

A preliminary analysis of acoustic tagging data for estimating the possibility of double counting same fish schools in recruitment monitoring survey by trolling

ピストンライン曳縄加入調査における同一魚群をダブルカウントする可能性を評価するための音響タグ行動データの予備的解析

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Summary

Fine-scale fish horizontal distribution is a key component of estimating fish abundance and interpreting the survey results when large pelagic predators move quickly in and out of local ecosystems. Acoustic tagging research has been carried out on southern bluefin tuna (SBT) in the southern Western Australia. This is the same region where a fishery-independent acoustic and trolling survey for recruitment abundance index of juvenile SBT has been historically undertaken. We investigated the spatial and temporal distribution patterns of age-1 SBT population in and out of the acoustic survey area during three summer seasons (2004/05, 2005/06, 2006/07). The annual differences of distribution patterns revealed by acoustic tagging were characterized by two distinctive migration runs. Furthermore, we detected different residence times for SBT. Migration analysis of the effect of the survey area indicated that inshore-migrating seasons were underestimating the indices when a relatively high proportion of SBT were migrating out of the acoustic survey area. Moreover, analysis of cumulative duration of tagged SBT schools on the curtains frequency indicated that the majority (80 %) of the SBT occurring on the curtain stayed to 3.5 days there. This result suggest that if same schools go on staying during 3 days, the researcher should collect up some part of same SBT schools.

要約

空間精度の高い魚群の水平分布情報は、資源評価、さらに漂泳性捕食魚類が局所的な生態系から急速な移出入がある場合の資源加入調査の解釈について、鍵となる要素となる。これまで、音響タグ行動調査は、オーストラリア南西海域でミナミマグロ幼魚（SBT）を対象に実施されてきた。この行動調査は、漁業から独立した加入指標を得るための音響・曳縄調査が行われている海域で、実施されてきた。我々は、2004-2006 年度のオーストラリアの夏季に、音響加入調査海域の内外で SBT1 歳魚の時空間分布パターンを調べた。分布パターンの年変動は、2つの明瞭な（「沿岸に滞在」または「陸棚域を回遊」）回遊経路で特徴化された。また、海域における SBT の滞在日数も経年で変化した。2004 年度のように沿岸付近の小海山に SBT が偏在する年の加入指数は、過小評価に陥っていた可能性がある。さらに、陸棚上の音響受信機列への出現日数に関する累積度数分布の結果は、SBT の 80%が約 3.5 日間以内で陸棚の局所的な海域に滞在することを示している。仮に同一魚群が平均で 2-3 日間程度局所海域に出現し続けるならば、現行の曳縄加入調査のプロトコルでは、同一魚群からの‘ダブルカウント’があるかもしれない。

INTRODUCTION

The acoustic index predicted the low recruitment levels of 1999 – 2001 year classes of southern bluefin tuna (SBT) so that it was likely to be a reliable index in some extents. However, the survey was ceased after the final survey in 2006 due to the budget restriction. Alternatively, a type of survey that can be done with lower cost was sought. Since 2006/2007 season, NRIFS have conducted a feasibility survey that a chartered Australian F/V go-and-back on a single straight line between inshore and shelf break off the Bremer Bay, Western Australia (WA) and find SBT schools with trolling catch (Itoh and Kurota 2007).

Current SBT recruitment-index assessment models do not take into account small-scale spatial variation in SBT distribution. If SBT aggregated in the area when the survey was conducted, it is possible that the research vessel may encounter and sample same fish schools. Thus, to reduce the possibility of “double counting” the same animals, it would be important to understand fish residence pattern in the survey area.

The successful use of data collected by the acoustic tagging and monitoring projects in the analysis has been an important achievement of the Recruitment Monitoring Program (RMP, 2002-03 to 2004-05), and subsequently via independent Japan-Australia collaboration (2005-06 to 2006-07). Smart tag technology developed and/or used extensively within the RMP are now tools-of-choice in tuna research programs throughout the world to examine critical questions about habitat preferences, migration and residence patterns, and physiology (Heupel et al. 2006).

Our principal objectives were to:

- Identify annual fluctuations in fish positioning and aggregation as a function of temporal variation in a specific habitat using the behavioural data obtained during the summer migration of juvenile SBT population in 2004/05, 2005/06 and 2006/07 seasons and
- Examine the residence times of age-1 SBT on the listening station arrays between inshore and shelf break.

In this report, we discuss the possibility of “double counting” the same fish during the recruitment survey. It would be important to understand fish residence pattern in the survey area.

MATERIALS AND METHODS

Research sites

The study was conducted along the coast of southern Western Australia (SWA) between Albany (35.01°S, 118.01°E) and Esperance (33.52°S, 121.53°E) (Fig. 1). The width of the continental shelf was 30-60 km and on the shelf, the waters are mostly less than 80 m in depth. There were many lumps in this coastal area, which are known to attract tuna. Acoustic recruitment-monitoring survey (ARS) has been conducted to monitor the relative abundance of 1-year old SBT based on a line transect survey till 2005/06 season. And, then the Recruitment Trolling-Survey (RTS) was carried out on the shelf off Bremer Bay in SWA (Fig. 1a). The RTS has been established to monitor the recruitment index of age-1 SBT. In the survey, a chartered Australian vessel goes and back on the same straight line (piston-line) off Bremer Bay using trolling for about a week (Fig. 1b).

