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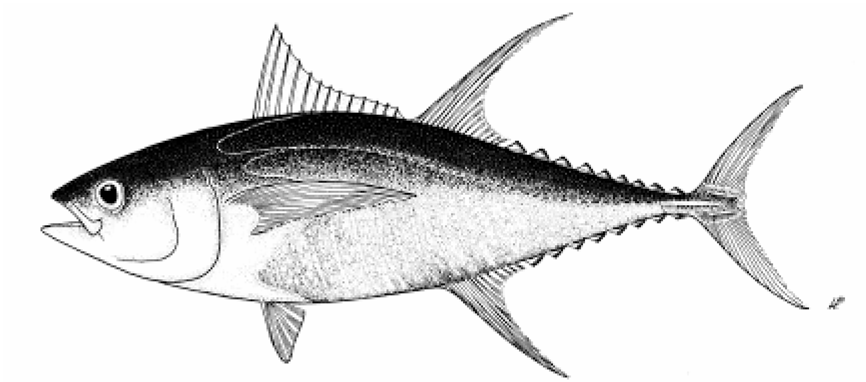
Movement of bigeye tuna (Thunnus obesus) determined from archival tag light-levels and sea surface temperatures



N.P. Clear, K. Evans, J. S. Gunn, J. Hampton, S. Bestley, K. Hartmann, T. Patterson & J. Sibert

Division of Marine Research, CSIRO, Hobart, Tasmania, Australia.
Oceanic Fisheries Program, Secretariat of the Pacific Community, Noumea, New Caledonia.
Joint Institute of Marine and Atmospheric Research, University of Hawai'i at Manoa, Honolulu, Hawai'i, USA.

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Movement of bigeye tuna (*Thunnus obesus*) determined from archival tag light-levels and sea surface temperatures

N. P. Clear[1], K. Evans[1], J. S. Gunn[1], J. Hampton[2], S. Bestley[1], K. Hartmann[1], T. Patterson[1], J. Sibert[3].

[1]Division of Marine Research, CSIRO, GPO Box 1358, Hobart, Tasmania, Australia.
[2]Oceanic Fisheries Program, Secretariat of the Pacific Community, BP D5, 98848 Noumea, New Caledonia.
[3]Joint Institute of Marine and Atmospheric Research, University of Hawai'i at Manoa, Honolulu, Hawai'i, USA.

Abstract

Conventional and archival tags were deployed on bigeye tuna (*Thunnus obesus*) in waters off the north eastern coast of Australia in the years 1999-2001 as part of a study investigating the movement patterns and habitat preferences of this species in the Coral Sea/western Pacific Ocean area. Of the 269 conventional tags (CTs) and 161 archival tags (ATs) released, 66 (24.5 %) and 17 (10.6 %) have been recovered respectively to date. Time at liberty ranged 16 to 1,441 days and tuna were recaptured between 9.6 to 7,873.2 nautical miles (nmi) from their place of release, with 90 % of all tagged fish recaptured within 150 nmi of their release position. Returns were seasonal in nature, reflecting CPUE within the domestic fishery and were similar to the results of previous conventional tagging studies in the area. Light data retrieved from 14 of the ATs were used to generate estimates of longitude using light-based geolocation techniques. Because of substantial errors associated with light-based latitude estimates, sea surface temperature matching between those data collected by the tag and those determined using remote sensing was used to determine latitude. Latitude estimates were further refined using a movement filter. Calculated position estimates suggest that, for the large part, bigeye tuna remained within the area of release for the entire time at liberty. Only three fish with ATs and two fish with CTs undertook large scale movements into the greater Coral Sea and WPO, with two recorded as returning to waters close to their release location. Limitations in the accuracy of geolocation derived position estimates confounded the establishment of finer-scale movements, although comparisons with post-processing filtering techniques (SST-matched position estimates and Kalman filtered position estimates) suggest there may be some limited movements in a north-south direction. The results of this study suggest that the east coast waters of Australia largely comprises localised populations of bigeye tuna, a proportion of which are transitory, either making cyclical large-scale movements east and into the broader WPO before returning to the Coral Sea or dispersing into areas outside of the Coral Sea. The limitations of using light-based geolocation techniques to estimate location for a sub-tropical, deep-diving predator such as bigeye tuna are discussed.

Introduction

A rapid rise in the catches of bigeye tuna (*Thunnus obesus*) in waters along the east coast of Australia from 20 to 1,050 tonnes during the 1990s has increased the value of this fishery to over $AU25 million (Ward & Bromhead 2004). As a result, bigeye have become one of the most valuable components of the east coast tuna and billfish fishery (ET&BF). These increased catch rates, an associated expansion of the fishery both spatially and temporally and recent debate over potential declines in bigeye stocks (Hampton et al. 1998) have prompted questions relating to the links between bigeye throughout the Pacific Ocean, and in particular, between those fish in the western and central Pacific Ocean (WPO and CPO).

Population studies on bigeye in the Pacific Ocean have found little evidence of genetic heterogeneity (Grewe & Hampton 1998) and, as a result, bigeye tuna caught off the east coast of Australia have been assumed to belong to a Pacific-wide stock. Conventional tagging programs carried out in the Australian fishing zone (AFZ) of the Coral Sea have observed longer-term recaptures of fish over 2,500 km from their point of release indicating that bigeye are capable of large-scale migrations (Miyabe 1994; Hampton & Gunn 1998). Such migrations provide evidence that mixing (and gene flow) across the western Pacific could occur. However, the majority of fish tagged as part of these studies (> 90 %) were recaptured within the Coral Sea, suggesting the possibility of widespread residency throughout the population.

The spatial distribution of recaptures from conventional tagging programs and a marked seasonality in recaptures, reflecting seasonality in catch rates within the fishery, has led to the proposal of two possible scenarios for bigeye in the ET&BF: (1) long residence times for the majority of fish with individuals demonstrating seasonal changes in behaviour, resulting in seasonal changes in catchability, or (2) a possible cyclic migration pattern with fish returning to the Coral Sea each year resulting in seasonal changes in availability (Hampton & Gunn 1998). A lack of any recaptures south of 25°S has also prompted questions as to the links between those fish in the northern part of the Coral Sea and those further south in the southern Coral and Tasman Seas.

Archival tags (ATs) are widely recognised throughout the international pelagic fisheries research community as an effective tool for examining movement and behaviour of large, pelagic higher order predators that remain constantly submerged (and therefore are not suitable for satellite telemetry) such as bigeye tuna (Kitagawa et al. 2000; 2004; Block et al. 2001; Gunn & Block 2001; West & Stevens 2001; Schaefer & Fuller 2002; Musyl et al. 2003; Teo et al. 2004). In an effort to test the hypotheses proposed in Hampton & Gunn (1998) and to resolve those issues concerning the relationships between bigeye stocks both within the AFZ and across the broader WPO, an archival tagging program was initiated to gather additional information on the long term movements and behaviour of bigeye. However, in determining reasonable estimates of distribution and movement of bigeye tuna within the Coral Sea and broader WPO, a number of issues relating to the accuracy of position estimates derived from light-level geolocation data needed to be addressed.

Previous studies investigating the accuracy of light level geolocation estimates have demonstrated that estimates of latitude are less accurate than those of longitude. Additionally, both longitude and latitude estimates are compromised by the diving behaviour of fish species through degradation of light attenuation curves used in calculating surface light levels at depth (Gunn et al. 1994; Welch & Eveson 2001; Beck et al. 2002; Bradshaw et al. in press; Schaefer & Fuller 2002; Itoh et al. 2003; Musyl et al. 2003). Latitude estimates are further compromised during periods surrounding the equinoxes, when differing latitudes have a similar day length preventing the calculation of latitude on the basis of day length.

In an effort to improve light-based geolocation estimates, particularly those associated with latitude, several studies have incorporated environmental data into position estimation calculations as a means of reducing the potential area in which an individual could be found (and therefore the error around the estimate). These have included bathymetry (West & Stevens 2001; Beck et al. 2002), tidal data (Hunter et al. 2003), sea surface temperature, temperature-at-depth, sea surface height, chlorophyll and ocean currents (Inagake et al. 2001; Beck et al 2002; Bradshaw et al 2002; Itoh et al. 2003; Kitigawa et al. 2004). Other techniques employed to reduce errors in light-based position estimates have included the application of models such as state-space Kalman filter statistical models which provide best-estimate predictions of the location of an animal given the light-based geolocation estimates provided to the model (Sibert & Fournier 2001; Sibert et al. 2003).

Here we present the results of investigations into the seasonal and long-term movements of bigeye tuna tagged in the western Coral Sea, providing insights into the relationships between stocks both within the ET&BF and with that of the broader WPO, information that is essential for the effective future management of these populations. Additionally, we present here the results of investigations into the use of remotely sensed sea surface temperatures as a means of improving latitude estimation and in doing so, highlight issues pertinent to the use and future improvement of geolocation techniques in resolving the movement patterns of deep diving species such as bigeye tuna.

Methods

Tags and tagging operations

A total of 161 archival tags (Mk7, Wildlife Computers, Redmond WA) and 269 pairs of conventional tags were deployed on bigeye tuna during tagging operations in the northern part of the eastern tuna and billfish fishery (ET&BF) over the period 1999-2001 (Figures 1 and 2). Fish were caught using either handlining on surface schools or longlining techniques. After capture, fish were lifted without gaffing on board the vessel and placed onto a tagging cradle. A wet cloth was placed over the eyes of the fish in an effort to calm the fish while the hook was removed and the fork length measured. Only fish less than 30 kg were made available by operators for tagging and as a result, the majority of fish tagged ranged 75-85 cm in length. The life status and condition of each fish was assessed by the person carrying out tagging operations and only those that were vigorous and retained good colour were tagged.

Conventional tags

Two conventional tags (Hallprint, Australia) bearing an identifying number and return information were inserted into the dorsal musculature on either side of the second dorsal fin approximately four cm behind the origin of the fin and one cm below the mid-dorsal body line. The dart head was orientated towards the head of the fish and inserted through, and anchored in, the basal bone elements (pterygiophores) of the fin rays.

A total of 189 of those fish tagged with conventional tags (CTs) were additionally injected with 5 ml of strontium chloride solution for age validation. Capture, tagging, strontium chloride injection and returning the fish to the water took approximately 30 seconds.

Archival tags

Archival tags were placed internally within the body cavity of each fish. An incision approximately four cm long on the ventral surface of the fish between the anal and pelvic fins was made and the peritoneum was torn using a gloved finger. A broad-spectrum antibiotic (2.5 ml) was syringed directly into the body cavity and the tag inserted, orientating the stalk in a posterior direction towards the tail. The incision was closed with an absorbable suture and the fish was returned to the water. In the case of the four fish caught during longlining operations (May 2000), individuals were additionally tagged with a pair of CTs as an alert mechanism for recapture. All other fish were tagged only with an archival tag. Archival tagging procedures in general took less than one minute to complete.

Tags were programmed to record and store internal and external temperature, light and pressure every four minutes. Each tag was printed with an identifying number, information about a reward offered and where to return the tag.

