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Seasonal changes in pod characteristics of eastern Australian humpback whales *(Megaptera novaeangliae)*, Hervey Bay 1992–2005

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ABSTRACT

We investigated the characteristics and composition of 4,506 humpback whale pods observed in Hervey Bay between 1992 and 2005. We use these data to analyze and model the variability of pod size and composition, and to assess the importance of Hervey Bay for particular classes of humpback whales. Pods ranged in size from one to nine individuals. Pairs were the most frequent pod type (1,344, 29.8%), followed by mother-calf alone (1,249, 27.7%), trios (759, 16.8%), singletons (717, 15.9%), and 4+ whales (437, 9.7%). Of the 4,506 pods, calves were present in 40%, and 10.8% of all pods had one or more escorts present. Of the 1,804 pods observed with calves present, 1,251 (69.4%) were mothers alone with their calves. The size and composition of pods in the study area varied significantly as the season progressed. Pods with calves present were rarely recorded early in the season but dominated later in the season. A significant increase over years in larger groups may be related to social and behavioral changes as the population expands. The data indicate that Hervey Bay is important to immature males and females early in the season, to mature males and females in mid-season, and to mother-calf pairs (either alone or with escorts) in mid-to-late season.

Key words: humpback whale, *Megaptera novaeangliae*, Hervey Bay, Australia, social behavior, pod size, pod composition.

Humpback whales (*Megaptera novaeangliae*) are found in all oceans of the world and maintain an annual migratory cycle from low-latitude winter breeding grounds to high-latitude summer feeding areas in both the Northern and Southern Hemispheres (Chittleborough 1965, Dawbin 1966, Baker *et al.* 1986, Clapham 2000). Winter assemblages of humpback whales occur in tropical and subtropical waters either around islands or along continental coastlines (Dawbin 1956). Relatively shallow and sheltered warm-water areas appear to be a preferred habitat for calving females (Dawbin 1966, Whitehead and Moore 1982, Smultea 1994, Clapham 2000, Craig and Herman 2000, Ersts and Rosenbaum 2003).

Eastern Australian humpback whales commence the southern migration from the breeding grounds to their Antarctic feeding areas in July each year and return at some point by June the following year (Dawbin 1966). Chittleborough (1965) suggested that there is no particular latitude along the eastern coast of Australia where migration ceases and breeding activities commence.

One of many places that are used by humpback whales during the winter is Hervey Bay in Queensland; this is slightly west of the main northward migratory stream and 2° south of the Great Barrier Reef lagoon. Humpback whales do not enter Hervey Bay on their northward migration that peaks during June and July. The migration stream passes Breaksea Spit to the northeast of Hervey Bay and then inclines to the northwest, with whales dispersing widely between the outer Great Barrier Reef and the Australian coast (Paterson 1991).

Previous studies suggested that the large inter-reef lagoon of the Great Barrier Reef, between 16°S and 23°S, represents the primary overwintering and breeding grounds of eastern Australian humpback whales (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999). There are no recent published data on aggregations of humpback whales north of Hervey Bay.

On the southward migration, large numbers of humpback whales make a slight diversion from the southern migratory pathway and pass inside Breaksea Spit to enter Hervey Bay (Paterson 1991). It has been suggested that the proportion of eastern Australian (E1 breeding ground) humpbacks entering Hervey Bay is 30%–50% (Chaloupka *et al.* 1999). Humpback whales move into Hervey Bay from late July and during August, September, and October. They enter and leave from the north and aggregate in shallow water close to the western shore of Fraser Island in the eastern part of the bay (Corkeron *et al.* 1994). Aerial surveys have shown that pods are not randomly distributed but tend to aggregate in clusters (Corkeron 1993). Mother and calf pods are the final cohort to migrate southwards (Dawbin 1966, 1997) and enter Hervey Bay during September and October (Corkeron 1995, Corkeron and Brown 1995). On leaving the area, humpback whales initially travel north, rounding Breaksea Spit to the east before rejoining the southward migratory stream (Corkeron 1993, Corkeron *et al*. 1994).

Calves are frequently observed in Hervey Bay, singers are heard, and competitive groups are observed in the bay (Corkeron 1993, Corkeron *et al*. 1994); the latter involve intrasexual competition among males for access to females (Clapham 2000). Previous studies of humpback whales in Hervey Bay in the late 1980s and early 1990s examined migratory movement, distribution, pod size, residency, relative abundance (Corkeron 1993, Corkeron *et al*. 1994), behavioral response to whale watching vessels (Corkeron 1995, Corkeron and Brown 1995), seasonal abundance trends, and survival probabilities (Chaloupka *et al.* 1999). Corkeron *et al.* (1994) suggested that the nonrandom clustering of humpback whales aggregating in Hervey Bay might be related to social factors. However, there were no data indicating that Hervey Bay was of importance to any particular class of humpback whale (Corkeron *et al.* 1994).

In this study, we investigate the sizes and composition (classes of whales) of 4,506 humpback whale pods observed in Hervey Bay between 1992 and 2005. The primary objective of the study was to investigate and analyze pod size and composition over years and within season, and to use these data to assess the importance of Hervey Bay for particular classes of humpback whales.

