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Mid-migration humpback whale feeding behavior off Eden, NSW, Australia

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ABSTRACT

There is some evidence of humpback whale feeding opportunistically at low- to mid- latitudes in known breeding grounds and during migration. However, feeding behavior in east Australia has been observed more regularly than anywhere else in the world. Here we report on the frequency and behavior of feeding humpback whales off Eden, New South Wales (1995 -2010). Whales were observed feeding every year, except in 2001 with the greatest number of whales observed feeding in 1995, 1996, and 2005-2010. Preliminary analysis of the relationship between Sea Surface Temperatures and the proportion of whales observed feeding during 1995, 1996, and 2006-2009 occurred during the coldest water temperatures in the area for the same period suggesting strong upwelling events. The increased 2005 feeding was likely fueled by nutrient-rich upwelling promoted by the East Australian Current (EAC). Lateral lunge feeding was prevalent and sometimes occurred in echelon formation performed by multiple individuals. The majority of whales feeding were sub-adults suggesting they stand the greatest advantage from this opportunistic activity. A better understanding of the year-to-year oceanographic processes off Eden, and adjacent regions, and of the age-class composition of feeding pods is crucial. We suggest that this geographic area is more important as a feeding area to migrating humpback whales than previously thought, and that areas off the coast of southeastern New South Wales may serve as extralimital foraging grounds, especially for sub-adult whales.

KEYWORDS: FORAGING, FEEDING GROUND, EAST AUSTRALIA, HUMPBACK WHALE, FEEDING BEHAVIOR

INTRODUCTION

Humpback whales (*Megaptera novaeanglieae*) feed worldwide at high latitudes and migrate toward tropical and subtropical areas in both hemispheres to breed (Dawbin, 1966). While on the breeding grounds, humpback whales are known to fast through the breeding season (Chittleborough, 1965; Dawbin, 1966; Stone *et al*. 1990).

Long migrations and breeding behavior can be energetically costly (Read, 2001) and poor body condition has been shown to affect migration timing, offspring sex ratio and survival rates in other species as well as whales (Price *et al.*, 1988; Wiley and Clapham, 1993; Sandberg and Moore, 1996). Therefore migratory whales should optimize intake high quality prey (Witteween *et al.* 2011) and even opportunistically take advantage of ephemeral food sources when they became available.

Humpback whale feeding behavior depends largely on the type of prey sought and its density (Jurasz and Jurasz, 1979; Watkins and Schevill, 1979; Hain *et al.*, 1982; Baker 1985). Lunge feeding is a costly behavior for baleen whales (Acevedo-Gutiérrez *et al.*, 2002; Goldbogen, 2008). Therefore, a threshold prey density is required to make these costs worthwhile for the whale. In fact, threshold foraging behavior is typical of higher vertebrates that feed on highly aggregated prey (Piatt and Methven, 1992).

Lack of feeding by humpback whales in their breeding grounds has been related to lack of sufficient prey densities (Corkeron and Connor, 1999). However, feeding events away from the feeding grounds have been reported in many areas of the world such as Hawaii (Salden, 1989), Brazil (Danilewicz *et al.*, 2008; Pintode sa Alvez, 2009), the Dominican Republic (Baraff *et al.*, 1991), Mexico (Gendron and Urban, 1993), Virginia, United States (Swingle *et al.*, 1993), New Zealand (Dawbin, 1966), east Australia near Moreton Island and Cairns, Queensland (Stockin and Burgess, 2005; Tim North, pers comm.), off southeastern New South Wales (Paterson, 1987; Kaufman and Naessig, 2000; Kaufman *et al*., 2006; Stamation *et al*., 2007; Gales *et al*., 2009), off Tasmania (Gill *et al*., 1998) and along the migration route to Antarctica (Anderson *et al.*, 2010).

Understanding what triggers these feeding events in areas where feeding does not normally occur is important. The observations of feeding away from historical feeding areas has been presumed to involve mostly juveniles based on body size (Salden, 1989; Baraff *et al.* 1991, Swingle *et al.* 1993; Pinto de sa Alvez, 2009). Opportunistic feeding on sporadic prey patches of enough density may be critical to survival of juvenile whales, who have thinner blubber layers than adults (Pinto de sa Alvez, 2009). However, substantial data sets involving feeding in extralimital areas are scanty.

