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Classifying and combining herd surface activities and individual dive profiles to identify summer behaviours of beluga from the St. Lawrence Estuary, Canada

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ABSTRACT: Studies of the behaviour of diving animals usually focus on either individual dives or surface group activities, but these complementary observations are seldom combined in the same study. We here study the summer (June-October) behaviour of St. Lawrence Estuary belugas (*Delphinapterus leucas* (Pallas, 1776)) by combining fine-scale individual diving data from 27 time-depth-speed recorder deployments (conducted in 2002-2005) with surface activity data from 1413 focal herd follows (conducted in 1991-2012). We classified 6312 dives into seven dive types based on shape and swim speed. Dives were then combined into five bout types, including three pelagic, one benthic and one near-surface. We classified surface activities of herds into six clusters, differentiated primarily by their associated movement patterns (milling or directional) and further by herd structure and dispersion and occurrence of acrobatic surface events. Finally, we used herd focal follows conducted while tracking an individual beluga, to relate dive and bout types to surface activities. Results indicate that milling at the surface was more frequently related to benthic dives and potentially associated with behaviours such as benthic foraging, resting, socializing, and care of young. Directional surface movements were more frequently associated with pelagic dives likely used during pelagic foraging, exploration and travelling.

Key Words : Behaviour • St. Lawrence beluga • Dive classification • Surface activities •

Delphinapterus leucas

INTRODUCTION

A first step in studying behaviour often consists of defining large functional categories of behaviour or activity states (such as foraging, socializing, resting and travelling) which can then be associated with other ecological factors (Altmann 1974; Huntingford 1984; Janik 1999). For cryptic and wide-ranging species, behaviour classification is often based on movement patterns, either observed or inferred from telemetry data (e.g. Bailey and Thompson 2006; Jonsen et al. 2007), or on indicators, such as dive patterns, obtained using data-logging technologies (Ropert-Coudert et al. 2009). In the case of diving animals, the definition of behavioural classes is particularly challenging because they exhibit only a small fraction of their behavioural repertoire at the surface (Slooten 1994; Boyd et al. 2010).

The development of bio-logging technologies and animal-borne tags has enabled the remote measurement of surface and sub-surface behaviour at fine spatial and temporal scales (Mann 1999; Ropert-Coudert et al. 2009). While early biologgers documented only depth changes (Kooyman 1981; Schreer et al. 2001), the availability of other sensors, such as velocimeters (Lesage et al. 1999b; Doniol-Valcroze et al. 2011), thermometers (Lesage et al. 1999b), accelerometers, magnetometers (Fletcher et al. 1996; Burgess et al. 1998; Johnson and Tyack 2003; Goldbogen et al. 2006) and video-cameras (Marshall 1998), has furthered our understanding of the underwater movement patterns and behaviours of diving animals.

Logistic challenges and costs often limit sample size and thus our capacity to infer patterns at the level of populations from findings obtained from tracking a few individuals (Mann 1999; Whitehead 2004). Surface observations from focal group

follows (e.g. herds or pods) offer an alternative to study behaviour and can be particularly powerful in answering a variety of questions when applied in the context of long-term population monitoring. In this context of focal group follows, surface observations can be classified into different behaviours or surface activities by using metrics related to group geometry, size and composition, swimming patterns and dynamism, as well as information on individual movement characteristics within these groups (e.g. Lusseau 2003; Bearzi 2005; Canadas and Hammond 2006; Garaffo et al. 2007), or in exceptional cases, direct evidence of a behavioural event (e.g. prey capture).

In general, classification schemes are developed based on inferences about the relationship between observed surface activities and presumed underwater behaviours. While behavioural studies relying on focal group follows often have less spatial and temporal resolution compared to studies relying on individual tracking, they have the advantage of sampling a greater proportion of a population, a greater diversity of behaviours and of being less prone to sampling biases linked to selection of individuals (Mann 1999; Whitehead 2004). For social species, following groups also allows for measuring social behaviour at the relevant social unit level, often missed by individual tracking (Whitehead 2004).

Traditional surface focal follows can however be enriched by the use of technology by improving our understanding of the relationship between surface and underwater behaviours of animals. When recorded simultaneously, metrics describing the surface activities of a group and the diving behaviour of an individual within the group can enhance our definitions of surface behavioural classes. Conversely, surface activity information of a tagged individual and its group can shed light on the at-depth behaviour

and reduce the uncertainty associated with dive type definitions (Mann 1999; Shamoun-Baranes et al. 2012). Coupling of fine-scale measurements of underwater diving patterns of individuals with the classification of surface activities of their groups (or herds and pods) have however only rarely been attempted (but see Visser et al. 2014) and, not in the context of long-term population studies.

In this study, we illustrate the usefulness of combining fine-scale diving data from a small number of remotely tracked individuals with coarser data on surface activities obtained using group follow protocols in defining behavioural classes, using data collected from St. Lawrence Estuary (SLE) beluga (*Delphinapterus leucas* (Pallas, 1776)). Specifically, individual tracking documenting the diving behaviour of 27 belugas using bio-logging techniques and direct observation of their surface behaviour and that of their herd, are combined with a long-term dataset of over 1400 focal herd follows, documenting surface activities and movement patterns, to classify beluga behaviour. We hypothesized that herd surface movement patterns, configuration and structure varies according to the underwater behaviour of the individuals composing the herd. Hence, we predict that there will be a relationship between dive profiles of tracked individuals and herd surface characteristics.

MATERIALS AND METHODS

1. Classification of herd surface activities

Data collection

We followed over 2500 beluga (*Delphinaterus leucas*) herds between June and October of 1989–2012 within the summer distribution of the population. During this period, important life processes and behaviours, including socializing, mating, feeding, calving and nursing of neonates, and care of young are known to take place (Michaud 2005; Mosnier et al. 2010). One research team acquired most of the data, but a second team, trained by the first team, contributed to sampling in 2003–2005 and 2009–2010. We selected survey areas according to weather conditions, while avoiding resampling areas covered the previous days. Survey areas covered the various sectors of a large portion of the population summer distribution, and a broad range of habitats, but were neither randomly nor systematically sampled for beluga herds. The study area encompassed the full extent of the summer distribution (ca. 4,845 km²) before 1996, but was limited to its central portion from 1996–2012 as a result of a concurrent study on social networking (Fig. 1). One or two observers compiled observations aboard a 9–10 m vessel, from a platform located 4-m above water.

We defined a herd as an assemblage of groups in which inter-group distances were small compared with the extent of the herd, generally within a few tens or hundred meters of each other. Groups were composed of animals swimming within one body length of each other, generally in a coordinated fashion. We initiated a *herd follow* by collecting preliminary information on herd composition and size while maintaining a distance of 300–500 m from the herd. After 15 min, the research vessel proceeded into the herd at slow cruising speed (< 5 knots). We described herd characteristics in a systematic way every 30 min through *summary surveys*, which comprised information on: herd size, type (adult: white individuals only; adult-grey: white individuals, and grey colored sub-

adults and young; adult-grey-calf: white individuals, grey colored sub-adults and young, and young of the year) and radius of the herd spatial extent, geometrical structure (form, structure, and dispersion), predominant movement patterns (hereafter PMP), swimming dynamism, acrobatic surface events (breach, body-rolling, tail or pectoral slapping, spitting, fish chasing, etc.), and surface vocalizations (Table 1). We also noted the GPS position of the research vessel and prevailing weather conditions. Herd follows lasted generally 3h at the most (~6 summary surveys), but duration varied depending on sampling protocols (e.g., photo-identification, biopsy sampling, tagging) and prevailing conditions.

Cluster analysis

We used *summary survey* data in a cluster analysis to classify and characterize the herd's surface activities (hereafter SA). We selected seven variables for this analysis, and retained *summary surveys* for which all variables were recorded (Table 1). Variables were ordinal, nominal, or asymmetrically nominal, and were introduced into the cluster analysis by first calculating a distance matrix using PROC Distance in the SAS[®] software and the DGOWER method, which allows calculating a dissimilarity matrix from different variable types. We used this matrix as the input to a hierarchical clustering using PROC Cluster (SAS) and the Ward method, while excluding 10% of the observations through the TRIM option to remove outliers to which this analysis is sensitive (Hair et al. 1995). We chose the best cluster solution based on the concordance between the pseudo F and pseudo T criteria (SAS Institute 1999). Multivariate analyses were conducted using

SAS[®]; all other statistical analyses were conducted in R (R Development Core Team, 2013).

We identified unique characteristics of the identified clusters (i.e., any unique combination of variables found in only one cluster type) to post-classify *summary surveys* not included in the analysis due to missing data, but for which sufficient information (i.e. presenting one of the unique variable combination) was available for an *a posteriori* classification. We examined further the relationship between herd characteristics and SA clusters using three additional variables: herd radius, herd size and herd type. Differences in herd radius (log) and size (log) among SA clusters were tested using one-way ANOVA's and post-hoc Tukey's test. Conformity to ANOVA assumptions of absence of outliers, homoscedasticity and normality of residuals were investigated through visual inspection of residuals histograms, QQ plot and outlier routine detection in R. We investigated differences in the relative frequency of use of the various SA among herd types using a Chi-square test, with a post-hoc evaluation of the contribution of individual frequencies of herd types per SA to significance (package *polytomous* in R).

2. Classification of radio-tracked individual diving behaviour

Data collection

From 2001 to 2005, we deployed archival tags on 45 individual beluga, sampled from the central portion of the summer population distribution, where all gender and age classes are encountered (Fig. 1, see Michaud 1993). Tags included a time-depth-velocity recorder (TDVR, Mk8, Wildlife Computers Inc., Redmond, USA) and a 300 g radio transmitter (Telonics, 932 E. Impala Avenue Mesa, AZ, USA). We tagged and tracked

belugas from a small vessel equipped with a six-element Yagi antenna. Tags were attached to belugas with a suction cup (Hooker and Baird 1999) using either a cross-bow or a 3-m pole. A magnesium cap, designed to corrode and release suction after 4-6 h, served as a mechanism to retrieve tags from the whales. TDVRs recorded time, depth (± 0.25 m), and swim speed ($\pm 0.05 \text{ m}\cdot\text{s}^{-1}$) every second, from which other dive characteristics were extracted for analysis (Appendix A).

Principal Components and Cluster analyses

We classified dives using a combination of multivariate data analysis following the method developed by Lesage et al. (1999b). In summary, a principal components analysis (PCA) with a VARIMAX rotation first reduced the number of variables to a smaller set of uncorrelated factors or principal components (PCs). This prevented the over-weighting effect of incorporating collinear variables on the similarity index used in cluster analysis (Hair et al. 1995). Factor scores were then introduced into a hierarchical complete linkage cluster analysis ran on a random sample of 1000 dives to identify the best cluster solution describing the dataset and to obtain the corresponding cluster centroid values. Using these cluster centroids as seeds, we finned-tuned the classification using a non-hierarchical K-means clustering procedure. Details of the analysis can be found in Appendix A.

To interpret the potential function of dives, we used surface tracking data to evaluate the distance of the dives to the sea floor bottom. The details of the individual surface tracking and data manipulation can be found in Lemieux Lefebvre et al. (2012). Briefly, surface tracks were interpolated linearly (i.e. not considering underwater

horizontal movements) to obtain a beluga position every second to match dive records. Proportional distances of the sea floor relative to diving depth were calculated for each interpolated positions using bathymetric data at a 5 m resolution corrected for tidal water levels (Canadian Hydrographic Service, Fisheries and Oceans Canada). The percentage of dives within a 3 m reach of the sea floor was also calculated for each dive type.

