

Behaviour of gray whales (*Eschrichtius robustus*) summering off the northern California coast, from Patrick's Point to Crescent City

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This study quantifies basic dive characteristics and behaviour patterns of undisturbed gray whales (*Eschrichtius robustus*) observed summering at four northern California locations: the Big Lagoon – Patrick's Point area, Orick, Klamath River mouth, and Crescent City. Observable behaviours were limited to several locomotions (swim slow, swim moderate, swim fast, and floating) seen in different behavioural contexts (milling, circling, pluming, and transit). Sixteen behaviours were observed and they fit naturally into locomotive–context categories (i.e., swim-milling, swim slow – circling, etc.). Each behaviour was described using behavioural observations and dive characteristics. Behaviours that did not appear goal oriented or directed, i.e., milling and floating, had highly variable dive characteristics. More specific behaviours, such as circling and pluming, were less variable. Some specific and less directed behaviours appeared functionally related and usually occurred together. Apparent bottom feeding was observed and the Big Lagoon – Patrick's Point area appeared to be a favoured feeding site, as evidenced by mud plumes and repetitive circling of surfacing animals. Feeding was composed of at least three observable behaviours: circling, circling with pluming, and milling with pluming. Locomotive–context categories are useful in refining broad behavioural definitions and quantifying basic behaviour patterns. This approach can enhance the interpretation of observable surface behaviours.

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Les caractéristiques de base de la plongée et les variations du comportement ont été étudiées chez des Baleines grises (*Eschrichtius robustus*) de Californie dans leurs territoires d'été au large de quatre points sur la côte, dans le nord de la Californie : site de Big Lagoon – Patrick's Point, Orick, embouchure de la rivière Klamath et Crescent City. Les comportements observés semblent restreints à divers types de mouvements (nage lente, nage modérée, nage rapide et flottement) reliés à des situations diverses (déplacements erratiques, déplacements circulaires, rejets de boue et déplacements d'un endroit à un autre). Seize comportements ont été observés et ils correspondent tout naturellement à des catégories de contextes de locomotion (i.e., nage lors de déplacements erratiques, nage lente lors de déplacements circulaires, etc.). Chaque comportement est décrit, tenant compte à la fois des observations du comportement lui-même et des caractéristiques des plongées. Les comportements qui ne semblent pas avoir de direction ou de but précis, par exemple les déplacements erratiques et les flottements, sont reliés à des caractéristiques de plongée extrêmement variables. Les comportements plus spécifiques, tels les déplacements circulaires et le rejet de boue, sont moins variables. Certains comportements spécifiques moins orientés semblent avoir une relation fonctionnelle et se produisent ordinairement en même temps. Les baleines semblent se nourrir sur le fond de l'eau et le site de Big Lagoon – Patrick's Point est apparemment un site d'alimentation de prédilection, du moins à en juger par le rejet de boue et les déplacements circulaires répétés des animaux qui refont surface. L'alimentation suppose au moins trois comportements différents : déplacements circulaires, déplacements circulaires avec rejet de boue et déplacements erratiques avec rejet de boue. Les catégories de contextes de locomotion sont des outils commodes pour raffiner les définitions trop vagues de certains comportements et pour quantifier les comportements de base. Cette approche offre la possibilité d'une interprétation plus juste des comportements de surface observés.

[Traduit par la rédaction]

Introduction

The migratory pathway of gray whales (*Eschrichtius robustus*) extends from calving lagoons in Baja California, Mexico, along the west coast of North America to feeding areas in the Bering, Chukchi, and (occasionally) Beaufort seas (Rice and Wolman 1971; Rugh and Fraker 1981). However, detailed information about individual migratory patterns, coastline utilization, and summertime distributions is usually not available (Pike 1962; Rice and Wolman 1971; Wilke and Fiscus 1961). Censuses conducted at Unimak Pass, Alaska (Hall et al. 1977; Rugh and Braham 1979; Rugh 1984), indicate that by summer, the majority of gray whales end their migration at these northern feeding grounds. Groups of summering whales, however, have been observed in many coastal areas along the migratory pathway. Summertime sightings have occurred off British Columbia, Washington, Oregon, and California (Darling 1978, 1979, 1984; Dohl et al. 1981; Gilmore 1960; Pike 1962; Rice and Wolman 1971). Small groups of whales (six to eight per group) reside in at least four northern California locations during the summer months: the St. George Reef offshore from

Crescent City, at the Klamath River mouth, in the Big Lagoon – Patrick's Point area, and in waters adjacent to the Farallon Islands (Dohl et al. 1983). The presence of summering whales in these areas offers an opportunity to observe identified individuals (using natural markings as described in Darling 1984) over extended time periods. Such observations are usually not possible for animals in the inaccessible northern seas or migrating far offshore.

Few detailed behavioural observations and dive characteristics have been reported for summering gray whales and the available literature deals mainly with feeding activity. Thus, behaviours such as bottom feeding by summering whales (Hatler and Darling 1974; Oliver et al. 1983; Oliver and Kvittek 1984) must usually be inferred from the muddy plumes of surfacing animals or resultant bottom depressions (Nerini 1984). Using indirect evidence of feeding, Guerrero (1989) reported that significantly different patterns in the apparent feeding behaviour of summering gray whales were related to the patchiness and mobility of two different benthic prey items.

Some gray whale behaviours are defined broadly and could

reflect behavioural contexts rather than specific actions. For example, several specific behaviours may occur during "feeding," each having different dive characteristics. Taken together, these behaviours represent a feeding context rather than a specific feeding behaviour. Noting only that an animal is "feeding," therefore, may not accurately reflect the actions of that animal. Dive characteristics can be obtained by monitoring respiratory blows of surfaced whales (Sumich 1983; Würsig et al. 1986) and have been described by Harvey and Mate (1984) using radio-tagged animals. Combining visual observations of gray whales with their corresponding dive patterns can enhance the interpretation of many broadly defined behaviours, but this practice has been limited to only a few studies (Guerrero 1989; Harvey and Mate 1984; Murison et al. 1984; Oliver et al. 1984; Würsig et al. 1986). Admittedly, individual variability exists among whales exhibiting these behaviour patterns. This study, however, attempts only to describe observable behaviours common to most of the study animals rather than specify the behaviours of each individual.

