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**Varying depth and swarm dimensions of open-ocean Antarctic
krill *Euphausia superba* Dana, 1850 (Euphausiacea) over diel
cycles**

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ABSTRACT Diel vertical migration (DVM) behaviour in swarms of Antarctic krill (*Euphausia superba* Dana, 1850) is notoriously variable, with swarms being found at a range of depths and in different shapes, sizes, and packing concentrations throughout the day-night cycle. Because social aggregation can potentially serve the same purpose as DVM in minimising predation risk, krill may use both strategies to varying extents. Diel variation was examined in swarm depth, length, perimeter, area, thickness, and packing concentration across 4,130 open-ocean swarms in the Scotia Sea during summer. Inter-relationships between each of the swarm descriptors were complex but multivariate analyses identified pairings in levels of similarity between area and perimeter, thickness and packing concentration, and depth and length. Second-stage analysis further identified diel cyclicality in these relationships. Swarm parameters were more variable than depth over the diel cycle, identifying swarming to be the primary diel response to which DVM is a secondary contributor.

Key Words: behaviour, diel vertical migration (DVM), echosounder, Southern Ocean

INTRODUCTION

In amassing in swarms that are often hundreds of metres in length, and hundreds of thousands of tonnes in biomass, Antarctic krill (*Euphausia superba* Dana, 1850) form some of the largest aggregations of biomass in the animal kingdom and it is a behaviour that dominates their ecology (Hamner & Hamner, 2000). Krill are noted for their pronounced diel vertical migrations (DVMs) in which vertical distances, sometimes of the order of hundreds of metres, are traversed each night and day (Tarling *et al.*, 2001). Although there may be some advantages in exhibiting both swarming and DVM, it raises the question of whether both are necessary, given that they are being driven by the same trade-off between energetic demand

and predator avoidance (Ritz, 1994). This overlap in function leads to some complex outcomes in terms of variable patterns of vertical migration and swarm structure over diel cycles (Godlewska, 1996) that have proven difficult to predict (Alonzo & Mangel, 2001; Cresswell *et al.*, 2009). Understanding these interactions is nevertheless fundamental to predicting how this species will respond behaviourally to changes in its environment (Smetacek & Nicol, 2005).

Even the earliest studies of DVM in Antarctic krill noted its variability. Marr (1962) stated that there was no obvious pattern in the vertical movements of krill swarms, with subsurface swarms liable to be encountered at any depth to 150 m virtually at any hour of the day or night. Hardy & Gunther (1935) also refer to apparently erratic vertical movement of krill. Some subsequent studies have nevertheless reported a pronounced difference in krill swarm depth over diel cycles. Nast (1979), for instance, calculated a mean depth of 20 m during the night and 136 m during the day. Witek *et al.*, (1981) found swarms moved upwards at dusk to the upper 40 m and downwards at dawn to around 90 m. Further studies have noted periods of dispersion during night-time and a consolidation back into swarms during the day (Kalinowski, 1978; Everson, 1983). There are even reports of reverse migration, where swarms are closer to the surface during the day than at night (Kalinowski & Witek, 1985). For every study that has distinguished a DVM pattern, however, there is another that fails to find any diel change in vertical position or levels of dispersion (Shulenberger *et al.*, 1984; Daly & Macaulay, 1988; Higginbottom & Hosie, 1989; Azzali & Kalinowski, 2000; Lowe *et al.*, 2012)

In an attempt to resolve this complex picture, Godlewska (1996) carried out a major synthesis of acoustic and net catch data across a number of ocean sectors. She noted that a number of vertical migration patterns existed in different environments or under different circumstances, but, underlying this, she proposed that there was a universal pattern which

could be modelled with a periodicity of 12 or 24 h. According to Godlewska (1996), adults are more likely to exhibit a 24 h migration cycle over large amplitudes, whereas juveniles have a greater tendency to have 12 h cycles and shallower migrations. Furthermore, when food is scarce, migrations are shallower and have a 12 h cycle, but a 24 h deeper migration cycle is reverted to when food is abundant. In a model of feeding activity in relation to depth and time of day, however, Morris & Ricketts (1984) found that neither stomach nor hepatopancreas nor gut fullness varied with depth and only stomach fullness showed any significant variation with time of day, concluding that the links between feeding, swarming, and vertical migration are tenuous.

Variability in diel rhythmicity is also exhibited at the individual level. Gaten *et al.*, (2008) maintained Antarctic krill in activity-monitors exposed to either constant darkness or a light-dark cycle and found complex rhythms made of two circadian components, one shorter than 24 h and one longer than 24 h. Furthermore, krill did not display a robust 24 h rhythm even under a light-dark cycle, which suggests that light may not be a dominant coordinating factor (*Zeitgeber*).

Cresswell *et al.*, (2009) modelled the trade-off between packing concentrations and vertical position in the water column in terms of relative risk to predators and accessibility to surface productivity. Individuals migrating deeper and packing closer experienced lower predation risk but at the cost of lowered feeding success. By contrast, individuals moving closer to the surface and becoming more dispersed achieved a greater reward from feeding but at a greater risk. This conceptual approach benefits from considering the interactions between DVM and swarming since neither acts in isolation from the other. The study nevertheless found a lack of responsiveness in the swarming parameter (i.e., packing concentration) indicating that either the costs or benefits of this trait were not fully captured in the model or there are further swarm parameters that may be more responsive. For

instance, Tarling *et al.*, (2009) found swarm length, thickness, area, and distance to nearest swarm neighbour as all being responsive to changes in environmental conditions.

Although net sampling in early studies has provided a great deal of information about the Antarctic krill, the greatest focus of research in the last decades has been through the use of active acoustics (Watkins *et al.*, 2004; Tarling *et al.*, 2009; Krafft *et al.*, 2012). Acoustic surveys can cover large distances rapidly and now incorporate sophisticated multifrequency techniques which enable Antarctic krill to be distinguished from other types of swarming pelagic organisms (Madureira *et al.*, 1993a, 1993b, Korneliussen *et al.*, 2009). Furthermore, swarm detection algorithms can analyse the echograms for features meeting the set criteria for Antarctic krill swarms (e.g., SHAPE Shoal Analysis and Patch Estimation System; Coetzee, 2000), generating swarm inventories that can amount to thousands of swarms that are each measured in multiple dimensions, including perimeter, length, area, thickness, depth, and backscattering strength. These advances do not completely obviate the need for net samples, which are still required to assess typical individual size and age structures of populations with which to generate target strength models and estimate packing concentrations (Demer & Conti, 2003, 2004). Advances in acoustics and processing nevertheless mean that analyses at the level of swarms can be performed over extensive temporal and spatial extents using objective methods.

We analysed the structure and depth of Antarctic krill swarms over diel cycles using acoustic data collected continuously over a large-scale survey of the Scotia Sea (Fig. 1). This sector of the Southern Ocean is suited to this type of study since more than 30% of the circumpolar population of krill is found within it (Atkinson *et al.*, 2008) and it covers a range of environmental conditions in, for instance, temperature (0 to 5°C), distance from sea-ice and land (0 to 1000s km), and levels of primary productivity (0.2 to 3 mg m⁻³) that are likely to influence swarm structure (Tarling *et al.*, 2009), making it likely that a wide variety of

swarm structures will be encountered. Our study only considered the open-ocean situation (>100 km from nearest land) to avoid confounding our analyses with inshore influences on swarm structure, as these can be considered to be a special case (Klevjer *et al.*, 2010). Multivariate statistical analyses were performed in order to synthesise variability across a number of swarm structure parameters so as to reveal any dynamics in the relationship between swarm structure and swarm depth over diel cycles. In particular, we employed a two-stage technique following Clarke *et al.*, (2006) where, firstly, we considered multivariate relationships between swarm descriptors (e.g., length, depth, packing concentration, and other factors) and, secondly, we determined how these relationships change over hourly intervals across the diel cycle. Our overall aim was to evaluate the relative influences of swarming behaviour and DVM on diel variability in open-ocean krill swarms.

