JAPANESE LONGLINE CATCHES OF BLUEFIN TUNA IN THE ATLANTIC OCEAN, 1950-1970

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SUMMARY

From 1957 to 1970, Japanese longliners targeting tropical tunas in the Central Atlantic encountered Atlantic bluefin tuna. During this period, catches of bluefin tuna were widely disbursed within the region. This event is one of the most fascinating changes in bluefin tuna spatial distribution observed in the second half of the twentieth century. In particular, the catches that occurred off the coast of Brazil have received much attention in the scientific literature. However, the overall catch data alone provides an incomplete picture. ICCAT is now in the process of conducting a Management Strategy Evaluation of Atlantic bluefin tuna and these older Japanese longline catches are to be incorporated in this process. ICCAT may find it useful to examine these catches more closely with a view toward ensuring that assumptions regarding this data are correct. Therefore, a survey of the scientific literature for discussion of and data pertaining to Japanese longline activity in the Atlantic Ocean during this period may yield some answers to important questions.

RÉSUMÉ

De 1957 à 1970, les palangriers japonais ciblant les thonidés tropicaux dans l'Atlantique central ont observé du thon rouge de l'Atlantique. Au cours de cette période, les captures de thon rouge ont été grandement réparties dans la région. Cet événement est l'un des changements les plus fascinants de la distribution spatiale du thon rouge observés au cours de la seconde moitié du XXe siècle. En particulier, les captures effectuées au large des côtes du Brésil ont occupé une place importante dans la littérature scientifique. Cependant, les données générales sur les captures ne fournissent pas à elles seules une image complète. L'ICCAT est actuellement en train de mener une évaluation de la stratégie de gestion du thon rouge de l'Atlantique et ces anciennes captures réalisées par des palangriers japonais doivent être intégrées à ce processus. L'ICCAT peut juger utile d'examiner ces captures de plus près afin de s'assurer que les hypothèses concernant ces données sont correctes. Par conséquent, une étude de la littérature scientifique pour discussion et les données relatives à l'activité des palangriers japonais dans l'océan Atlantique au cours de cette période peut apporter des réponses à des questions importantes.

RESUMEN

Entre 1957 y 1970, los palangreros japoneses que se dedicaban a la pesca de túnidos tropicales en el Atlántico central se encontraron atún rojo del Atlántico. Durante este periodo, las capturas de atún rojo se devolvieron ampliamente en la región. Este evento es uno de los cambios más fascinantes en la distribución espacial del atún rojo observados en la segunda mitad del siglo XX. En particular, las capturas que se produjeron frente a las costas del Brasil han recibido mucha atención en la literatura científica. Sin embargo, los datos generales de captura por sí solos proporcionan una visión incompleta.ICCAT se encuentra ahora en el proceso de realizar una evaluación de la estrategia de ordenación del atún rojo del Atlántico y estas capturas japonesas de palangre más antiguas se incorporarán a este proceso. ICCAT puede considerar útil examinar estas capturas más detenidamente con miras a asegurar que los supuestos relativos a estos datos sean correctos. Por lo tanto, un estudio de la literatura científica para el debate y los datos relativos a la actividad de los palangreros japoneses en el océano Atlántico durante este período puede dar algunas respuestas a preguntas importantes.

KEYWORDS

Japanese longline, Atlantic bluefin tuna, Southern bluefin tuna, Brazilian Episode

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Introduction

Management Strategy Evaluation (MSE) is presently in development by ICCAT for the purpose of testing existing management strategies for Atlantic bluefin tuna (ABFT) and to identify a set of possible alternative management strategies. In the main, MSE, "..involves using simulation to compare the relative effectiveness for achieving management objectives of different combinations of data collection schemes, methods of analysis and subsequent processes leading to management actions" (Punt *et al.* 2014). One key component of the MSE process for ABFT, therefore, is the collection of valid catch data correctly applied to the east and west Atlantic bluefin stocks.

For many years, ABFT stock assessments conducted by the SCRS incorporated catch data going back no earlier than 1970 or 1974, even though catch data dating back to the 1950's and earlier, has existed in ICCAT's databases. There were significant reasons for the decision to limit historical catches to 1970 or 1974 when conducting assessments. Notably, catch-at-size/catch-at-length/catch-at-age data associated with purse seine and other catches for the period prior to the 1970s was sparse. Catch size data relative to these earlier landings was infrequently available until the early 1970s (Mather *et al.* 1995). However, the assumption regarding these JpnLL catches is that they were composed of large medium and giant BFT. Therefore, the decision by the SCRS to not use older catch data in stock assessments may have resulted in the longline data from 1950-1970 having been less well-examined than more recent catch data and therefore benefits from a closer examination before committing this data to the MSE catch database.

Here, we are examining harvesting of BFT by a longline fleet that was wide-ranging in coastal and distant-water regions of the Central Atlantic, on both side of the Atlantic. The data in ICCAT's database does not reveal the amount of catch by geographical location. Further, it becomes clear that the so-called Brazilian catch represents only a portion of the total JpnLL catch for the period.

Unlike the lengthy history of commercial exploitation of ABFT in northern, temperate regions in the Atlantic, we have only 14 years of data to work with in examining harvesting in the southern regions of the Central Atlantic and Southern Hemisphere. Consequently, due to the unusual nature of this migratory pattern, there may be difficulties in apportioning this catch to east and west stocks.

The Japanese Longline Fleet

The Japanese longline fleet (JpnLL) was the only wide-ranging, distant water fleet targeting ABFT in the Atlantic during the period, 1950-1970. JpnLL has been active in the Atlantic basin beginning in the early 1950s. Targeting of ABFT began in the Gulf of Mexico in 1964. However, bluefin catch in this area was very low until 1974 (Mather *et al.* 1995). JpnLL fishing in New England and off New York began in 1972, aimed at bigeye, albacore and bluefin. The Cape Hatteras fishery was exploited by JpnLL, first from 1964-1966 and then again in more recent years. The Bay of Biscay fishery for small and medium sized ABFT was exploited by JpnLL in 1974-1975, but declined rapidly thereafter. The Straits of Gibraltar region was exploited by JpnLL for bigeye and bluefin beginning in 1974. Finally, the Mediterranean was first exploited by JpnLL beginning in 1974 (Shingu *et al.* 1980), although ICCAT catch data for the Mediterranean indicates that JpnLL catches began there in 1972. Mather *et al.* 1995 states, "After the decline of their Atlantic bluefin tuna catches in the late 1960s and early 1970s, the Japanese shifted much of their effort to the eastern Atlantic and the Mediterranean. The remaining effort was concentrated in the northern Gulf of Mexico in May and June, when giant bluefin spawn there, and in the area south of the Grand Banks through much of the year."

Missing from the above description of JpnLL activity in the Atlantic is a period of 14 years (1957-1970) in which JpnLL were actively catching BFT in the Central Atlantic. The "Brazilian Episode", several consecutive years of catches by JpnLL off the coast of Brazil, was one event that occurred during this period.

