# Preliminary analysis of satellite transmitter data from tagged blue- and shortfin mako sharks indicates significant connectivity across the ICCAT-IOTC boundary

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**ABSTRACT**

Pelagic sharks, including the blue shark *Prionace glauca* and the shortfin mako *Isurus oxyrinchus,* exhibit extensive spatial distributions that may extend across jurisdictional boundaries of tuna Regional Fisheries Management Organisations (tRFMOs). Such transboundary movements present challenges for data reporting, stock assessment and management. Using satellite telemetry of a small number of individuals tagged off South Africa, this study demonstrates that both species routinely cross the IOTC/ICCAT boundary at 20°E. For blue sharks, although only three individuals' tracks were used, their movements suggest the potential for localised residency in addition to broad-scale dispersal. Furthermore, previous research has provided evidence for parturition habitats within the Benguela–Agulhas transition zone that straddles the boundary. Since this boundary encompasses an area of biological importance that is closely linked to dynamic environmental conditions, the location and extent of parturition habitats are likely to fluctuate over time, further complicating the delineation of management units and the interpretation of fisheries-dependent indices. Shortfin mako sharks displayed consistent site fidelity to the Agulhas Bank shelf edge, with movement patterns strongly associated with the Agulhas Current retroflection and associated mesoscale eddies. These findings align with previous work (e.g. Parker et al. 2017), which highlighted how the application of the IOTC/ICCAT boundary can introduce spurious variability into reported shortfin mako statistics. Collectively, the results indicate that truncating datasets or CPUE indices at this boundary is biologically unjustified and potentially risks introducing bias into assessments of wide-ranging pelagic sharks.

***Keywords***

RFMO boundary, mixed stock, movement, satellite, blue shark, shortfin mako shark

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## INTRODUCTION

South Africa's Exclusive Economic Zone (EEZ) incorporates the jurisdictional boundary between the International Commission for the Conservation of Atlantic Tunas (ICCAT) and the Indian Ocean Tuna Commission (IOTC) at 20°E, off Cape Agulhas. This region, known as the Agulhas Bank, is a highly dynamic and productive marine ecosystem (Hutchings, 1994) where the temperate waters of the Atlantic Ocean converge with the subtropical waters of the Indian Ocean (Lutjeharms 2006) , generating elevated levels of biodiversity (Smale et al. 1994; Griffiths et al. 2010) and supporting substantial aggregations of fish (Götz et al. 2014), including large pelagic species (Smale et al. 1994; Japp et al 1994). The ecological significance of the Agulhas Bank, combined with its accessibility, has resulted in concentrated fishing effort (DFFE, 2025), and a considerable proportion of South Africa's reported large pelagic catches can be traced to this area (DFFE, 2025). However, the coincidence of this fishing ground with an RFMO boundary presents challenges for data accuracy and reporting. Fishing operations that traverse the IOTC / ICCAT must be partitioned at this boundary for all species caught, reflecting the constraints of management jurisdictions rather than the biological realities or natural spatial distribution and boundaries of the fisheries resources themselves.

This jurisdiction boundary of the two tRFMOs (i.e. IOTC/ ICCAT) remains administratively necessary, however, it raises scientific and management challenges for South African researchers. Large pelagic species managed under the competence of any tRFMO exhibit broad migratory ranges that transcend political boundaries, while fishing operations frequently cross these lines. This creates complications for stock assessments, as catch data may not accurately reflect biological stock structures or spatial distributions. Key considerations include the extent of mixing between stocks, whether intermixed populations are reproductively isolated, and how catches should be allocated across neighbouring stock assessments (Parker et al. 2017).

The complexities associated with data reporting at the IOTC/ ICCAT boundary have been previously demonstrated for shortfin mako *Isurus oxyrinchus* (Parker et al. 2017). An analysis of South African Longline catches revealed that reporting catches according to the 20°E boundary could generate artificial fluctuations in annual catch rates. These fluctuations highlight the potential for RFMO boundaries to artificially inflate interannual variability, particularly in hotspot areas located near this boundary, and generate inconsistent indices that may bias stock assessments.

