Cue rates and surfacing characteristics of sei whales (*Balaenoptera borealis*) in the Falkland Islands

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ABSTRACT

The cue rate (CR: blows per whale per hour), surfacing characteristics and swim speeds of sei whales (*Balaenoptera borealis*) were quantified from focal follows carried out at Berkeley Sound (East Falkland) between January and May 2017 and off the west coast of West Falkland between February and April 2018. In Berkeley Sound, focal follows were conducted from Cape Pembroke lighthouse and from a small boat. In West Falkland all focal follows were conducted from a yacht. Thirty-seven focal follows of sei whale individuals or groups (2–5 individuals) were analysed to produce CRs ranging from 21.99 to 46.73, with a mean of 31.46 (SD = 5.12). There was no significant difference in the CRs observed from shore vs. boat platforms or between the two study areas. Maximum submergence times exceeding 13min were recorded from both individuals and groups. The durations of 51 whale surfacing events had a mean of 6.4s (SD = 1.7). The average swim speed during boat-based sei whale focal follows was 5.7kmh−1. The inter-breath intervals (IBIs) recorded from 13 solitary individuals ranged from 77.2 to 180.1s, with an overall mean of 118.6s (SD = 137.6). A combined approach incorporating IBI parameters and sequence pattern was used to classify 270 IBIs into surface dives (mean = 37.2s), intermediate dives (mean = 113.7s) and true dives (mean = 332.6s). Individuals showed marked variation in dive pattern, with some exhibiting clear cycles of true dives interspersed with surface bouts while others routinely took intermediate-duration dives interspersed by single surfacings. Sei whales in Berkeley Sound exhibited a higher proportion of surface dives than whales in West Falkland, and those surface dives were of lower mean and median IBI. Individual sei whales had surface bouts comprising a mean of 3.8 blows and a mean IBI of 33.4s. These are the first quantifiable data on surfacing-dive patterns and CRs for sei whales in the Falkland Islands and across the wider range of the species. The data have conservation and management relevance, including addressing availability bias for line transect and cue count abundance estimates, incorporation into vessel strike modelling, and understanding foraging behaviour.

KEYWORDS: CUE RATES; DIVING; FALKLAND ISLANDS; SOUTH ATLANTIC; SOUTHERN HEMISPHERE; SURVEY – AERIAL; SURVEY – SHORE-BASED; SURVEY – VESSEL; SWIM SPEED

INTRODUCTION

The collection of data on cetacean dive duration and surfacing behaviour is relevant to several aspects of their management and conservation including assessing energetic costs (Sumich, 1983; Acevedo-Gutiérrez *et al.,* 2002), investigating responses to anthropogenic disturbance (Ljungblad *et al.,* 1988; Argüelles *et al.,* 2016), and producing estimates of the amount of time that animals are at the surface and thus available for visual detection during abundance and cue-counting surveys (Øien *et al.,* 1990; Hiby, 1992; Heide-Jørgensen and Simon, 2007). In addition, knowledge of the breath frequency, dive interval, surfacing behaviour and swim speed of whales is important for understanding the conditions in which whale encounters can lead to vessel strikes (Nowacek *et al.,* 2001; Argüelles *et al.,* 2016). Consequently, the dive behaviour of most large baleen whale species has been studied, including the North Atlantic right whale (*Eubalaena glacialis*: Nowacek *et al.,* 2001), southern right whale (*E. australis*: Argüelles *et al.,* 2016), bowhead whale (*Balaena mysticetus*: Würsig *et al.,* 1984; 1985; Ljungblad *et al.,* 1988), blue whale (*Balaenoptera musculus*: Lagerquist *et al.,* 2000; de Vos *et al.,* 2013), fin whale (*B. physalus*: Stone *et al.,* 1992; Jahoda *et al.,* 2003; Heide-Jørgensen and Simon, 2007), Bryde's whale (*B. brydei*: Alves *et al.,* 2010), common minke whale (*B. acutorostrata*: Stockin *et al.,* 2001; Heide-Jørgensen and Simon, 2007), Antarctic minke whale (*B. bonaerensis*: Friedlaender *et al.,* 2014), humpback whale (*Megaptera novaeangliae*: Heide-Jørgensen and Simon, 2007; Witteveen *et al.,* 2008) and the gray whale (*Eschrichtius robustus*: Sumich, 1983).

The duration and surfacing behaviour of cetaceans has been monitored using various techniques including satellite telemetry (Lagerquist *et al.,* 2000), time-depth recorders (TDRs) attached by suction-cups (e.g. Friedlaender *et al*., 2014; Argüelles *et al.,* 2016) and visual observations (e.g. Stone *et al.,* 1992; Heide-Jørgensen and Simon, 2007; de Vos *et al.,* 2013). It has been monitored from a wide variety of platforms including aircraft (e.g. Würsig *et al.,* 1984; Ljungblad *et al.,* 1988), boats (e.g. Jahoda *et al.,* 2003; de Vos *et al.,* 2013) and shore vantage points (e.g. Stone *et al.,* 1992; Heide-Jørgensen and Simon, 2007).

The dive behaviour of the sei whale (*Balaenoptera borealis*) has been little studied in comparison with other baleen whales, perhaps primarily due to the offshore, pelagic habitat usually occupied by the species and its unpredictable occurrence in many areas (Horwood, 1987). During a small number of sightings in the Magellan Strait (Chile) sei whales were reported to take 5–7min dives, followed by four or five blows at the surface (Acevedo *et al.,* 2017), although systematic recording of dive times was not reported. Some respiration intervals were also recorded from whale watching vessels in the Gulf of Maine in 1986, where sei whales mostly undertook shorter dives (≤ 90s) consistent with observations of surface feeding but also exhibited longer dives of 6–11min duration (Schilling *et al.,* 1992). Two sei whales were tagged with acoustic time-depth transmitters off Japan in 2013, providing data for 10 and 32hr respectively and revealing overall mean dive durations of around 3min and a maximum dive of 12.2min (Ishii *et al*., 2017).

During 2017 and 2018, research was conducted on sei whales in the Falkland Islands to collect baseline information on their distribution, ecology and behaviour (Weir, 2017; 2018). This paper presents data on the cue rate, swim speed, and the dive and surfacing characteristics of sei whales in coastal areas off East and West Falkland. The data were primarily collected to generate correction factors for an aerial abundance survey carried out in Berkeley Sound in 2017, but also because of their relevance to ongoing work including foraging behaviour and understanding vessel interactions.

METHODS

Data collection

A sei whale survey was carried out between January and May 2017 in the Berkeley Sound candidate Key Biodiversity Area (cKBA) on the east coast of the Falkland Islands (Fig. 1). A second study occurred off West Falkland between February and April 2018, focussing on the King George Bay and Queen Charlotte Bay cKBAs (Fig. 1). Both study areas were located in coastal waters with depths of ≤ 60m.

