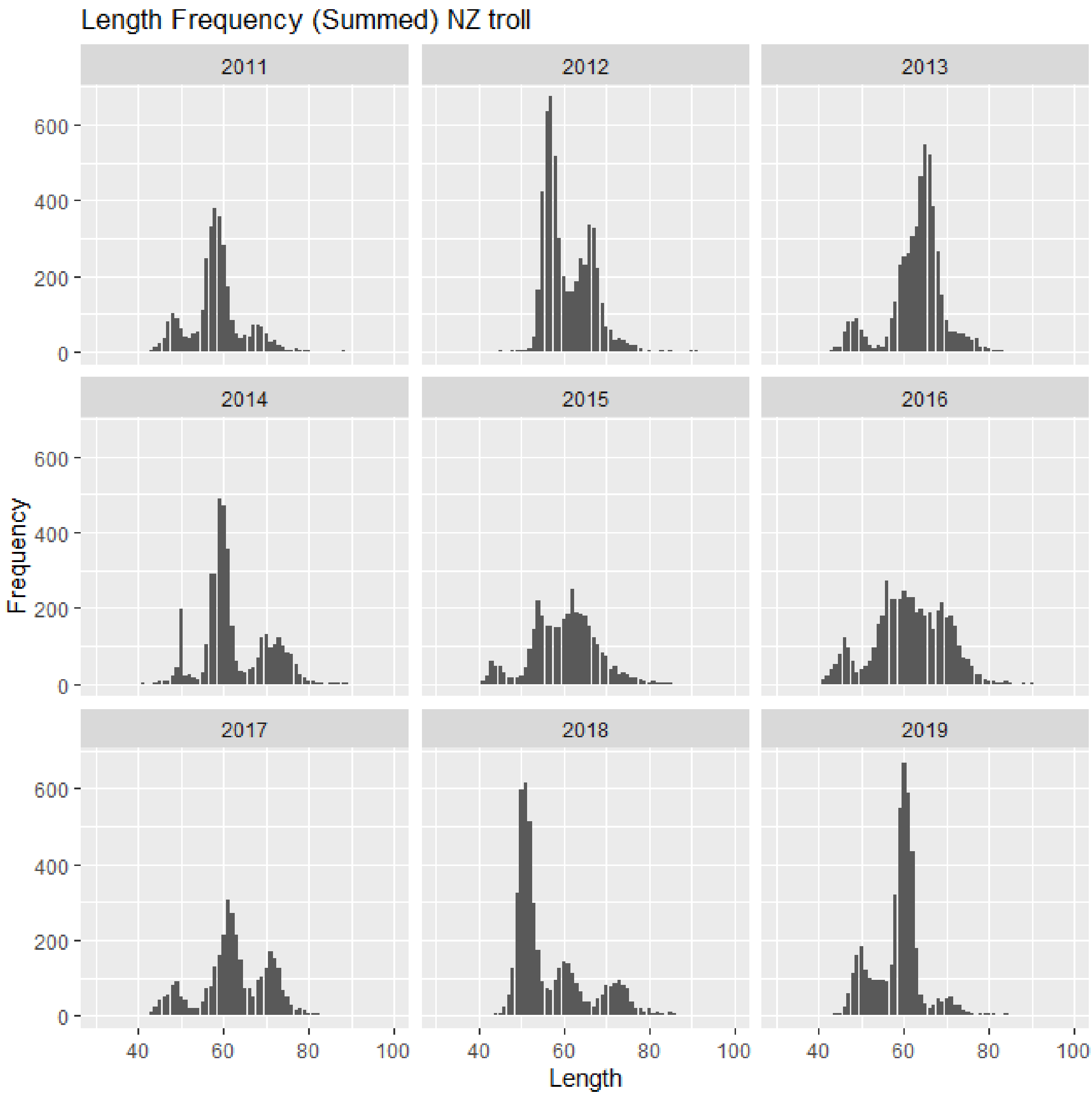

Figure 10: Length frequencies by year of albacore sampled from the New Zealand troll fishery in the South Pacific.