Similar issues have been observed in studies on the population structure of swordfish *Xiphias gladius*. Microsatellite analysis identified an admixture zone between 14°E and 27°E, with evidence of bidirectional gene flow (West, 2016; West et al. 2023). Although weak differentiation suggests that the Indian Ocean and Atlantic Ocean support largely separate, philopatric stocks, both passive larval drift and active dispersal of adult dispersal contribute to admixture and genetic homogenisation. Consequently, small shifts in distribution across the IOTC/ICCAT boundary may result in marked annual variability in catch data. Reflecting this, South African swordfish datasets are routinely subset at 29 ° E for use in stock assessments.

Biologically meaningful stock delineation is important beyond the reporting of catch data and extends to biological data and estimates such as size structure, ageing, reproductive maturity, recruitment estimates, mortality rates etc., datasets integral to stock assessments. For example, nursery areas situated on or near the IOTC/ICCAT boundary, such as the one identified for blue sharks *Prionace glauca* are likely to contribute substantial interannual variability in reported data (da Silva et al. 2010). In recognition of these complexities, South Africa provided CPUE indices covering the full extent of its EEZ for the 2025 IOTC blue shark and ICCAT shortfin mako assessments.

The extent to which stock dynamics fail to conform to the IOTC/ICCAT boundary, and by extension the impact on how South Africa reports catch statistics and biological data to the respective tRFMOs, has not been comprehensively examined for other large pelagic species. Previous studies have touched on mixing or potential mixing across the IOTC/ICCAT boundary, using some of the multifaceted approaches to discern boundaries between stocks; such as, genetic evidence in albacore of dispersal of early life history stages across the Agulhas region (Nikolic *et al.*, 2020) which was supported by otolith microchemistry (Labonne *et al.*, 2024), genetic evidence in yellowfin tuna of a mismatch between biological units and this boundary (Mullins *et al.*, 2018), satellite tagging of swordfish that documents extensive movements, consistent with cross-region mobility of swordfish (West *et al.*, 2012), genetics study on swordfish that highlights the IOTC/ICCAT boundary region as a key interface where management splits may not fully align with biology (Muths *et al.*, 2013), and multiple genetic studies on blue shark indicating broad connectivity and potential mixing across the boundary (Bailleul *et al.*, 2018).

This paper seeks to justify the provision of CPUE indices covering the full extent of its EEZ, using satellite tag positional data from blue and shortfin mako sharks to investigate movement and connectivity between the IOTC and ICCAT, and to encourage constructive dialogue among CPCs and the IOTC Secretariat.

## METHODS

### Shark Capture and Tagging

Pelagic sharks were captured off South Africa during national pelagic longline surveys conducted between 2010 and 2016 aboard the *R/V Ellen Khuzwayo* as part of a long-term tagging programme conducted by the Department of Forestry, Fisheries and the Environment (DFFE) in collaboration with Oceans and Coasts and the Southwest Indian Ocean Fisheries Project (SWIOFP) off South Africa. Fishing gear consisted of drifting pelagic longlines, rigged in a manner consistent with American commercial longline operations, using a monofilament mainline deployed from a Lindgren-Pitman spool off the stern. Live sharks were brought alongside the vessel and carefully lifted into a specially designed cradle. Once secured, individuals were restrained, their gills irrigated continuously with seawater, and their eyes covered to minimize stress. All handling and tagging procedures followed best-practice protocols developed by the DFFE in collaboration with researchers tagging sharks in South Africa.

During tagging, sharks were sexed and measured. To secure the tag, four small holes were drilled into the distal portion of the leading edge of the dorsal fin. Tags were attached using two PVC plates with a thin layer of neoprene between the plate and the fin. Stainless-steel trace was looped at the end and fitted over a plastic bolt though the plate and secured with a partially cut Nyloc nut to ensure eventual shedding of the tags. Individuals in good condition were fitted with SPOT, MiniPAT, or PAT tags, depending on tag availability, with size constraints on early PAT tags (Table 1). Handling times from capture to release ranged from 4 to 13 minutes (mean = 8 minutes). PAT tags were programmed to either 90 or 180 days (Table 1).

### Data Collection and Preparation

Tracking data was obtained via the ARGOS satellite system. Raw data underwent rigorous quality control procedures, including the removal of duplicate records, temporal duplicates within individuals, and entries with missing or invalid coordinates. To reduce potential bias associated with post-release recovery behaviour, the first week of data for each individual was excluded from analyses.