Acoustic receivers

Seventy VR2 acoustic receivers (Vemco Ltd, Halifax, Canada) were deployed on the shelf in the southern coast of Western Australia (Fig. 1a). Each receiver was fastened to a vertical wire cable on a mooring anchor (125 kg section of railway track). Listening stations with a receiver consisted of time-scheduled electronic releaser, 50 meters of release rope in a PVC canister, and four/five floats. When deployed, the receivers were set to at depth of 20-25 meters, just below the subsurface floats in waters up to 150 meters deep. Listening stations were aligned equidistantly into 'curtains' in three cross-shelf lines initialing from the coast at each location (Fig. 1a, western curtain from Bald Island (Line1); middle curtain from Point Henry (Line2); eastern curtain from West Island (Line3)). In addition, 3 listening stations were deployed at each of three coastal topographic features (Lumps) located between Line1 and Line2 in depths of 40-60 meters. Some topographic lumps occur in this coastal area, and are known to attract pelagic fishes of several species, including juvenile SBT (Hobday and Campbell 2009).

During the summer season in 2004/05, listening stations were deployed on December 3 (Line1), December 4 (Line2 and Lumps) and December 5 (Line3) and retrieved in March 15-19, 2005. In 2005/06 season, listening stations were deployed on December 1 (Line1), December 2 (Line2 and Lumps) and December 3 (Line3) and retrieved in May 9-11, 2006. In 2006/07 season, listening stations were deployed on December 1 (Line1 and Lumps) and December 2 (Line2 and Lumps), and December 3 and January 14 (Line3) and retrieved in May 29-31, 2007. All receivers continuously monitored the passage of any tagged individuals over a 3-month period.

Acoustic transmitters

The transmitters used to tag SBT were V8, V9 and V16 coded pingers (Vemco Ltd). They each transmit a unique pinging sequence at a frequency of 69 kHz, which is repeated after a random delay of between 20 and 60 seconds. Battery life is rated at 365 (V8/V9) and 700 (V16) days. Receivers were separated by approximately

1500 m. This spacing decision was based on a desire to cover the width of the shelf; a tag detection range of up to 450 m (V8) and 800 m (V16) were expected based on detection experiments (Hobday et al. 2005).

The same protocol used for the capture and selection of SBT for conventional tagging was followed for the acoustic tagging (Hobday 2002). In brief, fish were caught by polling or trolling at the stern of the vessel (F/V Quadrant) and immediately placed in a tagging cradle. Caudal fork length (FL) was measured to the nearest centimeter. For acoustic transmitters, a 1-1.5cm horizontal incision was made about 0.5-1 cm off the midline and anterior to the vent by about 2-3 cm. The body wall was penetrated until the membranes of the peritoneum were observed. The membrane was then torn by a gloved finger, and a space in the visceral cavity (where the transmitter would be inserted) was carefully wedged out to help ensure no damage occurred to internal organs. The incisions were closed with one (or two) sutures. The entire implantation procedure generally took less than 2 minutes. Fish were also tagged with conventional plastic dart tags placed between the pterygiophores adjacent to the insertion of second dorsal fin. All fish were tagged by a single experienced operator.

For 2004/05 season, a total of 79 fish (FL: 41-64 cm) were tagged in the area between Line1 and Line2, and we released 22 tagged fish at December 7 2004 and 57 tagged fish in January 3-9 2005. For 2005/06 season, a total of 81 fish (FL: 43-73 cm) were also tagged in the area between Line1 and Line2, and we released 8 tagged fish in December 5-8 2005 and 73 tagged fish during January 6-10 2006. For 2006/07 season, a total of 84 fish (FL: 44-93 cm) were tagged in the western areas from Line2 wider than 2004/05 and 2005/06 season, and we released 54 tagged fish at December 4-10 2006 and 30 tagged fish in January 8-12 2007. The tagged and release locations of west-east range were 34.202°S/117.950°E-34.448°S/119.509°E (mean: 34.741°S/118.847°E), 35.201°S/117.961°E-34.539°S/119.265°E (mean: 34.756°S/118.840°E) and 34.521°S/115.288°E-34.565°S/118.979°E (mean: 34.779°S/118.082°E), respectively.

Data analyses

Some applications using acoustic tracking data have examined migration patterns of released individuals (Comeau et al. 2002; Stark et al. 2005). These studies typically look for individuals that pass a specific point or through a line (curtain) of receivers to define migration. These data are used to calculate the rate of progression through the area and also to examine swimming speed based on movement past known points.

