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ARTICLE

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

S. Lemieux Lefebvre, V. Lesage, R. Michaud, and M.M. Humphries

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 additionally 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, 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*.

Résumé : Les études du comportement des animaux plongeurs se concentrent habituellement sur les plongées individuels ou les activités de groupes en surface, mais ces observations complémentaires sont rarement combinées dans une même étude. Nous étudions le comportement estival (de juin à octobre) de bélugas (*Delphinapterus leucas* (Pallas, 1776)) de l'estuaire du fleuve Saint-Laurent en combinant des données à fine échelle sur des plongées individuels obtenues de 27 déploiements d'enregistreurs de temps–profondeur–vitesse (de 2002 à 2005) à des données sur l'activité en surface de 1413 suivis de troupeaux (réalisés de 1991 à 2012). Nous avons classé 6312 plongées en sept types de plongées en fonction de la forme et de la vitesse de nage. Les plongées ont ensuite été combinés en cinq types d'épisodes, dont trois pélagiques, un benthique et un près de la surface. Nous avons classé les activités en surface des troupeaux en six groupes se distinguant principalement par leurs motifs de déplacements associés (erratiques ou directionnels), puis selon la structure et la dispersion du troupeau et la présence d'évènements acrobatiques à la surface. Enfin, nous avons utilisé des suivis de troupeaux réalisés durant le suivi d'un individu en particulier pour relier les types de plongées et d'épisodes aux activités en surface. Les résultats indiquent que les déplacements erratiques à la surface étaient plus fréquemment associés à des plongées benthiques, potentiellement, à des comportements comme l'approvisionnement benthique, le repos, la socialisation et le soin des jeunes. Les mouvements directionnels en surface étaient plus fréquemment associés à des plongées pélagiques vraisemblablement utilisés durant l'approvisionnement pélagique, l'exploration et le déplacement sur de longues distances. [Traduit par la Rédaction]

Mots-clés : comportement, béluga du Saint-Laurent, classification des plongées, activités en surface, *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) that 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 biologging technologies and animal-borne tags has enabled the remote measurement of surface and subsurface behaviours at fine spatial and temporal scales (Mann 1999; Ropert-Coudert et al. 2009). Although early biologgers documented only depth changes (Kooyman 1981; Schreer et al. 2001), the availability of other sensors, such as velocimeters (Lesage et al. 1999*b*; Doniol-Valcroze et al. 2011), thermometers (Lesage et al.

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1999*b*), 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. Although behavioural studies relying on focal group follows often have less spatial and temporal resolution compared with 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 biologging techniques and direct observation of their surface behaviour and that of their herd are combined with a long-term data set 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 vary 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

Classification of herd surface activities

Data collection

We followed over 2500 beluga 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 the majority 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, as well as 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. 4845 km^2) before 1996, but was limited to its central portion from 1996 to 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 the water.

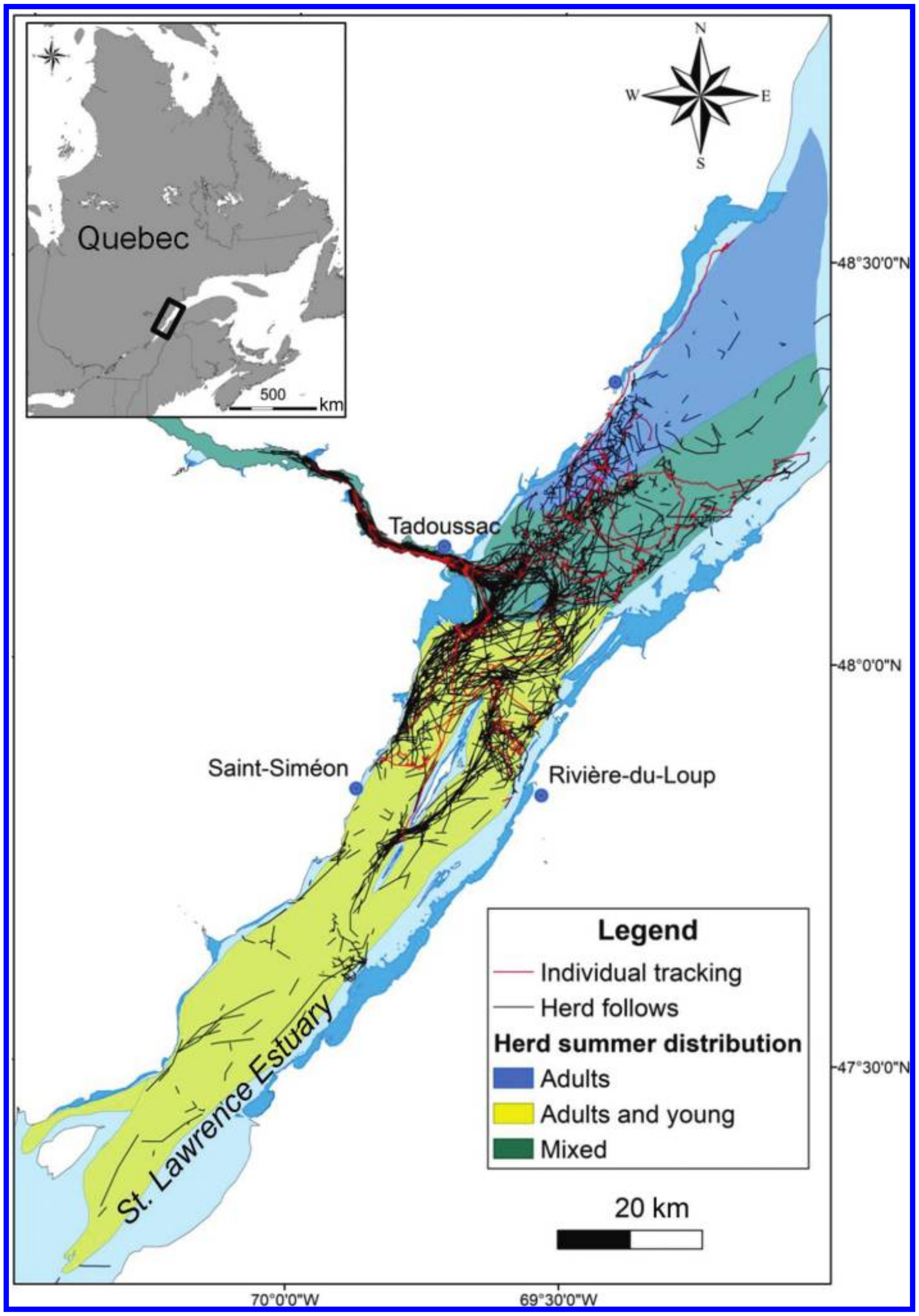
We defined a herd as an assemblage of groups in which intergroup distances were small compared with the extent of the herd, generally within a few tens or hundred metres of each other. Groups were composed of animals swimming within one body length of each other, generally in a coordinated fashion. We 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 consisted of information on herd size, herd type (adult: white individuals only; adult–grey: white individuals and grey colored subadults and young; adult–grey–calf: white individuals, grey colored subadults and young, and young of the year), and radius of the herd spatial extent, as well as 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 3 h 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 the pseudo t^2 criteria (SAS Institute Inc. 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 postclassify 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 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 ANOVAs and post hoc Tukey's test. Confor-