Some Important Questions

The ICCAT catch database contains catches for both east and west Atlantic bluefin expressed as total annual landings by region i.e. Mediterranean and west and east Atlantic. **Table 2** contains a summary of annual landings by JpnLL allocated to east and west Atlantic stocks for the period 1950-1970. However, the amount of landings in each geographical area in which JpnLL interacted with BFT during this period is a matter of some speculation. The ICCAT database includes 39,400 MT of catches attributed to JpnLL for the period 1950-1970. Where did these catches occur? Given the wide-ranging nature of JpnLL fishing operations, covering numerous coastal and

remote areas on the high seas in the Central Atlantic, is it possible to speculate as to the distribution of these catches? Would answers to these questions effectively assist in apportioning these catches to east or west stocks? And finally, what can be said about the natal origin of these catches?

Locations and Quantities of Japanese Longline Catches of BFT

The seasonal distribution pattern of bluefin tuna based upon JpnLL catches for the period 1956-1968 is illustrated in **Figure 3** (Wise and Davis 1973) and **Figure 4** (Mather *et al.* 1995) but is more clearly depicted in **Figure 5** (Takeuchi *et al.* 2009). **Figures 3** and **4** depict fishing activity by JpnLL for the period 1956-1968 whereas **Figure 5** provides the clearest data on monthly location of and density of catches by JpnLL, although it is limited to one year: 1964. However, in all three cases, the amount of catches which occurred in each geographical area are unavailable.

Table 1 plots the catches found in Takeuchi *et al.* 2009 to the ICCAT Statistical Areas (**Figure 1**) as well as the MSE Statistical Areas (**Figure 2**). The ICCAT Statistical Areas are included in **Table 1** only for the purpose of illustrating the wide-ranging aspect of Japanese fishing operations in the Atlantic at that time.

With regard to the amount of bluefin catches that took place along the Brazilian coast during this period, Fromentin and Powers 2005 states, "This episode was a short period from 1962 to 1967 during which Japanese longliners caught 5,000 to 12,000 tonnes of ABFT in an area where they usually caught tropical tuna." The same amount of catches are also mentioned in Fromentin 2009. This latter document also contains two charts (**Figures 6 & 7**) based upon official catches of Atlantic bluefin tuna reported to ICES and ICCAT for the period 1950-2003: **Figure 6** splits catches into the three main geographical areas i.e. the Mediterranean Sea, the East and the West Atlantic. **Figure 7** compares catches in the "Brazilian area" with that of the Norwegian area.

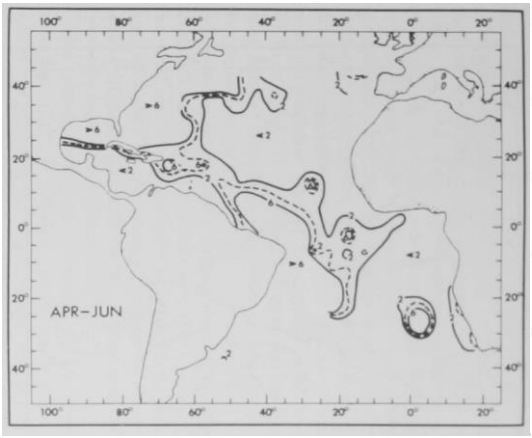
Takeuchi *et al.* 2009 states that catches in Venezuelan-Brazilian waters, "…increased rapidly reaching a peak in 1964 of about 13,000 t…". The inclusion of Venezuelan catches in this estimate does not enable us to understand the volume of either the Venezuelan or the Brazilian catches.

Fonteneau 2011 offers a summary of the historical changes in bluefin fishing zones by Japanese longline, based upon data developed for the purpose of conducting CPUE analysis (see **Figure 6**) but it is difficult to understand the amount of catches.

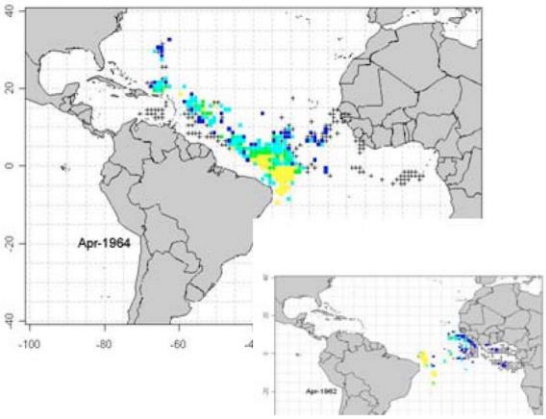
In Fromentin *et al.* 2014, for the purpose of quantifying catches in the Brazilian Episode, the authors estimated all the catches of the JpnLL fleet which occurred solely in the tropical belt, defined as between 20° N and 20° S. The stated result was that the highest catches, 1,200 – 8,300 MT, occurred during the four-year period, 1962-1965.

Consequently, there is no consensus in the literature as to the amount of the Brazilian catches or of the amount of catches elsewhere in the Central Atlantic.

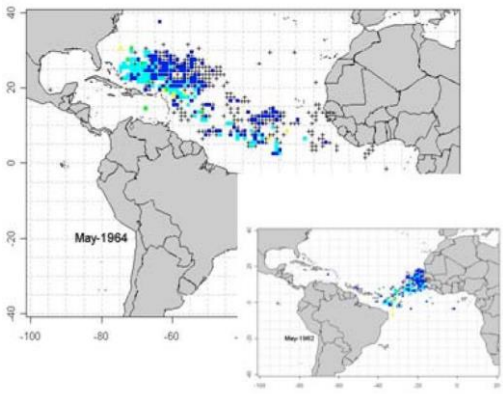
The amount of attention that has been focused in the literature on the Brazilian Episode is disproportionate to the role the Brazilian catches played in the total amount of JpnLL landings of BFT during the period. The question arises: Why has so much attention been given to these Brazilian catches? This would appear to be due, at least in part, to the unusual nature of the Brazilian catches which may have attracted scientists to the study of this singular event; that bluefin could be caught in such quantity in tropical waters in the Central Atlantic and in the Southern Hemisphere at a time when they were not spawning. Importantly, significant catches also occurred elsewhere, in other areas in the tropical Atlantic, far from Brazil, but discussion of these catches is only occasionally found in the literature. As an example, important catches occurred in the months of April, May and possibly June approximately 700 nm northeast of Brazil (See below). In September, a high concentration of catches occurred in the central Atlantic at the approximate latitude of Guyana (0°-10° N) but closer to Senegal than to South America (see below).



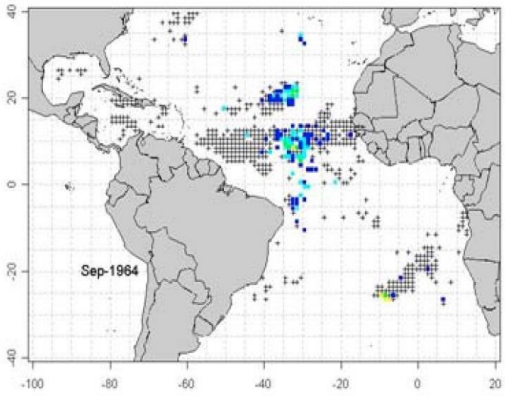
Distribution of JpnLL catches of BFT in April - June 1956-63 (Wise and Davis 1973)



Distribution of JpnLL catches of BFT in April 1963 (Takeuchi *et al.* 2009)