Humpback whales of Breeding Stock E1 generally spend the period between June and October along the extensive and complex coastline (over 3,000 km) of East Australia (Paterson and Paterson, 1989) where extralimital feeding has been frequently observed (Stockin and Burgess, 2005; Paterson, 1987; Kaufman and Naessig, 2000; Kaufman *et al*., 2006; Stamation *et al*., 2007; Gales *et al.*, 2009).

In East Australia humpback whales have been reported feeding on coastal krill (*Nyctiphanes australis*) and small teleost fish, including sardines (Gill *et al*., 1998; Kaufman and Naessig, 2000; Stockin and Burgess, 2005; Kaufman *et al*., 2006; Stamation *et al*., 2007, Gales *et al*., 2009).

We report the results of long-term opportunistic humpback whale feeding behavior observations on the frequency of feeding by humpback whales off East Australia in the area off Eden, New South Wales between 1995 and 2010. This is the most extensive record of extralimital feeding currently in existence for this area. The data we report on are preliminary and the beginning of more systematic observations and analysis to better understand the frequency of occurrence of extralimital feeding, the sex and age groups of the whales involved and the relationship between the frequency of occurrence of feeding and oceanographic variables.

METHODS

Study Area

The study area is located along the East Coast of Australia in the state of New South Wales (Figure 1) within 20 km offshore between Green Cape (Lat: 37º15'S; Long: 150 º 3'E) and Merimubula (Lat: 36 º 54'S; Long: 149 º 56'E), and inside Twofold Bay (33 km^2 in size with a mean depth of 18 m). The fishing town and Port of Eden is at the head of Twofold Bay. The linear distance between the edges of the study area is 36 km (Figure 1).

Data Collection
Data were obtained from two sources: commercial whalewatch and a research vessel. Data between 1995 and 2005 and in 2008 were opportunistically collected from the commercial whalewatch vessel 'Cat Balou', a 16m aluminum catamaran powered by 2 x 300hp Cummins diesel motors. Data were collected during the course of routine whalewatching operations. Research vessel data were collected between 2006 and 2010. The vessel was launched from Snug Harbour, Eden (Lat: 37 º 04'19.7"S; Long: 149 º 54'34.4"E). Surveys were conducted from a 6.2m rigid hull inflatable, equipped with a 150-hp outboard motor.

Collection protocols were similar for both platforms in that the study area was searched in a non-systematic way on all good weather days (Beaufort scale of 0 - 5) for the presence of whales, and the vessel was directed to areas where whale concentrations were seen. When whales were sighted and approached, the number of whales present and their behavior was documented, including feeding. The date, time, GPS location (*e.g.*, GPS location was not available for data prior to 2006), group size and composition of whale pods (*e.g.*, calf, adult, sub-adult), general activity of the whales was recorded and identification photographs were taken.

We considered specific behavioral sequences observed at the surface as evidence of feeding, specifically lunge feeding and echelon feeding which are typical of Southern Hemisphere humpback whales. Lunge feeding was defined as described by Hain *et al.* (1982). Additional evidence of feeding was the presence of prey at the surface, in the mouths of the whales, and/or picked up by closely associated birds, the expansion of the whale's ventral pleats followed by their contraction, and the opening and closing of the mouth just under the surface of the water (Stockin and Burgess, 2005). Two types of lunges have been described in East Australia: lateral (Figure 2) and vertical (Stamation *et al*., 2005), which we named 'bucket feeding' (Figure 3). Echelon feeding occurs when multiple whales laterally lunge in formation (Figure 4).

Because vessel-based environmental covariates were limited to observations collected after 2005, we also obtained remote-sensing derived monthly estimates of Sea Surface Temperature (SST) from the Advanced Very High Resolution Radiometer (AVHRR). The SST values were for September and October from 1995 to 2009, for the area of observed feeding approximately 8-10 miles off the coast from Eden.

Data analysis
To test whether one-or-more age classes were more commonly observed feeding than non-feeding, we performed a two-way chi-squared test for independence of factors on age classes and feeding behavior. The test was performed using the total numbers of feeding and non-feeding Adults, Sub-Adults and Calves, from 2006 - 2009, when age-classes were know, with all unknown age-class observations discarded.