Dive bout analyses

Dives occur in sequences, with dives that occur in rapid succession being generally more similar in characteristics compared those occurring after longer intervals. These series of dives, generally referred to as *bouts* (Mori et al. 2001), are often used to define distinct behavioural units (Luque and Guinet 2007). Given the expectation that beluga engage in multiple distinct behaviours over the period of tag deployment, we used the similarity in dive characteristics among successive dives (Boyd et al. 1994) to identify distinct dive bouts and a cluster analysis to classify bouts into distinct bout types. Further details of the dive bout analyses are presented in Appendix B.

We investigated the association between dive types and bout types using a Chi-square test, and post-hoc evaluation to identify dive types that differed in frequency among bout types. Each bout type was also described based on its duration and its dive characteristics, including general dive shape, diving velocity and dive depth relative to the sea floor.

3. Association between individual dives and herd surface activities

We used *summary surveys* of herd surface characteristics obtained while tracking tagged individuals to link herd SA with the tracked individual diving behaviour. All individual dives occurring during the period described by a classified *summary survey* were associated to its corresponding SA. The bout type that was most characteristic (i.e. longer lasting) of the period covered by a *summary survey* was also associated to the corresponding SA. We then used pairwise Fisher exact tests to compare the frequency distribution of the various dive types and bout types among SA. We used standardized Pearson's residuals to interpret unique cell contribution to observed differences, as unique frequency contribution to significance cannot be obtained for Fisher exact tests (Agresti 2013). All tests were made in R and the Benjamini-Hochberg correction was used to adjust p-values for multiple tests.

RESULTS

1. Classification of herd surface activities

A total of 3585 summary surveys, obtained from 1413 beluga (*Delphinapterus leucas*) herds followed between June and mid-October of 1991 to 2012, were retained for the analysis (Fig. 1). This represents 40% of all the summary surveys (8799) conducted during this period. Sufficient information for *a posteriori* classification was available for 287 summary surveys, corresponding to 8% of those retained for the analysis. The descriptors of herd surface characteristics were relatively uniformly distributed among categories for most variables, but were closer to a Poisson distribution for the 'form' and 'structure' variables, which were categorized as *broken* and *uniform*, in 94% and 88% of the cases, respectively (Table 1). Approximately half of the herds had a *directional* PMP,

a *moderate* dynamism and a relatively *tight* configuration, with infrequent surface events and vocalizations (Table 1).

Pseudo F and t^2 criteria indicate that herd surface characteristics are best described using 6 SA types (S1²). SA were mainly differentiated by their associated predominant movement patterns, but also their structure, degree of dispersion and the occurrence of surface events and vocalizations (Table 2). Herd type (Chi-square test: $X^2 = 101.76$, $df = 10$, $p < 0.0001$), size ($F = 25.33$, $df = 5$, $p < 0.001$) and radius ($F = 147.1$, $df = 5$, $p < 0.001$) also varied significantly among SA (Table 2).

Milling SA

Cluster 1 (hereafter Milling SA) and 3 (hereafter Milling-E SA) both included herds with a *milling* PMP. Herds involved in Milling-E SA regularly displayed surface events and surface vocalizations (Table 2), were tightly dispersed and were generally of a larger size than those involved in other SA (Table 2). Herds during Milling generally presented a reduced dynamism (low to moderate), included more frequently calves (and more rarely herds of adults only) and were distributed over a small radius.

Mixed SA

Cluster 2 represented herds that had two main PMP, *milling* or *directional*, but herds exclusively showing a *clustered* group structure, as opposed to a uniform group distribution within the herd (hereafter Mixed SA). Herds involved in Mixed SA were also

² Supplementary Figure S1 : Dendrogram of the cluster analysis of herd surface activities.

generally of a smaller size than herds involved in other SA, but were distributed over the largest mean radius (617 m).

Directional SA

Cluster 5 was composed of herds that exclusively displayed a *multi-directional* PMP (hereafter Directional-M SA), combined generally with a reduced dynamism (low to moderate), but no other singular characteristics (Table 2).

Cluster 4 and cluster 6 were composed of herd SA that had a *directional* PMP; herds in cluster 4 (hereafter Directional-D SA) were generally moderately or highly dispersed over a large mean radius, whereas herds in cluster 6 (hereafter Directional-T SA) had a tighter dispersion and the smallest mean radius (190 m). The Directional-T SA was also usually characterized by a higher dynamism, occasional *front* or *line* forms and accompanied by surface events and vocalizations (Table 2). In proportion, herds composed solely of adults were more often involved in Directional-D and less so in Directional-T, whereas herds with calves were more frequently involved in Directional-T than in Directional-D.

2. Classification of radio-tracked individual diving behaviour

Forty-five VHF tags were successfully attached to beluga but only forty-four were retrieved after deployment. Of these, 32 provided data on individual and herd surface behaviour, but five failed to record diving data. The remaining 27 follows provided 6,312 true dives (i.e. non-respiratory), of which a third (2,204 dives) had valid velocity data. Beluga reached the maximum depth of the St. Lawrence Estuary (335 m), and dove for a

maximum of 1149 s (19.2 min). However, median maximum depth and duration were much lower at 9 m (mean = 16 m, SD = 22 m) and 74 s (mean = 130 s, SD = 136 s), respectively. Approximately 15% of the 3125 dives with estimates of their distance relative to the sea floor reached depths within 3 m from it.

Hierarchical complete linkage cluster analyses ran on two sets of random sample of 1000 dives, including or not velocity variables, both indicated a 7 cluster solution to describe individual dives characteristics (Appendix A, S1³).

Dive types

Square dives

Two different types of square dives were identified (type 5, 7). The U-shape of these dives was inferred from the low ratios of maximum depth to dive duration, high ratios of bottom time to dive duration and high ratios of maximum depth to bottom time. Dives in cluster 5 were long, relatively deep and comprised wiggles (hereafter square-W dives) (Table 3). During these dives, 52% of the time was spent in the bottom phase, 18% in the descent phase, and 30% in the ascent phase. These square-W dives were performed in mid-water (63% of the water column), with about a third (30%) reaching the bottom.

Dives in cluster 7 were also square in shape, had relatively long duration and bottom phase, but contained no wiggles (hereafter square-U dives). They had the highest ratio of bottom time to dive duration, and of bottom time to maximum depth (Table 3). During these dives, 73% of the time was spent in the bottom phase, 13% in the descent phase, and 14% in the ascent phase. Similar to square-W dives, square-U dives were performed in mid-water (53% of the water column), and had the highest proportion of the dives (33%) reaching the bottom.

³ Supplementary Figure S2 : Dendrogram of the cluster analysis of individual diving profiles.

V shaped dives

Three different types of V shaped dives were identified (cluster 1, 3 and 4), i.e. dives generally characterized by high ratio of maximum depth to dive duration, intermediate ratio of bottom time to dive duration, and low ratio of maximum depth to bottom time (Table 3). Type 4 dives were relatively shallow and short v-Deep dives, only slightly deeper and longer than type 1 dives, characterized by a fast ascent rate (hereafter v-Fast dives), making them slightly skewed to the left. Some of the dives had a bottom phase longer than for dives of type 1 and 3, making dives in this category intermediate in characteristics between v-Deep and square dives (Table 3). During these dives, 37% of the time was spent in the bottom phase, 36% in the descent phase, and 26% in the ascent phase. These v-Fast dives rarely occurred near the bottom (5.5%).

Type 1 dives were short and shallow (hereafter v-Slow dives), and were characterized by the lowest average dive duration, maximum depth and bottom time (Table 3). They were also generally slightly skewed to the right, with a slower ascent than descent rate. During these dives, 35% of the time was spent in the bottom phase, 24% in the descent phase, and 41% in the ascent phase. Being generally shallow, only 3% of these dives were made within a 3 m reach from the sea floor.

Type 3 dives were deep V dives with fast ascent and descent rates (hereafter v-Deep dives). They were characterized by the highest average depth, descent rate, ascent rate, ratio of maximum depth to dive duration, and the lowest ratio of bottom time to maximum depth (Table 3). During these dives, 45% of the time was spent in the bottom phase, 26% in the descent phase, and 29% in the ascent phase. These dives occasionally

reached the bottom (16%) but were performed on average in mid-water (i.e. mean maximum depth corresponding to 45% of the full water column).

Trapezoidal dives

Two dive types had a trapezoidal shape (type **2**, **6**). Dives in this category were characterized by unequal rates of ascent and descent, intermediate ratios of maximum depth to dive duration, low ratios of bottom time to dive duration, and intermediate ratios of maximum depth to bottom time. Type 2 dives were relatively long and deep with the longest ascent rate making them strongly skewed to the right (hereafter skew-R dives). During these dives, 30% of the time was spent in the bottom phase, 19% in the descent phase, and 51% in the ascent phase (Table 3). These dives were also performed in mid water (46 % of the water column) but rarely (13%) reached the bottom.

Type **6** dives were skewed to the left due to slow descent rates (hereafter skew-L dives), with the least amount of time spent in the bottom phase relative to dive duration (Table 3). During these dives, 25% of the time was spent in the bottom phase, 53% in the descent phase, and 22% in the ascent phase. Similar to skew-R dives, skew-L dives were made in mid-water (37% of the water column), reaching the sea floor in 14% of the instances.

Frequency of use of dive types

The most common and least common dive types were v-Slow and v-Deep dives, with a frequency of 22% and 10%, respectively. The other dive types were similarly frequent, varying in frequency from 12 % to 16 %. However, when accounting for dive

duration, belugas spent 30% of their time performing square-W dives, and 20% and 19% doing skew-R and square-U dives. Thus, the three dive types characterized by deeper depths and longer bottom times represented about 69% of the time budget of tracked individuals when considering non-respiratory dives. The three v-Deep shaped dive types accounted for 4% (v-Slow), 10% (v-Deep), and 4% (v-Fast) of the time budget spent diving, for a total of 18%. The remaining 13% of the diving time was spent performing skew-L dives.

Dive bouts

The classification of dives into bouts resulted in the identification of five clusters or bout types (S1⁴), which were all significantly different in the relative frequency of the various dive types (all $p < 0.001$; Fig. 2). Bout types fell into three general categories based on the depth and distance relative to the sea floor of their dives: three were mostly pelagic, one was mostly benthic and one was mostly near the surface (Table 4).

Near-surface bouts

Dives in cluster C bouts (hereafter Near-Surface) were generally short and shallow, with particularly slow ascent and descent rates, as well as low velocities. The v-Slow dives were the most frequent dive type performed during Near-Surface bouts, although skew-L dives were also more frequently performed during these than other bout types (Fig. 2). Dives in Near-Surface bouts were performed on average closer to the surface compared to dives performed during other bout types, and rarely (8%) to the

⁴Supplementary Figure S3 : Dendrogram of the cluster analysis of dive bouts.

bottom (Table 4). They represented the most frequent and shortest bout type, lasting on average 21 min (SD = 19 min).

Benthic bouts

Bouts in cluster D (hereafter Benthic) were intermediate in duration, and were comprised of dives with the longest mean bottom time and thus, were generally U shaped. Accordingly, square-U dives were significantly more frequent during these bouts than during any other bout types (Fig. 2). Dives performed during Benthic bouts were relatively shallow, but often reached the bottom (49% of dives with available measurements), and presented the highest ratio of mean distance to the bottom (69%) (Table 4).