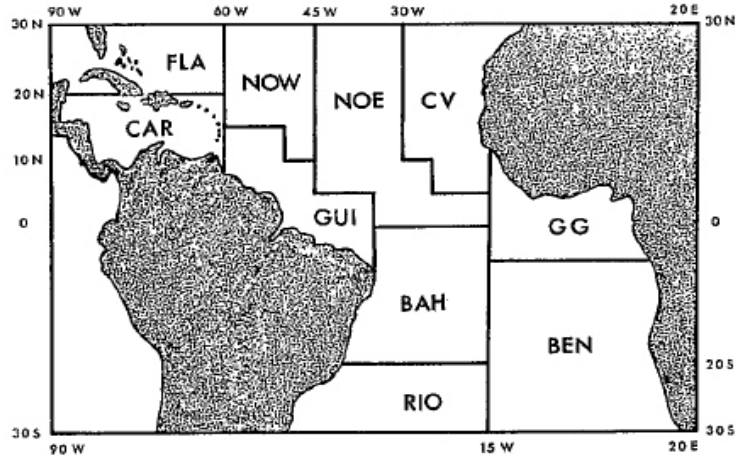


Distribution of JpnLL catches of BFT in May 1964 (Takeuchi *et al.* 2009)



Distribution of JpnLL catches of BFT in September 1964 (Takeuchi *et al*. 2009)

With regard to the differences in catches plotted by Wise and Davis 1973 (**Figure 3**) and that of Takeuchi *et al.* 2009 (**Figure 5**), one possible theory is that the catches plotted for 1964 in Takeuchi *et al.* 2009 are not precisely representative of the location of earlier catches during the period. Wise and Le Guen 1969 is the oldest document referenced here and it is focused on catches that occurred during the period 1956-1963. It is important to note that at this time, the JpnLL fleet was operating predominantly between 30° N and 30° S., targeting yellowfin, albacore, bigeye, bluefin, blue marlin, white marlin, black marlin, other marlin and swordfish. Wise and Le Guen 1969 also contains catch and effort (number of hooks used) for all the aforementioned species. JpnLL fishing activities in this document are geographically separated according to the schema in the chart below. Given the level of fishing effort in each of these sectors, it is possible to understand that bluefin might be caught off Namibia, Angola or seaward of the Gulf of Guinea, as the JpnLL extensively exploited these areas for tropical species. This data allows us to understand that JpnLL did not venture into more remote areas (Angola, Namibia, west of Gulf of Guinea, etc.) solely for the purpose of catching bluefin tuna.



Statistical areas used in analyses of catch and effort of the Japanese longline fishery (Wise and Le Guen 1969)

ICCAT Data

According to ICCAT data, 33,347 MT of bluefin catches has been attributed to the West Atlantic stock and 6,053 MT to the East Atlantic stock for a total amount of Atlantic-wide catches of 39,400 MT over the period 1957-1970 but no explanation was found as to how this catch was apportioned to east and west stocks.

Question of Natal Origin of JpnLL Catches 1950-1970

The question of natal origin of the JpnLL catches during this period is critical to the usefulness of this data within the MSE process. With the possible exception of those bluefin catches said to be Southern bluefin, there is no evidence available to positively identify the natal origin of any of the catches that occurred during the period. Fromentin *et al.* 2014 states, "The lack of biological archives of fish caught in the equatorial Atlantic during the 1960s does not allow us to retrieve the natal origin of those fish and thus to draw any firm conclusion on this specific issue." Equally importantly, given that no spawning areas have been documented in the southern hemisphere to date, the present assumption is that ABFT do not spawn there. The concept of an "ecological bridge" (Fromentin *et al.* 2014) is an important theory that could explain the presence and subsequent absence of ABFT in the southern hemisphere.

Catches of Southern Bluefin Tuna (*Thunnus maccoyii*)

The area around South Africa is considered to be feeding grounds for immature and adult southern bluefin tuna (Farley & Davis 1998). With regard to SBT catches by JpnLL in the Atlantic during this period, Wise and Davis 1973 state: "The published Japanese statistics did not separate the (Atlantic) bluefin and the southern bluefin previous to 1966. In the period 1966-68 about 30% of the total catch of both species was Southern bluefin, but less than 100 Southern bluefin were caught north of lat 20° S. About 75% of the catch south of lat 20° S was reported as Southern bluefin. We shall generally consider concentrations north of lat 20° S as (Atlantic) bluefin and concentrations south of 20° S as Southern bluefin." This is the earliest mention of SBT having been caught by JpnLL during this period. Mather *et al.* 1995 also mentions SBT being caught by JpnLL when fishing south of 20° S. Fromentin *et al.* 2014 states, "…southeastern Atlantic feeding grounds (offshore of South Africa, Namibia and Angola) may well have been shared by ABFT and southern bluefin tuna during the 1960s". SBT catch by JpnLL in the south Atlantic during this period is also supported in Takeuchi *et al.* 2009.

If we consider that SBT was the dominant bluefin catch south of 20° S, we should note that this latitude falls along the coast of the Brazilian state of Belo Horizonte, about 250 nm north of Rio di Janeiro. If we apply the same criteria to the West African coast, 20° S is located in Namibia, approximately 200 nm south of the Angola border.

Conclusion

With regard to the U.S. and Canadian purse seine catches that took place on the U.S. and Canadian East Coast during 1950-1970, there may be a solution that will result in arriving to a quantity of catch for this time series that represents only spawners. It would require a pro rata adjustment to the catch over the period based upon the assumption that length distribution for the nearest period in which catch size data from purse seine is reliably available can also be applied to the catches during this period. In addition, present understandings regarding the mixing of east and west BFT stocks on these U.S. and Canadian fishing grounds may influence the apportionment of this catch to both stocks.

Catches of BFT by JpnLL during the same period do not have the same problem i.e. they are all assumed to be of large medium or giant BFT. However, with regard to the question of natal origin, there are a few assumptions that can be made. Catches in the Gulf of Mexico and the Gulf of Campeche, although small, may be reliably considered to be primarily composed of Gulf spawners. Similarly, a certain percentage of catches off Cape Hatteras may be considered to be of Gulf spawners. Further, a certain percentage of catches taken east of Cuba could reasonably be considered to be of Gulf spawners due to this region's proximity to the Gulf of Mexico.

The catches having taken place east of the Bahamas Bank may be associated with a spawning area found to exist in the Bahamas, approximately 80nm east of West Palm Beach (Mather *et al.* 1995). This raises the question: to which stock should these catches be applied?

In connection with catches that are said to be of SBT it is of course possible to be definitive as to natal origin. However, the amount of such catches having taken place south of 20° S is a matter of some conjecture.

Finally, for catches that occurred in the central Atlantic, east of the Windward Passage, west of the Gulf of Guinea, along the north coast of South America and off the coast of Angola and Namibia, no guidance could be found as to the quantity of the catches in these areas. We can assume that a significant percentage of the total of 39,400 MT of catch recorded by ICCAT for the period has occurred in these regions. This difficulty together with the absence of any data supporting natal origin of all catch with the possible exception of catch considered to be SBT as well as limited catch in the Gulf of Mexico, as noted, presents the biggest challenge in preparing this data for use in the MSE project.

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Table 1. Locations of catches of bluefin tuna by Japan Longline by month, 1964.