METHODS

General survey details

A survey encompassing eight transects was carried out by the RRS *James Clark Ross* across the Scotia Sea between 9 January and 16 February 2003 (Fig. 1). The majority of transects were transited at speeds of 5 to 10 knots, depending mainly on ice conditions. Acoustic data were collected continuously over the 24 h cycle using a Simrad EK60 echosounder (Kongsberg Maritime AS, Horten, Norway) connected to hull-mounted split-beam 38 kHz, 120 kHz, and 200 kHz transducers. Only data from the 38 kHz and 120 kHz transducers were analysed to identify krill swarms to a maximum depth of 300 m. The beam angles, and hence sampling volumes, of both these frequencies were the same (7°) so allowing direct comparisons to be made for the purposes of swarm identification across most depths. An offset of the two sounders means, however, that the beams were not overlapping at depths shallower than 25 m. Although this could lead to the misidentification of some krill swarms,

we worked on the assumption that swarms of that shape, size, and backscattering strength were unlikely to be anything other than Antarctic krill in this part of the Southern Ocean. The surveys encompassed both open-ocean and shelf regions, but all shelf data (data < 100 km from nearest land) were excluded from the present analysis.

Krill net sampling

A number of swarms were captured by net sampling to ground-truth the acoustic records, principally for the purpose of establishing an acoustic target strength for krill. Krill swarms were located using the Simrad echosounder and then sampled with a rectangular midwater trawl (RMT8). The RMT8 was rigged with two remotely operated opening/closing nets, which had the capacity to sample separate swarms in close vicinity to one another. A random subsample was made from each catch to assess the body length frequency, sex composition, and maturity status of the sampled swarm. Krill body length was measured from front of eye to tip of telson. Sex and maturity categorisations were based on the scheme of Makarov & Denys (1980). Krill sampling took place mostly during the hours of darkness.

Acoustic data and processing

An acoustic system calibration was undertaken at Stromness Bay (54°9.44'S, 36°41.99'W) on 17 February 2003 using the standard sphere method (Foote *et al.*, 1987, 1990). Calibration was carried out with a 60 mm copper sphere for the 38 kHz transducers and a 23 mm copper sphere for the 120 kHz transducers (see Tarling *et al.*, 2009 for details).

Raw acoustic data from the 38 kHz and 120 kHz transducers were processed using Sonardata Echoview version 4.0 following the protocol of Hewitt *et al.*, (2004) with the aim of excluding all backscatter not attributable to krill aggregations. Background noise levels were estimated and subtracted from the 38 kHz and 120 kHz echograms (Watkins & Brierley, 1996). Filters were applied to exclude the upper 13 m of the water column and depths below

the detected bottom (where applicable) and other “bad data” resulting from interference or bad weather. Smaller spikes were removed from the data by restricting the final swarm detection to those regions of the echogram where the 7×7 (pings \times samples where the ping interval was 1.5 s and sample length, 0.1867 m) convolution filtered data were above a threshold of -80 dB at 120 kHz. A threshold of -70 dB at 120 kHz was used in the subsequent swarm delineation, as advised by Lawson *et al.*, (2008).

Krill swarm delineation

A swarm detection algorithm was applied to the processed 120 kHz echogram data using Sonardata Echoview version 4.0 “School detection module” (Sonardata Pty, Tasmania, Australia), which employs a SHAPES algorithm (Coetzee, 2000). This algorithm identifies data points that can be determined as “swarm candidates”, which are groups of cells that meet minimum criteria for length and height. These individual swarm candidates are then linked together to form a larger swarm candidate if the horizontal and vertical distances between them are less than the specified maximum linking distances. After any linking has been carried out, swarms are recognised if the final swarm candidates are larger than the defined minimum total swarm length and height. With a ping interval of 1.5 s, and standard cruising speed of 10 knots, the minimum horizontal resolution was around 7.5 m. We set the minimum total swarm length to 15 m, which is double the minimum horizontal resolution. Transmit pulse duration was 1024 μ s, giving an approximate pulse length of 1.5 m and a minimum vertical distance between 2 resolved targets of ~ 75 cm. The minimum total swarm height was set to 2 m, which was again double the minimum level of resolution. As swarm candidate dimensions must logically be smaller than or equal to the total swarm size parameters, minimum swarm candidate length and height were set to 10 m and 1 m, respectively. The maximum horizontal linking distance was set to 15 m, following Woodd-Walker *et al.*, (2003), and the maximum vertical linking distance was set to 5 m. Swarms

where the relative school length image compared to the beam width (Nb_i) was less than 1.5 were excluded from the dataset, following Diner (2001).

Swarms were detected from the 120 kHz echograms, and physical and acoustic descriptors for the detected swarm-regions were exported from both 38 and 120 kHz data. These dimensions were corrected for known beam geometry according to the system of Diner (1998) within Sonardata Echoview 4.0. These swarms were then interrogated to determine whether or not they were krill using a variable $\Delta S_{v120-38}$ identification technique (CCAMLR, 2005) following the steps outlined in Tarling *et al.*, (2009), including the allocation of different krill total lengths to different survey regions in line with corresponding net catch results. This had a relatively minor influence on estimated krill target strength (TS) across the survey grid, with minimum values of -76.63 dB and maximum, -74.48 dB, equal to a difference of 0.45 individuals m^{-3} at the survey average Sv value of -63.64 dB.

Swarm descriptors

A number of physical properties for each swarm were calculated (Fig. 2), including 1) swarm depth (m), 2) swarm thickness (m), 3) swarm length (m), 4) swarm perimeter (m), and 5) swarm area (m^2). Each of these parameters was corrected according to its beam geometry following the system of Diner (1998). A further descriptor, 6) packing concentration (individuals m^{-3}), relies on the estimation of the target strength (TS) of individual krill, which was carried out using the SDWBA model described in Tarling *et al.*, (2009). Although there are a number of other parameters that can be used to describe swarms, our choice reflects major axes of variability in water column position, shape, and internal organisation. We standardised these variables as a fourth root transformation given wide numerical ranges and large levels of variability within certain parameters. This was preferred to other transformations (e.g., $\log(1+x)$) since it is less severe on large abundances and is also invariant to scale change when calculating similarity matrices (Clarke *et al.*, 2014).

Data analysis

The general approach to data analysis was to examine relationships between the six swarm descriptors over the population of 4,130 swarms. We then sought to determine the influence of time of day on these patterns on these relationships by dividing the datasets into hourly intervals and making intercomparisons of similarity in swarm-descriptor relationships. We maintained time in GMT, relative to which local time was offset by -3 h. Day-time during the period of study was between 0600 and 0000 h GMT, night-time, 0200 to 0400 h, dusk, 0100 h and dawn, 0500 h, local midday was at 1500 h, local midnight, 0300 h.

To establish relationships in patterns of variability across the whole swarm dataset, we used the analytical package Primer 7 (version 7.0.11, Primer-E, Plymouth, UK). We provide an overview of the analytical steps in Figure 2. A resemblance matrix was generated to determine levels of similarity between swarm descriptors using Euclidean distance. The resemblance matrix was subsequently subjected to cluster analysis using average linkage with a SIMPROF test to determine the level of significance in the identified structure. The same resemblance matrix was also examined using non-metric multi-dimensional scaling (nMDS). Two and three-dimensional ordinations were generated and overlaid by the SIMPROF groups identified in the cluster analysis.

To examine the influence of time of day on these relationships, the fourth root transformed dataset was split up according to the hour of observation and a resemblance matrix generated for each of the 24 datasets using Euclidean distance (Fig. 2). The resulting 24 resemblance matrices were then subjected to a second-stage analysis in which a further resemblance matrix based on the Euclidean distance data was generated by determining the pairwise Spearman rank correlation coefficient between hours. Hierarchical clustering and nMDS were used to visualise structure in the data, with the level of correlation separating the

main clusters in the former being projected onto the latter to aid inter-comparison of the two techniques (only nMDS was subsequently plotted).

The second-stage analysis identified four principal groups that were interrogated further to identify what separated the groups as regards patterns of variability in swarm-descriptor variables and the interrelationships between them. The fourth root transformed dataset was split according to these four groupings, and Euclidean distance resemblance generated for each group, subsequently visualised with hierarchical clustering (not plotted) and nMDS and overlaid by SIMPROF groups. The contribution of each of the six swarm descriptors to the level of dissimilarity between the four groups was examined using SIMPER analysis of Euclidean distance similarity coefficients.

RESULTS

There were some clear relationships between the six descriptors, particularly between perimeter and area, length and area, and length and perimeter (Fig. 3). Depth did not appear to have a strong relationship with any other swarm descriptor apart from length, although there was considerable scatter at mid-depth intervals. Thickness exhibited a non-linear positive relationship with area and perimeter and a more diffuse positive relationship with packing concentration (individuals m^{-3}). Packing concentration did not exhibit strong relationships with any other swarm descriptors.