Recovery procedures

Posters detailing the objectives of the tagging program, the deployment of tags, the rewards given for returns and how to return tags were distributed to all operators in the ET&BF and in several languages to vessels outside the ET&BF working around the Coral Sea rim. Additional information on the objectives of the program and updates on its progress were distributed to fishers in the ET&BF by mail, newsletters and port visits and to the general public through media articles.

On return, ATs were checked for physical damage, sensor functioning, and clock drift. Any clock drift present was corrected (assuming a constant and progressive drift in time across time at liberty) and the data were then downloaded using custom software (Wildlife Computers, Redmond, WA). Tags from which data failed to download were returned to the manufacturer for further attempts at data retrieval. Once downloaded, data were visualised using in-house purpose software (Arctag, CSIRO Marine Research) to determine the exact time of release and recapture. Data collected by the tag either side of release and recapture were removed and the file was checked for erroneous data and post-processing depth drift. Depth drift was corrected using standard zero offset correction (ZOC) techniques. Erroneous data were flagged to ensure they were not used in subsequent processing or analyses before the complete dataset for each tag was archived in a central database. The details of all CT recaptures were also archived in a central database.

Analyses

Recaptures of CTs and ATs were investigated for seasonality in returns in the context of fishery effort. Return rates and possible seasonality in returns were then compared with previous CT returns in the Coral Sea region (Hampton & Gunn 1998).

Light-based geolocation

Daily estimates of longitude were calculated using proprietary software (GeoControl v2.01.0002; Wildlife Computers, Redmond). Light level curves are generated from light data collected by each AT and associated with a range of zenith angles (the angle between the vertical and observed centre of the sun) corresponding to a range of dawn, dusk and twilight values (Hill & Braun 2001). An approximate time of midday is input into the program as a reference point and midnight is calculated from the midpoint of the dawn-dusk events using a folding method involving overlaying the dawn and dusk light curves across one another. Standard astronomical equations are then used to calculate an estimate of longitude.

The regular crepuscular diving behaviour of bigeye tuna often severely affected the shape of the light curves displacing the attenuation of light levels with depth and therefore compromising estimation of longitude. Position estimates from days affected by such diving behaviour were not used in further analysis. Due to the interactive and thereby subjective nature of position calculations, processing of all light data was carried out by only one of the authors (KE) in an effort to standardise position estimation.

Estimating latitude using sea surface temperatures.

In an effort to address the problems associated with the calculation of latitude using light-based geolocation techniques, estimates of daily latitude were derived by comparing surface temperatures recorded by ATs with remotely sensed sea surface temperatures (SST).

A daily surface temperature for each tag was estimated from the median external temperature recorded by the tag across 0-20 m. Drift in the depth sensors of the tags used occurred over a period of months and ranged from 5-10 m up to a maximum of 15-20 m. Although ZOC techniques allowed some correction of depth drift, this did not correct for all drift across time at liberty. Zero correction techniques rely on data points collected at the surface which are then able to be adjusted back to 0 m. Datasets collected from bigeye tuna often contained very few data points collected at the surface (0 m), thereby resulting in the application of ZOC techniques to only a small number of data points temporally located large distances apart in the data record. As a result, a smaller degree of depth drift often occurred between the points at which ZOC techniques could be applied. Using a median across the top 20 m accounted for any depth drift remaining in the data record after ZOC techniques were applied and ensured that the true surface was included. Throughout the area encountered by tagged bigeye, the top 20 m appeared to be well mixed with little difference in water temperatures at the surface and 20 m. Overall, mean (±SD) differences between the water temperatures in the top 1 m and the median calculated for 0-20 m were 0.06 ± 0.12°C.

The matching process compared tag temperatures with an interpolated weekly SST product [optimum interpolation SST v2 (OI SST v2)] on a 1° grid centred along a strip of longitude based on the daily longitude estimate. Errors associated with longitude estimation [based on those calculated in Itoh et al. (2003) and Teo et al. (2004)] and those associated with sensor error [± 0.5°C associated with OI SST v2 SSTs (Reynolds et al. 2002) and ± 0.2°C associated with the temperature sensor of the tag] were incorporated into the matching process. This resulted in the matching process searching across a strip ± 1° in longitude either side of the estimated longitude and ± 0.7°C around the calculated median SST. Due to the spatial resolution of the OI SST v2 data, the strip of longitude searched either included the pixel in which the geolocation derived longitude lay and the closest adjacent pixel (resulting in a total of 2° of longitude included) or if the estimated longitude was exactly in the centre of a pixel then both adjacent pixels were included (resulting in a total of 3° of longitude included). No hemispheric limitation was placed on the SST matching process allowing all SSTs between 90°N and 90°S to be included in analyses.

Filtering of sea surface temperature derived positions

Initially, all latitudes at which tag SSTs matched satellite SSTs along the longitude strip were considered equally likely candidates for the latitude of the true location of an individual. In order to further refine the SST matching process, candidate latitudes were subjected to a movement filter. This involved determining if an individual could have reached a candidate position from any of the previous day's positions, starting with the position of release. An ellipse was generated for each candidate position determined by a 1° uncertainty in the estimate of longitude (as described above) and a 3° uncertainty in the estimate of latitude (based on error calculations around latitude estimates presented in Schaefer and Fuller (2002), Itoh et al. (2003) and Teo et al. (2004)]. If the distance between the ellipse around the previous days position and the ellipse around the current day's position was less than 1°, identified as the maximum daily swimming distance [based on daily speeds as derived from acoustic tracking studies (Carey 1992; Dagorn et al. 2000)], the position was accepted and used in the following day's calculations. The process was repeated for every day that longitude data estimates and candidate latitudes were available. If a candidate latitude was not available for a given day (due to either missing or poor longitude estimates or a lack of temperature matches) the maximum swimming distance was doubled to 2°. This was continued up to a maximum of ten days. If the recapture position of the fish was known and light data were available to the day of recapture, the filtering process was repeated backwards in an effort to further refine estimates with an exact known position. Remaining candidate latitudes were used to generate a density plot of likely positions in 1° grid squares for each day at liberty.

Comparison with position estimates as derived using Kalman filter analysis of light-based geolocation data

Latitude and longitude estimates as derived from light-based geolocation were analysed using a modified version of a state-space extended Kalman filter statistical model to produce a most probable track for each tag at liberty. Details of the methodology associated with this model can be referred to in Sibert et al. (2003). A qualitative comparison of position estimates from the Kalman filter model and those derived using SST matching techniques was made in an effort to identify discrepancies in estimating positions between the two techniques.

Results

Tag Returns

Conventional tags

Of the 269 tags released, 66 (24.5 %) have been recovered to date (Figure 1), 61 of which were recovered with recapture position information and 62 with a recapture date. Time at liberty ranged from 16 to 1,290 days with a mean of 369.6 ± 242.9 days (±SD). Distances between release and recapture positions (displacement) ranged from 9.6-1,116.0 nautical miles (nmi) with a mean displacement of 80.2 ± 192.0 nmi. Of those tags recovered 55 (90.2 %) were recaptured within 100 nmi of their release position.

Of the 66 CTs recovered, 57 were from fish injected with strontium, from which otoliths were collected from 23 and subsequently incorporated into an age validation study (Farley et al. 2003).

Archival tags

Of the 161 ATs released between 1999 and 2001, 17 (10.6 %) have been recovered to date (Figure 2). Time at liberty ranged from 47 to 1,441 days and the mean time at liberty was 578.0 ± 351.1 days. Displacement ranged 11.9-7,873.2 nmi and the mean distance displaced was 666.7 ± 1,915.1 nmi. Ten tags (76.5 % of all recovered) were recovered within 100 nmi of their release position and 14 of the 17 tags (82.4 %) were recovered within 250 nmi of their release positions. Of the tags released, the majority were released north of 18°S (97.5 %) with only four archival tags released in the southern part of the fishery (south of 18°S). Of the four tags released south of 18°S, one (25 %) has been recaptured to date.

Temporal variability in tag returns

Both CTs and ATs demonstrated a clear seasonality in returns, reflecting CPUE within the domestic Australian fishery (Figure 3). Recaptures of tagged fish (both conventional and archival) occurred through out the year, but were highest in the month of September (CT: 35.5 %; AT: 35.3 %). Relatively higher numbers of CT returns also occurred in the months of April (11.3 %), November (17.7 %) and December (14.5 %). One AT was recaptured in November 1999, one month after release and eight CTs were recaptured one month after release in 2001. The highest numbers of both CT and AT returns occurred in 2002 (Figure 3), the year after the final release of tags and at a time when the highest number of tags were present within the fishery. Prior to 2002, six ATs (35.3 % of recaptures) and 11 CTs (17.7 %) had been recaptured.

Longitude calculation and longitudinal movement

Of the 17 ATs recovered, a total of 3,482 days of light data were retrieved from 14 (Table 1), with data unable to be retrieved from three due to tag failure. Of those tags from which data could be retrieved, data for the complete period at liberty were only available for four tags, with either sensor failure or tag failure occurring in all other tags (Table 1).

A total of 3, 236 estimates of longitude were calculated using light-based geolocation techniques, representing 45.5 % days of the total 7,105 days tags were at liberty and 92.9 % of days for which light data were available(Table 1). Twelve of the 14 tags demonstrated an average displacement in longitude (difference between release longitude and individual longitude estimates across time at liberty) of less than 3° (range: 0.8 ± 0.6 to 2.7 ± 2.2°), suggesting the majority of tags did not make significant movements in an east-west direction during the period for which data were available. The other two tags demonstrated substantial east-west movements moving from release positions at approximately 147°E to as far as 168°E (98-353) and 163°E (99-213; Figure 4). Both bigeye, although released in different years, initiated eastward movement in the December after their release, with 99-213 initiating a second eastward movement in the December of the following year. Although the light sensors failed on both tags, recapture positions suggest 98-353 undertook at least a second eastward migration (it was caught at 164°E) and that 99-213 returned to an area of the same longitude as that of its release.

One AT recovered, but from which no data were able to be retrieved, was caught at 178°E and a CT released as part of this project was recaptured at 165°E, demonstrating that these bigeye had also undertaken at least one significant eastward movement during their time at liberty. There is some indication that two other bigeye tagged in the western Coral Sea also initiated similar east-west movements or east-west movements of a smaller scale (Figure 4). Both tags appeared to move beyond 155°E (98-372, 99-243), again in December, however, the extent of their movement could not be confirmed due to tag failure.

The error associated with light-based longitude estimates was calculated from the difference between the release position (recorded from the tagging vessel's GPS) and the longitude estimate for the first ten days after release (Figure 5) and for those ATs for which light data were available, the last ten days before recapture. Differences between release positions and the calculated longitude for the day of release ranged from 0.03 to 1.6° (mean±SD: 0.3 ± 0.4; n = 13) and those for the second day of release ranged 0.04 to 4.0° (0.9 ± 0.7; n = 14). Of the four tags for which light data were available on recapture, differences between recapture positions and the calculated longitude for the day of recapture (Figure 5) ranged 0.3 to 2.5° (1.4 ± 1.5; n = 2). Differences between recapture positions and the day before recapture ranged 0.1 to 1.2° (0.5 ± 0.5; n = 4).