Month	*Location*	*ICCAT Stat. Area*	*MSE Stat. Area*
January	Gulf of Campeche (Mexico)	BF60	1: GOM
	Off Rio Grande do Norte - Pernambuco (Brazil)	BF64	2: WATL
February	North of Yucatan/Campeche	BF60	1: GOM
	Central Atlantic (37°W - 44°°W, 8°N - 16°N)	BF64, BF62, BF65	2: WATL, 4: SATL
	South Atlantic, west of G. of Guinea (18°W - 2°W, 7°S - 6°N)	BF65	4: SATL
	South - So. Brazil (40°W - 30°W, 15°S - 5°S)	BF64, BF68	2: WATL
March	North of Guyana (57°W - 45°W, 5°N - 13°N)	BF64	2: WATL
	Equatorial Atlantic, off Senegal 28°W - 15°W, 2°N - 10°N)	BF62, BF65	4: SATL
	Minor catches off Brazil	BF64, BF68	2: WATL
	Central Atlantic (47°W- 40°W, 8°N - 14°N)	BF64, BF65	2: WATL, 4: SATL
April	Equatorial Atlantic 20° W off Senegal	BF64, BF62, BF65	2: WATL, 4: SATL
	East of Windward Islands	BF64, BF61	2: WATL
	Coastal Guyana, Suriname and French Guyana	BF64	2: WATL
	Central Atlantic (67°W - 64°W, 25°N - 33°N)	BF61, BF55	2: WATL
	Central Atlantic (40°W - 25°W, 5°N - 10°S) off Brazil	BF64, BF 65	2: WATL, 4: SATL
May	North of Cuba	BF61, BF67	2: WATL
	East of Bahamas	BF61, BF67	2: WATL
	East of Windward Islands	BF67, BF64	2: WATL, 4: SATL
	East of Suriname	BF64, BF65	2: WATL, 4: SATL
	Central Atlantic 24° W, closer to Sierra Leone	BF65	4: SATL
June	East of Bahamas	BF61	2: WATL
	North of Dominican Republic	BF61	2: WATL
	Central Atlantic (65°W - 45°W, 18°N - 30°N)	BF61, BF67	2: WATL
	Equatorial Atlantic (30°W - 20°W, 2°N - 7°N)	BF65	4: SATL
	Central Atlantic (60°W - 40°W, 15°N - 30°N)	BF67, BF62, BF57	2: WATL, 4: SATL
July	Off Cape Hatteras	BF55	2: WATL
	East of Bahamas Bank	BF61	2: WATL
	Central Atlantic (65°W - 38°W, 15°°N - 30°N)	BF67, BF62, BF57	2: WATL, 4: SATL
	Central Atlantic (45°W - 35°W, 5°N - 15°N)	BF64, BF65	2: WATL, 4: SATL
	West Africa, off Namibia/Angola (0°E - 10°E, 20°S - 15°S°)	BF65, BF66	4: SATL

Table 1. (Continued).

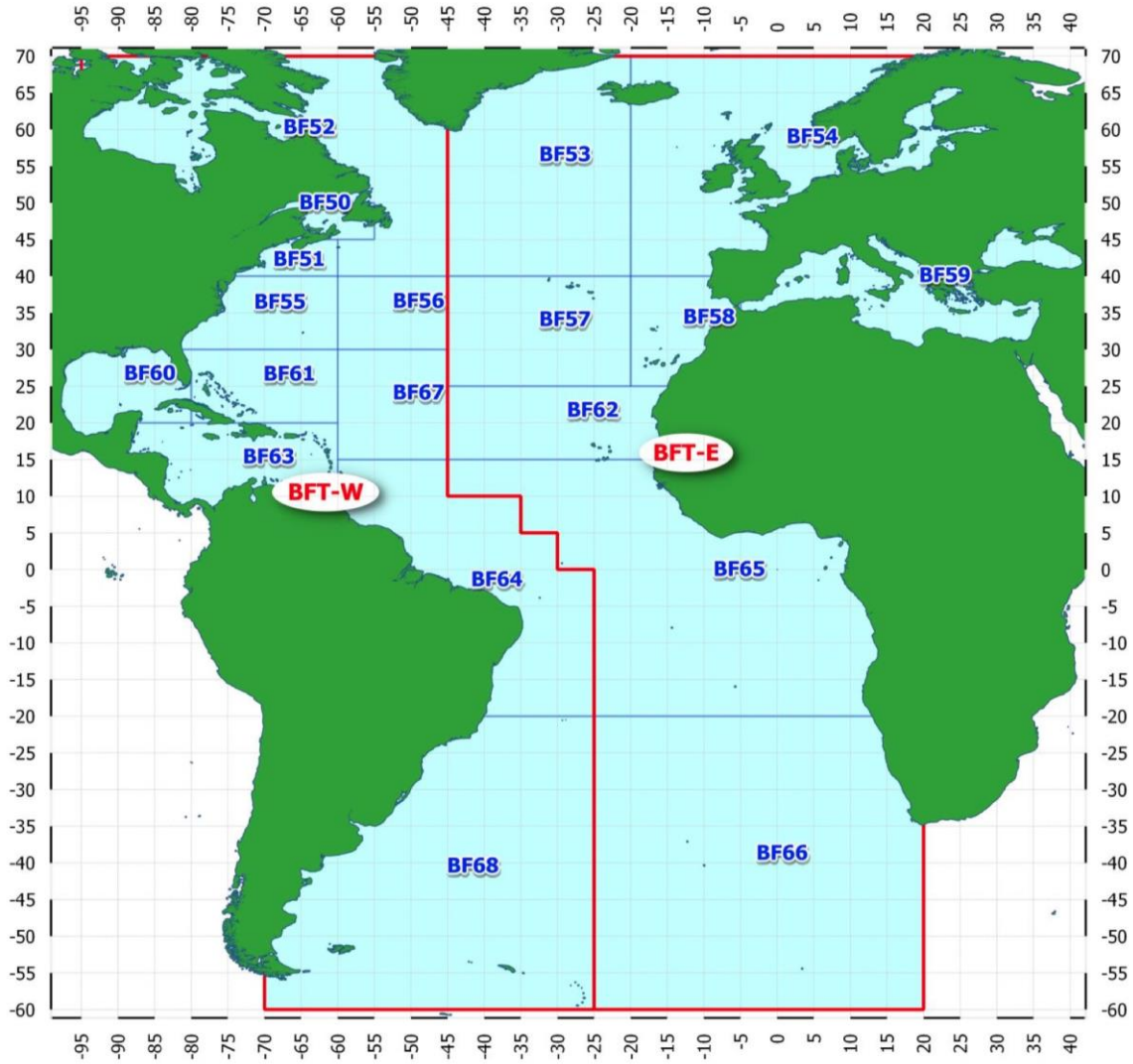
Month	*Location*	*ICCAT Stat. Area*	*MSE Stat. Area*
August	Mid Atlantic, close to Sierra Leone (30° W, 5° N)	BF62, BF65	4: SATL
	South Atlantic, west of Angola/Namibia border (0° E, 18° S)	BF65, BF66	4: SATL
	Central Atlantic (55°W - 20°W, 5°N - 15°°N)	BF64, BF65, BF62	2: WATL, 4: SATL
September	off Recife/Fortaleza (Brazil)	BF64	2: WATL
	Central Atlantic (30°W - 40°W, 5°N - 10°N)	BF64, BF65, BF62	2: WATL, 4: SATL
	Off Recife/Fortaleza (Brazil)	BF64	2: WATL
	South Atlantic, off Namibia (5°W-5°E, 17°S-27°S)	BF65, BF66	4: SATL
	Central Atlantic (40°W - 32°W, 15°N - 25°N)	BF62	4: SATL
October	South Atlantic, off Namibia (10°E, 22°S)	BF66	4: SATL
	South Atlantic, west of Namibia/Angola (5°W - 25°W, 10°S - 25°S)	BF65, BF66	4: SATL
	South Atlantic, off Espirito Santo-Rio (35°W - 46°W, 22°S - 35°S)	BF68	2: WATL
	South Atlantic off Bahia (Brazil)	BF64, BF65	2: WATL, 4: SATL
	South Atlantic off Ceara (Brazil)	BF64	2: WATL
	South Atlantic off Rio Grande do Sul (South Brazil)	BF68	2: WATL
	Equatorial Atlantic (45°W - 25°W, 5°N ° - 10°S)	BF64, BF65	2: WATL, 4: SATL
November	South Atlantic (Brazil) (43°W - 30°W, 28°S - 20°S)	BF64, BF68	2: WATL
	South Atlantic (35°W - 20°W, 4°S - 18°S)	BF64, BF65	2: WATL, 4: SATL
	Central Atlantic (55°W - 30°W, 0° - 7°N)	BF64, BF65	2: WATL, 4: SATL
	Southeast Atlantic, SW of G. of Guinea (10°W - 2°W, 2°S - 17°N)	BF65	4: SATL
	Coastal Mauritania/Senegal (16°W, 15°N - 19°N)	BF62, BF65	4: SATL
December	North Central Atlantic (38°W - 25°W, 33°N - 38°N)	BF57	5: NATL, 6: EATL
	East of French Guyana (45°W - 50°W, 5°N - 10°N)	BF64	2: WATL
	East of Pernambuco, Brazil (35°W - 25°W, 5°S - 12°S)	BF64	2: WATL
	South Central Atlantic (10°W - 30°W, 15°N - 30°N)	BF68, BF66	2: WATL, 4: SATL
	East of Sao Paulo (35°W - 43°W, 15°S - 18°S)	BF68	2: WATL