Fig. 1. Summer distribution of St. Lawrence Estuary (SLE) beluga (*Delphinapterus leucas*) in Quebec, Canada, with sectors were mainly herd of adults are encountered shown in blue, sectors with herds of adults and young shown in yellow, and sectors were 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; years 1991–2012), whereas red lines correspond to the radio-tracking positions of individual equipped with a time–depth–velocity recorder, which provided the data used to classify individual diving profiles (n = 27; years 2001–2005).



mity to ANOVA assumptions of absence of outliers, homoscedasticity, and normality of residuals were investigated through visual inspection of histograms of residuals, 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 χ^2 test, with a post hoc evaluation of the contribution of individual frequencies of herd types per SA to significance (package polytomous in R).

Classification of radio-tracked individual diving behaviour

Data collection

From 2001 to 2005, we deployed archival tags on 45 individual belugas, 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, Washington, USA) and a 300 g radio transmitter (Telonics Inc., Mesa, Arizona, 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 crossbow 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 (±0.05 m/s) every second from which other dive characteristics were extracted for analysis (Appendix A).

Table 1. Categories and description of each input variables used for the cluster analysis of St. Lawrence Estuary (SLE) belugas (*Delphinapterus leucas*) herd surface activities.

Variable	Type	Categories	Description	Frequency of occurrence: Absolute number	Frequency of occurrence: % relative to total number
Predominant movement pattern	Nominal	Directional	Continuous unidirectional movement	1727	48
		Multidirectional	Directional movement with frequent deviation of the principal axes	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 <100 m	1720	48
		Loose	Distance between individuals or groups = 100–300 m	1116	31
		Dispersed	Distance between individuals or groups >300 m	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

Principal components and cluster analyses

We classified dives using a combination of multivariate data analysis following the method developed by Lesage et al. (1999*b*). 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 data set and to obtain the corresponding cluster centroid values. Using these cluster centroids as seeds, we fine-tuned the classification using a nonhierarchical *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 position 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 with 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 belugas 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 χ^2 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.

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's 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's 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

Classification of herd surface activities

A total of 3585 summary surveys, obtained from 1413 beluga 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; however, the "form" and "structure" variables, which were

Table 2. Relative frequencies (%) for ordinal, nominal, and seminominal variables and means for numerical variables associated with the six herd surface activity types identified from surface focal follows of SLE belugas (*Delphinapterus leucas*) (n = 3585; years 1991–2012).

		Surface activity types					
Variable	Categories	Milling-E	Milling	Mixed	Dir-D	Dir-M	Dir-T
Predominant movement pattern	Directional	0	0	62	100	0	97
	Multidirectional	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 (no. of individuals)	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

Note: Main characteristics for the various surface activities are as follows — 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); multidirectional movements (Directional-M or Dir-M); directional movements in tight herds (Directional-T or Dir-T).

categorized as broken and uniform, in 94% and 88% of the cases, respectively, were closer to a Poisson distribution (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 six SA types (Supplementary Fig. S1).[1] SA were mainly differentiated by their associated PMP, but also their structure, degree of dispersion, and the occurrence of surface events and vocalizations (Table 2). Herd type (χ^2 test: $\chi^2_{[10]} = 101.76$, $p < 0.0001$), size ($F_{[5,1]} = 25.33$, $p < 0.001$), and radius ($F_{[5,1]} = 147.1$, $p < 0.001$) also varied significantly among SA (Table 2).