SST-based latitudes

Depth and water temperature data were available from all 14 tags for a total of 3,373 days. Of these data, a median water temperature for the upper 20 m was able to be calculated for 3,364 days (99.7 % of all days available; Table 1). Matching between tag and satellite surface water temperatures did not result in single point estimates of latitude due to the low temperature gradient of surface waters throughout the tropics (resulting in the same water temperature occurring across large areas). As a consequence, for any given longitude estimate a number of latitudes could be considered as candidates for a tags position on any given day. A total of 81,934 candidate latitudes were calculated representing matches between remotely sensed and in situ SSTs for 3,236 light based longitude estimates. After application of the movement filter this total was reduced to 48,780 candidate latitudes (Table 1). During the summer months, when tropical sea surface temperatures are highest and thermal gradients are lowest, candidate latitudes were contiguous along each longitudinal strip, and in some records extended from the release area across the equator and into the Northern Hemisphere (Figure 6). During winter months when surface water temperatures are lower and thermal gradients are highest, candidate latitudes often resulted in two discontinuous bands of possible positions either side of the equator (Figure 6).

For those tags for which light data were available for the total time at liberty, the ability to run the movement filter backwards improved latitude estimation, reducing the number of candidate latitudes, particularly those associated with a gradual drift in SST matches across hemispheres (Table 1, Figure 6). This also improved the error (the difference between the recapture position as derived from the tagging vessel's GPS and the latitudes estimated) around latitude estimates with mean overall error for latitude estimates the day before recapture reduced from 5.1 ± 13.0° to 0.4 ± 0.4° and those for two days before recapture reduced from 6.9 ± 14.2° to 0.8 ± 0.6° (Figure 7). Mean error estimates for all tags calculated from the difference between the release position (recorded from the tagging vessel's GPS) and latitude estimates for the first ten days after release (Figure 8) ranged from 0.0 ± 0.0° to 0.1 ± 0.0° (n=4) on the day after release and 0.5 ± 0.0° to 1.0 ± 0.6° (n=9) for the day two days after release.

Final position estimates and comparisons with Kalman filter analysis of light based position estimates

Density plots of position estimates produced by the use of light-based longitude estimates and filtered SST matched latitudes demonstrated in all tags (except those that moved east) that the highest frequency of matches were located in the area of release (either the north-west Coral Sea or southern Coral Sea), indicating that bigeye were largely resident in the Coral Sea during their time at liberty (Figure 9). Latitude estimates for the two tags that demonstrated east-west movements suggest possible movements north, particularly in those areas furthest east. A further AT released in the northern part of the fishery was recaptured towards the south-eastern part of the fishery, however, determining the details of this movement (i.e. whether the individual moved further south before perhaps moving north again or whether movement in a north-south direction was linked with movement in an east-west direction) was inhibited by the failure of the tag.

Comparisons with those position estimates derived from a modified version of a state-space extended Kalman filter statistical model support the indication that bigeye were largely resident within the Coral Sea (Figure 10). These results also demonstrated that the two tags 98-353 and 99-213 made substantial east-west movements. However, the additional northward movement demonstrated by filtered SST matched latitude estimation, while evident in those position estimates derived from the Kalman filter for 98-353, was not evident for 99-213.

Discussion

Recapture rates – conventional vs. archival tags

Return rates for tags released on bigeye tuna as part of this study differed substantially between the two tag types, with CT returns more than twice that of AT returns. Such tag return rates differ from those reported from simultaneous releases of CTs and ATs on bigeye tuna in the eastern Pacific Ocean (EPO) which demonstrated comparable return rates between ATs and CTs (Schaefer & Fuller 2002; Musyl et al. 2003). Tag returns from southern bluefin tuna (*Thunnus maccoyii*; SBT) tagged with ATs and CTs in southern Australian waters have demonstrated an opposing pattern with higher return rates of ATs than those of CTs (CSIRO unpublished data).

The discrepancy in return rates between these studies may be a consequence of a number of possible factors such as (1) higher rates of mortality in bigeye tuna in this study as a result of the methodology used to deploy ATs; (2) a higher rate of post-tagging infection in the bigeye tuna released with ATs in this study (3) lower compliancy rates of reporting and returning of ATs throughout the ET&BF fishery than those elsewhere or (4) differences in sample sizes and sampling effort.

Although it is unknown to what extent methodology (published details account a similar methodology to that used in this study) and experience differed between this study and those conducted elsewhere on bigeye, both tagging methodology and the experience of personnel have been standardised across the bigeye and SBT tagging programs undertaken by the CSIRO. However, environmental conditions at the time of tagging are difficult to standardise across programs, particularly in differing geographic regions and differences in survival rates may occur as a result. It is possible that the need to handle individuals on deck when deploying tags may have resulted in a higher susceptibility of bigeye to overheating due to higher air temperatures in the sub-tropics in comparison to more temperate air temperatures in SBT tagging areas and may have resulted in the higher rates of returns observed in SBT. However, there was little evidence of this at the time of tagging; all fish tagged appeared lively and swam strongly away from the vessel after release. Further, the higher temperatures of sub-tropical waters may result in a higher susceptibility to post-release infection in bigeye tagged with ATs. It could be expected that incisions generated by the insertion of smaller CTs would heal more rapidly than the larger and deeper incisions resulting from insertion of ATs. In an effort to reduce this possibility of infection we flushed each incision liberally with a broad-spectrum antibiotic before insertion of the tag (therefore maximizing the possibility of absorption). Reports from processors on the state of fish with ATs when recaptured suggest little evidence of infection in individuals, although incisions were reported to remain partially open around the trailing stalk. Of those bigeye released in EPO waters, similar cases of failure of incisions to completely close were reported (Schaefer & Fuller 2002). Additionally, a number of individuals were reported to present signs of trans-intestinal expulsion of ATs, suggesting significant irritation of ATs in those cases. Without an ability to recover deceased fish in order to determine cause of death it is difficult to resolve these possibilities.

Archival tagging programs conducted by the CSIRO involving SBT have been in operation since the early 1990’s and have involved significant communication programs detailing the deployment of tags and the rewards involved across the nations involved in this fishery. Although substantial effort was put into informing those fisheries catching bigeye in the WPO of the deployment of ATs on bigeye and the rewards involved, the number of nations involved in this fishery, the significant increased liaison effort required and the smaller time period for awareness programs could have resulted in lower levels of reporting compliancy.

Return rates of tags are dependent on both the number of tags deployed and the amount of effort associated with their recapture. Substantial differences exist in both the number of tags deployed and the amount of effort associated with each of the bigeye studies (this study; Schaefer & Fuller 2002; Musyl et al. 2003) and those investigating SBT (CSIRO unpublished data). Although resolution of these differences is beyond the scope of this study, the potential for differences in tag returns associated with these issues should be noted.

Return rates for both CTs and ATs deployed in this study were higher than those reported from the Coral Sea region in the early 1990’s (6.1 %; Hampton & Gunn 1998). Whether this reflects higher exploitation rates of bigeye or depletion of stocks within the Coral Sea region is difficult to determine due to differences in sample sizes between the two studies and substantive temporal changes in effort and targeting in the Coral Sea.

Temporal variability in recapture rates and how this relates to the movement patterns of bigeye tuna throughout the western Pacific Ocean

Returns of both types of tag deployed in this study were highly seasonal, reflecting CPUE within the Australian domestic fishery and supporting the findings in Hampton & Gunn (1998). The seasonally variable catchability observed in Hampton & Gunn (1998) was hypothesised to be the result of two possible occurrences: (1) long residence times for the majority of fish with fish demonstrating seasonal changes in behaviour, resulting in seasonal changes in their catchability, or (2) a possible cyclic migration pattern with fish returning to the Coral Sea each year.

The majority of fish from which AT and CTs were returned appeared to largely be resident within the north-western Coral Sea, with only five (three ATs and two CTs) of the 83 returned able to be confirmed as moving beyond these waters and into the greater WPO. Further, the recapture of one AT released in the southern part of the fishery in close proximity to its release position and the apparent lack of movement of this fish outside of this area, coupled with only one return of a northern tagged fish towards the southern part of the fishery suggests that there is also substantial residency even within the ET&BF.

There is some difficulty however in determining the proportion of the bigeye that demonstrated movement outside of the north-west Coral Sea region. In addition to the two AT for which large-scale movements were documented, at least two ATs (98-372 and 98-479) were observed to initiate movement in an easterly direction; however calculation of the extent of these movements was prevented by tag failure. If these bigeye did undertake easterly movements similar to that recorded by archival tags 98-353, 98-357 and 99-213, the number of migrating individuals may have numbered five ATs (36 %). Whether this is a true reflection of the proportion of individuals within the population undertaking long-distance movements is difficult to determine without further tagging programs within the region.

The majority of long-distance movements observed in bigeye tagged as part of this study appear to be cyclical, suggesting a return of individuals to populations in the area of the ET&BF and a lack of gene flow outside this area. Whether the movement patterns of those CTs and ATs caught in areas north of the release areas and that of the tag caught to the south of it's release area were also cyclical in nature cannot be confirmed either due to failure of ATs or recapture data being derived from CTs. Without an accurate assessment of the proportion of bigeye in the region undertaking cyclical movement patterns, it is difficult to assess the effects of such movements of individuals into and out of the fishery on catch rates and any temporal variability in these. Genetic studies carried out to date have provided little evidence of genetic differentiation of bigeye tuna throughout the Pacific (Grewe & Hampton 1998; Chow et al. 2000), suggesting some mixing of individuals between populations and therefore the possibility that some of the large-scale movements undertaken by bigeye may not be cyclical in nature.

Bigeye tagged in other parts of the Pacific largely demonstrate residency to those areas of release (Itano & Holland 2000; Schaefer & Fuller 2002; Sibert et al. 2003), with behaviour involving movement away from the greater release area virtually absent among recaptures. In such areas bigeye have been observed to associate around both artificial and natural features in the ocean such as fish aggregation devices (FADs), weather buoys, seamounts and offshore island features such as reefs (Dagorn et al. 2000; Schaefer & Fuller2002; Musyl et al. 2003; Sibert et al. 2003). While little is known about the fine-scale distribution of bigeye along the AFZ, the distribution of the fleet appears to be associated with topographical features such as the edge of the Great Barrier Reef (GBR) and ocean frontal zones. Topographical features such as seamounts and oceanic features such as ocean frontal zones have been associated with enhanced prey density (Koslow et al. 2000; Fock et al. 2002; Seki et al. 2002) and in areas of low productivity such as the eastern AFZ (Ward & Elscot 2000), serve as important foraging areas for higher order predators such as tuna (Fiedler & Bernard 1987; Seki et al. 2002). It is likely that features such as ocean frontal zones, seamounts and other bathymetric features along the eastern AFZ serve as focal areas for species such as bigeye and if they provide a consistent forage resource, may serve as broad areas of residence.

Why migrate?

The trigger for a change in behaviour that resulted in some fish moving out of the north-west Coral Sea is unclear, but may be related to the end of spawning. Ripe female bigeye tuna have been caught in the ET&BF across the period of August to December (Farley et al. 2003) suggesting spawning across these months. All fish that undertook movements out of the broader release area, initiated their movement in the month of December towards the end of the spawning season. Given that only a proportion of all individuals tagged undertook large-scale movements, it could be proposed that only the mature portion of the population undertake long distance movements (largely cyclical in nature), with juveniles resident in the ET&BF year round.

