



Note

Cetacean Diversity of the Continental Shelf and Slope off Southern Australia

PETER C. GILL,¹ *Blue Whale Study, C/- Post Office Narrawong, Victoria 3285, Australia; and Deakin University, PO Box 423, Warrnambool, Victoria 3280, Australia*

REBECCA PIRZL, *Skadia Pty Ltd, PO Box 195, Natimuk, Victoria 3409, Australia, and Deakin University, PO Box 423, Warrnambool, Victoria 3280, Australia*

MARGIE G. MORRICE, *Blue Whale Study, C/- Post Office Narrawong, Victoria 3285, Australia; and Deakin University, PO Box 423, Warrnambool, Victoria 3280, Australia*

KIERAN LAWTON, *Skadia Pty Ltd, PO Box 195, Natimuk, Victoria 3409, Australia*

ABSTRACT We recorded a diverse cetacean assemblage from systematic aerial surveys in productive upwelling waters off southern Australia in 2002–2013. Surveys recorded 133 sightings of 15 identified cetacean species consisting of 7 mysticete (baleen) whale species, 8 odontocete (toothed) species, and 384 sightings of unidentified dolphins. This is the first assessment of cetacean diversity for the region and we found diversity to be comparable with other productive regions elsewhere. Differential spatial and temporal distributions of mysticete and odontocete species were apparent, and were associated with habitat variables and seasonal migration cycles. The study contributes new information to assist the environmental planning and management of activities in the region, including oil, and gas exploration and production, fishing, shipping, and renewable energy development. © 2015 The Wildlife Society.

KEY WORDS aerial surveys, baleen whales, cetacean diversity, distribution, dolphins, southern Australia, toothed whales.

Managing marine biodiversity requires an understanding of the species assemblages that inhabit marine systems (Zacharias and Gregt 2005). Such systems include upwelling regions, which typically support high densities of marine fauna (Mann and Lazier 1996), and high cetacean diversity (e.g., Ballance and Pitman 1998, Tynan et al. 2005, Burrows et al. 2012).

On the southern Australian continental shelf and slope, seasonal upwelling associated with the Flinders Current (Middleton and Cirano 2002) occurs between November and May when south-easterly forcing winds induce shelf-break and coastal upwelling between western Bass Strait and the eastern Great Australian Bight (Kampf et al. 2004, Middleton and Bye 2007, Levings and Gill 2010). During this time, daily primary productivity in certain hotspots is comparable to levels seen in Benguela and Humboldt boundary current systems (Van Ruth et al. 2010). Within this broader system, a prominent surface cool-water upwelling plume extending from Portland, Victoria toward Kangaroo Island, South Australia (the Bonney Upwelling), is the most predictable and intense upwelling off southern Australia (Butler et al. 2002, Nieblas et al. 2009).

The peak of the upwelling season is November to March, weakening into May (Nieblas et al. 2009). The region supports valuable commercial fisheries (reviewed in Larcombe et al. 2002) and large populations of marine birds and mammals, and is regarded as biogeographically distinct because of its unique cool-temperate flora and fauna (Butler et al. 2002).

The Bonney Upwelling region encompasses development activities that can affect cetaceans (Evans et al. 2004, Melcon et al. 2012, Christiansen et al. 2013). Gas exploration and production, major shipping lanes, and important commercial and recreational fisheries occur there, wave power generators are proposed, and commercial whale watching has been trialed. Interactions between cetaceans and these activities are the focus of significant environmental management effort by both government and industry, including impact, and risk assessments and setting mitigation requirements under environmental legislation, evaluation, and management of marine protected areas, development of operational guidelines, or regulations for marine industry, and establishment of mandatory reporting requirements for offshore operators. For these efforts to be effective, information about spatio-temporal patterns in cetacean density and habitat use is required but currently lacking.

Cetaceans of southern Australian shelf and slope waters are little studied (Bannister et al. 1996, Ross 2006) but include species listed as threatened under Australian legislation and on the International Union for Conservation of Nature (IUCN) Red List. The region is a summer feeding ground for pygmy blue

Received: 17 February 2014; Accepted: 21 February 2015
Published: 4 April 2015

¹E-mail: pete@bluewhalestudy.org
Present address: Blue Whale Study Inc., C/o Post Office Narrawong, Victoria 3285, Australia

whales (*Balaenoptera musculus brevicauda*; Gill 2002) and a winter breeding ground for southern right whales (*Eubalaena australis*; Bannister 1986). Environmental managers are often required to make decisions about minimizing the impact of human activities in the region in an information-poor environment. We adopted a broad-scale, rapid assessment approach to address contemporary conservation management information demands. We used data from cetacean aerial surveys between western Bass Strait and the Eastern Great Australian Bight 2002–2013 and flown primarily to detect pygmy blue whales (Gill 2002, Gill et al. 2011) to address the information deficit for management of other cetacean species in the region. We investigated the diversity, distribution, relative abundance, seasonality, and habitat associations of cetacean species. We aggregated data at taxonomic, spatial, and temporal resolutions to generate results suitable for informing regional-scale management, maximizing the utility of a long-term dataset within the constraints of some inconsistencies in data collection. We also provide species-specific results; however, because of low sample sizes we caution their use by conservation managers.

STUDY AREA

The surveyed area covered continental shelf and upper slope waters between 40°30' S, 144° E, and 33°20' S, 131°07' E, from western Bass Strait to the eastern Great Australian Bight (Fig. 1). The total area covered was approximately 63,000 km² and corresponded closely with the known extent of the broad-scale upwelling system described above.

METHODS

Data Collection

We conducted systematic line-transect aerial surveys designed to detect pygmy blue whales in the study area from 2002 to 2013. We used parallel transects spaced 11.1 km apart, perpendicular to bathymetry, and varying in length (from 27 km to 113 km) according to shelf width from western Bass Strait to Kingston SE, where the seasonal distribution of pygmy blue whales is reliable (Gill et al. 2011), and repeat surveys were more consistently funded (Fig. 1). We used saw-tooth transects between Kingston SE and Port Lincoln to achieve broader search coverage of an area where pygmy blue whales were less consistently observed (Gill et al. 2011). We used along-shelf transects west of Port Lincoln in the remote Eastern Great Australian Bight where we considered surveys to be exploratory. We directed survey effort to the continental shelf and upper slope; we did not survey open ocean habitat (Table 1, Fig. 1).