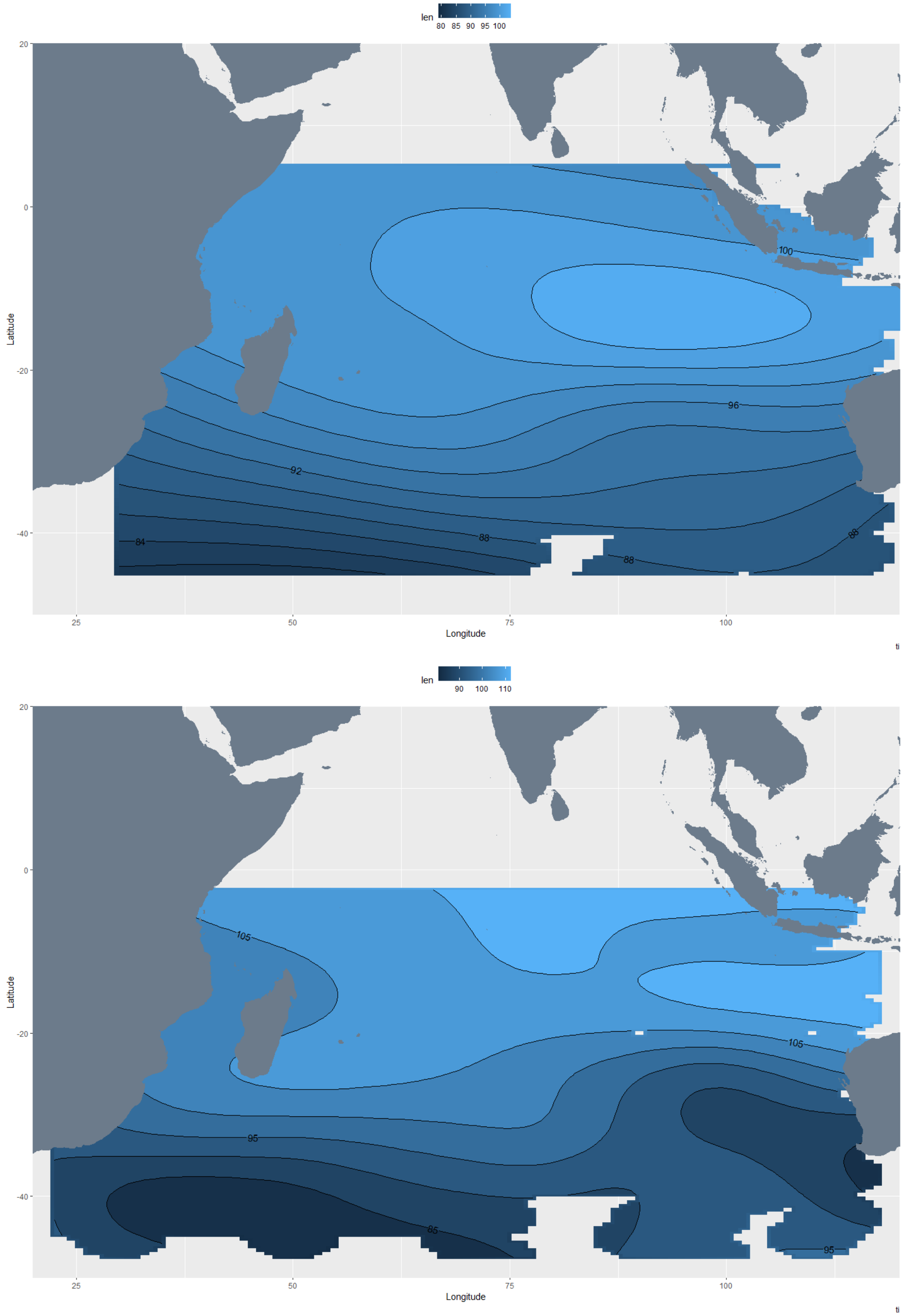

Figure 11: Spatial size patterns in Japanese longline catch samples of albacore tuna stratified at 10 by 20 resolution and sampled between 1965 and 2008 (above); and stratified at 5 x 5 resolution and sampled between 2009 and 2022 (below).

