# **Title:** The importance of seasonal sea-surface height anomalies for foraging juvenile southern elephant seals

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## Abstract

A novel classification system was applied to the sea-level anomaly environment around Marion Island. We classified the sea-level anomaly (SLA) seascape into habitat types and calculated percentage of habitat use of ten juvenile southern elephant seals (SES) from Marion Island. Movements were compared to SLA and SLA slope values indicative of ocean eddy features. This classification provides a measure of habitat change due to seasonal fluctuations in SLA. Some of the seals made two migrations in different seasons, each of similar duration and proportion of potential foraging behaviour. The seals in this study did not use any intense eddy features but their behaviours varied with SLA class. Potential foraging behaviour was positively influenced by negative SLA values (i.e., areas of below average sea-surface height). Searching behaviour during the winter was more likely at eddy edges where high SLA slope values correlated with low SLA values. Though the seals did not forage within newly spawned eddies they did forage near the Sub-Antarctic Front (SAF). Plankton and other biological resources transported by eddies formed at the subtropical convergence zone (SCZ) are evidently concentrated in this region and enhance the food chain there, forming a foraging ground for juvenile southern elephant seals from Marion Island.

## Keywords

Ocean habitat classification, Marion Island, sea level anomalies, southern elephant seal

## Introduction

The ‘ocean landscape’ (Steele 1989) varies in three dimensions both spatially and temporally, complicating the characterization of oceanic habitats at small and intermediate scales (Gregr and Bodtker 2007). Whilst being important for the management of conservation areas and resources (Costello 2009, Ward et al. 1999), landscape classification is also useful for understanding species’ responses to their environment (e.g. Townsend and Hildrew 1994). The knowledge of how species utilize their habitats, in turn feeds into conservation management decisions. Satellite telemetry data can be used to inform scientists how animals use their environments and associated environmental data can be used to assess conditions within those habitats.

Southern elephant seals (SES), *Mirounga leonina*, from Marion Island forage mostly in pelagic waters west of the Prince Edward Islands (Jonker and Bester 1998, McIntyre et al. 2011, Tosh et al. 2012, Massie et al. 2015). This area is characterised by above average kinetic energy created by ocean eddies formed from interactions between the west flowing Antarctic Circumpolar Current (ACC) and the South West Indian Ridge (SWIR) at the Andrew Bain Fracture Zone (ABFZ) (Ansorge et al. 1999, Ansorge and Lutjeharms 2005). Eddies are also spawned north of Marion Island, where the Agulhas Return Current (ARC) interacts with the Sub-Antarctic (SAF) and Subtropical (STF) fronts that form the Subtropical Convergence Zone (SCZ; Lutjeharms and Valentine 1988). We documented the movements of juvenile SES relative to those eddies and fronts near the SCZ in 2004.

Eddies spawned at some major frontal structures are known to be rich in zooplankton that form the basis of complex food chains (e.g., Pakhomov et al. 1994, Pakhomov and Perissonotto 1997, Nel et al. 2001). Warm core eddies generated at the SCZ transport subtropical zooplankton communities to sub-Antarctic waters (Pakhomov and Perissonotto 1997) increasing the biomass of micro-nekton and zooplankton species (Pakhomov and Froneman 2000). Cold core eddies originating at the intersection of the ABFZ and the SWIR have euphausiid communities comparable in biomass to the most productive regions of the Southern Ocean in summer (cf. Bernard et al. 2007). Those eddies concentrate the zooplankton prey of epipelagic fish and cephalopods which are the common prey of seabirds (Nel et al. 2001, Cotté et al. 2007), fur seals (Klages and Bester 1998, de Bruyn et al. 2009a) and southern elephant seals (Bailleul et al. 2010, Dragon et al. 2010, Massie et al. 2015).

The correlations between cyclonic (cold-core) eddies and negative sea-surface height anomalies and between anti-cyclonic (warm-core) eddies and positive sea-level anomalies (SLA) allows eddies to be identified from sea surface height measurements using earth-orbiting satellites (Ansorge and Lutjeharms 2003, Durgadoo et al. 2010). SES from Kerguelen Island showed enhanced foraging behaviour within cold-core eddies (Bailleul et al. 2010, Dragon et al. 2010) and at the edges of warm-core eddies near an interfrontal zone (Dragon et al. 2010). Some juvenile SES from Peninsula Valdés, Patagonia foraged more deliberately in association with eddies generated at the Brazil-Malvina confluence (Campagna et al. 2006). Ocean surface eddies around Marion Island are intense, productive features (Pakhomov and Perissonotto 1997, Bernard et al. 2007) that might be important foraging areas for predators that breed at Marion Island, including SES. We build on the regional findings of Tosh et al. (2012)

by exploring the use of eddies and associated sea surface features as important foraging areas for juvenile SES from Marion Island. We also propose a classification model of the eddy habitats near Marion Island to allow them to be evaluated relative to the dispersion and activity of juvenile SES. We compared the movements of juvenile SES from Marion Island and sea surface height, measured by earth-orbiting satellites to suggest whether seals were foraging versus transiting relative to ocean eddy systems. We identified differences in SLA's and SLA slopes relative to the seals' movements using a mixed model approach. Where SLA or SLA slope significantly influenced seal behaviour, we used generalised linear mixed models to test for differences in SLA and SLA slope values between searching behaviour occurring over two seasonally distinct migrations.

## Methods

We documented the movements of ten juvenile (< two years old) SES in 2004 (Table 1) using satellite relay data loggers (SRDLs), using the Argos Data Collection and Location Service (ADCLS). Age and sex were known for nine seals from uniquely numbered flipper tags that were attached soon after birth (de Bruyn et al. 2008). We chemically immobilised seals with intramuscular injections of ketamine hydrochloride (Bester 1988, Erickson and Bester 1993) and then glued the SRDLs to the dorsal cranial pelage of each seal with quick setting epoxy resin (Araldite ®, Ciba Geigy), a method shown not to be detrimental to the seals foraging behaviour or survival (Field et al. 2012). SRDLs were recovered from seals that were immobilized when they returned to shore or after they were shed with moulted skin. Tracking data are stored in the Publishing Network for Geoscientific and Environmental Data (PANGAEA;

www.pangaea.de). The list of relevant DOIs is available from the corresponding author.

We used location data to document movements of seals using a state-space approach (c.f., Breed et al. 2009). The model accounts for errors in Argos DCLS locations and also binary codes locations as searching mode (1) or transit mode (0) (Jonsen et al. 2005). The behaviour of moving seals was incorporated into the movement models based on assumptions that seals swim more slowly and deviate more in consecutive turning angles when searching (i.e., actively foraging) relative to when they are travelling. The correlated random walk model was fit to individual tracks (c.f., Breed et al. 2009) by running two Markov chain Monte Carlo (MCMC) chains for 10 000 iterations, with a burn-in of 7000, sampling all model parameters and each location estimate. Every fifth point of 3000 remaining samples was retained, resulting in 600 MCMC samples in each chain. A mean and variance value was calculated for each location estimate and model parameter from the 600 MCMC samples. Searching bouts were identified where five consecutive locations were modelled as searching locations and were separated by five consecutive transit locations. We counted the number of searching bouts and compared behaviour in each migration.

Modelled searching locations were plotted on sea-level anomaly (SLA) maps (Pascual et al. 2006) for the relevant time periods to identify their associations with SLAs. Intense eddy features were characterised by SLA values above or below 30cm average (Durgadoo et al. 2010). SLA values are useful indicators of ocean eddy features (Pakhomov et al. 2003, Durgadoo et al. 2010) but the ± 30cm cut off point describes less than 2% of SLA landscape values in the study area.

To describe which SLA habitats were used by seals, we reclassified SLA maps using a dynamic approach based on mean SLA values accounting for variation in different periods. Daily SLA data from AVISO (http://www.aviso.oceanobs.com/) coinciding with SES tracks were imported into ArcMap (ESRI 2011) as raster files, using Marine Geospatial Ecology Tools (Roberts et al. 2010). Raster files were then reclassified using the Reclass tool in Spatial Analyst (ESRI 2011). Reclassification using the standard deviation method with 7 intervals was specified. Low and high core habitats were specified as being -30cm or +30cm in ArcMap (ESRI 2011). We identified the following categories:

- low core (-30cm or -3 standard deviations from the mean)
- low edge ( -2 standard deviations from the mean)
- low background edge (-1 standard deviation from the mean)
- background (mean)
- high background edge (+1 standard deviation from the mean)
- high edge (+2 standard deviations from the mean)
- high core (+30cm or +3 standard deviations from the mean)

Each location estimate was assigned an SLA (aviso.oceanobs.com) and SLA slope value. SLA slope datasets were generated from SLA datasets using *DEM Surface Tools* (Jeness 2012) in ArcMap 10 (www.esri.com, 2010). A new raster dataset based on value differences between grid cells was generated using the 4-cell method (Zevenbergen and Thorne 1987). A slope value is given to a grid cell based on the following equation (Jeness 2012):

$$Degrees\_Slope = \frac{180\sqrt{\left(G^2 + H^2\right)}}{\pi}$$

where G equals the east-west gradient of three adjacent cells and H equals the north-south gradient of three adjacent cells.

The *DEM Surface Tool* was used to identify gradients in the SLA dataset and to identify edge habitats or transition areas between eddies and the surrounding ocean. The differences between searching and transit behaviour were tested using a mixed effects modelling approach in programming language R (lme4 package in R, Bates 2010; R Development core team 2013). Models were run with a logit link due to the binary nature of the response variable (i.e. behaviour, searching=1 and transit=0). A null model that included only individual seal as a random effect was constructed and all subsequent models were tested against the null model to assess the importance of SLA and SLA slopes for predicting searching behaviour. The effect of environmental variables on behaviour was explored by modelling environmental variables separately and together, as part of the full model. We also used log-likelihood ratio tests to compare models.

Where SLA or SLA slope values had a positive effect on searching behaviour, we assessed the different SLA and SLA slope values for migration stages (winter vs. spring migration). The response variables were recoded to represent binary outcomes and generalised mixed effects models were used to test for effect significance as outlined above.

## Results

*Seal movements*

We tracked 13 seals in 2004 and analysed the data of ten of them that were tracked for more than 40 days (Table 1, Fig. 1), accounting for 3774 state-space modelled location estimates. State-space models detected both transit (mode 0) and searching (mode 1) behaviour in tracks of nine seals. Searching behaviour was not detected for two seals even though they were tracked for 61 days (BB125) and 117 days (BB193). Both of those seals were tracked during the transit stage of their migrations until their transmitters failed. The model performed consistently for all seals with MCMC model runs converging for all individuals. Model outputs are available from the corresponding author.