We conducted surveys only in sea conditions with a Beaufort Sea State (BSS) Code ≤ 4 from twin-engine high-wing aircraft at 457 m altitude and a groundspeed of approximately 240 km/hr. Two observers, 1 on each side of the aircraft, searched a strip width from the track line out to 5.6 km (half the transect spacing), monitoring the outer limit of the search area with a hand-held clinometer (SuuntoTM, Vantaa, Finland). A 170 m-wide strip directly beneath the aircraft was not visible to observers and was not surveyed. We used a small number of observers, with at least 1, and 90% of the time both, being highly experienced. We recorded a global positioning system (GPS)

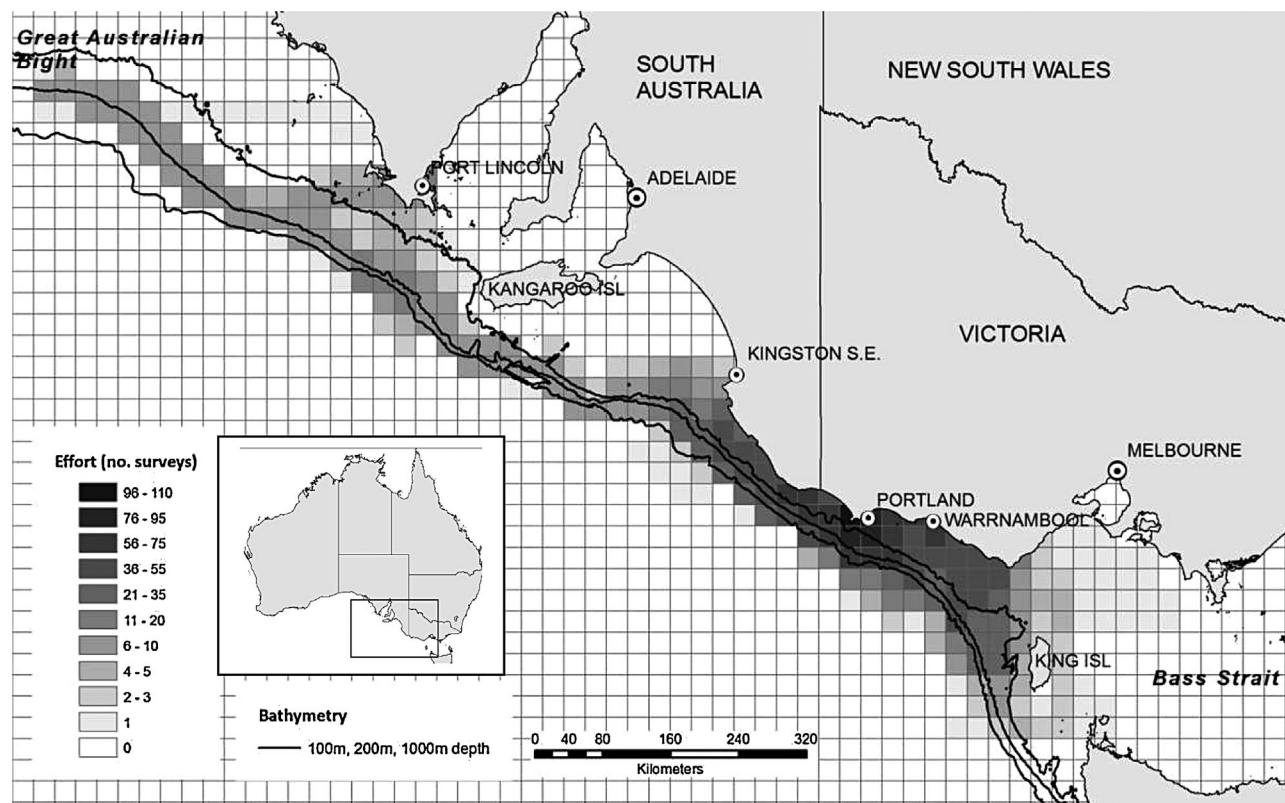


Figure 1. Aerial cetacean survey effort in continental shelf and slope waters off southern Australia 2002–2013. Grid cells are 25 km × 25 km. Darker shading indicates greater search effort.

Table 1. Number of surveys and kilometers flown (in parentheses) for each month and year during cetacean surveys in southern Australia, 2002–2013. Note that each upwelling year is defined as commencing in October. The period of highest seasonal effort was from November to April.

Year	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Total
2002–2003	0	3 (3,113)	12 (11,039)	4 (4,906)	3 (2,431)	4 (2,955)	1 (1,084)	3 (3,845)	0	0	1 (848)	0	31 (30,221)
2003–2004	1 (1,170)	5 (3,505)	10 (13,268)	2 (3,897)	1 (2,597)	1 (660)	1 (2,130)	0	0	0	0	0	21 (27,227)
2004–2005	0	6 (7,014)	5 (8,276)	2 (2,542)	1 (2,807)	2 (4,092)	1 (2,654)	0	0	0	0	0	17 (27,385)
2005–2006	0	0	1 (4,867)	0	1 (2,953)	2 (2,675)	0	1 (2,257)	1 (796)	0	0	0	6 (13,548)
2006–2007	0	0	1 (1,297)	0	0	0	2 (2,641)	2 (2,674)	2 (2,994)	1 (733)	0	0	8 (10,339)
2007–2008	0	1 (754)	0	0	0	0	1 (418)	1 (694)	0	0	0	0	3 (1,866)
2008–2009	0	0	0	1 (915)	0	0	0	0	0	1 (758)	0	0	2 (1,673)
2009–2010	0	0	0	0	0	1 (602)	0	0	0	0	0	0	1 (602)
2010–2011	0	0	0	0	5 (5,139)	0	0	0	0	0	0	0	5 (5,139)
2011–2012	0	2 (4,636)	3 (4,242)	6 (13,022)	5 (7,031)	2 (3,617)	0	0	1 (1,254)	1 (1,464)	1 (1,363)	2 (2,837)	23 (39,466)
2012–2013	1 (1,241)	1 (1,095)	1 (1,080)	1 (976)	1 (1,053)	1 (950)	0	0	0	0	0	0	6 (6,395)
Total	2 (2,411)	18 (20,117)	33 (44,069)	16 (26,258)	17 (24,011)	13 (15,551)	6 (8,927)	7 (9,470)	4 (5,044)	3 (2,955)	2 (2,211)	2 (2,837)	123 (163,861)

waypoint and the declination to each sighting (using a hand-held clinometer) from the track line as the aircraft passed perpendicular to it, and calculated georeferenced positions. We occasionally obtained georeferenced positions by flying directly overhead the sighting (e.g., when the aircraft broke from the track line to confirm species or estimate group size). We included only sightings made from the track line (on-effort) in analyses; we excluded additional sightings made at other times (off-effort). An experienced observer confirmed species identifications either in situ or post-flight using high-resolution digital photographs. We assigned sightings as like (e.g., like fin whale [*Balaenoptera physalus*]) if identification could not be confirmed and features closely matched that species (e.g., Branch and Butterworth 2001), or as unidentified if no identification was possible. In these analyses, we included like records with their relevant species. Dolphin sightings (excepting Risso's dolphins [*Grampus griseus*]) were difficult to identify to species level from the survey altitude; thus we aggregated them as dolphins for analyses. We recorded environmental conditions at the start of each transect and whenever conditions changed. The protocols conformed to standard aerial survey methods for a range of cetacean species, with the exception of dolphins, which are usually surveyed for at lower altitudes. For further details of methods see Gill et al. (2011).

We address the potential biases of line-transect survey methods (Burnham et al. 1980) in the following manner. We conducted surveys in BSS ≤ 4 and clear conditions to minimize detection bias caused by poor weather. Observers were trained and we used the same observers on most surveys to minimize observer bias. We controlled for double counting (recording the same animals from 2 adjacent transects) post-survey by discarding sightings from adjacent transects where the animal could have covered the intervening distance at a speed of

18.5 km/hr. This speed exceeds the highest recorded transit speed of blue whales (14.2 km/hr; Lagerquist et al. 2000), one of the faster cetaceans, so transit calculations using this speed likely eliminated double counting. We controlled for dependence among sightings during data collection by recording observations of the same species within 200 m of one another as one sighting. We considered the likelihood of dependence amongst sightings to be extremely low; post-processing checks revealed no tempo-spatial coincidence within 5 km, excepting dolphins where some dependence may be expected. Distance-from-line biases include under-representation of small or cryptic species and lower sighting rates toward the middle of transect spacing, both of which are caused by decreasing detectability farther from the track-line. The sparseness of data precluded reliable estimates of detection functions; thus, this remains an inherent bias. Similarly, inherent behavioral biases exist whereby species that spend more time at the surface or are more visible are likely to be over-represented in the data. The study's long time-span, low sample sizes, and a lack of data from which to calculate reliable detectability adjustments result in inherent challenges that we have addressed by controlling biases to the extent possible, applying conservative analysis methods, and conservative results interpretation.