Whale surfacing behaviour was monitored from shore and boat platforms. In Berkeley Sound, shore-based observations were conducted from the Cape Pembroke lighthouse at 28m eye height. The lighthouse provided unrestricted views over Port William and across a wide expanse of open Atlantic Ocean (Fig. 1). A single observer conducted standardised visual watches for whales during favourable weather conditions (Beaufort sea state ≤ 3, visibility ≥ 5km) using the naked eye and *Bushnell Marine* 7 × 50 binoculars with a

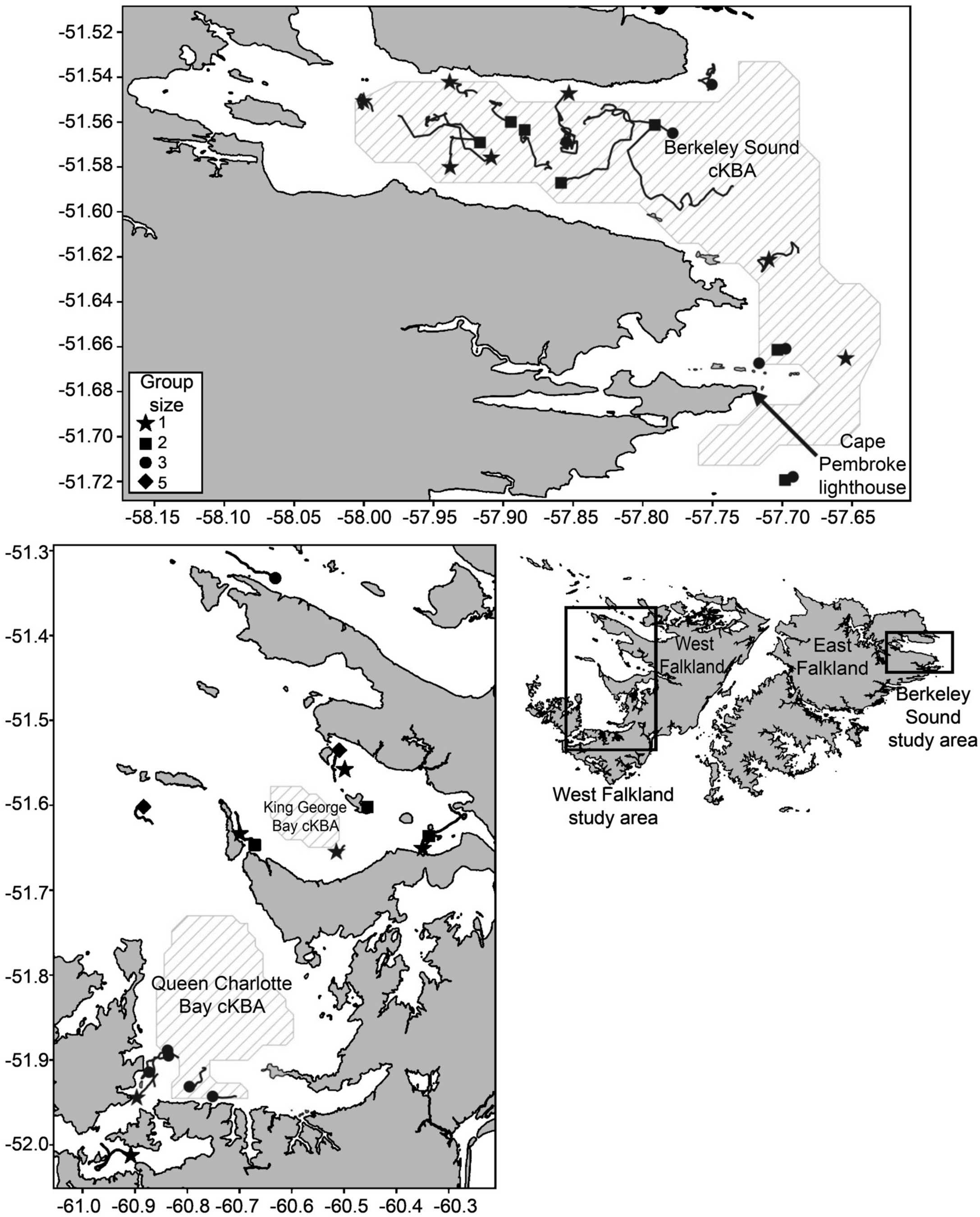


Fig. 1. Location of the Berkeley Sound and West Falkland study areas in the Falkland Islands, showing the spatial extent of the candidate Key Biodiversity Areas, the initial sighting locations for the 37 sei whale focal follows included in the study, and the tracks of the boat-based focal follows.

vertical reticle. Boat surveys were conducted in Berkeley Sound using a 6.5m rigid-hulled inflatable boat (RHIB) with twin 125-hp engines. A 19.5m motor-sailing vessel, providing a 5.1m observation eye height, was used throughout the West Falkland survey. At least two dedicated observers searched for whales continuously with the naked eye during boat surveys. More information on the general methods implemented during the surveys is available in Weir (2017; 2018).

Standardised information including group size, position and behaviour was logged for all sei whale sightings. A whale group was defined as a number of associated animals moving in the same direction and separated from one another by no more than three body lengths. Group size was visually estimated and, during small boat work, confirmed using photo-identification whenever possible. A dedicated focal follow (FF; Altmann, 1974) to collect surfacing data was initiated when the following criteria were met: (1) the sighting was at sufficient proximity that the observer was confident of detecting all blows; (2) the group size and spacing were stable so that the target animal(s) could be confidently tracked over time; and (3) prevailing light and sea conditions were favourable for detecting blows. Each focal follow ceased either: (1) when at least one hour of data had been collected; (2) if the focal animal or group was lost; or (3) immediately that group composition changed.

During each FF, whale surfacing events or 'cues' were logged verbally into a time-calibrated digital voice recorder (DVR) by the observer or directly into a laptop by a second person using a custom-designed Excel spreadsheet with an automatic timestamp (1s accuracy). A cue was defined as any appearance of a whale at the surface; this predominantly comprised the blow, but also included a small number (n = 7; 0.6%) of surfacings where the head, back or dorsal fin broke the surface without a visible blow being observed (consistent with Heide-Jørgensen and Simon, 2007).

A distance of at least 200m was usually maintained between the whales and the boat to minimise disruption to behaviour. At the end of each surfacing bout the vessel relocated to the position where the whales had submerged to maximise the detection of the subsequent surfacing. During RHIB surveys the engines were often switched off so that surfacing animals could be detected audibly as well as visually. Photo-identification data were collected using a 100–400mm zoom lens, either prior to commencing the behavioural work or opportunistically during the focal follow. Short video clips of sei whales were taken on an opportunistic basis using *GoPro* cameras (14–30fps) during 2017 and using a *DJI Phantom 4* drone (24–30fps) during 2018.

Data analysis

Only FFs that commenced when animals were < 5km from the lighthouse were included in the shore-based dataset, since it becomes difficult to accurately monitor behaviour when whales are ≥ 5km from a shore vantage point (Würsig *et al.,* 1985). For all datasets, FFs of < 20min duration were omitted from the analysis to reduce potential bias from long dives being under-recorded. A total of six shore-based FFs and 31 boat-based FFs were suitable for data analysis after this initial quality control.

The time (1s accuracy) of every whale cue logged verbally using the DVR method was extracted from the recordings using the software Audacity 2.1.2 (*http://www.audacityteam.org*). The cue rate (CR), defined as the number of cues per whale per hour, was calculated for each focal follow as: CR = $(B/D*60)/G$. Where, B is the total number of cues during D, minus 1; D is the total duration (min) of the FF, from the time of the first cue recorded to that of the last; and G is the number of individuals in the FF.

Since it was not possible to assess accurate dive duration of individual whales within a group (due to lack of overt natural markings that would make individuals recognisable at distance), a minimum dive duration (MDD) was produced for each FF. The MDD was defined as the maximum amount of time when all individuals within a focal group were submerged and provides an indication of the minimum dive duration of any individual within the focal group. A minimum average swim speed was calculated for boat-based FFs, by calculating the distance travelled by the boat during each FF using a QGIS (*https://qgis.org*) script. This definition produces a straightline horizontal swim speed across the surface and does not account for vertical movements or finer-scale spatial movements.

The duration of whale surfacing events (WSE; i.e. the time taken for an individual's body to complete a surfacing) was assessed from the video clips. Only WSEs where exact emergence and submergence times were evident were included in the analysis. Each WSE was analysed frame by frame, and the start time was extracted for the emergence of the rostrum or splashguard, or the appearance of a surge of water such as the bow-wave from the head or exhalations that commenced subsurface (i.e. any cue at the surface of the emerging whale). The completion of the WSE was defined as the total disappearance of the whale's body below the surface (usually ending with the dorsal fin tip).