Hierarchical cluster analysis combined with SIMPROF found significant structure within the data, identifying three significantly different groups of swarm descriptors (Fig. 4). A major division between swarm descriptors occurred at a group average distance of 121.5, where the swarm descriptors divided into two branches. In one branch, perimeter and area were significantly linked at a group average distance of 58.5. In the other branch, significant

linkages were apparent between thickness and packing concentrations (individuals m^{-3}) and between depth and length at distances of 48.0 and 56.0, respectively.

Non-metric MDS, superimposed with group structure identified by SIMPROF, similarly showed a distinct separation into the same three pairs of swarm descriptors (Fig. 5). The relative distances between these pairs were smallest between thickness and packing concentration (individuals m^{-3}) and largest between perimeter and area. Each pair was separated almost equidistantly from the other two.

A second-stage analysis examined the relationship between the Bray-Curtis similarity matrices generated for each hourly interval. This derived a second-stage correlation matrix that was analysed by hierarchical clustering and non-metric MDS. This generated two major groups, bounded by a correlation level of 0.87, and two outliers (Fig. 6). The larger of the two groups contained all hourly intervals between 0600 h and 0000 h, which corresponded to all the hours of local daylight. The latter contained the intervals, 0200 h, 0300 h, and 0400 h, the local hours of darkness. The two outliers corresponded to local dusk (0100 h) and local dawn (0500 h).

Further non-metric MDS analyses carried out on each of the four time-period groupings (day-time, dusk, night-time, and dawn) revealed changes in the ways the swarm-descriptor pairs related to each other (Fig. 7). In the day-time group (0600 to 0000 h), the relationship closely resembled that seen in the original analysis (Fig. 5), with three distinct groups, identified as being significantly different by SIMPROF. In the night-time group (0200 to 0400 h), thickness and packing concentration (individuals m^{-3}) remained significantly different to depth and length and both pairs were significantly different to both area and length. In the dawn outlier (0500 h), perimeter and area remained significantly different to depth and length and both pairs were significantly different to thickness and packing concentration. In the dusk outlier (0100 h), thickness and packing concentration were

significantly different to the new pairing of length and area, and both pairs were significantly different to both depth and length. Overall, the relationship between swarm descriptors altered over the diel cycle, with the pairings of thickness and packing concentration and perimeter and area showing the greatest sensitivity to the diel cycle.

When considering the swarm descriptors that contributed most to the dissimilarity between the four time-period groupings, it was apparent that perimeter, area and packing concentration consistently made the greatest contributions, with length, thickness, and depth being more similar between time-period groups (Table 1). Perimeter and area were the greatest contributors to dissimilarity between day and night, as well as between day and dusk and night and dusk. Levels of dissimilarity between dawn and the other three time-period groups were more influenced by packing concentration in combination with area. Out of the six parameters, depth mostly ranked fifth in terms of its contribution to dissimilarity between time-period groups with the exception of night *versus* dawn, where it was ranked fourth and contributed 8% to total dissimilarity levels.

To provide an overview of the patterns of change between swarm parameters over the diel cycle, we plotted their respective means (\pm 95% CI) for each time-period group (Fig. 8), with parameter values further detailed in Table 2. These summaries were determined in the raw, untransformed values. It is apparent that there are distinct increases in packing concentration at dawn (0500 h) and dusk (0100 h) relative to typical day-time or night-time values, which explains the high contribution of packing concentration to levels of dissimilarity between dawn and the other time-period groups. Meanwhile, values for perimeter and area were four to five times higher during day-time than the other time-period groups which underpins the dominant contribution of these two parameters to dissimilarity levels between day-time and night-time and day-time and dusk. Dusk values for perimeter and area were similarly around 20% higher than those observed at night-time, which again is

reflected in these two parameters being the largest contributors to dissimilarity levels between those respective time-period groups. Changes in depth between the time-period groups were of a smaller magnitude but indicate an approximate doubling of depth during the night-time to 80 m from an average day-time depth of 40 m. Depth during dusk and dawn was intermediate between these two values.

DISCUSSION

We considered how depth and the structure of open-ocean swarms of the Antarctic krill altered over diel cycles. Our approach was, firstly, to perform non-parametric multivariate analyses on a number of measures of swarm structure, as well as swarm depth, to determine if there were any natural relationships between these swarm descriptors. We then investigated in what ways these relationships altered over the course of the diel cycle. Considered individually, each of the swarm descriptors exhibited a rather complex pattern of change and variability over the course of the 24-hour cycle. The multivariate analyses identified relationships between these swarm descriptors and the ways in which these relationships altered at key periods of the diel cycle. Our study revealed that when swarm descriptors are considered in combination, krill exhibit some relatively coherent diel behavioural patterns.

Vertical migration

In terms of the depth distribution of swarms, we observed a pattern of reverse migration with swarms being closer to the surface during the day compared to at night, and dusk and dawn having intermediate depths. The difference in day and night depths was nevertheless around 40 m, with average swarm depth during night being around 80 m whereas in the day it was around 40 m but with a much larger degree of variability. Although small in relation to total ensonified volume, this depth change may still be quite an important difference to air-breathing predators (Croxall *et al.*, 1988, Boyd *et al.*, 1994). The dusk and dawn levels of

variability were similar to night-time, with average depths of around 50 m and 70 m, respectively. One possibility is that swarms during night-time move out of the ensonified region and go either deeper than 250 m or shallower than 13 m. Demer & Hewitt (1995) found that krill biomass estimated from acoustic surveys dropped during night-time, most likely as a result of krill migrating above the depth of the echosounder transducer on the ship's hull. Although this cannot be ruled out, one would expect at least the bottom parts of these swarms to be resolved by the echosounder. The vast majority of resolved swarms at night-time were well below the top 40 m, with very little evidence of swarms in the top few metres of the echograms. Similarly, if swarms did migrate below 250 m at this time, there was no indication of a transition to deeper depths in the hours of dusk and dawn, given that average swarm depths during these times were around 50 m and 70 m, respectively. A further possibility is that krill within swarms closer to the surface disperse to a level where they are no longer resolvable by the swarm detection algorithms. They may also be harder to detect nearer the surface because of the reduced sampling volumes closer to the transducer.

Kalinowski & Witek (1983), in their spatially extensive study of Antarctic krill vertical migration patterns, found that, although the classical vertical migration pattern of descent at dawn and ascent at dusk was evident in the majority of regions, a reverse migration pattern was found around South Georgia. Marr (1962) and Everson (1982, 1983) also reported situations where there were distributions that were shallower during the day than at night. In all these case studies the reverse migration occurred in rather limited spatial regions. The reverse migrations we describe appear to occur over a wide region of the Scotia Sea as well as the offshore regions close to South Georgia, a considerably greater geographic region than considered in any previous studies.

Across the realm of pelagic organisms, reverse DVM has mainly been reported for smaller species, such as copepods, predated on by tactile predators such as ctenophores that

are themselves avoiding predation by high-performance visual hunters (Ohman, 1990; Frost & Bollens, 1992). Tactile predation is not known to be a major source of mortality in Antarctic krill populations. Another source of non-visual predation, however, is from baleen whales, which locate their prey acoustically. Willis (2007, 2014) considered the potential impact of increasing levels of whale predation on krill behaviour using state-dynamic trade-off models. He assumed that whales may present an equal if not greater threat in the deeper layers as they do at the surface and, accordingly, the models predicted that krill would spend a greater period of time in the surface layers when whales became the dominant source of mortality. This does not explain, however, why distributions become deeper during the night.

Satiation sinking during the hours of darkness may contribute to deeper average night-time distributions and potentially a drop in the overall biomass contained within swarms as they tend towards less aggregated formations. Tarling & Thorpe (2017) identified diel changes in downward velocities imparted by krill swarms, which they interpreted as an indication of greater levels of satiation sinking during night-time. Assuming that feeding increases as soon as light levels drop, a descent in swarm depth may result through the sinking of individuals within swarms and possibly a shrinkage in swarm size as individuals on the peripheries descend beyond the body of the swarm. It is also expected, however, that individuals return to the surface layers once digestion has taken place in order to resume feeding (Pearre, 2003). The mixed layer throughout much of the Scotia Sea is relatively deep, ranging between 40 m and 106 m, with euphotic depths that can reach beyond 80 m (Korb *et al.*, 2012) and deep chlorophyll-a maximum levels sometimes between 70 m and 90 m (Holm-Hansen *et al.*, 2004). Thus, a return to the surface may not be strictly necessary since krill swarms may be capable of feeding as successfully in their deeper night-time positions of around 80 m as in the shallower positions they occupy during the day.

