

Biophysical correlates of relative abundances of marine megafauna at Ningaloo Reef, Western Australia

Jai C. Sleeman^{A,G}, Mark G. Meekan^B, Steven G. Wilson^C, Curt K. S. Jenner^D,
Micheline N. Jenner^D, Guy S. Boggs^A, Craig C. Steinberg^E
and Corey J. A. Bradshaw^F

^AGIS and Remote Sensing Group, Charles Darwin University, Darwin, NT 0909, Australia.

^BAustralian Institute of Marine Science, P.O. Box 40197, Casuarina MC, NT 0811, Australia.

^CHubbs–SeaWorld Research Institute, 2595 Ingraham Street, San Diego, CA 92109, USA.

^DCentre for Whale Research (Western Australia) Inc., P.O. Box 1622, Fremantle, WA 6160, Australia.

^EAustralian Institute of Marine Science, PMB No. 3, Townsville, Qld 4810, Australia.

^FSchool for Environmental Research, Institute of Advanced Studies, Charles Darwin University,
Darwin, NT 0909, Australia.

^GCorresponding author. Email: jai.sleeman@cdu.edu.au

Abstract. Changes in the relative abundance of marine megafauna (whales, dolphins, sharks, turtles, manta rays, dugongs) from aerial survey sightings in the waters adjacent to Ningaloo Reef between June 2000 and April 2002 are described. Generalised linear models were used to explore relationships between different trophic guilds of animals (based on animal sighting biomass estimates) and biophysical features of the oceanscape that were likely to indicate foraging habitats (regions of primary/secondary production) including sea surface temperature (SST), SST gradient, chlorophyll-*a* (Chl-*a*), bathymetry (BTH) and bathymetry gradient (BTHg). Relative biomass of krill feeders (i.e. minke whales, whale sharks, manta rays) were related to SST, Chl-*a* and bathymetry (model [AIC_c] weight = 0.45) and the model combining these variables explained a relatively large amount (32.3%) of the variation in relative biomass. Relative biomass of fish/cephalopod feeders (dolphins, sharks) were weakly correlated with changes in SST, whereas that of other invertebrate/macroalgal feeders (turtles, dugong) was weakly correlated with changes in steepness of the shelf (bathymetry gradient). Our results indicate that biophysical variables describe only a small proportion of the variance in the relative abundance and biomass of marine megafauna at Ningaloo reef.

Additional keywords: aerial surveys, chlorophyll-*a*, marine megafauna, Ningaloo Reef, sea surface temperature.

Introduction

Ningaloo Reef in northern Western Australia is the world's third largest fringing coral reef (spanning ~260 km of coastline) (Spalding *et al.* 2001). The proximity of the continental shelf to the reef allows for the convergence of warm and cold oceanographic currents, providing the necessary biophysical conditions to support a diverse array of organisms. Although the Ningaloo region is commonly known for its resident marine intertidal communities such as corals and reef fishes, it also plays host to a large suite of resident marine megafauna including sharks, dolphins, dugongs and manta rays (Preen *et al.* 1997). Some marine megafauna such as humpback (*Megaptera novaeangliae*) and pygmy blue whales (*Balaenoptera musculus brevicauda*) migrate past Ningaloo Reef en route to breeding grounds (Chittleborough 1965; Jenner *et al.* 2001), whereas others such as turtles migrate to Ningaloo Reef to feed and nest (Preen *et al.* 1997). Other migratory megafauna such as whale sharks have predictable seasonal occurrences at Ningaloo Reef for reasons that are not yet clearly understood (Wilson *et al.* 2001).

Throughout the Ningaloo region, large species such as turtles and whales were subjected to exploitative hunting practices up until the mid-1970s (CALM 2005). In 1987, the Australian waters adjacent to Ningaloo Reef were declared a Marine Park and are actively managed by the state of Western Australia. Further, national legislation was instituted in 1999 (EPBC Act) to protect migratory marine species. In recent decades, whales, whale sharks and manta rays have attracted increasing interest among eco-tourism industries, and as such, these operations are of great importance to the regional economy (Davis *et al.* 1997; Davis 1998). Dugong and turtles are also recognised for their important cultural (Aboriginal) and conservation value within the region (Marsh *et al.* 1997; Limpus *et al.* 2001).