Analysis

We assigned sightings to 1 of 4 groups based on foraging niche to overcome low sample sizes in species-level data (Table 2). This approach provides information about functional groups suitable for broad-scale conservation planning. Sightings were assigned to 1) rorquals ($n = 42$; fin, sei [*Balaenoptera borealis*], minke [*B. acutorostrata* and *B. bonaerensis*], humpback [*Megaptera novaeangliae*]), which forage on krill or small schooling fish (Best 2007, Croll et al. 2008); 2) dolphins ($n = 22,532$;

Table 2. Cetacean species recorded during aerial surveys 2002–2013 in southern Australia.

Taxon	Common name	Species group ^a	<i>n</i> sightings	<i>n</i> individuals	Mean group size (\pm SD)
Baleen whales					
<i>Eubalaena australis</i>	Southern right whale	SRW	12	52	4.2 \pm 4.2
<i>Caperea marginata</i>	Pygmy right whale		1	100	100
<i>Balaenoptera physalus</i>	Fin and like fin whale	ROR	7	8	1.1 \pm 0.4
<i>B. borealis</i>	Sei and like sei whale	ROR	12	14	1.3 \pm 0.5
<i>B. acutorostrata</i>	Dwarf minke whale	ROR	1	1	1
<i>B. bonaerensis</i>	like Antarctic minke whale	ROR	1	1	1
<i>Megaptera novaeangliae</i>	Humpback whale	ROR	10	18	1.8 \pm 1.0
Toothed whales					
<i>Physeter macrocephalus</i>	Sperm whale	ODO	34	66	1.9 \pm 2.2
<i>Tasmacetus shepherdi</i>	Shepherd's beaked whale	ODO	1	6	6
<i>Hyperoodon planifrons</i>	Southern bottlenose whale	ODO	1	2	2
<i>Mesoplodon</i> spp.	Unidentified beaked whales	ODO	1	20	20
<i>Orcinus orca</i>	Killer whale	ODO	6	21	3.5 \pm 2.8
<i>Globicephala melas</i>	Long-finned pilot	ODO	40	1853	46.3 \pm 46.7
<i>Grampus griseus</i>	Risso's dolphin	ODO	1	40	40
<i>Lissodelphis peronii</i>	Southern right whale dolphin	ODO	1	120	120
<i>Tursiops</i> spp.	Bottlenose dolphin	DOL	4	363	90.8 \pm 140.1
	Dolphins	DOL	384	22169	58 \pm 129.6
Unidentified large whales			3	3	1
Unidentified small whales			2	2	1

^a SRW = southern right whales; ROR = rorquals; ODO = other odontocetes; DOL = dolphins.

presumed bottlenose [*Tursiops* sp.] or short-beaked common [*Delphinus delphis*]; BWS unpublished data), which feed on small schooling fish, and squid (Ross 2006, Best 2007, Puserini et al. 2007); 3) other odontocetes ($n = 2,135$; sperm [*Physeter macrocephalus*], long-finned pilot [*Globicephala melas*], beaked whales [Family Ziphiidae], killer whales [*Orcinus orca*], southern right whale dolphins [*Lissodelphis peronii*], Risso's dolphins), which prey predominantly on squid but also on fish (except killer whales that occur widely and take a range of pelagic prey; Baumgartner 1997, Davis et al. 1998, Morrice 2004, Best 2007, Azzellino et al. 2008, Praca and Gannier 2008); and 4) southern right whales ($n = 52$), which fast in the study region and are absent during the upwelling season (Pirzl 2008). We made a single sighting of a pygmy right whale [*Caperea marginata*] group, but we excluded it from analysis because too little is known of the species to assign it to a foraging niche group (Kemper et al. 2013). We measured effort as the distance flown calculated from aerial survey tracks in ArcGISTM (Environmental Systems Research Institute, Inc.) for each month (calendar) and year (12-month period beginning in Oct when upwelling-forcing winds commence).

Temporal occurrence.—We calculated encounter rate, a measure of relative abundance, for each species, each month (all years pooled), and each year (2002–2003 to 2012–2013). We divided the number of sightings for each specified period by the distance flown in kilometer, then calculated an encounter rate of individuals per 1,000 km flown, and compared encounter rates between species. We report encounter rates even for very small sample sizes as they contribute insight in the currently data-poor environment.

Spatial distribution.—We applied density kernel analysis to represent the relative density distribution of rorquals, dolphins, and other odontocetes groups. We generated a grid of 25 \times 25 km cells in ArcGISTM and overlaid the grid

with aerial survey tracks and sightings. We chose this resolution to subsume dependence among sightings and geo-referencing inconsistencies arising from the long-term nature of the dataset (e.g., observer bias, positioning technology), and to resolve distribution patterns at a scale suitable for broad-scale management planning (tens of kilometers). We extracted an effort value for each cell according to the number of survey tracks passing through it (e.g., Keller et al. 2012). We then gave each cell a value (for each species group) representing the probability of sighting based on the actual number of sightings weighted for effort. We calculated an index of animals per search effort (WPSE) by dividing the number of animals sighted (in each species group) by the effort value. To allow comparisons across the distributions of each of the species groups, we converted the WPSE data to a proportion of the total WPSE across the survey area. This gave an index of animals per unit effort (WPUE) relative to the other groups in the analysis. We calculated kernel distributions for each species group in ArcViewTM 3.2 (Environmental Systems Research Institute, Inc.) using the Animal Movement extension (Hooze and Eichenlaub 1997). We used WPUE data to weight kernel distributions, so if two grid cells had WPUE values of 2 and 10 respectively, either 1) the effort was the same, but we sighted 5 times more animals where WPUE = 10, or 2) we spent 5 times more effort searching where WPUE = 2 but sighted the same number of animals in each grid cell. We used the least-squares cross-validation method to calculate the smoothing factor (*H*-value) for each data set (Seaman and Powell 1996). We used isotropic smoothing, assuming independence of space. We plotted the density kernels using Vertical MapperTM 3 (Northwood Technologies Inc., London, United Kingdom) and MapInfoTM 10 (Pitney Bowes, Stamford, CT) and presented them as density plots representing the entire kernel distribution. Because the

kernel data are based on WPUE and not WPSE, the plots show relative indices of cetacean distribution and abundance over the period of the surveys.

Depth and slope associations.—We investigated species and group associations with depth (m), depth range, and slope (m/km) to explore relationships with environment. We derived depth and slope values for all sighting locations from the General Bathymetric Chart of the Oceans (GEBCO) 1-Minute World Bathymetry Grid using Vertical MapperTM v3.0 extension in MapInfoTM v.10 (resolution approximately 1 nm² at the study area latitude), and calculated means (\pm SD) for each species and group. We chose 4 depth ranges: 0–100 m (inner shelf), 101–200 m (outer shelf), 201–1,000 m (upper slope), and >1,001 m (lower slope to abyssal plain). The 100-m isobath represents a transition from the gently sloping inner shelf to the more steeply sloping outer shelf. The shelf break at 200 m marks a transition to the steeper upper slope, and the 1,000 m isobath represents an ecological boundary because it coincides with a layer of Antarctic Intermediate Water below the Flinders Current (Currie et al. 2012). We compared depth, depth range, and slope differences between groups using Kruskal-Wallis tests, and Mann-Whitney *U* tests for pairwise comparisons in RTM v3 (R Core Development Team, Vienna, Austria).