Only FFs conducted on solitary sei whales (n = 13; see Table 1) were used for detailed investigation of dive types and cycles. Inter-breath intervals (IBIs) were calculated as the time elapsed between two consecutive surfacings by an individual. Only data from complete dive cycles were used to ensure adequate representation of longer dives. A complete dive cycle was defined as a long, deeper dive (i.e. true dive) followed by a full surfacing bout, or vice versa (depending on where in the dive cycle the focal follow had commenced). Initial examination of IBIs against dive sequence number for each whale revealed obvious inter-individual differences in sei whale dive pattern (Fig. 2). Consequently, it was not considered useful to define dive types by merging the IBIs from all whales and determining a single IBI cut-off point via a log-survivorship analysis (e.g. Stone *et al.,* 1992; Kopelman and Sadove, 1995; Jahoda *et al.,* 2003). Rather, a combined approach was developed that allowed for inter-individual variation in dive pattern and dive type duration. Firstly, the dive sequences for each individual were visually-inspected to determine whether or not differentiated dive types (i.e. dives that were clearly surface or true) were apparent based on duration and pattern of occurrence. For individuals that clearly exhibited differentiated dive types (n = 9), each dive was visually-categorised as surface, true or intermediate based solely on examination of that individual's dive sequence and prioritising pattern over IBI

Table 1

Sei whale cue rates recorded during 37 focal follows (FF) in the Berkeley Sound (BS) and West Falkland (WF) study areas using shore, rigid-hulled inflatable boat (RHIB) and yacht platforms. Behaviour is abbreviated as: T = Travel, F = Forage, M = Milling.

FF No.	Date	Start time (UTC)	Platform	Photo-ID no.	FF durn. (min)	Group size	Average speed (kmh^{-1})	Overall behaviour	Total no. of blows	Cue rate (cues/whale/hr)
BS–1	07/02/17	15:45	Shore	–	33.1	1	–	T	16	27.2
BS–2	07/02/17	19:05	Shore	–	39.2	2	–	T	42	31.4
BS–3	08/02/17	12:41	Shore	–	123.8	2	–	T	113	27.1
BS–4	14/02/17	17:31	Shore	–	58.2	3	–	T	108	36.8
BS–5	19/03/17	14:00	RHIB	BS–55	60.4	1	3.5	F	48	46.7
BS–6	02/04/17	13:27	RHIB	BS–62, 72	93.3	2	7.2	T	96	30.5
BS–7	09/04/17	17:54	RHIB	BS–62	21.6	1	7.5	T	12	30.5
BS–8	09/04/17	13:48	RHIB	BS–74	40.3	1	7.1	F	27	38.8
BS–9	09/04/17	15:46	RHIB	BS–73	51.3	1	7.3	F	36	41.0
BS–10	17/04/17	17:46	Shore	–	54.0	3	–	F	105	38.5
BS–11	17/04/17	19:15	Shore	–	46.2	3	–	T	72	30.8
BS–12	23/04/17	16:35	RHIB	BS–62, 88	21.9	2	8.1	T	23	30.1
BS–13	23/04/17	15:12	RHIB	BS–85, 86, 87	48.1	3	6.1	F	80	32.8
BS–14	08/05/17	15:47	RHIB	BS–97	49.5	1	3.8	F	20	23.0
BS–15	08/05/17	17:10	RHIB	BS–82, 89, 94	42.0	3	7.1	N/K	73	34.3
BS–16	16/05/17	13:59	RHIB	BS–82, 89	74.4	2	6.9	T	95	37.9
BS–17	16/05/17	16:05	RHIB	BS–95, 99	47.1	2	6.1	N/K	51	31.9
BS–18	16/05/17	17:07	RHIB	BS–94	83.0	1	4.7	T	34	23.8
BS–19	22/05/17	14:50	RHIB	BS–97, 99	68.8	2	5.5	F	52	22.2
BS–20	29/05/17	14:38	RHIB	BS–89, 97, 99	56.3	3	6.4	T	79	27.7
WF–1	25/02/18	15:08	Yacht	WF–2, 3, 5	84.7	3	5.4	F	137	32.1
WF–2	03/03/18	09:45	Yacht	–	90.0	1	–	F	44	28.7
WF–3	03/03/18	13:03	Yacht	WF–9, n/a	96.8	2	6.0	T	104	31.9
WF–4	03/03/18	17:51	Yacht	WF–12, n/a	53.5	2	4.8	T	55	30.3
WF–5	03/03/18	18:46	Yacht	WF–12	38.2	1	4.6	T	15	22.0
WF–6	05/03/18	13:02	Yacht	–	22.2	3	8.3	T	37	32.4
WF–7	06/03/18	12:09	Yacht	WF–15, n/a	109.2	3	4.1	T	165	30.0
WF–8	06/03/18	17:06	Yacht	WF–16, 17, 18	61.4	3	4.3	N/K	90	29.0
WF–9	06/03/18	18:37	Yacht	WF–19, 20, 21	23.8	3	3.7	T	40	32.7
WF–10	10/03/18	16:51	Yacht	WF–24, 25, 26, 27, 28	66.4	5	4.6	T	171	30.7
WF–11	15/03/18	14:16	Yacht	–	24.6	1	4.8	N/K	14	31.7
WF–12	15/03/18	15:50	Yacht	WF–39	72.2	1	3.6	M	37	29.9
WF–13	16/03/18	10:48	Yacht	WF–55, 56, 57, 58, 59	38.1	5	5.3	T	111	34.7
WF–14	19/03/18	19:43	Yacht	WF–61, 88	34.3	2	–	M	41	35.0
WF–15	24/03/18	19:52	Yacht	WF–15, 97, 98	62.1	3	6.0	T	105	33.5
WF–16	25/03/18	18:08	Yacht	WF–100	85.7	1	7.7	T	43	29.4
WF–17	26/03/18	14:40	Yacht	–	54.1	1	5.9	T	25	26.6

duration. For example, dives 13 and 32 during BS-18 were classified as surface dives based on the consistent sequence of true dives interspersed by shorter surface dives (Fig. 2g), even though their IBIs were more than double those of most other surface dives exhibited by that individual.

Secondly, the percentage difference of each IBI (pcIBI) from the overall mean IBI of all dives combined was calculated separately for each individual whale, as a method to incorporate intra-individual variation in the classification of the dive types. The pcIBI values were ranked in order for the nine individuals that exhibited differentiated dive types to assess whether they comprised non-overlapping categories with respect to the visually-identified dive types. All pcIBI values of ≤ 55.8 related to visually-identified surface dives. All pcIBI values of > 147 were related to true dives. All pcIBI values of 72.7 to 140.4 had been visually-classified as intermediate dives. However, a small number of dives that had been visually-allocated to surface or intermediate types ($n = 23$) occurred in a zone of overlapping pcIBI value (56.1 to 72.6) and therefore remained uncategorised using this method.

The third method incorporated inter-individual variation in the duration of dive types, by ranking the IBIs of the nine whales that exhibited differentiated dive types to assess the cut-off values that distinguished between the visually-identified dive types. All dives with an IBI of ≤ 64s related to visually-identified surface dives. All IBI's > 169.7s were related to true dives, while IBI's of 117.2 to 126s formed a non-overlapping group of intermediate dives. However, there were areas of overlap in IBI duration between visually-identified surface and intermediate dives ($n = 40$; 64.7–116s) and between intermediate and true dives ($n = 13$; 126.1–165s), and those dives therefore remained uncategorised.

The pcIBI and IBI cut-off values identified for each dive type using the above methods were then applied to categorise the dives recorded in the four non-differentiated focal follows. An overall dive type was then assigned. For the nine whales with differentiated dive patterns, a final dive type was allocated only when at least two of the three methods produced the same dive type category (thus potentially allowing the visually-identified dive type to be over-ruled by the IBI approaches). For the four whales with undifferentiated dive patterns, a final type was allocated only when the pcIBI and IBI methods produced the same dive type.