### State-Space Modelling

All pelagic shark movement data were analysed using correlated random walk state-space models (CRW-SSM) implemented in the *aniMotum* R package. Although SPOT tags provide more accurate positions than light-based geolocation PAT tags, state-space models (SSMs) or correlated random walk (CRW) approaches, such as those implemented in the *aniMotum* R package, are used for several reasons. First, SPOT transmissions are irregular in time, so SSMs interpolate tracks to regular intervals, making them directly comparable across individuals. Second, even ARGOS and GPS positions carry error, especially lower ARGOS classes, and SSMs incorporate this uncertainty explicitly rather than relying only on filtering. Third, CRW models impose biologically realistic movement patterns, avoiding unrealistic straight-line connections between sparse points. Fourth, SSMs provide confidence intervals around predicted positions, which is essential for downstream analyses such as habitat use, home range, or speed estimation. Finally, using a common modelling framework allows consistency when combining SPOT data with less accurate sources like SAT tracks. In short, SSMs add rigor, realism, and uncertainty quantification to SPOT-based tracking, making them highly valuable despite the relatively high accuracy of the raw positions.

. The SSM approach accounts for observation error inherent in ARGOS location data and estimates the most probable movement path by fitting a continuous-time movement process to irregular satellite observations. Model parameters included a maximum swimming speed constraint of 3.0 m/s for blue sharks and 4.47 m/s for shortfin mako sharks (Vaudo et al., 2017), minimum time interval of 1 hour between observations, and regularized predicted locations at 24 -hour intervals.

The CRW-SSM assumes movement follows a correlated random walk with temporally autocorrelated velocity components. These thresholds represent biologically plausible maximum speeds for the species and serve to remove extreme outlier locations (Saraiva et al., 2023; Gibson Banks et al., 2025). This produced one modelled position per day for each shark.

Data transmission patterns were characterized by calculating temporal gaps between consecutive ARGOS transmissions for each individual. The proportion of gaps <24 hours was computed as an indicator of data continuity and tracking quality. This metric provides insight into the temporal resolution of movement data and potential biases in behavioural interpretation and justifies predicting locations at 24-hour intervals.

Confidence regions representing positional uncertainty or directional displacement were derived from state-space model standard errors. Elliptical confidence polygons were constructed using x (longitude)- and y (latitude)-axis standard errors from the SSM fitted locations, with a subset of locations visualized to avoid plot overcrowding. Where ellipse construction failed due to computational constraints, circular confidence regions were generated as an alternative uncertainty representation.

## RESULTS AND DISCUSSION

This study reports on 14 pelagic sharks fitted with satellite transmitters (SPOT, MiniPAT, and PAT) between 2010 and 2016 (Table 1) to illustrate movements across the IOTC/ICCAT boundary.

The size range of tagged blue sharks was 2110–2445 mm TL, while shortfin mako sharks ranged from 1560–2150 mm TL. Male maturity was assessed through clasper calcification and articulation: the singular male blue shark was mature, while only one of the four male shortfin mako sharks was mature. Based on published estimates of length at maturity, none of the female shortfin makos approached maturity ($L_{50}$ = 2650–2800 mm TL; Jordaan and Parker, 2022). By contrast, the female blue sharks were mature or nearing maturity, as the estimated $L_{50}$ for the species is 1940 mm TL (Jolly et al., 2013).

Among the three tag types deployed, SPOT tags exhibited the greatest retention times, with several units remaining attached for multiple months. In contrast, PAT and MiniPAT tags tended to detach earlier, due to factors such as tag failure, premature shedding or mortality. Blue sharks transmitted for 34–120 days (median = 78 days), yielding a total of 676 positions. Of the raw Argos locations, 82% of temporal gaps were <24 hours. Shortfin makos transmitted for 15–133 days (median = 110 days), yielding 4,611 locations, with 95% of temporal gaps <24 hours. These thresholds represent biologically plausible maximum speeds for the species and serve to remove extreme outlier locations (Saraiva et al., 2023; Gibson Banks et al., 2025). This produced one modelled position per day for each shark.

Both species displayed consistent use of the Agulhas Bank, with a high degree of fidelity around the shelf edge. The SSM movement tracks of the three blue sharks are shown in Figure 1. The tracks highlight individual variability, ranging from wide-ranging offshore movements to localized residency near Madagascar and South Africa, only partially influenced by time at liberty. Despite the limited sample size, the results indicate that blue sharks do cross the ICCAT / IOTC management boundary. The movement tracks of 11 shortfin makos are shown in Figure 2, revealing pronounced inter-individual variability but consistent use of South African waters and adjacent offshore habitats and several examples of transboundary movement.