Milling SA

Cluster 1 (hereafter Milling SA) and cluster 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 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 comprised herds that exclusively displayed a multidirectional 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 comprised 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,

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[1] Supplementary figures are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0015.

Table 3. Mean (±SD) values of time–depth derived variables per dive type identified based on the final *K*-mean clustering of the full data set (*n* = 6312) for radio-tracked SLE belugas (*Delphinapterus leucas*) (years 2001–2005).

	Dive types						
							
Variable	Square-W	Square-U	v-Fast	v-Slow	v-Deep	Skew-R	Skew-L
Dive duration (s)	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 (s)	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
Maximum 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/maximum 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
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
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
Ascent rate/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
Descent rate/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
Number of wiggles	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
Ascent velocity	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
Descent velocity	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
Bottom velocity	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
% 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
% less 3 m	29.62	32.54	5.49	3.20	16.43	12.96	13.83

Note: Characteristics related to velocity data (*n* = 2206) and distance relative to the sea floor (*n* = 3125) are calculated based only on dives with available data. Velocity statistics are presented relative to the maximum recorded for each individual and thus are unitless.

whereas herds with calves were more frequently involved in Directional-T than in Directional-D.

Classification of radio-tracked individual diving behaviour

Forty-five VHF tags were successfully attached to belugas but only 44 were retrieved after deployment. Of these, 32 provided data on individual and herd surface behaviours, but 5 failed to record diving data. The remaining 27 follows provided 6312 true dives (i.e., nonrespiratory), of which one-third (2204 dives) had valid velocity data. Belugas 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 median 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 seven cluster solution to describe individual dive characteristics (Appendix A; Supplementary Fig. S2[1]).

Dive types

Square dives

Two different types of square dives were identified (types 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 one-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.

V-shaped dives

Three different types of V-shaped dives were identified (clusters 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 dives of types 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%).

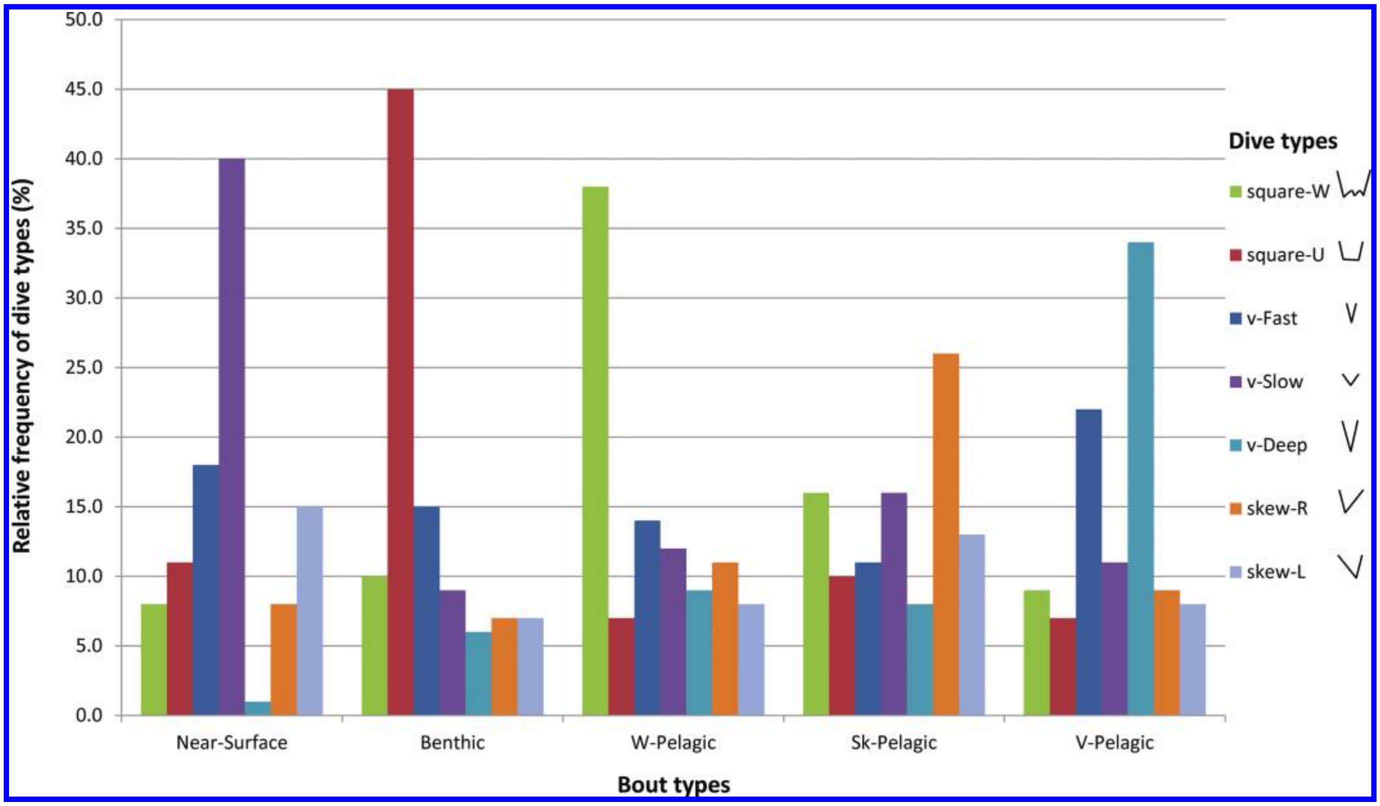
Type 1 dives were short and shallow (hereafter v-Slow dives) and were characterized by the lowest dive duration, maximum depth, and bottom time (Table 3). They were also generally slightly skewed to the right, with a slower ascent than descent rate. During these dives, 35% of the time was spent in the 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 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 (types 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 rela-