We determined the size of two relevant research areas relative to the array of acoustic receivers: one was an area inside the ARS area and the second was an area outside of the ARS area (Fig.1c). The area inside the ARS area was 4215.5 km² (54%) and outside of the ARS area was 3613.8 km² (46%). To compare the spatial usage and migratory direction of tagged SBT between in and out of ARS area, site preference of SBT was determined using acoustic tracking data. We

calculated the proportion of residence time between in and out of the ARS area from migration time (days) across some two receivers. In other words, the time ratio indicated time of completing the migrations in and out of the ARS area. Time, distance and speed (rate of movement) were calculated for each movement recorded between the receivers (curtains, curtains and Lumps, and Lumps) (Comeau et al. 2002). Migration time (MT) was the period between the last detection at one receiver and the first detection at next receiver. Distance was measured between the positions of two relevant receivers. The movement and tagging patterns are described in a companion paper (Hobday et al. 2007). Here we report the residence patterns relative to the ARS area, and the potential impact on density/abundance estimates.

In order to determine the duration of tagged SBT schools on the curtains (DC), DC was the period between the first detection at one receiver on one curtain and the last detection at the receiver of the curtain. We showed the cumulative frequency of DC from acoustic tagging data. Notice that the RTS conducted just on the Line 2.

Residence times (RT) in the acoustic tracking area (Fig. 1a) for SBT were based on survival analyses conducted with the Kaplan-Meier method and compared using the two-sample *t*-test in accordance with a previous study (Ohta and Kakuma, 2005). The statistical analysis was performed using the statistical software package StatView 5.0 (SAS Institute, Inc., Cary, NC, USA), and a *p* value less than 0.05 indicated statistical significance.

RESULTS

Detections and migrations

A total of 60 (86 %), 58 (83 %) and 62 (89 %) receivers were retrieved each year, and provided sufficient sites to determine migration between receivers. The total number of tagged SBT detected at the receivers was 55 (70 %) in 2004/05, 68 (84 %) in 2005/06 and 62 (73 %) in 2006/07.

Migration between receivers in the survey area were calculated as 10 migration pathways (Line1-Lumps, Line2-Lumps, Line3-Lumps, Line1-Line2, Line2-Line3, Line1-Line3, Between Lumps, Along curtain, Between adjacent receivers along curtain, Between adjacent receivers in Lumps) each season (Table 1). The total number of migrating SBT were 2744, 416 and 662, respectively. The proportion of migrations associated with Lumps were 93% in 2004/05, 21% in 2005/06 and 68% in 2006/07, conversely, 7%, 79% and 32% were occurred just on the shelf (curtain), respectively.

Spatial usage in the survey area

Tagged SBT in 2004/05 and 2006/07 migrated mostly around the inshore (very little shelf-migration), in 2005/06, large number of fish migrated not only between Lumps and the continental shelf, but also between curtains (Table 1). This result indicates that the estimated residence time out of ARS area (84.5% and 65.0%)

during 2004/05 and 2006/07 season was greater than in ARS area (15.5% and 35.0%). On the other hand, unlike 2004/05 and 2006/07 seasons, tagged SBT during 2005/06 stayed in ARS area (63.3%) rather than out of ARS area (36.7%).

Residence patterns

While the tagged SBT were present on curtains of shelf and Lumps all three research seasons, we found a remarkable change of spatial distribution patterns and residence time for all of tagged fish between both years. In 2004/05 season, tagged SBT were present mostly at the Lumps every day during the research period and 91.3% of all detections ($n = 27,855$) were recorded by the receivers at the Lumps, although a small number were recorded on the curtains on shelf (Fig. 2a). In 2005/06 season, tagged SBT were widely distributed on the shelf, and there were few detected at the inshore Lumps. The total number detected was 5,214, 93% of all detections occurred at each shelf receiver; in contrast, a small number were detected at the Lumps (7%) (Fig. 2b). In 2006/07 season 88% of all detections ($n = 18,514$) was found at the Lumps, and 12% occurred at the curtains on the shelf (Fig. 2c). Residence patterns in this region were clearly different than the two migration runs: inshore-migrating both 2004/05 and 2006/07 seasons, and shelf-migrating in 2005/06 season.

Cumulative DC frequency gathered from all three years indicated that the majority (80 %) of the SBT occurring on the curtain stayed less than 3.5 days (Fig. 3a). Cumulative DC frequencies were similar for each year (Fig. 3b-d); however, in 2004/05 it (DC) was shorter (2.2 days) than another years (2005/06: 3.7 days, 2006/07: 5.1 days). In 2006/07, tagged SBT also occasionally made longer residence on the curtain (three individuals on 15 days in Fig. 3d). These observations indicate our SBT in each year occupied different spatial habitats and that its remarkable habitat choices alone are not sufficient to quantify the DC.