Definitions of size at maturity are varied among bigeye tuna, with minimum sizes varying from 64 cm (Hisada 1973) up to 125 cm (McPherson 1992) in the north-west Coral Sea. Fork lengths of bigeye at 50 % maturity during the spawning season in the north western Coral Sea have been reported as 102 cm in females and 87 cm in males with 90 % maturity occurring at 122 cm in females and 120 cm in males (Farley et al. 2003). Of those bigeye recaptured, on release two individuals with ATs and 16 with CTs were equal to or greater than 87 cm in length and only one conventionally tagged was of 102 cm in length. At the time of recapture, all individuals with ATs and 49 with CTs were equal to or greater than 87 cm in length and six (ATs) and 42 (CT) were of 102 cm in length. Although sex allocation of individuals was not made, if we assume that all individuals recaptured were male, at least five individuals with ATs and at least 25 individuals with CTs would have been sexually mature. If we assume that all were female, at least three with ATs and 21 with CTs would have been sexually mature, substantially more individuals in either case than those with CTs documented to undertake large-scale migrations and comparable to the number of individuals with ATs documented to undertake large-scale migrations. However, if large-scale movements are cyclical in nature, only those individuals with CTs caught outside the greater release area would be positively identified as undertaking such large-scale movements. As a result, it is highly likely that the number of individuals documented as undertaking large-scale movements is underestimated. All individuals for which large-scale migrations were positively identified ranged 84-89 cm in length on release and all are likely to have been greater than 120 cm on recapture (two were 121 and 129 cm in length, the remainder, although total lengths on recapture were not provided, taking into account time at liberty and average growth rates would have been of a similar length).

The information on movement provided by the analysis of light-based geolocation data presented here suggest bigeye tuna display a range of movement behaviours; residency, cyclical migration and dispersion. Other fish species such as Atlantic cod have been observed to display a similar range of movement behaviours, with the majority of cod resident to particular areas and a smaller number dispersing and undertaking cyclical movements between feeding, overwintering and spawning grounds (Robichaud and Rose 2004). The incidence of migrators and dispersers amongst groups of cod was associated with population size and was dependent on the carrying capacity of the area in which the cod were tagged. Atlantic bluefin tuna (*Thunnus thynnus*) have been observed to demonstrate a range of movement behaviours also, with fish tagged in the waters of North Carolina demonstrating cyclical migration to either spawning areas in the western Atlantic or the Mediterranean or to non-spawning areas in the western Atlantic and dispersion to the Mediterranean (Block et al. 2001). The reasons behind large scale movements in bigeye are unclear, but may also be associated with movement between spawning and foraging grounds and the proportion of migrators may also be associated with the carrying capacity of the north-west Coral Sea. A need to maximize fitness and reduce competition for resources in a seasonal environment may result in a proportion of the population undertaking such large scale movements. Further collection of data on movements in bigeye via archival tagging coupled with the collection of size and sex information is required to resolve this question.

Estimating position using light-based longitudes and filtered SST matched latitudes

Using SST at low latitudes to derive precise position estimates is problematic. Near the equator, temperatures within the bounds of the errors placed on the matching process used in this study can be present across a wide range of latitudes, thereby broadening the potential area in which a fish may be located. Studies located in higher latitudes do not face as substantial a problem in determining potential locations due to steeper latitudinal gradients in sea surface temperatures which serve to reduce the number of potential candidates for latitude estimates. This was further exacerbated by allowing the parameters of filtering process to run unconstrained, i.e. latitudes along the longitude strip across both hemispheres could be considered as candidates for SST matches. Movement constraints on the basis of hemisphere such as those utilised for temperate species of tuna (which are unlikely to cross the equator; e.g. Teo et al. 2004) could not be considered for the movement patterns of sub-tropical species such as bigeye tuna, which has been observed to cross the equator in previous tagging studies (Hampton & Gunn 1998; Schaefer & Fuller 2002). As a result, unique SST-based latitudes were only able to be calculated on 0.04 % (17 days) of all days bigeye recaptured in this study were at liberty, a figure far less than the 80 % reported for temperate species such as Pacific bluefin tuna (*Thunnus orientalis*; Itoh et al. 2003).

Estimates of error surrounding geolocation-derived positions for the first day of release were comparable to those calculated using similar comparisons to known locations elsewhere. Comparisons between light-based geolocation estimates and known recapture positions of bigeye tagged in the waters of Hawai'i were calculated as 0.2° and 0.3° for latitude and 0.2° and 0.1° for longitude (Schaefer & Fuller 2002). Direct comparisons between position estimates derived from light-based longitude estimates and SST-matched latitude estimates and Argos-based satellite positions in a double tagging experiment on two species of shark resulted in the calculation of root mean square errors of 0.9° and 0.6° for longitude and 1.5° and 1.2° for latitude (Teo et al. 2004). In the same study, light-based longitude estimates and SST-matched latitude estimates derived from both pop-up satellite tags (PSATs) and ATs deployed on Atlantic bluefin tuna were compared with Argos-based PSAT end points and GPS recapture locations, resulting in root mean square errors of 0.8° and 1.3° for light-based longitudes and 0.9° and 1.9° for SST latitudes derived from ATs and PSAT tags respectively.

The accuracy of position estimates using geolocation has been tested using several other methods such as mooring experiments and deployment of tags on fish in captivity, resulting in similar or worse error estimates than those presented in this study. Welch & Eveson (2001) placed tags on a fixed subsurface mooring at high latitudes, calculating average position errors of 30 km longitude and 44 km in latitude. In a similar mooring experiment at mid-latitudes, position errors calculated were of 0.1° to 0.3° in longitude and 0.8° to 3.5° (Musyl et al. 2003). Gunn et al. (1994) estimated errors of 0.5 ± 0.1° for longitude and 1.5 ± 0.2° for latitude around position estimates derived from tags deployed on SBT in a towed cage. Errors of 2.4 ± 0.4° and 0.5 ± 2.5°for longitude and 1.8 ± 2.0° and 1.3 ± 5.3° for latitude were determined from light data collected from two tagged Pacific bluefin tuna placed in stationary pens (Itoh et al. 2003).

Differences between the SSTs measured by the external sensor of the tag and those remotely sensed via satellite have been identified as an important source of error when calculating SST-matched latitudes, with this effect strongest where latitudinal SST gradients are shallowest (Teo et al. 2004). These differences may be compounded by response times of the thermistor on the tag, drift in depths recorded by the tag and the effects of atmospheric and oceanographic conditions on the accuracy of remotely sensed SSTs. The tags used on bigeye in this study incorporated a temperature sensor located on the end of a stalk located external to the fishes' body. Response times reported by the manufacturer were relatively fast and in the order of 6 s. Drift in pressure sensors was recorded in almost all tags recaptured and ranged from 5-10 m up to a maximum of 15-20 m. In an effort to reduce the error caused by drift in the pressure sensors of the tag, we used the median temperature calculated across temperatures recorded between 0-20 m. Due to the well mixed nature of the top 20 m of the water column with the Coral Sea differences between water temperatures recorded between 0-1 m and the median of the top 20 m were less than 0.2°C and generally less than the error associated with the tags temperature sensor. The product we used, optimum interpolation SST v2 (OI SST v2), is an interpolated weekly SST product, which, although through interpolation on such a time scale, reduced the effect of cloud cover on estimated SSTs, combined both day and night passes thereby including heating/cooling effects at the surface related to day and night (Robinson et al. 1984; McClain et al. 1985). In an effort to overcome these errors, the OI SST v2 incorporates in-situ temperature data from observations from ships and buoys, converting the temperature of the "skin" (about a micron in depth) to a "bulk" (0.5-1 m in depth) SST, thereby correcting for day/night differences (Reynolds et al. 2002). Corrections are also incorporated into OI SST v2 for the negative temperature bias in SSTs when clouds are present.

Verification and further development of the position estimation method

Position estimates calculated after application of a modified state-space Kalman filter model on light-based latitudes and longitudes supported the findings resulting from our analysis of light-based longitudes and filtered SST-matched latitudes. One advantage of analysing position estimates with a state-space model is that it not only provides a "most likely track", it also calculates an estimate of error associated with each position estimate (Jonsen et al. 2003; Sibert et al. 2003). However, estimating latitudes at equinoxes still poses a problem and a limitation of the Kalman filter model is that it depends on the model estimates rather than the observed estimates at these times. While we were unable to determine the details or extent of any north-south movement of bigeye, particularly on smaller scales within the north-west Coral Sea, the Kalman filter appeared to record such movements among a number of tags. However, it is difficult to determine whether this apparent movement was related to serial correlation in the geolocation derived position estimates (each position is dependent on the calculated position from the previous day), rather than true movement. One possible way of reducing these biases and reduce the effect of the equinoxes may be to extend a similar state-space model to include SST matching. Further work investigating the sensitivity and validity of the results of differing state-space models (e.g. Kalman filter, Markov chain Monte Carlo, advection-diffusion methods) should also be encouraged.

Rather than providing a point estimate of position for each day a tag was at liberty, the imprecision in the SST-matching process for geolocation in equatorial waters resulted in "clouds" of possible latitudes from which a most likely region of occupancy could be determined. This, as a result, prevents the ability to estimate the position of individual on a fine scale, and subsequently limits any fine-scale investigations examining the relationship between individuals and their environment. As tag manufacturers continue to improve light based geolocation methodology, estimates of longitude and latitude at times other than the equinoxes will also continue to improve, reducing the spatial scale at which inferences on movement can be made. However, estimating latitude at times around the equinoxes will continue to be a problem. As remote sensing and modeling of temperature-at-depth improves the ability to use temperatures other than surface temperatures, possible means of reducing the number of candidate latitudes may include matching of temperatures across a range of depths. Advances in tag technology involving a reduction in pressure sensor depth drift, faster response times in thermistors and enhanced accuracy in temperatures and depths recorded will serve to improve the accuracy in determining temperatures for matching. Similarly, advances in remotely sensing SSTs will reduce spatial scales at which matching can be made and improve accuracy in temperature matching.

While determining the best estimate of position using ATs, particularly in equatorial waters is not a simple process (Figure 11), this study has demonstrated that combining both SST matching and movement filters can substantially improve our ability to estimate broad-scale movements of bigeye tuna. While movements between the north-western Coral Sea and the greater WPO were evident among some bigeye tagged as part of this study, our ability to determine that proportion of the population that undertake large-scale movements is restricted. However, our results suggest a broad-scale residency of bigeye within the Coral Sea. Further, the lack of returns of northern released fish in the southern part of the fishery and *vice versa* suggests that there is also substantial residency of individuals within populations throughout the ET&BF. Further tagging studies involving deployment of tags throughout the entire ET&BF would serve to provide greater insight into the possibility of resident sub-populations throughout the ET&BF and provide information essential for the effective and sustainable management of this species.

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Table 1. Details of light data, longitude estimates and latitude estimates using sea surface temperature (SST) matching and filtering methods for all archival tags deployed in the Coral Sea 1999-2001.