As an exploratory analysis of the influence of oceanographic variables on the feeding behavior of humpback whales, we performed a parametric regression (General Linear Model, under a Quasi-Binomial distributino) of the log-odds of the proportion of whales feeding versus the Sea Surface Temperature (SST, for September). Because of the influence of extreme values (particularly 2009) and non-normality of the data (n = 15) we also calculated the non-parametric Spearman's

rank correlation coefficient (ρ) between SST and the proportion of feeding whales. We performed a non-parametric bootstrap estimate of the correlation coefficient's 95% confidence interval.

All analyses were performed using the open-source R language for statistical computing (R Development Core Team, 2011).

RESULTS

During the fifteen years of observation, humpback whale feeding was recorded every year, except in 2001. A total of 4,852 humpback whale sightings were recorded, with 857 (17.7%) showing feeding behavior (Table 1).

Research vessel effort between 2006 and 2010 varied by year but always occurred between September and October with 4 survey-days (112 nm; 15h) in 2006, 4 (23h) in 2007, 25 (1555 nm; 135h) in 2009 and 10 (783 Km; 64h) in 2010. In 2008, the research crew was on board of the whalewatch vessel *Cat Balou* (29 days and 135 h).

The annual proportion of whales feeding seemed to have a U-shaped temporal trend, whereby earlier years (1995, 1996) and later years (2005 – 2010) had greater proportions of feeding whales than years between 1997 and 2004. Analysis showed an apparent inverse-relationship between Sea Surface Temperature (monthly composite for September) and the proportion of whales feeding each year (Figure 6). The relationship is marginally significant when using a General Linear Model under a Quasi-binomial distribution (p value of 0.042; R-squared value of 0.31), such that every degree increase in temperature resulted in a 46% decrease in the odds of whales' feeding. This result is dampened by the 2009 observation, which has a much greater proportion of feeding whales than expected by the model, and appears to be an outlier. Repeating the analysis, but using a non-parametric Pearson's rank correlation test, we estimated a significant correlation of -0.643, and a 95% Confidence Interval of -0.877 to -0.206 (non-parametric bootstrap).

Based on data from 1995 to 2005, the proportion of whales seen feeding during early, middle and late migration season varied from year to year and there appeared to be fewer whales feeding during the late portion of the breeding season (Figure 7).

Between 2006 and 2010, feeding whales were generally found outside of Twofold Bay (Figure 8) and whale concentrations tended to shift from year to year over an area up to 20 km offshore within the study area (and could extend beyond but there was no effort that far from shore). In 2009, all feeding whales used the lateral lunge behavior during feeding bouts observed. In 2010, type of feeding was only reported five times and was mostly lateral lunge feeding with one instance of bucket feeding. Echelon feeding was prevalent in 2007.

About half of the feeding whales (46.7%) were sub-adults and the proportions of age classes involved in feeding changed from year to year (Table 2). Sub-adults seemed to be consistently more commonly seen feeding than other age-classes. The two-way Chi-squared test for independence of factors suggested strong evidence for a difference in the proportions of age classes seen feeding (Chi-squared statistic of 131.07 and p-value < 0.0001).

DISCUSSION

Feeding behavior in east Australia has been observed more regularly than anywhere else in the world (Kaufman *et al*., 2006). The data and analyses presented here suggest that humpback whales of Breeding Stock E1 may take advantage of spikes in productivity activated by oceanographic circulation patterns and water temperature gradients as suggested by Stamation *et al.* (2005).

Feeding behavior appears to be widespread and not confined to one or two individuals like in other reported cases. In addition, the proportion of whales seen feeding after 2005 has increased and has been between a minimum of 25% in 2008 to a maximum of 68% in 2009. This suggests that waters off south-east Australia may be an important extralimital feeding ground, and feeding opportunities may have increased due to favorable environmental conditions for this population and the energy gained by this opportunistic feeding may be substantial to the fitness of individual whales.

Dalla Rosa *et al.* (2008) documented variability in the foraging strategies of individual whales off Area V of Antarctica, both related to local food availability and to individual 'choices' to maximize food intake. This plasticity of behavior may be one of the reasons for seemingly consistent opportunistic feeding in waters off East Australia.