The change in the number of tagged fish remaining in the research area is shown Figure 4a, b. This result indicates that following the initial tagging, when tagged fish left and were never detected, half of the detected fish remained in the research area for the next 56 days following tagging and then moved out of the area in 2004/05 season. In contrast, in the 2005/06 season, half of the detected fish moved quickly out of the area by the next 14 days following tagging; however, 18% of tagged fish remained for over 100 days after tagging. The trend in residence time of the 2004/05 season was significantly different compared to the 2005/06 season (two-sample t -test, $P < 0.05$) (Fig. 4a) indicating that a difference was found among inshore- and shelf-migration run seasons. In 2006/07 season, the half of detected fish remained for the next 47 days, which was longer than the shelf-migrating season in 2005/06. For both inshore-migrating seasons (e.g. 2004/05 and 2006/07), there was no significant differences between the residence time curves (two-sample t -test, $P > 0.05$) (Fig. 4b).

DISCUSSION

We found that the spatial and temporal distribution patterns investigated by acoustic tagging system were characterized by two distinctive migration runs. The majority of 1-age SBT showed a strong association with coastal topographic features (Lumps) in 2004/05 and 2006/07. These inshore-migrating SBT mostly moved between curtain and Lumps and around Lumps (Table 1). Conversely, in 2005/06, shelf-migration SBT were occurred at higher rates not only between curtain and Lumps, but also between curtains (Table 1). Tagged SBT in this widely shelf-migration did not stay continuously around the Lumps, while inshore-migrating seasons persisted the features (Fig. 2a-c). Moreover, inshore-migrating SBT could leave (below 20%) by the end of summer (Dec-Feb), in contrast, shelf-migrating SBT moved mainly on shelf in the summer-autumn period (Dec-Apr). In other words, more than 20% of detected SBT during all seasons remained in the survey region during the ARS period (Jan-Feb), but decrease trends of residence time were significant different ($P < 0.05$) between inshore-migrating SBT and shelf-migrating SBT (Fig. 4a). The summer habitat use by 1-age SBT had interannual variations of two patterns on fine-scale excursion. The spatial and temporal differences could affect interannual fluctuations of the recruitment abundance indices for reason that the ARS were conducted the same survey area just on the shelf every year.

To monitor recruitment level of 1-age SBT, an acoustic survey has been conducted for several summer seasons (1996/97-2004/05). For instance, in 2004/05 season, the transect survey using scanning sonar and the design of the zigzag transect line in ARS area was conducted between January 14 and February 17 in 2005 (Itoh et al. 2005). When the information from the ARS is combined with the spatial and temporal variation observed in the acoustic tagging, it seems obvious that most of the tagged fish recorded by acoustic receivers seemed to be moving in coastal waters (Fig. 2a) and hence 84.5% migrated out of the ARS area (Table 1). They would thus be 'hidden' from the acoustic survey vessel. Itoh (2005) reported that the calculated acoustic index of 2004/05 season have been at the lowest level since 1999/2000. While it should be noted that there are some issues regarding the reliability of the acoustic indices based on the biomass of SBT schools estimated by sonar specialists (Itoh and Tsuji 2004), our results based on tagged fish indicated that the majority of 2004/05 SBT migrated mainly inshore (i.e. out of ARS area). Our results suggest that the sonar specialists may detect more fish schools than the ARS area, if the acoustic survey could include more inshore regions. Thus, the main factor causing the indices variation in the ARS could be age-1 SBT population migrating into and out of the ARS dead zone. The indices could change on an annual basis as a result of changes in fish horizontal density and detection efficiency.

While Japanese research vessel for acoustic survey use high performance omni-scan sonar to detect SBT schools in the ARS area, it would be too dangerous for this vessel to conduct acoustic surveys along inshore areas as the vessel is too large. Furthermore, coastal waters include some topographic features that are

unsurveyed. An alternative method to estimate recruitment indices of SBT were proposed by Itoh et al. (2005). They have proposed a trolling catch indices by using the piston lined survey set off Bremer Bay (center of the ARS area) and extending toward the shelf break offshore as a line between two points (34.31°S/119.27°E, 34.47°S/119.41°E), which was conducted along the Line2 in our acoustic receivers (see Fig. 1a, b). They have already conducted a piston line survey from 2004/05 season (9 round trips off Bremer Bay during January-February). The results between the three summer seasons (2004/05, 2005/06, 2006/07) may be seen as an increasing trend of the recruitment index from the 2004 to the 2006 year class (Itoh 2007). However, the trend was different from our probable result. Because, the high proportion of migrating SBT around topographic features in 2004/05 and 2006/07 seasons (Fig. 2a,c) will cause fewer catches and lower indices than during the shelf migration season in 2005/06. Moreover, for both inshore-migrating seasons, there were no significant differences between the residence time in survey region during the periods ($P > 0.05$) (Fig. 4b). Those results suggest that the catchability on the piston line survey could be the same conditions for reasons that both seasons consistent with horizontal distribution and residence time (density-dependent catch efficiency or a density-dependent horizontal distribution). Therefore, in 2004/05 and 2006/07, it is possible that the recruitment index could be an underestimate given that the majority of the age-1 SBT population might have shifted away from the piston line survey area. But in fact in 2006/07, the recruitment index was estimated at a high level caused by the large number of catches ($n = 213$), while a fewer catch ($n = 32$) in 2004/05. The catches and the index in 2006/07 were relatively higher than 2004/05. In addition, SBT catches in the 2006/07 were larger than 2005/06 seasons ($n = 141$) of mainly migrated on the shelf including the survey area (Fig. 2b). The catches were not made a simple comparison between 2004/05 and 2006/07 when both residence patterns were significantly different ($P < 0.05$). These results suggest that the recruitment abundance of age-1 SBT population in 2006/07 may be substantively increased in levels in comparison with 2004/05. We have demonstrated that the interpretation can be determined by examining ecological issues. Our hypothesis could be verified by recruitment and nominal catch over several years.