Fig. 2. Relative frequency of dive types per dive bout types for radio-track SLE belugas (*Delphinapterus leucas*) equipped with time–depth–velocity recorders (years 2001–2005). Dive types are represented based on their general shape and time–depth–velocity characteristics as follows: Square-W corresponding to long and relatively deep dives with wiggles; Square-U corresponding to square-shaped with long duration and bottom phase dives; v-Fast corresponding to fast, short, and shallow dives; v-Slow corresponding to slow, short, and shallow dives; v-Deep corresponding to deep v-shaped dives; Skew-R corresponding to long, deep, and skewed to the right dives; 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 as follows: Near-Surface bouts mostly related to shallow and v-Slow dives; Benthic bouts related to Square-U dives occurring near the sea floor; W-Pelagic bouts related to pelagic Square-W dives; Sk-Pelagic bouts related to pelagic and Skew-R dives; V-Pelagic bouts related to pelagic and v-Deep dives.



tively 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, 20% doing Skew-R dives, and 19% doing 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 nonrespiratory dives. The three V-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 (Supplementary Fig. S3),[1] 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 with dives performed during other bout types and rarely (8%) to the 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 consisted 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

Table 4. Mean (±SD) variable values for dives of radio-tracked SLE belugas (*Delphinapterus leucas*) (years 2001–2005) from the full data set (n = 5816) within each dive bout cluster.

	Bout types				
Variable	Near-Surface	Benthic	W-Pelagic	Sk-Pelagic	V-Pelagic
n	158	50	41	87	68
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 (s)	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 (s)	30.44±51.50	112.36±116.16	95.01±110.85	67.41±80.40	48.21±68.69
Maximum 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/maximum depth	4.04±4.77	9.14±8.82	4.11±4.01	3.62±3.56	2.15±2.00
Ascent rate (m/s)	0.30±0.18	0.49±0.28	0.43±0.26	0.34±0.21	0.63±0.30
Descent rate (m/s)	0.31±0.20	0.54±0.33	0.56±0.34	0.51±0.33	0.60±0.33
Ascent rate/descent rate	1.38±1.62	1.49±2.30	1.07±1.10	0.98±1.08	1.33±1.07
Descent rate/ascent rate	1.49±1.69	1.51±1.96	1.87±1.96	2.07±2.11	1.22±1.41
Number of wiggles	0.14±0.46	0.16±0.44	0.92±1.32	0.29±0.66	0.16±0.49
Ascent velocity	0.33±0.12	0.38±0.13	0.38±0.13	0.40±0.13	0.43±0.11
Descent velocity	0.33±0.12	0.37±0.12	0.34±0.11	0.39±0.12	0.42±0.11
Bottom velocity	0.34±0.14	0.37±0.15	0.33±0.13	0.38±0.13	0.40±0.14
% to bottom	0.22±0.27	0.69±0.26	0.48±0.30	0.42±0.36	0.34±0.34
% less 3 m	7.94	49.39	10.51	17.23	13.00

Note: Velocity (n = 2034) and relation to bottom (n = 2873) are calculated for dives with available values among the full data set. For definitions of bout types refer to the main text.

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) consisted 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 with 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 to 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.

Association between individual dives and herd surface activities

Fisher's 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 frequency of bout types 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 SA (Fig. 4).

Mixed

Dive types performed by tagged individuals in herds displaying a Mixed SA were characterized by higher frequencies of v-Slow (26%) and Square-U (19%) dives, as well as higher occurrence of Sk-Pelagic (27%) and Benthic (36%) bouts (Fig. 4).

Directional-D

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

Directional-M

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

Table 5. Pairwise comparison of the frequency of dive types among surface activity clusters, obtained from SLE belugas (*Delphinapterus leucas*) equipped with time–depth–velocity recorders and from herds surface focal follows, respectively (years 2001–2005).

	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**

Note: Adjusted *p* values from Fisher's test are presented. Values in boldface type are statistically significant ($\alpha = 0.05$).