Swarm-descriptor relationships

To consider the complexities of the individual patterns of diel variability in swarm-descriptor values, we invoked non-parametric multivariate analytical techniques. These analyses were carried out in two stages, the first establishing relationships between swarm descriptors and the second considering how these relationships changed on an hourly basis over the diel cycle. At the first level, it was apparent that there were significant differences between certain pairs of parameters, with perimeter paired with area being significantly different to length paired with depth, and both these being significantly different to packing concentration paired with thickness. At the second level, what emerged was a pattern of clustering according to the four cardinal periods of the diel cycle, namely day-time, dusk, night-time, and dawn. In essence, time of day had a large effect on how each swarm descriptor related to its partner as well as to other swarm descriptors. In the day-time group, which contained by far the longest period of time (0600 to 0000 h GMT, a total of 18 h), the relationships remained similar to those established across the entire dataset. The structure of these relationships was nevertheless quite different at night-time as well as at dusk and dawn.

Further insight into how swarm-descriptor relationships alter over diel cycles was given by SIMPER analysis, which identified those swarm descriptors that are responsible for the greatest levels of dissimilarity between respective groups. Perimeter, area, and packing concentration were found to be the most dissimilar between the four cluster groups (day, dusk, night, and dawn). Specifically, the major response between the day-time and night-time groups was an alteration in swarm area and perimeter. Meanwhile, during both dusk and dawn, packing concentration appeared to make a major contribution to dissimilarity levels.

There appears to be two major changes regarding the day-to-night difference in the area-to-perimeter relationship. Firstly, both of these swarm descriptors become considerably smaller in the night-time group, being around 20% of average day-time values. Secondly, the relative relationship alters, with perimeter increasing in relation to area during the night.

Night-time swarms thus decrease in size and adopt an alternative shape compared to those typical of day-time.

The occurrence of smaller swarms during the night than during the day suggests that swarms break up into smaller units during night-time. The break up and dispersion of swarms during night-time has been previously reported by Everson (1982, 1983) in waters around South Georgia, while Zhou & Dorland (2004) reported that swarms in Crystal Sound, Antarctic Peninsula, were smaller during the night than during the day. The increased perimeter-to-area relationship indicates that either swarm shape has changed or the edge of the swarm has become more intricate (or rough). Shapes that increase perimeter relative to area generally involve elongation of one axis relative to another, but neither length nor thickness altered in a manner consistent with such a pattern and, in fact, length became shorter during the night. It thus appears that the swarm edge became rougher in night-time swarms. This could be in response to a relaxation of threat of predation, allowing individuals to aggregate more loosely and increasing roughness at the swarm edge, as modelled by Brierley & Cox (2010). Individuals may also be feeding more actively at night and performing satiation sinking (see above). Rougher perimeters may also result from individuals at the swarm edges increasing nearest neighbour distances to operate their feeding baskets.

The second-stage analysis also identified a significant crepuscular response, where swarm-descriptor values during dusk and dawn appeared to be very different to those during day and night. Probably the most dramatic change was in packing concentration which increased from average values of around 25 individuals m^{-3} during both day and night to values that were, on average, 75 and 150 individuals m^{-3} at dusk and dawn, respectively. One potential explanation is that the acoustic target strength of the krill changed between the different phases of the day as a result of changed orientation of the krill relative to the

echosouder. This was invoked by Everson (1982) in relation to an 8 dB difference between day-and-night values of a krill patch monitored continuously for five days. Demer & Hewitt (1995) considered changed orientation to be responsible for high densities which occurred a few hours after sunrise and shortly prior to sunset. How orientation changes at dusk and dawn to affect target strength nevertheless remains unknown.

The higher estimated packing concentrations during dusk and dawn may otherwise be an accurate reflection of smaller nearest-neighbour distances within krill swarms during those periods. Such behaviour is consistent with greater levels of predation threat (Olson *et al.*, 2013), which may occur during the intermediate light levels of the crepuscular periods. From a predator's perspective, intermediate light conditions are antipredation windows when light is sufficient for planktivorous fishes to locate prey but insufficient to render these fishes vulnerable to piscivores. For instance, in considering the interaction between the Arctic euphausiid *Thysanoessa inermis* (Krøyer, 1846), and the planktivorous fishes, the Norway pout *Trisopterus esmarkii* (Nilsson, 1855) and *Maurolicus muelleri* (Gmelin, 1789), Kaartvedt *et al.*, (1996) found that their relative vertical distributions changed across a front where levels of light attenuation changed abruptly. Planktivores were more likely to be found in the krill layers in the intermediate light levels on one side of the front, where they could presumably feed at less risk from their predators. Myctophid fishes are known to feed on Antarctic krill (Saunders *et al.*, 2015) and are themselves a major dietary item of penguins and seals (Cherel *et al.*, 2010), making crepuscular periods potentially key times for myctophids to feed on their prey. In turn, the antipredation response of krill may drive the more densely packed formations observed at these times.

Swarming and DVM as a dual strategy

The diel cycle of light is probably the most predictable environmental change that pelagic animals experience, yet there has been very little consensus between Antarctic-krill studies

about the diel response of these organisms (Everson, 1983, Morris & Ricketts, 1984, Godlewska, 1996). Here we considered whether a robust diel behavioural cycle could be revealed through assessing both DVM and swarming as part of a dual strategy in balancing the trade-off between predation threat and individual physiological needs. Our approach was to consider swarming through the inclusion of multiple variables measuring size, shape, and the concentration of individuals. The depth at which the swarm resides was not given special status but considered as just one further swarm descriptor that was added to the matrix of possible diel responses. The data suggested that krill behaviour varied over the course of the diel period, and that these changes in behaviour were reflected in a clear diel change in the ways in which the combination of these swarm descriptors related to each other. The analysis was also able to identify the swarm properties that varied the most to this diel response, with area, perimeter, and packing concentration being the most dissimilar between the four phases of diel cycle. Although a diel change in depth was apparent, with swarms appearing to be shallower during the day than at night, its total range was rather small (around 40 m) and the day-time depth showed considerable variability. DVM made only a minor contribution to the repertoire of krill swarm behaviour over the diel cycle. As an overall strategy, it thus appears that Antarctic krill within swarms exhibit a distinct diel response that is dominated by the swarm size, the roughness of the swarm-edge, and how regularly they are organised within the swarm. Depth can often be highly variable and appears to be only a secondary contributor to the diel response.

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Table 1. Swarm descriptors with the greatest percentage contributions to average (SD) dissimilarity between respective time-period groups. The top two contributors to dissimilarity are shown for each time period group as well as *Depth*, which is included for comparative purposes.

Swarm descriptor	Average dissimilarity (SD)	Contribution %	Rank
Time-period group	Night vs Dawn		
Individuals m ⁻³	2.57 (0.47)	43.63	1 st
Area	1.51 (0.65)	25.55	2 nd
Depth	0.49 (0.75)	8.35	4 th
	Night vs Day		
Area	3.23 (0.25)	38.11	1 st
Perimeter	2.82 (0.25)	33.32	2 nd
Depth	0.57 (0.76)	6.74	5 th
	Dawn vs Day		
Area	3.05 (0.25)	32.57	1 st
Perimeter	2.60 (0.23)	27.79	2 nd
Depth	0.41 (0.65)	4.33	5 th
	Night vs Dawn		
Area	1.63 (0.48)	26.12	1 st
Individuals m ⁻³	1.62 (0.49)	25.93	2 nd
Depth	0.65 (0.82)	10.37	5 th
	Dawn vs Dusk		
Individuals m ⁻³	2.69 (0.53)	39.14	1 st
Area	1.63 (0.51)	23.65	2 nd
Depth	1.35 (0.74)	7.14	5 th
	Day vs Dusk		
Area	3.34 (0.26)	34.51	1 st
Perimeter	3.27 (0.28)	33.73	2 nd
Depth	0.33 (0.62)	3.38	5 th

Table 2. Average (95% CI) values for swarm descriptors in each of the 4 time-period groups.

Time-period groups	Number of swarms	Depth (m)	Length (m)	Thickness (m)	Perimeter (m)	Area (m ²)	Individuals m ⁻³
Night	190	79.87 (8.41)	46.24 (4.94)	5.65 (0.67)	217.40 (36.98)	103.60 (24.74)	32.49 (18.13)
Dawn	58	64.58 (12.88)	42.06 (5.04)	6.63 (1.30)	199.01 (39.25)	127.78 (45.75)	158.63 (109.92)
Daytime	3779	38.37 (0.87)	107.94 (14.50)	6.62 (0.23)	717.01 (155.08)	540.28 (146.79)	26.09 (2.16)
Dusk	103	45.21 (8.18)	76.88 (31.70)	4.64 (0.72)	263.45 (108.74)	128.72 (71.10)	77.07 (34.60)

Figure legends

Figure 1. Cruise track along which swarm identification was performed. The locations of swarms of *Euphausia superba* used in our analyses are marked with circles. Bathymetry is shaded in 1000 m intervals. The mean sea ice edge during January and February 2003 is marked (dashed line); SG is South Georgia, AP, Antarctic Peninsula

Figure 2. Schematic diagram of the second-stage multivariate analysis procedure, following Clarke *et al.*, (2006). The first stage considers the dissimilarity between swarm descriptors across all time periods. The second-stage analysis produces an nMDS plot that summarises the concordance in pattern of time periods with similar relationships between swarm descriptors.