Of the pelagic shark tracks analysed in this study, 5 of the 14 individuals crossed the IOTC / ICCAT tRFMO boundary at least once during the relatively short monitoring period. Although the sample size for blue sharks is limited, the SSM-derived movements around the Agulhas Bank are consistent with their known distribution in South African fisheries catches. Long-distance movements were also observed: for example, blue shark BSH1 crossed the IOTC / ICCAT boundary toward Madagascar, a result consistent with the well-documented wide-ranging behaviour of the species (Nakano and Stevens 2008; Vandeperre et al. 2014; Campana et al. 2011). Such long-distance movements have been previously recorded from South Africa, including the trans-Atlantic recapture of a juvenile blue shark (923 mm FL) originally tagged locally and later recovered in Uruguay (da Silva et al. 2010). In addition to long-distance movement, the da Silva et al (2010) study highlighted the presence of a parturition area for blue sharks associated with the Benguela Agulhas Current transition filaments/ subtropical convergence. These dynamic features fluctuate seasonally and interannually across the edge of the Agulhas Bank and thus straddle the IOTC / ICCAT boundary. As blue sharks frequently cross this boundary and critical habitats such as parturition grounds shift with environmental conditions, truncating data at 20°E for stock assessment purposes is biologically unjustifiable.

For shortfin mako sharks, a potential nursery area has been suggested along the Agulhas Bank shelf edge, although this remains unconfirmed.  The present study nonetheless demonstrates strong site fidelity to this region, with distribution patterns reflecting either residency on the highly productive Agulhas Bank fishing grounds, transient use of the Agulhas current retroflection to move offshore, or northwest dispersal via Agulhas Current mesoscale eddies and Benguela current along the west coast of South Africa. Site fidelity is further highlighted by recaptures, one shortfin mako shark was recaptured near its release site 169 days post-tagging. Two additional shortfin mako sharks, not included in this study, were also recaptured within 90 days, notably by the same vessel that had assisted with tagging deployments.

Comparable complex movement strategies have been documented elsewhere, ranging from localized fidelity to shelf and slope habitats to extensive transoceanic migrations (Rogers et al., 2015). For example, a long-distance migration of 25,550 km was recorded across the Indian Ocean, from the Great Australian Bight to southeast of Madagascar, interspersed with short periods of fidelity to several oceanic areas *en route*. Juvenile shortfin makos typically exhibited site fidelity within mid-outer shelf, shelf edge, and slope habitats characterized by pronounced bathymetric relief and oceanographic frontal gradients. Building on these earlier observations, the present study strengthens the hypothesis that the Agulhas Bank shelf edge constitutes an ecologically important habitat for juvenile shortfin makos. As with blue sharks, these patterns indicate that movements are not constrained by the tRFMO boundary but instead shaped by dynamic oceanographic processes and prey availability.

In summary, both species display wide-ranging movements that routinely extend across the IOTC / ICCAT boundary, with ecologically important habitats, including parturition and potential nursery grounds, straddling this artificial management line. Given the high probability of boundary crossings and the biological irrelevance of 20°E as a dividing line, truncating data for stock assessment at this longitude introduces serious biases and misrepresents the true population dynamics of these highly migratory sharks. A holistic approach that integrates data across the entire South African EEZ, rather than an arbitrary boundary, is therefore essential for robust and ecologically meaningful stock assessments.

