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Site-specific female-biased sex ratio of humpback whales (*Megaptera novaeangliae*) during a stopover early in the southern migration

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Abstract: Previous research on humpback whales (*Megaptera novaeangliae* (Borowski, 1781)), in both the Northern and Southern hemispheres, has reported site-specific male-biased sex ratios in breeding grounds and along migratory corridors. However, one recent Southern Hemisphere study reported a female-biased sex ratio in a feeding area within a coastal migratory corridor, indicating that females may preferentially occupy some habitats. We investigated the classes and relative seasonal timing of humpback whales using Hervey Bay (Queensland, Australia) as a stopover early in the southern migration. Modeling and analyzes were undertaken using data from resighting histories of 361 individually identified whales between 1992 and 2009. The data consisted of 2131 sightings categorized by either sex, age, reproductive status, or maturational status. A female-biased sex ratio of 2.94:1 indicates that Hervey Bay is a preferential stopover for females. The data revealed that the bay is important for mature females who co-occur with immature males and females during August. During September and October, mothers with calves accompanied by a few escorts dominate the Bay. Immature males and females socialize with mature females during August and September. The data support the hypothesis that habitat preferences and differential migration of females and males provide a plausible explanation for site-specific sex-bias in breeding grounds, migratory stopovers, and along migratory corridors.

Key words: humpback whale, *Megaptera novaeangliae*, Hervey Bay, mature and immature males and females, calves, escorts, preferential habitat, sex ratio.

Résumé : Des travaux antérieurs sur les baleines à bosse (*Megaptera novaeangliae* (Borowski, 1781)), tant dans l'hémisphère nord que dans l'hémisphère sud, ont fait état de rapports de masculinité penchant vers les mâles dans les aires de reproduction et le long de couloirs de migration. Une étude récente dans l'hémisphère sud fait toutefois état d'un rapport de masculinité penchant vers les femelles dans une aire d'alimentation à l'intérieur d'un couloir de migration côtier, ce qui indique que les femelles pourraient occuper préférentiellement certains habitats. Nous avons examiné les classes de baleines à bosse et le moment saisonnier relatif de leur utilisation de la baie Hervey (Queensland, Australie) comme escale tôt durant la migration vers le sud. Une modélisation et des analyses ont été réalisées en utilisant des données d'historiques d'observations répétées de 361 baleines identifiées individuellement entre 1992 et 2009. Les données consistent en 2131 observations catégorisées selon le sexe, l'âge, l'état reproducteur ou la maturité. Un rapport de masculinité penchant vers les femelles de 2,94 : 1 indique que la baie Hervey est une escale privilégiée des femelles. Les données révèlent que la baie est importante pour les femelles matures qui cooccurrent avec des mâles et femelles immatures en août. En septembre et octobre, ce sont plutôt les mères avec baleineaux accompagnées par quelques escortes qui dominent dans la baie. Des mâles et femelles immatures interagissent socialement avec les femelles matures en août et en septembre. Les données appuient l'hypothèse voulant que les préférences en matière d'habitat et la migration différentielle des femelles et des mâles constituent une explication plausible du biais selon le sexe dans les aires de migration, dans les escales migratoires et le long de couloirs de migration. [Traduit par la Rédaction]

Mots-clés : baleine à bosse, *Megaptera novaeangliae*, baie Hervey, mâles et femelles matures et immatures, baleineaux, escortes, habitat privilégié, rapport de masculinité.

Introduction

Humpback whales (*Megaptera novaeangliae* (Borowski, 1781)) undertake long annual migrations between winter low-latitude breeding grounds and summer high-latitude feeding areas (Clapham 2000). Northern Hemisphere humpback whales travel from feeding areas in mid-latitudes to high latitudes to tropical breeding grounds such as Hawai'i and the West Indies, often without encountering continental shorelines (Baker et al. 1986; Smith et al. 1999; Stevick et al. 2003; Calambokidis et al. 2008). In contrast, Southern Hemisphere humpback whales predominantly migrate along the extensive continental coastlines and nearshore islands of South America, Africa, and Australia, en route to and from tropical breeding grounds (Chittleborough 1965; Dawbin 1966, 1997). Dawbin (1966, 1997) using whaling data investigated and described the timing and temporal segregation of reproductive and maturational classes of humpback whales during the Southern Hemisphere migrations.

The sex ratio in humpback whale populations does not vary significantly from parity (Clapham 2000). However, several studies have reported site-specific sex-ratio variation from parity at various stages of the migration. Herman et al. (2011) found a male-

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biased sex ratio in the Hawaiian breeding grounds. They undertook a comprehensive review of previous studies reporting male-biased sex ratios and discussed the reasons for the worldwide occurrence of male-biased sex ratios in winter breeding grounds. Brown et al. (1995) reported a male-biased sex ratio off Stradbroke Island, southeast Queensland (27°S), Australia, during the northern and southern winter migration. In contrast, Barendse et al. (2010) reported a female-biased sex ratio off Saldanha Bay, southwest Africa (33°S), in mid-spring during the southern migration.

Hervey Bay (25°S, 153°E) is located along the continental coast of southeast Queensland, slightly west of the main northward migratory pathway and 2° south of the Great Barrier Reef lagoon. Humpback whales do not enter Hervey Bay on their northward migration during June and July. The migration passes Great Sandy 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; Smith et al. 2012). On the southward migration, large numbers of humpback whales make a slight diversion from the southern migratory pathway and pass inside Great Sandy Spit to enter Hervey Bay (Paterson 1991). They aggregate in shallow waters close to the western shore of Fraser Island in the eastern part of the bay and enter and leave Hervey Bay from the north (Corkeron 1993; Corkeron et al. 1994; Franklin et al. 2011). The residency time of humpback whales visiting Hervey Bay is around 1.5 to 2 weeks (Franklin 2014). Hervey Bay is neither a calving ground nor a terminal destination, but rather a stopover early in the southern migration (Franklin et al. 2011; Franklin 2012).

Past aerial surveys have shown that within Hervey Bay, pods aggregate in nonrandom clusters (Corkeron 1993). Corkeron et al. (1994) suggested that the clustering of pods may be related to social factors. However, there were no data indicating that Hervey Bay was of importance to any particular class of humpback whale. Franklin et al. (2011) investigated pod characteristics in Hervey Bay and reported that pod size and composition varied significantly during August, September, and October. Pod composition in August appeared to be related to the presence of mature females and immature males and females. During September and October, mothers with calves dominated pod composition, accompanied by few escorts.