For the nine individuals with differentiated dive patterns, complete dive cycles were extracted to examine surface bout parameters. Surfacing bouts that included intermediate dives were omitted. The surfacing bout duration (SBD) was

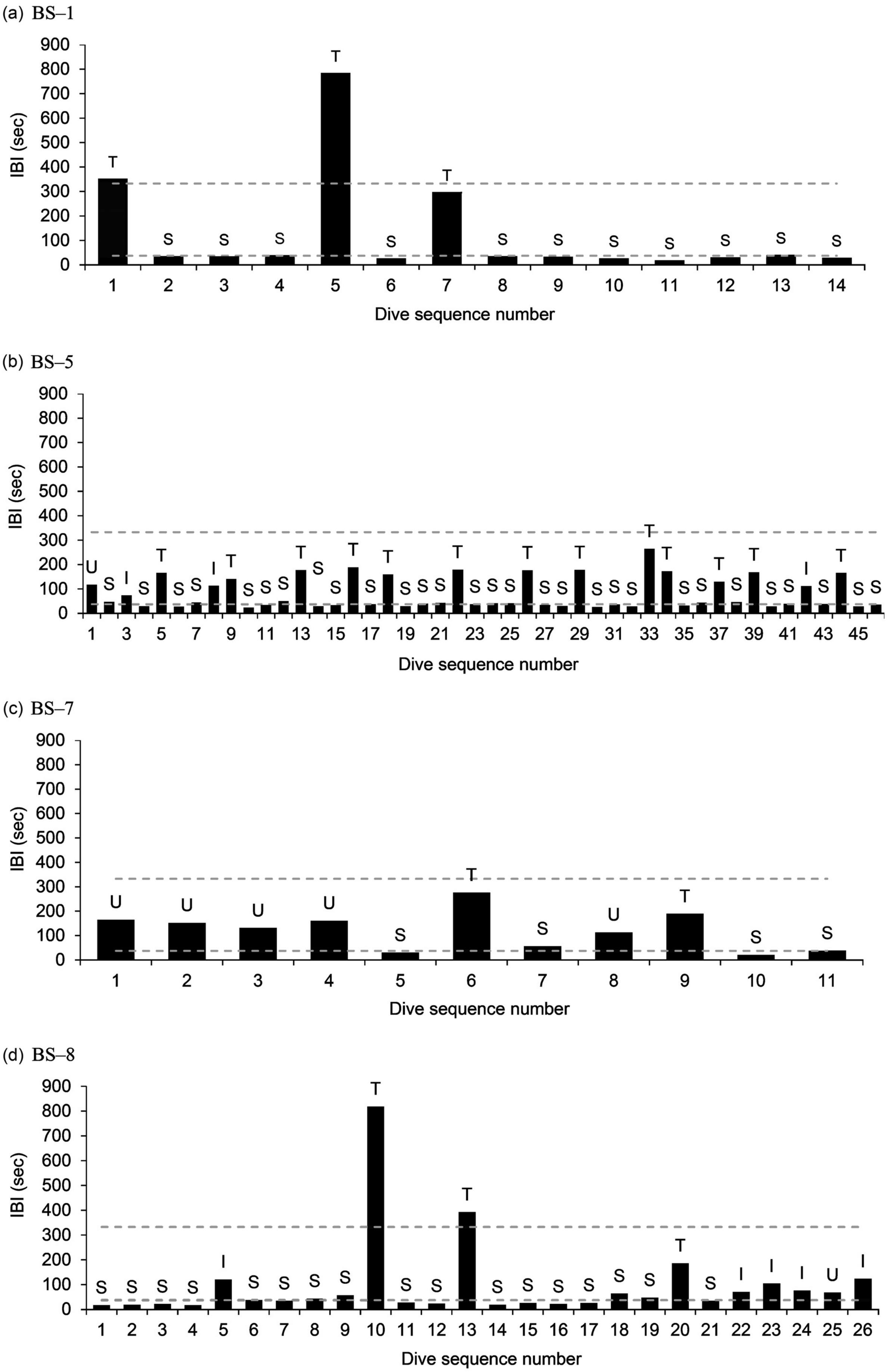
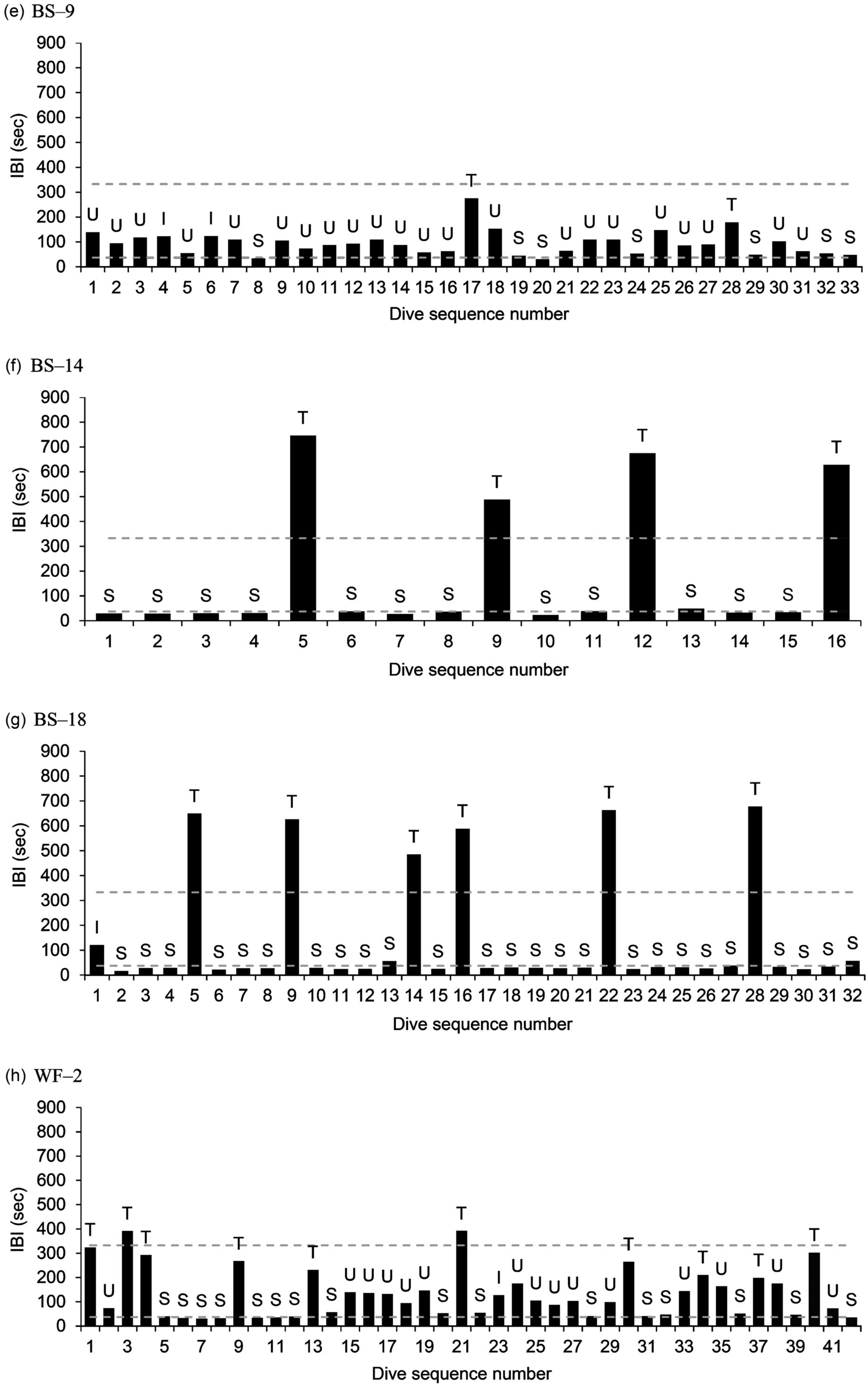


Fig. 2. Inter-breath intervals (IBIs) for complete dive cycles recorded during focal follows (FF) of 13 individual sei whales (a–m). Dashed lines show the mean IBI for surface and true dives for the combined dataset. Dive types assigned during the analysis are labelled: S – Surface, I – Intermediate, T – True, U – Unclassified.