Each of six seals (YY428, YY191, YY232, YY302, BB277 and TO340) made two migrations, the first after they moulted in April (M1) and the second after they hauled out briefly in winter (July-Sept, M2). Searching behaviour peaked in June and July (50% of search locations) during M1 and in October (50% of search locations) in M2 (Fig. 2). About 43% of searching behaviour occurred during the initial searching bout (F1) of M1 which lasted 32 days, on average (range: 10 – 129 days, n=8). Subsequent search bouts were recorded during M2, with 50% of search locations in the second search bout (F2), which lasted an average of 34 days (range: 12-119 days, n=4).

*Habitat use*

SLA habitat classification: We divided SLA landscapes into seven classes. Most searching locations were situated in the background habitat class for both seasons (Fig. 3). The distribution of SLA and SLA slope values that were used by seals correlated with classified habitat types (Fig. 4a and b). The background habitat class had an average SLA value of -0.46 ± 3.10 cm and the high-core habitat class had an average SLA value of 21.59 ± 6.99 cm. Seals did not appear to forage in low-core habitats (-3 standard deviations from the mean). The highest SLA slope values used by the seals corresponded with the high edge and low edge habitat types (Fig. 4b). The sea-surface temperatures of the different SLA classes were not constant and varied according to the timing of the migrations. Sea-surface temperatures were lowest in the background habitat types during the first migration (M1) (Fig. 4c). They were highest in the low edge and low background edge habitat types during the second migration (M2) (Fig. 4c).

Post-moult migration (M1): Most M1 searching behaviour was in the background SLA class, with equal proportions of it in the high edge and low background edge classes (Fig. 3). The background SLA class was characterised by low sea-surface temperatures, low SLA slope values, and SLA values close to zero. Those locations were all south of the SWIR (Fig. 5a). Searching behaviour was not associated with any intense features (Fig. 5a) though it was influenced by weak, positive and negative anomalies (Fig. 5b).

Post-winter haulout migration (M2): Searching behaviour occurred more in the low background edge and high background edge SLA habitats (Fig. 6a) in the M2 migration (Fig. 3), where SLA slope values were higher than they were during M1 (Fig. 4b). Two seals (BB277: 7 days and YY191: 3 days) had brief searching bouts in the high SLA habitat (Fig. 6a and b).

*Mixed effects models*

Searching behaviour was more likely than transit at locations with lower SLA values but with higher SLA slope values (Table 2). There was no significant difference in SLA between searching locations recorded in M1 and M2 but SLA slope values were higher during the M1 migration (Fixed effects estimate = 138.89 ± 19.69, Z =7.052, p=0.0001). Searching was significantly influenced by an interaction between SLA slope values and absolute SLA values during the M2 migration (Fixed effects estimate = 8.61±2.06, Z=4.178, p=0.0001). The probability of searching was greatest where SLA slope values were high and SLA values were low, indicating increased searching at eddy edges.

## Discussion

The habitat classification scheme using SLA values facilitated assessment of seal behaviour among seasons and comparison of habitat types according to slope values and sea-surface temperatures. Marine habitats have been classified according to substrate characteristics (sediments (Connor et al. 2003)), remotely sensed data (chlorophyll-a concentration (Hardman-Mountford et al. 2008)) or features that dominate oceanography (major ocean currents (Gregr et al. 2012)). Marine habitats are predominantly classified for the identification of important pelagic conservation areas (Campagna et al. 2007, Gregr et al. 2012). We propose that marine classifications associated with specific features such as eddies and sea-level anomalies (this study) can also aid in understanding the habitat use of seabird and seal predators. The use of eddies as important foraging areas is significant in areas where these features are common (Nel et al. 2001, Polovina et al. 2006) and understanding seasonal changes related to sea level anomaly usage by top predators will provide clues about seasonal productivity changes and long term dynamics of these features.

Eight to 12 anti-cyclonic eddies are usually generated at the Sub-tropical convergence (STC) each year (Pakhomov and Perissinotto 1997), which then move south and transport pelagic plankton communities into sub-Antarctic waters (Froneman and Perissinotto 1996). Eddies may last from four to six months and move as far south as 45° (Lutjeharms and Gordon 1987). As they drift into sub-Antarctic waters they generally cool and re-join the SAF mainstream or are reinforced by boundary currents (Pakhomov and Perissinotto 1997). The tendency of juvenile SES from Marion Island to forage in the SAF during 2004 (Tosh et al. 2012), could be an artefact of the interaction between those dissipating eddies and the possible retention of prey within the frontal zone. Dissipating anti-cyclonic eddies, which typically correlate with lower SLA values relative to surrounding water and with upwelling at the eddy edges (Bakun 1996), are also generally associated with divergence of plankton and nutrients at the edges. The physical processes and forces that cause the retention of eddies (Bakun 1996) might also result in the concentration of prey species at these interfaces and keep them from dissipating for at least short periods.

Juvenile southern elephant seals undertake two different migrations. The first migration (M1) occurred just after seals moulted in summer and most foraging behaviour then was during a primary foraging bout (F1) in June before they returned to land. The second migration (M2) was after the mid-winter haulout when most seals foraged during several bouts in October. It is not clear why some juvenile or under-yearling SES haul-out in mid-winter (Kirkman et al. 2001, Hofmeyr et al. 2012), other than perhaps simply to rest. As they reach reproductive age (~ 3 to 4 yrs old), female SES stop hauling out in winter though males, who mature later, continue to haulout in winter well into their sixth year (Kirkman et al. 2001). Survival seems unaffected by these differences (Pistorius et al. 2002), suggesting mechanisms not related to energy acquisition or growth (cf. Reisinger et al. 2011, Hofmeyr et al. 2012).

Even though the seals apparently used the same areas during the M1 and M2 migrations in 2004 (Fig. 1) the environmental conditions associated with searching differed between them (Fig. 4). Most searching in 2004 was within 1° latitude of the SAF (Tosh et al. 2012). Although those locations were within the frontal zone, most of them were in areas of mean SLA values, or the background habitat class (this study). Intense eddies (30cm above or below the mean) had little influence on searching behaviour of juvenile SES (Fig. 5a and 6a). The intense positive features created by the STC were far beyond the northern limit of SES movements in 2004 and the one intense cyclonic feature identified from altimetry data at the intersection of the ABFZ and the SWIR was not used (Fig. 5a). The increased use of low edge and low background edge habitat types in the M2 migration suggests that seals might be using decaying anti-cyclonic (warm core) eddies to locate prey and forage (e.g., Fig. 4c, Fig. 6c). Much foraging during the M2 migration was in the background habitat type at the interface between areas of low and high SLA (Fig. 6a). Those areas had higher SLA slope values during the M2 migration where myctophid fishes are generally abundant (Brandt 1983).

Juvenile SES from Marion Island evidently explore eddies and areas of divergent SLA similar to SES from Kerguelen Island (Bailleul et al. 2010, Dragon et al. 2010). Juvenile seals from Marion Island used warm eddy habitats that originated north of the sub-Antarctic Front in contrast to seals from Kerguelen Island that mainly foraged in cold eddies (Bailleul et al. 2010) or areas with lower SLA values (Dragon et al. 2010). The geographic location of Marion Island in relation to the STC has an important regional effect on available resources, evident in the foraging behaviour of sea-birds from Marion Island (Nel et al. 2001) and elephant seals tracked in other years (Oosthuizen et al. 2011, Tosh et al. 2012).

SES foraging behaviour is evidently influenced by a variety of biotic and abiotic factors including sea temperature (Biuw et al. 2007), bathymetric features (Tosh et al. 2012), frontal zones (Bost et al. 2009), and sea-ice concentration (Tosh et al. 2009, Bestley et al. 2013). Measuring actual foraging activity and success requires direct documentation of behaviour data (Bestley et al. 2010, Schick et al. 2013). Using models of searching behaviour of SES we infer that movements of juvenile seals are influenced by SLA though we think that these inferential hypotheses about foraging activity need to be directly tested. Northward shifts in foraging behaviour might indicate enhanced availability of prey caused by increased eddy shedding from the STC. More eddies that last longer and move farther south as a result of the poleward shift of the southern ocean westerlies in recent decades (Meredith and Hogg 2006, Backeberg et al. 2012) might result in correlative changes in use of ocean habitats by SES from Marion Island. The Agulhas Current leakage and the associated shedding of eddies at the SCZ appear to be important elements in the movement and foraging ecology of juvenile SES and could be an important starting point for studying the implications of ocean climate change on SES foraging patterns and demography.

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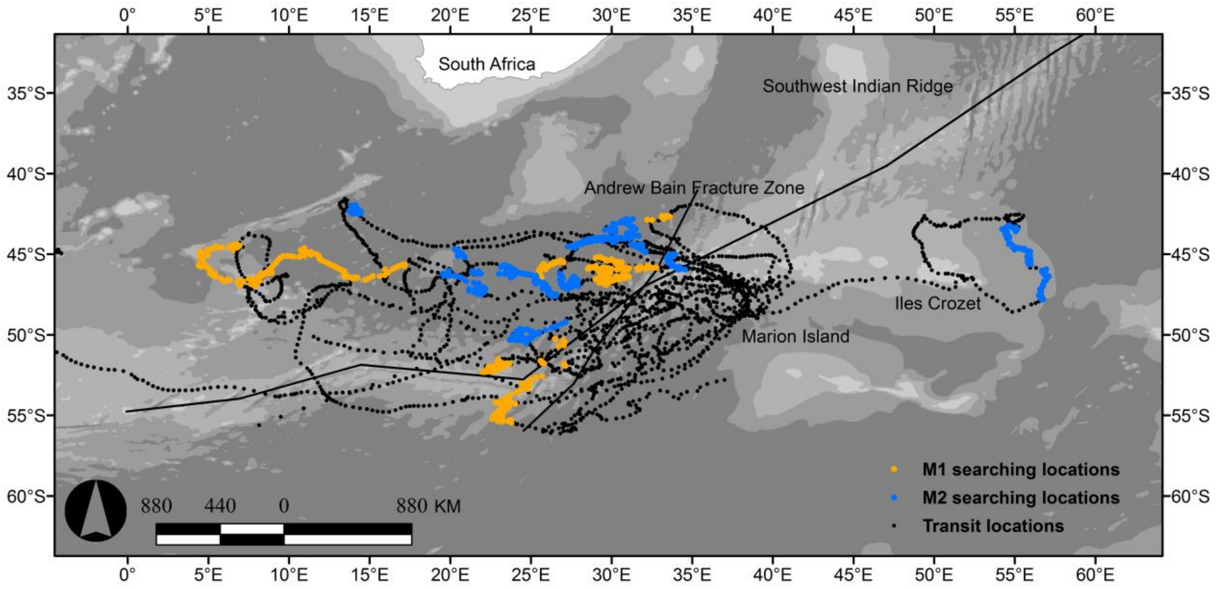


Figure 1. State-space modelled location estimates for ten juvenile southern elephant seals tracked from Marion Island in 2004. Searching behaviour (mode 1) recorded in the post-moult migration (M1) and post-winter haul out migration (M2) are indicated. Locations are overlayed onto a bathymetric map of the region where darker shades indicate deeper depths.