Methods

Study Area and Timing of Surveys

Hervey Bay, formed by Fraser Island and the mainland, is located at 25°S, 153°E on the eastern coast of Queensland (Fig. 1). It is a wide, shallow bay approximately 4,000 km^2 in area and is generally less than 18 m deep, with a sand and mud bottom (Vang 2002). Fraser Island is 126 km long; it lies along a northeasterly axis and its northern end bridges the continental shelf. The most southerly islands of the Great Barrier Reef are directly north of Hervey Bay at a distance of between 111 and 222 km (Fig. 1).

Paterson (1991) reported that the southern migration from the Great Barrier Reef began in late July, with humpback whales moving into and out of Hervey Bay from early August to mid-October. Additional information from the Queensland Environment Protection Agency (QEPA) and the whale-watching industry confirmed the presence of humpback whales in the bay from the first week of August to mid-October between 1987 and 1991. Accordingly, a 10 wk survey commencing on the first Sunday after 5 August each season was chosen to provide a representative sample of the seasonal flow of humpbacks in Hervey Bay.

Definitions

Pod—Refers to either a lone whale (singleton)[1] or two or more humpback whales swimming side-by-side within one–two body lengths of each other, generally moving in the same direction and coordinating their speed of travel (Whitehead 1983, Clapham 1993, Corkeron *et al.* 1994). Although in some species, for example, *Orcinus orca*, the term pod is used to describe stable groups, our use of the term "pod" does not imply stable groups.

Adult—For the purpose of this study, the term "adult" is used in the results and modeling, to describe the number of whales in a pod that were not calves. The term

[1]Although a single whale is not a pod, for convenience we include singletons under the term for the purpose of these analyses.

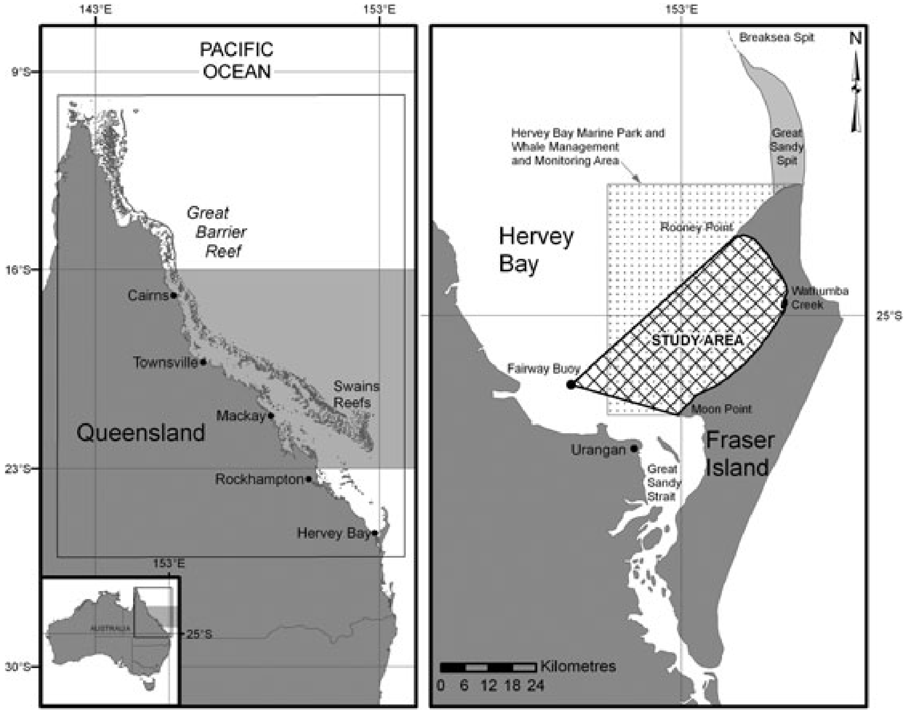

Figure 1. The location of Hervey Bay on the eastern coast of Australia and its geographic relationship to the reefs and inter-reef lagoon of the Great Barrier Reef is shown in the left side map. The primary overwintering and breeding ground for eastern Australian humpback whales is believed to be off the Queensland coast within the Great Barrier Reef inter-reef lagoon between 16°S and 23°S (shaded). The study area and the Hervey Bay Marine Park boundaries are shown on the eastern side of Hervey Bay.

"adult" is therefore used for convenience to identify all noncalves but does not imply sexual maturity. A proportion of the whales here classified as adults are likely to be immature whales and they are not identified separately as such in this paper.

Calf—An individual whale was considered to be a calf if it appeared to be less than half the length of a particular adult with whom it maintained a constant and close relationship. In most observations, no other whale was seen coming between a mother and calf (Tyack and Whitehead 1983). The adult in the dyad was assumed to be the mother.

Escort—Is defined as a whale accompanying a mother and her calf. Escorts have been generally found to be male and may be mature males waiting for a postpartum estrous mating opportunity (Glockner and Venus 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Clapham 2000).

Surveys

Vessel surveys for this study were conducted for nine weeks in 1992 and for ten weeks each year between 1993 and 2005, commencing on the first Sunday after

5 August until mid-October. The study area (Fig. 1) is approximately 27.8 km from Urangan Boat Harbour, Hervey Bay. Fieldwork was planned for 6 d each week, leaving Urangan harbor at 0800 each Sunday and returning at 1500 the following Friday. Planned daily operations were from 0930 to 1700 on Sunday, 0700 to 1700 Monday to Thursday, and from 0700 to 1330 on Friday.