Peaks in food availability in waters off Eden may be fueled by a variety of processes. The years 1995, 1996, and 2006-2010, when the largest proportion of whales was seen feeding, were also the years that registered the coldest water temperatures in the area for the same period suggesting strong upwelling was occurring. In 2005 feeding was likely fueled by nutrient-rich upwelling promoted by the East Australian Current (EAC) as suggested by Stamation *et al.* (2005) who also saw a peak in feeding during this year. The EAC is a complex and highly energetic western boundary system in the south-western Pacific dominated by a series of mesoscale eddies (Ridgway and Dunn, 2003). These eddies regularly move onto the continental shelf and close inshore and influence local circulation patterns. The strength of the upwelling depends on the topographic features of an area (Oke and Middleton, 2000).

We would like to emphasize that the data we have available and the correlations with SST are preliminary. The data were collected opportunistically in an unsystematic way. Nonetheless, the results are encouraging and suggest that closer attention should be paid to oceanographic patterns in relation to whale activity in this area in the future, especially in light of climate change and the shifting strength of the East Australian Current.

CONCLUSIONS

A better understanding of the functioning of oceanographic processes on a year-to-year basis off Eden and adjacent regions is crucial to improve our knowledge of humpback whale feeding. We suggest that this geographic area is more important as a feeding area to migrating humpback whales than previously thought, and that areas off the coast of New South Wales may serve as extralimital foraging grounds.

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analysis of stable isotopes: implications on prey and resource quality. *Aquatic Mammals* 37(2): 101-110.

Table 1 – Total whale sightings and the percentage of whale feeding between 1995 and 2010. Data from 1995 to 2005 and 2008 were collected from operators of whalewatch vessel *Cat Balou* and data in 2006. 2007, 2009 and 2010 (in bold) were collected as part of our research effort from R/V *Naiad.*

Year	Total whales sightings	Whales not feeding	Whales feeding	% whales feeding
1995	100	51	49	0.49
1996	217	212	59	0.27
1997	477	441	36	0.08
1998	461	439	22	0.05
1999	288	281	7	0.02
2000	278	248	30	0.11
2001	357	357	0	0.00
2002	282	268	14	0.05
2003	309	287	22	0.07
2004	304	298	8	0.03
2005	345	266	79	0.23
2006	**60**	**43**	**17**	**0.28**
2007	**189**	**133**	**56**	**0.30**
2008	917	566	351	0.38
2009	**392**	**126**	**266**	**0.68**
2010	**269**	**169**	**100**	**0.37**

Table 2 – Summary of proportion of age classes seen feeding between 2006 and 2010.

Year	% Adults	% Sub-Adults	% Calves
2006	18	36	0
2007	21	36	8
2008	43	57	11
2009	55	77	53
2010	31	62	5