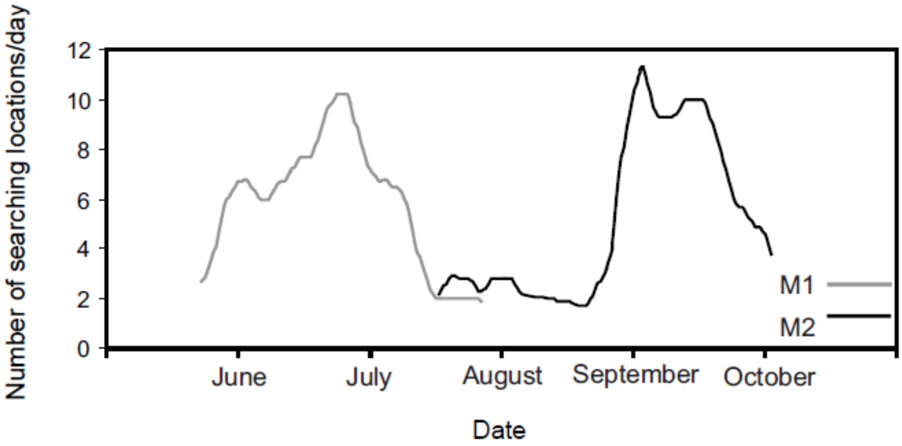


Figure 2. Timing of searching locations (state-space modelled: mode 1) recorded during the post-moult migration (M1) and the post-winter haul-out migration (M2) of 10 juvenile southern elephant seals from Marion Island.

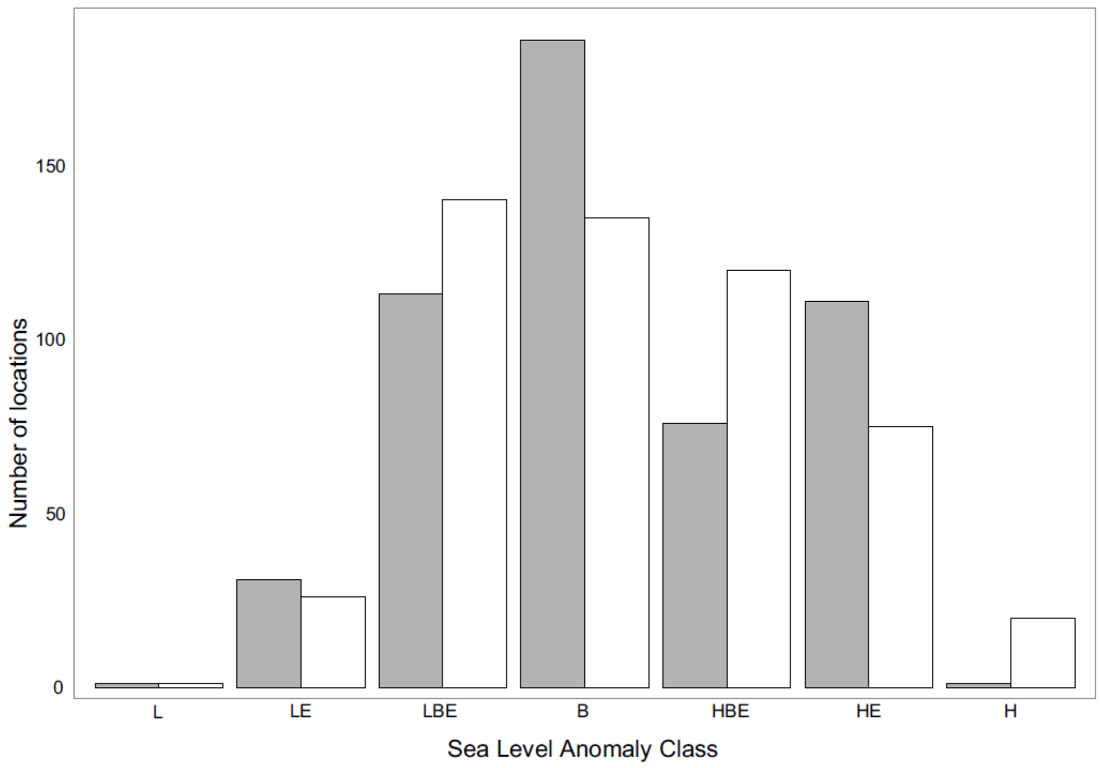


Figure 3. Number of searching locations (state-space modelled: mode 1) per SLA class (L: low, LE: low edge, LBE: low background edge, B: background, HBE: high background edge, HE: high edge, H: high) occurring during the different migrations of ten juvenile southern elephant seals from Marion Island. Post haul-out migration (M1: grey bars) and the post-winter migration (M2: white bars). M1 searching locations peaked in July and M2 searching locations peaked in October. No searching behaviour was recorded in the Low SLA habitat class.

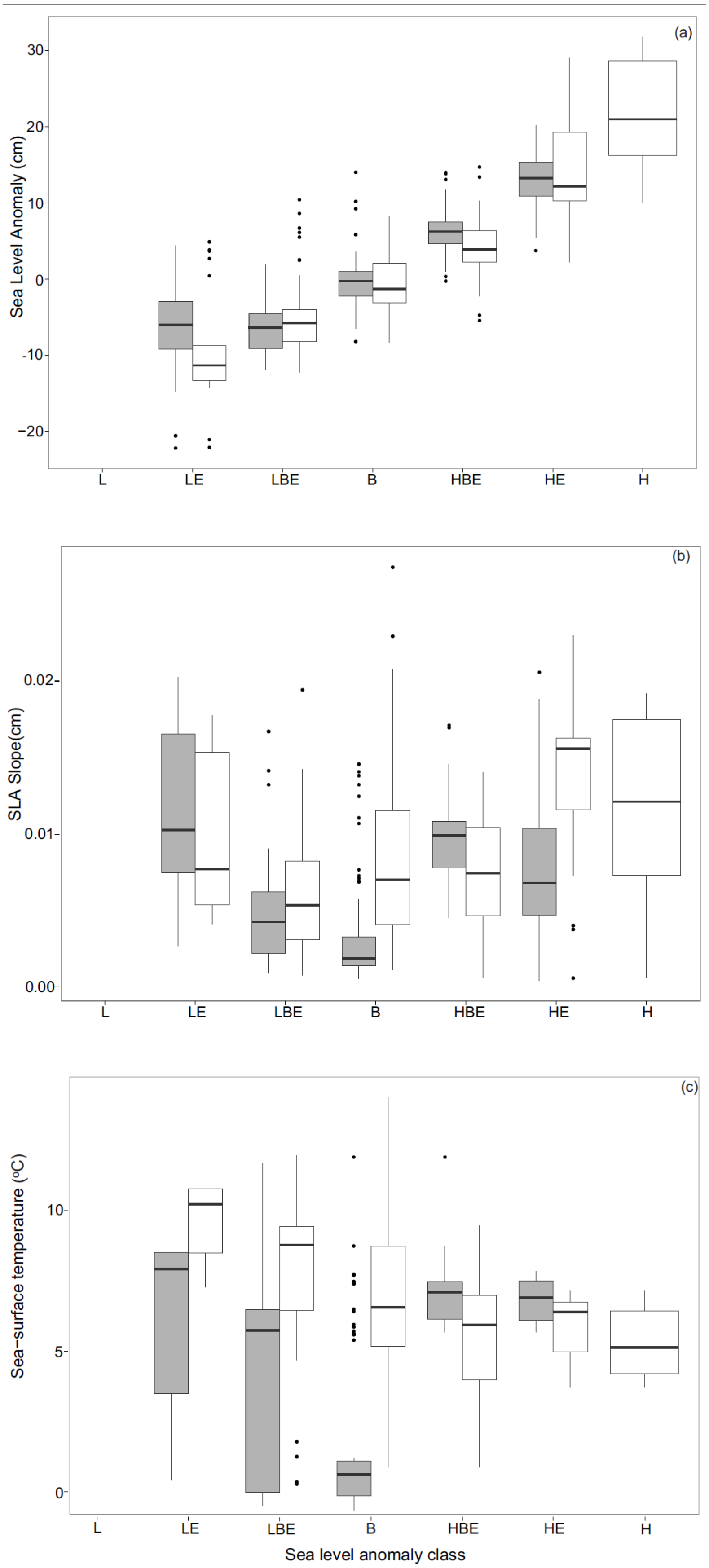

(a)
Sea Level Anomaly (cm)
30
20
10
0
-10
−20
L
LE
LBE
B
HBE
HE
H
(b)
SLA Slope(cm)
0.02
0.01
0.00
L
LE
LBE
B
HBE
HE
H
(c)
Sea−surface temperature (ºC)
10
5
0
L
LE
LBE
B
HBE
HE
H
Sea level anomaly class

Figure 4: Box and whisker plots for (a) sea level anomaly (SLA) values of the SLA classes (L: low, LE: low edge, LBE: low background edge, B: background, HBE: high background edge, HE: high edge, H: high) identified for the searching locations, (b) SLA slope values of the SLA classes of searching locations and (c) sea-surface temperatures (°C) of the SLA classes identified for the searching locations the post-moult migration (M1: grey bars) and the post-winter haulout migration (M2: white bars). Bars represent median values, boxes represent the interquartile range, whiskers represent the minimum and maximum values whilst the dots represent outliers.