Before this study, I observed undisturbed (from boat traffic, planes, divers, fishing operations, etc.) summering gray whales in the Big Lagoon – Patrick's Point area, California, during 1979 and 1980. These whales exhibited different behavioural contexts such as transit between areas, milling, and apparent feeding. Locomotions, ranging from floating to fast swimming, were noted throughout the observations and they did not occur with equal frequency in each behavioural context. All observable behaviours could be naturally grouped into locomotive-context categories (i.e., swim slow – milling, swim fast – transit, etc.). These categories showed that it was possible for many of the swimming movements to have different meanings or functions dependent upon the context in which they occurred. The meaning of some animal behaviours is known to change in different contexts (i.e., Smith 1965). Noting the context in which specific behaviours occur can improve the interpretation of those behaviours.

Locomotive-context categories offer a new approach to understanding gray whale behaviour by refining broad behavioural definitions. Much informal knowledge of gray whale behaviour exists, but little of it has been quantified. Swartz and Jones (1980) stated that in their study, much of the gray whale behaviour was anecdotal and requires additional study for quantification. This indicates that in general, gray whale behaviour needs additional quantification and a need exists for additional descriptions of base-line behaviours. Using the locomotive-context approach, this study will quantify some basic dive characteristics and base-line behaviour patterns of undisturbed gray whales that spend the summer off the northern California coast.

Methods

Four northern California locations served as observation sites: the Big Lagoon – Patrick's Point area, Orick, the Klamath River mouth, and Point St. George in Crescent City (Fig. 1). These sites afforded unobstructed views of the coastline and ranged from 6 to 50 m above the water surface. Observations were made 2 days each week from September 1986 through October 1987, and May 1988 through August 1988. The 1st year of observations provided information as to whether the summering whales migrated, and if so, their approximate departure and arrival times. Beginning in May 1987, observation time at each site was distributed approximately equally through the daylight hours so that daily behavioural changes could be observed. Each site was visited once or twice daily, 2 days a week, in the morning, afternoon, or evening. My previous sightings in 1979, 1980, and 1986 indicated that

approximately 70% of sightings occur within the 1st hour of observation time. A 60-min minimum waiting period was therefore established before abandoning the site. When a sighting occurred, observations continued until the whale left the area. The remaining sites were then sampled as time permitted.

During a sighting, data used for calculating dive characteristics were recorded on respiration, location, locomotion, and general behaviour of each visible whale. A time, direction, compass bearing, and distance were noted for every surfacing. Because the whales were close to the shoreline, their distance offshore was estimated subjectively using offshore landmarks where distances were predetermined using a topography map. A similar technique of estimating distance subjectively has been used successfully by Poole (1984). Instead of a topography map, Poole used a surveyor's transit to determine the distance of offshore landmarks. He then estimated subjectively the distance offshore of migrating gray whales.

Observations were limited to behaviours at or above the water surface. Changes of direction in successive surfacings, however, were assumed to occur underwater. Surfacing with visibly exhaled water vapour were noted as blows. Remaining surfacings were noted as no-blows. When the animals dove after a surfacing, it was noted if the flukes were raised completely or partially above the water surface, or not at all. Visible flukes may indicate when the whales begin a long dive (sounding) and could be useful in determining their next surfacing. Whales were generally 100–500 m from shore and could be individually identified from scars and pigmentation patterns on the back, head, and sides (i.e., Darling 1984).

Previous observations determined that dive durations could be naturally grouped into surface-dive sequences of long and short dives. A surface-dive sequence was defined as one long dive (≥ 60 s) followed by a variable number of shorter surface respirations. A locomotive pattern and the context in which it occurred were assigned to all the observed surface-dive sequences. The surface-dive sequences were placed in locomotive-context categories and divided into duration of long dive, blow interval, number of blows per surfacing, and duration of surfacing. Dive characteristics were obtained for each categorical division by calculating the mean and standard deviation. Significant differences between categories were determined by using analysis of variance and *t*-tests.

When observing the summering whales prior to this study, I noted that at least three distinct swimming speeds could be observed. Approximate swimming speeds, therefore, were calculated in an attempt to quantify observable changes in speed. Because offshore distance was estimated subjectively, calculated swimming speeds were never intended to be extremely accurate. Instead, these swimming speeds were grouped into six gross categories of locomotion (Table 1).

Swimming speeds were determined by plotting the compass bearings onto topography maps and calculating the time and distance between surfacings. Based on the topography map scale, with 100 m as the smallest division, accuracy could have been within ± 10 m for the distance between surfacings. Offshore distances, however, were estimated subjectively, which probably reduced accuracy by an unknown amount. Accuracy, therefore, was greater than ± 10 m, but in my estimation, probably less than ± 50 m (one-half of the smallest division). The whales were always observed within one of the following contexts: transit, milling, circling, and pluming. Contexts and locomotions are defined in Table 1.

Results

Summering whales were observed during 29 sightings at all observation sites between the dates of September 1 and October 31, 1986; May 1 and October 31, 1987; and May 1 and August 31, 1988. Whales sighted between the beginning of May and the end of October were considered summering whales. These animals remained close to shore and never appeared to be migrating. A total of 50 summering whales (representing a smaller number of resighted individuals) were observed. Thirty-one animals were observed at the Big Lagoon – Patrick's Point