In this study, we use long-term resighting histories of 361 individually identified humpback whales derived from photo-identification in Hervey Bay between 1992 and 2009. We use these data to investigate the relative timing of age, sex, and reproductive and maturational classes of humpback whales using the bay during August, September, and October. The importance of Hervey Bay for particular classes of eastern Australian humpback whales during the southern migration is discussed. Sex-bias, site-specific habitat preference and differential migration of females and males at a migratory stopover and along migratory corridors are also discussed.

Materials and 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 east coast of Queensland (Fig. 1). It is a wide shallow coastal embayment approximately 4000 km^2 in area with a mean depth of 20 m (Ribbe 2014). Fraser Island is 126 km long; it lies along a northeasterly axis and its northern end bridges the continental shelf (Ribbe 2014; also see Fig. 2). The study area is located in the eastern bay against the western shore of Fraser Island (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 Hervey Bay 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. Consequently, we conducted vessel-based photo-identification and observations of humpback whale pods in the Hervey Bay study area from early August until mid-October each year between 1992 and 2009 with consistent annual weekly effort.

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

Field observations

A pod was defined as either a lone whale (singleton) or two or more humpback whales swimming side-by-side within one to two body lengths of each other, generally moving in the same direction, and with coordinated speed of travel (Whitehead 1983; Clapham 1993; Corkeron et al. 1994).

Pods were chosen for observation on a "first pod available" basis with no a priori selection of any particular pod class. During the weekly study period, a variable overnight anchorage within the study area was selected based on the location of the final pod observed, weather conditions, and tidal movements. Each morning, subject to weather and sea-state conditions, travel was commenced along a different transect each day until a pod was sighted. However, if information about the location of pods was available from one of the local commercial whale-watching vessels, then travel was commenced toward that location. If a pod was sighted en route, then it was selected for observation.

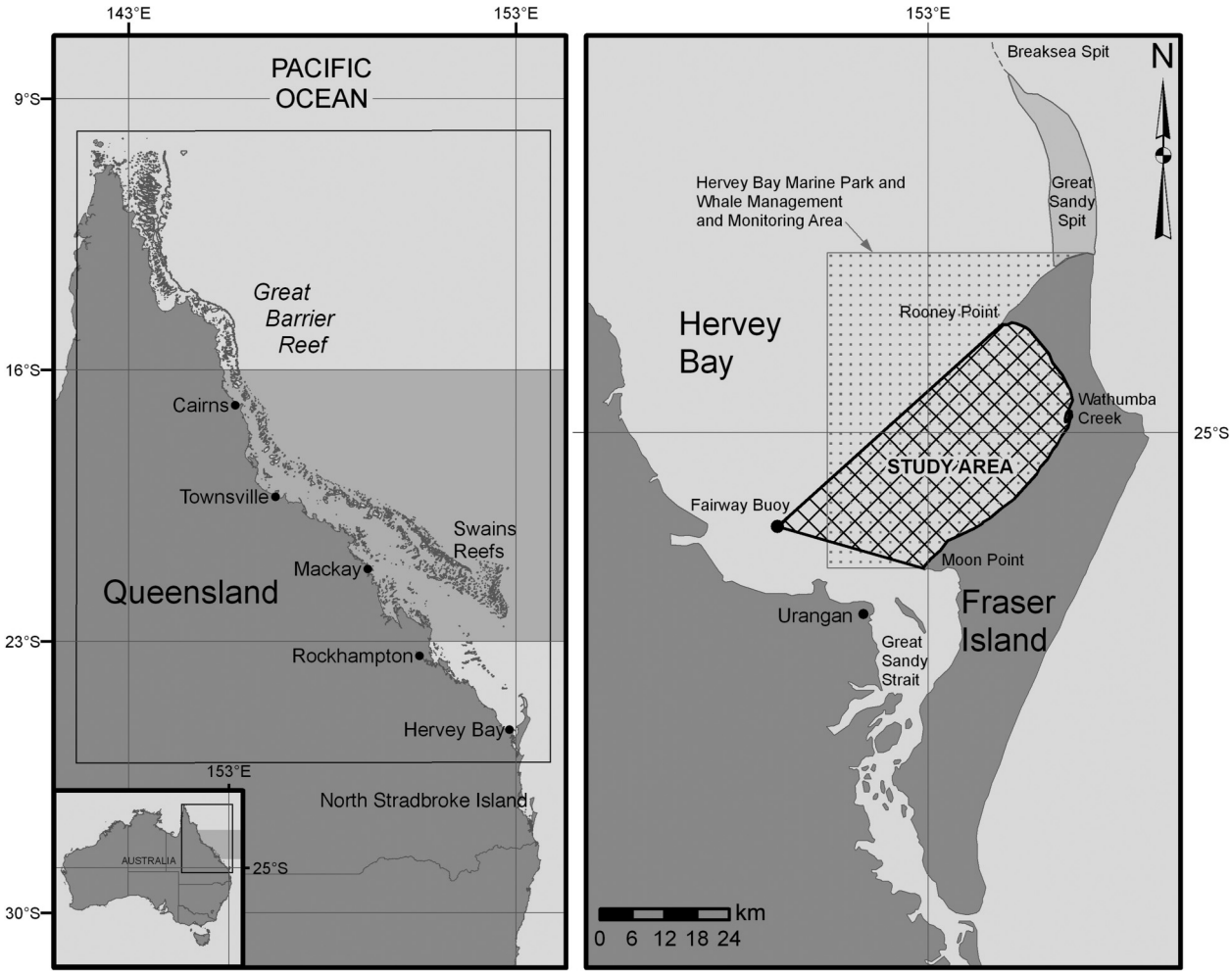
We were supported each season by research assistants who were undergraduate students or graduates participating in environmental or marine science degrees at Southern Cross University and (or) other Australian and overseas universities. Weekly volunteer interns were rostered and supervised by the research assistants to assist with fieldwork. A minimum of six interns were rostered on morning and afternoon shifts. The roster duties were to scan and search for pods; take field notes, GPS readings, weather readings, and environmental readings; and to complete the daily data entry.

Each pod selected for observation was assigned an identification code. Data collected during observations included date, time, and GPS location at commencement every 15 min during and at completion of the observation. The number of individuals, composition, and surface behaviors of pods (continuous sampling; Altmann 1974) were recorded. Information on sex-identification was obtained where possible (see definitions below for sex-identification methods). All pod and observation data were recorded daily in field notes and entered into a FileMaker Pro database each evening.