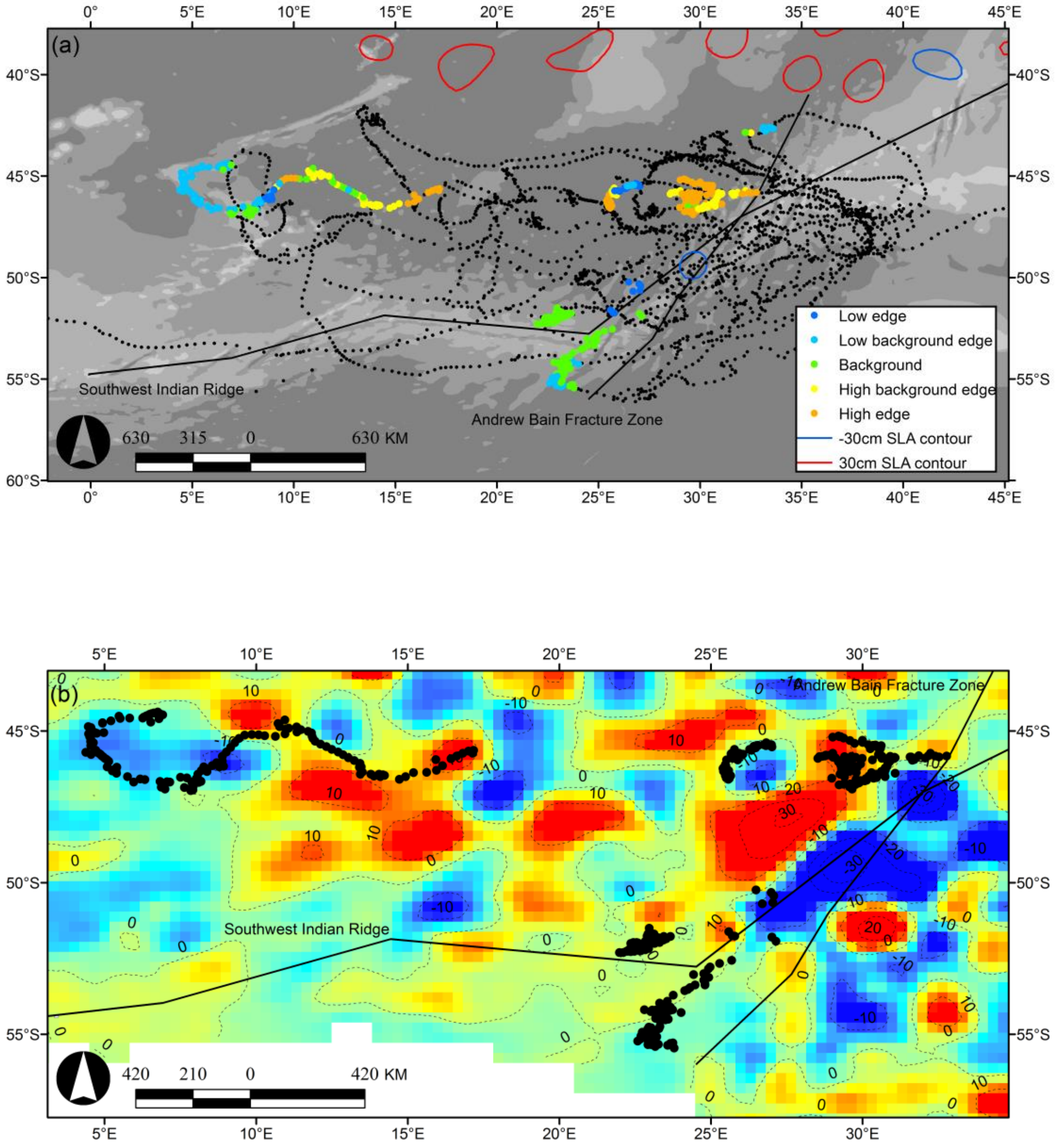
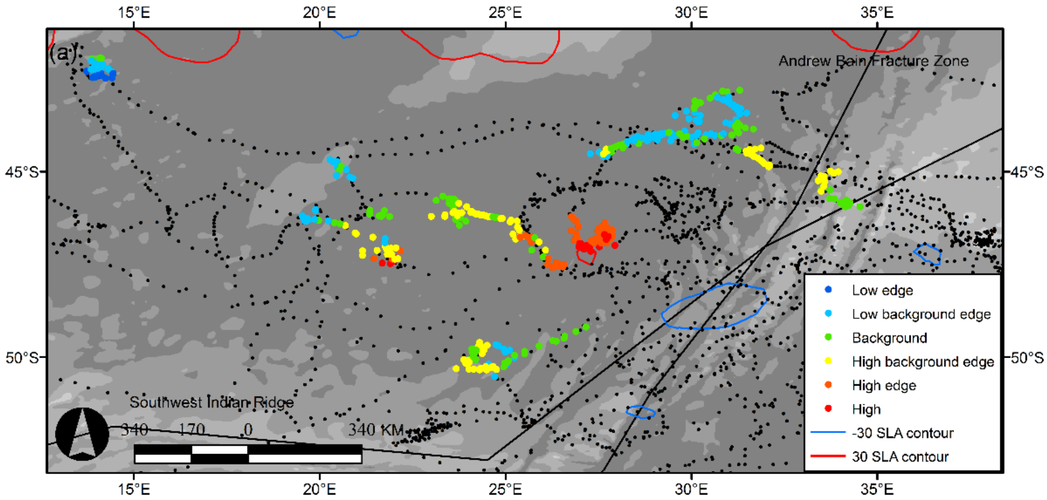
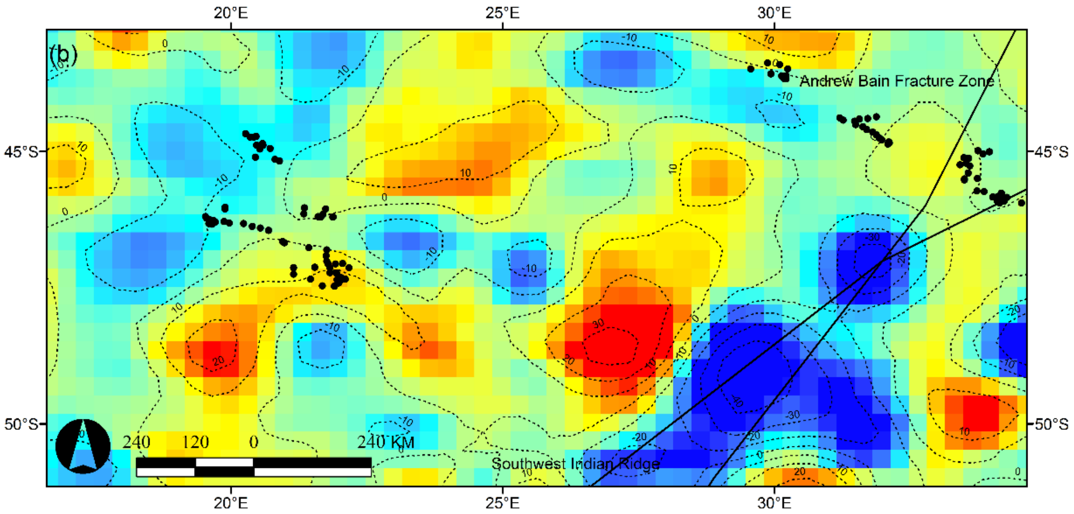


Figure 5. State-space modelled searching locations recorded during the M1 migration. (a) Habitat classes of locations are indicated, as well as intense eddies (more or less than 30 cm from the mean), (b) searching locations recorded in the M1 migration are overlayed onto a composite SLA map, created by averaging weekly SLA datasets for the months of June and July. The contours give an indication of SLA values.


(a)
15°E
20°E
25°E
30°E
35°E
45°S
50°S
Andrew Bain Fracture Zone
Southwest Indian Ridge
340
170
0
340 KM
● Low edge
● Low background edge
● Background
● High background edge
● High edge
● High
-30 SLA contour
30 SLA contour


(b)
20°E
25°E
30°E
45°S
50°S
Andrew Bain Fracture Zone
Southwest Indian Ridge
240
120
0
240 KM

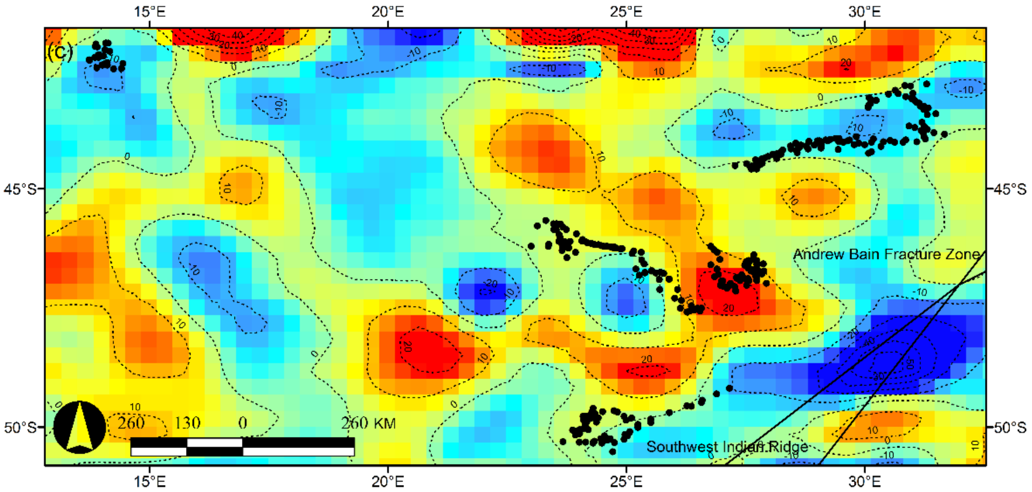

(c)
15°E
20°E
25°E
30°E
45°S
50°S
Andrew Bain Fracture Zone
Southwest Indian Ridge
260
130
0
260 KM

Figure 6. State-space modelled searching locations recorded during the M2 migration. (a) Habitat classes of locations are indicated, as well as intense eddies (more or less than 30 cm from the mean), (b) searching locations recorded in the M2 migration are overlayed onto a composite SLA map, created by averaging weekly SLA datasets for the months of August and (c) October. The contours give an indication of SLA values.