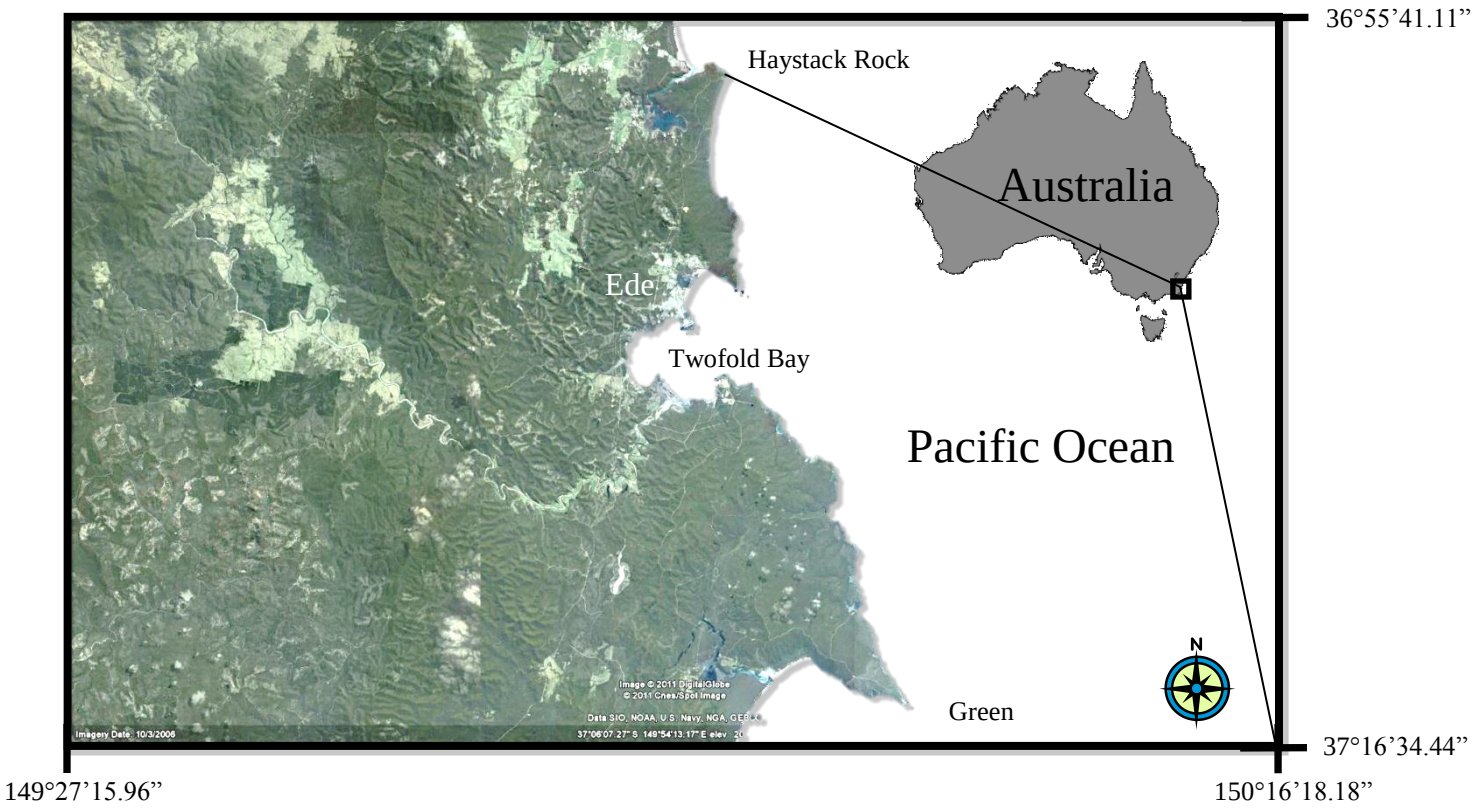


Figure 1 – Map of the study area

Figure 2 – Humpback whale 'lateral lunge feeding' off Eden, New South Wales, Australia on 23 September, 2009.

Figure 3 – Humpback whale ‘bucket feeding’ off Eden, New South Wales, Australia on 9 October, 2010.

Figure 4 – Three humpback whales ‘echelon feeding’ off Eden, New South Wales, Australia on 9 October, 2010.