Behavior.—We reported descriptive behavioral observations where they provided unique or new information about the species. In data-poor environments such as this study region, insights into habitat function inferred from behavior can improve information available for management.

RESULTS

Survey effort was biased toward coverage of upwelling seasons, corresponding with pygmy blue whales' seasonal occurrence (Nov–Apr; 103 of 123 surveys), and relatively little survey effort occurred during 2008–2011 (11 of 123 surveys; Table 1). We recorded 133 sightings of 15 identified cetacean species, 1 sighting identified to genus-level, 384 sightings of unidentified dolphins, and 5 sightings of unidentified cetaceans (Table 2). Three baleen whale families were represented (Balaenidae [right whales], Neobalaenidae [pygmy right whales], and Balaenopteridae [rorquals]) as were 3 toothed whale families (Physeteridae [sperm whales], Ziphiidae [beaked whales], and Delphinidae [dolphins and their relatives including killer and pilot whales]).

Relative abundance data (Tables 3 and 4) should be interpreted in the context of effort distribution (Table 1) and the low sample sizes for many species (Table 2). Few conclusions about temporal occurrence can be drawn because of unequal effort distribution across seasons and the rarity of most species. We encountered southern right and humpback whales most often May–September, despite low survey effort in those months. We sighted fin, sei, and pilot whales only from November–May (upwelling season), although this may be an artifact of their relative scarcity overall and low survey effort at other times of year. Dolphins were sighted most consistently across years.

Modeled spatial distribution of rorquals, dolphins, and other odontocetes showed that rorquals and dolphins were

widely distributed in shelf waters, whereas other odontocetes were mainly associated with the steeper terrain of the upper slope (Fig. 2). Kernels represent the probability of occurrence based on empirical data corrected for survey effort (see Fig. 1 for effort distribution, which was mainly in shelf, and upper slope waters). Kernels are unlikely to occur in areas of low sightings and high effort, but may occur in areas of low sightings when effort is also low. Probabilities of occurrence for dolphins (Fig. 2c) and other odontocetes (Fig. 2b) coincided spatially alongshore; however, dolphins had a greater probability of occurrence farther inshore on the shelf in comparison to other odontocetes, which were more likely to be sighted on the slope (consistent with depth and slope associations, see below). Density distribution of rorquals (Fig. 2a) was focused in the eastern half of the study area, in the region of the main Bonney Upwelling productivity plume and waters further east. A single minke whale was sighted near 135° E, in an area of low effort (Fig. 2a).

Mean depth (\pm SD) distribution for all 4 rorqual species occurred in shelf waters (humpback: 57 ± 31 m, $n = 10$; minke: 93 ± 79 m, $n = 2$; sei: 160 ± 137 m, $n = 12$; fin: 162 ± 90 m, $n = 7$) with a difference among humpback, sei, and fin whales (minke whales excluded because of low sample size; Kruskal-Wallis, $K = 13.19$, $P < 0.01$). Dolphins were also distributed in shelf waters (mean depth 134 ± 197 m, $n = 384$). Other odontocetes occurred on the slope (59% of sightings on upper slope and 39% on lower slope, $n = 85$; Fig. 3). Killer whales (mean depth 171 ± 135 m, $n = 6$) were predominantly on the shelf close to the shelf-break, pilot whales (mean depth 634 ± 494 m, $n = 40$) were on the upper slope (closer to the shelf break), and beaked (mean depth $1,283 \pm 606$ m, $n = 3$) and sperm (mean depth $1,220 \pm 628$ m, $n = 34$) whales were predominantly on the lower slope. Sperm, killer, and pilot whales occurred at significantly different depths (Kruskal-Wallis, $K = 33.13$, $P < 0.001$; beaked whales and odontocetes represented by a single sighting excluded because of low sample size). Southern right whales, rorquals, dolphins, and other odontocetes occurred at different depths (Kruskal-Wallis, $K = 219.50$, $P < 0.001$; Fig. 3). Pair-wise comparisons indicated that southern right whales occurred in shallower water than all other groups (Mann-Whitney *U*; rorquals $U = 371$, $P < 0.001$; dolphins $U = 4,645$, $P < 0.001$; other odontocetes $U = 1,011$, $P > 0.001$) and other odontocetes occupied deeper water than any other group (rorquals $U = 129$, $P < 0.001$; dolphins $U = 1,725$, $P < 0.001$), whereas we found no difference in the depth occupied by rorquals and dolphins (Mann-Whitney *U*; $U = 6,022$, $P > 0.05$). These results correspond with the occurrence of 48% of rorquals and 59% of dolphins on the inner shelf, 42% of rorquals, and 30% of dolphins on the outer shelf, and 10% of rorquals and 9% of dolphins on the upper slope.

Rorqual species (fin, sei, and humpback whales) occupied areas of similar slope (Kruskal-Wallis; $K = 3.02$, $P > 0.05$), whereas we found a difference in slope among some other odontocetes (killer, sperm, and pilot whales; Kruskal-Wallis; $K = 16.72$, $P < 0.001$). As expected, southern right whales occurred in the shallowest depths and in areas where slope was similar to mid-

Table 3. Temporal occurrence across months of cetaceans sighted during aerial surveys from November 2002 to March 2013 in southern Australia. Numbers denote animals sighted per 1,000 km survey distance for each month, pooled for all years (i.e., the 12-month period from Oct–Sep). The period of highest seasonal effort was from November to April.

Species	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Southern right whale	0	0	0	0	0	0	0	0	0.8	3.1	6.8	8.8
Pygmy right whale ^a	0	0	0	0	0	0	0	0	19.8	0	0	0
Fin whale	0	0.10	0.14	0.07	0.08	0	0	0	0	0	0	0
Sei whale	0	0.25	0.07	0.04	0.08	0.19	0	0.21	0	0	0	0
Minke whale ^a	0	0	0.02	0	0	0	0.12	0	0	0	0	0
Humpback whale	0	0.05	0.07	0	0	0	0	0.11	0.99	1.0	0	0.35
Sperm whale	1.7	1.2	0.23	0.53	0.08	0.13	0.75	0.85	0	0	0	0
Southern bottlenose whale ^a	0	0	0	0	0.08	0	0	0	0	0	0	0
Shepherd's beaked whale ^a	0	0	0	0	0.25	0	0	0	0	0	0	0
Unidentified beaked whale ^a	0	0	0.47	0	0	0	0	0	0	0	0	0
Killer whale	0	0	0.19	0	0	5.0	0	6.0	0	0.68	0	0
Pilot whale	0	59.6	7.0	19.3	4.0	39.5	0	26.3	0	0	0	0
Southern right whale dolphin ^a	0	59.6	0	0	0	0	0	0	0	0	0	0
Risso's dolphin ^a	0	0	0	0	1.7	0	0	0	0	0	0	0
Bottlenose dolphin	0	1.5	7.7	0	0	0	0	0	0	0	0	1.1
Dolphins	545.1	120.3	105.0	151.8	105.6	233.4	26.9	257.6	155.8	2.7	0	0

^a species sighted 2 or fewer times.

shelf (0.7 ± 0.8 m/km), probably because of shoaling waters near-shore. Slope varied among the rorquals, dolphins, southern right whales, and other odontocetes (Kruskal-Wallis, $K = 173.16$, $P < 0.001$). Other odontocetes were strongly represented in areas of relatively steep slope (4.6 ± 2.3 m/km, $n = 85$), steeper than either rorquals, southern right whales, or dolphins (Mann-Whitney U ; $U = 177$, $P > 0.001$; $U = 950$, $P < 0.001$; $U = 2,463$, $P < 0.001$, respectively). All other species groups were distributed in areas of similar slope (Mann-Whitney U ; rorquals-southern right whales $U = 149$, $P > 0.05$; rorquals-dolphins $U = 6,816$, $P > 0.05$; southern-right whales-dolphins $U = 1,551$, $P = 0.05$; Fig. 4).