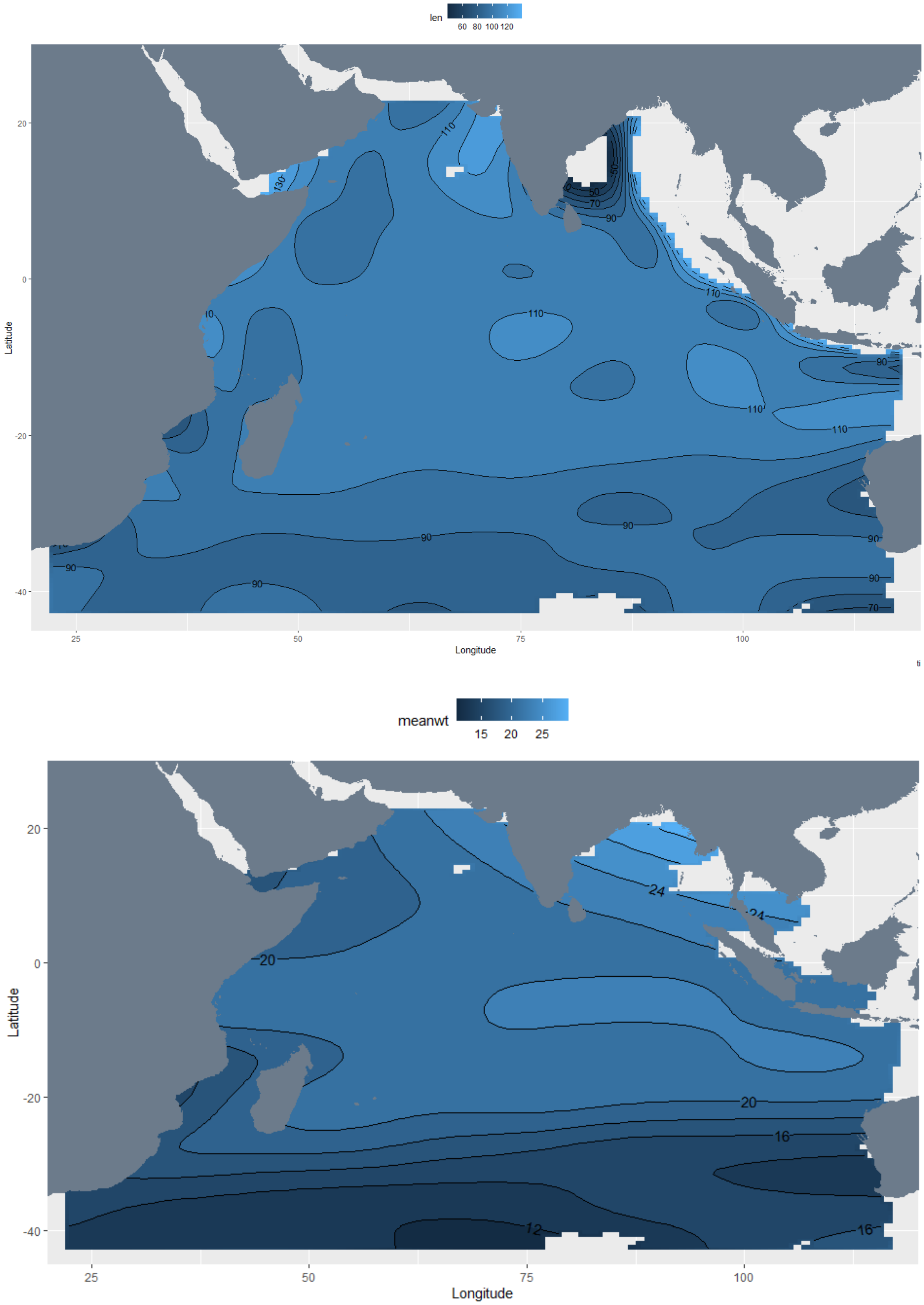

Figure 12: Spatial patterns of length frequency (above) and mean weight (below) in Taiwanese longline catch samples of albacore tuna, stratified at 5x5 resolution and sampled between 1980 and 2022.