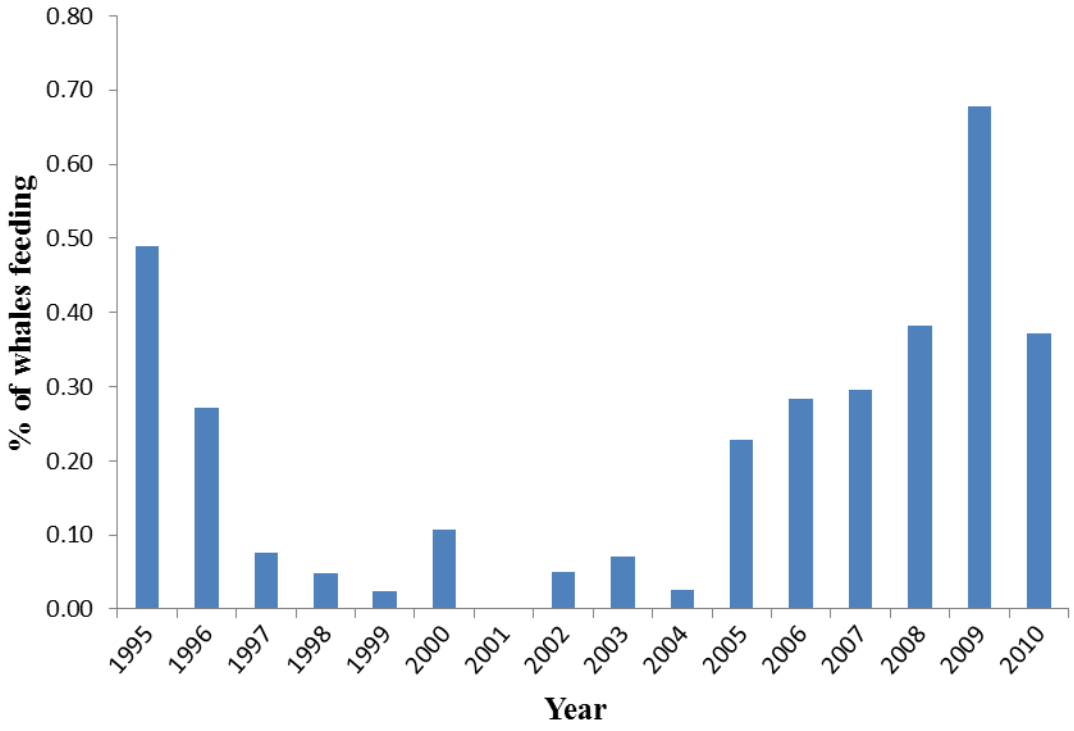


Figure 5 – The percentage of whales feeding by year

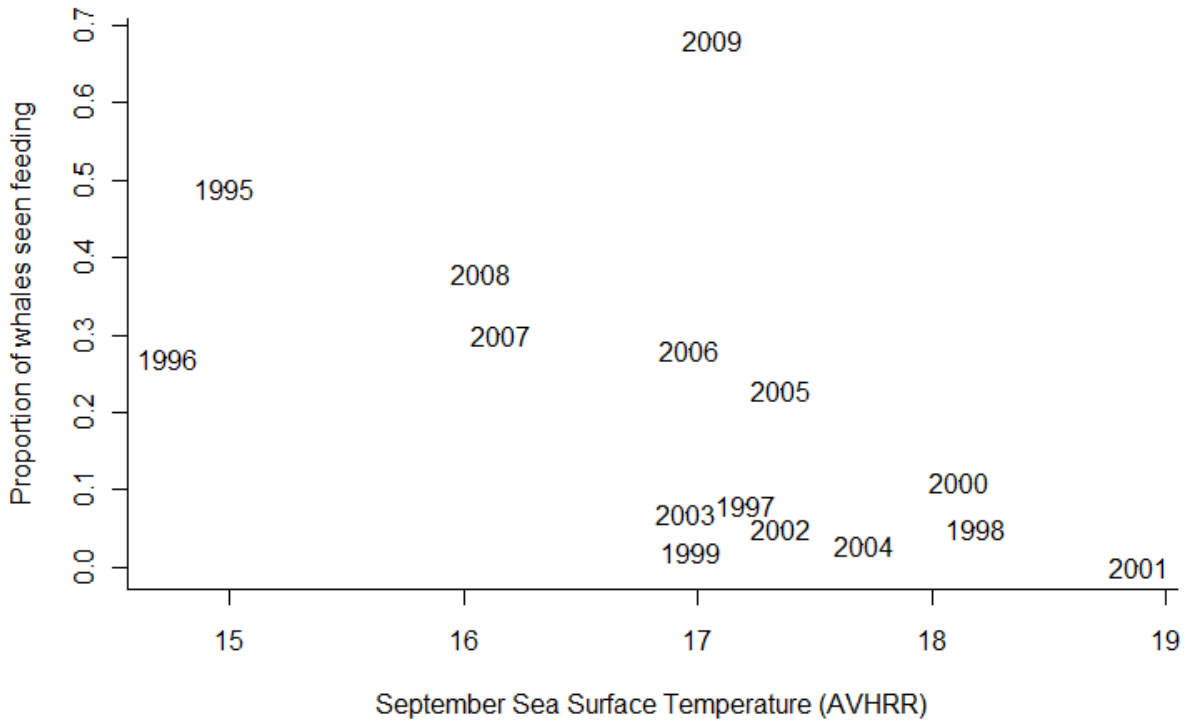


Figure 6- Correlation between September Sea Surface Temperature and the proportion of humpback whales seen feeding in water off Eden, Australia, from 1995 to 2009. The Spearman's Rank Correlation Coefficient is -0.64 (95% C.I. of -0.88 -0.21).