Tag	DAL	Days of light data	Days of median ST (0-20m)	Light-based longitude estimates	SST-matched latitude estimates	One-way filtered latitude estimates	Two-way filtered latitude estimates
98-347	934	277	277	274	5,315	2,370	–
98-353	874	218	253	198	5,672	1,110	–
98-363	758	522	519	519	14,060	10,120	–
98-372	969	84	92	80	1,736	781	–
98-463	281	60	58	58	978	497	262
98-479	47	47	47	46	711	313	–
99-190	378	378	370	378	6,048	2,973	2,746
99-213	697	436	338	436	12,459	3,759	–
99-216	351	205	202	204	7,041	4,840	–
99-224	254	254	242	252	7,381	5,145	3,717
99-237	636	224	219	224	6,991	5,125	–
99-243	224	224	224	222	4,257	946	–
99-262	350	267	243	244	5,533	3,899	–
00-112	352	286	280	101	3,752	1,902	–
Total	**7,105**	**3,482**	**3,364**	**3,236**	**81,934**	**48,780 (8,615)^**	**6,725**

DAL: days at liberty
^: total for tags for which the two-way filter could be applied

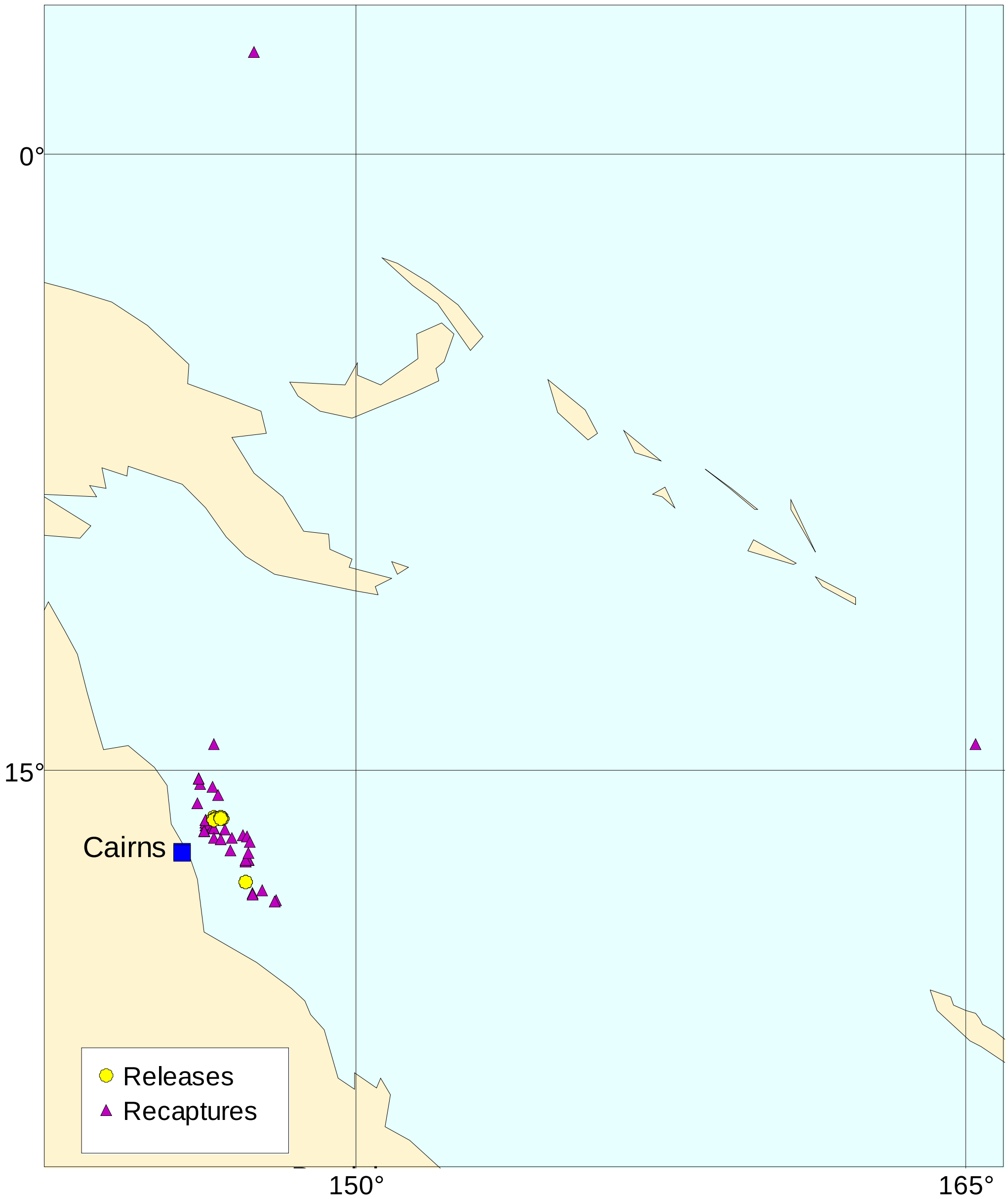

Figure 1. Release and recapture positions of conventional tags deployed on bigeye tuna in the Coral Sea.

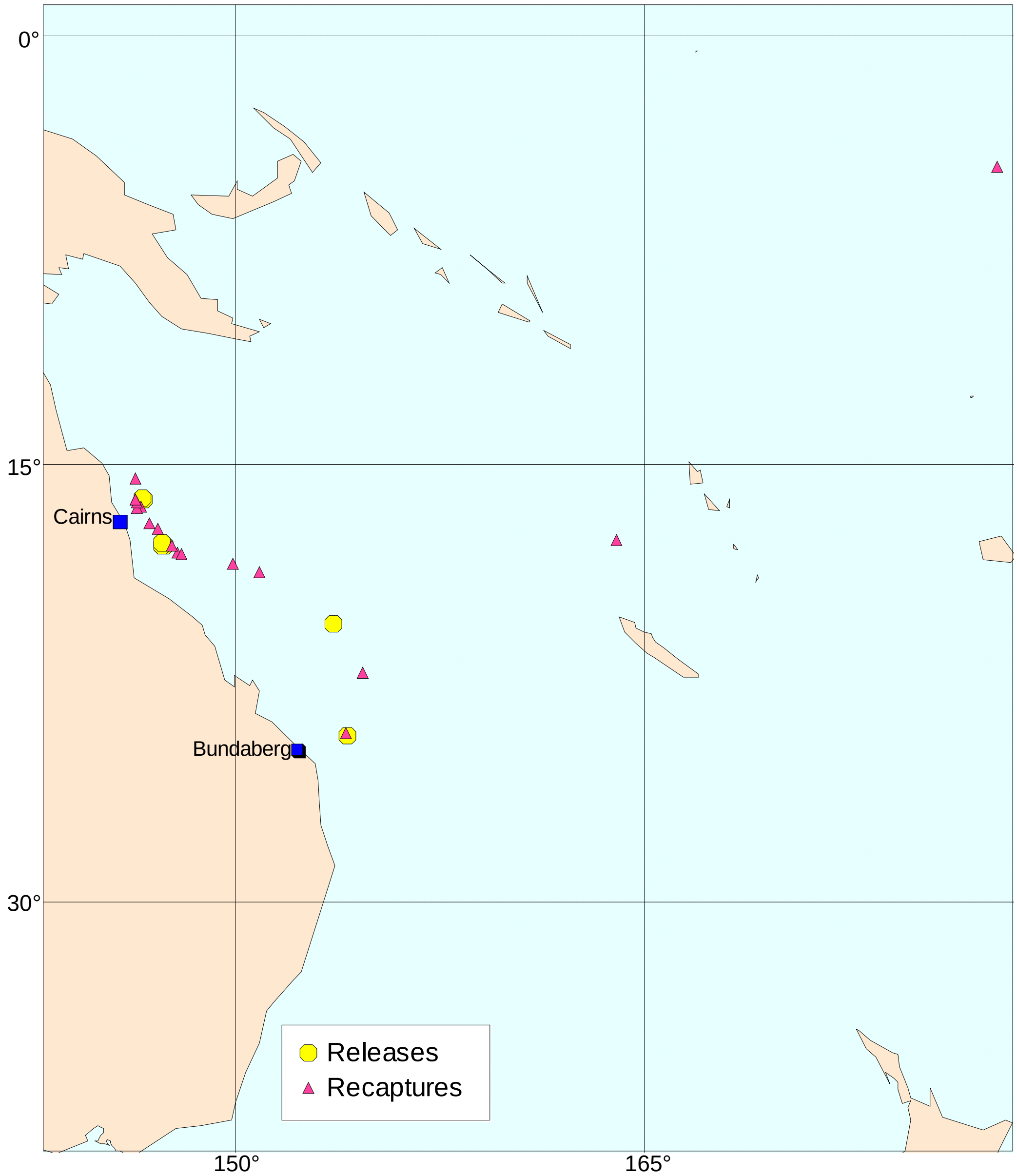

Figure 2. Release and recapture positions for archival tags deployed on bigeye tuna in the Coral Sea.

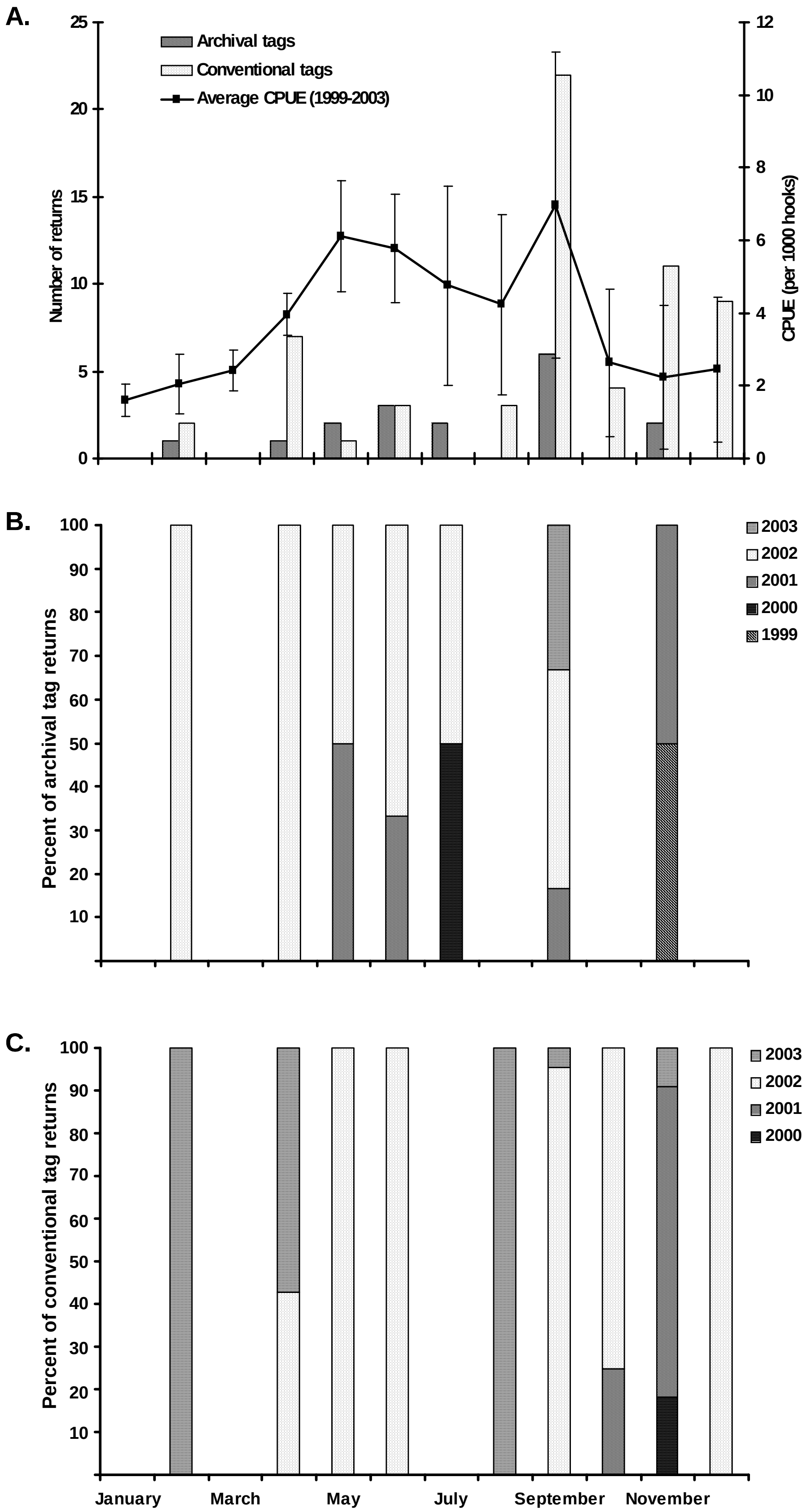

Figure 3. Conventional and archival tag returns (a) across months in relation to average CPUE for 1999-2003; (b) and (c) per year.