Aerial survey techniques are useful for assessing the relative abundance and distribution of large migratory marine organisms, particularly over broad spatial scales (10s to 100s of km) (Preen *et al.* 1997; Chaloupka and Osmond 1999; Evans and Hammond 2004). Although they are usually biased indicators of relative abundance because they only target individuals visible at

or near the surface, when repeated at regular intervals and correction factors for observer bias (perception and availability bias) are applied (Marsh and Sinclair 1989), aerial surveys can provide improved estimates of relative abundance and distribution of megafauna without the use of expensive and logistically challenging techniques such as satellite telemetry (Mate *et al.* 1997; Hays *et al.* 2004; Wilson *et al.* 2006). Furthermore, broad-scale survey data can be compared with surrogates of the physical and biological properties of ocean surface waters to provide heuristic interpretations of the environmental conditions influencing relative abundance patterns (Jaquet and Whitehead 1996; Kasamatsu *et al.* 2000; Schick *et al.* 2004).

Fluctuations in the relative abundance and distribution of marine megafauna at broad spatial scales have been attributed to oceanographic processes that operate in a 'bottom-up' fashion by influencing the availability of food. For example, sea surface temperature (SST), SST gradient (SSTg), chlorophyll-*a* (Chl-*a*) concentration and bathymetry can be used as surrogate variables for primary production. Many studies have demonstrated correlations of these variables to the relative abundance and distribution of zooplankton (Myers and Hick 1990; Sugimoto and Tadokoro 1998; Kideys *et al.* 2000; Wilson *et al.* 2002). In turn, zooplankton can structure the relative abundance and distribution of fish (Agenbag *et al.* 2003; Schick *et al.* 2004), and for this reason, surrogate measures of zooplankton biomass have been used to model marine mammal (Bradshaw *et al.* 2004; Littaye *et al.* 2004) and reptile (Polovina *et al.* 2004) distributions and behaviour. However, plankton distributions may be altered by factors that are not responsible for their production and growth (Guinet *et al.* 2001; Bradshaw *et al.* 2004). Forcing factors are also susceptible to dilution effects through the food web (El-Sayed 1988; Guinet *et al.* 2001). For these reasons, it seems likely that distributions of species feeding on lower trophic-level prey species will be more closely correlated with variables such as SST and Chl-*a* than the distributions of higher trophic-level species (Gende and Sigler 2006).

In this paper we examine spatial and temporal patterns in the distribution, relative sighting occurrence and biomass of marine megafauna species observed at Ningaloo Reef, Western Australia. Occurrence of megafauna and fish/krill schools was estimated using aerial surveys flown at roughly weekly intervals between June 2000 and April 2002. These estimates of occurrence were compared with the physical and biological oceanography of the region characterised by satellite remote-sensing data. We aimed to identify important spatial and temporal patterns of habitat use by this suite of marine fauna and determine whether there were useful physical and biological correlates to explain some of the variation in their relative abundance. We examined the hypothesis that the strength of any correlations found varies depending on trophic level, with stronger correlations expected for those species feeding on lower trophic-level organisms such as invertebrates and algae.

Materials and methods

Oceanographic setting

The oceanography of the Ningaloo region of northern Western Australia is dominated by the Leeuwin Current that drives warm, low-nutrient surface waters south along the continental

shelf and influences the production and recruitment of invertebrate and fish communities depending on its strength (Caputi *et al.* 1996). The Current is strongest during autumn and winter (April–September) (Godfrey and Ridgeway 1985), and weakens during the summer (September–April) as a result of southerly winds that drive the Ningaloo Current (Taylor and Pearce 1999). As a wind-driven current, the Ningaloo Current is limited to the surface (<50 m) (Gersbach 1999; Woo *et al.* 2006a), but is sufficient to influence cold water upwelling (Woo *et al.* 2006b) that generates high primary production and phytoplankton biomass (Hanson *et al.* 2005).