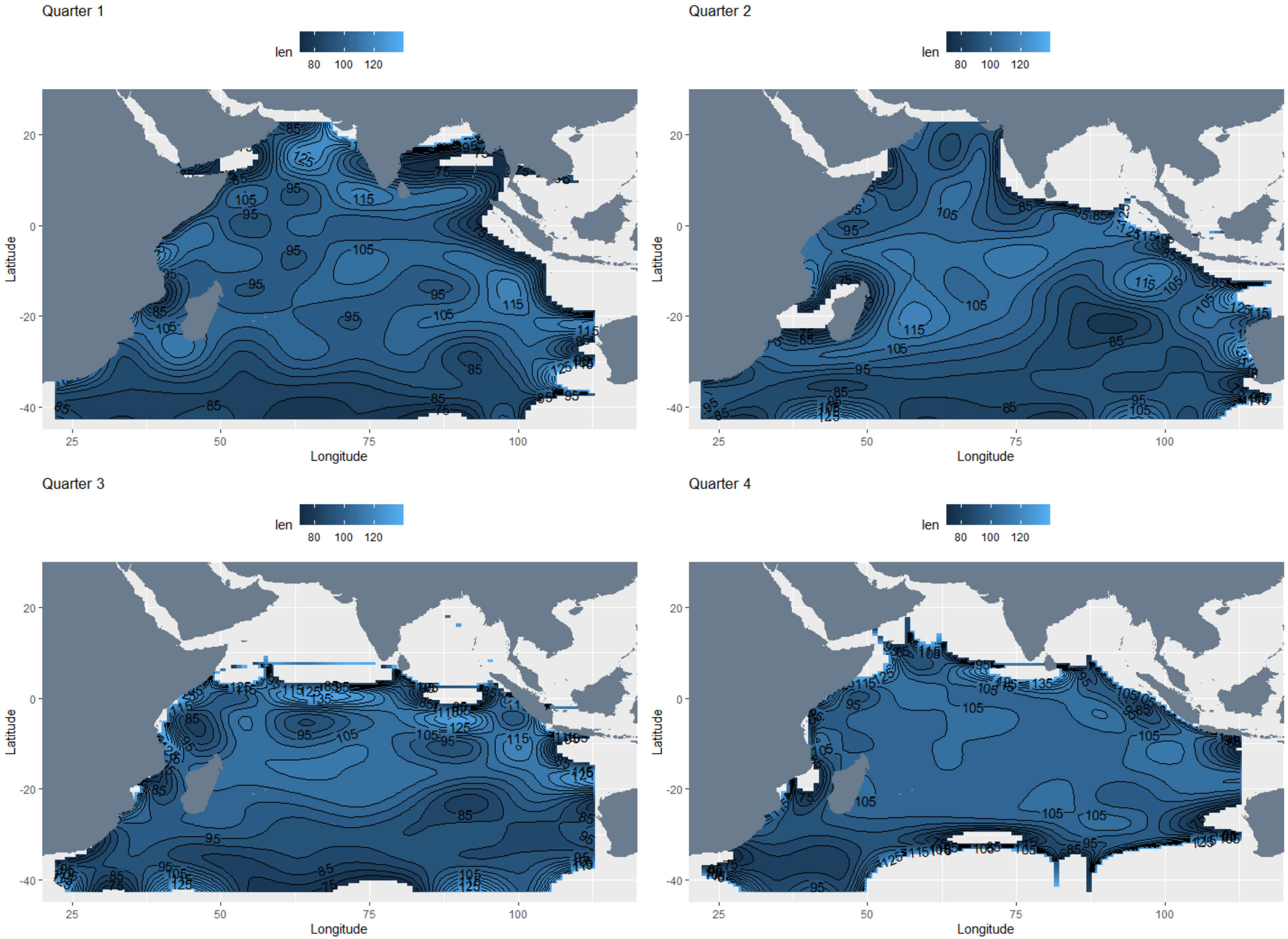

Figure 13: Spatial patterns of length frequency by quarter in Taiwanese longline catch samples of albacore tuna stratified at 5 by 5 resolution and sampled between 1980 and 2022.