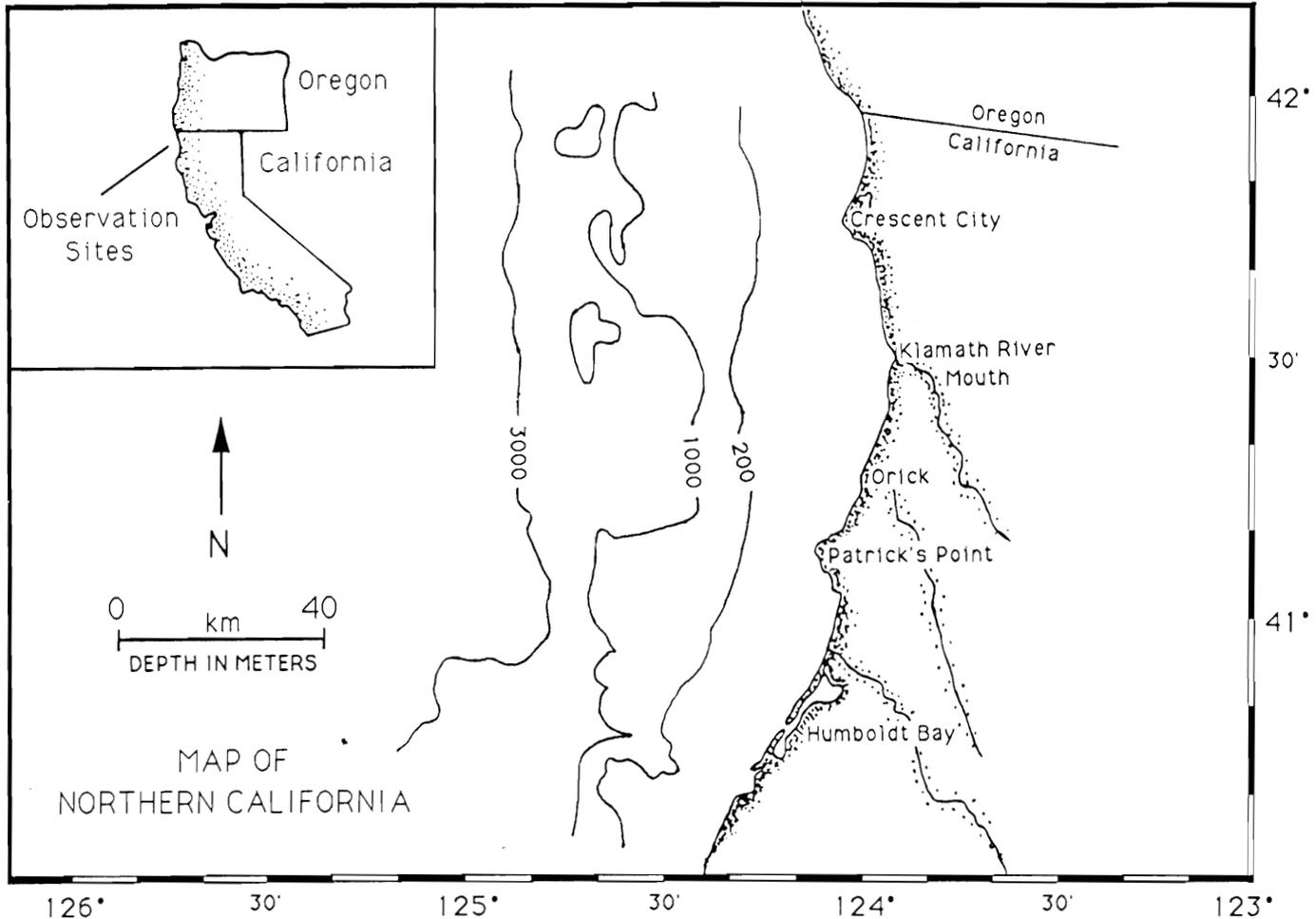


FIG. 1. The four observation sites used to observe gray whales summering off the northern California coast: Crescent City, Klamath River mouth, Orick, and Patrick's Point.

TABLE 1. Definition and probable function of the four behavioural contexts and six locomotions observed in gray whales summering off the coast of northern California

Term	Definition	Probable function
Context		
Transit	Forward movement from area to area	Travel
Milling	Forward and numerous directional changes in movement within a restricted area	Searching
Circling	Constant directional changes in movement within a restricted area	Bottom feeding
Pluming	Sea floor disturbance resulting in surface mud patches and plumes	Bottom feeding
Locomotion		
Swim slow	Minimal forward progress ($0.5-1.0 \text{ km} \cdot \text{h}^{-1}$)	Bottom feeding
Swim moderate	Constant forward progress ($3.0-4.0 \text{ km} \cdot \text{h}^{-1}$)	Travel
Swim fast	Rapid forward progress with occasional white water ($7.0-8.0 \text{ km} \cdot \text{h}^{-1}$)	Unknown
Float	No forward movement	Resting/orientation
Float then swim slow	—	Searching
Float then swim fast	—	Searching

area. Three to five whales were observed at each of the remaining observation sites, including opportunistic sightings at Crescent Beach (three whales) and Dry Lagoon (three whales). The majority of whales were seen at the Big Lagoon – Patrick's Point area because fog and rain severely reduced observation time at Point St. George and the Klamath River mouth. All observed summering whales were judged to be

“adults” and usually were sighted as individuals with occasional groups of two or three animals.

Because many whales were in transit and swam out of view before specific behaviours could be noted, behavioural analysis was limited to 13 sightings and a total of 12 different whales. One whale (identified by distinct natural markings) was observed in 3 of the 13 sightings, once with another whale and

TABLE 2. Number of observed surface-dive sequences per behaviour (locomotive-context category) seen during the 13 sightings

Observed locomotion	Context					
	Circling	Circling with pluming	Transit	Milling	Milling with pluming	None
Swim slow	38 (2)	9	2 (1)	92	15	*
Swim moderate	4 (4)	0	41 (11)	16 (16)	0	*
Swim fast	1 (1)	0	2	1 (1)	0	*
Float	5 (4)	*	*	*	*	14 (6)
Float then swim slow	6	*	*	*	*	2
Float then swim fast	1	*	*	*	*	0

NOTE: The numbers in parentheses represent the contribution made by one whale in the two sightings not used in statistical analysis.

*Behaviours that cannot take place. For example, a whale cannot simultaneously float and transit.

twice alone. To avoid repeated observations of the same whale (which would bias statistical analysis), two of these sightings were not included in the statistical analysis, which was limited to 11 sightings and 12 different whales. Six locomotive behaviours were seen across five behavioural contexts resulting in 16 observable behaviours (locomotive-context categories) (Table 2). The division of long and short dives was determined by inspecting the frequency distribution of all observed dive durations. An apparent break in dive duration occurred at 60 s and correlated well with the observed behaviours.

Locomotive behaviours

These behaviours ranged from variable speeds of forward movement to floating at the water surface (Tables 1 and 2). Swim slow was minimal forward movement seen in animals milling and apparently feeding. Slow swimming comprised 62.7% ($n = 156$) of observed surface-dive sequences. The swim moderate behaviour was also used while milling but rarely seen during apparent feeding. The majority of swim moderate surface-dive sequences were observed during transit when an animal would move from one area to another. Of observed surface-dive sequences, 24.5% ($n = 61$) were during swim moderate. Swim fast was observed rarely and never during apparent feeding (i.e., circling and pluming). Only 1.6% ($n = 4$) of observed surface-dive sequences were swim fast.