Aerial censuses

Between June 2000 and April 2002, Woodside Energy Ltd commissioned the Centre for Whale Research (CWR) and CSIRO Marine Research to conduct a series of aerial surveys of marine megafauna in the waters adjacent to Ningaloo Reef, from North West Cape (21°47'S, 114°09'E) to south Amherst Point, south of Coral Bay (23°37'S, 113°36'E) to establish a baseline description of the region as part of an environmental impact assessment (Woodside 2003). A total of 26 surveys were carried out by CWR at roughly 8-day intervals (weekly) depending on weather and aircraft availability between June and November in 2000 and 2001. CSIRO Marine Research did a total of 12 surveys between January and May in 2001 and January and April 2002. Between January and March, surveys were carried out monthly by CSIRO and between April and May, surveys were carried out fortnightly. All surveys used a twin engine over-head wing Partenavia P68B aircraft fitted with bubble windows to maximise the field of view beneath the plane. The survey teams comprised two observers positioned on opposite sides of the aircraft who logged sighting occurrence and positions of animals using a GPS or a palm-top computer synchronised with a GPS logger at regular 1-s intervals. Survey routes used by CWR consisted of 16 NW–SE oriented transects running perpendicular to the coastline, spaced ~5 nm (9.3 km) apart and averaging a total distance of 1041.45 km (Fig. 1a). A standardised flight path consisting of 12 inshore–offshore transects spanning a total distance of 637.87 km was flown on each of the CSIRO surveys (Fig. 1b). One month following the commencement of the CSIRO surveys (February–May 2001 and January–April 2002), a single observer recorded positions and sighting occurrence of animals with a GPS when transiting between Learmonth and Carnarvon (24°53'S, 113°38'E). Unlike the standardised survey route, this deviated flight path ran adjacent to the coast at a distance of 300–400 m seaward of the front of Ningaloo Reef and covered a total distance of ~403 km (Fig. 1b). The inclusion of this additional survey dataset during the period of the CSIRO surveys provided better control of survey effort, with the approximate distance surveyed at each transect interval being around 1040 km (Table 1). No estimates were made of transect width on any of the survey flights because the overhead position of the wings prevented the attachment of reference streamers needed for defining transect width. As such, no estimates of animal densities could be made.

For the aerial surveys conducted by CSIRO, observers used clinometers (Suunto PM-5/360PC) and compass boards to report the relative vertical and horizontal position of sighting to the