Takeuchi *et al.* 2009

Table 2. Japanese Longline Catches in Atlantic 1950-1970.

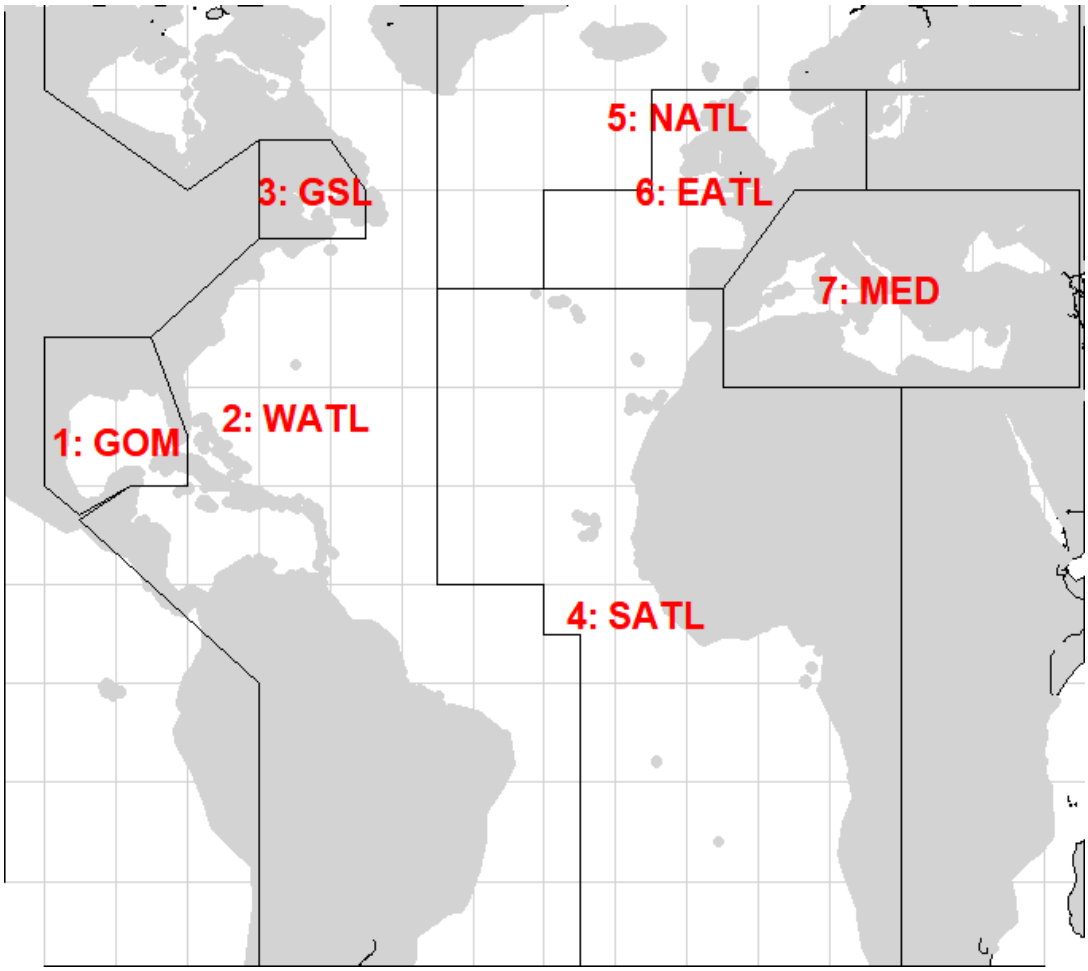
Year	***Attributed to West Stock (MT)***	***Attributed to East Stock (MT)***
1950	0	0
1951	0	0
1952	0	0
1953	0	0
1954	0	0
1955	0	0
1956	0	0
1957	30	33
1958	32	2
1959	200	56
1960	339	481
1961	373	204
1962	219	2,484
1963	1,219	1,618
1964	6,191	585
1965	12,044	404
1966	9,147	50
1967	2,471	100
1968	694	13
1969	272	2
1970	116	21
Total	**33,347**	**6,053**

Source: ICCAT.