We recorded calves with all species except sperm whales, indicating that the region is used for breeding, or rearing young by many of the species sighted. We observed humpback, fin, and sei whale cow-calf pairs once each, and as expected, recorded southern right whale cow-calf pairs and mating behavior regularly in winter. We often observed pilot whales and dolphins with calves. The southern right whale dolphin sighting contained calves, and the pygmy right whale sighting contained a range of size classes including calves. Of our sperm whale sightings, 68% were of solitary mature males, and the remainder (32%) were groups of 2–12 similarly sized animals, possibly bachelor schools. Group sizes for sperm, beaked, and pilot

Table 4. Temporal occurrence over years of cetaceans sighted during aerial surveys from November 2002 to March 2013 in southern Australia. Years are defined as the 12-month period from October–September. Numbers denote encounter rates (animals sighted per 1,000 km) for each year, segregated by the slash symbol (/) into the periods of high and low survey effort (high = Nov–Apr; low = May–Oct). Survey effort was low from 2007–2008 to 2010–2011.

Species	2002–2003	2003–2004	2004–2005	2005–2006	2006–2007	2007–2008	2008–2009	2009–2010	2010–2011	2011–2012	2012–2013
Southern right whale	0/0.64	0	0	0/0.66	0	0	0/ 17.8	0	0	0/5.6	0
Pygmy right whale ^a	0	0	0	0	0/ 15.6	0	0	0	0	0	0
Fin whale	0.12/0	0.15/0	0	0	0	0	0	0	0	0.03/0	0
Sei whale	0.20/0	0.15/0	3	3	0	0	1	0	0	0	0
Minke whale ^a	0.12/0	0.04/0	0	0	0/0.94	0	0	0	0	0/0.87	0.16/0
Humpback whale	0.04/0	0.04/0	0	0	0	0	0	0	0	0	0
Sperm whale	0.35/0	0.45/0	0.62/0	0/2.6	0	0	0	0	0	0.31/ 0.29	1.3/0
Southern bottlenose whale ^a	0	0.08/0	0	0	0	0	0	0	0	0	0
Shepherd's beaked whale ^a	0	0	0	0	0	0	0	0	0	0.18/0	0
Unidentified beaked whale ^a	0.78/0	0	0	0	0	0	0	0	0	0	0
Killer whale	0.12/ 1.3	0.30/0	0	0	0/0.31	0	0	0	0	0.06/0	0
Pilot whale	8.9/ 54.2	3.7/0	0.47/0	6.2/0	0	0	0	0	0	26.7/0	19.5/0
Southern right whale dolphin ^a	0	0	0	0	0	0	0	0	0	1.2/0	0
Risso's dolphin ^a	0	0	0	0	0	0	0	0	0	0	18.8/0
Bottlenose dolphin	0	12.2/0	0	0	0	0	0	0	0	0/0.43	4.7/0
Dolphins	63.8/ 190.0	134.8/0	164.7/0	36.6/ 340.0	301.8/ 208.1	47.0/0	337.0/0	0.0	30.2/0	119.2/0	448.6/0

^a species sighted 2 or fewer times.

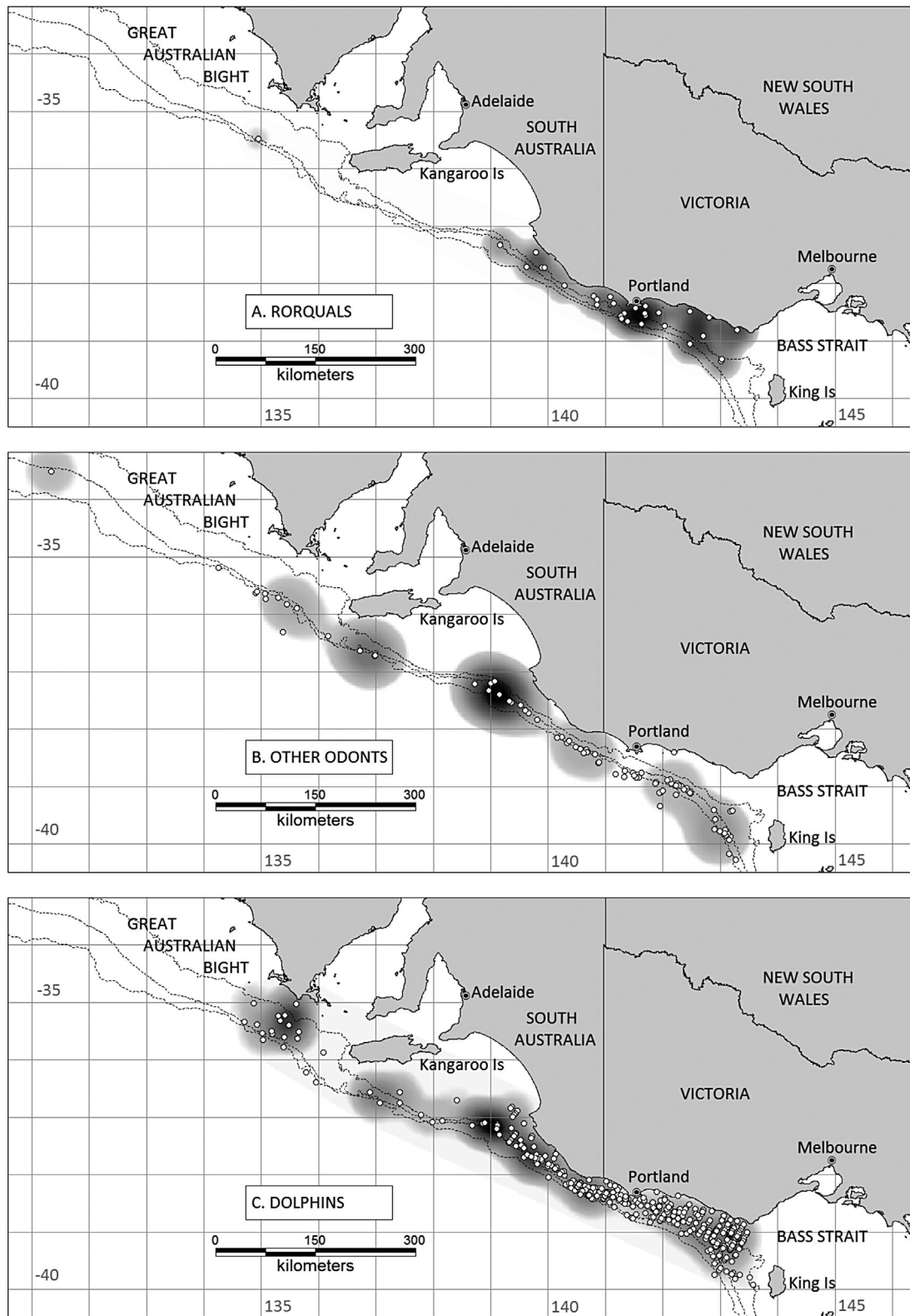


Figure 2. Density kernels and point sightings (white dots) in southern Australia, 2002–2013, for cetacean species groups: (A) rorquals, (B) other odontocetes (odonts), and (C) dolphins. Kernel shading indicates the relative probability of encountering an individual from the relevant species group at a given point (black highest probability). Lack of kernel coverage does not imply that we did not record sightings there, but that after we considered effort, the probability of sightings was low. We show 100 m, 200 m, and 1000 m isobaths (dashed lines) to indicate shelf and slope depth.