Figure 3. Scatter plots of each of the swarm-descriptor variables against each other. Swarm-descriptor data have been pre-treated with a fourth root transformation.

Figure 4. Hierarchical cluster analysis of swarm-descriptor variables over the entire datasets of swarms, using group average linkage. Red lines indicate significant linkages in the data structure, as determined by a SIMPROF test (Primer version 7.0.11).

Figure 5. Non-metric multi-dimensional scaling (nMDS) on swarm-descriptor variables over the entire dataset of swarms using a Kruskal fit formula to minimise stress in the projections. The nMDS is overlaid by ellipsoids representing significant linkages in the data structure identified by a SIMPROF test (Primer version 7.0.11).

Figure 6. Non-metric multi-dimensional scaling (nMDS) of a second-stage analysis (Clarke *et al.*, 2006) formulated within Primer (version 7.0.11) on swarm descriptor variables split into hourly intervals and each analysed to determine resemblance matrices. A Kruskal fit formula was used to minimise stress in the projections. The nMDS represents a subsequent analysis of these matrices, based on the generation of a further resemblance matrix

considering levels of similarity between each hourly interval. The plot is superimposed by ellipsoids which represent the level of correlation separating the main clusters in an accompanying hierarchical cluster analysis (87%). Numbers refer to hourly intervals, which are in GMT. Local noon was 1500 h, local midnight 0300 h.

Figure 7. Non-metric multi-dimensional scaling (nMDS) of swarm-descriptor variables using a Kruskal fit formula to minimise stress in the projections. The original data set was split into four time-period groups based on the outcome of the second-stage analysis, namely day-time (0600–0000 h), dusk (0100 h), night-time (0200–0400 h), and dawn (0500 h). Each of the nMDS plots is superimposed by ellipsoids representing significant linkages in the data structure identified by a SIMPROF test (Primer version 7.0.11).

Figure 8. Mean and 95% confidence intervals of the swarm descriptors for swarms occurring within each time-period group.