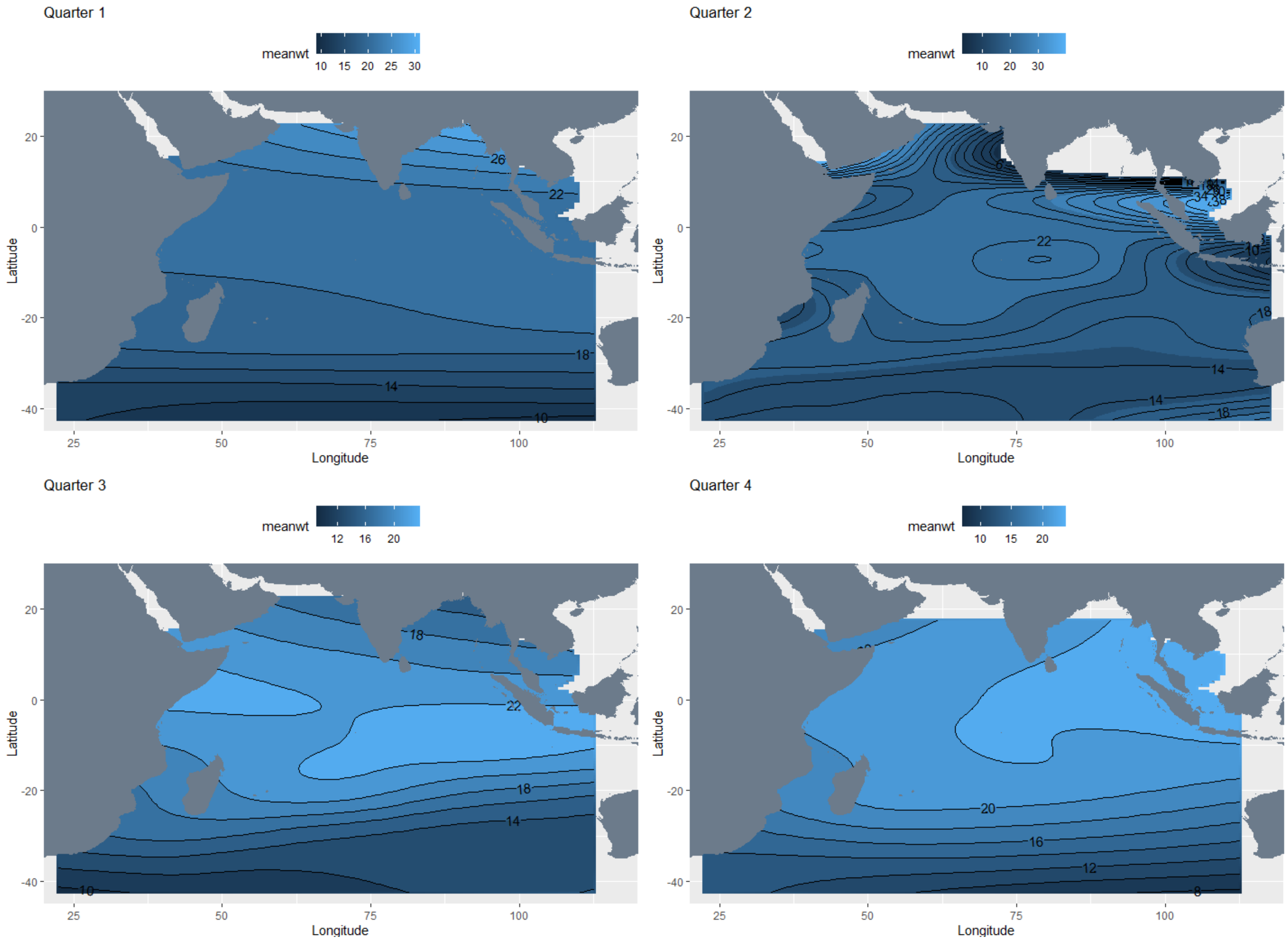

Figure 14: Spatial patterns mean weight by quarter in Taiwanese longline catch samples of albacore tuna stratified at 5 by 5 resolution and sampled between 1980 and 2022