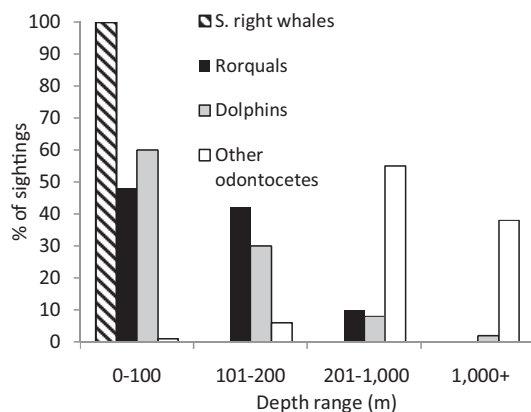


Figure 3. Depth range selection by cetacean species group in southern Australia, 2002–2013. Southern right whales $n = 12$; rorquals $n = 31$; other odontocetes $n = 85$; dolphins $n = 388$.

whales may be under-estimates due to short observation periods and the usually longer dive times of these species. We observed feeding behavior in sei, fin, humpback, and sperm whales and dolphins. We observed sei whale feeding behavior on 5 occasions, and they included bubble clouds, lunging, and skim feeding near visible krill swarms or baitfish schools, and orange-red defecation indicating a krill diet (Drummond and Macwalter 1935). We observed a fin whale bubble cloud near krill, an orange-red fin whale defecation, and a young humpback whale lunge feeding near surface krill swarms. We observed sperm whales defecating a dark cloud twice, possibly indicating undigested ink from a squid diet. We often observed dolphins feeding, either on baitfish schools or sometimes in krill surface swarms.

DISCUSSION

Cetacean species diversity in the study region (minimum 15) was comparable with diversity in other productive areas worldwide, including the northern California Current (22 species; Burrows et al. 2012), northern Gulf of Mexico (13 species; Davis et al. 1998), the Eastern Tropical Pacific (30 species; Ballance et al. 2006), the Mozambique Channel (17 species; Kiszka et al. 2007), and off the Canary Islands

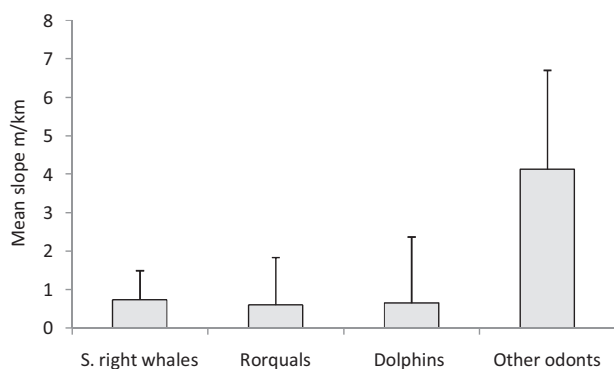


Figure 4. Mean slope (+SD) associations for cetacean species groups in southern Australia, 2002–2013. Southern right whales $n = 12$; rorquals $n = 31$; other odontocetes (odonts) $n = 85$; dolphins $n = 388$.

(16 species; Carrillo et al. 2010). The upwelling there is considered Australia's most intense and productive (Butler et al. 2002), and probably aggregates cetacean prey species to a degree not found around most of the Australian continent. High cetacean diversity November to May (9 of 15 species) is likely attributable to upwelling-linked productivity seasonally supporting prey, including large biomass of krill (Morrice 2013), small pelagic fish (Bulman et al. 2011), and cephalopods (Jackson et al. 2005).

Cetacean species' occurrence patterns generally accorded with their known ecology. Southern right whale occurrence was consistent with their known winter-spring migration to breed in coastal waters off southern Australia (Bannister 1986). Humpback whale occurrence corresponded with the timing of migration to and from calving grounds off Northern Australia (Dawbin 1966), and evidence of autumn feeding is consistent with opportunistic feeding observed in migration routes off eastern Australia (Stamation et al. 2007). Sperm whale feeding in the study region would be consistent with known feeding in adjacent Tasmanian waters (Evans and Hindell 2004), but the apparent occurrence of sperm, and pilot whales mainly during the upwelling period may be an artifact of higher search effort; both species have stranded in southern Australia in other months: sperm whales in August and pilot whales in September and October (McManus et al. 1984). Sporadic killer whale presence is consistent with photo-identification evidence that individuals move between regions (e.g., western Victoria and Southern New South Wales, Australian Orca Database, unpublished data).

To the best of our knowledge, the records of feeding sei and fin whales reported here are the first for Australian waters, and indicate that the region is used for at least opportunistic feeding by rorqual whales. We did not observe any southern right whales away from the coast, which is notable in that the surveys do not indicate offshore occurrence during the winter period; migratory movements within the region remain unknown. The single sighting of pygmy right whales was noteworthy because it was the largest group ever recorded, near an area where abundant krill surface swarms were present at the time (Gill et al. 2008).

Low encounter rates or species absence could be due to variable detectability and/or survey effort, in particular between 2007–2008 and 2010–2011 and between May and October in most years. In the case of rare, cryptic, or deep or long-diving species (e.g., beaked whales) a high threshold search effort may be required before even 1 occurrence is detected. Low encounter rates may be determined as much by ecology and behavior as by actual abundance.

Patterns of distribution in relation to depth and slope generally accorded with what is known for species and groupings elsewhere. Southern right whale occurrence in shallow near-shore waters is consistent with winter habitat preference (Pirzl 2008). Rorquals occurred mainly in waters where productivity is highest, and their depth and slope distribution was comparable to pygmy blue whales, which forage mostly on the shelf in the study region (Gill et al. 2011, Morrice 2013). Highly variable depths are occupied by rorquals

in other feeding areas, suggesting different factors, such as prey depth distribution, at play in different regions (Hain et al. 1995, Tynan 2005, Canese et al. 2006). Shelf and slope distributions of other odontocetes accord with observations elsewhere (Davis et al. 1998, Canadas et al. 2002). The depth distributions of dolphins and killer whales may be particularly affected by the temporal and spatial variability of pelagic fish and their predators across the shelf and water column in this upwelling system (Ward et al. 2006, Morrice 2013). Praca and Gannier (2008) and Azzellino et al. (2008) speculated that partitioning of pilot and sperm whales into discrete depth ranges reduced competition, which may explain their upper and lower slope distribution in our surveys.