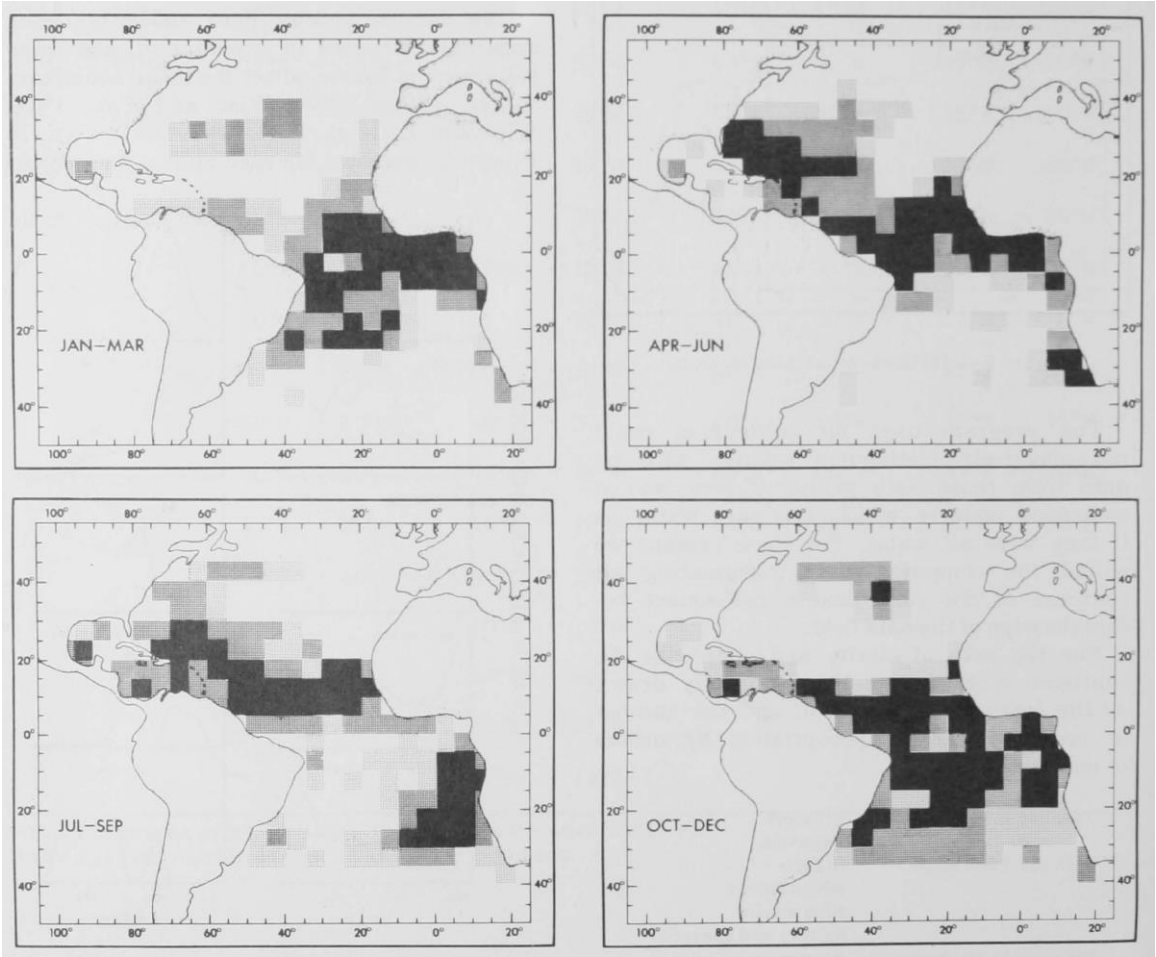
Source: SCRS

Figure 1. ICCAT Statistical Area chart for Atlantic bluefin tuna.



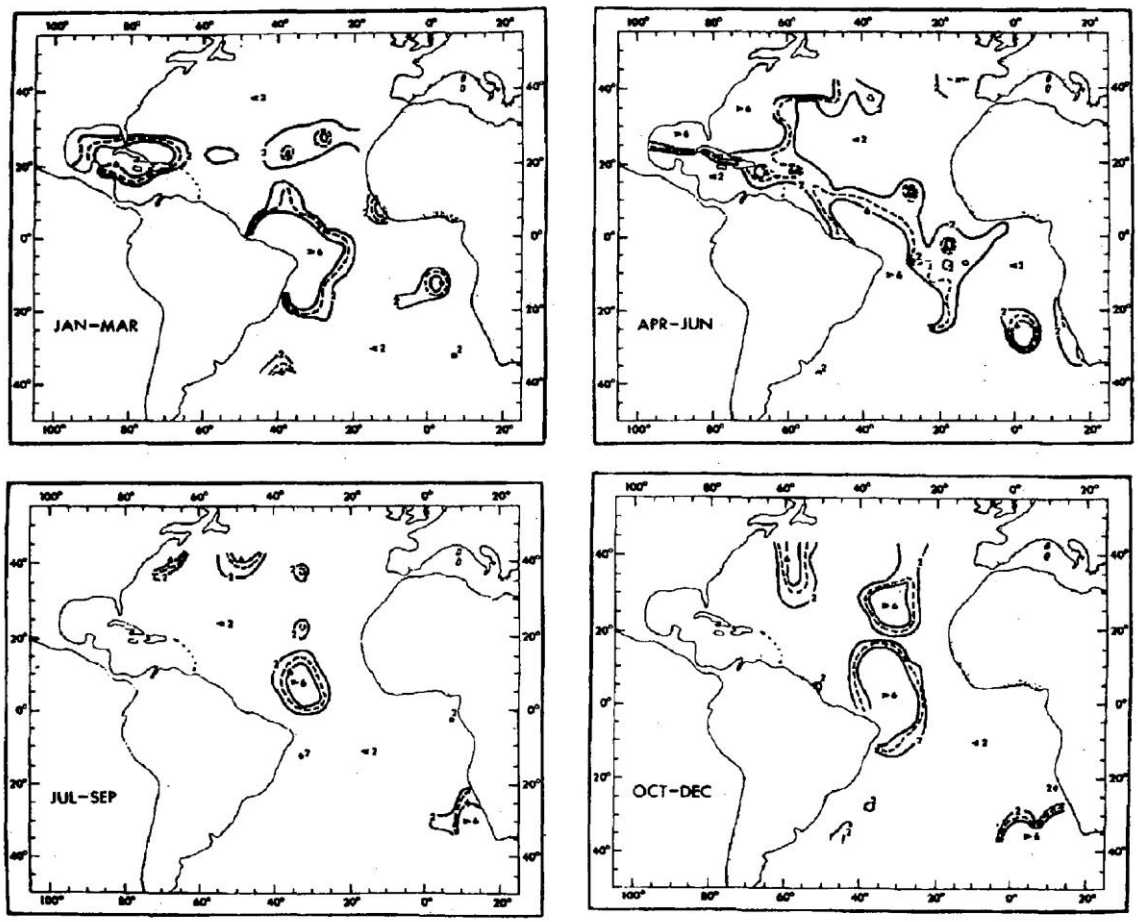
Source: SCRS

Figure 2. MSE Statistical Areas for Atlantic bluefin tuna.