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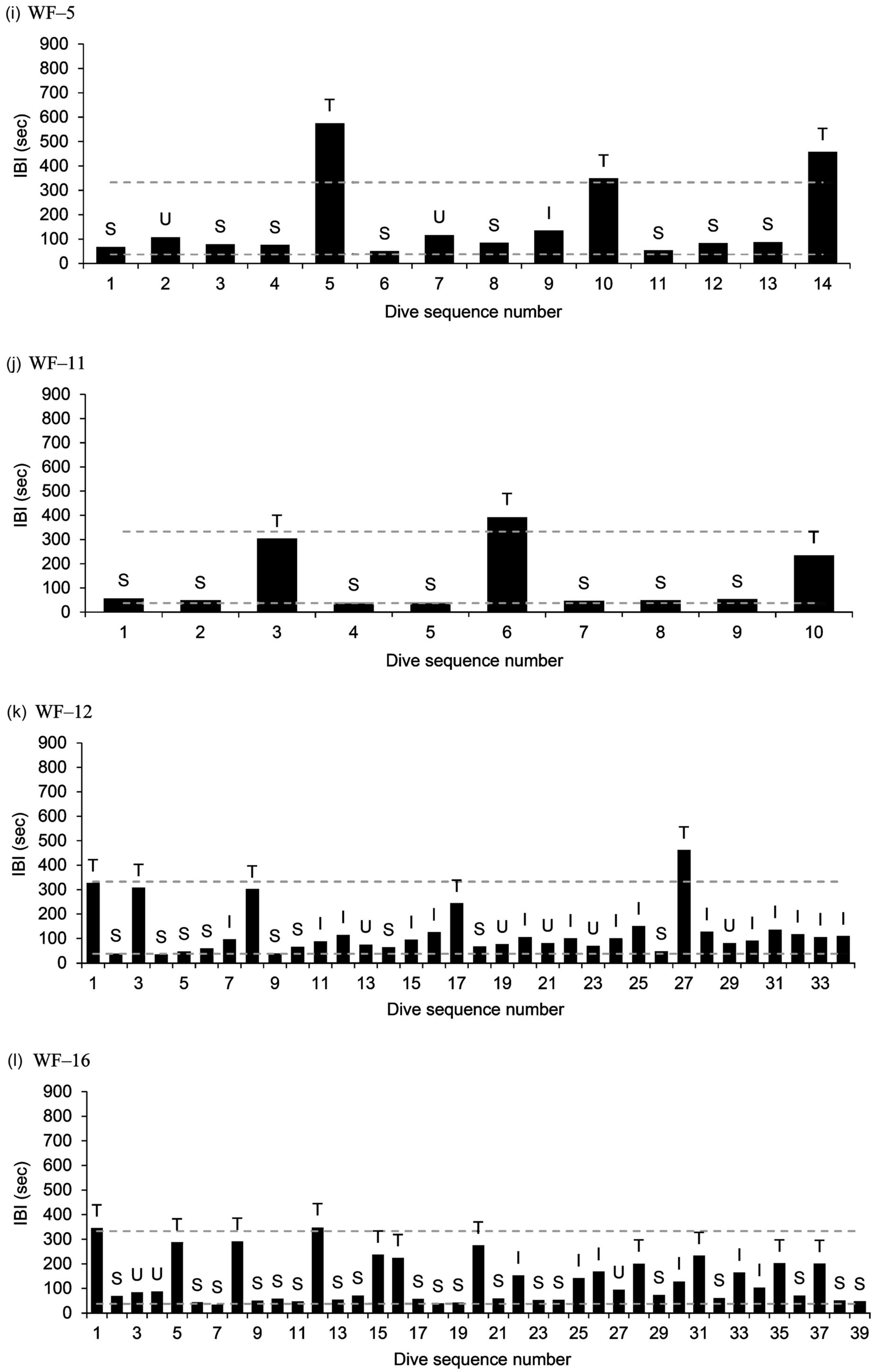

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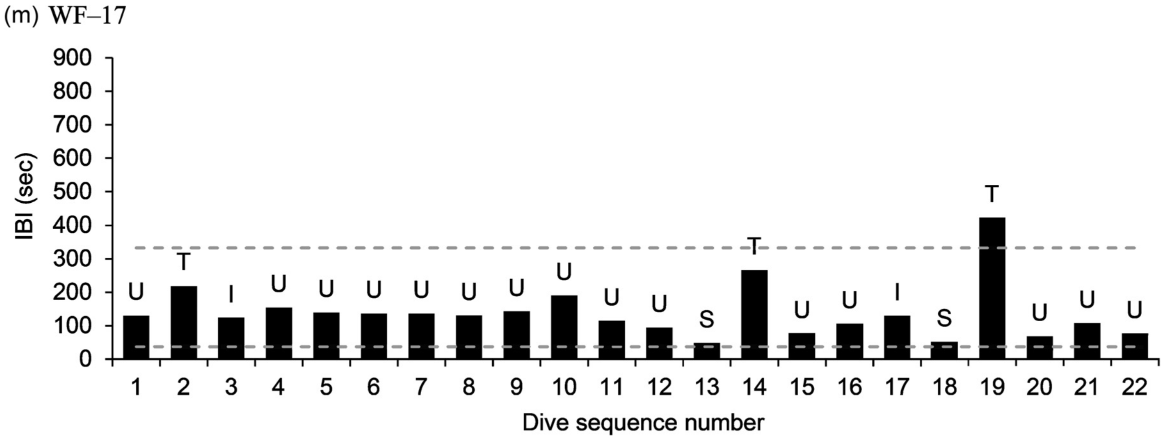

Fig. 2. Concluded.

defined as the sum of consecutive IBIs that were classified as surface dives. The true dive time (TDT) was defined as the IBI of longer true dives, i.e. dives between surfacing bouts. The number of blows per surface bout (BSB) was defined as the number of breaths per surfacing bout.

RESULTS

Cue rates

A total of 37 FFs were carried out on sei whale individuals or groups, including 20 in Berkeley Sound and 17 in West Falkland (Fig. 1). The CR ranged from 22 to 46.7 (Table 1), with an overall mean of 31.5 (SD = 5.12) and a median of 30.8. Mean CRs of 32.3 (n = 20, SD = 6.4, median = 31.1, range = 22.2–46.7s) and 30.6 (n = 17, SD = 3.1, median = 30.7, range = 21.9–35s) were recorded in Berkeley Sound and West Falkland respectively. Following Anderson-Darling Tests for normality, a two sample t-test of CR between Berkeley Sound and West Falkland was not significant (p = 0.346). Two sample t-tests also showed no significant difference between the CRs obtained from shore versus boat platforms, either using only the Berkeley Sound dataset (p = 0.924) or also including the West Falkland dataset (p = 0.781). The mean CR for each of the recorded group sizes was 30.7 (n = 13, SD = 7.3, median = 29.4) for single animals, 30.8 (n = 10, SD = 4.2, median = 31) for pairs, 32.6 (n = 12, SD = 3.1, median = 32.6) for groups of three whales, and 32.7 (n = 2, SD = 2.8, median = 32.7) for groups of five whales.

Dive and surfacing durations

There were 57 occurrences of submergences exceeding 300s (5mins), including 29 accurate dive times recorded from individuals and 28 MDDs recorded from groups of 2 or 3 whales. In Berkeley Sound the longest dive recorded from an individual of 815.2s (13.6mins) was similar to the longest group MDD of 800.1s (13.3mins). In West Falkland, the longest submergences were 574s (9.6mins) by an individual and 363s (6.1mins) as a group MDD. Altogether there were 20 dives recorded from single individuals or groups of whales (2 or 3 individuals) that exceeded 480s (> 8mins) duration, with the majority occurring during eight focal follows in Berkeley Sound and only a single occurrence in West Falkland.