Pelagic bouts

Bouts in cluster E (hereafter W-Pelagic) were comprised of generally long and deep dives of variable shapes, although square-W dives were particularly abundant in this bout type (Fig. 2). They were the second longest bout type, lasting on average 54 min (SD = 34 min; Table 4). Among pelagic bouts, this type was associated with the lowest number of dives occurring near the bottom, with only 10.5%.

Cluster A (hereafter Sk-Pelagic) bouts were the longest on average (mean = 57 min; SD = 51 min). They comprised dives that were relatively deep, but intermediate in other characteristics compared to other bout types, and that had faster descent than ascent rates (Table 4). Accordingly, skew-R dives were significantly more often associated with Sk-Pelagic bouts (Fig. 2) than with any other bout types, except type E (or W-Pelagic)

bouts. Square-W dives were also significantly more frequently performed as part of this bout type. Dives with valid velocity data occurring during Sk-Pelagic presented the second highest mean velocities in all three phases of the dive. Only 17% of the dives occurring during this bout type reached the sea floor.

Dives in cluster B bouts (hereafter V-Pelagic) had the highest mean ascent and descent rates and velocities, and presented the highest ratios of maximum depth/ dive duration, being relatively deep but of short duration (Table 4). Accordingly, they were frequently associated with v-Deep and v-Fast dives (Fig. 2). Only 13% of the dives occurring during this bout type reached the sea floor.

3. Association between individual dives and herd surface activities

Fisher exact tests revealed overall significant differences in the relative frequency of dive types (Table 5, Fig. 3) and bout types (Table 6, Fig. 4) among SA categories (both $p < 0.001$). Most SA differed significantly from one another in the relative frequency of their associated dive types, except for Milling vs. Mixed, and for Directional-D vs. Directional-M or Directional-T (Table 5). However, fewer significant differences in bout types frequency between each SA were found, probably due to smaller sample size. Only Milling and Milling-E differed significantly from Directional-M and Directional-T in their relative frequency of associated bout types (Table 6). A summary of the main characteristics of SA and of their main associations with different dive and bout types are presented in Table 7.

Milling-E

Of the summary surveys recorded during individual beluga VHF tracking, only four herds were classified as being involved in Milling-E. Despite this rare occurrence, this SA differed significantly from all others by being associated with a higher frequency of v-Fast (37%) and square-U (26%) dives (Table 5; Fig. 3). Three of the four diving bouts recorded in association with this surface activity were Benthic bouts (75%) and one was a W-Pelagic bout (25% ; Fig. 4).

Milling

During Milling, tagged beluga performed v-Slow (27%) and square-U (23%) dives more frequently, and skew-R (6%) and v-Deep (3%) dives more rarely (Fig. 3). Near-Surface (29%) and Benthic (43%) bouts also occurred more frequently in association with this surface activity (Fig. 4).

Mixed

Dive types performed by tagged individuals in herds displaying a Mixed surface activities were characterised by higher frequencies of v-Slow (26%) and square-U (19%) dives, and higher occurrence of skew-Pelagic (27%) and Benthic (36%) bouts (Fig. 4).

Directional-D

Directional-D surface activity was strongly associated with skew-R (17%) and v-Deep (16%) dives, although all dives types were fairly frequent during this SA (Fig. 3). No bout type was particularly more frequent or infrequent during this surface activity (Fig. 4).

Directional-M

In proportion, tagged whales in herds performing Directional-M surface activity used square-W (21%) and skew-L (12%) dives more often than during the other surface activities, and performed more frequently the three pelagic bout types (skew-Pelagic = 35%, V-Pelagic = 22%, and W-Pelagic = 35%) (Fig. 4).

Directional-T

Belugas among herds involved in Directional-T more frequently performed v-Slow dives (23%) and less frequently square-U dives (9%). V-Pelagic bouts (33%) and Near-Surface bouts (25%) also occurred more frequently during this SA, with no Benthic bouts (0%) being recorded (Fig. 4).

DISCUSSION

Most previous studies used predefined characteristics and classes to identify surface activities or behaviours during group follows in the field (Lusseau 2003; Canadas and Hammond 2006; Garaffo et al. 2007; Miller et al. 2010; Visser et al. 2011; Filby et al. 2013; Lunardi and Ferreira 2013). However, using an automated statistical approach to classifying surface activities is highly valuable when direct identification of behaviours in the field is challenging. Here, we provide a new rigorous and objective way of identifying key characteristics and their relative value in discriminating among behavioural states. Our results confirmed the importance of movement patterns for describing surface behavioural states in marine mammals (Lusseau 2003, 2004; Bearzi 2005; Miller et al.

2010; Degraati et al. 2013) with the PMP representing a driving factor in surface activities clustering (> 97% frequency for one PMP in 5 of the 6 SA clusters, Table 2).

However, other variables (occurrence of surface events and surface vocalisations, degree of dispersion, and structure) were important for further differentiating herds displaying similar PMP, but different surface activities (Table 2). Hence, considering only movement patterns to identify surface activities would likely have reduced the behavioural repertoire that can alternatively be identified using multiple metrics. On the other hand, two variables, form and dynamism, were not decisive in separating the identified SA clusters and both included categories that were rarely observed in the field throughout the years. This highlights the need to measure variables (and their categories) that are observed in the field more often than anecdotally.

Dives types identified in SLE belugas were generally similar to those identified in other diving animals. In diving animals, square dives with long bottom times are often considered foraging dives (Martin et al. 1998; Lesage et al. 1999b; Austin et al. 2006; Dragon et al. 2012). Square dives with wiggles are typically associated with foraging on pelagic (escaping) preys, with the wiggles resulting from depth adjustments during pursuit (Hochscheid et al. 1999; Schreer et al. 2001; Kuhn et al. 2009; Dragon et al. 2012). These W-dives are most likely also used for foraging by SLE beluga, as they represented the longest lasting dives and accounted for 16% of the dives of tracked individuals. Although most square-W-dives were pelagic dives, almost 30% still reached the sea floor, which could reflect active foraging on demersal fishes (Vladykov 1946) or depth adjustment to bathymetric features during benthic dives (Martin et al. 1998).

Square or U-dives without wiggles have often been related to benthic foraging that necessitate less variation in dive depth due to lesser mobility of benthic preys (Schreer et al. 2001). In SLE belugas, this category comprises the highest proportion of dives attaining the sea floor, supporting that one of their potential functions is benthic foraging dives. However, two thirds of the dives did not reach the sea floor, suggesting they are also used for other purposes.

The most frequent dives performed were v-Slow dives, and their low velocity and shallow depth suggest that these dives may be linked to slow travelling and/or to resting or recovery behaviours amid activities necessitating deeper dives and greater energy expenditure (Kooyman and Ponganis 1998; Le Boeuf et al. 2000; Austin et al. 2006). The similar v-Fast dives could serve analogous functions, but their faster/ascent rate, longer duration and maximum depth indicate that they could be related to more active behaviours, such as active or more dynamic travelling, shallow foraging or social interactions. The presence of dives with intermediate shapes between v and u dives within this cluster can involve increased horizontal displacement, similar to the “shallow active” dives reported in pinnipeds (Baechler et al. 2002; Wilson et al. 2014).

Deeper V dives are usually associated with either exploration, predator avoidance or travelling (Schreer et al. 2001; Austin et al. 2006; Dragon et al. 2012). The SLE beluga being presumably free of predation pressure (Mosnier et al. 2010), and v-Deep dives being on average their deepest dives, it is most likely that these dives are associated with foraging exploration where the individual would transit at a similar and fast descent and ascent rate to explore the water column in search of an adequate food patch (Schreer and Testa 1996).

Trapezoidal dives have been less often identified in other species and their attributed functions vary in the literature. Among these functions, they have been mainly related to prey pursuit, foraging, food processing and resting (Lesage et al. 1999b; Schreer et al. 2001; Sala et al. 2011). In SLE belugas, skew-R dives present characteristics, in terms of depth, duration and relation to the bottom, similar to those of v-Deep dives, and thus could constitute a type of exploratory dives with an added search or foraging component during the ascent phase, a function suggested for harbour seals (Lesage et al. 1999b). skew-L dives in SLE belugas are relatively long and shallow with below-average velocities, which resemble resting drift dives identified in many pinniped species (Thums et al. 2008; Kuhn et al. 2009; Sala et al. 2011).

Grouping dives into bouts allowed specifying further their functions, and also highlighted the variability of behavioural contexts of their use. As expected, square-W dives were primarily associated with W-Pelagic bouts during which only 10% of the dives reached the sea floor, a pattern consistent with a pelagic foraging behaviour. Despite belugas reaching the bottom only 30% of the time when performing square-U dives, this dive type was strongly associated with Benthic bouts, during which half of the dives reached the bottom, a pattern again consistent with a benthic foraging function. Hence, the primary function of U dives seems to be benthic foraging but despite that, they may also be used in other contexts.

The high frequency of v-Slow dives during the low velocities Near-Surface bouts confirmed these dives to be likely used for slow travelling and/or resting. However, the relatively frequent association of v-Slow dives (>15%) with skew-R dives in skew-Pelagic bouts suggests that they can also be used during bouts of activity involving higher

swim velocity, and low ascent and descent rates. These characteristics could potentially translate into an increased horizontal movement during active travelling. For their part, v-Fast dives were relatively frequent (>10%) during all bout types suggesting they can be associated with different dive types and be used in a variety of contexts. This would be consistent with their use for travelling, a function that can be part of different behaviours. For example, during V-Pelagic bouts, belugas most likely use v-Fast dives to travel while concurrently exploring the water column in search of prey using the deeper V dives.

Skew-R dives were frequently associated with square-W dives during skew-Pelagic bouts, where variation in dive shapes and durations could reflect differences in the distribution, density or types of prey targeted by belugas during pelagic foraging. Dive association within these bouts also confirms that skew-R dives most likely serve as exploratory and/or foraging pelagic dives. Skew-L dives, for their part, were not particularly frequent during any specific bout type, despite being more often used during the low velocity Near-Surface bout, supporting a possible resting function.

Establishing the link between surface activities and diving behaviour of individuals (either dive types or bout types) can provide additional insights into the potential functions and behaviours related to the identified surface activities. For example, in other studies, *milling* have often been related to either foraging, socializing and resting or classified as a behaviour in itself with no obvious function related to it (Pippard and Malcolm 1978; Watts and Draper 1986a; Lesage et al. 1999a; Mymrin and Huntington 1999; Heide-Jørgensen et al. 2001; Canadas and Hammond 2006; Markowitz and McGuire 2007; Steckenreuter et al. 2012; Castellote et al. 2013; Degradi et al. 2013). Here however, the three SA of belugas that involved a *milling* PMP - Milling, Milling-E

and Mixed - were associated more often than expected with square-U dives and with the corresponding Benthic bouts, although they varied in other associated characteristics, allowing us to relate the use of milling to various distinct behaviours (Table 7).

Herds involved in Milling-E displayed surface events and vocalization, were the largest in size, and frequently performed v-Fast dives. These characteristics suggest that Milling-E was most likely related to benthic foraging or socializing. Behaviours similar to the milling surface activity described for SLE beluga were described in belugas from the High Arctic, moving “*very little distance horizontally*” when suspected to forage on patchily distributed Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum, 1792)) (Martin and Smith 1992, 1999). Pippard and Malcolm (1978) also described foraging in SLE belugas as being characterized by individuals going back and forth within limited areas where they executed tight circles, half circles and reversals of direction. Similar movement patterns were described by Watts and Draper (1986b) when observing Hudson Bay beluga foraging on capelin (*Mallotus villosus* (Müller, 1776)) aggregations.