Figure

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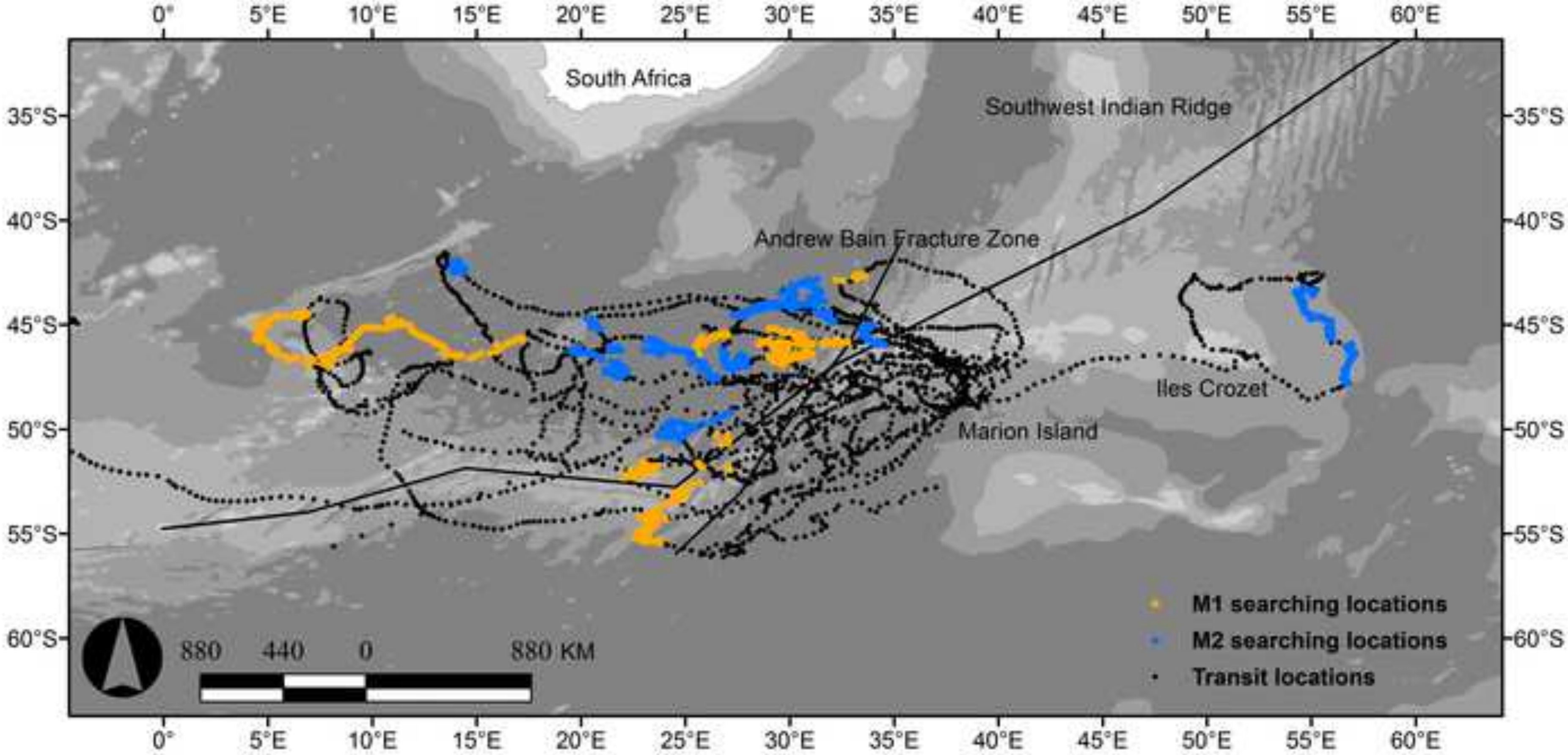
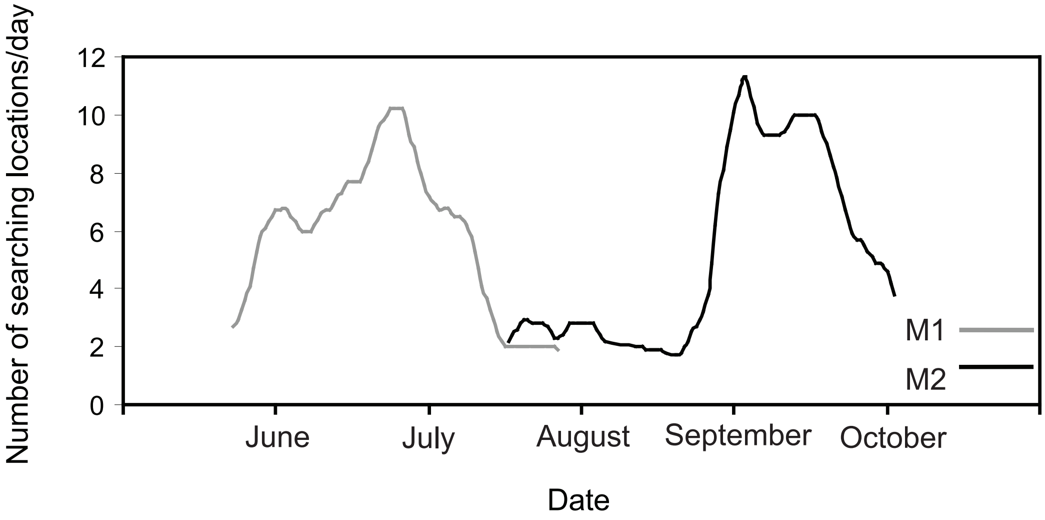
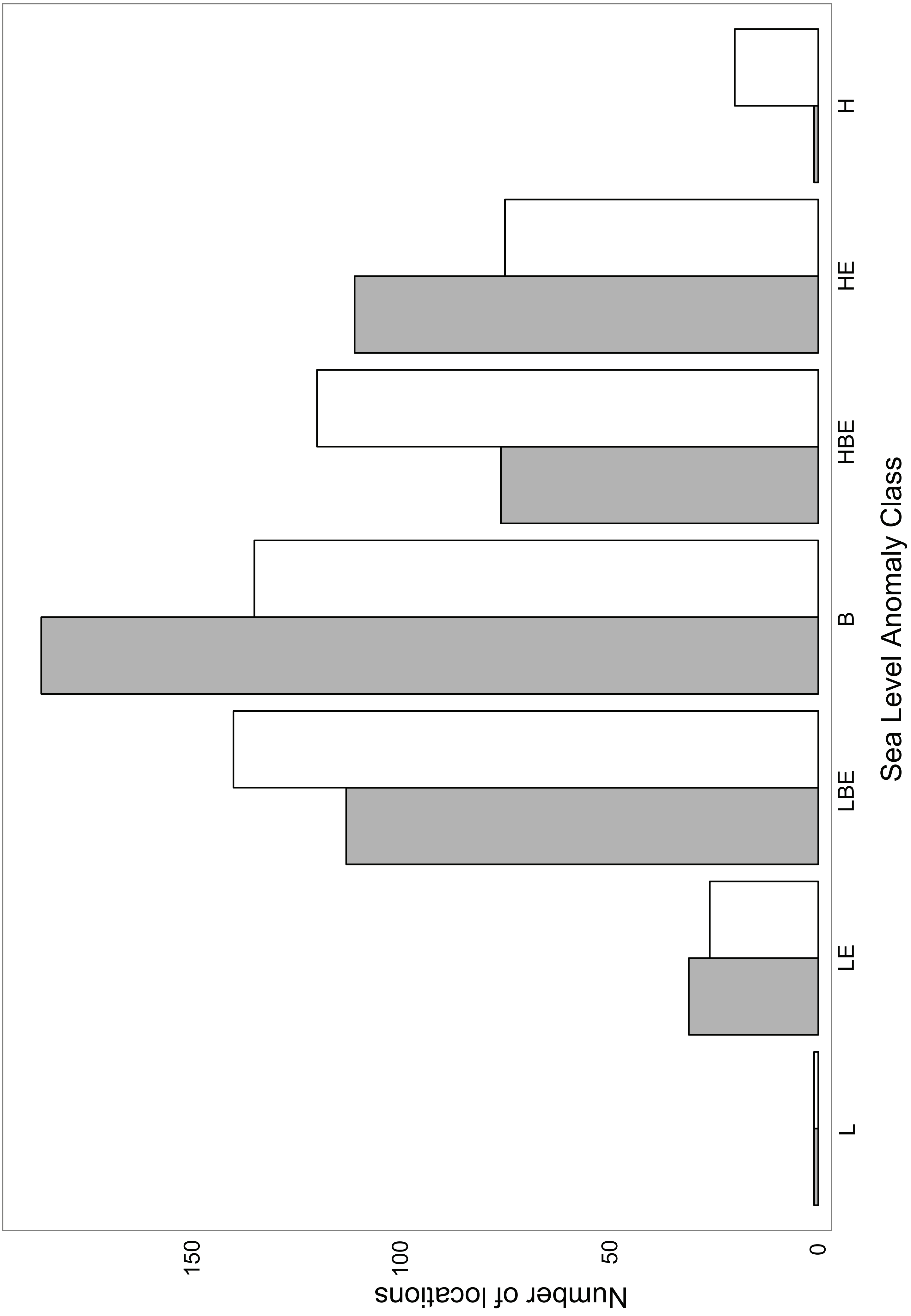


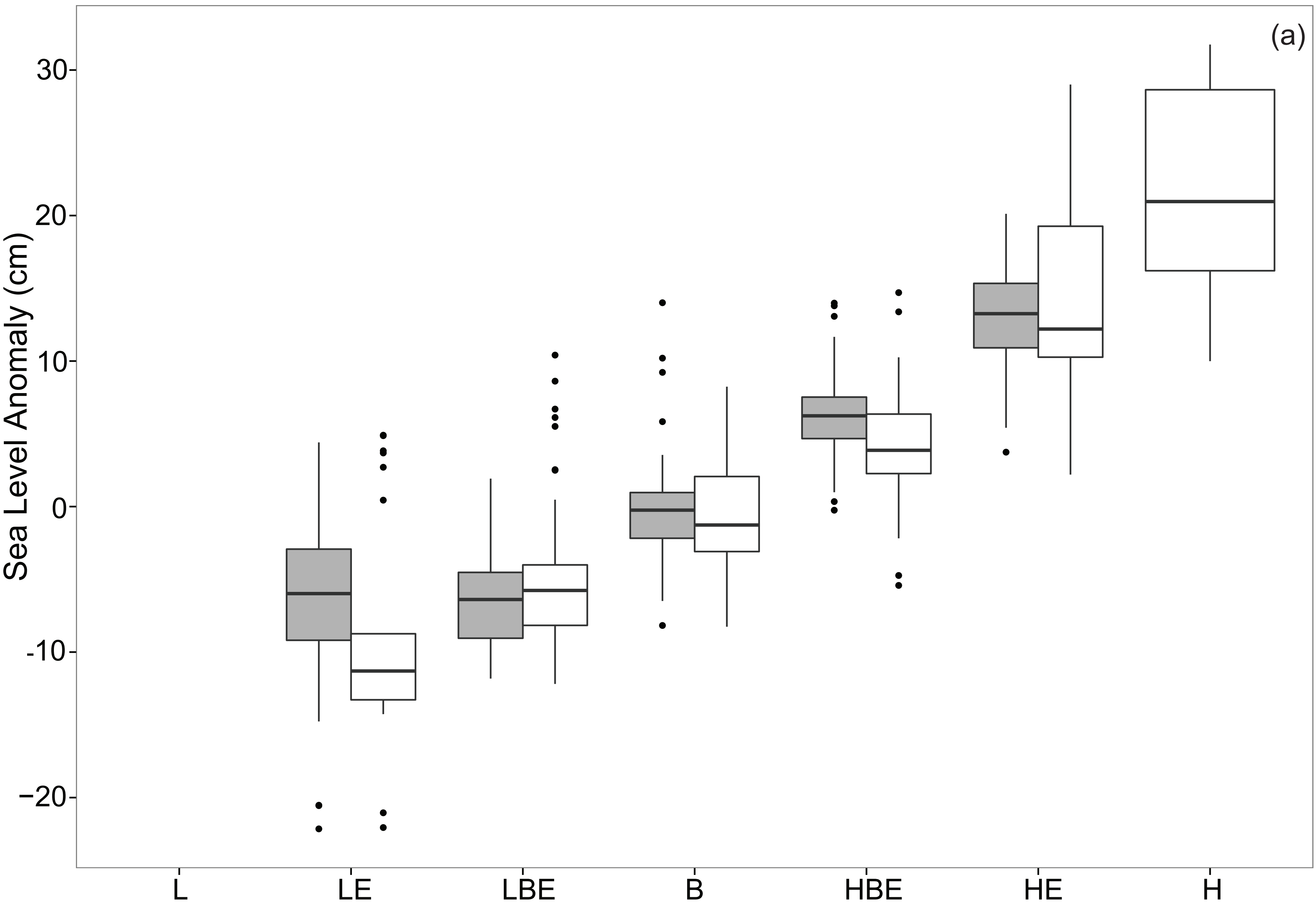
Figure


Number of searching locations/day
12
10
8
6
4
2
0
June
July
August
September
October
Date
M1
M2