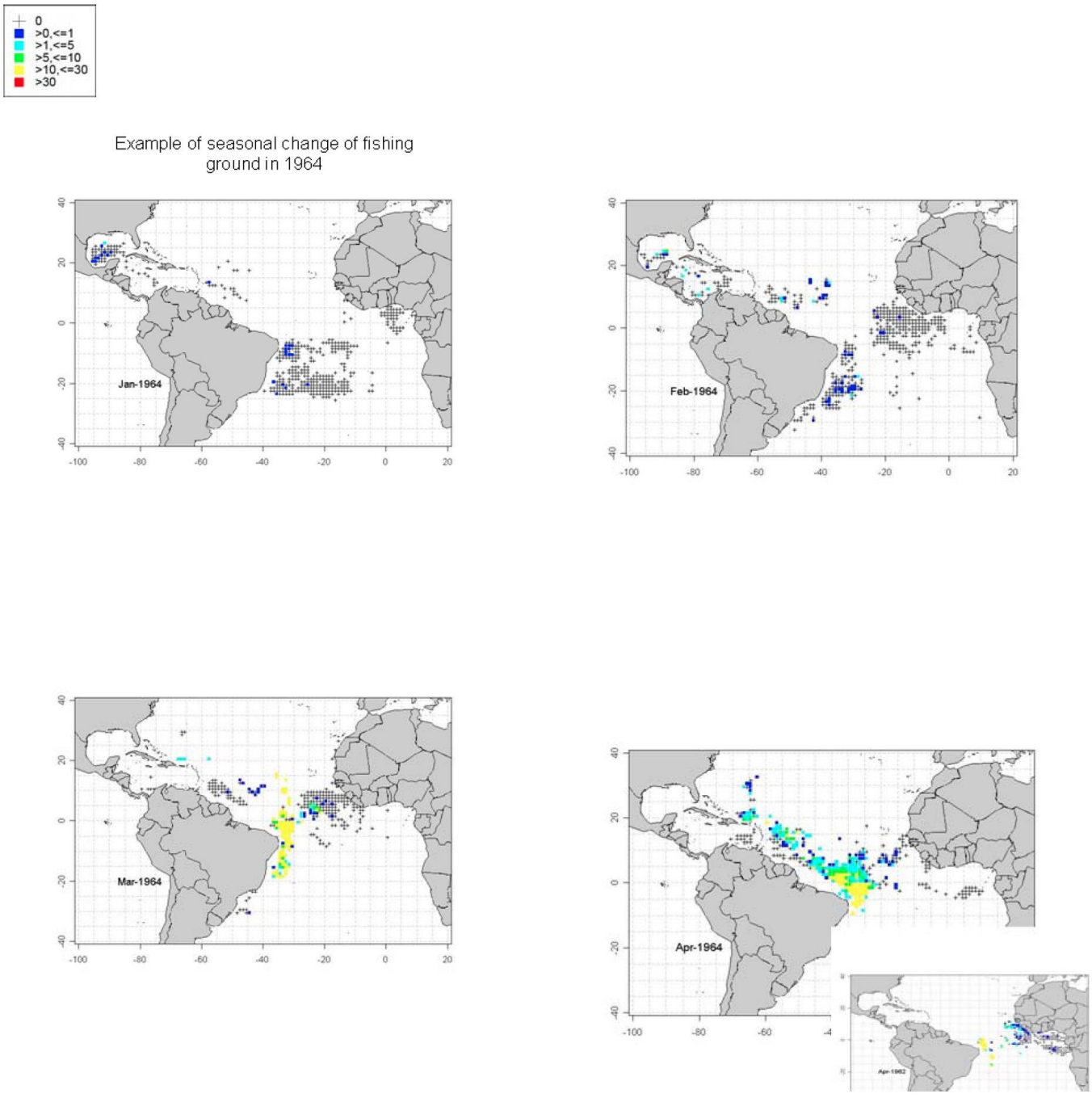
Darkest portion includes 75% of the effort; intermediate shading plus darkest portion includes 95% of the effort; all shaded areas include 99% of the effort. (Source: Wise and Davis 1973).

Figure 3. Relative amounts of fishing by Japanese longline fleet in the Atlantic, 1956-1968.



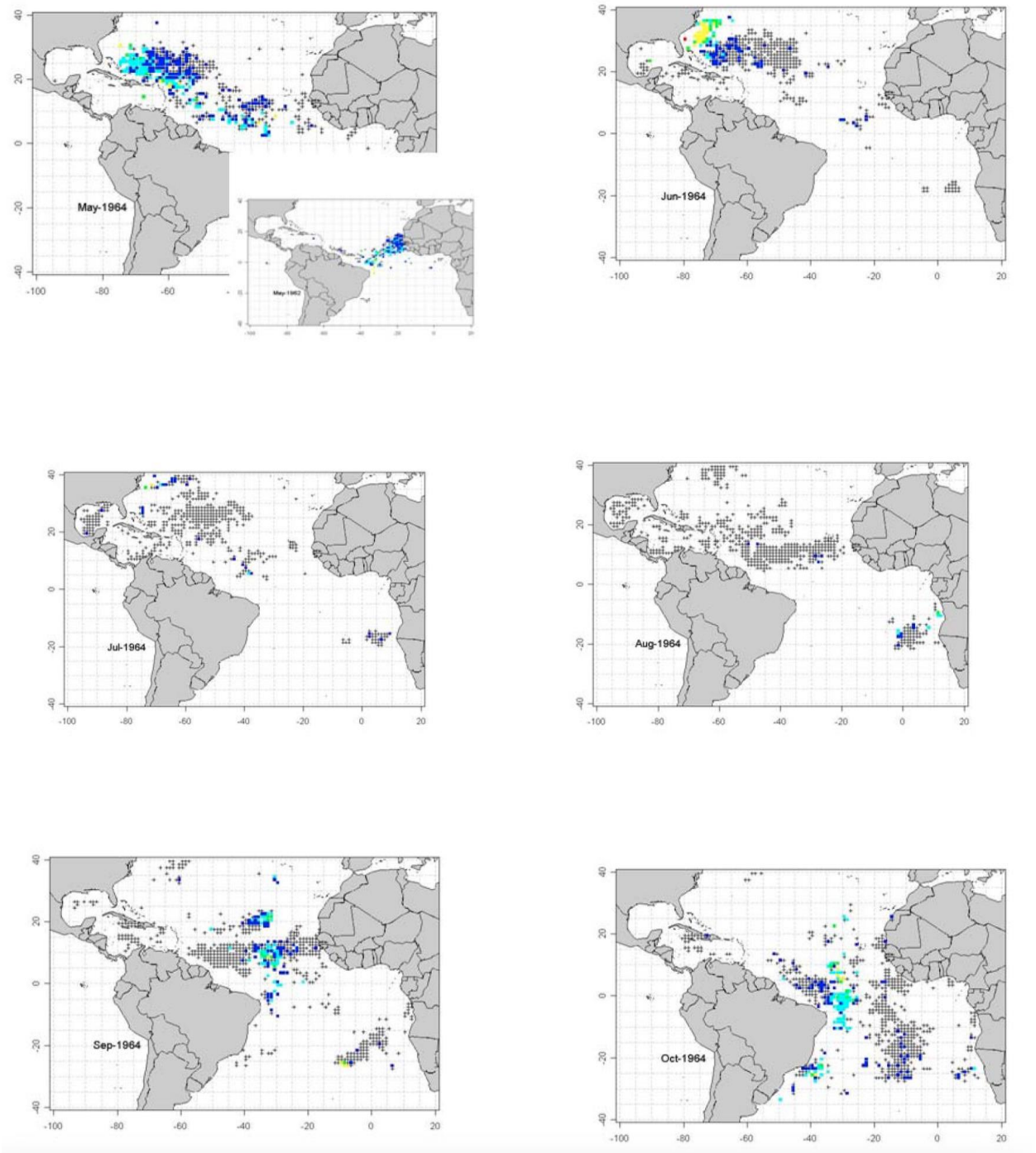
Source: Mather *et al.* 1995

Figure 4. Distribution of oceanic catches of bluefin tuna (per 10,000 hooks in the four quarters of the year, 1956-1968.