The large size of herds involved in milling is consistent with a foraging behaviour, where forming larger groups may be an advantage when targeting certain elusive prey. This has been hypothesized for belugas (Cosens and Dueck 1991), and shown in many other species (Benoit-Bird and Au 2009). Chances of social interactions are likely to increase with herd size and thus, it is unsurprising to have milling-E associated with larger herd sizes. Belugas are recognised as a highly social species, and frequent social interactions are an essential part of their life style (Michaud 2005). Surface events (including chasing, rubbing, rolling) and vocalisations have been previously linked to social interactions in beluga (Sjare and Smith 1986; Lesage et al.

1999a; Panova et al. 2012) and represent the best metric available to identify socializing in this species.

The Milling SA is most likely related to either/or benthic foraging, resting and care of young. The high occurrence of Benthic bouts during Milling suggests that it is related to benthic foraging. Resting in cetaceans generally involve individuals remaining motionless or swimming slowly near the surface (Canadas and Hammond 2006; Degraati et al. 2008; Stelle et al. 2008), a pattern similar to our description of milling, during which Near-Surface bouts were frequent and dynamism was low. Herd of female belugas accompanied by calf and juveniles are known to prefer shallower waters (Michaud 1993; Mosnier et al. 2010). This is in agreement with the shallow depth of Benthic and Near-Surface bouts observed during Milling and the high prevalence of calves in herds in this state. These shallower bouts could be used by female belugas accompanied by calves to either favor access to shallower benthic preys, to minimize the time young spend alone at the surface while females are feeding, or to favor social interactions by the young (Loseto et al. 2006; Gibson and Mann 2008; Tyson et al. 2012).

The Mixed SA combined two movement patterns, *milling* and *directional* and was often associated with both skew-Pelagic bouts and Benthic bouts (Fig. 4). Accordingly, it showed characteristics intermediate between SA that involved milling or directional PMP. Herds observed during Mixed SA were also, on average, the smallest herds although they were spread over the largest radius (Table 7). Concordant with the clustered structure observed, this surface activity seems to encompass both benthic and pelagic behaviours during which individuals are scattered and seemingly less interactive, despite being spatially associated. In this manner, it resembles the feeding behaviour

described by Panova et al. (2012) for Myagostrovsky belugas and probably also involve both benthic and pelagic foraging in SLE belugas. Herds displaying Mixed SA were rarely seen in herd where calves were observed, suggesting that this behavioral strategy, where individuals and groups are highly dispersed, may not be suitable for individuals caring for young.

The last three SA (Directional-D, Directional-M and Directional-T) were characterised by different types of directional PMP. Directional movement can be used for different purposes, but with travelling being the behaviour most often associated with a directional movement pattern (e.g. Lusseau 2003; Stelle et al. 2008; Steiner 2011; Degradi et al. 2013). Directional movement could also be part of exploration and prey searching behaviour where the displacement is used to spatially investigate a habitat of interest. Directional movement can further be used during foraging to pursue escaping prey or to move between prey patches within a foraging bout. The three directional SA were here associated mainly with pelagic dives and bouts and, when considered together, appeared to be related to the same behaviours (i.e. travelling, exploration and pelagic foraging) but with varying frequency of use of these behaviour (Fig. 3 and 4).

The multi-directional PMP observed during Directional-M is characterised by frequent deviations from the main movement axis, which could depict prey pursuit (Simon et al. 2007; Lunardi and Ferreira 2013). We believe that Directional-M SA is primarily linked to pelagic foraging during which beluga herds exhibit pelagic exploration and travelling between prey patches. Herds involved in this SA also included the individuals with the highest proportions of square-W dives and W-Pelagic bouts, strongly supporting the link of this SA with pelagic foraging. The high occurrence of

skew-Pelagic bouts also confirms that this type of bout is related to pelagic foraging, serving either for exploration or as a modified type of pelagic foraging bout.

The specific functions of Directional-D SA are most likely similar to those of Directional-M and Directional-T SA, given they are associated with similar dive types. The highest frequency of skew-R and v-Deep dives in individuals evolving within herds displaying Directional-D suggests a higher importance of exploration during this SA. Dispersion can help cover more area in search for food. However, no bout type was strongly associated with this SA, suggesting a mixed use of behaviours by individuals in herds involved in Directional-D. Furthermore, herds displaying Directional-D showed characteristics similar to Mixed-SA (large radius, small herd, mostly adults) and it is possible that herds showing a clustered structure or a dispersed and directional pattern are using similar behaviours but that result in distinct surface activities.

The frequent use of shallow v-Slow and v-Fast dives by individuals within herds observed in Directional-T suggests that this SA is mostly related to travelling. Directional movement with shallow diving is generally considered as travelling behaviour in belugas (Sjare and Smith 1986; Lydersen et al. 2001; Markowitz and McGuire 2007; Panova et al. 2012) and other diving cetaceans (Bearzi 2005; Canadas and Hammond 2006; Degradi et al. 2008; Stelle et al. 2008). The tight and elevated dynamism of herds in Directional-T SA also supports that Near-Surface bouts occurring during this SA are related to active travelling rather than resting. The frequent use of V-Pelagic bouts by individuals in herds displaying Directional-T suggests some exploration, despite that these individuals are not using V-dives frequently. Finally, the relatively frequent occurrence of both square-W

dives and W-pelagic bouts indicates that some pelagic foraging can also take place when herds are in Directional-T.

Relative frequency of use of the different SA also varied among herd types. A sexual segregation occurs in SLE belugas during summer, with herds of females with calves occupying a different portion of the Estuary than herds of sub-adult and adult males (Michaud 1993; Michaud 2005). Reasons for this segregation can be related to multiple factors (Michaud 2005; Mosnier et al. 2010) and our observations show that it results in differences in frequency of use of some behaviours. Generally, females with calves seem to favor behaviours with increased proximity among individuals of the herd, rarely using the Mixed SA and more frequently the Directional-T, compared to herds composed solely of adults. This could be related to the benefits of communal life among females such as care for young, defence against predators, harassment from males and infanticide (Michaud 2005) or to differences in habitat use and exploitation (Mosnier et al. 2010).

This study highlighted dive types, bout types and associated surface activities indicating that SLE beluga perform a variety of behaviours during the period from June to October, including resting, socializing, and care of young, exploration and travelling, as well as foraging. These findings are consistent with what we know about their life cycle, foraging habits and diet. In the SLE, belugas give birth mainly from June to August, and the species is known to feed their calf for at least one full year, likely close to two years (Matthews and Ferguson 2015). While seasonal variations in energy requirements and foraging intensity are poorly known for SLE beluga (see Lesage 2014 for a review), it is suspected, based on historical data from hunted individuals and local

knowledge, that the spring is a period of intensive feeding in the SLE. However, foraging also occur on a regular basis during summer, a finding which is supported by the regular occurrence of foraging bouts in all herd types in this study. There is little information on the contemporary diet of SLE beluga (Lesage 2014). The data available is, however, consistent with a study conducted in the 1930s indicating that belugas have a diverse diet, which varies seasonally, and which incorporates both invertebrates and fish prey, from benthic, demersal and pelagic habitats (Vladykov 1946). The documentation of what appears to be pelagic and benthic foraging in this study is therefore consistent with a diet composed of these species.

Some rarer but important behaviours known to occur during summer, such as calving (Michaud 2005), were not identified by this classification and would require further investigation. As hypothesized, herd surface behaviour varied according to the diving behaviour of individuals. However, association patterns between dive profiles and surface activities were complex, and multiple behaviours were often associated with a given dive type or surface activity. These results reflected our perception that classifications may not allow to identify exclusive behavioural classes, and that variations in the use of behaviours has to be considered. Despite these limitations, general patterns emerged when combining multiple sources of information, forming a firm basis to better understand the behaviour of this cryptic species that could be used to further study the characteristic of the habitat selected by St. Lawrence belugas for specific functions.

This study demonstrates the added value of using information from individual dives to enhance the understanding of behaviours related to surface activities of herds collected during long-term population studies. In a next step, the behaviours attributed to

the 1400 herds analysed here could be used in a spatially and temporally explicit framework for identifying foraging habitats and important prey, as well as habitat used for other important life functions during the summer period.

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1 **TABLES**

2 **Table 1.** Categories and description of each input variables used for the cluster analysis of St. Lawrence Estuary (SLE) belugas
3 (*Delphinapterus leucas* (Pallas, 1776)) herd surface activities. Frequency of occurrence for each category is presented in absolute
4 number and relative to the total (%).








5

Variable	Type	Categories	Description	Freq. (%)
Predominant Movement Pattern	Nominal	Directional	Continuous unidirectional movement	1727 (48)
		Multi-Directional	Directional movement with frequent deviation of the principal axe	930 (26)
		Milling	Circular movement at the surface resulting in low net displacement	928 (26)
Dynamism	Ordinal	Low	Level of energy displayed by individuals at the surface	823 (23)
		Low to Moderate		321 (9)
		Moderate		1967 (55)
		Moderate to High		257 (7)
		High		217 (6)
Form	Nominal	Broken	Individuals and groups do not show a precise configuration	3376 (94)
		Front	Individuals or groups are abreast from one another forming a front	78 (2)
		Line	Individuals or groups are following one another forming a line	131 (4)
Structure	Nominal	Uniform	Individuals or groups are uniformly distributed within the herd	3170 (88)
		Clustered	Individuals or groups are distributed in a few distinct clusters	415 (12)
Dispersion	Ordinal	Tight	Distance between individuals or groups < 100m	1720 (48)
		Loose	Distance between individuals or groups= 100- 300m	1116 (31)
		Dispersed	Distance between individuals or groups > 300m	336 (21)
Surface events	Asymmetrical nominal	Yes	Spy hoping, tail or pectoral slash, breach, body contacts	399 (11)
		No		3186 (89)
Surface vocalizations	Asymmetrical nominal	Yes	Vocalizations can be heard from the research boat	297 (8)
		No		3288 (92)

Table 2. Relative frequencies (%) for ordinal, nominal and semi-nominal variables and means for numerical variables associated with the six herd surface activity types identified from surface focal follows of SLE belugas (*Delphinapterus leucas* (Pallas, 1776)) ($n=3585$; 1991-2012). Main characteristics for the various surface activities are: milling and occurrence of surface events (Milling-E), milling movement patterns (Milling), milling and directional movements and a clustered herd structure (Mixed), directional movements in dispersed herds (Directional-D or Dir-D), multi-directional movements (Directional-M or Dir-M) and directional movements in tight herds (Directional-T or Dir-T).