Photo-identification procedure

The aim of the field photography was to obtain information to identify individual humpback whales within pods. Consequently, photographs of the ventral fluke patterns, dorsal fins, and lateral body markings were obtained where possible of each individual in each pod (Katona et al. 1979; Katona and Whitehead 1981; Hammond 1986). To facilitate photographic analysis a marker shot of Fraser Island was taken prior to commencement and after completion of photography on each pod. In addition, if a photograph of a dorsal fin was followed immediately by a fluke photograph of the same individual whale, then a marker shot (of the ship's railings) was taken to verify that the preceding series of

Fig. 1. The location of Hervey Bay on the eastern coast of Australia and its geographic relationship to the Great Barrier Reef and presumed breeding grounds (16°S–23°S; shaded area) of humpback whales (*Megaptera novaeangliae*) is shown on the left-side map. The study area and the Hervey Bay Marine Park boundaries are shown on the eastern side of Hervey Bay.



photographs were of the same individual whale. Between 1992 and 2002, 35 mm slide-film photographs were taken with a Canon Camera using a 100–300 mm lens. From 2003 to 2009, a Canon EOS digital Camera with a 100–300 mm lens was used. The 35 mm slide photographs selected for use in the analysis were scanned and digitized prior to analysis. All photographs used in the analysis were digitally archived as high-resolution JPEG files at a standard ratio of 1536 pixels × 1024 pixels at 300 dpi. The standard formatting enabled consistent display on Apple computers for photo-identification and matching throughout the study.

Field notes were imported into an integrated whale analysis FileMaker Pro database. All field photography was organized and archived by date, time, and pod. The file name of each data image included pod identification, date, and frame number. As well, a code for whether the image was of a ventral tail fluke (USF), left or right side lateral body (LSD or RSD, respectively), gender information (GEN), or of behavior (BH) was included. Photography of each pod was reviewed in conjunction with field notes. Then archive numbers of photographs supporting identification of individual whales were recorded in the database. Intraseason resightings of individuals were compiled and archived with supporting photography. Ventral fluke photographs were assessed for image quality (SPLASH; Calambokidis et al. 2008) prior to inclusion in each yearly catalogue.

Matching of yearly tail fluke catalogues was facilitated by using a proprietary matching system based on applying an array of coded discrete characteristics (ACDC) on the file name of each tail fluke photograph (Franklin 2012). The ACDC categories were based on individually unique and stable patterns of black and white pigmentation on ventral tail flukes (Katona et al. 1979; Katona and Whitehead 1981). The system allowed each tail fluke to be visually displayed for matching in contiguous and discrete stratified categories when using Apple Preview software. When matching a tail fluke, it was pairwise matched with other photographs within its ACDC color and pattern category. If not matched, it was then subsequently compared with photographs within adjacent categories. As the majority of flukes were predominantly all white (63.5%; Franklin 2012), the shape and coloration of the trailing edge and notch were also important characteristics in the matching process (Carlson et al. 1990; Mizroch et al. 1990; Blackmer et al. 2000; Friday et al. 2000). To minimize misidentification, missed matches, and false negatives, dorsal fin and lateral body photography was used as secondary information to verify matches. One other experienced member of the research team independently verified all matches.

Resighting histories of individual humpback whales based on sightings over 2 or more years were compiled from matching yearly tail fluke catalogues and incorporated into an Excel capture–mark–recapture database for analyses. Database and photography files used in the photo-identification process were digitally backed-up and stored on and offsite for security.

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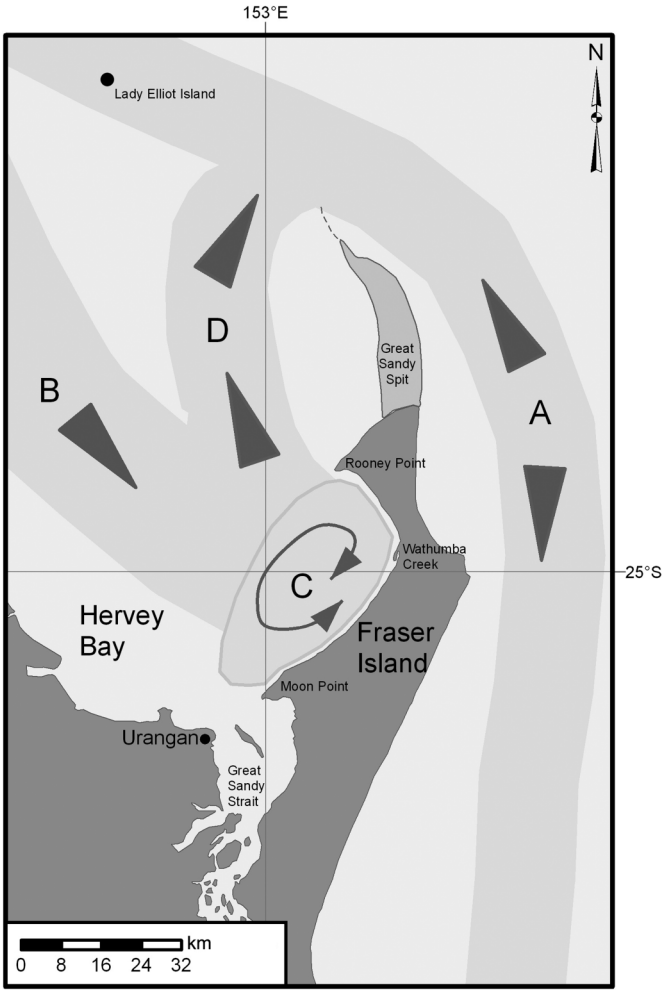
Fig. 2. Migratory pathways of humpback whales (*Megaptera novaeangliae*) into and out of Hervey Bay. Hervey Bay is a bowl-shaped coastal embayment with an area of 4000 km². Its northern entrance, east of the northern end of Great Sandy spit, is 80 km wide with an mean depth of 20 m (Ribbe 2014). Humpback whales enter (B) and leave Hervey Bay (D) to the north and aggregate and circulate in the eastern bay, off the western shore of Fraser Island (C) (Corkeron 1993; Franklin et al. 2011). To enter Hervey Bay, humpback whales make a slight diversion from the primary north–south migratory pathway (A) (Paterson 1991) and traverse shallow waters for approximately 40 km, contending with 3 m tidal movements and do not return to deeper water (Ribbe 2014) until they pass north of Great Sandy spit and rejoin the primary southern migratory pathway (A).