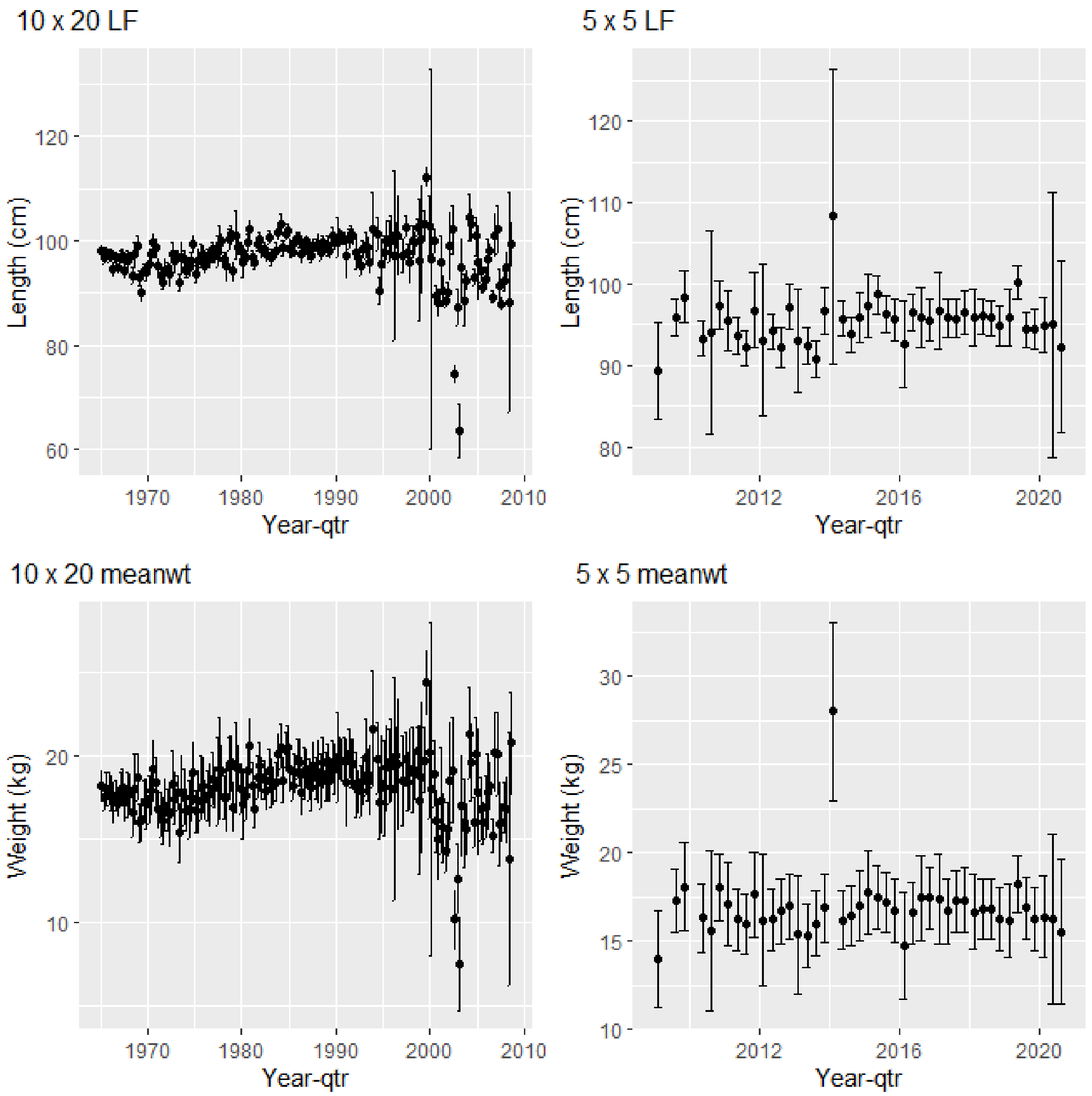

Figure 15: Temporal size patterns in Japanese longline catch samples of albacore tuna stratified at 10 by 20 resolution and sampled between 1965 and 2008 (left); and stratified at 5 x 5 resolution and sampled between 2009 and 2020 (right). Estimates are based on length frequency data (above) and mean weights (below).