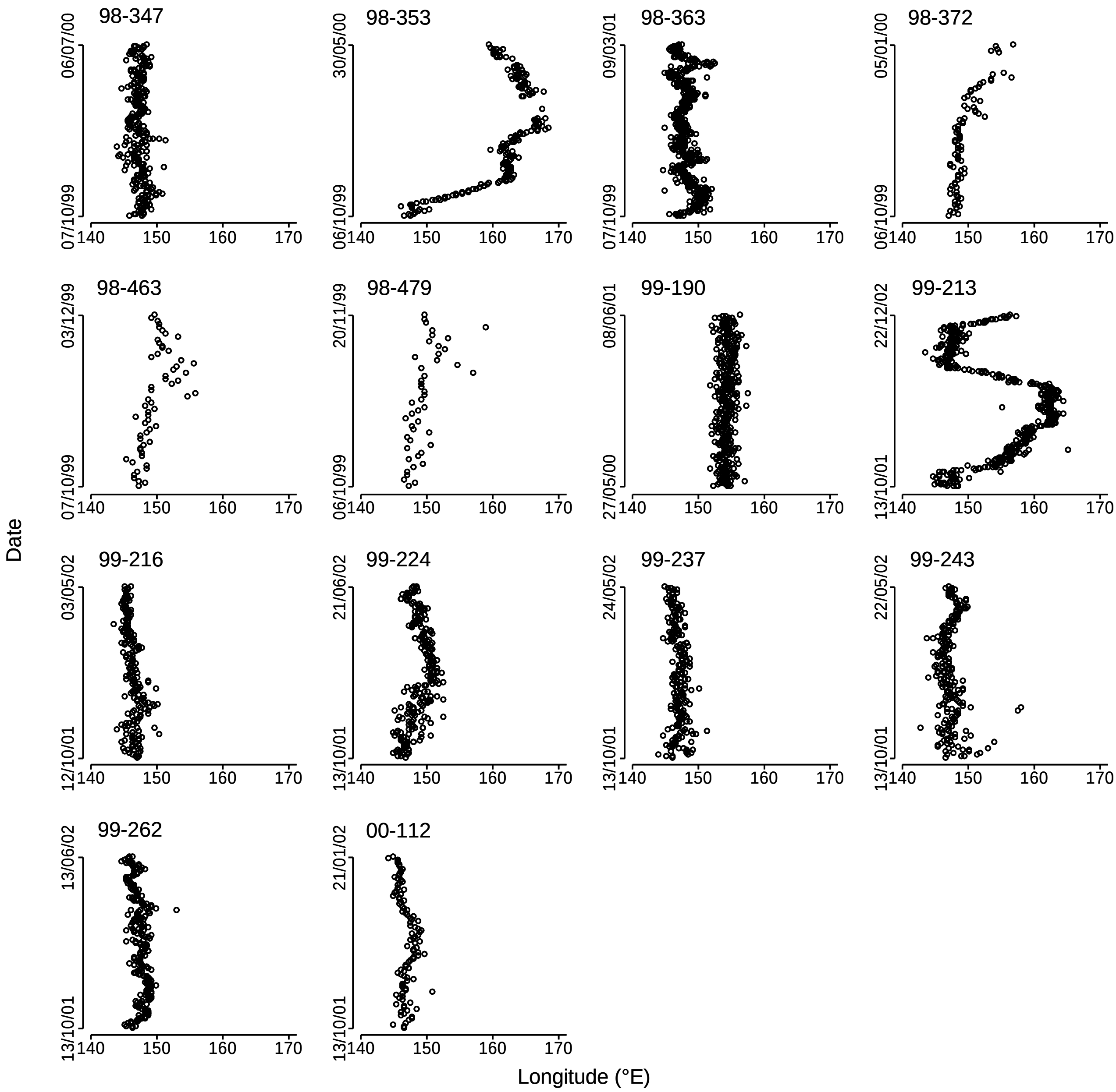

Figure 4. Longitude estimates derived from light-based analysis for all tags deployed in the Coral Sea 1999-2001.

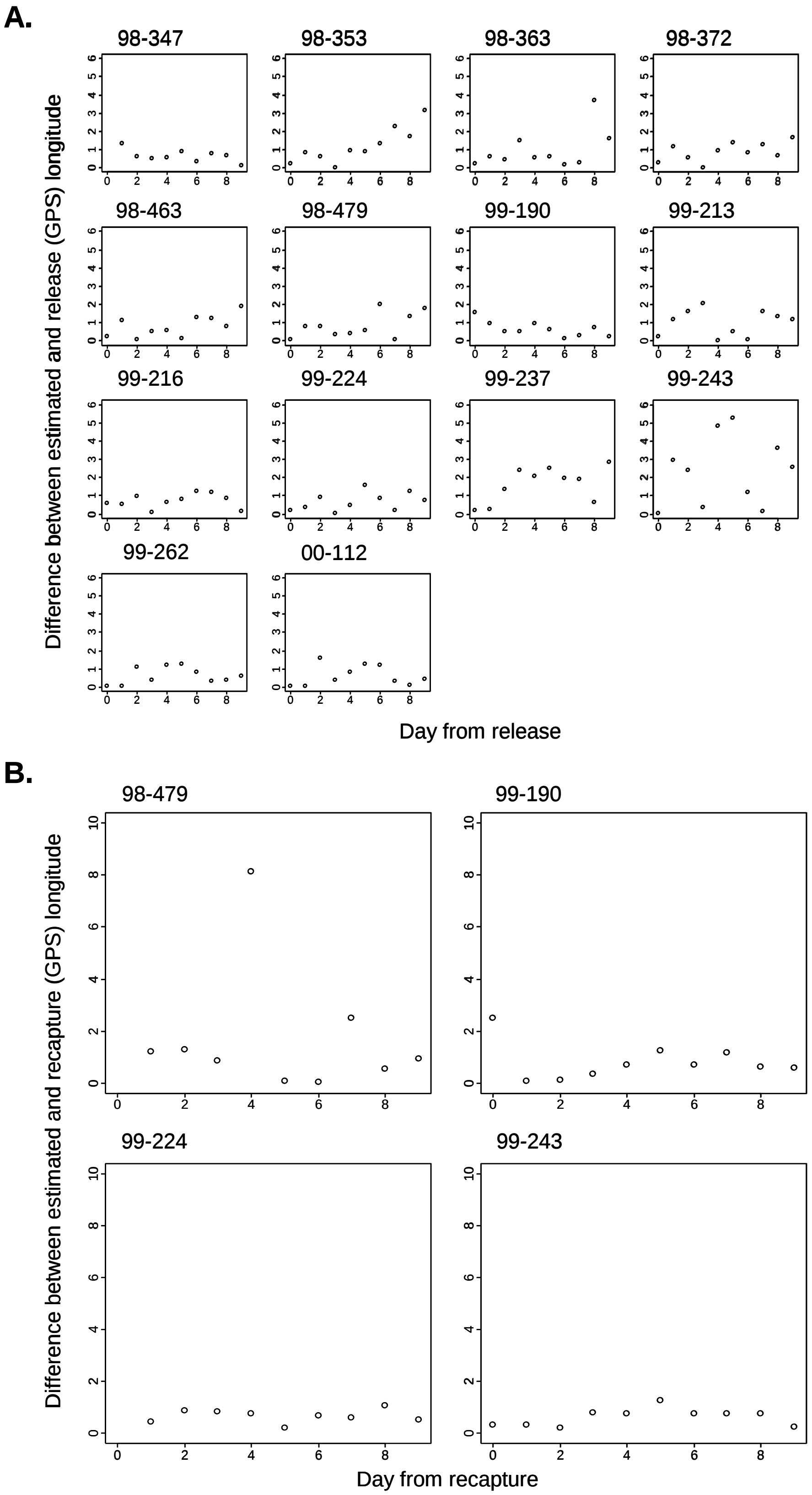

Figure 5. Difference between the (a) release and (b) recapture longitudes (as derived by GPS) and light-based longitude estimates derived from archival tags for the first and last ten days at liberty of archival tags released in the Coral Sea.