Four different motorized vessels were utilized as dedicated research platforms between 1992 and 2005: two were mono-hulls and two were catamarans, ranging in length from 11 to 27 m. When searching for humpback whale pods, the normal range of operational speed of the four research vessels was 12.9–18.5 km/h. Upon commencement of observations, the rate of travel of the research vessel was adjusted to match the speed of the pod.

Pods were chosen for observation on a "first pod available" basis with no *a priori* selection of any particular pod class. On arrival in the study area, or prior to departing an overnight anchorage within the study area, the nearest pod in sight was selected. If no pod was in sight, either a random direction of travel was commenced until a pod was sighted or, if information about the location of pods was available from one of the local commercial whale-watching vessels, travel was commenced toward that location. If a pod was sighted en-route, it was selected for observation.

The pod was used as the basic observational unit in analysis for the 4,506 pods observed. The hours spent weekly on survey and observing whales, the weekly total numbers of pods and whales observed, and the mean hourly rates of observation of pods and whales over weeks were documented prior to analysis of the size and composition of pods.

Statistical Analysis

To examine the variation in pod size and composition, we report the whole sample frequencies and percentages of pod sizes (all whales), and pod sizes categorized by no calves present, versus calves present. We also report the proportions of pods for the classes, calves and escorts in terms of the number of calves and the number of escorts present. For the variation over years and within season, we report the proportion of pods with a calf present and the proportion of all whales in the pod size categories (1, 2, 3, 4+ whales).

For further analysis, we report the frequencies by week (1–10) of the pod size categories 1, 2, 3, 4+ adults of pods in which a calf was present or not present, and the frequencies by week (1–10) of the pod size category 1, 2, 3, 4+ of all whales in pods with calves present.

A multinomial logistic regression model was developed to estimate variation in the proportion of pods of 1, 2, 3+ adults over years, and over weeks within year of pods in which a calf was present or not present.

Results

Effort and Observations

A total of 139 six-d survey periods (Sunday–Friday) were conducted in the Hervey Bay study area between 1992 and 2005. Data were obtained on 770 of the planned 834 survey days. Total survey time was 6,160 h and observations of humpback whale pods were conducted for a total of 2,760 h.

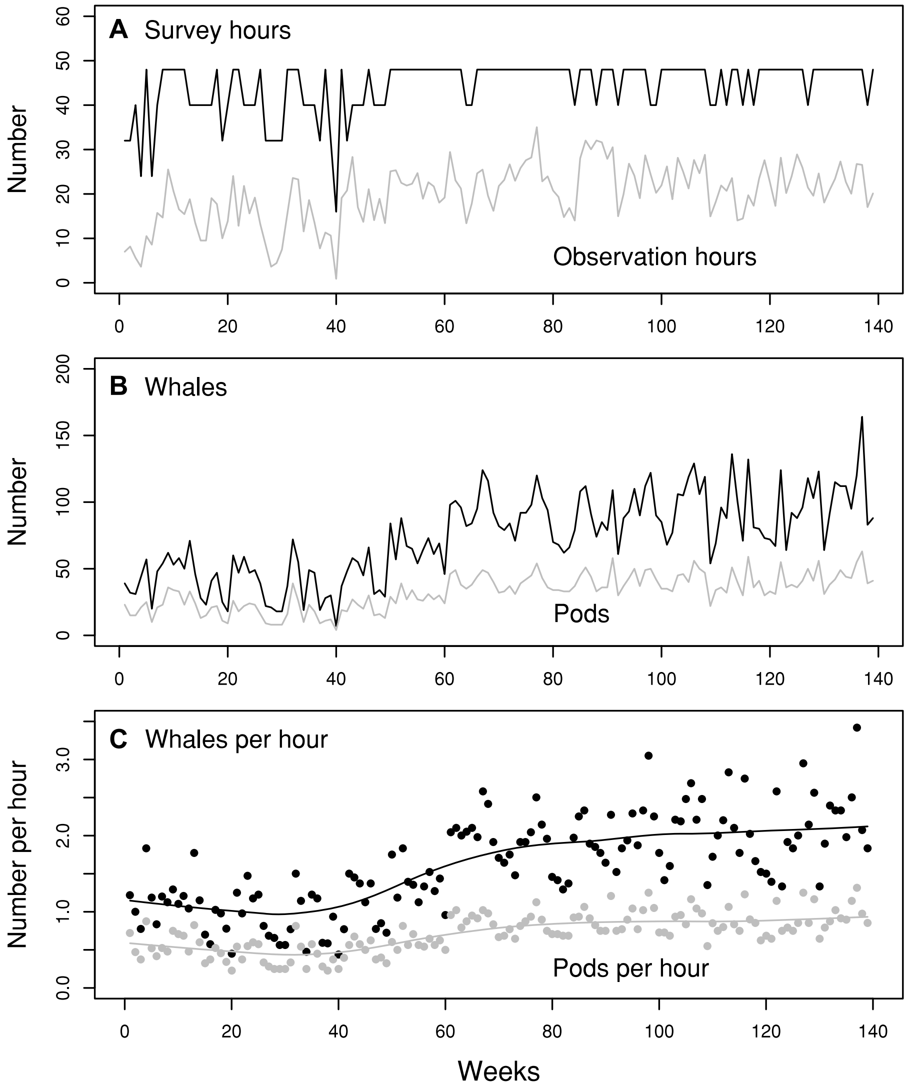

Figure 2. (A) Weekly survey and observation hours 1992–2005, (B) weekly observations of humpback whale pods and whales 1992–2005, (C) humpback whales and pods observed per hour in survey periods 1992–2005 with Loess growth curves.