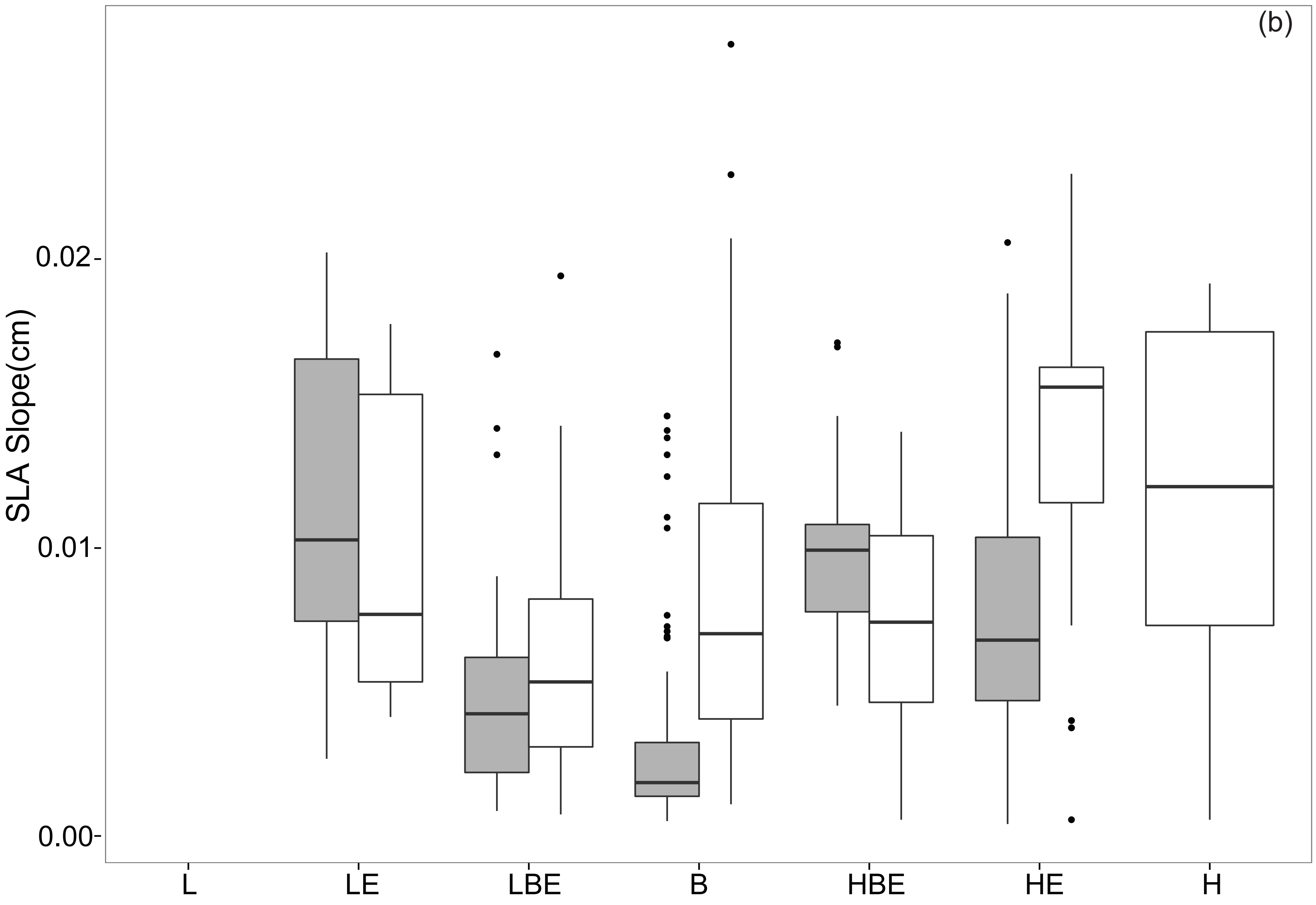
Figure


Number of locations
0
50
100
150
L
LE
LBE
B
HBE
HE
H
Sea Level Anomaly Class

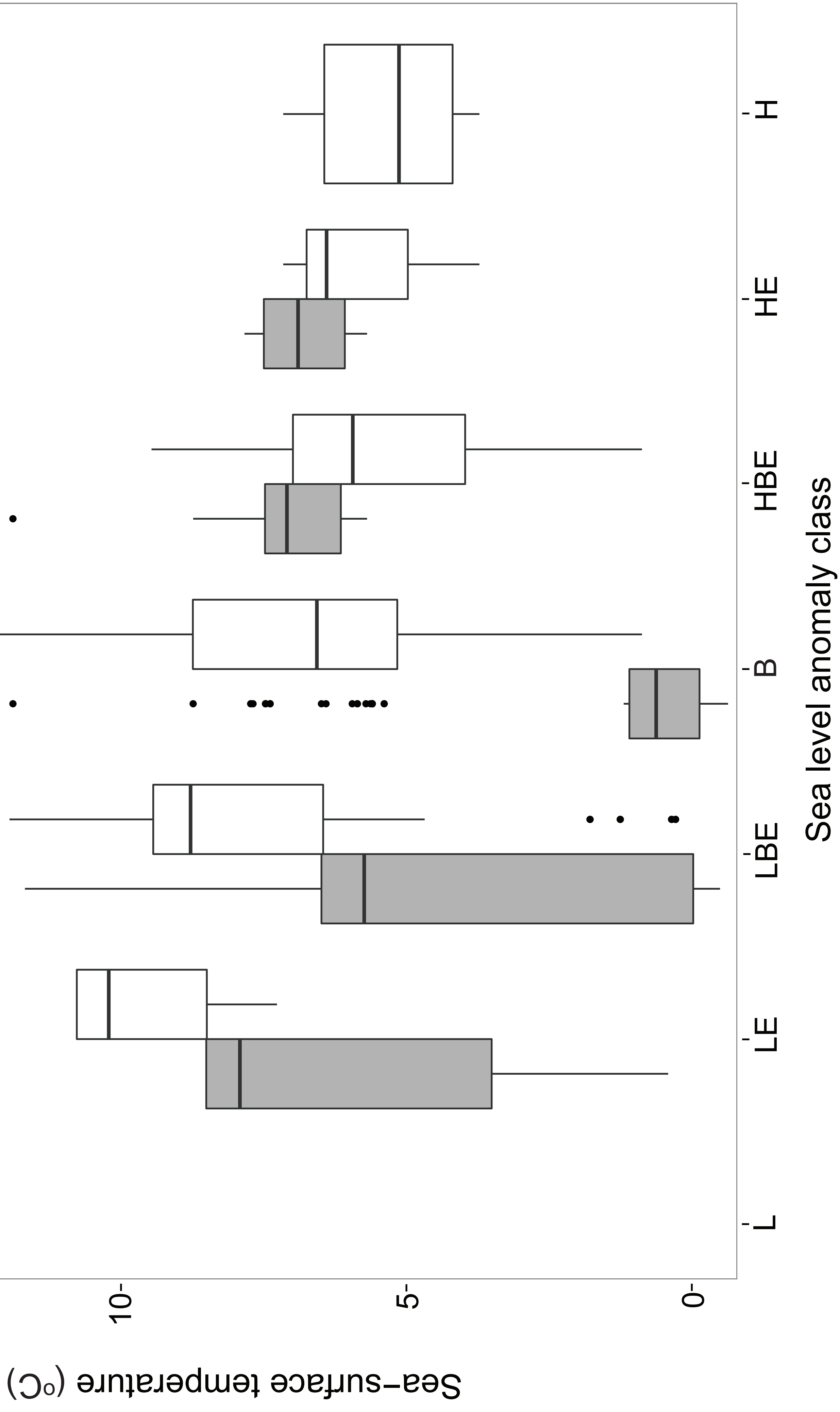
Figure

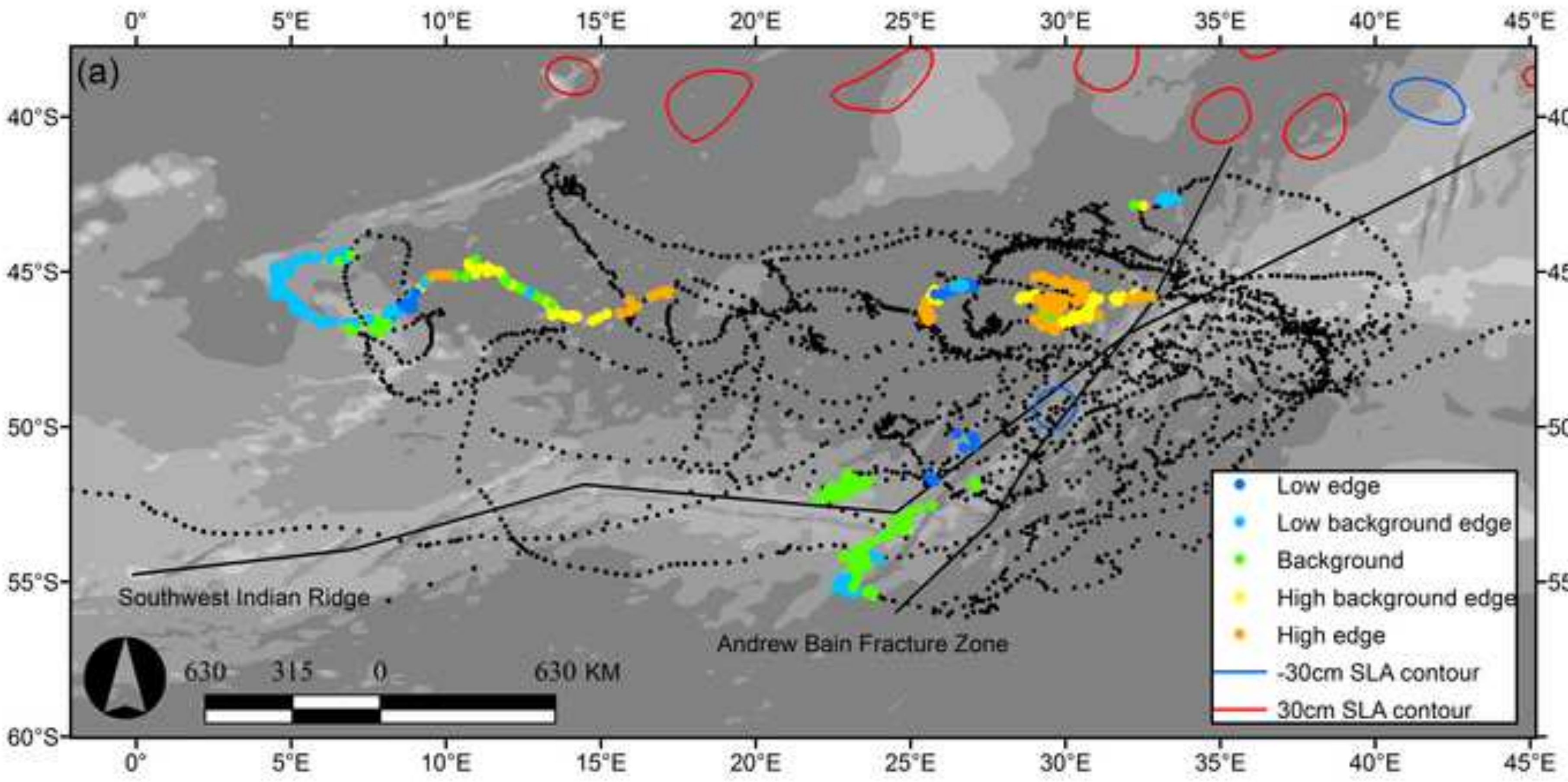


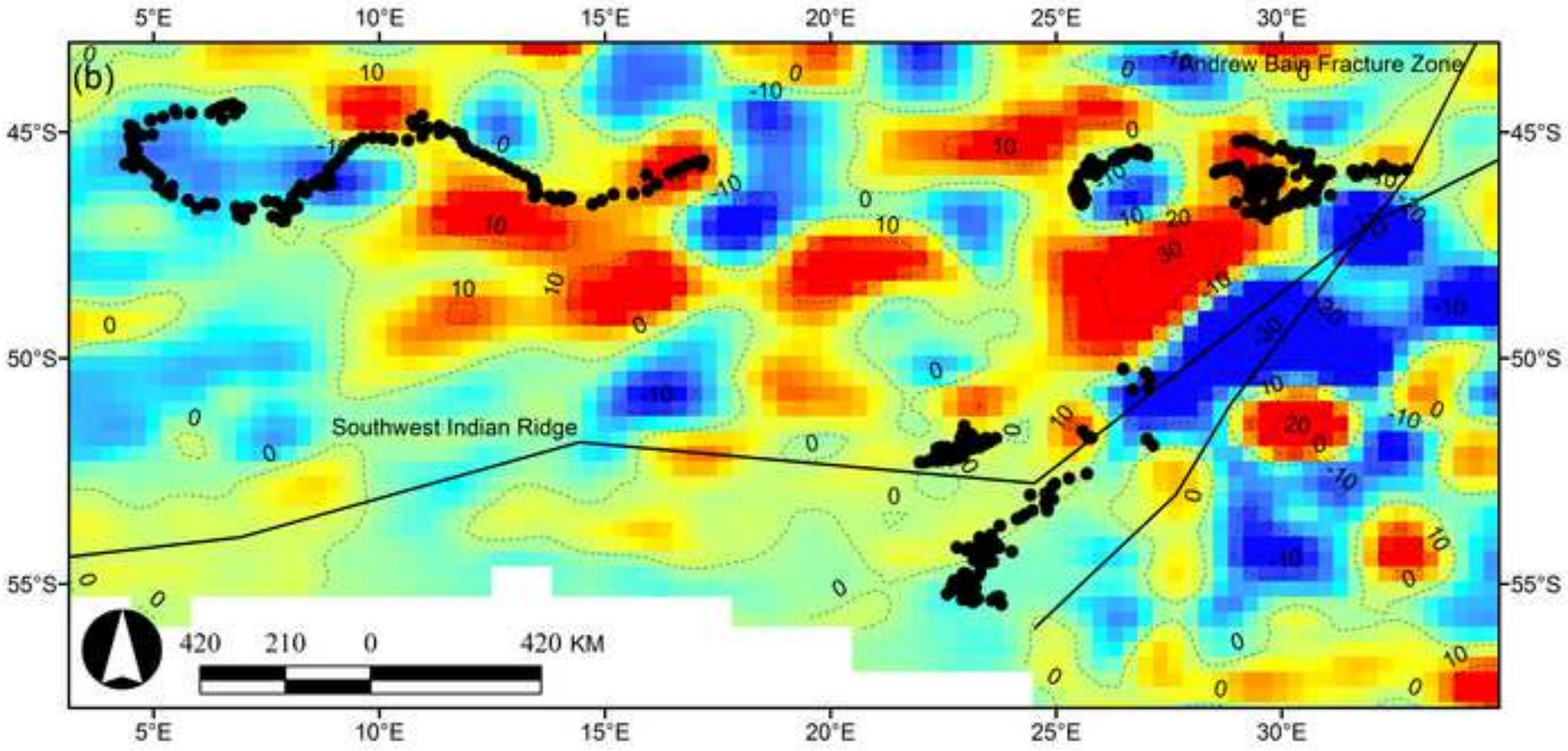
Figure

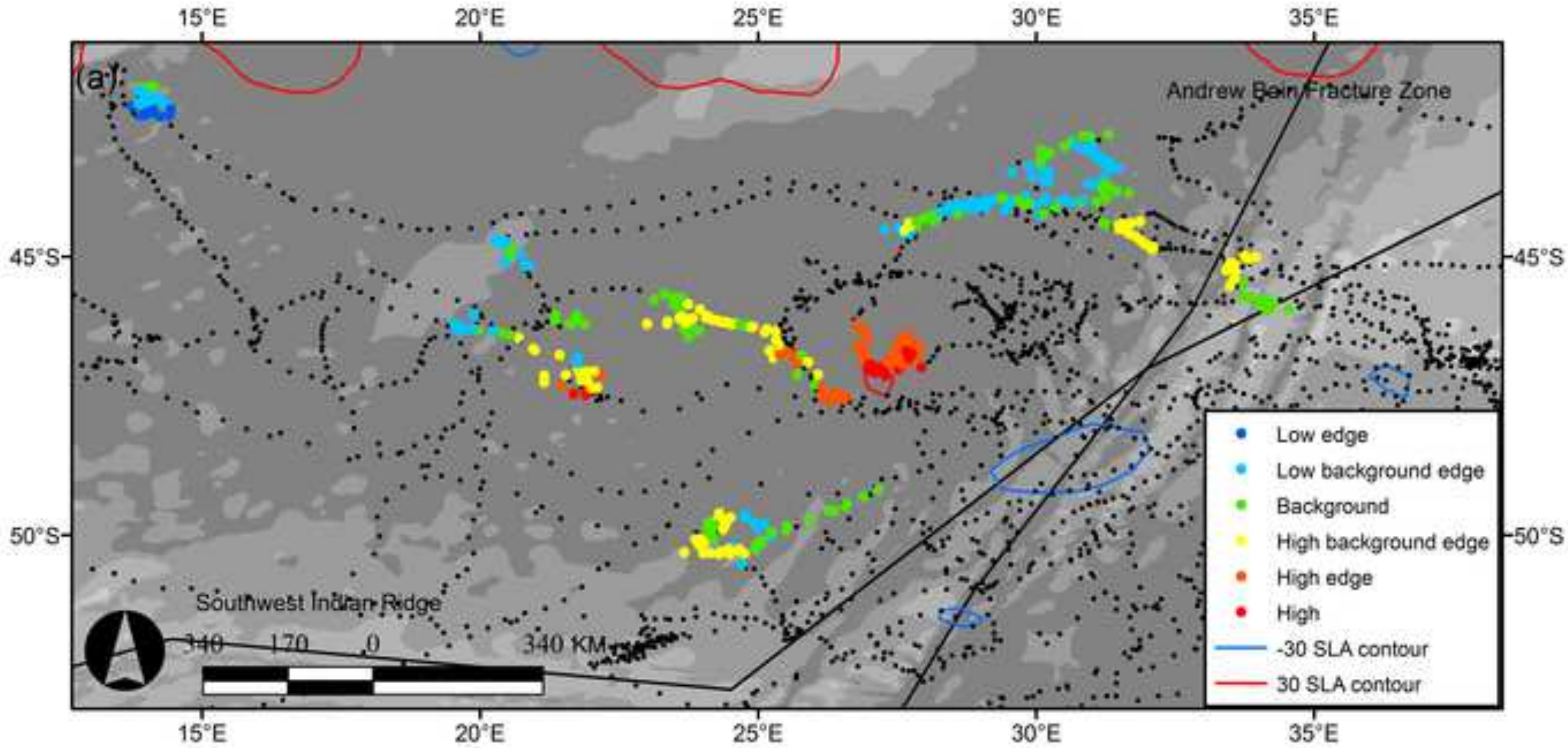


Figure


(c)
Sea−surface temperature (oC)
10
5
0
L
LE
LBE
B
HBE
HE
H
Sea level anomaly class


(a)
0°
5°E
10°E
15°E
20°E
25°E
30°E
35°E
40°E
45°E
40°S
45°S
50°S
55°S
60°S
Southwest Indian Ridge
Andrew Bain Fracture Zone
630
315
0
630 KM
● Low edge
● Low background edge
● Background
● High background edge
● High edge
-30cm SLA contour
30cm SLA contour


(b)
5°E
10°E
15°E
20°E
25°E
30°E
45°S
50°S
55°S
Andrew Bain Fracture Zone
Southwest Indian Ridge
10
-10
0
20
30
420
210
0
420 KM