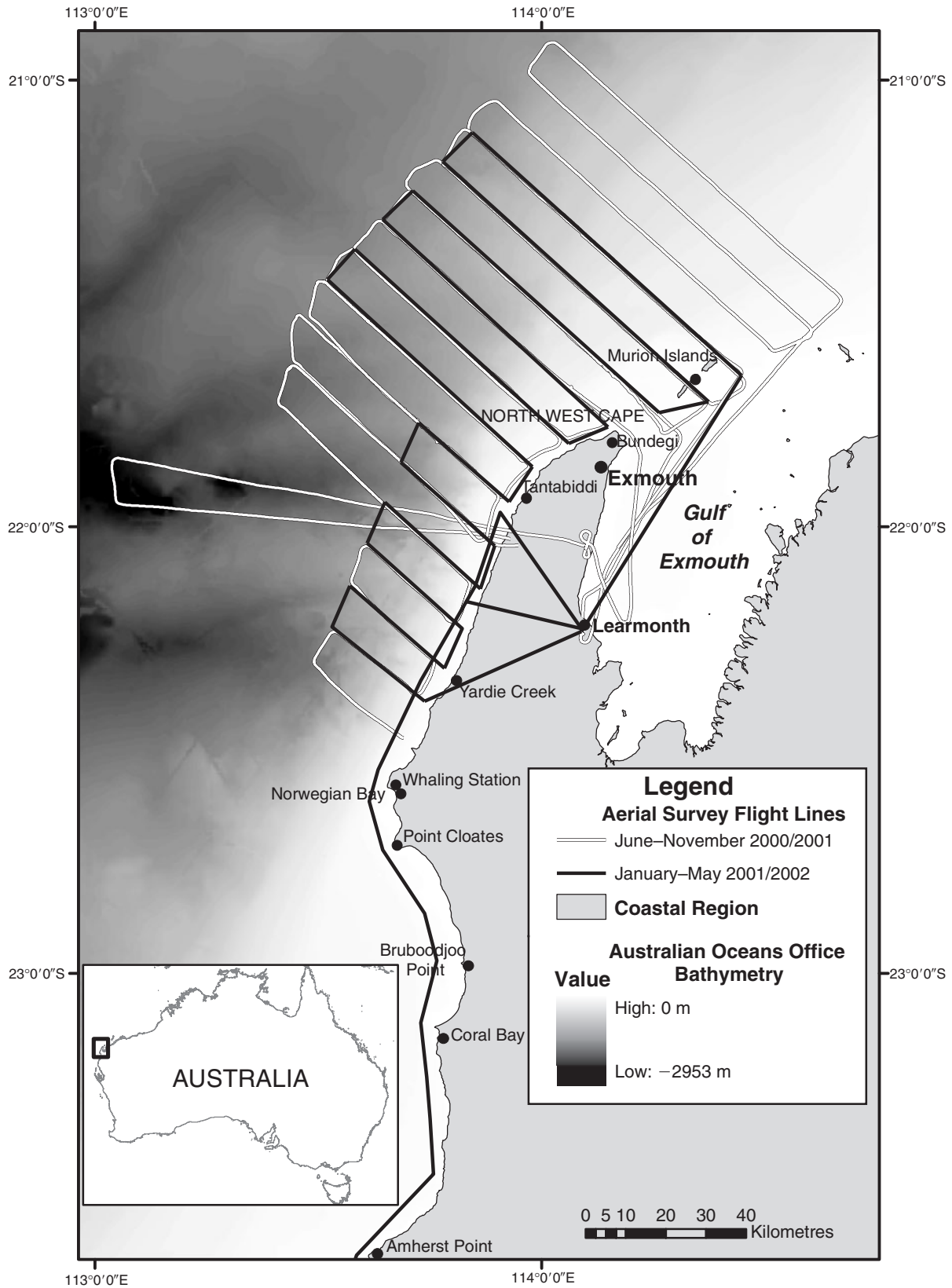


Fig. 1. Location and bathymetry of the Ningaloo region, Western Australia and aerial survey flights done by Centre for Water Research (CWR) between June and November, 2000 and 2001 and CSIRO between January and May, 2001 and 2002.

Table 1. The number of aerial surveys per year/month and the monthly total transect length (km) and ranges of Beaufort Sea States during the aerial surveys

Year	Month	Survey effort (no. of transects)	Total transect lengths (km)	Beaufort Sea State (range)
2000	June	4	~4165.8	1–5
	July	4	~4165.8	1–4
	August	3	~3124.35	1–4
	September	2	~2082.9	1–5
	October	3	~3124.35	1–4
	November	2	~2082.9	2–4
2001	January	1	~637.87	2–3
	February	1	~1040.87	2–3
	March	1	~1040.87	1
	April	2	~2081.74	1–3
	May	2	~2081.74	1–4
	June	4	~4165.8	1–3
	July	3	~3124.35	2–4
	August	2	~2082.9	2–3
	September	2	~2082.9	2–4
	October	1	~1041.45	2–4
	November	1	~1041.45	2–3
	2002	January	1	~1040.87
February		1	~1040.87	2–3
March		1	~1040.87	1–2
April		2	~2081.74	1–3

Table 2. The trophic guilds, the broad taxonomic groups contained within guilds and the specific taxonomic ‘species’ classes that also constituted guilds

Estimates of the approximate proportion (0–1) of taxa that were positively identified to a species level from aerial surveys are provided along with estimates of the approximate proportion (0–1) of each species that comprised a trophic guild