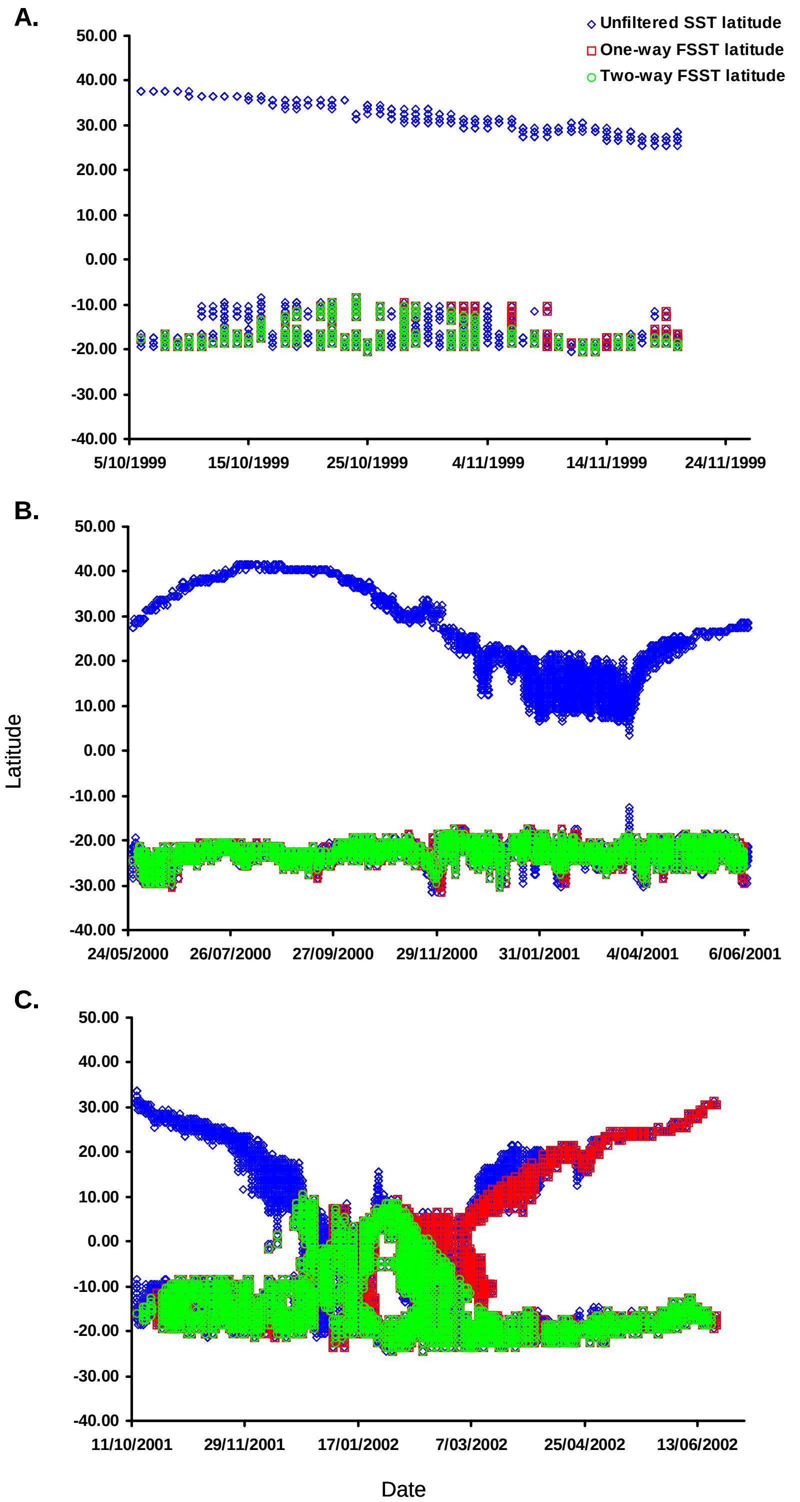

Figure 6. Latitude estimates derived from sea surface temperature (SST) matching without a movement filter, SST matching with a one-way movement filter using the known release position (one-way FSST) and SST matching with a two-way movement filter using both the known release and recapture positions (two-way FSST) for the archival tags (a) 98-479; (b) 99-190 and (c) 99-224.

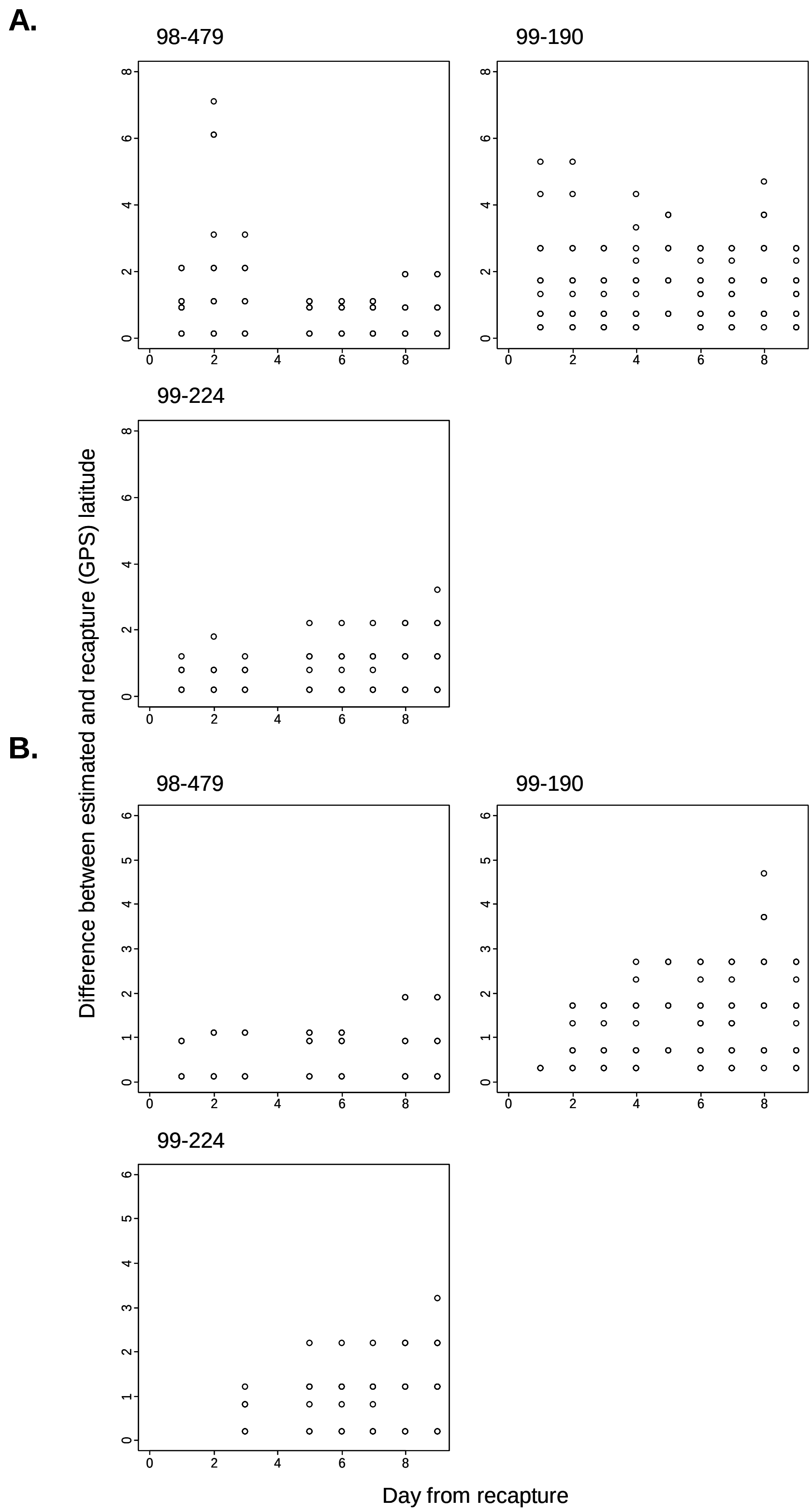

Figure 7. Difference between the recapture latitudes (as derived by GPS) and SST matched latitudes for the last ten days at liberty of archival tags released in the Coral Sea when using a movement filter (a) in only one direction (forwards) and (b) in two directions (forwards and backwards).

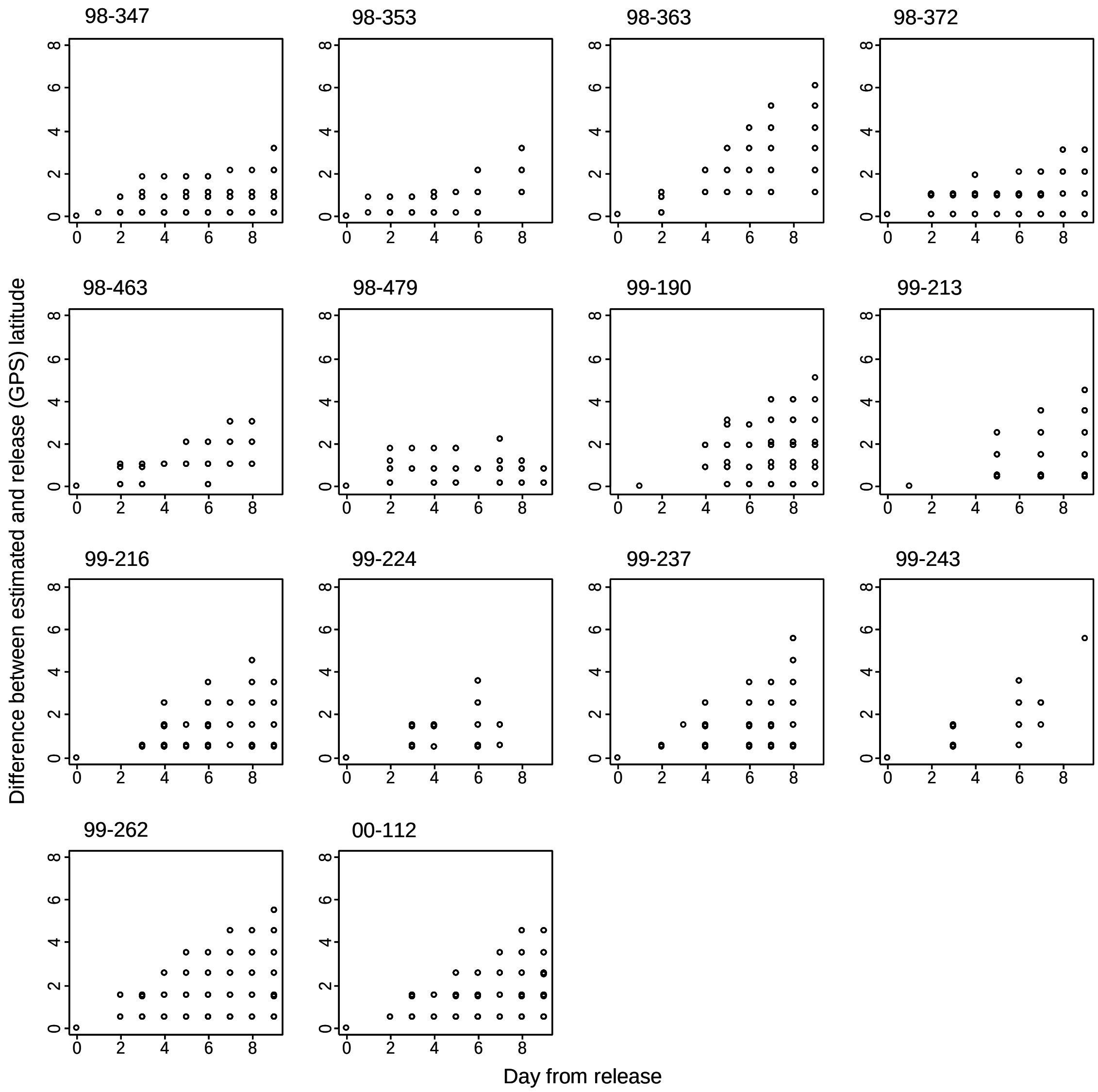

Figure 8. Difference between the release latitude (as derived by GPS) and SST matched latitude estimates for the first ten days at liberty of archival tags released in the Coral Sea.