Floating was also observed, in which the animals remained just below the water surface. Because floating required no forward movement, it was seen rarely during the observed behavioural contexts. Instead, floating was observed by itself or in combination with another locomotive behaviour during apparent feeding. These feeding surface-dive sequences began with the animal floating near the surface and ended with the whale swimming slowly in a semicircle. Floating was seen in 11.2% ($n = 28$) of observed surface-dive sequences.

Behavioural contexts

Throughout each sighting, the whales were always observed to be in one of four behavioural contexts: transit, milling, circling, and pluming. Transit involved forward movement from one area to another, usually in a straight line. A beeline course was altered only when the animals were rounding a headland or avoiding an obstacle. Otherwise, the shortest distance was taken between two areas. Of observed surface-dive sequences, 18.1% ($n = 45$) were transit. When the new area was reached and transit ended, either the milling or the

circling context would begin. Pluming was never observed immediately after transit.

Milling occurred in 43.8% ($n = 109$) of observed surface-dive sequences and involved swimming back and forth within a restricted area, usually a few 100 m in diameter. These areas were located approximately 50–500 m from rocky headlands, in the middle of bays, and occasionally at the Klamath River mouth. Milling usually involved only one or two animals. Six whales, however, were observed for 2 consecutive days at Patrick's Point milling near shore. During milling, the whales would swim throughout the area making many directional changes both above and below the water surface. Since individual whales would sometimes dive in one direction and surface in another, it was clear that directional changes occasionally took place underwater.

Some surface swimming patterns were repeated before diving. Within this context, the whales would swim in a semicircle before diving and then surface where the semicircle began, completing a circular route. The pattern would then be repeated numerous times with half the circle occurring at the surface and the other half apparently underwater. The majority of these circular patterns were in a clockwise direction (61.4%, $n = 35$) and never more than approximately 100 m in diameter. Circling comprised 22.1% ($n = 55$) of observed surface-dive sequences.

Occasionally, surface mud patches and plumes were seen during milling and circling. Mud patches about 20–25 m in diameter were present before the animals surfaced during milling. While at the surface, the whales never swam back or dove through the mud patches. If new mud patches were formed in succeeding dives, they would form near previous patches but never in the same location. During circling, mud patches formed semicircles before the animals surfaced and occasionally a whale surfaced with mud streaming from its mouth, forming mud plumes. Mud patches and plumes occurred in 6.0% ($n = 15$) of observed surface-dive sequences during milling and 3.6% ($n = 9$) during circling. Most sightings of mud patches and plumes involved one whale. If two animals were present, each formed mud patches or plumes independently of the other in different but nearby locations (approximately 100–300 m apart).

Behaviours (locomotive-context categories)

Table 3 provides descriptions of the most frequently observed behaviours. A frequent behaviour was defined to be a loco-

TABLE 3. Description of the most frequently observed behaviours (locomotive–context categories)

Behaviour (locomotive–context category)	Description	%*	n
Swim slow – milling	Most frequent behaviour. Tendency to surface facing the same direction. Constant positional changes for individual whales, ranging from 0 to 60°. Positional changes did not occur in a straight line, therefore constant directional changes occurred.	36.9	92
Swim slow – milling with pluming	Similar to swim slow – milling but involved the formation of mud patches and plumes. Tendency to surface facing the same direction. Occurred within smaller areas (0–14°) than swim slow – milling.	6.0	15
Swim slow – circling	Tendency for clockwise circling (63.2%, $n = 24$, of these observed surface–dive sequences). Surfaced facing different directions. Small positional changes (<10°). Occasional no-blows.	15.3	38
Swim slow – circling with pluming	Similar to swim slow – circling but involved the formation of mud patches and plumes. Clockwise circling in 57.1% ($n = 4$) of these observed surface–dive sequences.	3.6	9
Swim moderate – transit	Constant positional and distance changes. Always visible blows and surfaced facing the same direction.	16.5	41
Swim moderate – milling	Observed only in one whale. Similar to swim slow – milling but positional changes were smaller (0–15°). Occasional no-blows. Tendency to surface facing the same direction.	6.4	16
Swim moderate – circling	Observed only in one whale. Position never changed and surfaced facing the same direction. Occasional no-blows.	1.6	4
Float	Occurred at or near the water surface. Animals always faced the same direction. Numerous no-blows.	5.6	14
Float–circling	Same as float but whales' direction changed gradually with each succeeding respiration. They rotated (clockwise and counterclockwise) between 45 and 180° by the end of each surface–dive sequence. Numerous no-blows.	2.0	5
Float then swim slow – circling	Occasionally, floating preceded swim slow – circling within a surface–dive sequence. Respirations were visible and surfacing directions were always different.	2.4	6

*Percentage of all observed surface–dive sequences.

TABLE 4. Percentage of frequently observed behavioural surface–dive sequences in which the flukes or partial flukes (arched peduncle) were raised above the water surface before a long dive

Behaviour (locomotive–context category)	Flukes		Arched peduncle		Total %
	%	n	%	n	
Swim slow – milling	43.5	40	7.6	7	51.1
Swim slow – milling with pluming	53.3	8	6.7	1	60.0
Swim slow – circling	42.1	16	15.8	6	57.9
Swim slow – circling with pluming	66.7	6	—	0	66.7
Swim moderate – transit	14.6	6	—	0	14.6
Swim moderate – milling	50.0	8	—	0	50.0
Swim moderate – circling	100.0	4	—	0	100.0
Float	35.7	5	—	0	35.7
Float–circling	60.3	3	—	0	60.0
Float then swim slow – circling	50.0	3	—	0	50.0

motive–context category that was observed in a total of four or more surface–dive sequences. These behaviours occurred during swim slow, swim, float, and across most behavioural contexts. The majority of frequently observed behaviours were seen when the animals were swimming slowly within a restricted area.

When the animals completed a dive or surface respiration during swim slow – milling or swim slow – milling with pluming, they had a tendency to surface facing the same direction. For example, a whale that surfaced facing north did so during all of its swim slow – milling surface–dive sequences. The surfacing direction was different for each animal but usually remained constant throughout that animal's surface–dive sequences. The position or compass bearing, however,

changed throughout the surface–dive sequences, indicating that directional changes occurred during swim slow – milling. Because a whale surfaced facing the same direction, changes in direction occurred underwater during the dive.