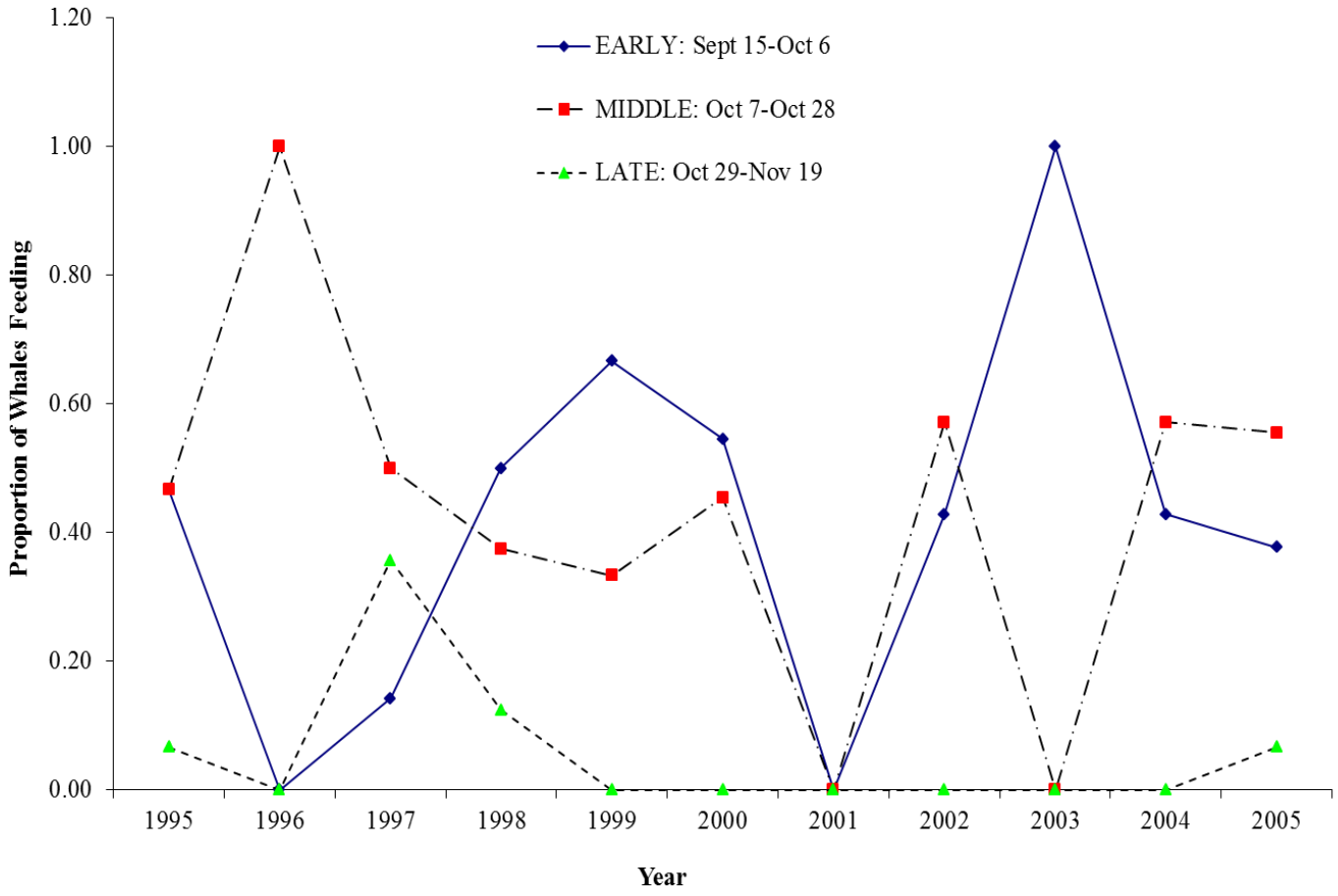
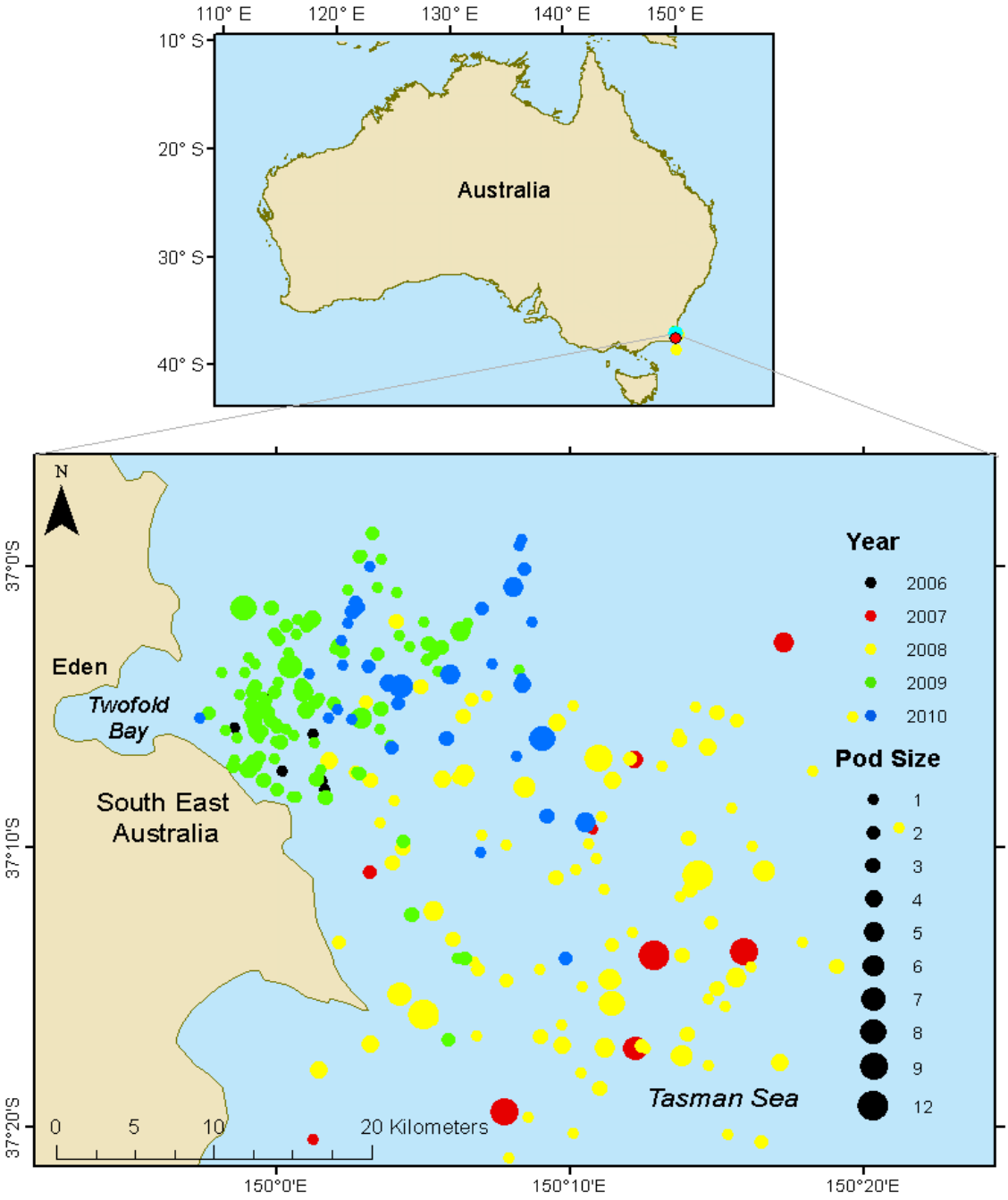


Figure 7 – Proportion of whales seen feeding during early, middle and late migration season off Eden New South Wales, Australia between 1995 and 2005 (data from whalewatch vessel 'Cat Balou').


110° E
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Eden
Twofold Bay
South East Australia
Tasman Sea
0
5
10
20 Kilometers
150°0'E
150°10'E
150°20'E
Year
2006
2007
2008
2009
2010
Pod Size
1
2
3
4
5
6
7
8
9
12

Figure 8 – Location of whales sighted feeding off Eden between 2006 and 2010 (color coded by year) with group size (coded by circle size).