A total of 51 WSEs were extracted from 11 different sei whale encounters on nine dates (Table 2). The durations ranged from 4.1 to 12.1s, with a mean of 6.4s (SD = 1.7) and a median of 6.1s. Mean durations per encounter varied from 5.1 to 9.9s (Table 2). The WSEs were of longer duration in West Falkland (n = 14, mean = 8s, SD = 1.8) than in Berkeley Sound (n = 37, mean = 5.8s, SD = 1.1).

Swim speed

The average linear swim speed during boat-based sei whale focal follows was 5.7kmh^{-1} (Table 1; n = 29, SD = 1.4, median = 5.9, range = 3.5–8.3kmh^{-1}). Swim speed was higher in Berkeley Sound (n = 14, mean = 6.2kmh^{-1}, median = 6.7) than in West Falkland (n = 15, mean = 5.3kmh^{-1},

Table 2

Number and mean duration of whale surfacing events (WSE) per sei whale encounter.

WSE No.	Date	Area	Method	Group size	WSE n	Mean durn. (s)	SD	Range (s)
1	23/02/17	Berkeley Sound	GoPro	3	7	5.1	0.8	4.1–6.3
2	23/02/17	Berkeley Sound	GoPro	4	3	5.4	1.5	4.4–7.1
3	27/02/17	Berkeley Sound	GoPro	4	5	5.4	0.6	4.9–6.1
4	28/03/17	Berkeley Sound	GoPro	3	6	5.1	1.0	4.3–6.9
5	08/05/17	Berkeley Sound	GoPro	6	5	6.1	0.7	5.1–7.1
6	13/05/17	Berkeley Sound	GoPro	4	10	6.8	1.1	5.5–8.6
7	16/05/17	Berkeley Sound	GoPro	2	1	6.6	n/a	6.6–6.6
8	24/03/18	West Falkland	Drone	3	4	7.1	1.1	6.1–8.3
9	26/03/18	West Falkland	Drone	3	4	6.6	1.7	6.1–7.5
10	26/03/18	West Falkland	Drone	4	1	8.2	–	8.2–8.2
11	27/03/18	West Falkland	Drone	5	5	9.9	1.6	7.6–12.1

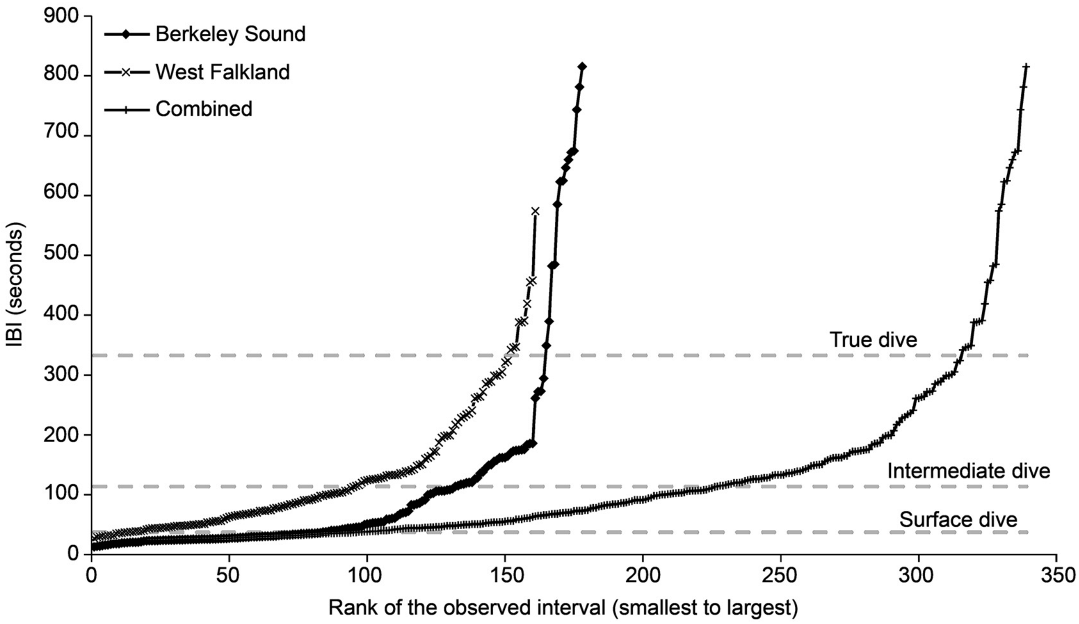

Fig. 3. Ranked order of Inter-breath intervals (n = 339) for complete dive cycles recorded from 13 individual sei whales, showing the mean values for surface, intermediate and true dives from the combined dataset.

Table 3

Inter-breath intervals (IBIs, n =339) recorded during full dive cycles of 13 sei whale focal follows (FF) in Berkeley Sound (BS) and West Falkland (WF).

FF No.	Dive pattern type	All combined (s)						Surface (s)			Intermediate (s)			True (s)			Unclassified (s)		
		n	Min	Max	Mean	SD	Median	*n*	%	Mean IBI	*n*	%	Mean IBI	*n*	%	Mean IBI	*n*	%	Mean IBI
BS–1	Diff.	14	15.2	781.2	124.3	217.0	31.6	11	78.6	28.7	0	0	–	3	21.4	475	0	0	–
BS–5	Diff.	46	20.0	261.1	77.2	64.8	39.1	29	63.0	32.2	3	6.5	95.4	13	28.3	170.7	1	2.2	113.82
BS–7	Undiff.	11	17.4	272.9	117.9	79.3	127.9	4	36.4	32.8	0	0	–	2	18.2	229.4	5	45.5	141.31
BS–8	Diff.	26	13.9	815.2	92.9	166.7	37.5	17	65.4	28.4	5	19.2	95.9	3	11.5	463	1	3.8	64.65
BS–9	Undiff.	33	27.5	271.9	91.6	48.7	86.2	7	21.2	41.4	2	6.1	120.1	2	6.1	223.8	22	66.7	92.9
BS–14	Diff.	16	19.6	743.2	180.1	273.4	31.4	12	75.0	29.8	0	0	–	4	25.0	631.1	0	0	–
BS–18	Diff.	32	12.8	674.4	139.1	233.1	25.9	25	78.1	26.5	1	3.1	117.2	6	18.8	611.7	0	0	–
WF–2	Undiff.	42	27.0	388.0	128	102.6	97.5	16	38.1	38.6	1	2.4	124	10	23.8	284	15	35.7	119.7
WF–5	Diff.	14	48.0	574.0	163.7	167.4	84	8	57.1	70.3	1	7.1	132	3	21.4	458.3	2	14.3	111.5
WF–11	Diff.	10	38.0	391.0	124.6	132.4	48.5	7	70.0	45.7	0	0	–	3	30.0	308.7	0	0	–
WF–12	Diff.	34	32.0	458.0	119.5	95.5	93	9	26.5	48.7	15	44.1	108.5	5	14.7	325.4	5	14.7	74.2
WF–16	Diff.	39	31.0	347.0	125.4	93.7	81	19	48.7	51.3	6	15.4	140.3	11	28.2	256.1	3	7.7	85.3
WF–17	Undiff.	22	45.0	419.0	136	81.6	126.5	2	9.1	46.5	2	9.1	123	3	13.6	299.7	15	68.2	116.9

median = 4.8). It was also slightly higher for FFs in which overall behaviour was considered to be travel (n = 17, mean = 6kmh^{-1}, median = 6) compared with foraging (n = 7, mean = 5.5kmh^{-1}, median = 5.5).