Variable	Categories	Surface activity types					
		Milling-E	Milling	Mixed	Dir-D	Dir-M	Dir-T
Predominant Movement Pattern	Directional	0	0	62	100	0	97
	Multi-Directional	0	0	4	0	100	0
	Milling	100	100	35	0	0	3
Dynamism	Low	16	30	19	26	32	11
	Low to Moderate	9	9	0	9	11	7
	Moderate	64	54	78	52	53	63
	Moderate to High	5	5	0	7	3	11
	High	7	3	3	6	2	8
Form	Broken	100	100	98	100	100	86
	Front	0	0	2	0	0	3
	Line	0	0	0	0	0	11
Structure	Uniform	89	100	0	100	100	100
	Clustered	11	0	100	0	0	0
Dispersion	Tight	75	67	25	0	40	92
	Loose	17	23	21	60	41	7
	Dispersed	7	10	54	40	18	1
Surface Events	No	0	100	100	100	90	95
	Yes	100	0	0	0	10	5
Surface Vocalization	No	56	100	100	100	95	91
	Yes	44	0	0	0	5	9
Herd Size (#ind)	2-225	44	28	20	23	27	28
Radius (m)	5-2000	343	276	617	541	429	190
Herd Type	Adult	12	12	20	25	19	11
	Adult-Grey	75	67	73	59	63	68
	Adult-Grey-Calf	13	22	6	15	18	21

15 **Table 3.** Mean values of time-depth derived variables per dive type identified based on the final K-mean clustering of the full-dataset
16 ($n=6312$) for radio-tracked SLE belugas (*Delphinapterus leucas* (Pallas, 1776)) (2001-2005). Characteristics related to velocity data
17 ($n=2206$) and distance relative to the sea floor ($n=3125$) are calculated based only on dives with available data. Standard deviations
18 are given in parenthesis.

Dive types							
	Square-W	Square-U	v-Fast	v-Slow	v-Deep	Skew-R	Skew-L
Dive Duration (sec)	286.58 (132.2)	187.55 (119.1)	30.30 (17.9)	22.13 (9.9)	124.32 (148.7)	195.23 (118.4)	153.41 (115.0)
Maximum Depth (m)	28.35 (22.1)	13.35 (9.2)	6.02 (3.1)	3.40 (1.4)	35.96 (45.4)	23.58 (17.6)	14.19 (13.2)
Bottom Time (sec)	148.23 (102.3)	136.19 (103.4)	11.29 (8.6)	7.76 (5.0)	55.91 (94.6)	58.37 (49.2)	38.09 (38.3)
Max. Depth / Duration	0.10 (0.1)	0.08 (0.0)	0.21 (0.1)	0.17 (0.1)	0.31 (0.1)	0.13 (0.1)	0.10 (0.0)
Bottom Time / Duration	0.51 (0.2)	0.69 (0.1)	0.36 (0.1)	0.35 (0.1)	0.38 (0.1)	0.29 (0.1)	0.24 (0.1)
Bottom Time /Max. Depth	6.81 (5.8)	11.53 (7.9)	1.89 (1.0)	2.47 (1.7)	1.39 (0.9)	2.82 (2.2)	3.13 (3.1)
\bar{x} Ascent Rate (m/s)	0.37 (0.3)	0.46 (0.3)	0.53 (0.2)	0.24 (0.1)	0.81 (0.3)	0.22 (0.1)	0.38 (0.2)
\bar{x} Descent Rate (m/s)	0.57 (0.3)	0.50 (0.3)	0.38 (0.2)	0.37 (0.2)	0.87 (0.3)	0.58 (0.3)	0.15 (0.1)
\bar{x} Ascent Rate / \bar{x} Descent Rate	0.92 (1.0)	1.20 (1.0)	1.58 (0.6)	0.73 (0.3)	1.06 (0.6)	0.43 (0.2)	3.33 (3.0)
\bar{x} Descent Rate / \bar{x} Ascent Rate	2.26 (2.2)	1.31 (1.1)	0.73 (0.3)	1.77 (1.2)	1.20 (0.6)	3.66 (3.4)	0.46 (0.3)
Wiggle (#)	1.71 (1.1)	0.03 (0.2)	0.00 (0.1)	0.00 (0.0)	0.07 (0.3)	0.07 (0.3)	0.24 (0.5)
\bar{x} Ascent Velocity (stand.)	0.36 (0.13)	0.38 (0.15)	0.41 (0.11)	0.34 (0.12)	0.45 (0.11)	0.39 (0.13)	0.35 (0.13)
\bar{x} Descent Velocity (stand.)	0.35 (0.11)	0.37 (0.13)	0.40 (0.10)	0.32 (0.12)	0.44 (0.10)	0.38 (0.11)	0.36 (0.13)
\bar{x} Bottom Velocity (stand.)	0.32 (0.12)	0.38 (0.16)	0.39 (0.15)	0.34 (0.14)	0.40 (0.13)	0.36 (0.13)	0.34 (0.14)
\bar{x} % to bottom	0.63 (0.10)	0.53 (0.12)	0.19 (0.05)	0.10 (0.03)	0.45 (0.11)	0.46 (0.11)	0.37 (0.10)

19

% less 3 meters	29.62	32.54	5.49	3.20	16.43	12.96	13.83
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Draft

Table 4. Mean variable values for dives of radio-tracked SLE belugas (*Delphinapterus leucas* (Pallas, 1776)) (2001-2005) from the full-dataset ($n=5816$) within each dive bout cluster. Velocity ($n=2034$) and relation to bottom ($n=2873$) are calculated for dives with available values among the full-dataset. Standard deviations are given in parenthesis.

Bout types	Near-Surface	Benthic	W-Pelagic	Sk-Pelagic	V-Pelagic
n	158	50	41	87	68
\bar{x} total duration (min)	20.77 (19.41)	38.52 (33.12)	53.59 (33.55)	57.07(50.78)	32.81 (32.21)
Dive Duration (sec)	75.95 (94.72)	164.41 (139.23)	201.18 (168.45)	163.04 (138.60)	112.58 (123.99)
Maximum Depth (m)	7.15 (8.83)	12.20 (9.66)	23.69 (23.75)	19.58 (19.62)	22.90 (32.92)
Bottom Time (sec)	30.44 (51.50)	112.36 (116.16)	95.01 (110.85)	67.41 (80.40)	48.21 (68.69)
Max. Depth / Duration	0.14 (0.07)	0.11 (0.08)	0.16 (0.09)	0.15 (0.07)	0.23 (0.10)
Bottom Time / Duration	0.47 (0.18)	0.59 (0.23)	0.42 (0.21)	0.37 (0.18)	0.38 (0.16)
Bottom Time /Max. Depth	4.04 (4.77)	9.14 (8.82)	4.11 (4.01)	3.62 (3.56)	2.15 (2.00)
\bar{x} Ascent Rate (m/s)	0.30 (0.18)	0.49 (0.28)	0.43 (0.26)	0.34 (0.21)	0.63 (0.30)
\bar{x} Descent Rate (m/s)	0.31 (0.20)	0.54 (0.33)	0.56 (0.34)	0.51 (0.33)	0.60 (0.33)
\bar{x} Ascent Rate / \bar{x} Descent Rate	1.38 (1.62)	1.49 (2.30)	1.07 (1.10)	0.98 (1.08)	1.33 (1.07)
\bar{x} Descent Rate / \bar{x} Ascent Rate	1.49 (1.69)	1.51 (1.96)	1.87 (1.96)	2.07 (2.11)	1.22 (1.41)
Wiggle (number of.)	0.14 (0.46)	0.16 (0.44)	0.92 (1.32)	0.29 (0.66)	0.16 (0.49)
\bar{x} Ascent Velocity (stand.)	0.33 (0.12)	0.38 (0.13)	0.38 (0.13)	0.40 (0.13)	0.43 (0.11)
\bar{x} Descent Velocity (stand.)	0.33 (0.12)	0.37 (0.12)	0.34 (0.11)	0.39 (0.12)	0.42 (0.11)
\bar{x} Bottom Velocity (stand.)	0.34 (0.14)	0.37 (0.15)	0.33 (0.13)	0.38 (0.13)	0.40 (0.14)
\bar{x} % to bottom	0.22 (0.27)	0.69 (0.26)	0.48 (0.30)	0.42 (0.36)	0.34 (0.34)
% less 3 meters	7.94	49.39	10.51	17.23	13.00

Table 5. Pairwise comparison of the frequency of dive types among surface activity clusters, obtained from SLE belugas (*Delphinapterus leucas* (Pallas, 1776)) equipped with time-depth-velocity recorders and from herds surface focal follows, respectively (2001-2005). Adjusted p values from Fisher test are presented.











		 Milling-E	 Milling	 Mixed	 Dir-D	 Dir-M
	Milling	<0.00	-	-	-	-
	Mixed	0.01	0.93	-	-	-
	Dir-D	<0.01	<0.00	0.02	-	-
	Dir-M	<0.01	<0.00	0.01	0.61	-
	Dir-T	<0.01	<0.00	0.19	0.56	0.04

Table 6. Pairwise comparison of the frequency of bout types among surface activity clusters, obtained from SLE belugas (*Delphinapterus leucas* (Pallas, 1776)) equipped with time-depth-velocity recorders and from herds surface focal follows, respectively (2001-2005). Adjusted p values from Fisher test are presented.

















					
	Milling-E	Milling	Mixed	Dir-D	Dir-M
 Milling	0.86	-	-	-	-
 Mixed	0.86	0.84	-	-	-
 Dir-D	0.53	0.53	0.86	-	-
 Dir-M	0.03	0.02	0.31	0.53	-
 Dir-T	0.01	0.03	0.06	0.52	0.31

Table 7. Summary of main characteristics of surface activity clusters derived from herd surface focal follows of SLE belugas (*Delphinapterus leucas* (Pallas, 1776)) ($n=3585$; 1991-2012) and of their associated dive and bouts types, both obtained from radio-tracked individuals equipped with time-depth-velocity recorders ($n=27$; 2001-2005), and potential behaviours.

Acronym	Surface activities					
						
	Milling-E	Milling	Mixed	Directional-D	Directional-M	Directional-T
PMP	Milling	Milling	Milling & Directional	Directional	Multi-directional	Directional
Radius	Medium	Small	Large	Large	Medium	Small
Herd size	Large	Average	Small	Small	Average	Average
Herd type	Mixed	With calf	Rarely with calf	Adults	Mixed	With calf
Other characteristics	Surface events & vocalizations	Reduced dynamism	Clustered	Dispersed	Reduced dynamism	Tight, elevated dynamism
Bouts	Benthic	Near-Surface Benthic	Sk-Pelagic Benthic	-	Sk-Pelagic V-Pelagic W-Pelagic	V-Pelagic Near-Surface
Dives	v-Fast; square-U	v-Slow; square-U	v-Slow; square-U	skew-R; v-Deep	square-W; skew-L	v-Slow
Potential main behaviour(s)	Socializing Benthic foraging	Benthic foraging Resting Care of young	Mixed	Pelagic exploratory	Pelagic foraging	Travelling

FIGURES

Figure 1. Summer distribution of St. Lawrence Estuary (SLE) beluga (*Delphinapterus leucas* (Pallas, 1776)) in Québec, Canada, with sectors where mainly herds of adults are encountered shown in blue, sectors with herds of adults and young shown in yellow and sectors where both type of herds are found shown in green. Black lines correspond to the focal surface follows used for the classification of herd surface activities ($n=3585$; 1991-2012), whereas red lines correspond to the radio-tracking positions of individual equipped with a time-depth-velocity recorders, which provided the data used to classify individual diving profiles ($n=27$; 2001-2005).