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

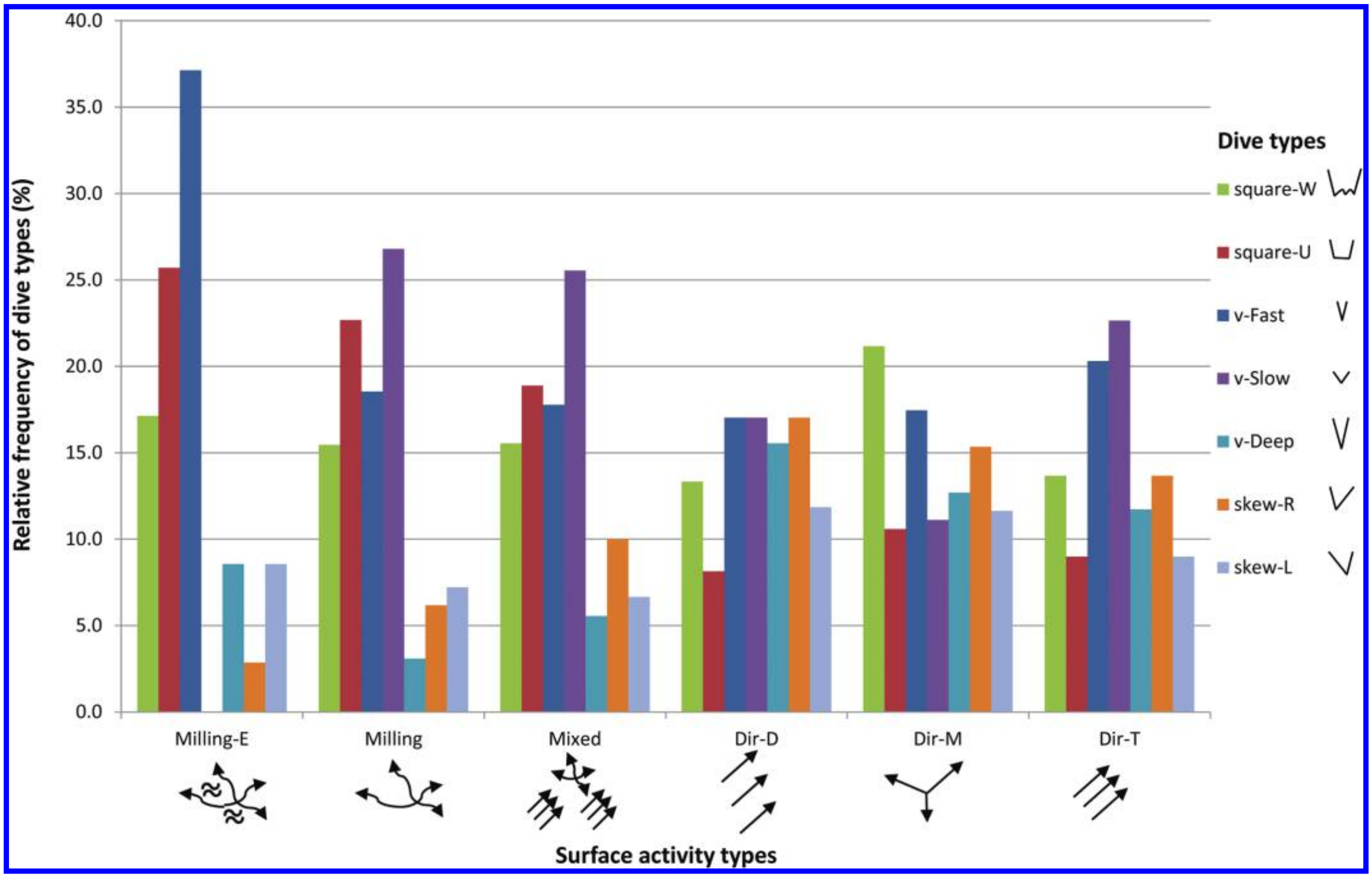


Table 6. Pairwise comparison of the frequency of bout types among surface activity clusters, obtained from SLE belugas (*Delphinapterus leucas*) equipped with time–depth–velocity recorders and from herds surface focal follows, respectively (years 2001–2005).

	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

Note: Adjusted *p* values from Fisher's test are presented. Values in boldface type are statistically significant ($\alpha = 0.05$).