Occasionally, when the animals sounded (beginning of a long dive) at the end of a surface–dive sequence, the peduncle area became arched severely or the flukes were lifted entirely out of the water. The percentage of surface–dive sequences in which this occurred is listed in Table 4 for each frequently observed behaviour.

The majority of observed surface–dive sequences were of whales swimming slowly. Fewer surface–dive sequences and behaviours were observed when the locomotion was swim moderate. Most of the swim moderate surface–dive sequences

TABLE 5. Summary statistics for dive characteristics seen in the 11 sightings (12 different whales) used for statistical analysis

	Duration of dive (s)			Blow interval (s)			No. of blows/ surfacing			Duration of surfacing (s)		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
Locomotion												
Swim slow	208.02	92.34	146	16.62	9.21	372	3.49	1.82	142	41.65	33.12	142
Swim moderate	145.41	64.17	29	30.12	13.54	57	3.07	1.75	27	62.44	65.28	27
Swim fast	156.50	50.20	2	19.33	7.02	3	2.50	0.71	2	29.00	24.04	2
Float	269.18	100.49	17	20.42	6.46	26	3.71	2.93	7	61.38	63.95	8
Context												
Milling	207.52	101.77	91	16.13	9.83	176	2.95	1.71	87	31.75	29.77	87
Transit	145.16	61.95	32	28.40	13.59	68	3.23	1.99	30	63.33	64.95	30
Circling	208.94	75.26	35	17.30	8.56	115	4.09	1.50	35	54.57	31.14	35
Pluming	213.63	75.45	19	16.40	8.41	73	4.53	1.71	19	57.16	27.40	19
Behaviour (locomotive-context category)												
Swim slow – transit	115.00	—	1	19.50	11.70	8	9.00	—	1	156.00	—	1
Swim slow – milling	207.52	101.77	91	16.13	9.83	176	2.95	1.71	87	31.75	29.77	87
Swim slow – milling with pluming	229.00	61.80	10	17.30	8.84	46	4.33	1.37	12	57.17	26.64	12
Swim slow – circling	208.94	75.26	35	17.30	8.56	115	4.09	1.50	35	54.57	31.14	35
Swim slow – circling with pluming	196.56	88.81	9	14.85	7.53	27	4.86	2.27	7	57.14	30.85	7
Swim moderate – transit	145.41	64.17	29	30.12	13.54	57	3.07	1.75	27	62.44	65.28	27
Swim moderate – milling*	225.00	133.20	16	18.00	7.95	49	4.13	1.68	15	54.27	33.54	15
Swim moderate – circling*	204.75	55.98	4	21.35	11.92	17	5.25	1.89	4	90.75	24.62	4
Swim fast – transit	156.50	50.20	2	19.33	7.02	3	2.50	0.71	2	29.00	24.04	2
Swim fast – milling*	166.00	—	1	18.00	—	1	2.00	—	1	18.00	—	1
Swim fast – circling*	242.00	—	1	12.67	2.29	9	10.00	—	1	114.00	—	1
Float	315.71	132.32	7	21.57	5.95	23	3.67	3.20	6	65.14	68.11	7
Float – circling	233.00	—	1	11.67	1.53	3	4.00	—	1	35.00	—	1
Float then swim slow	260.50	27.58	2	18.75	12.24	8	5.00	1.41	2	75.00	32.53	2
Float then swim slow – circling	238.00	72.16	6	16.52	7.27	29	5.83	2.23	6	79.83	49.08	6
Float then swim fast while circling	184.00	—	1	22.67	8.50	3	4.00	—	1	68.00	—	1

*Behaviours seen in repeated observations of only one whale. To avoid data bias, the remaining behaviours displayed by this animal were not incorporated into the other summary statistics.

were seen during transit in which the animals were usually passing through the immediate area. Less time, therefore, was spent observing animals in the swim moderate locomotion. Swim moderate was never seen during pluming and was observed only in transit, circling, and milling.

Floating, in one form or another, was seen in 11.2% ($n = 28$) of observed surface-dive sequences. Five variations of floating were observed, three of which were considered frequent behaviours. It was obvious when the animals were floating because the distance from shore and position never changed. The animals remained just under or at the water surface. They always remained low in the water and little of their bodies could be seen. During floating, many surfacings occurred with no visible blow and were therefore recorded as no-blows. When no-blows occurred, they were lumped together in particular surface-dive sequences. The remaining surface-dive sequences consisted mostly of visible respirations with occasional no-blows.

Surfacing and respiration characteristics

Although the aim of this study was to describe whale behaviour that occurred near or at the water surface, it was also possible to quantify these activities (Table 5). Surface-dive sequences for locomotion, context, and locomotive-context categories were analyzed for duration of dive, blow interval, number of blows per surfacing, and duration of surfacing. Frequency distributions of these four divisions are presented in Fig. 2. The distributions were skewed positively but when

transformed into logarithms, they became approximately normal. The use of parametric statistics, therefore, was appropriate.

Using ANOVA (99% confidence intervals), significant differences were found between contexts for duration of dive ($F = 5.67$, $p = 0.001$), blow interval ($F = 24.71$, $p = 0.0001$), and number of blows per surfacing ($F = 8.28$, $p = 0.0001$). No significant differences were found among contexts for duration of surfacing. Duration of dives was significantly longer during milling ($t = 3.52$, $df = 121$, $p < 0.001$), circling ($t = -3.65$, $df = 65$, $p < 0.001$), and pluming ($t = -3.33$, $df = 49$, $p < 0.002$) than during transit. When transit occurred, the blow interval was significantly longer than that seen during milling ($t = -8.01$, $df = 242$, $p = 0.0001$), circling ($t = 6.54$, $df = 181$, $p = 0.0001$), and pluming ($t = 6.39$, $df = 139$, $p = 0.0001$). During apparent feeding (circling and pluming), the number of blows per surfacing was significantly higher than during nonfeeding activities (milling and transit). Circling had more blows per surfacing than did milling ($t = -3.86$, $df = 120$, $p < 0.001$) and transit ($t = -2.83$, $df = 63$, $p < 0.007$). Pluming also showed an increase in the number of blows per surfacing over milling ($t = -3.48$, $df = 104$, $p < 0.001$) and transit ($t = -2.79$, $df = 47$, $p < 0.008$).