Dive types and cycles by individual whales

Accurate dive cycle timings were available for 13 solitary sei whales; those for which photo-identification images had been successfully obtained each comprised a unique individual (Table 1). The mean IBIs for individuals ranged from 77.2 to 180.1s (Table 3), producing an overall combined mean IBI of 118.6s (n = 339, SD = 137.6). Nine individuals were considered to have differentiated dive patterns (Fig. 2, Table 3). When ranked in order, the majority of the 339 IBIs recorded from full dive cycles occurred along a continuum, with little indication of distinct dive types based on IBI duration alone (Fig. 3). Using the combined-method approach a total of 270 (79.6%) IBIs were assigned to a dive type, while the other 69 (20.4%) dives remained unclassified (Table 3).

Using the combined dataset, the majority of IBIs (49%) comprised surface dives with a mean IBI of 37.2s and a median of 34.3s (Table 4). True dives with a mean IBI of 332.6s and a median of 278.9s comprised 20.1% of the dives. A relatively small number of dives (10.6%) were categorised as intermediate dives, with a mean IBI of 113.7s and a median of 116.1s. The remaining dives were unclassified, but their mean and median IBIs of 106.2s and 102.5s respectively indicated that they would be most-appropriately categorised as intermediate dives. The combined dataset contained overlapping IBI ranges between surface (12.8–86s) and intermediate (67.5–165s) dives, and between intermediate and true (126.1–815.2s) dives (Table 4). Within the Berkeley Sound and West Falkland study sites the surface, intermediate and true dives had non-overlapping IBI values, but the range of values differed between the sites. In particular, the mean and median IBIs of surface dives were notably higher in West Falkland than in Berkeley Sound (Table 4).

The nine individuals with differentiated dive patterns were, in most cases, characterised by a higher proportion (> 48%) of surface dives, a low proportion (< 15%) of unclassified dives, and median IBIs of < 85s (Table 3). The

Table 4
Inter-breath intervals (s) for sei whale dive types in Berkeley Sound and West Falkland.

	Combined dataset					Berkeley Sound					West Falkland				
Dive type	*n*	%	Mean	Range	Median	*n*	%	Mean	Range	Median	*n*	%	Mean	Range	Median
Surface	166	49.0	37.2	12.8–86.0	34.3	105	59.0	30.2	12.8–60.8	27.9	61	37.9	49.3	27.0–86.0	48.0
Intermediate	36	10.6	113.7	67.5–165.0	116.1	11	6.2	102.1	67.5–120.5	108.4	25	15.5	118.8	87.0–165.0	120.0
True	68	20.1	332.6	126.1–815.2	278.9	33	18.5	367.6	126.1–815.2	271.9	35	21.7	299.5	195.0–574.0	288.0
Unclassified	69	20.4	106.2	51.5–187.0	102.5	29	16.3	101.0	51.5–162.0	102.5	40	24.8	110.0	65.0–187.0	103.0
TOTAL	339	100.0	118.6	12.8–815.2	69.0	178	100.0	108.8	12.8–815.2	40.6	161	100.0	129.6	27.0–574.0	94.0

exception was WF-12 (Fig. 2k), which was considered to have a differentiated dive pattern but had a far higher proportion (44.1%) of intermediate dives and a lower proportion of surface dives (26.5%) compared with the other eight individuals. Four whales (BS-1, BS-14, BS-18 and WF-11) exhibited strikingly-differentiated dive patterns characterised by > 96.9% of their dives being either surface or true dives (Fig. 2). However, WF-11 had a higher mean IBI for surface dives and a lower mean IBI for true dives than the other three individuals (Table 3). The dives of BS-5 were generally consistent in pattern but with a less pronounced difference between surface and true dives than the other individuals with differentiated dive patterns; this individual had the lowest mean IBI for true dives (170.7 sec) and the smallest difference between the mean IBI of true and surface dives (Table 3; Fig. 2b). The dive patterns of BS-8, WF-5 and WF-16 were more variable (Fig. 2). While over 76% of the dives of these three individuals could be attributed to surface or true dives, they exhibited a higher proportion of intermediate or unclassified dive types (> 21%) compared with the other whales with differentiated dive patterns. Three individuals (BS-8, WF-12 and WF-16) appeared to alter their dive patterns over the duration of the focal follow, in all cases changing from defined sequences of true and surface dives to a more variable pattern of intermediate dives (Fig. 2).

All four individuals with undifferentiated dive patterns were characterised by high proportions (35.7–68.2%) of unclassified dive types, low proportions (9.1–38.1%) of surface dives and median IBIs of > 85s (Table 3). The mean IBIs of true dives for those whales were < 300s. All four individuals exhibited periods of successive intermediate or unclassified dive types (Fig. 2), with the majority (> 72%) of dives by BS-9 and WF-17 comprising those types.

Surfacing bout parameters were extracted for six individuals that exhibited regular dive patterns (BS-5, BS-8, BS-14, BS-18, WF-5 and WF-11). The BSB varied from 1 to 7 with a mean of 3.8 (n = 28, SD = 1.3). The mean IBI during surfacing bouts was 33.4s (n = 27, SD = 10.5, range = 20.8–72s) and the SBD had a mean of 97.1s (n = 27, SD = 45.7, range = 20.8–216s). The TDT had a mean of 387.7s (n = 28, SD = 226.3, range = 126.1–815.2s).

DISCUSSION

Cue rates and surfacing times

The overall mean CR of 31.5 obtained for Falkland sei whales was notably lower than the CRs published in other studies for baleen whales including minke (46.1), fin (52) and humpback (71) whales in Greenland (Heide-Jørgensen and Simon, 2007), fin whales in the Gulf of Maine (48 without boats and 51 with boats present; Stone *et al*., 1992), and minke whales in Norway (44; Øien *et al*., 1990). No differences in CR were apparent between shore and boat platforms or between different study areas. Additionally, the dataset included multiple FFs carried out in different years (but in similar seasons), dates, time of day and with different individuals. Consequently, we conclude that Falkland sei whales produce genuinely lower CRs than those published for minke and fin whales, highlighting the limitations of inferring data from other, even closely-related, species. The CR range for Falkland sei whales (22–46.7) was well within the range of variability reported for other baleen whales, for example minke whales (16–66; Øien *et al*., 1990), fin whales (17.4–90; Heide-Jørgensen and Simon, 2007) and humpback whales (22.1–156; Heide-Jørgensen and Simon, 2007).

The mean WSE recorded for Falkland sei whales (6.4s) was longer than that reported for minke (3.5s) or fin (4s) whales in Greenland (Heide-Jørgensen and Simon, 2007). While the difference from minke whales may be the result of the greater body size and stronger blow of sei whales, the longer WSE compared with the larger fin whale is less explainable. Heide-Jørgensen and Simon (2007) did report WSE variation of 2–11s for fin whales which is similar to that noted for sei whales. Possibly the shallower-surfacing behaviour and taller dorsal fin (which protrudes above the water for longer) of sei whales may account for them being visible longer above the surface even though their body size is smaller, or these differences may simply reflect variation in the behaviours of the sampled individuals. The WSE durations measured in this study should be treated as a minimum indication of 'availability' during a visual survey, since sei whales were certainly also visible from the air while submerged within the upper water column (as demonstrated by drone footage; Weir, 2018). Similar is true for Icelandic minke whales, with the WSE from boats (3.5s) being doubled when visible submergence time was included from aircraft (7.2s) (Heide-Jørgensen and Simon, 2007). It is likely that the apparent variation in WSE between the Falkland study areas was the consequence of small sample sizes, variation in method, and the differences in behaviour of whales during the video footage. Moreover, six surfacings in the West Falkland dataset related to two individuals that each surfaced three successive times, which may have biased the dataset (one of these animals produced the three highest WSE values).