Each sighting event in the capture–mark–recapture database was examined in conjunction with photo-identification and observation notes. Information on pod composition, behavior, and sex were reviewed. Where the relevant information was available, individual whales were categorized into the following sex, age, and reproductive and maturational classes for analyses: (1) males, mature not with lactating females; (2) males, mature escorting lactating females; (3) males, unknown maturity not with lactating females; (4) females, lactating; (5) females, not lactating; (6) known-age whales (male and female) as calves; (7) known-age whales (male, female, and unknown sex) 1–6 years; and (8) known-age whales (male and female) 7+ years. The classes selected for investigation were derived from Dawbin (1966, 1997), Franklin et al. (2011), and Franklin (2012) and were classified in accordance with the definitions below.

Definitions for class categorization, sex identification, and peak density

Male sex identification

Males were determined by either unequivocal observation and (or) photography of their genital area, or inferred as a male when observed in the social role of escort to a lactating female (see definition below), a singer, or a principal member of a competitive group (Tyack 1981; Glockner and Venus 1983; Baker and Herman 1984; Clapham et al. 1992; Herman et al. 2011). The presence of extensive vertical and horizontal scratch marks on the left and right lateral bodies was also used in conjunction with the behavioral observations to infer that an individual was a male (Chu and Nieukirk 1988).

Males observed both as escorts and not in the role of escorts

Males were identified as escorts when observed accompanying a female with calf and were classified "with lactating female". When the same males were observed either within or between seasons in pods with no calves present, they were classified as "not with lactating females".

Male maturational status — known mature or unknown maturity

Males were determined to be socially and sexually mature if the time between first sighting and subsequent resightings exceeded 6 years and were classified as "known mature" (Chittleborough 1965; Clapham 1992; Gabriele et al. 2007). If the time between first sighting and subsequent resightings of a male was 6 years or less, then they were classified as "maturity unknown".

Female sex identification

Females were determined by either unequivocal observation and (or) photography of their genital area and the presence of a hemispherical lobe posterior to the genital slit (True 1904; Glockner 1983), or inferred as female when observed in a constant and close relationship with a calf (Tyack and Whitehead 1983; Clapham et al. 1999; Herman et al. 2011).

Females lactating and nonlactating

Females observed in a constant and close relationship with a calf (Tyack and Whitehead 1983; Clapham et al. 1999; Herman et al. 2011) were inferred to be lactating. When the same females were observed in other seasons in pods with no calves present, they were classified as "nonlactating". If individual females were observed only in pods in a constant and close relationship with a calf throughout their resighting histories, then they were classified as "only lactating". If individual females were observed only in pods with no calves present throughout their resighting histories and were sex-identified by genital observation, then they were classified as "only nonlactating".

Female maturational status — known mature or unknown maturity

Females classified as "lactating" were determined to be both socially and sexually mature and classified as "known mature". Females classified as "only nonlactating" were determined to be socially and sexually mature and classified as "known mature" if the time between first sighting and subsequent resightings exceeded 6 years (Chittleborough 1955, 1965; Clapham 1992; Gabriele et al. 2007). If the time between first sighting and subsequent resightings was 6 years or less, then they were classified "maturity unknown".

Known-age whales

Known-age whales were individually identified whales first observed as calves or yearlings. An experienced observer identified yearlings to be unambiguously small relative to adults, but too large to be calves of the year (Clapham et al. 1999; Craig et al. 2003).

Table 1. Summary of collection effort for humpback whales (*Megaptera novaeangliae*) in Hervey Bay from 1992 to 2009.

	Fieldwork			Sightings (*n*)		
Year	First day	Last day	Field days	Pods	Whales	Yearly catalogues: tail flukes (*n*)
1992	10 August	9 October	42	189	387	4
1993	6 August	15 October	53	229	442	5
1994	7 August	14 October	50	163	380	47
1995	6 August	13 October	51	172	374	47
1996	4 August	11 October	48	185	410	70
1997	1 August	17 October	64	300	693	140
1998	9 August	16 October	58	410	934	190
1999	28 July	15 October	63	399	929	210
2000	6 August	13 October	58	380	815	206
2001	12 August	19 October	57	432	954	234
2002	11 August	17 October	59	409	968	268
2003	10 August	17 October	56	390	928	270
2004	5 August	15 October	60	419	952	303
2005	30 July	14 October	61	448	1 050	376
2006	3 August	13 October	58	420	984	341
2007	30 July	11 October	60	399	945	297
2008	7 August	17 October	61	508	1 283	407
2009	6 August	16 October	55	396	901	317
		Total	1 014	6 248	14 329	3 732

Known-age whales were classified as male or female from genital observations, or if no genital observations were available, were classified as sex unknown. They were then further categorized into four age categories: sightings as calves (male, female, or unknown sex); sightings as yearlings (male, female, or unknown sex); sightings as 2- to 6-year-olds (male, female, or unknown sex); and sightings from year 7 onwards, i.e., 7+ years (male and female). Sightings of known-age individual whales (males, females, and unknown sex) first sighted as calves, yearlings, or from 2 to 6 years were categorized as "known immature" and sightings of the same whales that exceeded 6 years, or if they were females observed lactating, were categorized as "known mature".

Peak density

Peak density is the model estimated mean occurrence, day within season, of the sightings of each of the sex, age, and reproductive and maturational classes analyzed in this study.

Statistical analysis and modeling

We constructed a database for the sightings of the individually identified whales in each class to investigate their timing during August, September, and October.

The response variable of primary interest was the day of each sighting during the months of August, September, and October (1 August = day 1, …, 19 October = day 80).

To further investigate the patterns of sightings and relative seasonal timings of the classes of humpback whales using Hervey Bay, a multilevel linear model, with day during August, September, and October as the response variable, was fitted with the seven classes of whales (calves excluded as necessarily accompanying the lactating females) as a factor, using the MIXED procedure in IBM SPSS Statistics version 19.0 (IBM, Armonk, New York, USA). Separate variances were fitted for the seven classes in the random effects part of the model. In the multilevel model for mean day within season, the data were modeled as a sample of sightings on each of a sample of whales.

Ten comparisons between classes were planned to investigate the relative timing and likely association of classes during August, September, and October. Based on the temporal segregation of migrating humpback whales described by Dawbin (1966, 1997), the first seven of these comparisons were expected to yield significant mean differences, whereas the last three were not. Each comparison was tested against a Bonferroni-adjusted p value of 0.005 to yield an overall α level of 0.05 for the 10 tests.

Results

Collection effort and photo-identification matching

Fieldwork in Hervey Bay was conducted for 181 weeks, involving 1014 operational days and 8122 h of field observations from 1992 to 2009, and weekly effort was constant in all years (Table 1).