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

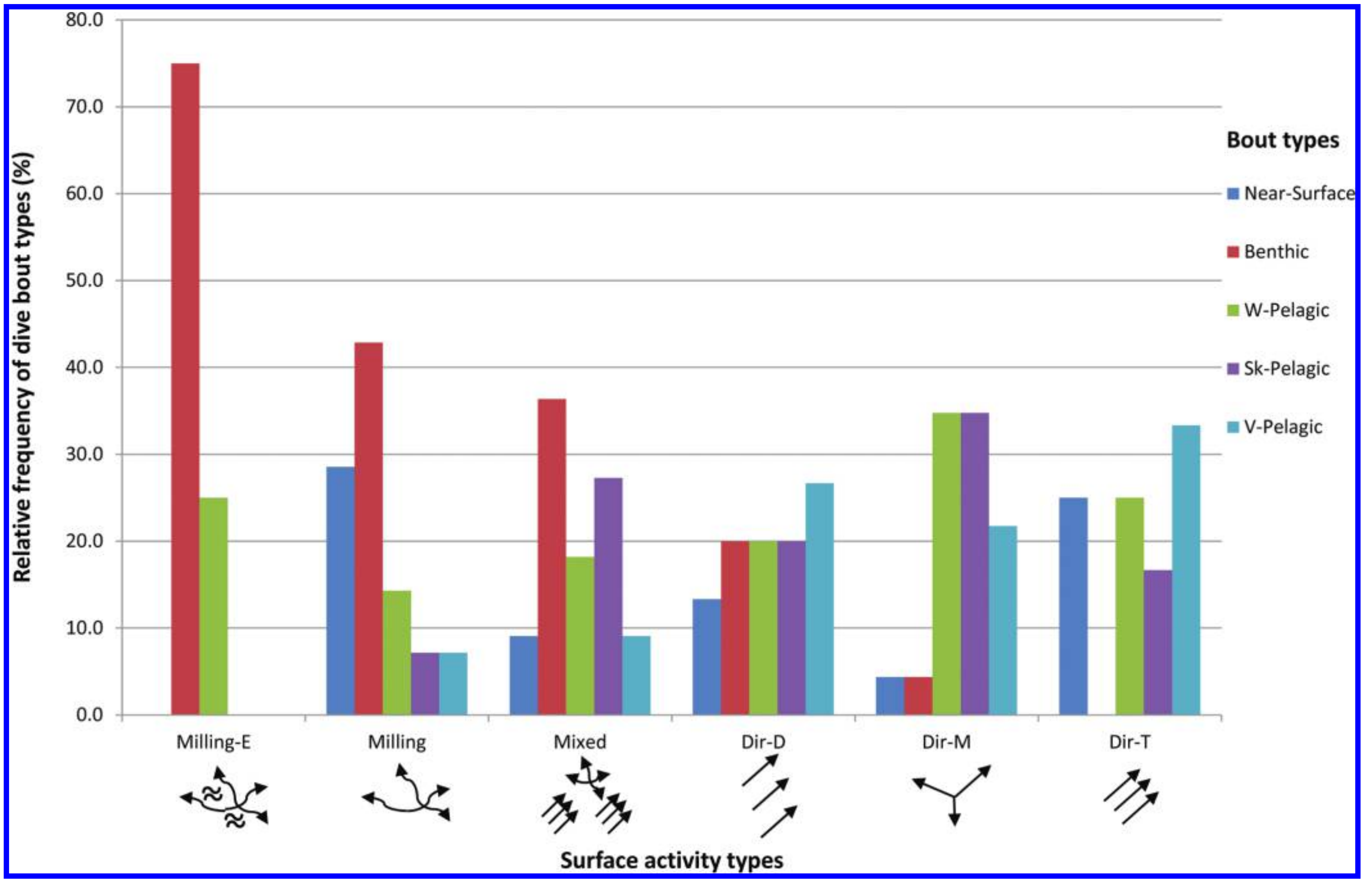
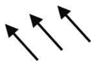
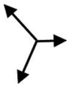
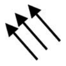


Table 7. Summary of main characteristics of surface activity clusters derived from herd surface focal follows of SLE belugas (*Delphinapterus leucas*) (n = 3585; years 1991–2012) and of their associated dive and bouts types, both obtained from radio-tracked individuals equipped with time–depth–velocity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

	Surface activities					
						
Variable	Milling-E	Milling	Mixed	Dir-D	Dir-M	Dir-T
Predominant movement pattern	Milling	Milling	Milling and directional	Directional	Multidirectional	Directional
Radius	Medium	Small	Large	Large	Medium	Small
Herd size	Large	Medium	Small	Small	Medium	Medium
Herd type	Mixed	With calf	Rarely with calf	Adults	Mixed	With calf
Other characteristics	Surface events and 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

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 SA 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 SA 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; Degrati et al. 2013) with the PMP representing a driving factor in SA clustering (>97% frequency for one PMP in five of the six SA clusters; Table 2).

However, other variables (occurrence of surface events and surface vocalizations, degree of dispersion, and structure) were important for further differentiating herds displaying similar PMP but different SA (Table 2). Hence, considering only movement patterns to identify SA 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.

Dive 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. 1999*b*; 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 belugas, 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 that they are also used for other purposes.

The most frequent dives performed were v-Slow dives; 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 the 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 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. 1999*b*; 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 dive with an added search or foraging component during the ascent phase, a function suggested for harbour seals (*Phoca vitulina* Linnaeus, 1758) (Lesage et al. 1999*b*). 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 Sk-Pelagic bouts suggests that they can also be used during bouts of activity involving higher swim velocity, as well as 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 that 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 Sk-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 SA 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 SA. 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 1986; Lesage et al. 1999*a*; 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; Degrati 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 SA described for SLE belugas 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 (1986) when observing Hudson Bay belugas 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), as well as 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 recognized 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 vocalizations have been previously linked to social interactions in belugas (Sjare and Smith 1986; Lesage et al. 1999*a*; 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 benthic foraging, resting, or 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; Degrati 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 Sk-Pelagic bouts and Benthic bouts (Fig. 4). Accordingly, it showed characteristics intermediate between SA that involved milling and SA that involved 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 SA 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 herds 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 characterized by different types of directional PMP. Directional movement can be used for different purposes, but travelling is the behaviour most often associated with a directional movement pattern (e.g., Lusseau 2003; Stelle et al. 2008; Steiner 2011; Degrati 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 (Figs. 3 and 4).

The multidirectional PMP observed during Directional-M is characterized 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 Sk-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 that 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 SA.