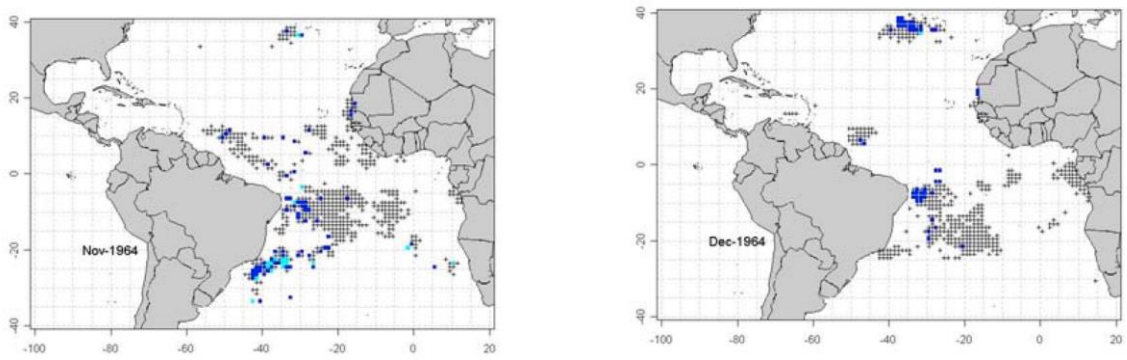
Takeuchi *et al.* 2009

Figure 5A. Example of season change of fishing ground expressed catch rate (no. of fish per 1,000 hooks) by month and 1 degree squares in 1964 (April and May 1962 are shown for comparison).



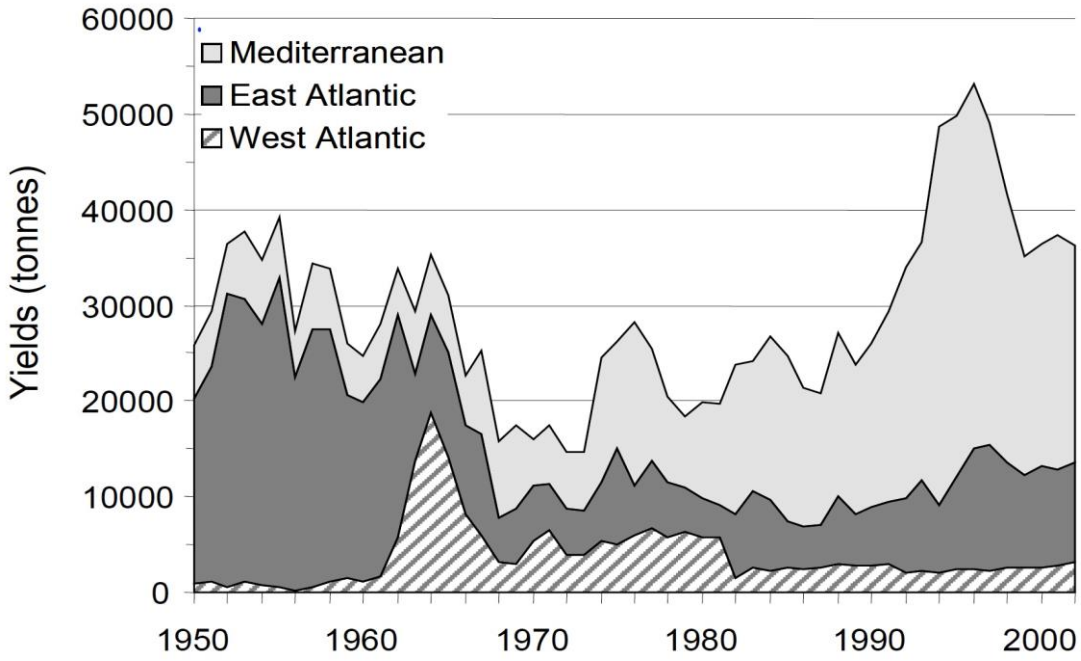
Takeuchi *et al.* 2009

Figure 5B



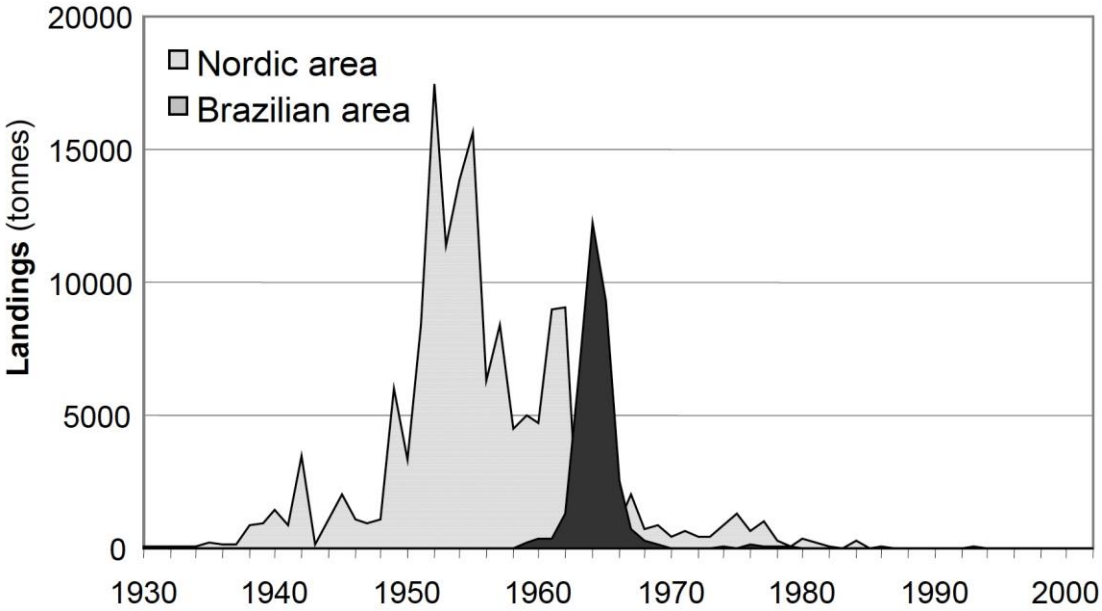
Takeuchi *et al.* 2009

Figure 5C



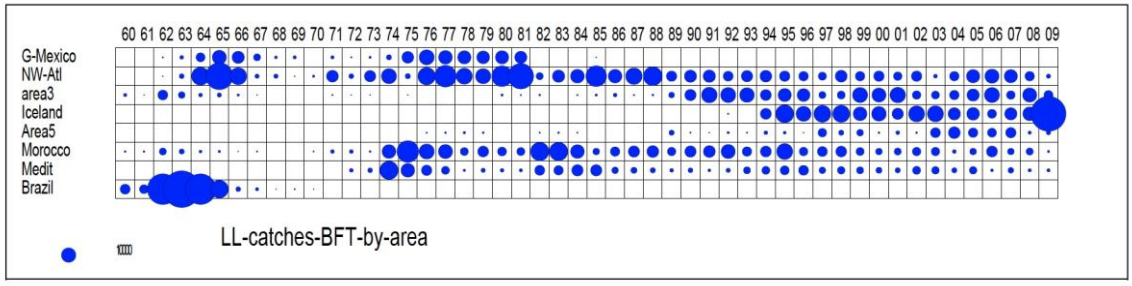
Fromentin & Powers 2005

Figure 6



Fromentin & Powers 2005

Figure 7



Fonteneau 2011

Figure 8