The 1992 to 2009 Hervey Bay reconciled tail fluke catalogue consisted of 2821 individual flukes. Progressive photo-identification matching of yearly catalogues between 1992 and 2009 yielded resighting histories of 578 individual humpback whales.

Assignment of individually identified whales to classes and sex ratio

There were 361 of the 578 individually identified whales with resighting histories, which could be assigned to classes and analyzed in terms of sex, reproductive category, and maturational status (summarized in Tables 2 and 3).

There were 262 resighting histories of individually identified females and 89 males (Table 2). The seasonal sex ratio of females to males in Hervey Bay was 2.94:1. There were also 10 resighting histories of individually identified known-age whales of unknown sex (Table 2).

Statistical analysis

There were a total of 2131 sightings, within and between seasons, of the 361 individually identified whales (Supplementary Table S1).[1] The results and statistics for each class are reported (Table 3) and the seasonal timing of sightings, by class, day within season, and by number of sightings are presented (Figs. 3*a*–3*h*).

Sightings of known-mature males not observed with lactating females (Fig. 3*a*) were less common during August and peaked

[1]Supplementary Table S1 is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0086.

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Table 2. Number and sightings of individually identified humpback whales (*Megaptera novaeangliae*) (classes *a*, *b*, *c*, and *d*) by sex, sex-identification method, reproductive category, and maturational status, as well as known-age whales (class *e*) by maturational status, age class (*i*, *ii*, *iii*, *iv*), and sex, if available.

Class, sex, sex-identification method	Reproductive category	Maturational status: Known immature	Known mature	Maturity unknown	Total sightings
(*a*) Males sighted as escorts, and the same males sighted not in the role of escorts (*n* = 77)					
Males: genital observation	Not with lactating females	0	11	12	23
Males: inferred	Not with lactating females	0	126	98	224
Males: genital observation	With lactating females	0	7	0	7
Males: inferred	With lactating females	0	185	0	185
	Total sightings of males (*n* = 77)	0	329 (74.9%)	110 (25.1%)	439 (100%)
(*b*) Females sighted lactating and the same females sighted nonlactating (*n* = 126)					
Females: genital observation	Lactating	0	109	0	109
Females: inferred	Lactating	0	490	0	490
Females: genital observation	Nonlactating	0	60	0	60
Females: inferred	Nonlactating	0	203	0	203
	Subtotal	0	862	0	862
(*c*) Females sighted only lactating (*n* = 96)					
Females: inferred	Lactating	0	544	0	544
	Subtotal	0	544	0	544
(*d*) Females sighted only nonlactating (*n* = 30)					
Females: genital observation	Nonlactating	0	2	110	112
	Subtotal	0	2	110	112
	Total sightings of females (*n* = 252)	0	1408 (92.8%)	110 (7.2%)	1518 (100%)
(*e*) Known-age (male, 12; female, 10; unknown sex, 10): first sighted as calves or yearlings (*n* = 32)					
(*i*) Calves	Male	14	0	0	14
	Female	12	0	0	12
	Unknown sex	5	0	0	5
(*ii*) Yearlings	Male	33	0	0	33
	Female	20	0	0	20
	Unknown sex	9	0	0	9
(*iii*) 2–6 years	Male	17	0	0	17
	Female	14	0	0	14
	Unknown sex	12	0	0	12
(*iv*) 7+ years	Male	0	23	0	23
	Female	0	12	0	12
	Unknown sex	0	3	0	3
	Total sightings of known-age whales (*n* = 32)	136 (78.2%)	38 (21.8%)	0 (0.00%)	174 (100%)
Total of number of individual whales (*n* = 361)		136 (6.4%)	1775 (83.3%)	220 (10.3%)	2131 (100%)

Note: Refer to the Materials and methods section for definitions for classification of whales and sex-identification methods used in the study.

Table 3. Sex, age, and maturational and reproductive classes of humpback whales (*Megaptera novaeangliae*) by number of known individual whales, number of sightings, first day class sighted, last day class sighted, and the median, mean, standard deviation (SD) of days of sightings of each class.

Sex, age, and maturational and reproductive classes	Whales (*n*)	Sightings (*n*)	First day	Last day	Median	Mean	SD
(*a*) Males (known mature, not with lactating females)	41	137	6	76	50.0	49.4	14.28
(*b*) Males (known mature, with lactating females)	73	192	19	77	57.0	56.7	12.32
(*c*) Males (unknown maturity, not with lactating females)	41	110	6	76	36.0	34.3	16.55
(*d*) Females (lactating)	222	1143	13	80	57.0	56.8	12.77
(*e*) Females (nonlactating)	156	375	3	73	24.0	26.3	13.68
(*f*) Calves (males and females)	7	31	37	77	67.0	64.7	10.12
(*g*) Males, females, and unknown sex (1–6 years)	32	105	1	62	22.0	25.3	13.84
(*h*) Males and females (7+ years)	14	38	18	64	51.5	45.4	14.83

Note: The classes *a*–*h* selected to investigate relative seasonal timing were derived from Dawbin (1966, 1997), Franklin et al. (2011), and Franklin (2012).

during September. Sightings of those same males when with lactating females (Fig. 3*b*) occurred mainly in September and early October, with very few sightings in August. Mature males leave Hervey Bay approximately 3–4 days before the last of the lactating females (Figs. 3*a*, 3*b*, and 3*d*). Sightings of males of unknown maturity not with lactating females (Fig. 3*c*) occur from early August through September and into early October. The spread of this class suggests that it may be composed of both immature and some mature whales. Sightings of lactating females (Fig. 3*d*) occurred mainly in September and October and these whales were rarely observed in August. Sightings of nonlactating females occurred predominantly in August with decreasing sightings during