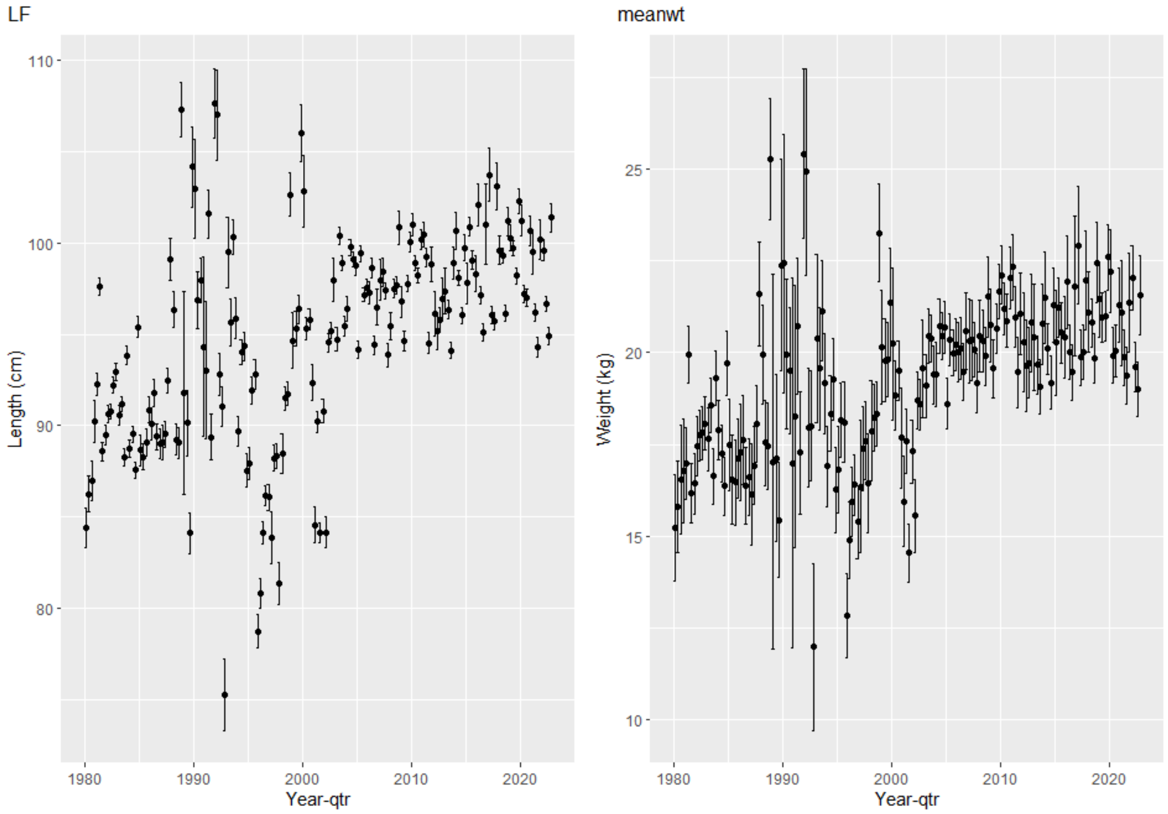

Figure 16: Temporal size patterns by quarter in Taiwanese longline catch samples of albacore tuna stratified at 5 by 5 resolution and sampled between 1980 and 2022. Estimates are based on length frequency data (left) and mean weights (right).

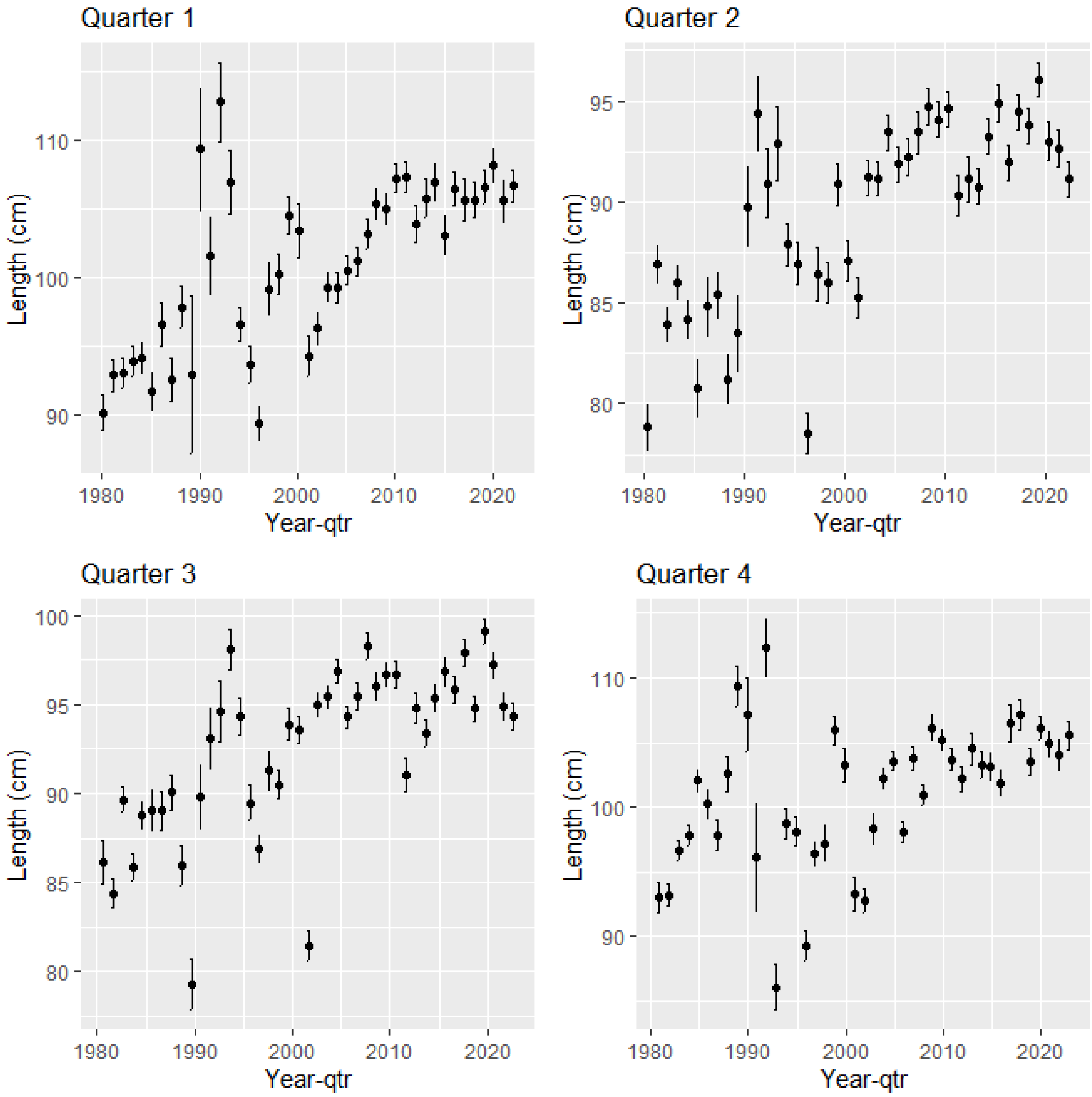

Figure 17: Temporal length frequency patterns by quarter in Taiwanese longline catch samples of albacore tuna stratified at 5 by 5 resolution and sampled between 1980 and 2022.