Trophic guilds	Broad taxonomic groups	Specific taxonomic classes	Proportion animals positively identified to species	Proportion animals in trophic guild
Krill feeders	Whales	Humpback whales (<i>Megaptera novaeangliae</i>)	1.0	~0.67
		Pygmy blue whales (<i>Balaenoptera musculus breviceauda</i>)	~1.0	~0.02
		Minke whales (<i>B. acutorostrata</i>)	~1.0	~0.01
	Whale sharks	Whale sharks (<i>Rhincodon typus</i>)	~1.0	~0.01
		Rays	Manta rays (<i>Manta birostris</i>)	<0.13
Fish/cephalopod feeders	Dolphins	Mobulid rays (<i>Mobula eregoodootenkee</i>)	?	
		Bottlenose dolphins (<i>Tursiops truncatus</i>)	<0.02	~0.89
		Indo-Pacific humpback dolphins (<i>Sousa chinensis</i>)	<0.01	
		Clymene dolphin (<i>Stenella clymene</i>)	?	
	Sharks	Risso’s dolphins (<i>Grampus griseus</i>)	?	
		Hammerhead shark (<i>Sphyrna</i> spp.)	<0.18	~0.11
		Requiem sharks (<i>Carcharhinus</i> spp.)	<0.03	
Invertebrate/macro-algae feeders	Turtles	Green turtles (<i>Chelonia mydas</i>)	?	~0.99
		Flatback turtles (<i>Natator depressus</i>)	?	
		Hawksbill turtles (<i>Eretmochelys imbricata</i>)	?	
		Loggerhead turtles (<i>Caretta caretta</i>)	?	
		Olive ridley turtles (<i>Lepidochelys olivacea</i>)	?	
	Leatherback turtles (<i>Dermochelys coriacea</i>)	?		
Dugong	Dugongs (<i>Dugong dugon</i>)	1.0	~0.01	

aircraft. Angle of drift for each transect was corrected so that horizontal angles reported from the compass boards could be made relative to direction of the flight path. Using trigonometry to calculate the approximate location of animals, most sightings occurred within a 500 m radius of the aircraft. In all surveys,

a mean altitude of 305 m and a speed of 120 knots were maintained. Of the animals identified, only large cetaceans, whale sharks, dugongs and some sharks were discernable to species level; thus, taxa were generally grouped as turtles, dolphins, sharks, etc. (Table 2). Although attempts were made to avoid

Table 3. The types of biophysical variables analysed, the spatial scale of analyses

Broad, averaged across Ningaloo region; fine, spatially explicit or equal to the spatial resolution of satellite data; data sources, temporal coverage and spatial resolution of data. AVHRR, Advanced Very High Resolution Radiometer; MODIS, Moderate Resolution Imaging Spectroradiometer

Biophysical variable	Scale of analysis	Data source	Temporal coverage	Spatial resolution (km)
Sea surface temperature	Broad	AVHRR Pathfinder (Version 5)	Weekly Composites	4
	Fine	MODIS Terra level 2 (Collection 4)	Daily	1
Sea surface temperature gradient	Broad	AVHRR Pathfinder (Version 5)	Weekly Composites	4
	Fine	MODIS Terra level 2 (Collection 4)	Daily	1
Chlorophyll- <i>a</i>	Broad	SeaWiFS level 3 (Version 5.1)	Weekly Composites	9
	Fine	SeaWiFS level 2 (Version 5.1)	Daily	~1
Bathymetry	Fine	National Oceans Office of Australia	?	0.250
Bathymetry gradient	Fine	National Oceans Office of Australia	?	0.250

surveying in sea surface conditions greater than Beaufort Sea State 3, this was not always possible. In preliminary analyses of the data, negative correlations between Beaufort Sea State and sighting occurrence of all taxonomic categories were found, indicating that marine fauna sighting were subject to observational biases related to poor sea-state conditions. Approximately 34% of the surveys were carried out in conditions with greater than Beaufort Sea State 3 (see Table 1). Although inclusion of these data for analysis was likely to increase perception bias relating to omission of animals owing to turbidity, it was necessary for increasing the statistical robustness by maximising the sample size of animal sighting of the relatively poorly represented species such as sharks, dugongs and some whales.