Observations were made and data collected on a total of 10,179 humpback whales in 4,506 pods during the 139 6-d survey periods. Six-day survey and observation hours, and numbers of pods and whales observed in each survey period, are plotted in Figure 2A and B. Figure 2C shows the hourly rates of pods and whales observed. A Loess curve (Cleveland 1979) was added to Figure 2C to show the growth of mean observation rates over time.

Table 1. Number of whales (*n*) in pods in Hervey Bay, between 1992 and 2005.

Number of whales in pods	All whales (calves included)	
	n	%
1	717	15.9
2	2,593	57.5
3	759	16.8
4	281	6.2
5	96	2.1
6	38	0.8
7	12	0.3
8	7	0.2
9	3	0.1
Total	4,506	100.0

Pod Sizes in Hervey Bay 1992–2005

The frequencies and percentages of pod sizes for the whole sample are summarized in Table 1, and divided into two categories by "no calves present, or calves present" in Table 2. Pods ranged in size from 1 to 9 individual whales (mean = 2.26, SD = 0.10). Pods with two whales present were the most frequently observed pod size (57.5%) followed by trios (16.8%), and singletons (15.9%). Only 9.7% of pods were composed of four or more whales (Table 1). Of the 4,506 pods, 2,702 (59.96%) had no calves present and 1,804 (40.04%) had calves present (Table 2).

Of the 2,593 pods with two whales in the whole sample (Table 1), 1,344 (51.8%, Table 2) were made up of two adults, and 1,249 (48.2%, Table 2) were composed of mothers alone with their calves. In pods with no calves present, 23.7% had three or more whales and in pods with calves present, 30.8% of pods had three or more whales present.

Observations of Pods with Calves and Escorts Present in Hervey Bay 1992–2005

The number of pods observed with calves present, and the number of pods with escorts present by number and percentage for the whole sample are summarized in Table 3. Of the 4,506 pods, 1,804 (40%) had one or more calves present; 38.2% had

Table 2. Number of whales (*n*) in pods by no calves present and calves present.

Number of whales in pods	Pods with no calves present		Pods with calves present	
	n	%	*n*	%
1	717	26.5	0	0
2	1,344	49.7	1,249	69.2
3	393	14.5	366	20.3
4+	248	9.2	189	10.5
Total	2,702	100.0	1,804	100.0

Table 3. Pods with calves/escorts present (by number and percentage).

Number of calves/ escorts present	Calves (number of pods)		Escorts (number of pods)	
	n	%	*n*	%
None present	2,702	60.0	4,019	89.2
1	1,721	38.2	371	8.2
2	75	1.6	71	1.6
3	8	0.2	37	0.8
4			4	0.1
5			3	0.1
6			1	0.0
Total	4,506	100.0	4,506	100.0

one calf present, 1.6% two, and 0.2% included three calves. One or more escorts were recorded in 10.8% of the 4,506 pods.

Trends in Pod Size and Composition in Hervey Bay 1992–2005

The proportion of pods with calves present and the number of whales in pods over years and within season are summarized in Figure 3A, B, C, and D.

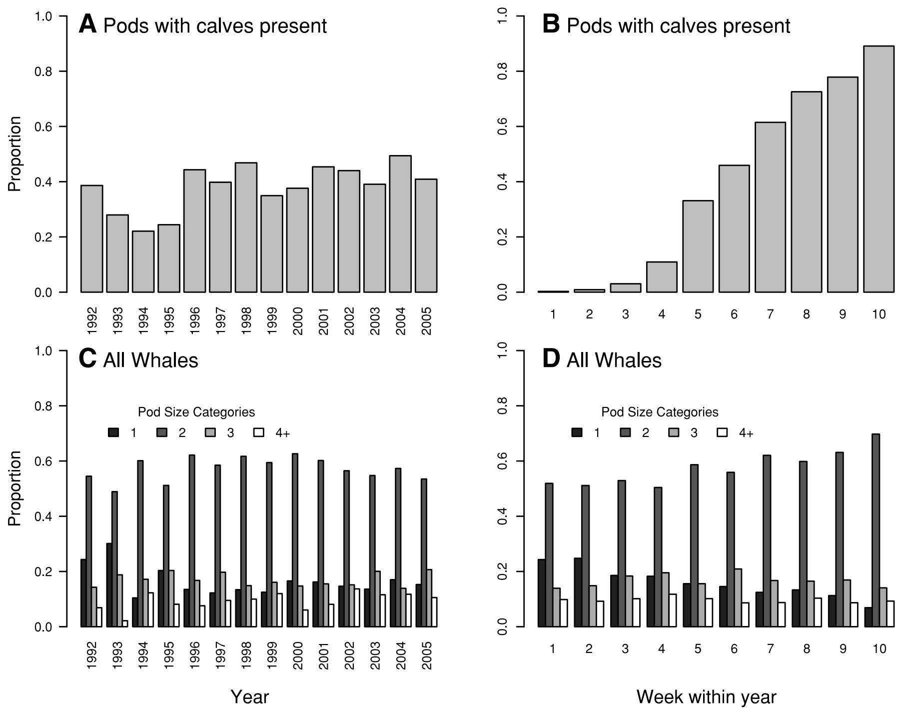

Figure 3. Observed proportions: (A) pods with calves present by year, (B) pods with calves present by week within year, (C) all whales in pod (calves included): pod size by year, (D) all whales in pod (calves included): pod size by week within year.