To avoid an overestimation of calculated indices due to the double counting of fish to same schools in the piston-line survey, it is important to compare between the DC of fish on the curtain and the duration during a round trip, when the vessel go-and-back on a single straight line between inshore and shelf break off the Bremer Bay. Basically, the piston line surveys were always conducted during the daytime (from 6:00 to 18:00) in the successive 13 days in January 2008 (Itoh and Sakai 2008). Analysis of cumulative DC frequency indicated that the majority (80 %) of the SBT occurring on the curtain stayed to 3.5 days there (Fig. 3a). This result suggest that if same schools go on staying during 3 days, the researcher should collect up some part of same SBT schools. To improve the estimates of the indices, the arrangement of the piston line-survey or is needed.

Examining the SBT residence time on the shelf, where the piston line survey was conducted, thus considered crucial to correctly interpret the abundance indices and assess population trends of this exploited species. Key needs were to determine how quickly juvenile SBT move east along the southern Western Australia coast during the austral summer, and how, based on behavioural information by acoustic tagging data, re-modify the calculated indices.

Our annual analyses based on large number of fish tracking showed that it is more likely that the indices leading to large interannual fluctuations of abundance estimates are caused by temporal and spatial distribution patterns. Especially, the recruitment abundance indices were underestimated on inshore-migrating seasons. In order to a narrower fluctuation range than in the past, we propose that the recruitment survey should carry out a trolling catch at coastal topographic features in addition to the piston line survey during the same period, and combine catch information from both the topographic features and on the shelf. Shelf-migration season, the catchability (depend on horizontal distribution) can be higher on the piston line survey and lower on a survey around Lumps than inshore-migration season, the opposite results will occur in inshore-migration season based on our results in Figure 2 (piston line survey conducted in the vicinity of Line2). In that case, the plan will offset the influence of the annual population distribution differences both patterns.

In order to predict the migration timing across the piston line survey area before the survey start, the underlying mechanism of migration dynamics in relation to the annual fluctuations of oceanographic conditions responsible for the temporal precision and movement patterns displayed by migratory SBT must be further investigated.

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Table 1. Details of the number of migration recorded between receivers and residence time in and out of acoustic recruitment-monitoring survey area (ARS area) estimated by analysis based on straight-line distance-time rates.

Migration route	2004/05 season			2005/06 season			2006/07 season		
	No. of migrations	in ARS (day)	out of ARS (day)	No. of migrations	in ARS (day)	out of ARS (day)	No. of migrations	in ARS (day)	out of ARS (day)
Line1-Lumps	40	4.4	210.0	30	0.0	139.7	28	0.3	149.2
Line2-Lumps	23	37.6	126.1	14	25.8	48.7	26	72.9	143.7
Line3-Lumps	5	49.3	30.6	2	103.7	12.4	6	83.4	111.0
Line1-Line2	11	101.5	42.3	21	140.4	105.4	8	193.6	77.2
Line2-Line3	8	30.9	38.1	28	529.4	74.7	18	140.9	26.2
Line1-Line3	2	12.7	4.7	2	103.7	12.4	2	17.7	1.9
Between Lumps	88	0.0	287.3	13	0.0	75.1	15	0.0	31.1
Along curtain	104	57.7	189.5	158	262.4	189.3	93	94.9	462.6
Between adjacent receivers along curtain	79	1.3	51.6	118	94.6	49.5	88	56.6	43.5
Between adjacent receivers in Lumps	2384	0.0	634.8	30	0.0	22.8	378	0.0	179.2
Total	2744	295.3	1615.0	416	1260.0	730.0	662	660.3	1225.6
%		15.5	84.5		63.3	36.7		35.0	65.0