Significant differences were also observed among locomotions (at the 99% confidence interval) for duration of dive ($F = 8.32$, $p = 0.0001$) and blow interval ($F = 28.00$, $p = 0.0001$). Dive duration was significantly longer when the whales swam

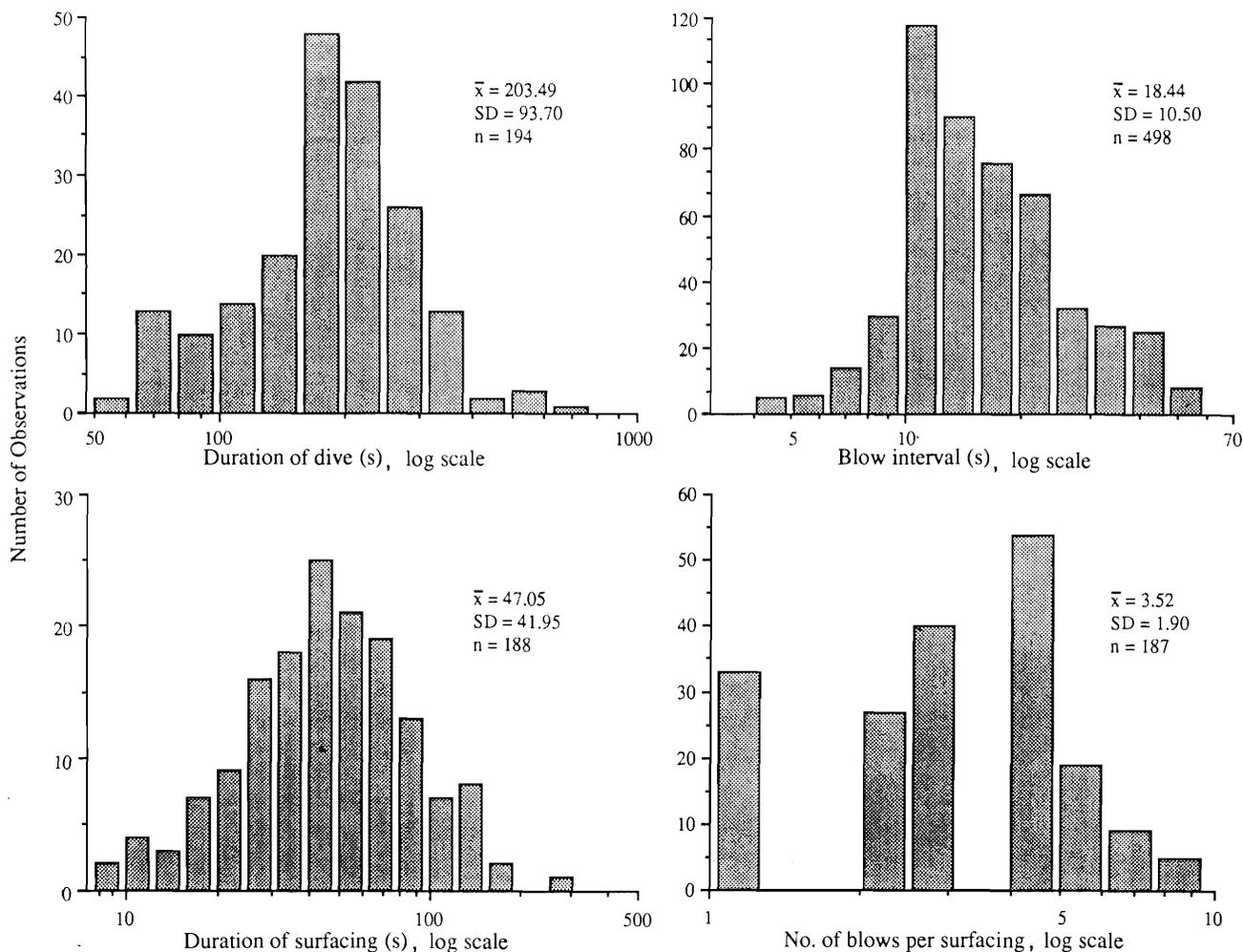


FIG. 2. Frequency distributions of the dive, respiration, and surfacing divisions. The \bar{x} and SD are the observed measurements and are not log transformed numbers.

slowly rather than moderately ($t = 3.91$, $df = 173$, $p = 0.0001$). During float, dive duration was longer than that of swim moderate ($t = -4.81$, $df = 44$, $p = 0.0001$) and swim slow ($t = -2.47$, $df = 161$, $p < 0.02$). The blow interval during swim moderate was longer than the blow intervals in float ($t = 2.91$, $df = 81$, $p < 0.005$) and swim slow ($t = -8.77$, $df = 427$, $p = 0.0001$). While floating, however, the whales had longer blow intervals than they did during swim slow ($t = -2.95$, $df = 396$, $p < 0.004$). Sample sizes for swim fast were too small for statistical analysis in all four divisions. For duration of surfacing, float sample sizes were also too small for analysis and there was no significant difference between swim slow and moderate. No significant differences were found among locomotions for number of blows per surfacing.

Discussion

A dive pattern of one long dive followed by a surfacing sequence of one or more shorter dives (blow intervals) was constant throughout all the observed behaviours. There was undoubtedly a real distinction between long and short dives. This distinction becomes apparent by inspecting the frequency distribution of all observed dive durations. An apparent break in dive duration occurred at 60 s. This break could have been a chance sampling effect, but it correlated well with the observed

behaviours. This study, therefore, used 60 s as the division between long and short dives. In Harvey and Mate's (1984) study of gray whale diving patterns, they also used 60 s as the division between long and short dives. After a long dive, the whales produced a sequence of blows separated by short, and doubtless, shallow dives. It is the overall duration of this surface sequence that is summarized in the duration of surfacing column in Table 5. It appears that gray whales must conform to a respiratory pattern of one long dive followed by one or more shorter dives and that the observed variability in respiration patterns can be correlated with the behaviours. Although the respiratory patterns observed in this study were those of summering gray whales, they appear to correspond with the "clumped" dive patterns observed by Harvey and Mate (1984) in gray whales wintering in Mexican lagoons, between southward and northward migrations.