While the variation over years (Fig. 3A and C) does not have an obvious pattern except for the decline in the proportion of pods with calves present between 1992 and 1993, the variation over weeks within year was more systematic (Fig. 3B and D). The proportion of pods with calves present increased strongly from week 4 to the end of the season (late August–September, to mid-October; Fig. 3B).

For all whales (Fig. 3C and D), pods with two whales consisted of either two adults, or a mother alone with her calf (Table 2). For all whales, the number of pods with two whales present—expressed as a proportion of all pods—increased with time during the season, while the proportion representing singleton pods decreased. The proportion of all pods represented by larger pods (3 and 4+ whales) increased from week 1 to about week 6 (early August to mid-September) and decreased thereafter (Fig. 3D).

The Effect of the Presence or Absence of Calves on Seasonal Variation in Pod Size and Composition

Singletons as a proportion of all pods were highest in the first four weeks when pods with calves were rarely seen; however, in the same period there were still more pairs than singletons (Fig. 3D). The proportion of pods with a calf present increased in the second half of the season and was associated with a rapid increase in the proportion of mothers alone with their calves (Fig. 3B and D).

To analyze and compare the size and composition of pods with calves present and pods with no calves present, we adopted the approach used by Mobley and Herman (1985) of counting and analyzing the number of adults in pods. Table 4 summarizes the pod data by week within year, categorized by the number of adults in pods with no calves present, all whales in pods with calves present, and the number of adults in pods with calves present.

Of the 1,804 pods observed with calves present (Table 4c), 1,251 (69.4%) included one adult, who were mothers alone with their calves, 23.4% had two adults, and 7.2% had three or more adults. Where no calves were present (Table 4a, 2,702 pods), pairs were the dominant pod type (49.7%); singletons (26.5%) and 23.7% had 3 or more adults.

Of singleton pods (Table 4a), 51.9% occurred in the first four weeks of the season when pods with a calf present were rarely seen. Similarly, 64.1% of adult pairs and 69.1% of 3 and 4+ pods with no calves present occurred in the first four weeks of the season. In contrast, during the last four weeks of the season, when the majority of pods had calves present, the occurrence of singleton pods was 29.1%, adult pairs 14.7%, and 3 and 4+ adults, 11.4% (Table 4a).

Statistical Model

A statistical model was designed to examine the number of adults in pods over years, and over weeks within season, and to compare the number of adults in pods in which a calf was present or not present. The pod sizes were summarized to the categories 1, 2, 3+ adults for this analysis. These categories were chosen to simplify the model, and to ensure that there were reasonable numbers in the cells of the design while capturing the main features in the data.

An ordered multinomial logistic regression model (Hosmer and Lemeshow 2000) was fitted to the data using MLwiN V2.02 software (Rasbash *et al.* 2005) to assess

Table 4. Number of pods by week within year for size categories (1, 2, 3, 4+), for: (a) number of adults (in pods with no calves present), (b) all whales (in pods with calves present), and (c) number of adults (in pods with calves present). Relevant percentages are reported below columns.

	(a) Number of adults in pods with no calves present					(b) All whales in pods with calves present				(c) Number of adults in pods with calves present[a]				
Week \ size	1	2	3	4+	Total	2	3	4+	Total	1	2	3	4+	Total
1	89	190	50	36	365	0	1	0	1	0	1	0	0	1
2	110	223	66	41	440	4	0	0	4	4	0	0	0	4
3	86	239	80	42	447	6	5	5	16	6	5	4	1	16
4	87	209	77	51	424	31	16	5	52	31	16	3	2	52
5	72	169	40	28	309	102	32	19	153	102	33	11	7	153
6	64	117	42	15	238	129	50	23	202	129	55	9	9	202
7	64	102	15	17	198	217[b]	71	28	316	219[b]	81	13	3	316
8	67	53	10	8	138	248	73	44	365	248	84	22	11	365
9	52	31	11	8	102	260	67	32	359	260	84	7	8	359
10	26	11	2	2	41	252	51	33	336	252	63	13	8	336
Total	717	1,344	393	248	2,702	1,249	366	189	1,804	1,251	422	82	49	1,804
% of Total	26.5	49.7	14.5	9.2	100					69.4	23.4	4.5	2.7	100

[a]For the number of adults (Table 4c), if one adult is present it was a mother alone with her calf, two adults can either be two mothers together, or a mother with an escort. Similarly, if three adults are present, they can be a combination of up to three mothers (two mothers with one escort, or one mother with two escorts), while 4+ can be a combination of up to three mothers and escorts.

[b]There were two observations of a mother with two calves present in this week in different years, which accounts for the differences in this row between "All whales, in pods with calves present" and "Number of adults, in pods with calves present."

Table 5. Ordered multinomial logistic regression model for the proportions of size categories 1, 2, 3+ adults (calves excluded from count): fixed effects parameter estimates, their standard errors and *P*-values.