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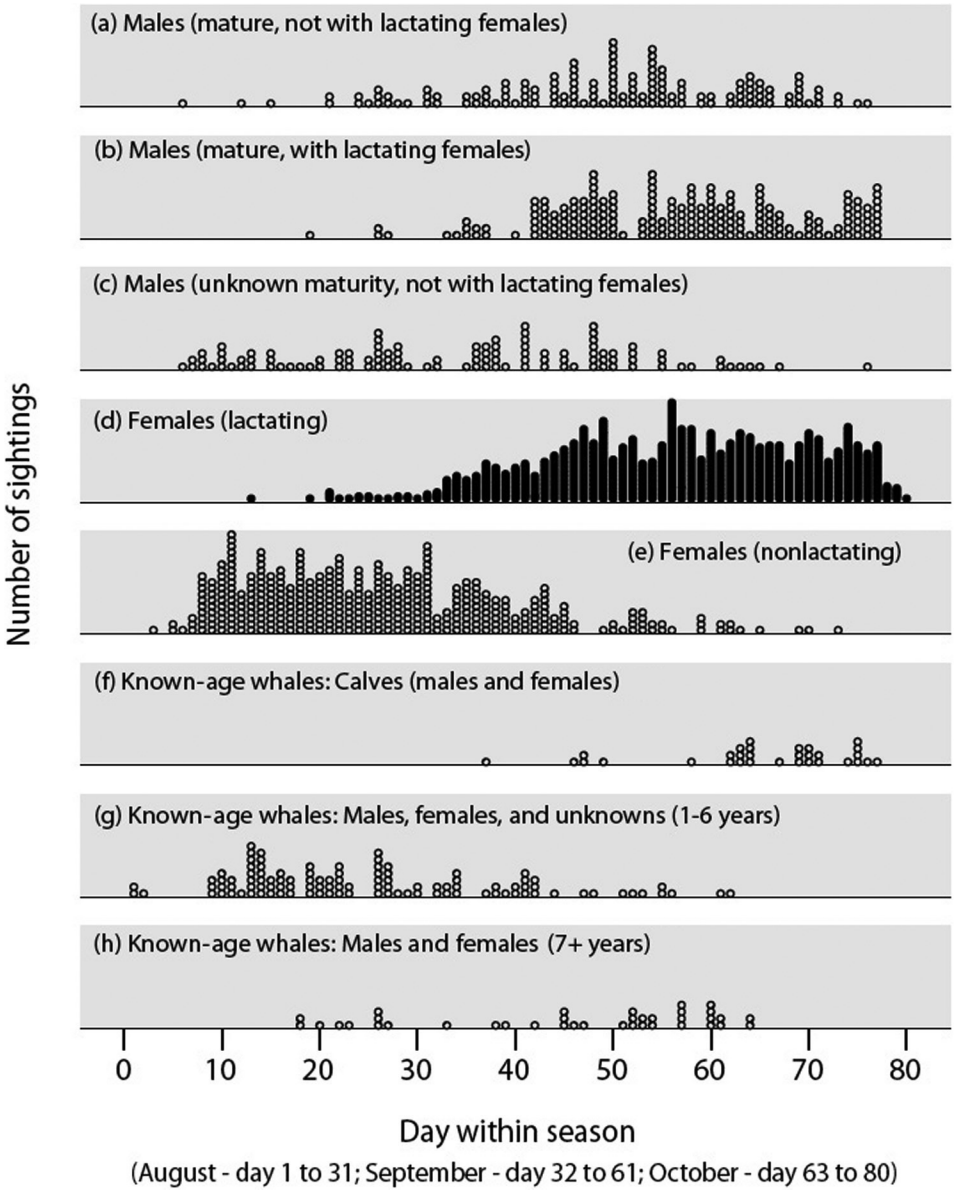
Fig. 3. Sightings of individually identified humpback whales (*Megaptera novaeangliae*) by class, day within season, and number of sightings. Classes *a*, *b*, and *c* represent sightings of the 77 males. Class *d* (shaded black) and class *e* (shaded grey) represent sightings of the 126 females that were sighted both lactating and nonlactating. Classes *f*, *g*, and *h* represent sightings of the same 32 known-age whales.



September and very few sightings in October (Fig. 3*e*). Although there is overlap of sightings of lactating females (Fig. 3*d*) and nonlactating females (Fig. 3*e*) in September and less in October, there is a clear segregation of these two classes.

The sightings presented in Figs. 3*f*, 3*g*, and 3*h* are of the same known-age individual whales. The data show that calves sighted in September and October, as expected, coincide with the sightings of lactating females (Figs. 3*d* and 3*f*). They return in subsequent years as yearlings and immature whales in August or early September (Figs. 3*f* and 3*g*). As mature whales (7+ years), they are sighted in late August through September and early October (Fig. 3*h*).

Multilevel modeling of classes

The class factor was found to be highly significant ($F_{[6,46.57]}$ = 155.90, $p < 0.0001$). The model-estimated means (peak density of each class), their standard errors, degrees of freedom, and 95% confidence intervals are reported (Table 4) and the results of the 10 planned comparison tests between the classes are also reported (Table 5).

The first seven comparisons were all highly statistically significant and the last three comparisons were nonsignificant, with all 10 tests meeting the Bonferroni-adjusted p value of 0.005.

Reproductive category of selected females based on long-term resighting histories

Of the 252 individually identified females in the database (Table 2), 111 (44%) had adjacent year sightings and were able to be assigned to more specific reproductive categories, which are reported (Table 6). These more specific reproductive categories were not used in the statistical analysis and modeling above. The results are used when discussing nonlactating and lactating females.

There were 62 occurrences of resting and early pregnant females: 49 (79%) in August, 12 (19.3%) in September, and 1 (1.6%) in early October. There were 24 occurrences of either resting or early

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Table 4. Multilevel model estimated mean values (peak density) of each class of humpback whales (*Megaptera novaeangliae*), as well as their standard errors (SE) and lower and upper 95% confidence intervals (95% CI).

				95% CI	
Sex, age, and maturational and reproductive classes	Mean	SE	df	Lower	Upper
Males (known mature, not with lactating females)	51.58	2.052	32.966	47.41	55.76
Males (known mature, with lactating females)	57.00	1.213	64.391	54.57	59.42
Males (unknown maturity, not with lactating females)	35.35	2.251	38.924	30.79	39.90
Females (lactating)	57.74	0.729	223.307	56.31	59.18
Females (nonlactating)	25.89	0.936	149.466	24.04	27.74
Males, females and unknown (1–6 years)	25.72	2.005	27.177	21.61	29.83
Males and females (7+ years)	45.97	3.259	12.822	38.91	53.02

Note: The dependent variable is day within season.

Table 5. Results of the 10 planned pairwise comparison tests between sexual, reproductive, and maturational classes of humpback whales (*Megaptera novaeangliae*) based on estimated marginal mean values.