Dive types and cycles by individual whales

Many visual observation studies of baleen whale diving behaviour have defined only two dive types based on an IBI cut-off. For example, several fin whale studies used log-survivorship analysis of merged datasets to define cut-off IBI durations between surface and true dives of 25–28s (e.g. Stone *et al.,* 1992; Kopelman and Sadove, 1995; Jahoda *et al.,* 2003). However, the duration of dives considered as 'true' or 'surface' may vary between individuals. Øien *et al*. (1990) noted that Norwegian minke whales exhibited considerable intra- and inter-individual variation in surfacing behaviour, and in the Falklands it was evident that the dive durations that comprised surface and true dives for one sei whale (e.g. BS-18) were different from the durations that comprised the same dive types for other individuals (e.g. WF-11). Moreover, a continuum of dive durations was exhibited, and the overlapping IBI ranges between dive types in the combined Falkland dataset indicated that IBI duration alone was not a clear indicator of dive type. Incorporating dive sequence pattern and the pcIBI into the classification of sei whale dives allowed variables such as behavioural context (i.e. occurrence in the dive sequence pattern) and inter-individual variation to be factored in to what constituted a particular dive type.

Although sei whales in Berkeley Sound and West Falkland exhibited similarities in their overall range of dive behaviour, the proportions and parameters of dive types varied between the regions. The mean and median IBIs of intermediate, true and unclassified dives were broadly comparable, indicating that the differences between the sites were best explained by surface dive parameters and by the overall dive type ratios. Sei whales in Berkeley Sound exhibited a higher proportion of surface dives than whales in West Falkland (59 vs. 37.9%), and those surface dives were of much shorter mean and median IBI than in West Falkland. As a consequence, individuals in Berkeley Sound undertook far fewer intermediate dives than those in West Falkland (15.5 vs. 6.2% of the total dives, increasing to 40.4 vs 22.5% if unclassified dives are also included as intermediate dives).

The underlying reasons for these differences are unclear, but could relate to variation in foraging conditions and behaviour between the two regions. The larger numbers of sei whales encountered in West Falkland compared with Berkeley Sound (Weir, 2017; 2018), could be considered to reflect higher prey densities or enhanced foraging conditions (for example, prey located closer to the surface resulting in reduced energetic demands) in that area. It is feasible that although the overall durations of true dives were similar between the two sites, whales in Berkeley Sound may have been diving deeper to reach their prey resulting in the necessity to take a greater number of breaths at the surface between foraging dives. Alternatively, whales in West Falkland may have been foraging less during daylight hours than those in Berkeley Sound and spending more time resting or travelling, with the differences in dive parameters reflecting different overall behaviour during the focal follows. In Japan, the mean dive durations of two tagged sei whales were significantly longer during the day than at night, and the whales also dove deeper during the day (Ishii *et al*., 2017). The changes were related to the depth of the dense scattering layer (which migrated closer to the surface at night), suggesting that sei whales altered their diving depth and sequence in response to changes in the depth distribution of their prey (Ishii *et al*., 2017). In the Falklands, initial indications from faecal sampling work are that sei whales target lobster krill (*Munida gregaria*: Weir, 2017; 2018), the shoals of which vary considerably in their horizontal and vertical spatial distribution according to environmental factors (Diez *et al*., 2016).

Lunge-feeding in baleen whales is a very energetically-costly behaviour (Goldbogen *et al*. 2008, 2011). In general, baleen whales maximise their energetic gains by increasing the number of lunges per dive with increasing depth and prey density (e.g. Friedlaender *et al*., 2016). Therefore, surfacing bouts after long and deep dives should include increased surface times and ventilation rates to recover used oxygen stores. Shallower feeding however, in which whales perform a single or fewer number of lunges could be difficult to discern from a travelling dive based on dive time alone, as whales can maximise feeding rates by incorporating breathing into the cycle of prey processing (Ware *et al*., 2011). In these situations, the whales are likely conserving oxygen, unlike in deep feeding when foraging rates could lead to oxygen debts (Hazen *et al*., 2015). The surfacing patterns found in this study suggest a substantial amount of shallow diving behaviour and determining the proportion of feeding occurring during this time would help shed light on the ecological interactions between sei whales and their prey around the Falkland Islands.

Unfortunately, it proved difficult to unequivocally assign behavioural categories to sei whales in the study areas to determine whether the regional differences in dive pattern reflected the sampling of different behaviours, since the animals were generally cryptic and exhibited little overt behaviour at the surface. Consequently, their behaviour was mostly judged in the field from their dive pattern and by the extent and speed of their spatial movements, which essentially voided any objective assessment of whether the dive patterns varied according to behaviour.

Intra-specific comparisons

The surfacing behaviour reported for Falkland sei whales broadly overlaps with the limited information available for the species elsewhere; however, the inconsistencies in methods used to describe dive types hinders intra-specific comparisons. For example, Avecedo *et al*. (2017), Schilling *et al*. (1992) and Ishii *et al*. (2017) did not describe IBI parameters or dive cycles either due to the more generalised nature of the studies (which were not specifically assessing behaviour) or due to limitations inherent to the methods used (e.g. tag data resolution and detection range). The 5–7min dives noted by Avecedo *et al*. (2017) for Chilean sei whales do fall within the Falkland dive duration range. The maximum dive times recorded for sei whales in the Gulf of Maine (11min; Schilling *et al*., 1992) and off Japan (12.2mins; Ishii *et al*., 2017) are similar to those recorded in the Falklands (13.6mins), despite being recorded in different habitats including open shelf waters (Gulf of Maine), nearshore shallow waters (Falklands) and open ocean of around 5,000m depth (Japan). These likely reflect longer foraging dives since all three of these regions are considered to represent sei whale feeding areas. The shorter dive times (≤ 90s) recorded regularly by Schilling *et al*. (1992) were correlated with numerous observations of surface-feeding during that study, whereas the whales monitored in the

Falklands and Japan were predominantly feeding sub-surface (Ishii *et al*., 2017; Weir, 2017; 2018).

The average swim speeds recorded for Falkland sei whales were inherently limited by methods, since the GPS positions reflect the locality of the boat rather than the movements of the whales themselves. These estimates therefore reflect minimum average speeds. The Falkland results (3.5–8.3kmh^{-1}) are lower than those recorded during two boat-based focal follows in Japan (8.1 and 10kmh^{-1}; Ishii *et al*., 2017), but comparable to the mean speeds of 6.2 and 7.4kmh^{-1} (for migration and non-migration) reported by Prieto *et al*. (2014) from satellite-tracking in the Azores. It is likely that different methods, varying focal follow duration, and behaviour of the animals in different studies will affect the results. Fast bursts exceeding 22kmh^{-1} were recorded by Falkland sei whales on occasion (Weir, 2017), and the species may therefore vary its speed and surfacing characteristics according to behaviour.

CONCLUSION

This study of Falkland sei whale cue rates and surfacing behaviour provides novel systematic information that will be useful to inform abundance estimates and to better understand differences in behaviour between habitats around the Islands. Other baleen whale species vary their diving behaviour according to factors including prey type, group size, time of day, geographic area, season, behaviour and habitat (Würsig *et al.,* 1985; Stone *et al.,* 1992; Kopelman and Sadove, 1995; Stockin *et al.,* 2001; Alves *et al.,* 2010), and consequently the most appropriate datasets for correcting whale abundance estimates are those collected on the same species, in the same geographic area and at the same time of year as the abundance survey is carried out (Heide-Jørgensen and Simon, 2007). The collection of cue rate, dive cycle and WSE data are relevant to addressing availability bias for line transect and cue count methods, and the data presented here should therefore be directly applicable to future sei whale abundance surveys in the Falklands. In addition, understanding the natural surfacing behaviour of sei whales is an integral component of vessel strike modelling, assessing potential disturbance from human activities, and maximising fieldwork approaches for photo-identification, tagging and biopsy sampling. While visual methods have produced useful initial data, they are restricted to daylight hours and periods of favourable weather. The collection of full diurnal datasets (i.e. including the hours of darkness) and information on the underwater behaviour of sei whales via the use of tags would be useful for generating ethograms of behaviour over spatio-temporal scales relevant to the whales around the Falklands to better inform future management decisions.

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