$\gamma_{3j} = \pi_{3j}$, $\gamma_{2j} = \pi_{3j} + \pi_{2j}$, $\gamma_{1j} = 1$[a]	Logit (γ_{2j})			Logit (γ_{3j})		
Parameter	Estimate	SE	P^c	Estimate	SE	P^c
Intercept[b]	0.942	0.105	<0.0001	−1.601	0.129	<0.0001
Year	0.007	0.009	0.436	0.044	0.012	<0.0002
Week	−0.231	0.024	<0.0001	−0.138	0.032	<0.0001
Week × Week	−0.048	0.012	<0.0001	−0.020	0.015	0.182
Calf	−1.646	0.110	<0.0001	−1.136	0.155	<0.0001
Week × Calf	0.161	0.056	0.004	−0.069	0.078	0.376
Week × Week × Calf	0.038	0.020	0.058	0.046	0.029	0.112

[a]Model: response_{ij} = ordered multinomial (pod_j, π_{ij}), where π_{ij} = probability of i (1, 2, 3+) adults (calves excluded from count), and reference category = 1 adult.
[b]Year referred to 1992, week centered at week 6, Calf referred to "calf not present."
[c]Two-tailed *P*-values based on z = Estimate/SE.

the joint effects of year, week within year, and presence of a calf on the probabilities of occurrence of 1, 2, 3+ adults. It was necessary to aggregate the first three weeks within years in order to fit the presence of the calf by week within year interaction effect because so few calves were observed early in the seasons. A linear effect for year and a quadratic effect for week within year were employed to smooth and describe the systematic pattern in the data.

Table 5 summarizes the parameter estimates, their standard errors and *P*-values from an ordered multinomial logistic regression model for the proportions of size categories 1, 2, 3+ adults as a function of year (linear), week within year (quadratic), absence or presence of calf, and the interaction of week within year by presence of calf.

The estimates reported in Table 5 were based on a parameterization using the size category of one adult as the reference category. The column labeled Logit (γ_{2j}) compares (on the natural logarithm scale) the probability of encountering two or more adults relative to a single adult, and the column labeled Logit (γ_{3j}) compares the probability of encountering three or more adults relative to a single adult.

The *P*-values in Table 5 indicate that there were significant effects for variation in relative pod size probabilities by year (linear), week within year (quadratic), presence of calf in a pod, and the interaction of week within year by presence of calf.

The model parameter estimates reported in Table 5 were used to calculate the estimated probabilities of the three response categories, 1, 2, 3+ adults by year, week within year, and absence or presence of calf. The estimated probabilities of 1, 2, or 3+ adults are plotted by year in Figure 4A, by week for pods with no calf present in Figure 4B, and by week for pods with calves present in Figure 4C.

The effects estimated by the model are more readily interpreted from the size category probabilities in Figure 4A, B, and C than from the Logit scale estimates in Table 5.

The proportion of 3+ adults increased significantly over years relative to the proportion of one adult and of either one or two adults. The increase in the proportion of 3+ adults over years (increased from 23% to 31%) corresponded with a greater

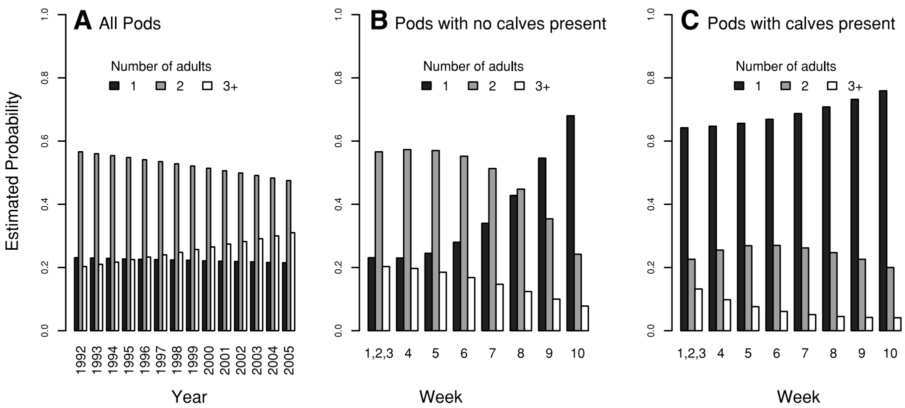

Figure 4. Estimated probabilities of 1, 2, or 3+ adults: (A) by year, (B) by week within year for pods with no calves present, and (C) by week within year for pods with calves present. (Note: In Fig. 4C the single adult category represents mothers alone with their calves and the 2 and 3+ categories are adults accompanying a calf or calves).

relative decrease in the proportion of two adults (decreased from 57% to 47%) than in the proportion of one adult (decreased from 23% to 21%) (Fig. 4A).

To the extent that the relative size probabilities changed over weeks, those changes differed significantly between pods where a calf was present and pods where a calf was not present (Table 5). A comparison of Figure 4B with Figure 4C shows that there was much greater variation over weeks in the number of adults where a calf was not present than the number of adults where calves were present.

For pods where a calf was not present (Fig. 4B), the proportion of singleton pods increased rapidly from about week 4 (late August) (increased from 23% to 68%) with an accompanying decrease in the proportions of larger pods (pods with two adults decreased from 57% to 24% and pods with 3+ adults decreased from 20% to 8%). Where a calf was present (Fig. 4C), the proportion of pods that included only the mother increased (from 64% to 76%) while the proportions of larger pods decreased over weeks (pods with two adults went from 23% to 20% via a peak of 27% in mid-September, and pods with 3+ adults decreased from 13% to 4%).