For most frequent behaviours, locomotions, and contexts, coefficients of variation indicated that behavioural variability was high. This may reflect individual variability in behaviour patterns; nevertheless, some behaviours and contexts appeared more variable than others. For example, milling and floating did not appear goal oriented or directed and had the highest overall variability in respiration patterns. The more specific and directed behaviours like circling and pluming were less variable. Circling and pluming had extremely similar numbers in all

four dive characteristic divisions. Both had the lowest overall behavioural variability of any locomotion or context. Their similarity reflects that these observations are probably the same and were only separated into different contexts because mud was not always visible.

While observing the whales, distinguishing between the different contexts and locomotions was not difficult. It was obvious when the whales were in transit, since they swam in a straight line and out of view. Circling and milling also appeared different from one another. Aside from significant differences in the number of blows per surfacing, it was obvious when the whales were circling as opposed to milling. During milling, the whales surfaced facing numerous directions, which they did not do during circling, and they also utilized a much wider area. Floating was also obvious because the whales did not move forward. In addition, significant differences in dive duration and blow interval were observed between swimming slowly and moderately.

My observations indicated that behaviours could be split naturally into two different groupings: context and locomotion (locomotive–context categories). Statistically significant differences between contexts were found for measures of dive duration, blow interval, and number of blows per surfacing; significant differences among locomotions were found for duration of dive and blow interval. Since I was unable to compare my observations with those of a second observer working independently, the reliability of the behavioural groupings needs to be established. Nevertheless, I believe that the differences between the various context and locomotive categories are real and provide a more refined and biologically meaningful view of previously defined behaviours (i.e., feeding).

Some specific behaviours and less goal-oriented behaviours appeared to be functionally related and usually occurred together. The best example was swim moderate – milling and swim moderate – circling. These two behaviours were seen numerous times as shown by one whale (Table 5). Although swim moderate – milling could happen alone, swim moderate – circling always occurred during swim moderate – milling. Swim moderate – milling had the highest variability in dive duration times of any behaviour. Swim moderate – circling had the second lowest dive duration variability. Duration of surfacing was also more variable during swim moderate – milling than during swim moderate – circling. When these behaviours occurred together, the whale would mill for five or six sets within a restricted area and then spend one or two sets circling at a specific location. This pattern of highly variable milling sets followed by a short series of less variable circling behaviours was repeated by this whale, sometimes for hours. Five other whales exhibited the same behaviour pattern using similar paired behaviours. Three of these whales used swim slow – milling with swim slow – circling and the remaining two used swim slow – milling (occasionally with pluming) with swim slow – circling with pluming. In all cases, the duration of dives and surfacings were more variable during milling than circling. From this behaviour pattern, it can be hypothesized that during milling, the whales appeared to be searching for a specific feeding site or object. When the feeding site was located, the whales began to circle and dive at this location. When pluming was observed, the whales were probably feeding. Even if mud was not observable, the whales still could have been feeding or perhaps verifying that this was an appropriate feeding site.

During circling, circling with pluming, and milling with pluming, the whales were apparently feeding. True feeding

could not be verified and instead apparent feeding was divided into the three observable contexts. Pluming is a strong indication that the whales were bottom feeding and is associated with two of the feeding contexts. Mud patches and plumes have been reported during apparent feeding activity (Dohl et al. 1983; Harrison 1979; Hatler and Darling 1974; Norris et al. 1977; Wilke and Fiscus 1961), but most behavioural descriptions are general and do not include dive times. Two exceptions are Oliver et al. (1984) and Würsig et al. (1986), both of whom observed summering gray whales producing mud plumes and apparently feeding. The number of blows per surfacing, duration of surfacing, and dive duration were recorded. The locomotion and swim patterns were described as milling; circling was never mentioned. The dive times for these animals, therefore, could have reflected both milling and circling. Nerini (1984), in a review of gray whale feeding activities, concluded that whales feeding during migration or summering usually consume benthic resources, such as several species of amphipods and isopods. Because pluming has been associated with bottom feeding, the apparent feeding observations in this study support Nerini's conclusions and the summering gray whales observed pluming were probably bottom feeding. Feeding, however, may also take place without obvious pluming.

Circling (without pluming) was also associated with feeding. Although the whales appeared to be feeding exclusively on benthic organisms, it is possible that during circling they may have been feeding near the surface or throughout the water column. Guerrero (1989) described the significantly different surface behaviours observed in gray whales feeding on benthic amphipods (*Ampelisca agassizi*) and free-swimming mysids (*Neomysis rayii*). The whales feeding on benthic amphipods dove and surfaced for longer periods and respired more times during surfacings than the whales feeding on swarms of mysids. In addition, respiratory patterns of mysid-feeding whales did not differ greatly from those engaged in nonfeeding activities, i.e., travel. The whales in this study exhibited similar respiratory patterns during apparent feeding activities, including circling (without pluming). There was a tendency for their dives and surfacings to be longer, with an increased number of blows per surfacing during apparent feeding activities than during nonfeeding activities. Guerrero also reports that during feeding on mysids, the whales she observed would initiate dives by rolling onto the side and exposing only one fluke. This did not occur with the whales feeding on benthic amphipods nor with the whales in this study. The feeding activities of the whales in this study, therefore, were probably oriented towards the sea floor rather than throughout the water column.

Although swim moderate – circling was observed only four times in one whale, on average this whale spent three times longer at the surface during swim moderate – circling than other whales did during swim slow – milling. Circling was observed to be associated with sea floor disturbances (swim slow – circling with pluming) and has been observed during feeding in other gray whales (Nerini 1984; Pike 1962; Sund 1975). The increased time spent at the surface during this behaviour may reflect the need to manipulate (i.e., swallow, spit out, sort out, etc.) the material obtained from the seabed. (It may also reflect individual variability in behaviour.) Although pluming was not associated with swim moderate – circling, the ingestion of food was still possible. A more likely possibility is that dives during swim moderate – circling may be more strenuous than those of swim slow – milling. A longer recovery period could be needed at the surface before another attempt is made at circling. Würsig

et al. (1986) reported similar findings in feeding gray whales, which had longer dive and surface durations and more blows per surfacing than nonfeeding whales. Duration of surfacings and dives and the number of blows per surfacing have also been found to be correlated positively with water depth not only in gray whales (Würsig et al. 1986) but also in bowheads (*Balaena mysticetus*) (Würsig et al. 1984) and humpbacks (*Megaptera novaeangliae*) (Dolphin 1987a, 1987b). In this study, however, water depth was not measured and the whales did not show an increase in dive duration or number of blows per surfacing during apparent feeding.