Figure 2. Relative frequency of dive types per dive bout types for radio-track SLE belugas (*Delphinapterus leucas* (Pallas, 1776)) equipped with time-depth-velocity recorders (2001-2005). Dive types are represented based on their general shape and time-depth-speed characteristics, with square-W corresponding to long and relatively deep dives with wiggles, square-U to square-shaped with long duration and bottom phase dives, v-Fast to fast, short and shallow dives, v-Slow to slow, short and shallow dives, v-Deep to deep v-shaped dives, skew-R to long, deep and skewed to the right dives, and skew-L to skewed to the left dives. Bout types are named based on the characteristics and distance relative to the sea floor of their associated dives, with Near-Surface bouts mostly related to shallow and v-Slow dives, Benthic bouts to square-U dives occurring near the sea floor, W-Pelagic bouts to pelagic square-W dives, Sk-Pelagic bouts to pelagic and skew-R dives, and V-Pelagic bouts to pelagic and v-Deep dives.

Figure 3. Relative frequency of dive types per surface activity types of SLE belugas (*Delphinapterus leucas* (Pallas, 1776)). Dives types are described in Fig. 2. Surface activity types are represented based on the predominant movement pattern of the herd and other differentiating characteristics, Milling-E being associated with a milling movement patterns and occurrence of surface events, Milling to milling movement patterns, Mixed with both milling and directional movements and a clustered herd structure, Directional-D to directional movements in dispersed herds, Directional-M to multi-directional movements and Directional-T to directional movements in tight herds.

Figure 4. Relative frequency of dive bout types per surface activity types for radio-tracked SLE belugas (*Delphinapterus leucas* (Pallas, 1776)) equipped with time-depth-velocity recorders and herds surface focal follows (2001-2005). Bout and surface activity types are described in Fig. 2 and Fig. 3, respectively.

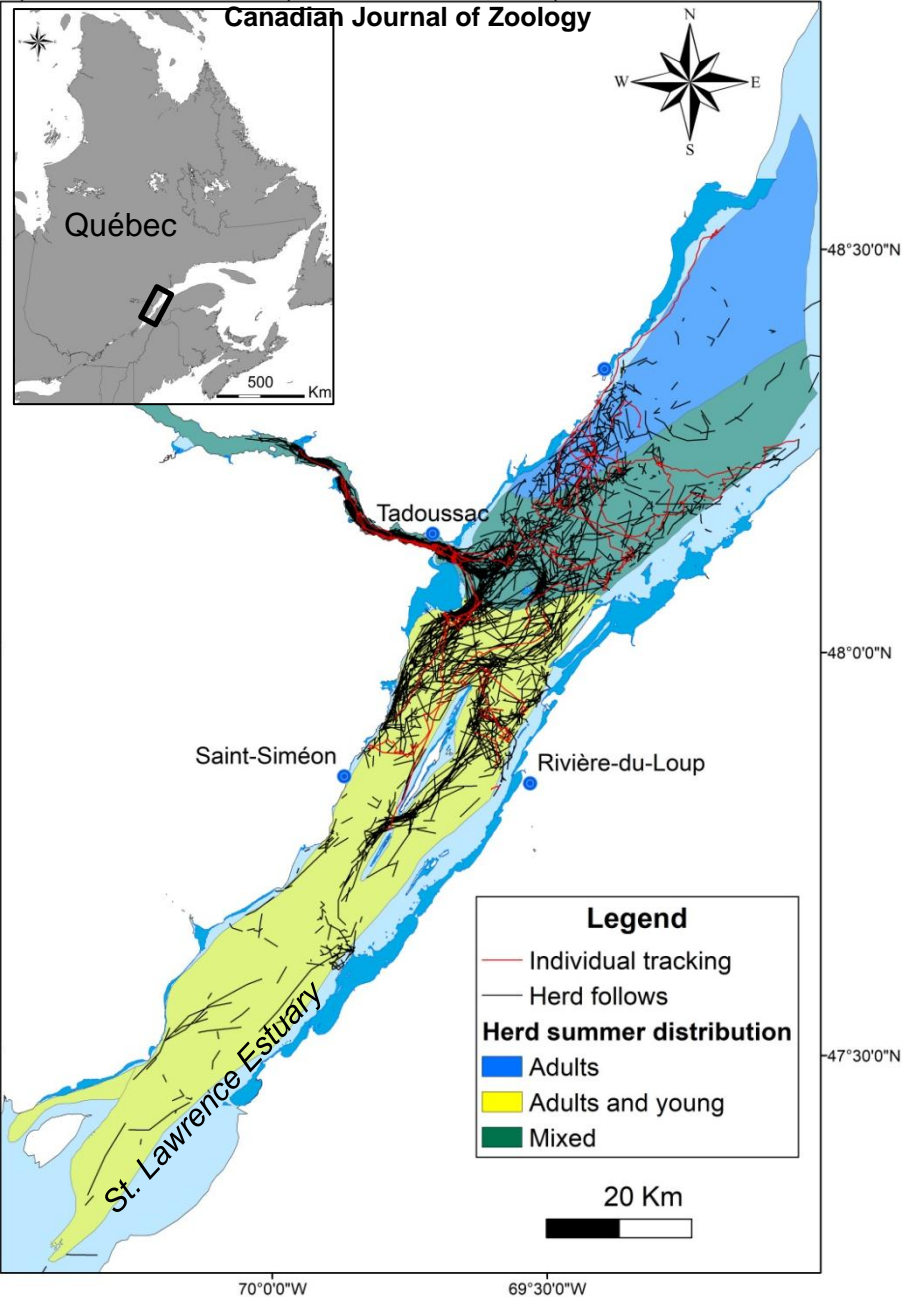
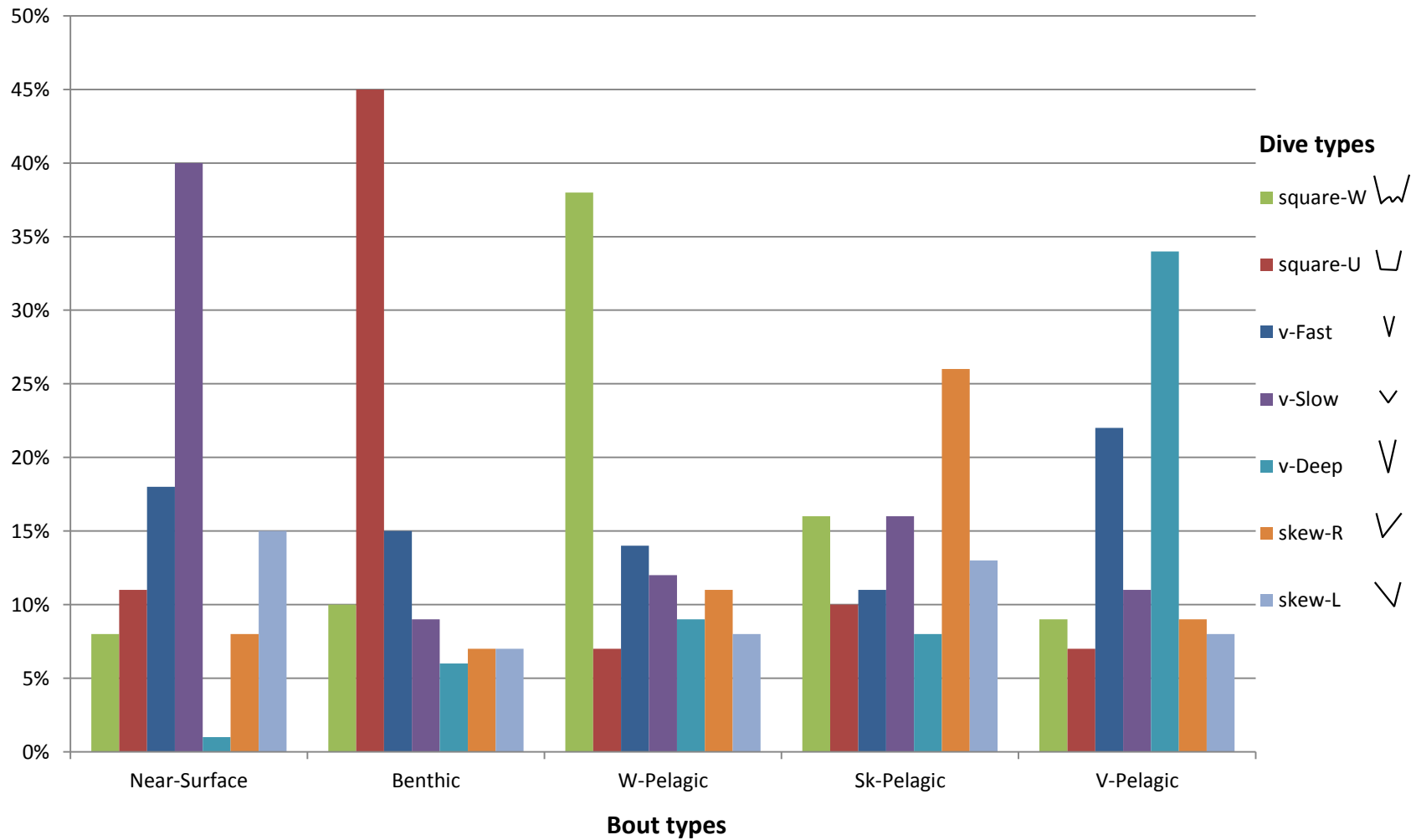
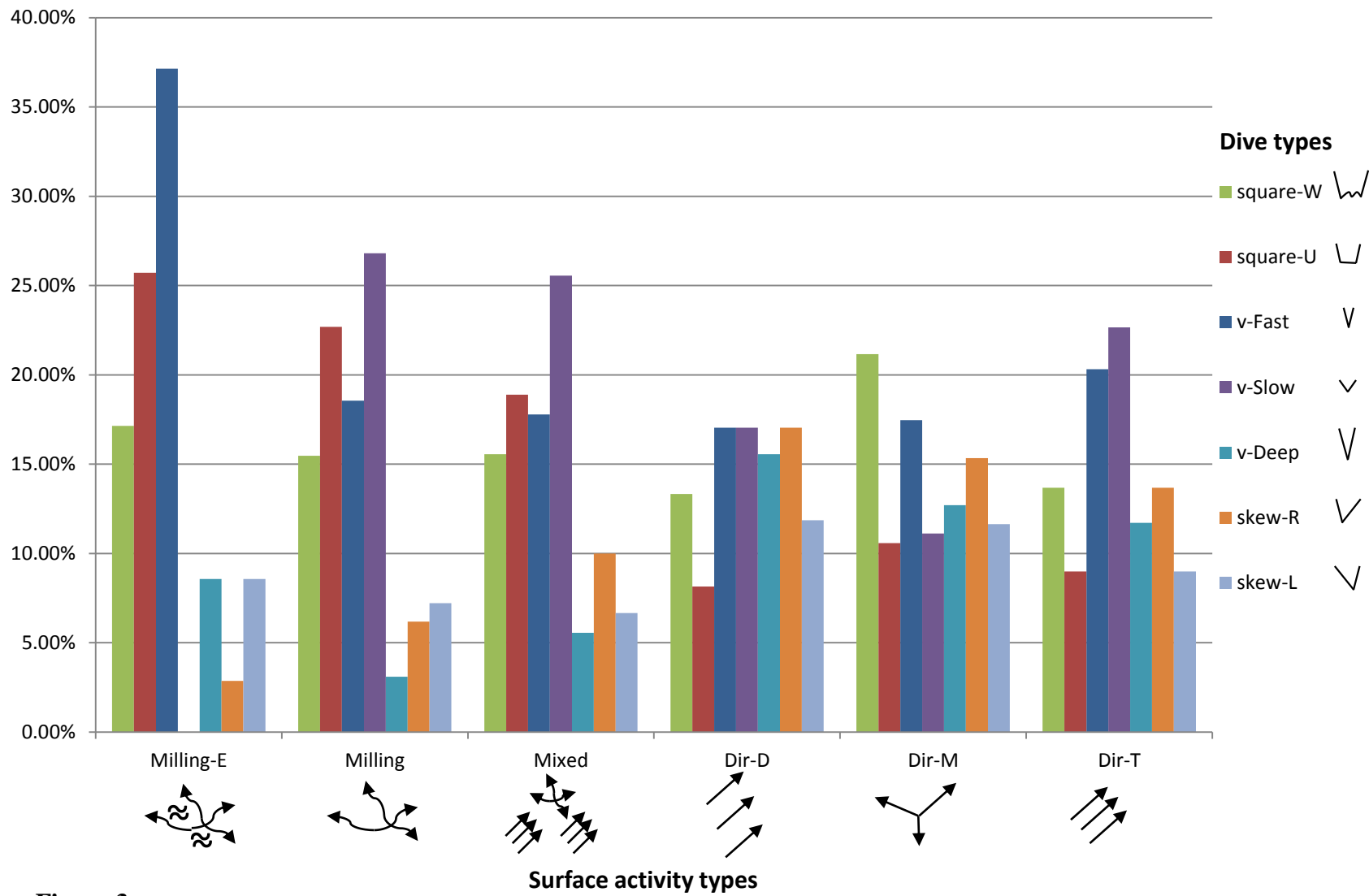