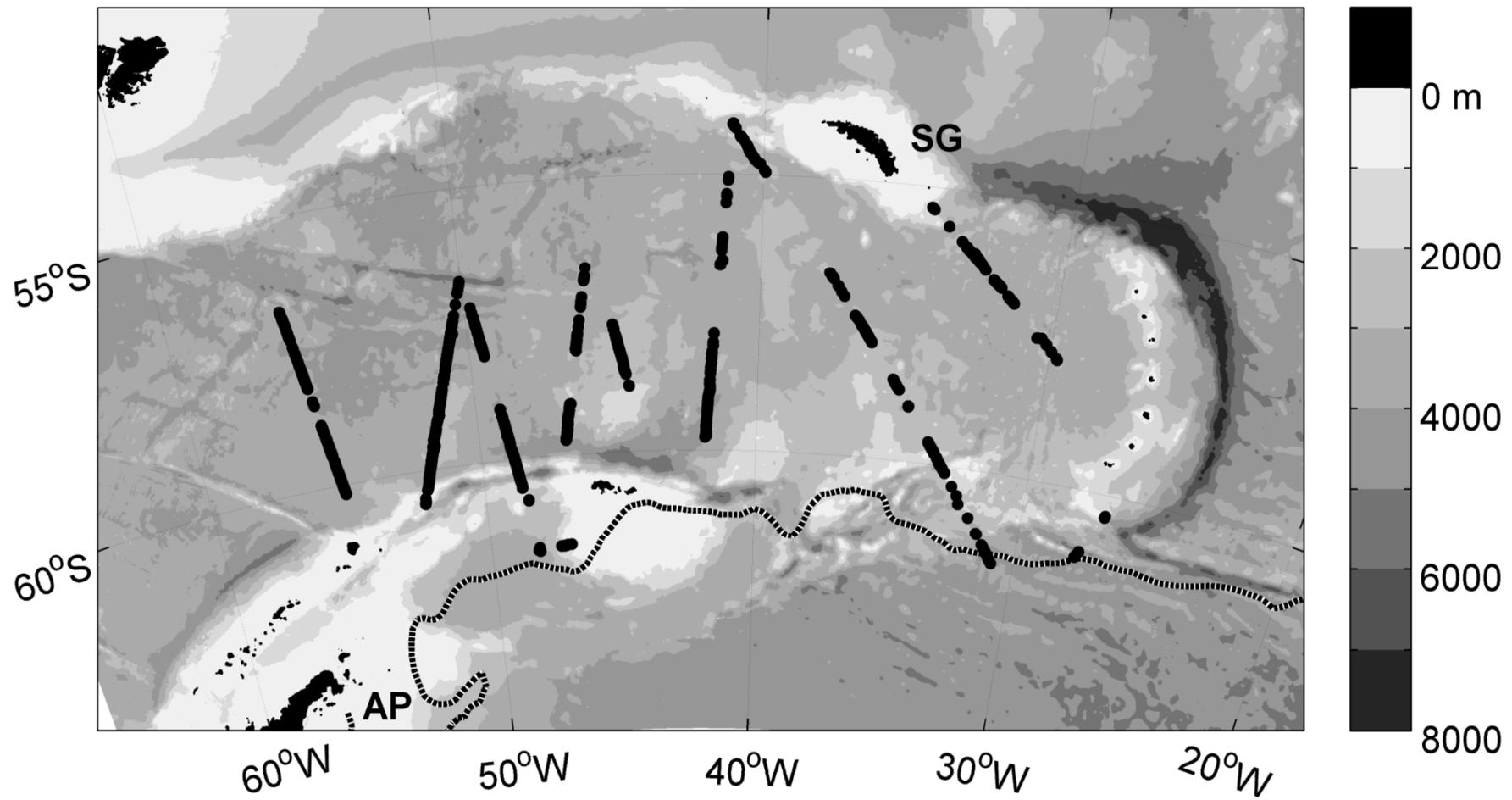


Fig. 1

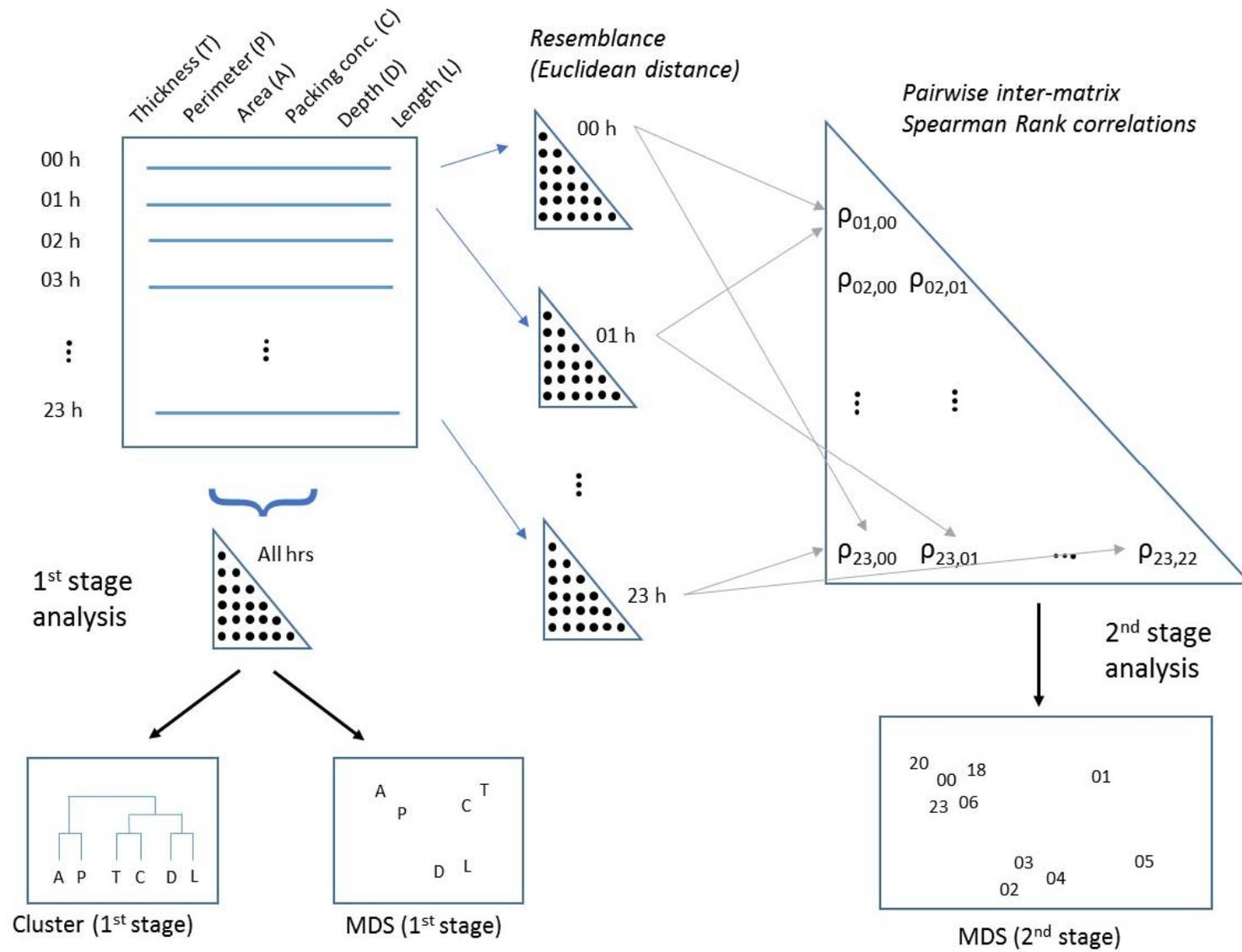


Fig. 2

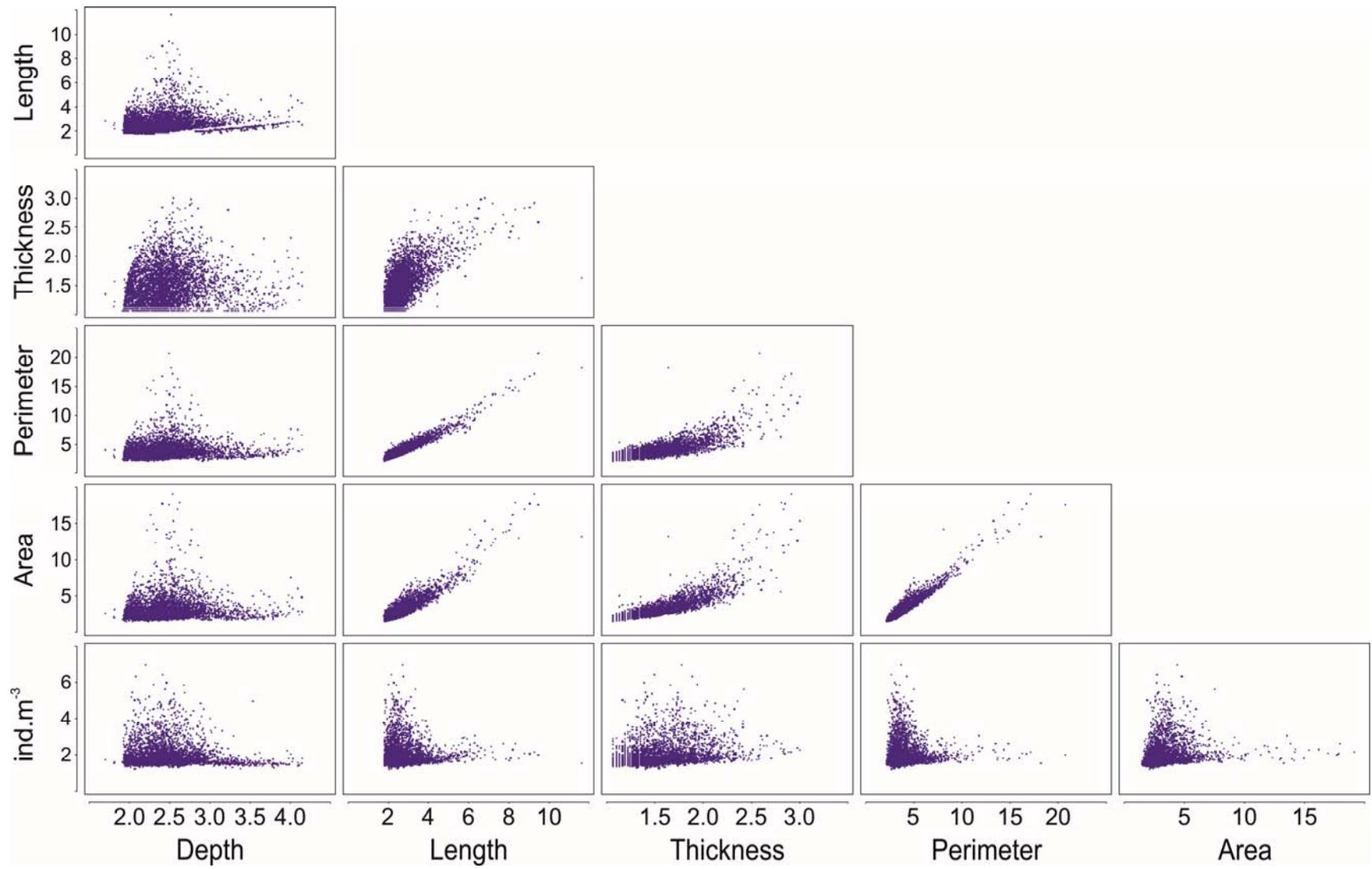


Fig. 3

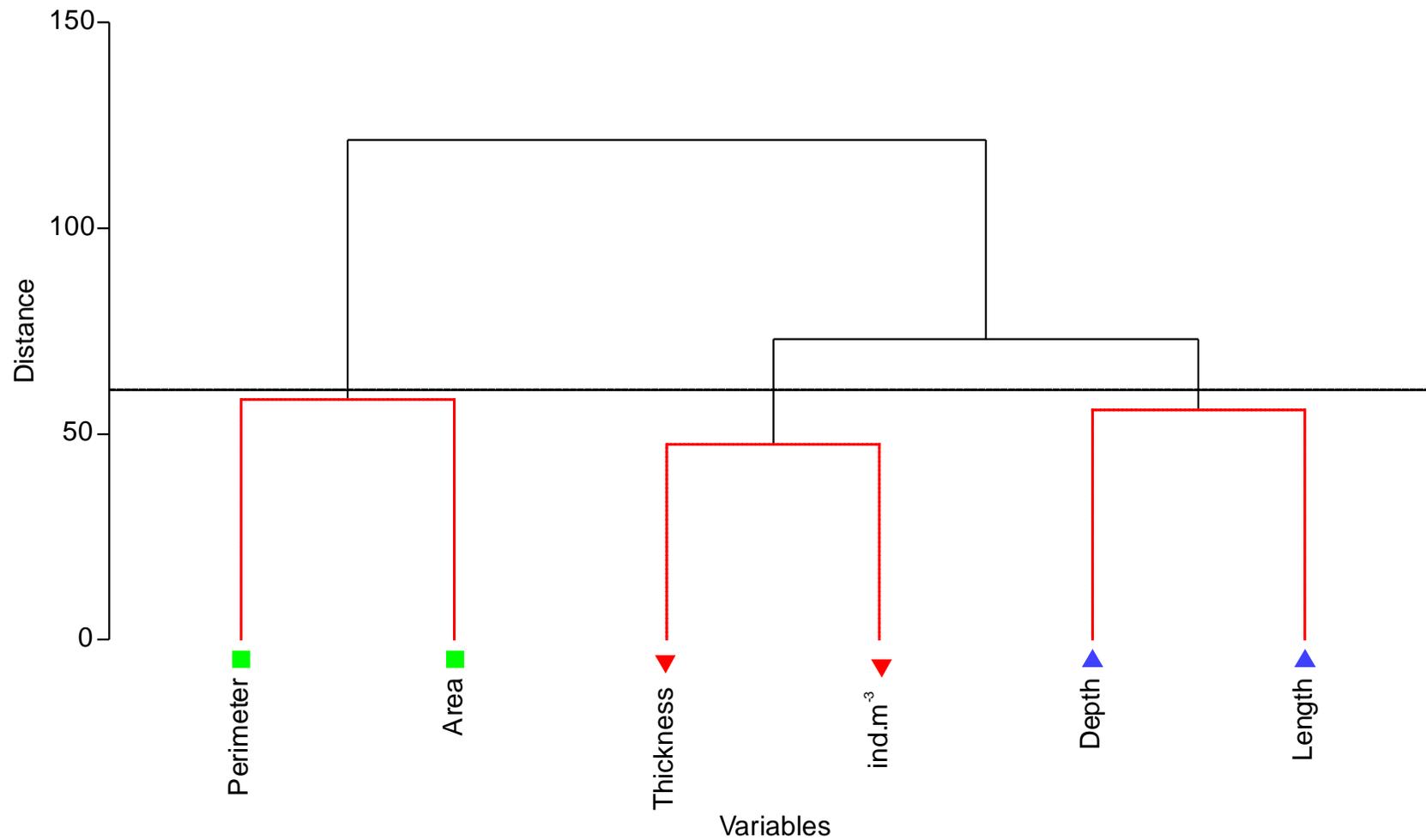