MANAGEMENT IMPLICATIONS

This upwelling region, considered Australia's most intense and productive (Butler et al. 2002), supports a significant diversity of cetacean species, some of them rarely sighted in Australian waters, and probably aggregates cetacean prey species to a degree not found around most of the Australian continent. The study area is at least an opportunistic feeding area for several rorqual species, a breeding area for southern right whales, and is used by migrating humpback whales. Apparently low abundances of many species implies that although cetaceans probably aggregate to forage in this productive upwelling system, it may not be a key feeding area for many, with the exception of pygmy blue whales (Gill et al. 2011, Morrice 2013). The aggregations of southern right whales are significant as population recovery in this formerly heavily occupied region is likely to be facilitated by social aggregation and site fidelity expression (Pirzl 2008). For these reasons, we suggest that maintaining the integrity of this habitat through the precautionary approach and effective, data-based decision making is important for cetacean conservation in the Australasian region. The upwelling region is subject to human activities that potentially affect cetaceans (e.g., Panigada 2006, MacLeod 2009, Di Iorio and Clark 2010, Castellote et al. 2012, Christiansen et al. 2013), and this publication provides managers and operators with information for marine planning and operations to minimize interactions and impacts.

ACKNOWLEDGMENTS

Data collection was funded by the Australian Government through the CERF Program, Natural Heritage Trust, Marine Species Protection Program and Australian Marine Mammal Centre, Australian Geographic Society, Origin Energy Resources Ltd, Bight Petroleum Pty Ltd, Santos Ltd, Beach Petroleum, and the Whale and Dolphin Conservation Society. Thanks to observers D. Glasgow, A. Levings, C. Levings, D. Levings, M. Garcia, M. Watson, S. McKay, and G. Palmeri, and to J. McKenzie for help with kernel density mapping. Production of this manuscript was funded by the International Fund for Animal Welfare.

LITERATURE CITED

- Azzellino, A., S. Gaspari, S. Airoidi, and B. Nani. 2008. Habitat use and preferences of cetaceans along the continental slope and the adjacent pelagic waters in the western Ligurian Sea. *Deep-Sea Research I* 55:296–323.
- Ballance, L. T., and R. L. Pitman. 1998. Cetaceans of the western tropical Indian Ocean: distribution, relative abundance and comparisons with cetacean communities of two other tropical ecosystems. *Marine Mammal Science* 14:429–459.
- Ballance, L. T., R. L. Pitman, and P. C. Fiedler. 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. *Progress in Oceanography* 69:360–390.
- Bannister, J. L. 1986. Southern right whales: status off Australia from twentieth-century 'incidental' sightings and aerial survey. Reports of the International Whaling Commission (Special Issue 10):153–158.
- Bannister, J. L., C. M. Kemper, and R. M. Warneke. 1996. The Action Plan for Australian Cetaceans. Australian Nature Conservation Agency Project Number 30, Canberra, Australian Capital Territory, Australia.
- Baumgartner, M. F. 1997. The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. *Marine Mammal Science* 13:614–638.
- Best, P. B. 2007. Whales and dolphins of the southern African subregion. Cambridge University Press, Cambridge, United Kingdom.
- Branch, T. A., and D. S. Butterworth. 2001. Estimates of abundance south of 60°S for cetacean species sighted frequently on the 1978/79 to 1997/98 IWC/IDCR-SOWER sighting surveys. *Journal of Cetacean Research and Management* 3(3):251–270.
- Bulman, C. M., S. A. Condie, F. J. Neira, S. D. Goldsworthy, and E. A. Fulton. 2011. The trophodynamics of small pelagic fishes in the southern Australian ecosystem and the implications for ecosystem modelling of southern temperate fisheries. Final report for FRDC project 2008/023. CSIRO Marine and Atmospheric Research, Hobart, Tasmania, Australia.
- Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monographs* 72:1–202.
- Burrows, J. A., J. T. Harvey, K. M. Newton, D. A. Croll, and S. R. Benson. 2012. Marine mammal response to interannual variability in Monterey Bay, California. *Marine Ecology Progress Series* 461:257–271.
- Butler, A., F. Althaus, D. Furlani, and K. Ridgway. 2002. Assessment of the conservation values of the Bonney Upwelling. A component of the Commonwealth Marine Conservation Assessment Program 2002–2004. CSIRO report to Environment Australia. CSIRO Marine and Atmospheric Research, Hobart, Tasmania, Australia.
- Canadas, A., R. Sagarminaga, and S. Garcia-Tiscar. 2002. Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. *Deep-Sea Research I* 49:2053–2073.
- Canese, S., A. Cardinali, C. M. Fortuna, M. Giusti, G. Lauriano, E. Salvati, and S. Greco. 2006. The first identified winter feeding ground of fin whales (*Balaenoptera physalus*) in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* 86:903–907.
- Carrillo, M., C. Perez-vallazza, and R. Alvarez-Vasquez. 2010. Cetacean diversity and distribution off Tenerife (Canary Islands). *Marine Biodiversity Records* 3:1–9.
- Castellote, M., C. W. Clark, and M. O. Lammers. 2012. Acoustic and behavioural changes by fin whales (*Balaenoptera physalus*) in response to shipping and airgun noise. *Biological Conservation* 147:115–122.
- Christiansen, F., M. Rasmussen, and D. Lusseau. 2013. Whale watching disrupts feeding activities of minke whales on a feeding ground. *Marine Ecology Progress Series* 478:239–251.
- Croll, D. A., B. R. Tershy, and K. M. Newton. 2008. Filter feeding. Pages 421–425 in W. F. Perrin, B. Würsig, and J. G. M. Thewissen, editors. *Encyclopedia of marine mammals*. Academic Press, San Diego, California, USA.
- Currie, D. R., S. McClatchie, J. F. Middleton, and S. Nayar. 2012. Biophysical factors affecting the distribution of demersal fish around the head of a submarine canyon off the Bonney Coast, South Australia. *PLoS ONE* 7(1): e 30138.
- Davis, R. W., G. S. Fargion, N. May, T. D. Leming, M. F. Baumgartner, W. E. Evans, L. J. Hansen, and K. Mullin. 1998. Physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico. *Marine Mammal Science* 14:490–507.
- Dawbin, W. H. 1966. The seasonal migratory cycle of humpback whales. Pages 145–170 in K. S. Norris, editor. *Whales, dolphins and porpoises*. University of California Press, Berkeley, USA.