Figure 1. <https://mc06.manuscriptcentral.com/cjz-pubs>

**Figure 2.**



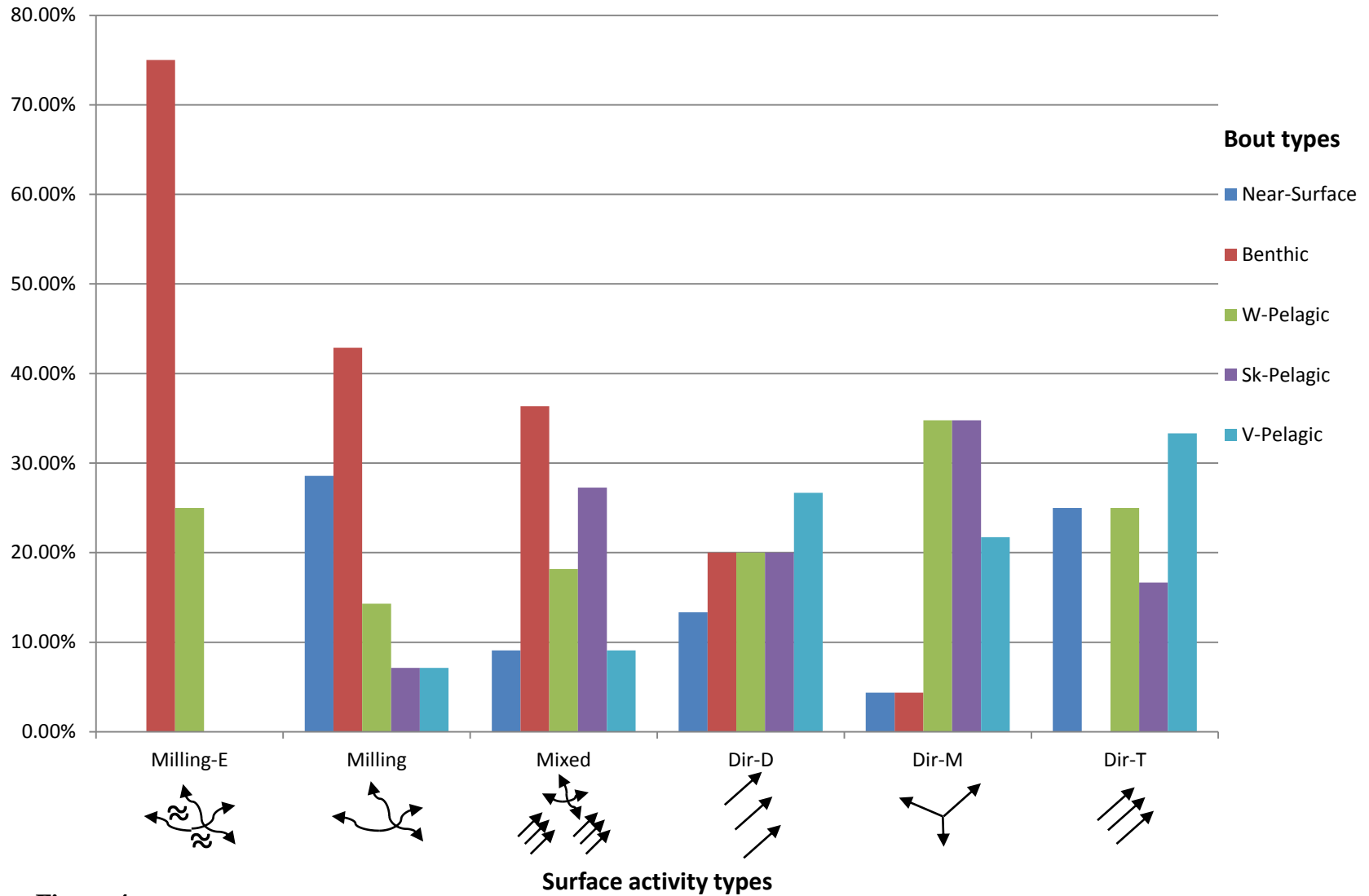


Figure 4.

APPENDIX A.

Classification of radio-tracked individual diving behaviour

METHODS

Dive record manipulation

We corrected drift of the pressure transducer manually using the program Instrument Helper (Wildlife Computers Inc.). Swim speed recording is known to vary among instruments, as well as according to tag position on the body and possibly, whale size (Baird 1997). Calibration of swim speed was achieved by dividing each velocity reading by the maximum speed recorded during a given deployment, resulting in values from 0 to 1. We excluded deployments where tags had an obstructed flow to the velocimeter, i.e., facing the body of the animals, or with unusually low maximum velocities and small variability among readings.

We analyzed dive records using a custom program to identify dives (depth ≥ 0.5 m), and extract various statistics, including: dive duration, maximum depth, bottom time, mean descent rate, mean ascent rate, mean ascent velocity, mean bottom velocity, mean descent velocity, number of wiggles. The bottom phase was defined as the interval between the first and last depths of a dive that exceeded 80% of maximum dive depth. Wiggles were defined as upward vertical excursions of ≥ 3 m. Index of relative duration of bottom time, dive shape and skewness were obtained through the following ratio-variables: bottom time/dive duration, bottom time/maximum depth, maximum depth/dive duration; descent/ascent rate, ascent/descent rate.

We used a log-survivorship analysis to identify break-points in dive duration between dives that were part of a breathing sequence and true dives, as the former are

expected to be shorter and more abundant than the latter. We selected break-point values independently for each individual since variation in individual physiology and behaviour is likely to affect diving patterns. We excluded dives associated with breathing sequences, the first true dive after tagging, and dives that were missing an ascent or a descent phase as a result of their short duration.

Principal Components and Cluster analyses

Variables were checked for normality (KS test) prior to the PCA, with transformations applied when improving distribution. We included all variables in the analysis, regardless of degree of normality attained since the series of statistical methods used in this study are robust to departure from normality, although normality helps maximising clarity of the results (Hair et al. 1995; Lesage et al. 1999). However, we excluded a set of 7 dives, characterized by particularly long post-dive intervals from the multivariate analyses; those were recorded from a single animal resting near the surface, and would have been considered as outliers in the analysis. Variables were standardized to a mean of 0 and a standard deviation of 1 to account for the sensitivity of PCA to variability in scale among variables.

Given that only about a third (2204 dives) of the 6312 retained dives had valid velocity data, we developed an approach that relied on observations with valid velocity data to classify observations with missing velocity data (Fig. A1). We ran the PCA twice, once using only the 2204 dives with valid velocity data and so, all 14 variables (*sub-dataset*) (PCA #1 in Fig. A1), and a second time using the full set of 6312 dives but using only the 11 depth/duration related variables that were common to all observations (*full-*

dataset) (PCA #2 in Fig. A1). This had the effect of producing principal components (PCs) with coefficients that reflected the inclusion or exclusion of the variables related to swim speed. Using only the 2204 observations with valid velocity data we randomly selected two sets of 1000 dives to run two parallel hierarchical complete linkage cluster analyses while trimming 10% of outlier dives (PROC Cluster and option TRIM in SAS) to compare the number of identified clusters when including or excluding velocity data.

The first hierarchical cluster analysis (Hierarchical cluster #1 in Fig. A1) used scores for all 6 PCs that were obtained from the PCA#1. The second hierarchical cluster analysis (Hierarchical cluster #2 in Fig. A1) used scores for PCs 1 to 5 obtained from the PCA #2, i.e. considering only depth/duration-related variables (Fig. A1). The number of clusters best describing each dataset was determined based on the concordance between the cubic clustering, the pseudo F , and pseudo t^2 criteria (SAS user Guide, Chapter 8). PCs scores and cluster assignments obtained from the hierarchical cluster analysis including velocity data (i.e., PCs 1 to 6 from PCA #1 and clusters from Hierarchical cluster #1 in Fig. A1) were used to calculate mean PCs scores for each cluster, i.e., cluster centroids. Centroids for each cluster were then used as seeds in a non-hierarchical, hard-k means cluster analysis to classify all 2204 dives with swim speed data and assign them to a specific cluster (K-means #1 in Fig. A1).

To obtain cluster assignment for the 4108 dives missing velocity data, we recalculated fine-tuned centroids using PC scores of the 2204 dives that were assigned a cluster identification number in the previous analysis (K-means #1, Fig. A1) although this time, centroids for each cluster were calculated using PC1 to PC5 scores for these 2204 dives that were obtained from the PCA ran on the full-dataset of 6312 dives (i.e. PCA #2,

Fig. A1). These fine-tuned centroids summarized into 5 depth/duration PCs but developed based on cluster assignments accounting for velocity data, were used as seeds in a final K-means cluster analysis (K-means #2 in Fig. A1) to obtain final cluster assignment, mean PCs scores and other statistics for the full-dataset. Each classification was validated from misclassification rates using a discriminant function analysis and cross-validation approach, i.e., recalculating the discriminant functions while leaving out the one observation to be classified.

RESULTS

Principal Components and Cluster analyses

When run on the full-dataset while excluding velocity-related variables, the PCA reduced the 11 depth/duration related variables to 5 uncorrelated factors, which retained 97% of the initial variance. Running the PCA on the sub-dataset containing only dives with valid velocity data resulted in 6 uncorrelated factors retaining 96% of the variance, with all velocity-related variables loading on a single, and additional factor (Table A1). Variables related to dive depth and duration, including bottom time were strongly correlated with factor 1, whereas those defining skewness of dives loaded heavily on factor 2 (Table A1). Variables that loaded heavily on factor 3 included those defining the relationship between bottom time and dive duration and depth. Variables most correlated with factor 4 were related to ascent and descent rates, and relationship between maximum depth and dive duration. Factor 5 captured the variability in the number of wiggles, while factor 6 described velocity data.

Using PCs scores from these two PCAs to classify two sets of 1000 dives randomly drawn from the sub-dataset (Fig. A1) resulted in both cases in a 7 cluster solution, i.e., the inclusion of velocity variables, i.e., using 6 factors, had no effect on the number of clusters identified. The final error rate associated with the classification of all 6312 dives, which was made using fine-tuned centroids summarized into 5 depth/duration PCs but developed based on cluster assignments accounting for velocity data, was 3%.