Except for apparent feeding behaviours, almost all the remaining behaviours were seen at each observation site. Circling and pluming, however, were seen only in the Big Lagoon – Patrick's Point area. Hatler and Darling (1974) suggest that significant feeding grounds for gray whales may not exist south of Vancouver Island. Milling and apparent feeding, however, were the majority of behaviours observed at Patrick's Point, and of the four observation sites, Patrick's Point appeared to be a bottom feeding area for the summering gray whales.

The areas chosen as observation sites for this study were reported by Dohl et al. (1983) to be occupied by small groups of summering gray whales. The groups were indeed small and only once did I see more than two to three individuals during a sighting. This resulted in a low but adequate sample size. Opportunistic sightings between observation sites indicated that the whales transit between these areas and may utilize a large portion of the coastline rather than only a specific area. I am currently photographically identifying the summering whales to see if they utilize more than one area and if the same individuals return each year. One individual whale was sighted during each of the three summers I collected data and at different observation sites (twice at Patrick's Point – Big Lagoon area and once near Point St. George). This indicates that some whales may not only return to their previous summering grounds but also utilize a large portion of the coastline.

During transit, surface time was highly variable (Table 5). The whales were observed making a consistent forward progression and a high surface time variation was not expected for such a steady pace. The dive characteristics indicated that transit was not as directed as it appeared during observation. Transit may be undirected because all that is required is travelling from point A to point B. How the whales accomplish this may not be a specific process. Transit was associated with near-shore travel along the coastline and occasional observation of terrestrial landmarks may aid the animals in navigation. An increase in surface time variability would be expected under these circumstances, but behaviours such as spy hopping, which may increase long distance viewing of terrestrial reference points (Daugherty 1972; Pike 1962; Walker 1971), were never observed. The observation sites, however, were high bluffs and headlands that could be seen easily if the whales were looking for landmarks.

All calculated swimming speeds were grouped into three gross categories: swim slow ($0.5\text{--}1.0\text{ km}\cdot\text{h}^{-1}$), swim moderate ($3.0\text{--}4.0\text{ km}\cdot\text{h}^{-1}$), and swim fast ($7.0\text{--}8.0\text{ km}\cdot\text{h}^{-1}$). (Floating and its variations have been omitted here; see Table 1.) During observations, the different speed categories were easily distinguishable. Because distance from shore was estimated subjectively, the calculated swimming speeds are only estimates. They indicate, however, that the speeds of each category are different from one another, a difference that could be appreciated visually. Although many gray whales probably do not limit

their swimming speeds to these categories, a tendency may exist for gray whales to utilize only certain ranges of speed. Mate and Harvey (1984) reported that gray whales average $127\text{ km}\cdot\text{day}^{-1}$ ($5.3\text{ km}\cdot\text{h}^{-1}$) during the last 29 days of the northward migration. During most of the migration, however, the whales average $85\text{ km}\cdot\text{day}^{-1}$ ($3.5\text{ km}\cdot\text{h}^{-1}$), which is within the swim moderate category range. Gray whales appear to swim faster during the southward migration at an average speed of $2.0\text{ m}\cdot\text{s}^{-1}$ ($7.2\text{ km}\cdot\text{h}^{-1}$) (Sumich 1983). The summering whales in this study displayed behaviours not usually associated with migration, but their swimming speeds could be categorized into distinct groups with swimming speeds similar to those observed in migrating animals. Why gray whales would swim within certain speed ranges is unknown. Perhaps swimming metabolism is more efficient at certain speed ranges and the whales tend to stay within them.

During the past observations of summering gray whales, I observed that their flukes would occasionally be lifted above the water surface as the animals began a long dive. This behaviour is common in migrating gray whales (Leatherwood et al. 1982). Observations of flukes raised above the water surface were recorded and found to be a reliable indication of when a surface–dive sequence ended (the beginning of a long dive). When raised flukes occurred, they were always at the end of a surface–dive sequence. The whales, however, did not always lift their flukes before a long dive. Occasionally, the flukes did not come out of the water completely and instead a severely arched peduncle was observed at the end of a surface–dive sequence.

Flukes were seen most frequently during apparent feeding and floating behaviours but almost never during transit. When the flukes were lifted above the water, the animals appeared to be entering a steep dive in which their bodies became almost perpendicular to the sea floor. W. J. Richardson (personal communication), however, observed similar behaviour in bowheads where raised flukes were seen when they dove in water only 4–5 m deep, less than half their body length. Raised flukes, therefore, may not be indicative of deep and near vertical dives in gray whales. Raised flukes, however, seem appropriate during feeding but unusual for floating animals. Float surface – dive sequences occurred independent of apparent feeding and tended to occur in a series. Flukes were seen rarely, indicating that the animals were actually resting. The frequency of flukes observed in float–circling and float then swim slow – circling, however, was the same as in apparent feeding behaviours. These two floating behaviours occurred occasionally during apparent feeding and never in a series. Under these conditions, the whales appeared inactive but were probably engaged in apparent feeding activities. Because transiting animals rarely show their flukes, they probably take shallower and most certainly less inclined long dives than during apparent feeding. Making shallow dives is consistent with whales that seem intent on travelling from one area to another.

In summary, locomotive–context categories, in conjunction with dive characteristics, has helped refine broad behavioural definitions and quantify several basic gray whale behaviour patterns not reported before this study. (i) Behaviours that did not appear goal oriented or directed, i.e., milling and floating, had highly variable dive characteristics. More specific behaviours, such as circling and pluming, were less variable. (ii) Some specific and less goal-oriented behaviours appeared functionally related and usually occurred together, i.e., swim slow – milling and swim slow – circling. (iii) Feeding was

composed of at least three observable behaviours: circling, circling with pluming, and milling with pluming. Even an obvious behaviour such as floating had several variations. (iv) The Big Lagoon – Patrick's Point area appeared to be a main feeding site for many gray whales summering off the northern California coast.

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