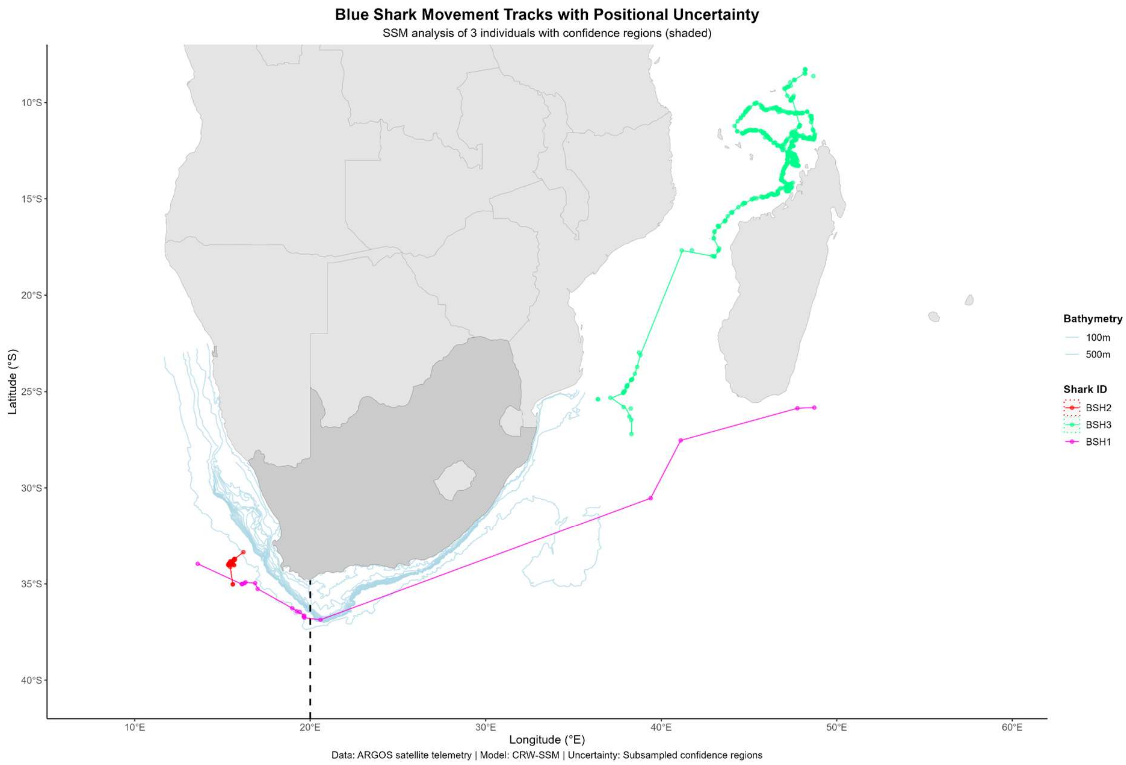


**Figure 1.** State-space modelled movement tracks of 3 satellite-tagged blue sharks *(Prionace glauca*) in South African waters. Coloured lines represent individual tracks derived from ARGOS telemetry data, with corresponding shark IDs indicated in the legend. Bathymetric contours (100 m, 500 m, and 1000 m) are shown to illustrate the relationship between shark movements and continental shelf features.