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 to be 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; Degrati 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 St. Lawrence Estuary than herds of subadult and adult males (Michaud 1993, 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 with 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 SA indicating that SLE belugas 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 St. Lawrence Estuary, 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). Although seasonal variations in energy requirements and foraging intensity are poorly known for SLE belugas (for a review see Lesage 2014), it is suspected, based on historical data from hunted individuals and local knowledge, that the spring is a period of intensive feeding in the St. Lawrence Estuary. However, foraging also occurs on a regular basis during summer, a finding that 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 belugas (Lesage 2014). The available data are, 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 SA were complex and multiple behaviours were often associated with a given dive type or SA. These results reflected our perception that classifications may not allow one 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 SLE belugas for specific functions.

This study demonstrates the added value of using information from individual dives to enhance the understanding of behaviours related to SA 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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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 extracted various statistics including dive duration, maximum depth, bottom time, mean descent rate, mean ascent rate, mean ascent velocity, mean bottom velocity, mean descent velocity, and number of wiggles. The bottom phase was defined as the interval between the first and the 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 rate/ascent rate, ascent rate/descent rate.

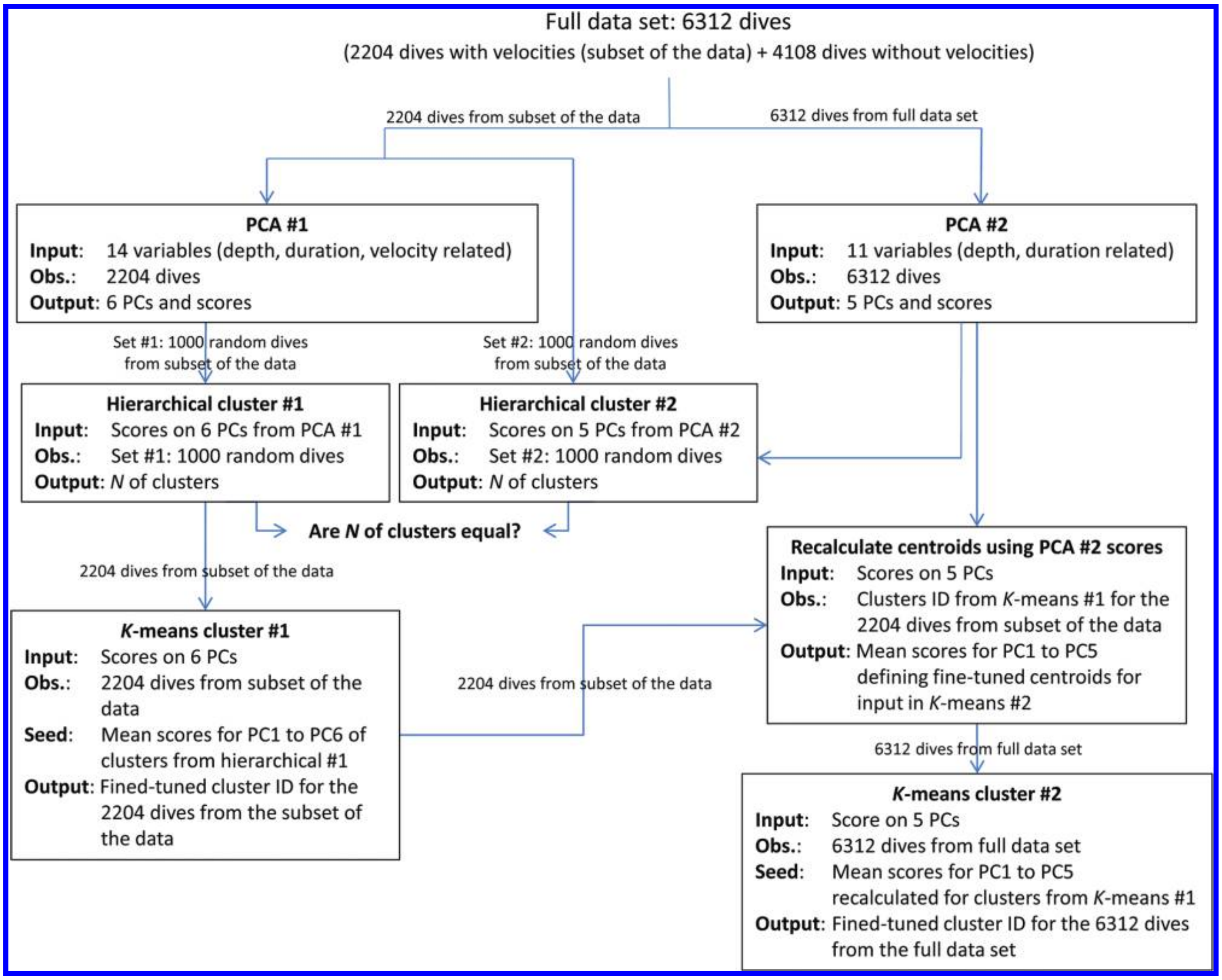
We used a log-survivorship analysis to identify breakpoints in dive duration between dives that were part of a breathing sequence and true dives, as the former are expected to be shorter and more abundant than the latter. We selected breakpoint values independently for each individual because variation 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 (Kolmogorov–Smirnov test) prior to the PCA, with transformations applied when improving distribution. We included all variables in the analysis regardless of the degree of normality attained because the series of statistical methods used in this study are robust to departures from normality, although normality helps to maximize clarity of the results (Hair et al. 1995; Lesage et al. 1999). However, we excluded a set of seven dives, characterized by particularly long postdive intervals, from the multivariate analyses; those were recorded from a single animal resting near the surface and would have been considered to be 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 one-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 (subset of the data) (PCA #1 in Fig. A1), and a second time using the full set of 6312 dives but using only the 11 depth- and duration-related variables that were common to all observations (full data set) (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,