					95% CI	
Pairwise comparisons tested	Mean difference	SE	df	Two-tailed *p*	Lower	Upper
(1) Females (nonlactating) vs. females (lactating)	–31.856	1.186	309.763	<0.005	–34.190	–29.521
(2) Females (lactating) vs. males, females, and unknowns (1–6 years)	32.025	2.133	34.777	<0.005	27.694	36.357
(3) Males (known mature, not with lactating females) vs. females (nonlactating)	25.697	2.255	47.685	<0.005	21.161	30.233
(4) Males (known mature, with lactating females) vs. females (nonlactating)	31.109	1.532	142.084	<0.005	28.080	34.138
(5) Males (known mature, not with lactating females) vs. males (maturity unknown, not with lactating females)	16.237	3.046	71.904	<0.005	10.165	22.310
(6) Males (known mature, with lactating females) vs. males (maturity unknown, not with lactating females)	21.650	2.557	61.686	<0.005	16.537	26.762
(7) Males, females, and unknowns (1–6 years) vs. males and females (7+ years)	–20.247	3.826	22.818	<0.005	–28.166	–12.329
(8) Males (known mature, with lactating females) vs. females (lactating)	–0.747	1.416	115.013	0.599	–3.551	2.058
(9) Females (nonlactating) vs. males, females, and unknowns (1–6 years)	0.169	2.212	39.964	0.939	–4.302	4.641
(10) Males (known mature, not with lactating females) vs. males and females (7+ years)	5.619	3.851	23.566	0.158	–2.337	13.576

Note: The dependent variable is day within season. Pairwise comparisons were derived from Dawbin (1966, 1997). Standard error (SE), degrees of freedom (df), and lower and upper 95% confidence intervals (95% CI) are presented.

Table 6. Specific reproductive categories of female humpback whales (*Megaptera novaeangliae*) based on long-term adjacent year resightings.

Class and specific reproductive category	Whales (*n*)	Occurrences (*n*)
(*b*) Females both lactating and not lactating (*n* = 126; Table 2)		
Nonlactating, resting	16	18
Nonlactating, early pregnant	36	44
Nonlactating, either resting or early pregnant*	21	22
Lactating and postpartum estrous pregnant	17	26
(*c*) Females only lactating (*n* = 96; Table 2)		
Lactating and postpartum estrous pregnant	19	24
(*d*) Females only nonlactating (*n* = 30; Table 2)		
Nonlactating, either resting or early pregnant*	2	2
Total	111	136

*There was insufficient sighting evidence to determine a specific reproductive state, but there was sufficient evidence to categorize as "either resting or early pregnant".

pregnant females: 12 (50%) in August, 9 (37.5%) in September, and 3 (12.5%) in early October.

There were 50 occurrences of lactating and postpartum pregnant females (i.e., mature females simultaneously lactating and pregnant). Twenty-four individuals had one postpartum pregnant occurrence, 10 individuals had two postpartum pregnant occurrences, and 2 individuals had three postpartum pregnant occurrences. Of the 50 postpartum pregnant occurrences, 39 (78%) were observed during September and 11 (22%) were observed during October.

Discussion

Our results show a female-biased sex ratio in Hervey Bay as a consequence of mature females using the wide shallow bay as an extension of the core breeding area to the north. During August, mature resting and early pregnant females co-occur and socially interact with immature males and females. From early September through October, an increasing number of lactating females with older calves involved in maternal activities dominate the bay. Overall, few mature males are present in Hervey Bay in August,

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with a low proportion of escorts accompanying mother–calf pods in September and October. The female-biased sex ratio in Hervey Bay is in contrast with the male-biased sex ratio reported by Brown et al. (1995) off Stradbroke Island, approximately 300 km south of Hervey Bay (Fig. 1), suggesting that maternally directed philopatry may be a factor in the sex ratio evident in Hervey Bay.

Maternally directed philopatry

Photo-identification studies of individual humpback whales over long time periods have documented maternally directed philopatry and site fidelity to summer feeding and winter breeding destinations (Martin et al. 1984; Clapham and Mayo 1987; Baker et al. 1990; Katona and Beard 1990; Clapham et al. 1993; Palsbøll et al. 1997). Franklin et al. (2011) reported that during the early 1990s, there was a decrease to around 20% in the proportion of pods with calves present in Hervey Bay. However, from 1996 onwards, the proportion of pods with calves present increased sharply to 40% and remained at or above that proportion through to the mid-2000s. From the mid-1990s, the eastern Australian humpback whale population has maintained a high rate of growth of 11% per annum (Noad et al. 2016). During the same period, a constant proportion (34%) of the eastern Australian population used Hervey Bay with a high rate of survivorship and site fidelity (Franklin 2014). The female-biased sex ratio reported in this study together with the above relevant factors indicates that mature females began using the wide shallow embayment of Hervey Bay in the early 1990s as an extension of the primary overwintering grounds to the north. Therefore, it is highly likely that maternally directed philopatry contributes to the female-biased sex ratio reported in Hervey Bay.

Hervey Bay: a social and ecological niche for mature females

Hervey Bay is well to the west of the primary migratory pathway (Fig. 2). The bay's benthic geography and environmental conditions are consistent with breeding habitats used by mature females worldwide (Rasmussen et al. 2007). Although the eastern side of Hervey Bay provides a protected shallow habitat, entry to and from the area involves negotiation of sandbanks with strong 3 m tidal movements (Ribbe 2014; Fig. 2). Consequently, access to the area for calves, yearlings, and immature males and females is likely a learned experience from the mature females (also see Fig. 2).

This study confirms that mature females, including early pregnant and resting females, use Hervey Bay during August, are co-temporal with immature males and females, and precede lactating females by about a month. In a recent study in Hawai'i, Craig et al. (2014) tested and provided support for the hypothesis that spatial distribution of females is driven primarily by avoidance of males. The absence of mature males in August in Hervey Bay provides mature females and immature males and females the opportunity for social activity conducive to social development and reproductive success with minimal male harassment.

Barendse et al. (2013) investigated the occurrence and associations of humpback whales at a coastal feeding area off west South Africa early in the southern migration and found no long-term social associations. They reported a female-dominated presence including non-nursing (possibly pregnant) females and yearlings, which suggested female derived site fidelity possibly involving culturally transferred fidelity to a feeding area.

The timing and separation of classes of whales using Hervey Bay early in the southern migration (Franklin 2012) do not differ from the timing and temporal segregation of humpback whales described by Dawbin (1966, 1997) based on whaling data. The structure of the southern humpback whale migratory procession, with mature females at the vanguard of the migration involved in maternal care of yearlings and immatures and lactating females at the rear of the migration involved in maternal activity, may be an evolutionary feature of humpback whale social organization, which merits further research.