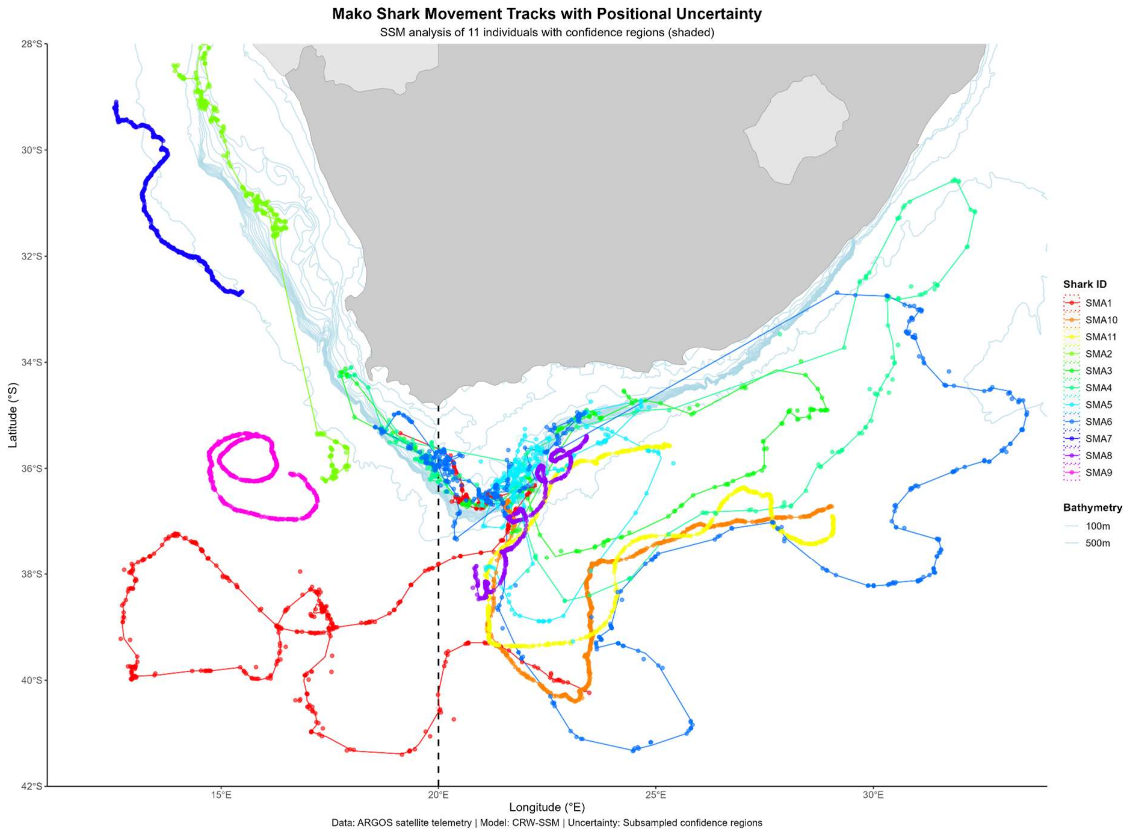


**Figure 2.** State-space modelled movement tracks areas of 11 satellite-tagged shortfin mako sharks *(Isurus oxyrinchus*) in South African waters. Coloured lines represent individual tracks derived from ARGOS telemetry data, with corresponding shark IDs indicated in the legend. Bathymetric contours (100 m, 500 m, and 1000 m) are shown to illustrate the relationship between shark movements and continental shelf features.

**Table 1.** Blue sharks (*Prionace glauca*) and shortfin mako sharks (*Isurus oxyrinchus*) tagged in South Africa. * recaptured within 169 days, ** mature male, ***near mature or mature female

| ID | First Detection Date | Last Detection Date | DAL | Species | Release position | TL mm | Sex | Tag |
|---|---|---|---|---|---|---|---|---|
| BSH1 | 2010/11/17 | 2011/02/04 | 79 | BSH | -35 03.931 S 018 15.170 E | 2110 | F | SPOT |
| BSH2 | 2011/01/29 | 2011/03/05 | 35 | BSH | -36 45.556 S 021 19.666 E | 2446 | M** | PAT (90 days) |
| BSH3 | 2011/10/27 | 2012/02/24 | 121 | BSH | -38 03.228 S, 27 51.200E | 2200 | F | SPOT |
| SMA1 | 2015/12/01 | 2016/04/08 | 129 | SMA | -35 27.00 S, 18 37.40 E | 2150 | M | SPOT |
| SMA2 | 2015/12/01 | 2016/04/08 | 129 | SMA | -35 27.00 S, 18 37.40 E | 1600 | M | SPOT |
| SMA3 | 2016/06/10 | 2016/09/29 | 111 | SMA | -36.34.10 S, 021 34.00 E | 2020 | F | SPOT |
| SMA4 | 2016/06/10 | 2016/10/17 | 129 | SMA | -36.34.40 S,021 35.4E | 1890 | F | SPOT |
| SMA5* | 2016/06/10 | 2016/10/22 | 133 | SMA | -36 33.40 S,021 32.9E | 1880 | F | SPOT |
| SMA6 | 2016/06/10 | 2016/10/19 | 131 | SMA | -36.33.80 S, 021 33.5E | 1590 | M | SPOT |
| SMA7 | 2016/02/27 | 2016/03/16 | 18 | SMA | -35 27.00 S, 18 37.40 E | 1600 | U | PAT (90 days) |
| SMA8 | 2016/06/01 | 2016/06/16 | 16 | SMA | -35 27.00 S, 18 37.40 E | 1860 | F | PAT (180 days) |
| SMA9 | 2016/02/26 | 2016/03/17 | 19 | SMA | -35 27.00 S, 18 37.40 E | 1810 | F | PAT(190 days) |
| SMA10 | 2016/06/12 | 2016/07/02 | 21 | SMA | -36.34.50 S, 021 37.60 E | 1760 | M** | miniPAT (90 days) |
| SMA11 | 2016/09/09 | 2016/09/30 | 22 | SMA | -36.34.50 S, 021 37.70 E | 1560 | F | miniPAt (90 days) |

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