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



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 six PCs that were obtained from the PCA #1.The second hierarchical cluster analysis (Hierarchical cluster #2 in Fig. A1) used scores for PC1 to PC5 obtained from the PCA #2, i.e., considering only depth- and duration-related variables (Fig. A1). The number of clusters best describing each data set was determined based on the concordance between the cubic clustering, the pseudo *F*, and the 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., PC1 to PC6 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 nonhierarchical, 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 in 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 data set of 6312 dives (i.e., PCA #2 in Fig. A1).These fine-tuned centroids, summarized into five depth and 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 data set. 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 data set while excluding velocity-related variables, the PCA reduced the 11 depth- and duration-related variables to 5 uncorrelated factors, which retained 97% of the initial variance. Running the PCA on the subset of the data containing only dives with valid velocity data resulted in six uncorrelated factors retaining 96% of the variance, with all velocity-related variables loading on a single additional factor (Table A1). Variables related to dive depth and duration, including bottom time, were strongly correlated with factor 1, whereas those defining skew-

Table A1. Varimax-rotated factor matrix for principal components analysis using 11 dive variables (from full data set) and 14 dive variables (from subset of the data) obtained from radio-tracked St. Lawrence Estuary (SLE) belugas (*Delphinapterus leucas*) equipped with time–depth–velocity recorders (years 2001–2005).

	Varimax-rotating factor loading						
Variable	1	2	3	4	5	6	Communality
Full data set (11 variables; depth, duration)							
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
Maximum 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/maximum depth	0.22	−0.03	**0.89**	−0.37	0.07		0.98
Mean ascent rate	0.18	−0.44	0.17	**0.83**	−0.03		0.95
Mean descent rate	0.29	0.59	0.15	**0.70**	0.00		0.95
Mean ascent rate/mean descent rate	0.00	**−0.96**	−0.03	−0.03	0.00		0.93
Mean descent rate/mean ascent rate	0.12	**0.94**	−0.05	−0.16	0.04		0.93
Number of wiggles	0.33	0.03	0.08	−0.06	**0.94**		1.00
Subset of the data (14 variables: depth, duration, speed)							
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
Maximum 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/maximum depth	0.19	−0.08	−0.05	−0.42	**0.87**	0.06	0.98
Mean ascent rate	0.14	0.17	−0.42	**0.85**	0.12	−0.04	0.95
Mean descent rate	0.26	0.12	0.63	**0.69**	0.08	−0.02	0.95
Mean ascent rate/mean descent rate	−0.01	0.02	**−0.96**	−0.04	−0.03	−0.02	0.92
Mean descent rate/mean ascent rate	0.11	−0.03	**0.94**	−0.17	−0.05	0.02	0.93
Number of wiggles	0.31	−0.07	0.03	−0.07	0.07	**0.94**	1.00
Mean bottom velocity	−0.07	**0.96**	−0.02	0.02	0.02	−0.04	0.93
Mean ascent velocity	0.06	**0.93**	0.02	0.13	−0.01	0.01	0.88
Mean descent velocity	0.08	**0.91**	−0.03	0.15	−0.06	−0.06	0.87

Note: Highest loading for each variables are shown in boldface type.

Table A2. Frequency distribution of the 2204 dives from radio-tracked SLE belugas (*Delphinapterus leucas*) equipped with time–depth–velocity recorders (years 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: classification based on the full data set						
	Clusters	1	2	3	4	5	6	7
Dive frequency/cluster: classification based on a subset of the data	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

ness 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, as well as relationship between maximum depth and dive duration. Factor 5 captured the variability in the number of wiggles, whereas factor 6 described velocity data.

Using PCs scores from these two PCAs to classify two sets of 1000 dives randomly drawn from the subset of the data (Fig. A1) resulted in both cases with a seven cluster solution, i.e., the inclusion of velocity variables (i.e., using six 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 five depth and 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 cluster 1, 3, 6, or 7 (Table A2). Cluster 4 from the classification based on a subset of the data comprised dives with the highest mean velocities of all clusters. Thus, including velocities 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 data set resulted in more short, shallow, and slightly skewed to the 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 a classification scheme that was not influenced by the presence or absence of velocities (Table A2).

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Appendix B: dive bout analyses

Methods

Dive bouts have been defined either by using a bout ending criterion (BEC) based on postdive 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). Although 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 it assumes homogeneity within behavioural unit in dive characteristics.

Given the expectation that SLE belugas 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 of the Boyd et al. (1994) approach to account for these aspects. We used the scores for factor 1 obtained from the PCA of the full data set (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 0 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 and deeper dives) or lower (shorter and shallower 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 to avoid bout termination as a result of one dive being different from the others. We compared the means using a Student's t test. If the means did not differ significantly, then the fourth dive was moved from the second to the first block, the mean score was recalculated over the four dives, and compared with the mean of the next three dives. These steps were repeated until a significant difference was found (Student's 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 five PCs obtained previously (PCA #2 in Fig. A1) and classified using a combination of nonhierarchical and hierarchical cluster analysis to identify the optimal number of distinct individual behavioural units (bout types).

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