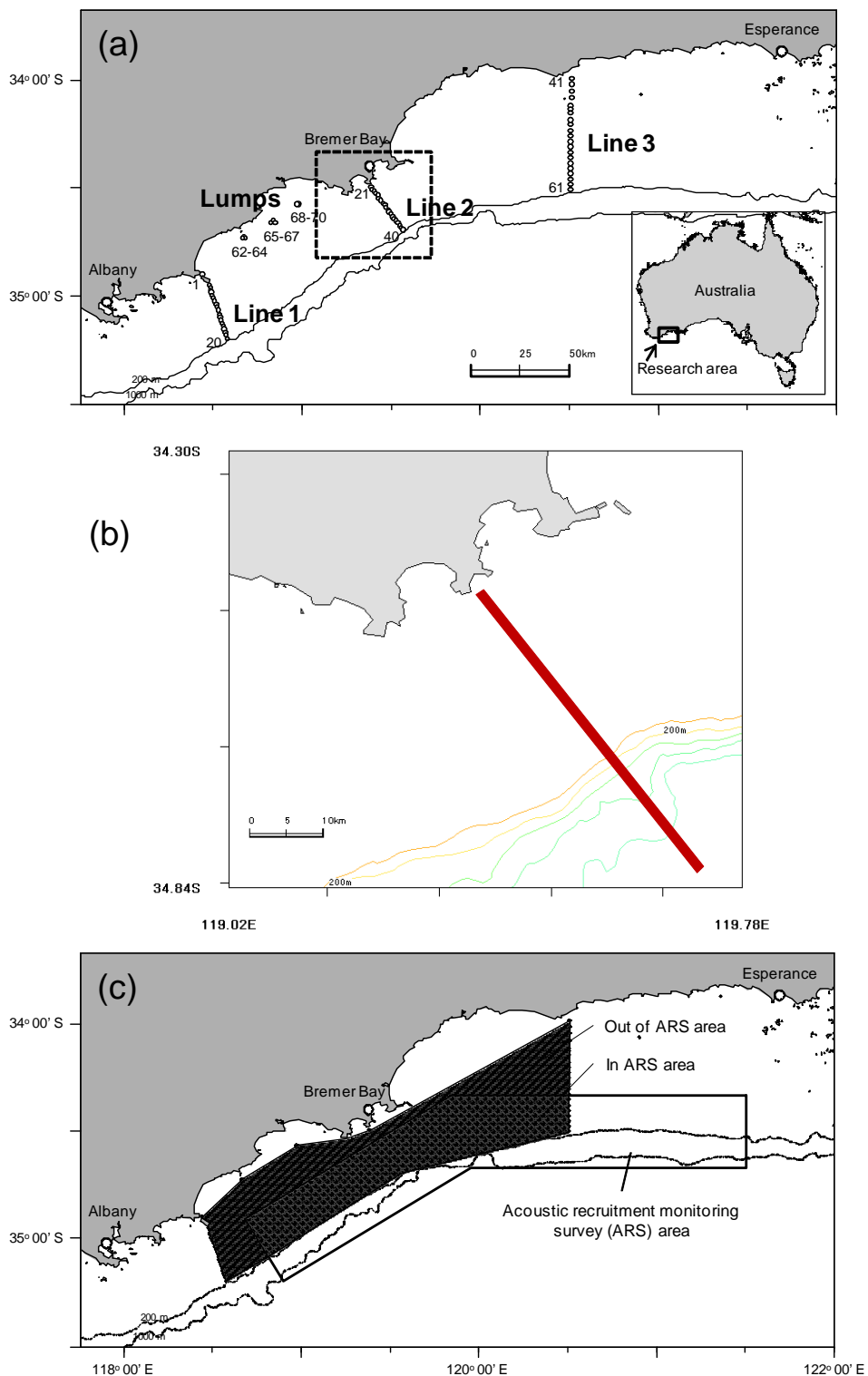


Figure 1. (a) Research area in southern Western Australia. Locations of acoustic receivers are represented by white circles (Line 1-3: $n = 20-21$ receivers per line, Lumps: $n = 3$ receivers on each lump). Receivers were aligned as a ‘curtain’ on the shelf. (b) Map showing the area researched: a straight line is the piston-line along line 2 of listening station array. (c) The area in the black line shows the acoustic recruitment-monitoring survey area (ARS area), the recruitment survey for juvenile southern bluefin tuna by omni-scanning sonar carried out since 1995/96, in the ARS area (dark diagonal area) and out of ARS area (light diagonal area).