The peak density of lactating females during September and October is a month later than the peak density of nonlactating females. During September and October, Hervey Bay offers mothers with older calves a shallow and sheltered habitat off the primary migratory pathway for maternal care (Franklin et al. 2011; Franklin 2012). Mothers spend 69.4% of their time alone with their calves, and when they do associate, they are more likely to associate with other mother–calf pods (Franklin et al. 2011).

There are few mature males searching for mating opportunities in Hervey Bay during September and October. The diving depths of individuals in competitive groups are reported to predominantly range between 50 and 298 m (Herman et al. 2008). However, Hervey Bay is, on average, less than 20 m deep (Ribbe 2014); hence, the shallow bay may inhibit the potential for male harassment of lactating females.

The results of this study show that some postpartum estrous females are present in Hervey Bay during September and October. Chittleborough (1958) reported that postpartum estrous may occur in a minority of cases (8.5%; 8 of 94); that this would likely occur 1 month after parturition; and that August is the peak birthing month. Mothers with calves are rarely present in Hervey Bay during August.

Dawbin (1956) suggested that humpback whales require some period in semitropical coastal waters for normal breeding behavior. Mothers with calves follow and prefer longer coastal routes and travel at a slow pace during the early southern migration (Felix and Guzman 2014). In this study, we suggest that as the eastern Australian population increased from the mid-1990s, mature females began using Hervey Bay as a social and ecological niche for maternal care. Several recent studies have reported similar social and ecological niche areas for mature females. Bruce et al. (2014) investigated the spatial use of Jervis Bay (35°S) by humpback whales during the late 2000s. They suggested that, associated with increases in the population, both calf and noncalf pods were using Jervis Bay as a resting area with mother–calf pods preferring shallower waters. Similarly, Carvalho et al. (2011) reported that the shallow waters near the Island of São Tomé (20°N) off the breeding area of west Africa had low levels of mating behavior and served primarily as a calving, nursing, and resting area for mother–calf pods. Barendse et al. (2010) found a female-biased sex ratio in an early feeding area off the southwest coast of Africa (33°S). We suggest that social and ecological niche areas for maternal care or early feeding behavior by mature females are important to the reproductive success and recovery of humpback whale populations.

Sex bias in breeding grounds, migratory stopovers, and migratory corridors

The sex ratio of humpback whale populations does not vary significantly from parity (Clapham 2000). However, site-specific variation of sex ratio from parity does occur during various stages of the migration (Brown et al. 1995; Craig and Herman 1997; Palsbøll et al. 1997; Smith et al. 1999; Jenner et al. 2006; Pomilla and Rosenbaum 2006; Barendse et al. 2010; Valsecchi et al. 2010; Herman et al. 2011; Herman 2017).

It has been suggested that individual males likely complete the migration to breeding grounds more often than females and that some early pregnant females may return to the feeding area before reaching the breeding grounds (Craig and Herman 1997). Herman et al. (2011) undertook a comprehensive review of reports of male-biased sex ratios in winter breeding grounds. They concluded that although male bias in winter grounds is consistent worldwide, its interpretation remains unclear and that it may reflect differential migration of males and females to the winter grounds.

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The only female-biased sex ratio reported in a coastal migratory corridor was off Saldanha Bay (33°S), southwest South Africa (Barendse et al. 2010), around 3000 km south of the known West African breeding grounds (Rosenbaum et al. 2009). The Barendse study had long seasonal coverage and reported a female-biased sex ratio from mid-spring (October) associated with early feeding. Barendse et al. (2010) suggested that a female-biased region associated with early feeding in the southern coast migratory corridor may offer a plausible explanation as to where "missing" females go while males complete the migration to breeding grounds. Similarly, Stamation et al. (2007) reported early feeding by humpback whales, including mother–calf pods, migrating past Eden (37°S), New South Wales, Australia, during the southern migration, but with no evidence of gender bias.

Brown et al. (1995) undertook biopsy sampling of humpback whale pods from May to October in 1992 during the northern and southern migrations. The study area off Stradbroke Island, southeast Queensland (27°S), is approximately 300 km south of Hervey Bay (Fig. 1). They reported a male-biased sex ratio of 2.4:1 and hypothesized that the male-biased sex ratio off Stradbroke Island may be because some females overwinter in Antarctica. The eastern Australian humpback whale population was severely depleted during the last phase of commercial whaling in Antarctica (Clapham et al. 2009). At the cessation of commercial whaling in the early 1960s, it is estimated that only about 200 eastern Australian humpback whales survived (Paterson et al. 1994; Jackson et al. 2009) with few mature breeding females (Chittleborough 1965). Recovery in eastern Australia was very slow between the early 1960s and 1990s, with the population estimated to have increased to only 1900 whales by 1992 (Paterson et al. 1994). In the late 1980s and early 1990s, population estimates of humpback whales visiting Hervey Bay were highly variable, increasing from 554 in 1988, to a peak of 1040 in 1991, before declining to 921 by the mid-1990s (Chaloupka et al. 1999). After the near total collapse of both Pacific and eastern Australian humpback whale populations from commercial whaling, it was hypothesized that the social aggregation of some remaining Oceania humpback whales with the eastern Australian population may have occurred (Clapham and Zerbini 2006, 2015). It has also been suggested that sex-specific longitudinal migratory behavior and low levels of migratory interchange of eastern Australian and nearby Pacific humpback whale populations might contribute to male-biased sex ratios in the eastern Australian migratory corridor (Valsecchi et al. 2010; Franklin et al. 2014). In the 25 years since 1992, there has been no substantiation of female humpback whales not migrating and remaining in Antarctic feeding areas during the winter months. Consequently, the male-biased sex ratio reported by Brown et al. (1995) based on sampling conducted in 1992 is likely to have involved differential migration of males. Also, it may have been related to the small size and state of recovery of eastern Australian humpback whales in the early 1990s.

Our evidence of a female-biased sex ratio in Hervey Bay, together with the above evidence on male and female-biased sex ratios, provides an alternative and plausible explanation for the occurrence of sex bias in breeding grounds at migratory stopovers and along coastal migratory corridors.

Preferential use of site-specific habitats by mature humpback females early in the southern migration is unlikely to be unique to Hervey Bay. Future research of similar Southern Hemisphere coastal habitats will be important for the monitoring, management, and conservation of humpback whales.

Our findings substantiate the importance of the shallow, protected embayment of Hervey Bay for mature humpback females with calves or accompanying immature whales early in the southern migration. We recommend that the southern boundary of the overwintering and breeding grounds for eastern Australian humpback whales be extended to include the Hervey Bay habitat within the Great Sandy Marine Park.

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