15°E
20°E
25°E
30°E
35°E
(a)
Andrew Bain Fracture Zone
45°S
45°S
50°S
50°S
Southwest Indian Ridge
340
170
0
340 KM
Low edge
Low background edge
Background
High background edge
High edge
High
-30 SLA contour
30 SLA contour
15°E
20°E
25°E
30°E
35°E

Figure

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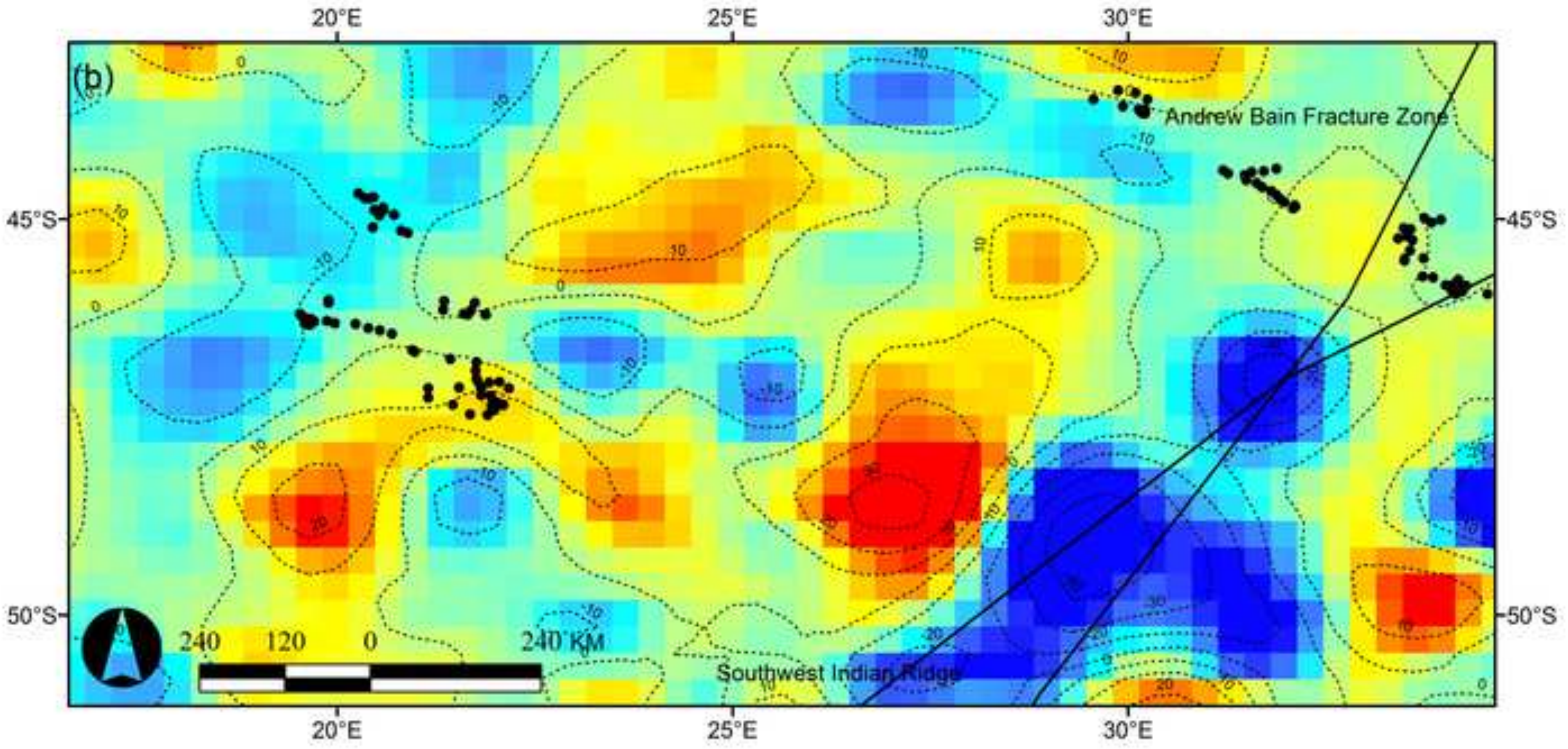

Figure

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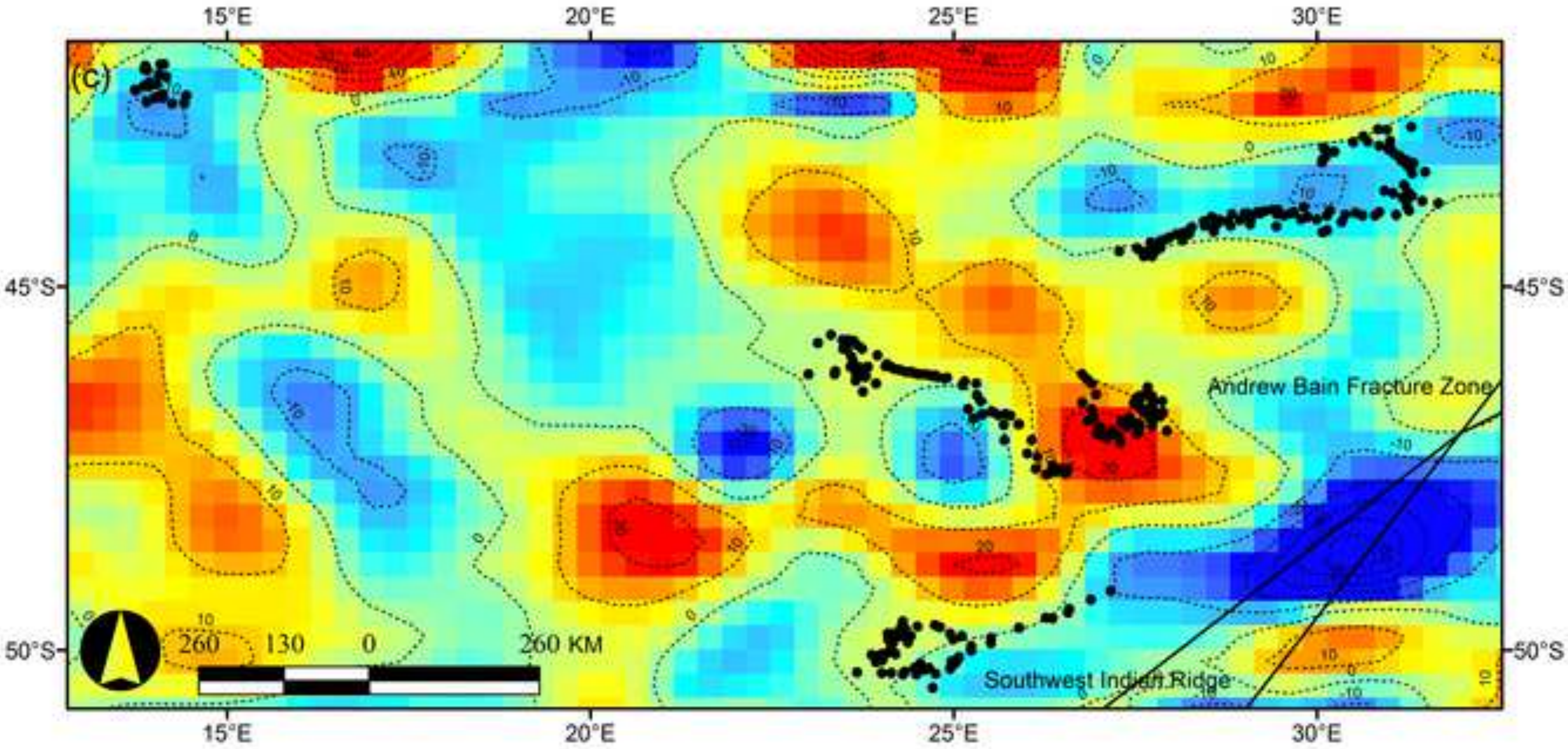

Table 1. Deployment details for ten juvenile southern elephant seals from Marion Island, 2004. Dates are given as year/mm/dd. M1=post-moult migration; M2=post-winter haul-out migration, F =searching bout number and duration (days).

| Tag | Sex (M/F) | Age (yr) | Transmitter type | Date deployed | Migration stage (duration) | Foraging bouts (duration) |
|---|---|---|---|---|---|---|
| YY428 | F | 0.5 | Sirtrack Kiwisat | 2004/04/13 | M1(90) | F1(51) |
| | | | | 2004/08/14 | M2(106) | F2(36) |
| YY191 | F | 0.5 | Telonics-ST10 | 2004/04/16 | M1(117) | F1(21)<br>F2(26) |
| | | | | 2004/08/10 | M2(112) | F3(13)<br>F4(3)<br>F5(34) |
| YY232 | M | 0.5 | SMRU/Series 9000 SRDL | 2004/04/16 | M1(104) | F1(42)<br>F2(2)<br>F3(3) |
| | | | | 2004/08/04 | M2(116) | F4(7) F5(8)<br>F6(36) |
| YY302 | M | 0.5 | Telonics-ST10 | 2004/04/27 | M1(100) | F1(37) |
| | | | | 2004/08/19 | M2(111) | F2(67) |
| BB277 | F | 1 | Sirtrack Kiwisat | 2004/04/13 | M1(65) | |
| | | | | 2004/06/30 | M2(158) | F1(21)<br>F2(43) |
| TO340 | M | 1 | SMRU/Series 9000 SRDL | 2004/04/18 | M1(43) | F1(7) |
| | | | | 2004/06/27 | M2(147) | F2(6)<br>F3(30) |
| BB032 | F | 1 | Sirtrack Kiwisat | 2004/04/15 | M1(102) | F1(10) |
| BB018 | F | 1 | Sirtrack Kiwisat | 2004/04/16 | M1(100) | F1(66) |
| BB193 | F | 1 | Sirtrack Kiwisat | 2004/04/17 | M1(117) | - |
| BB125 | M | 1 | Telonics-ST10 | 2004/04/18 | M1(61) | - |

Table 2. Summary of mixed effects models comparing sea level anomalies (SLA) and SLA slope values between searching (mode 1) and transit (mode 0) behaviour predicted by state-space models. The full model was significantly different from the null model. Individually modelled variables were also significantly different from the full and the null models.

| Fixed effects | AIC | ∆AIC | Log Likelihood | df |
|---|---|---|---|---|
| Null | 3470.2 | -296.9 | -1733.1 | - |
| SLA + SLA slope | 3173.3 | - | -1582.6 | 1 |
| SLA | 3421.7 | -248.4 | -1707.8 | 0 |
| SLA slope | 3212.6 | -39.3 | -1603.3 | 1 |