Fig. 4

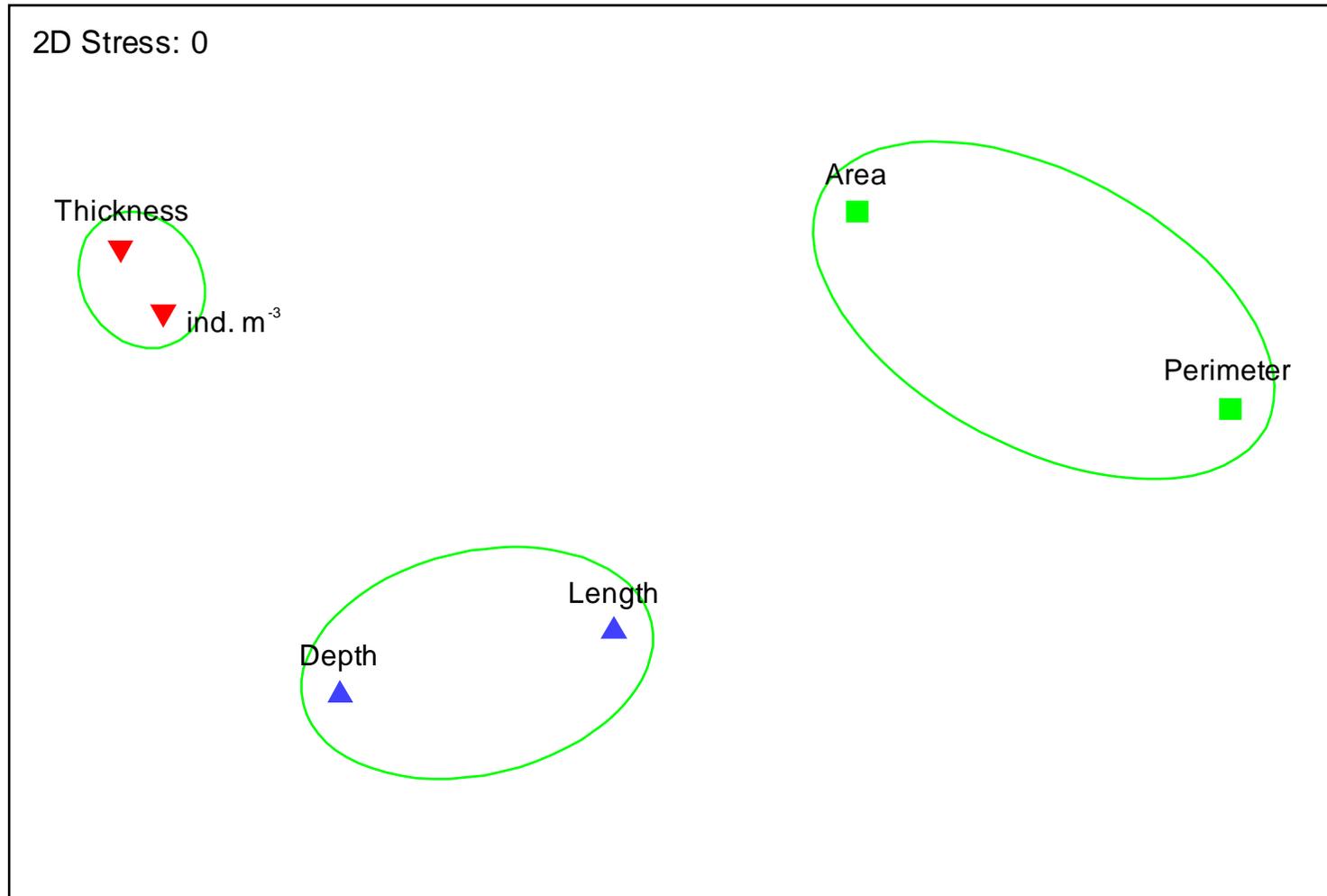


Fig. 5

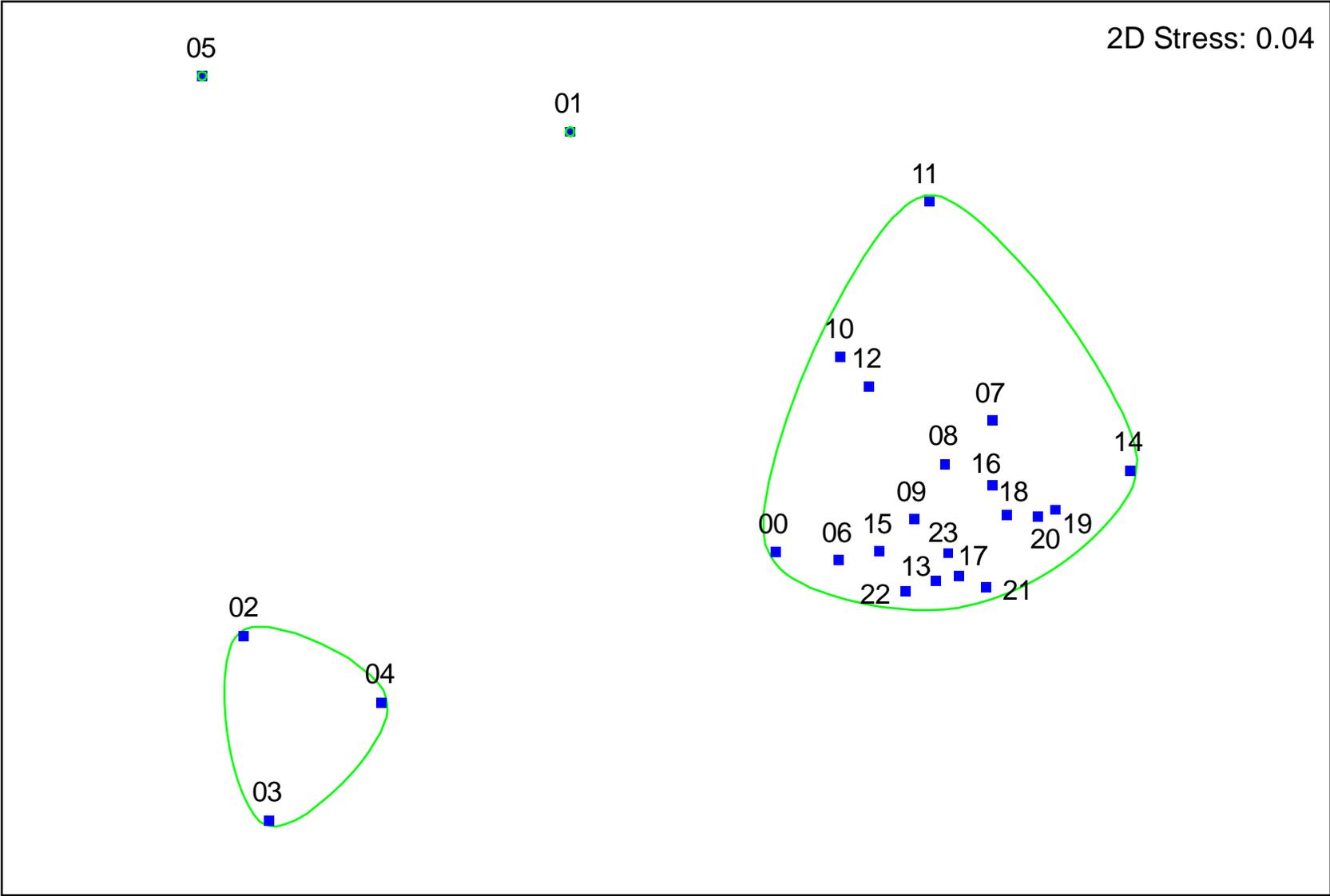


Fig. 6

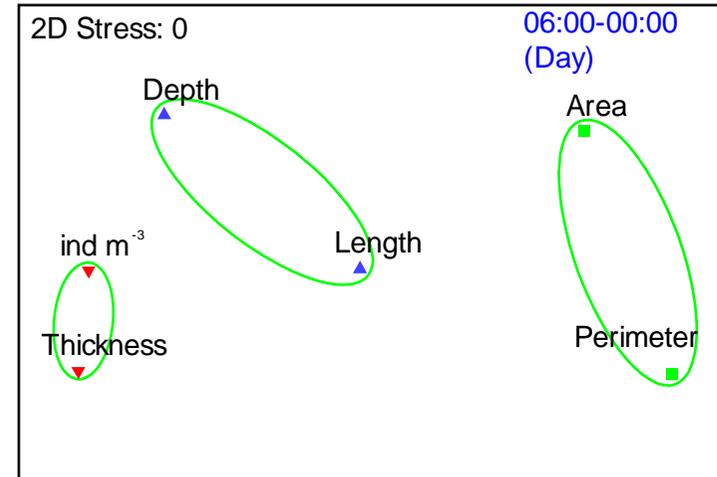