The proportion of pods where calves were present increased sharply from about week 4 (late August), so that by week 10 (mid-October) about 90% of all pods included calves (Fig. 3B). Consequently, the rapid increase in the proportion of singleton pods over weeks (Fig. 4B) occurred in the context of an ever-decreasing proportion of the total number of pods that did not include a mother and calf (Table 4a).

Discussion

Increase of Larger Pods in Hervey Bay over Years

In the Southern Hemisphere, at least seven populations of humpback whales are recognized (IWC 2006). Eastern Australian humpback whales are considered by the

International Whaling Commission (IWC) to be a relatively discrete breeding stock termed E1, and form part of the IWC's Antarctic Area V management area (130°E–170°W) (IWC 2006, Olavarría *et al.* 2006). Recent modeling suggests that, prior to the last period of commercial and illegal whaling (Clapham and Zerbini 2006, Clapham *et al.* 2009), the eastern Australian and Oceania humpback whale population may have ranged from 40,595 to 44,476 (95% CI 36,642–66,129, Jackson *et al.* 2006). In 1963, when the IWC declared complete protection for Southern Ocean humpback whales, it was estimated that there may have been fewer than 100 survivors in the eastern Australian population (Paterson *et al*. 1994). During the 30 yr from 1962 to 1992, the eastern Australian humpback whale population was estimated to have only increased to 1,900 whales (95% CI 1,650–2,150, Paterson *et al.* 1994). During the 14 yr of this study, 1992–2005, the eastern Australian humpback whale population is estimated to have increased to 7,024 (95% CI 5,163–9,685; Paton *et al.* in press).

Accordingly, the numbers of humpback whales available to enter Hervey Bay during the study period increased by a factor of approximately 3.7. The increase in the population of eastern Australian humpback whales in Hervey Bay may be one of the factors contributing to the significant increase (Table 5) over years of larger groups (pods with 3+ adults, Fig. 4A) compared to pods of one or two adults. Hence, as the population increased, larger groups became more common.

The increase in the number of pods observed over the study period (Fig. 2C) is consistent with the growth in the population, which is likely to have generated a skewed distribution in the population toward younger whales. Humpback whale males and females may reach sexual and social maturity as early as 5 yr (Chittleborough 1965, Clapham 1992), although a recent study suggests it could be 10 or more years in some populations (Gabriele *et al.* 2007). Consequently, male and female humpback whales in the early stages of sexual and social development may also have contributed to the significant growth in pods with 3+ adults (Fig. 4A) over years in Hervey Bay.

Dawbin (1956, 1966) suggested that humpback whales require some period in suitable semitropical coastal waters for normal breeding behavior, and that maximum aggregations can be expected to occur toward the northern part of the migration closest to the breeding grounds. Hervey Bay is near the putative breeding ground of eastern Australian humpback whales located in the Great Barrier Reef lagoon (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999). They do not migrate directly through Hervey Bay, but divert from the main migratory pathway to move into and out of the bay from the north. Humpback whales in Hervey Bay aggregate in nonrandom clusters on the eastern side of the Bay (Corkeron *et al*. 1994). Therefore, due to the density and movements around the bay by humpback whales, there is an increased likelihood of interactions (aggregation and disaggregation) among pods, which may also contribute to the formation of larger groups or to the probability of encountering recently aggregated pods.

There were significant changes in the pod characteristics of humpback whales utilizing Hervey Bay from the beginning to the end of the study, notably the increase in larger groups. Given that this population is known to have increased in size from about 1,900 to 7,000 whales (Paterson *et al.* 1994; Paton *et al.* in press) during the period 1992–2005, these changes may be indicative of social and behavioral changes that occur as a population expands. If so, it may be useful to review similar long-term data from other areas hosting recovering populations (notably Hawaii and the West Indies), to search for similar changes in pod characteristics and social behavior as populations expand over extended study periods. Studies from Hawaii have reported that the range of humpback whales has expanded as the population increased (Mobley *et al*. 1999, Johnston *et al*. 2007), and that whales regularly move between islands separated by 4° of longitude (Cerchio *et al*. 1998).

Seasonal Change in Pod Characteristics Early to Mid-Season

Dawbin (1966, 1997) reported that females in early pregnancy and resting non-lactating females were among the first to commence the southern migration and that they preceded lactating females by about a month. Furthermore, they were either accompanied or closely succeeded by immature males and females. Mature males and females follow immature males and females but also precede lactating females with calves and escorts. The timing and presence of the sexual and maturational classes as described by Dawbin (1966, 1997) is likely to contribute to the higher proportion and number of pairs in Hervey Bay during August.

In the early part of the season, when calves were rarely present, the highest proportion and numbers of pods were pairs (Fig. 4B, Table 4a). Recent genetic studies of humpback whales in breeding grounds off the coast of South Africa and Brazil reported that most pairs consist of male–female dyads (Pomilla and Rosenbaum 2006, Cypriano-Souza *et al.* 2010). Brown and Corkeron (1995) also reported that male–female associations represented the greatest proportion of pairs observed during the southern migration along the eastern coast of Australia.