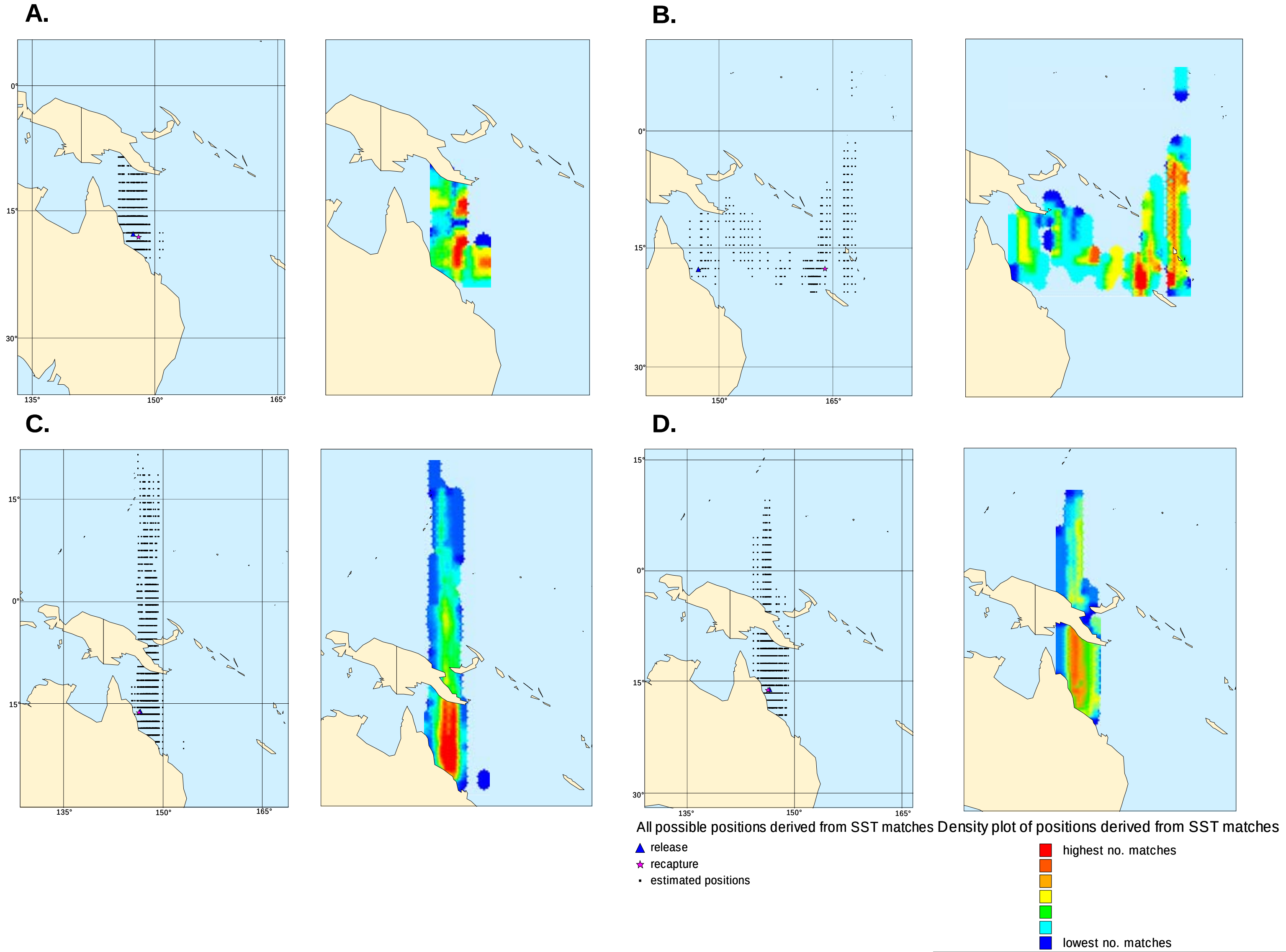

Figure 9. Position estimates and densities of position estimates for (a) 98-347; (b) 98-353; (c) 99-262; (d) 00-112.

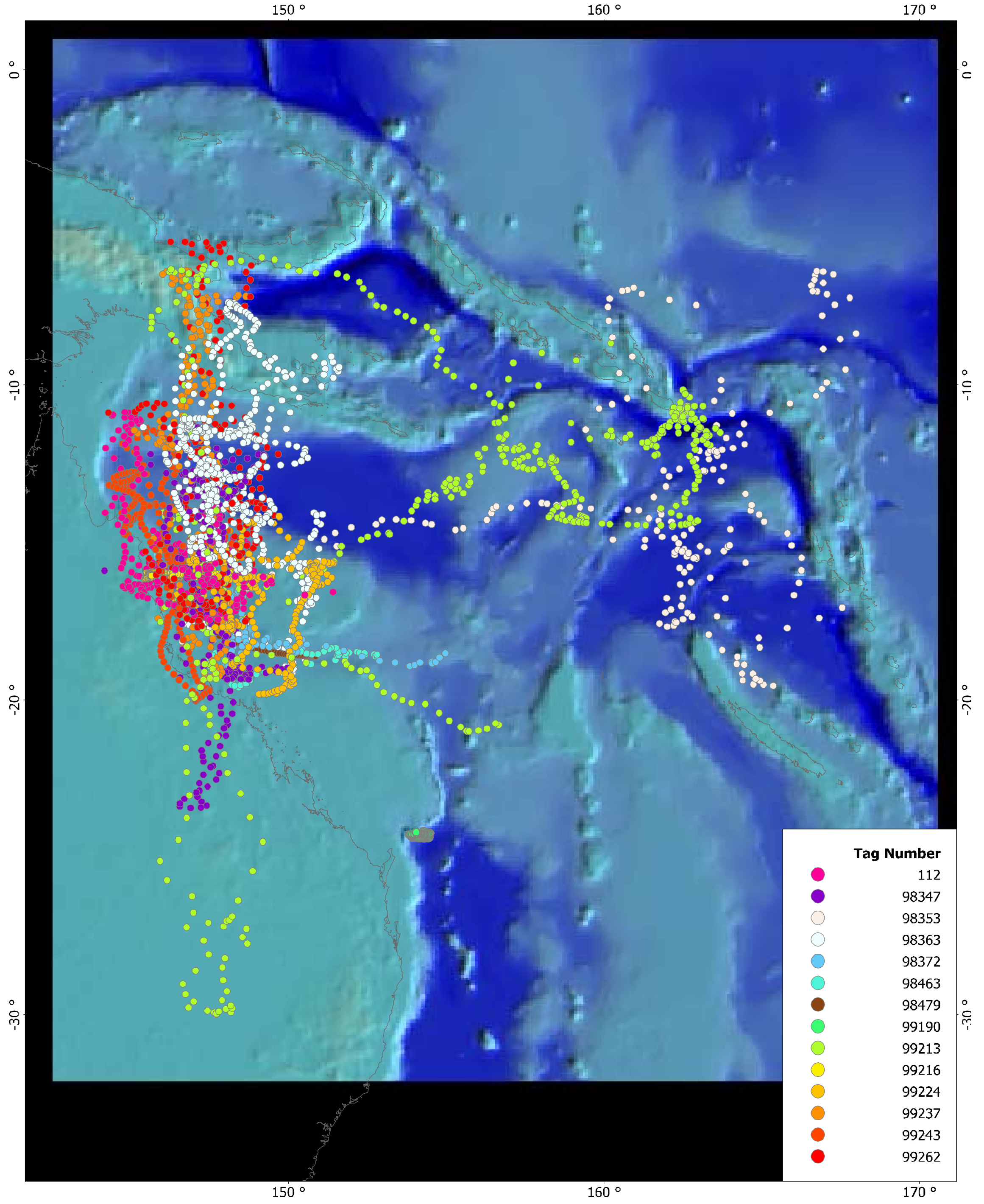

Figure 10. Estimates of position for bigeye tuna in the western Pacific Ocean as determined by analysis of geolocation data from archival tags using a modified state-space Kalman filter model.

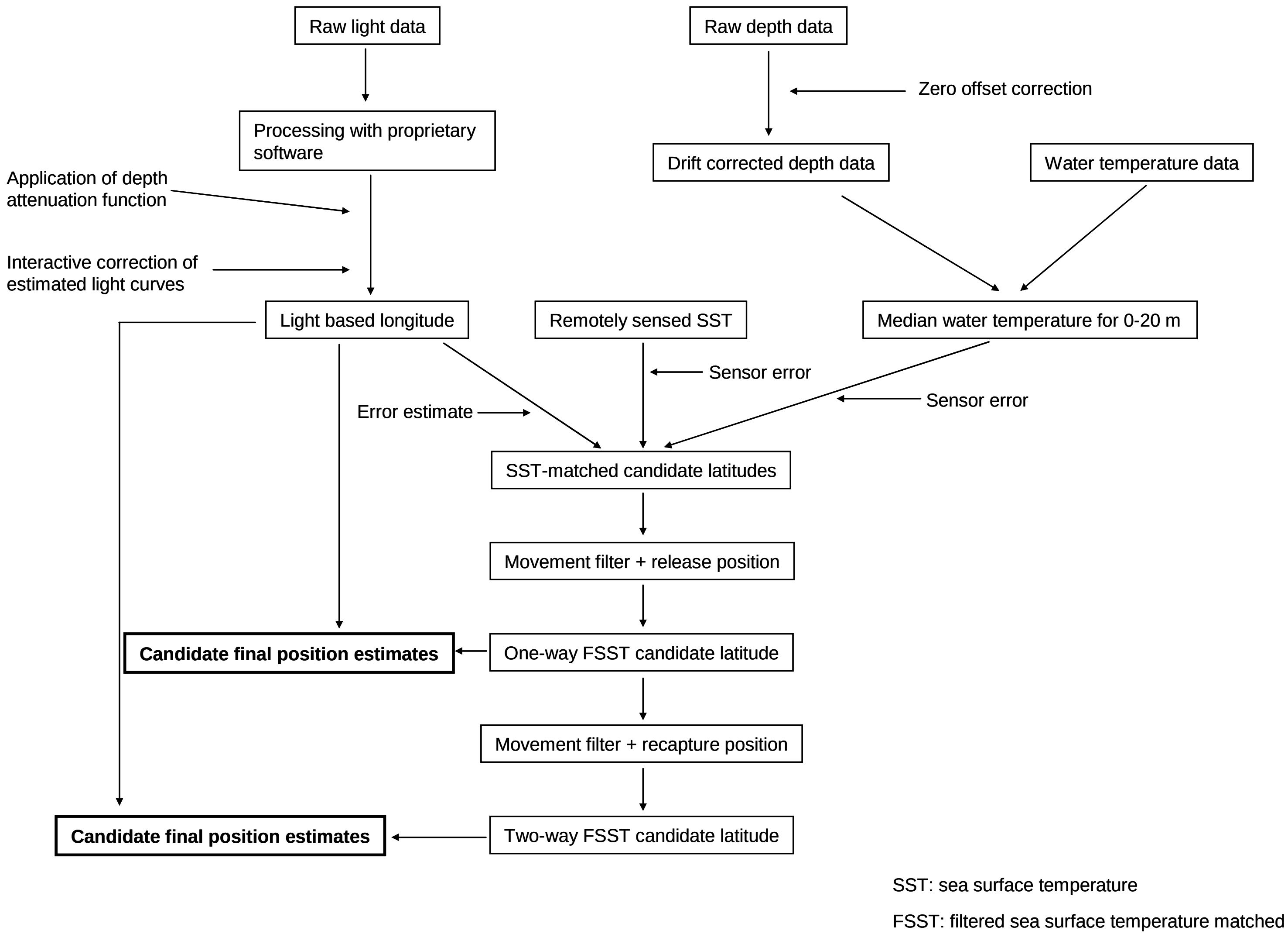

Figure 11. Schematic diagram of methodology used to calculate position estimates.