- Di Iorio, L., and C. W. Clark. 2010. Exposure to seismic survey alters blue whale acoustic communication. *Biology Letters* 6:51–4.
- Drummond, J. C., and R. J. Macwalter. 1935. Pro-vitamin A in the food of whales. *Journal of Experimental Biology* 12:105–107.
- Evans, K., and M. A. Hindell. 2004. The diet of sperm whales (*Physeter macrocephalus*) in southern Australian waters. *ICES Journal of Marine Sciences* 61:1313–1329.
- Evans, K., M. Hindell, and G. Hince. 2004. Concentrations of organochlorines in sperm whales (*Physeter macrocephalus*) from Southern Australian waters. *Marine Pollution Bulletin* 48:486–503.
- Gill, P. C. 2002. A blue whale (*Balaenoptera musculus*) feeding ground in a southern Australian coastal upwelling zone. *Journal of Cetacean Research and Management* 4:179–184.
- Gill, P. C., C. M. Kemper, M. Talbot, and S. A. Lyons. 2008. Large group of pygmy right whales in a shelf upwelling region off Victoria, Australia. *Marine Mammal Science* 24:962–968.
- Gill, P. C., M. G. Morrice, B. Page, R. Pirzl, A. H. Levings, and M. Coyne. 2011. Blue whale habitat selection and within-season distribution in a regional upwelling system off southern Australia. *Marine Ecology Progress Series* 421:243–263.
- Hain, J. H. W., S. L. Ellis, R. D. Kenney, P. J. Clapham, B. K. Gray, M. T. Weinrich, and I. G. Babb. 1995. Apparent bottom feeding by humpback whales on Stellwagen Bank. *Marine Mammal Science* 11:464–479.
- Hooze, P. N., and B. Eichenlaub. 1997. Animal movement extension to ArcView. Version 1.1. U.S. Geological Survey, Alaska Biological Science Center, Anchorage, USA.
- Jackson, G. D., S. Wotherspoon, and B. L. McGrath-Steer. 2005. Temporal population dynamics in arrow squid *Nototodarus gouldi* in southern Australian waters. *Marine Biology* 146:975–983.
- Kampf, J., M. Doubell, D. Griffin, R. L. Matthews, and T. M. Ward. 2004. Evidence of a large seasonal coastal upwelling system along the southern shelf of Australia. *Geophysical Research Letters* 31:L09310.
- Keller, C. A., L. Garrison, R. Baumstark, L. I. Ward-Geiger, and E. Hines. 2012. Application of a habitat model to define calving habitat of the North Atlantic right whale in the southeastern United States. *Endangered Species Research* 18:73–87.
- Kemper, C. M., J. F. Middleton, and P. D. van Ruth. 2013. Association between pygmy right whales (*Caperea marginata*) and areas of high marine productivity off Australia and New Zealand. *New Zealand Journal of Zoology* 40:102–128.
- Kiszka, J., P. J. Ersts, and V. Ridoux. 2007. Cetacean diversity around the Mozambique Channel island of Mayotte (Comoros archipelago). *Journal of Cetacean Research and Management* 9:105–109.
- Lagerquist, B. A., K. M. Stafford, and B. R. Mate. 2000. Dive characteristics of satellite-monitored blue whales (*Balaenoptera musculus*) off the central California coast. *Marine Mammal Science* 16:375–391.
- Larcombe, J., K. Brooks, C. Charalambou, M. Fenton, M. Fisher, M. Kinloch, and R. Summerson. 2002. Marine matters - atlas of marine activities and coastal communities in Australia's South-East Marine Region. Bureau of Rural Sciences, Canberra, Australian Capital Territory, Australia.
- Levings, A. H., and P. C. Gill. 2010. Seasonal winds drive water temperature cycle and migration patterns of southern Australian giant crab *Pseudosquilla in us gigas*. Pages 461–478 in G. H. Kruse, G. L. Eckert, R. J. Foy, R. N. Lipcius, B. Sainte-Marie, D. L. Stram, and D. Woodby, editors. *Biology and management of exploited crab populations under climate change*. Alaska Sea Grant, University of Alaska, Fairbanks, USA.
- MacLeod, C. D. 2009. Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. *Endangered Species Research* 7:125–36.
- Mann, K. H., and J. R. N. Lazier. 1996. *Dynamics of marine ecosystems*. Blackwell Science, Oxford, United Kingdom.
- McManus, T. J., J. E. Wapstra, E. R. Guiler, B. L. Munday, and D. L. Obendorf. 1984. Cetacean strandings in Tasmania Australia from Feb. 1978 to May 1983. *Papers and Proceedings of the Royal Society of Tasmania* 118:117–136.
- Melcon, M. L., A. J. Cummins, S. M. Kerosky, L. K. Roche, S. M. Wiggins, and J. A. Hildebrand. 2012. Blue whales respond to anthropogenic noise. *PLoS ONE* 7: e 32681.
- Middleton, J. F., and M. Cirano. 2002. A northern boundary current along Australia's southern shelves: The Flinders Current. *Journal of Geophysical Research* 107(9):3129.
- Middleton, J. F., and J. A. T. Bye. 2007. A review of the shelf-slope circulation along Australia's southern shelves: Cape Leeuwin to Portland. *Progress in Oceanography* 75:1–41.
- Morrice, M. G. 2004. Killer whales (*Orcinus orca*) in Australian territorial waters. Report for the Whale and Dolphin Conservation Society. School of Ecology and Environment, Deakin University, Warrnambool, Victoria, Australia, and Australocetus Research, Narrawong, Victoria, Australia.
- Morrice, M. G. 2013. Fine-scale foraging habitat and behavioural responses of pygmy blue whales. Dissertation, Deakin University, Warrnambool, Victoria, Australia.
- Nieblas, A. E., B. M. Sloyan, A. J. Hobday, R. Coleman, and A. J. Richardson. 2009. Variability of biological production in low wind-forced regional upwelling systems: a case study off southeastern Australia. *Limnology and Oceanography* 54:1548–1558.
- Panigada, S. 2006. Mediterranean fin whales at risk from fatal ship strikes. *Marine Pollution Bulletin* 52:1287–1298.
- Pirzl, R. 2008. Spatial ecology of *E. australis*: habitat selection at multiple scales. Dissertation, Deakin University, Warrnambool, Victoria, Australia.
- Praca, E., and A. Gannier. 2008. Ecological niches of three teuthophagous odontocetes in the northwestern Mediterranean Sea. *Ocean Science* 4:49–59.
- Puserini, C., V. Magnin, L. Meynier, J. Spitz, S. Hassani, and V. Ridoux. 2007. Food and feeding ecology of the common dolphin (*Delphinus delphis*) in the oceanic northeast Atlantic and comparison with its diet in neritic areas. *Marine Mammal Science* 23:30–47.
- Ross, G. J. B. 2006. Review of the conservation status of Australia's smaller whales and dolphins. Report to the Commonwealth of Australia. Department of the Environment and Heritage, Canberra, Australian Capital Territory, Australia.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.
- Stamaton, K. A., D. B. Croft, P. D. Shaughnessy, and K. A. Waples. 2007. Observations of humpback whales (*Megaptera novaeangliae*) feeding during their southward migration along the coast of southeastern New South Wales, Australia: Identification of a possible supplemental feeding ground. *Aquatic Mammals* 33:165–174.
- Tynan, C. T., D. G. Ainley, J. A. Barth, T. J. Cowles, S. D. Pierce, and L. B. Spear. 2005. Cetacean distributions relative to ocean processes in the northern California Current system. *Deep Sea Research II* 52:145–167.
- van Ruth, P. D., G. G. Ganf, and T. M. Ward. 2010. Hot-spots of primary productivity: an alternative interpretation to conventional upwelling models. *Estuarine Coastal and Shelf Science* 90:142–158.
- Ward, T. M., L. J. McLeay, W. F. D. Immlich, P. J. Rogers, S. M. McClatchie, R. Matthews, J. Kampf, and P. D. Van Ruth. 2006. Pelagic ecology of a northern boundary current system: effects of upwelling on the production and distribution of sardine (*Sardinops sagax*), anchovy (*Engraulis australis*) and southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight. *Fisheries Oceanography* 15:191–207.
- Zacharias, M., and E. Gregr. 2005. Sensitivity and vulnerability in marine environments: an approach to identifying vulnerable marine areas. *Conservation Biology* 19:86–97.

Associate Editor: James Sheppard.