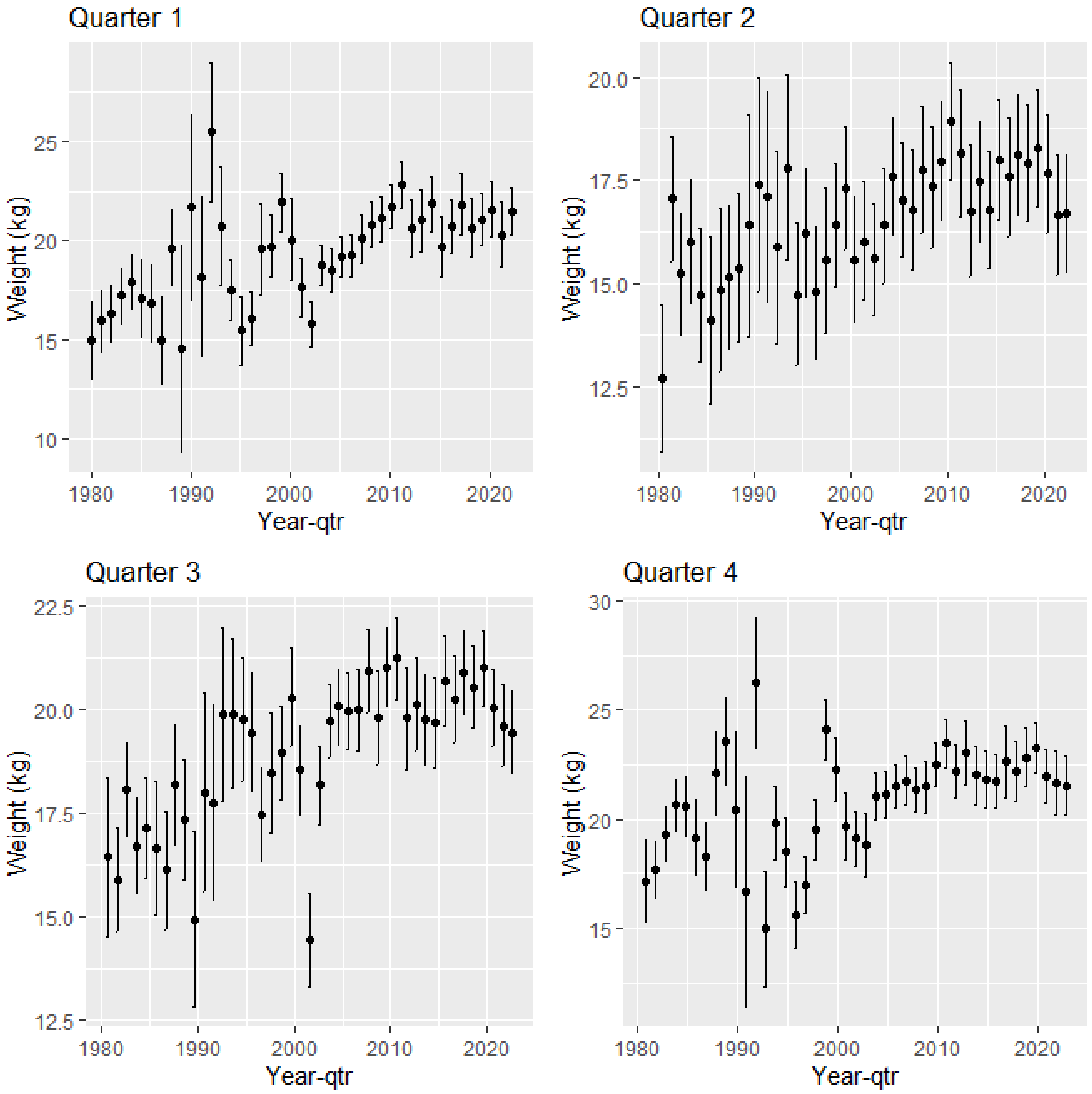

Figure 18: Temporal patterns in mean weights by quarter in Taiwanese longline catches of albacore tuna stratified at 5 by 5 resolution and sampled between 1980 and 2020.