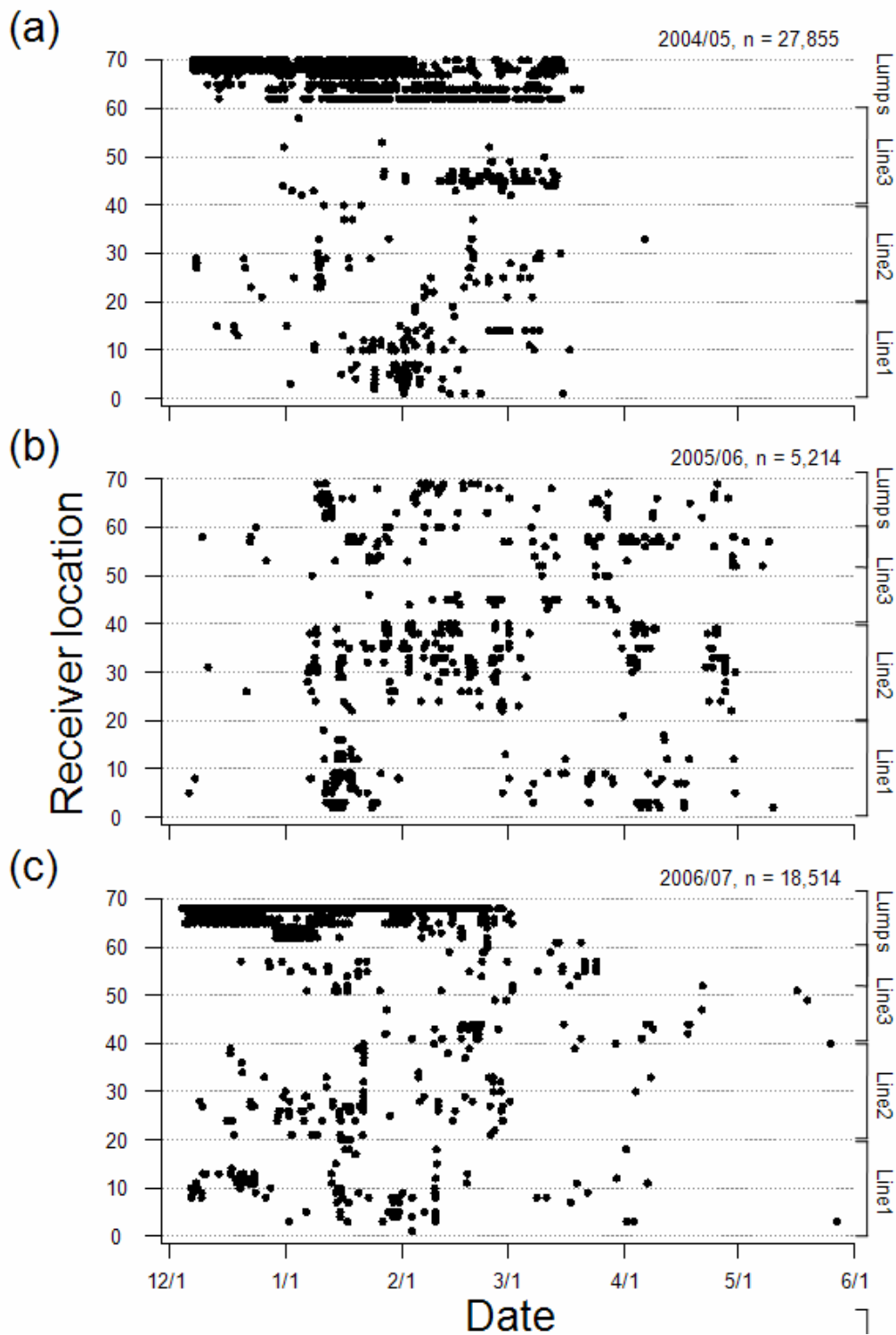


Figure 2. Time series of acoustic detections (represented by dots) for all tagged southern bluefin tuna by VR2 receivers from December to March in 2004/05 (a), and from December to May in 2005/06 (b) and 2006/07 (c). VR2 receiver's locations and numbers (No.1-20 (Line 1), No. 21-40 (Line 2), No. 41-61 (Line 3) and No.62-70 (Lumps)) are illustrated on Fig.1a.