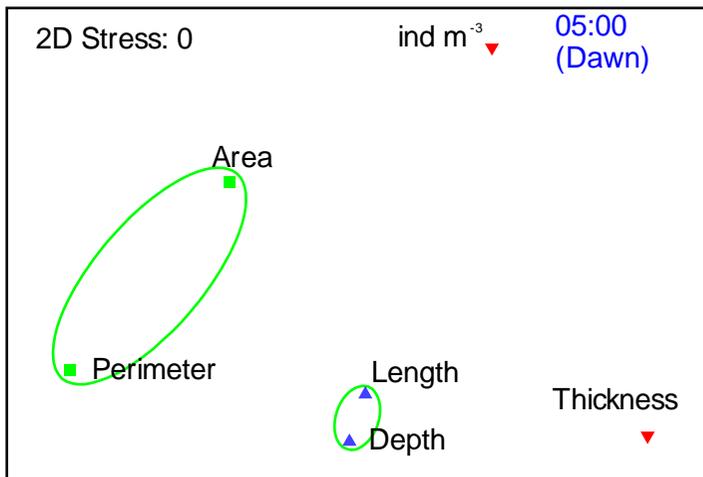
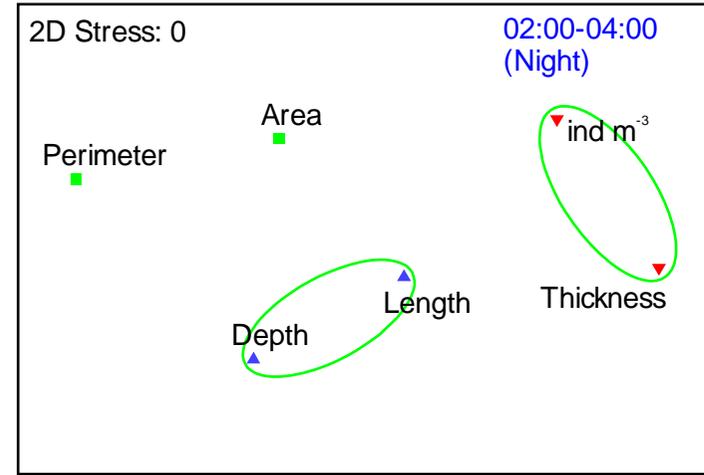
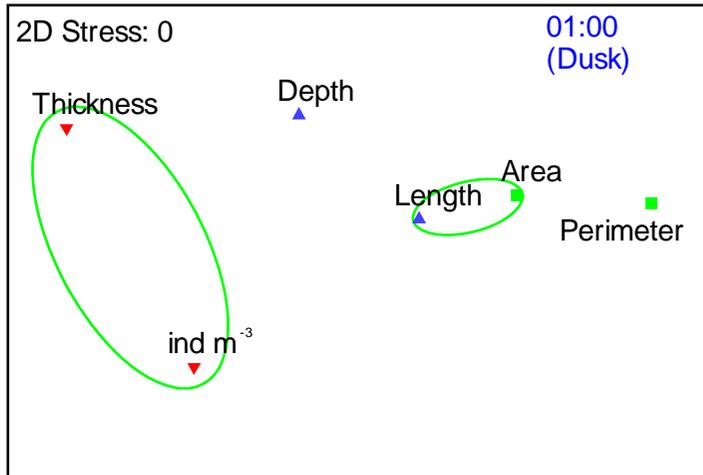


Fig. 7

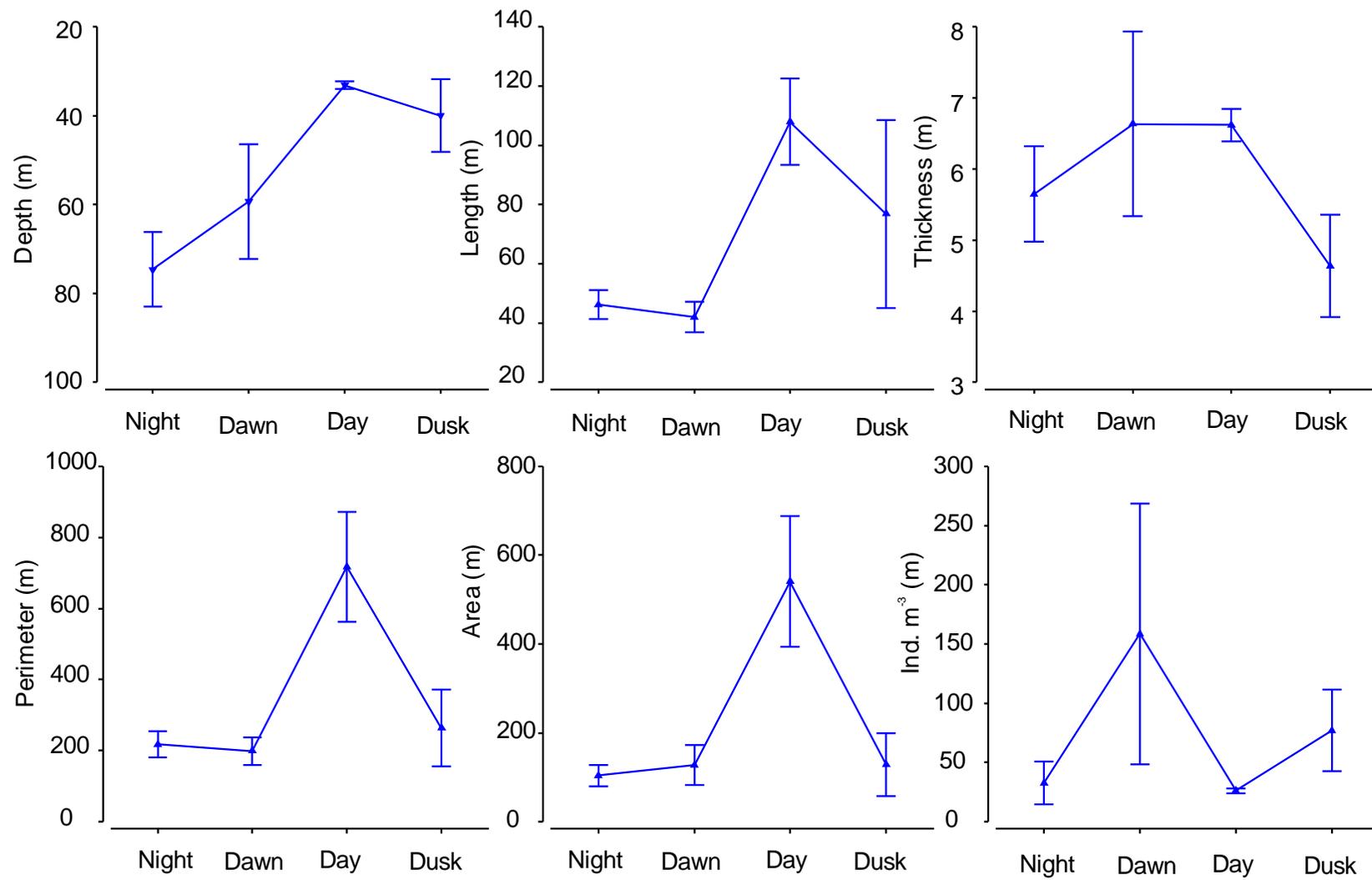


Fig. 8