Compared to pairs, there were relatively fewer singletons in the early part of the season (Fig. 4B). The proportion and number of singletons were higher during the first two weeks of August, compared to the last two weeks of August and the first week of September (Fig. 3D, Table 4a). Clapham (1994) showed that, in the southern Gulf of Maine, immature male and female humpback whales spent relatively more time alone in their early years, with solitary time diminishing as they approached sexual and social maturity. Specifically, he found that males were alone in 55.8% of observations at the age of one, but in only 26.8% of sightings by the age of six. The comparable figures for lone females were 49.9% at age 1 yr to 20.5% at 6 yr. Male and female humpback whales in the early stages of maturity are likely to contribute to the proportion of singletons observed in August.

Presence of Calves Affect Pod Composition after Mid-Season

Modeling of the systematic variability of observed pod size and composition within season in Hervey Bay revealed the significant influence of pods with calves present on pod size and composition in mid-to-late season (Fig. 4C, Table 4c).

Adult pairs and mothers alone with their calves were the most frequent pod size and type observed in Hervey Bay, with mothers alone with their calves accounting for just under half of such pods (Table 1, 2). However, the composition of pods with two whales present changed significantly over the season (Fig. 4B and C) as the mothers with calves moved into the bay from mid-season onwards and dominated the latter half of the season (Fig. 3B), coinciding with a rapid decrease of adult pairs (Fig. 4B). Mothers were alone with their calf in 69.4% of observations of pods with calves present, (Table 4c), and the proportion of lone mother-calf pods in Hervey Bay was greater than has been reported for other regions (Hawaii: Mobley and Herman 1985, Herman and Antinoja 1977; West Indies: Mattila and Clapham 1989, Mattila *et al*. 1994).

Mobley and Herman (1985) found that when they excluded calves from the count, the overall distributions of pod sizes were very similar. In contrast in Hervey Bay, there were significant differences in pod sizes in pods with and without a calf, when the calf was excluded from the count (Fig. 4B and C). One of the major differences between the Hervey Bay and Hawaiian studies was that the modal size for pods having a calf present was three, mother-calf and escort (Herman and Antinoja 1977, Herman *et al.* 1980, Glockner and Venus 1983). By contrast, in Hervey Bay in pods with calves present the modal size was two, because of the significantly higher proportion of mothers alone with their calf (Table 4c).

When mothers were not alone with their calves, they were either accompanied by an escort or escorts, or were mixing with other females with calves (Table 3, 4c). It has been reported that mother and calf pods rarely associate with other mother-calf pods in winter breeding grounds (Herman and Antinoja 1977, Baker and Herman 1984, Mobley and Herman 1985). In contrast in Hervey Bay, although the proportion of pods with more than one calf present is low, interaction between mother-calf pods does occur. Possibly by mid-to-late season in Hervey Bay, when the calves are more mature and mother-calf bonds are well established, mothers may be more comfortable mixing with other mother-calf pods (see below).

Hervey Bay as a Habitat for Mothers with Calves

Forty percent of all pods observed in Hervey Bay had one or more calves present (Table 3), and there were more mother-calf pods observed in Hervey Bay compared to earlier reports in other regions (Hawaii: Herman and Antinoja 1977, Mobley and Herman 1985, West Indies: Mattila and Clapham 1989, Mattila *et al*. 1994).

Hervey Bay is slightly off the migratory pathway and south of the putative breeding ground and may provide mothers and calves with a suitable and convenient location for maternal care in the early stages of the southern migration. Mothers of humpback calves exclusively provide maternal care in the form of food, protection, and preparation for their calves' first migration to high-latitude feeding areas (Clapham 2000). It has been suggested that females with calves prefer shallower waters close to shore to minimize predation by sharks and/or to avoid harassment by males (Whitehead and Moore 1982, Glockner and Venus 1983, Mattila and Clapham 1989, Smultea 1994), or as a function of social organization (Ersts and Rosenbaum 2003).

It has also been suggested that escorts may serve a protective function, and that it may be advantageous for mothers with calves to travel with an escort during migration (Herman and Antinoja 1977, Brown and Corkeron 1995). A recent study reported that females with a calf may tolerate a single escort as a "bodyguard" strategy to avoid harassment by other males (Cartwright and Sullivan 2009). However, the low proportion of escorts observed in Hervey Bay may provide a further advantage to mothers in that they have the opportunity of spending most of their time alone with their calves without having to take into account the presence of male escorts, or of being harassed by male escorts.

The first calves observed in Hervey Bay occurred in late August. Therefore, calves accompanied by mothers may be between a few weeks to 2 mo of age (Chittleborough 1953, 1958). Consequently, Hervey Bay does not appear to be a calving ground, but rather a suitable stopover for mothers to engage in maternal activity with older calves during the early stages of their southern migration.

Conclusions

Hervey Bay is south of the putative breeding grounds and is a habitat utilized by eastern Australian humpback whales during the early stages of the southern migration. These data on pod characteristics of humpback whales in Hervey Bay indicate that the shallow, sheltered waters of the eastern bay provide an important habitat for mothers and calves, as a temporary stopover during their initial southern migration to Antarctic feeding areas. In addition, Hervey Bay provides a suitable and important habitat for other classes of humpback whales primarily during the early part of the migratory season, specifically immature males and females in early August and mature males and females in late August. The significant seasonal changes in pod characteristics of humpback whales in Hervey Bay appear to be related to the different sexual and maturational classes of humpback whales using the bay.

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