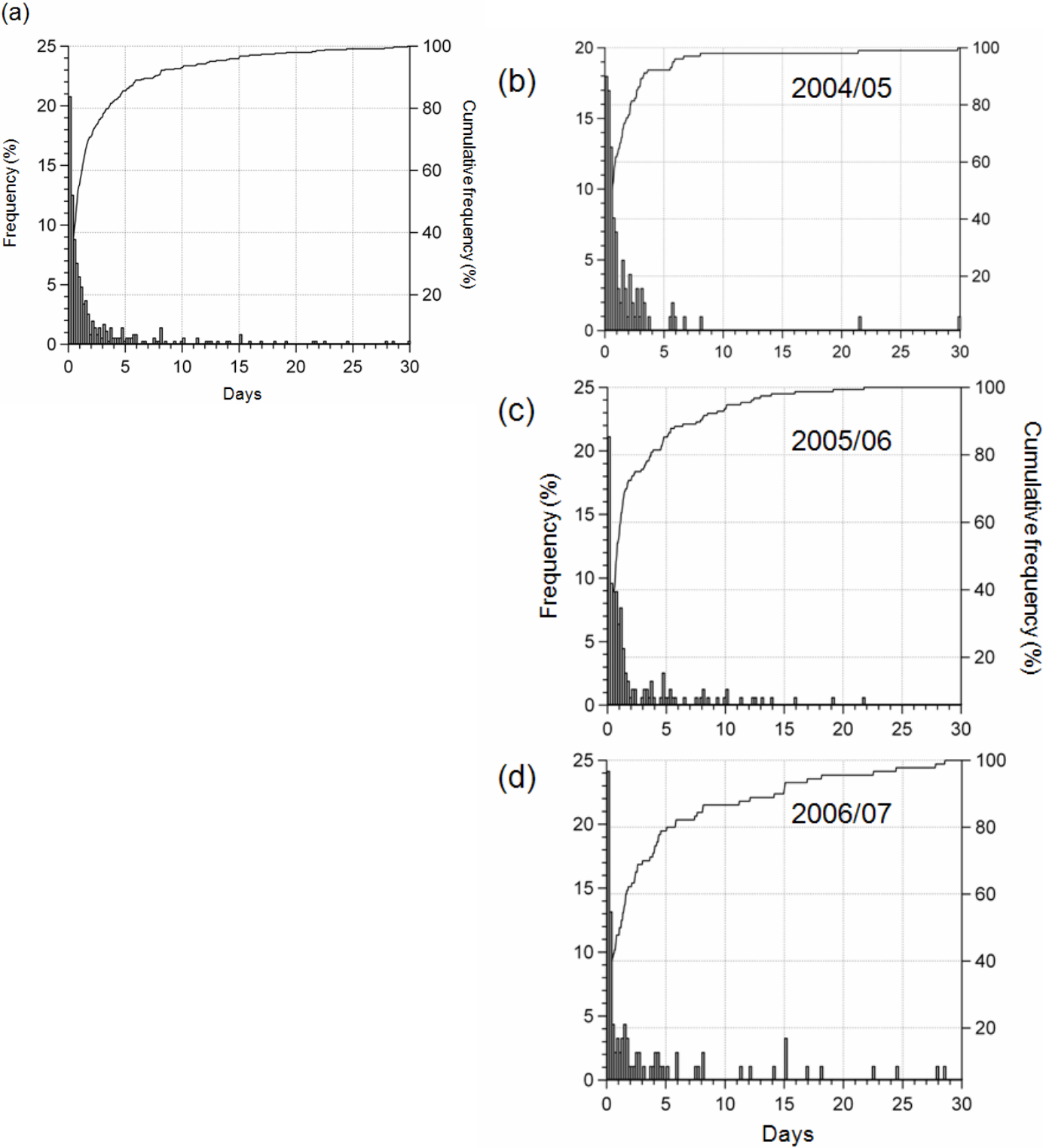


Figure 3. Cumulative frequencies of the duration on the curtain for all years data (a), 2004/05 (b), 2005/06 (c) and 2006/07.

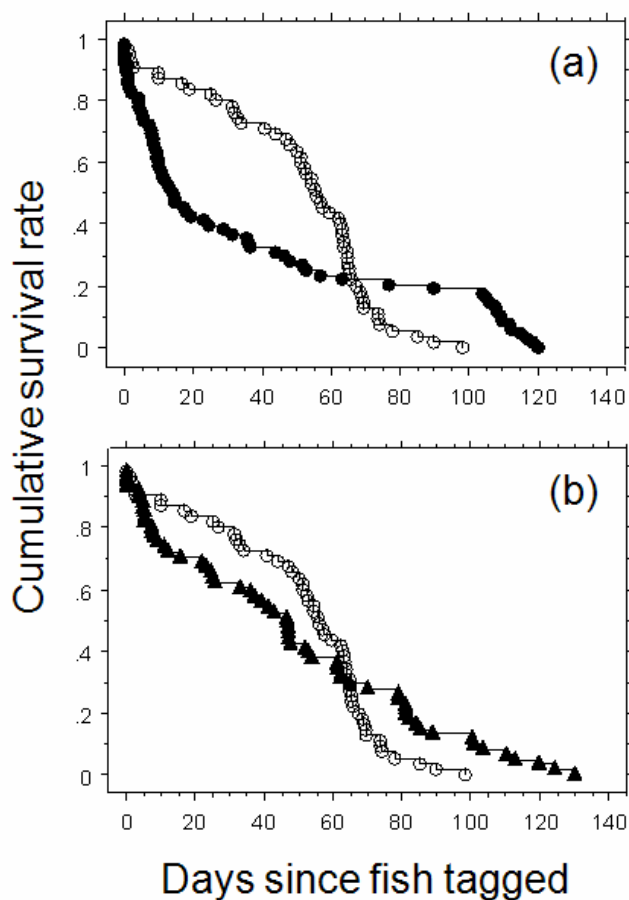


Figure 4. Kaplan-Meier curves for survival analysis of tagged fish in survey area during three seasons. (a) The residence time relationship between inshore-migrating season (2004/05; open symbols) and shelf-migrating season (2005/06; closed symbols), and (b) relationship of both inshore-migrating seasons (2004/05; open symbols, 2006/07; triangle symbols). There was significant differences between 2004/05 and 2005/06 (two-sample t -test $P < 0.05$), but no difference between 2004/05 and 2006/07 (two-sample t -test $P > 0.05$).