The comparison of cluster assignments for the 2204 dives with velocity data made while accounting and not accounting for velocity data in centroid definition indicated that 81 % of the dives were assigned to a cluster with similar characteristics (Table A2). The main effect (87% of the misclassified cases) of including velocity data to identify clusters was the interchange of dives between cluster # 4 and clusters 1, 3, 6 or 7 (Table A2). Cluster #4 from the sub-dataset classification comprised dives with the highest mean velocities of all clusters. Including velocities thus have led to more high velocity dives being classified in cluster #4 and conversely, less lower velocity dives being included in this cluster despite similarity in shapes. Excluding velocity variables in the classification of the full-dataset resulted in more short, shallow and slightly skew left dives being classified in cluster #4, and less high-velocity dives of various shapes being included in other clusters. Classifications of dives skewed right were very similar between the two classifications, suggesting that a high ratio of descent rate to ascent rate led to classification scheme that was not influenced by the presence or absence of velocities (Table A2).

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Table A1. Varimax-rotated factor matrix for principal components analysis using 11 dive variables (from full-dataset) and 14 dive variables (from sub-dataset) obtained from radio-tracked St. Lawrence Estuary (SLE) belugas (*Delphinapterus leucas* (Pallas, 1776)) equipped with time-depth-velocity recorders (2001-2005). Highest loading for each variables are shown in bold.

Full-dataset		Varimax-Rotating Factor Loading					
Variables (11: depth, duration)	1	2	3	4	5	Communality	
Duration	0.94	0.05	0.20	-0.17	0.20	0.99	
Maximum Depth	0.92	0.09	-0.05	0.31	0.17	0.98	
Bottom Time	0.80	0.05	0.56	-0.03	0.16	0.99	
Max. Depth / Duration	-0.23	0.03	-0.42	0.84	-0.09	0.94	
Bottom Time / Duration	0.09	0.01	0.96	0.20	0.03	0.98	
Bottom Time / Max. Depth	0.22	-0.03	0.89	-0.37	0.07	0.98	
\bar{x} Ascent Rate	0.18	-0.44	0.17	0.83	-0.03	0.95	
\bar{x} Descent Rate	0.29	0.59	0.15	0.70	0.00	0.95	
\bar{x} Ascent Rate / \bar{x} Descent Rate	0.00	-0.96	-0.03	-0.03	0.00	0.93	
\bar{x} Descent Rate / \bar{x} Ascent Rate	0.12	0.94	-0.05	-0.16	0.04	0.93	
Wiggle	0.33	0.03	0.08	-0.06	0.94	1.00	

Sub-dataset		Varimax-Rotating Factor Loading					
Variables (14 : depth, duration, speed)	1	2	3	4	5	6	Communality
Duration	0.95	-0.01	0.04	-0.18	0.17	0.17	0.99
Maximum Depth	0.91	0.07	0.12	0.32	-0.11	0.13	0.99
Bottom Time	0.82	0.01	0.05	-0.07	0.54	0.14	0.99
Max. Depth / Duration	-0.22	0.12	0.08	0.83	-0.42	-0.09	0.95
Bottom Time / Duration	0.08	0.04	0.03	0.14	0.98	0.02	0.98
Bottom Time /Max. Depth	0.19	-0.08	-0.05	-0.42	0.87	0.06	0.98
\bar{x} Ascent Rate	0.14	0.17	-0.42	0.85	0.12	-0.04	0.95
\bar{x} Descent Rate	0.26	0.12	0.63	0.69	0.08	-0.02	0.95
\bar{x} Ascent Rate / \bar{x} Descent Rate	-0.01	0.02	-0.96	-0.04	-0.03	-0.02	0.92
\bar{x} Descent Rate / \bar{x} Ascent Rate	0.11	-0.03	0.94	-0.17	-0.05	0.02	0.93
Wiggle	0.31	-0.07	0.03	-0.07	0.07	0.94	1.00
\bar{x} Bottom Velocity	-0.07	0.96	-0.02	0.02	0.02	-0.04	0.93

\bar{x} Ascent Velocity	0.06	0.93	0.02	0.13	-0.01	0.01	0.88
\bar{x} Descent Velocity	0.08	0.91	-0.03	0.15	-0.06	-0.06	0.87

Table A2. Frequency distribution of the 2204 dives from radio-tracked SLE belugas (*Delphinapterus leucas* (Pallas, 1776)) equipped with time-depth-velocity recorders (2001-2005) with velocity data among the seven dive clusters, when classified using a k-means approach and principal components accounting (vertical) and not accounting (horizontal) for velocity-related variables.

Dive frequency/cluster : full-dataset classification								
Dive frequency /cluster : sub-dataset classification	Clusters	1	2	3	4	5	6	7
	1	355	0	0	106	0	1	6
	2	4	296	6	5	0	1	15
	3	0	3	214	4	0	1	1
	4	33	0	110	172	0	0	0
	5	0	4	3	0	255	5	5
	6	0	1	0	53	0	229	0
	7	0	0	4	41	0	4	267

FIGURES

Figure A1. Flow chart describing the multivariate approach used for clustering of SLE beluga (*Delphinapterus leucas* (Pallas, 1776)) dives obtained from radio-tracked individuals equipped with time-depth-velocity recorders (2001-2005).

[2204 dives with velocities (Sub Dataset) + 4108 dives without velocities]

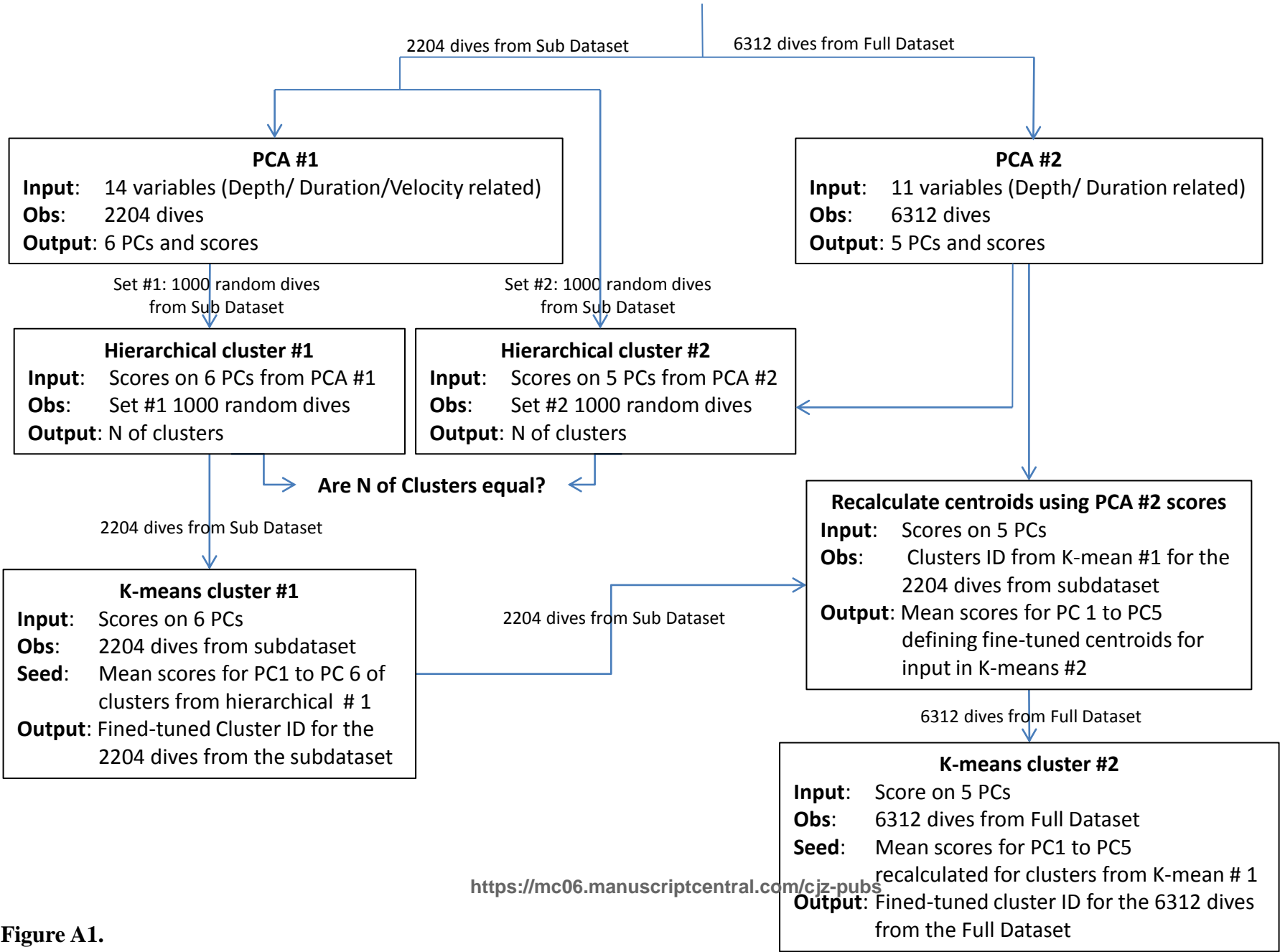


Figure A1.

APPENDIX B.

Dive bout analyses

METHODS

Dive bouts have been defined either by using a bout ending criterion (BEC) based on post-dive intervals or diving depths (Mori et al. 2001; Luque and Guinet 2007), or by comparing mean and variance of the characteristics of successive dives or blocks of dive to identify dissimilarities in characteristics using standard statistical tests (Boyd et al. 1994). While the BEC used in the first approach can take a different value from one individual to another, it assumes uniformity across time and activities for a given individual. The second approach allows more flexibility in the characteristics defining the end of a behavioural unit, but assumes homogeneity within behavioural unit in dive characteristics.

Given the expectation that St. Lawrence Estuary belugas (*Delphinapterus leucas* (Pallas, 1776)) engage in multiple distinct behaviours over the period of deployment, and building on previous studies which recognize that some heterogeneity in dive characteristics within a behavioural unit occurs (Halsey et al. 2007), we propose a modification the Boyd et al. (1994) approach to account for these aspects. We used the scores for Factor 1 obtained from the principal component analysis of the full-dataset (PCA#2 in Fig. A1) to determine the BEC. Factor 1 essentially captures variability in diving depth, duration and bottom time in our study (see Results). Given that the data were standardized to a mean of zero and standard deviation of 1, we defined the start of the first bout as the first sequence of three dives with Factor 1 scores uniformly higher (longer/deeper dives) or lower (shallower/shorter dives) than the mean, i.e., 0. We then

compared the mean score of these three dives with that of the following three dives, instead of just one as in Boyd et al. (1994), to acknowledge some degree of stochasticity in dive characteristics and avoid bout termination as a result of one dive being different from the others. We compared the means using a t-test. If the means did not differ significantly, the fourth dive was moved from the second to the first block, the mean score recalculated over the four dives, and compared to the mean of the next three dives. These steps were repeated until a significant difference was found (t-test, $p > 0.05$) corresponding to the end of a bout, and beginning of the next one.

Dive bouts were finally characterized using mean scores for the 5 PCs obtained previously (PCA#2 in Fig. A1), and classified using a combination of non-hierarchical and hierarchical cluster analysis to identify the optimal number of distinct individual behavioural units (bout types).

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