Remotely sensed data

Biophysical variables of SST, SSTg and Chl-*a* concentration were derived from satellite imagery and were used to describe (i) broad-scale (i.e. across the entire region) and (ii) fine-scale (spatially-explicit positions where animals were sighted) physical and biological surface oceanography at Ningaloo during the aerial survey transects. The variables (SST, SSTg and Chl-*a*) were selected for analysis because they were: (i) likely to act as surrogates for processes that influence primary production and food availability, (ii) could be classified accurately, without bias and classification methods could be easily replicated, (iii) could be resolved at fine spatial (kilometres) and temporal (daily) scales appropriate to the survey data, and (iv) relatively easy to access at little or no cost. Additionally, bathymetry and bathymetry gradient (see below) were also included in the analysis. A variety of data were used to derive the different biophysical variables in a form (spatial and temporal scale) appropriate for comparison and analysis with the aerial survey data (Table 3).

For the broad-scale analysis, we used remote-sensing data of SST and Chl-*a* that were generalised (averaged spatially) across the entire region and averaged temporally (from daily composites) on a monthly basis. Biophysical data used for the fine-scale analysis such as SST imagery were collected at approximately 4-day intervals (two images per 8-day period). This eliminated problems associated with atmospheric effects, which can render satellite imagery less useful and ensured that at least one image corresponded (approximately) with the dates and intervals of the aerial surveys. In every 8-day period only one image was

retained for analysis following a screening and removal of the image with the most incomplete data coverage (missing data as a result of clouds and/or sensor malfunctions). In spite of this, priority of selection was given to images that closely matched the dates of aerial surveys, thus temporal differences between datasets likely influenced the results negligibly.

HDF-EOS to GeoTIFF Conversion (HEG) Tool software provided by NASA's Earth Observing System (EOS) was used to geo-locate and convert files from Hierarchical data format (HDF) to GeoTIFF files usable within Environmental Systems Research Institute (ESRI) ArcGIS 9.1. The resulting data were converted into grids with a geographic projection (WGS84) and a spatial resolution of ~1 km. Cloud masks were used to remove (reclassify) erroneous data. SSTg was derived by reprojecting SST images into standard Mercator grids with equal interval *x*, *y* coordinates (m). A 3 × 3 neighbourhood function (Mennis *et al.* 2005) was used to evaluate the rate of change in the temperature values of adjacent cells and these values were subsequently outputted as a geo-referenced grid of temperature gradients.

NASA's SeaDAS 4.8 software (running on Linux Fedora Core 2) was used to geo-reference and subset Chl-*a* imagery for the Ningaloo region, which were then exported as ASCII files, uploaded and interpolated (inverse distance weighted) into raster coverages with ESRI ArcINFO. High-resolution bathymetry grid data with a spatial resolution (*x*, *y*) of 250 m were acquired from the National Oceans Office of Australia for the entire Ningaloo region. A map of bathymetric gradient was constructed by reprojecting the data as Mercator and applying a similar neighbourhood function as that used to generate the SSTg data. We used a macro in ArcGIS 9.1 to extract the values for each oceanographic variable (raster dataset) that corresponded to each animal observation from the aerial surveys (point dataset). Density distribution maps generated in ArcGIS 9.1 using a 5 km focal function were derived from the GPS point data of taxonomic groups that were recorded in large numbers during the surveys.

Weather station data

Wind data were used in a preliminary analysis to investigate how this variable influenced sightings given that southerly winds are known to influence the Ningaloo Current, which enhances nutrient upwelling and productivity in the region (Woo *et al.* 2006a). Wind speed and direction data were collected hourly

from a coastal weather station at Milyering (21°1.816'S and 113°55.316'E) in the northern section of the marine park. No wind data were available for the period between 26 April 2000 and 5 January 2001 owing to a technical fault. Wind direction and speed were decomposed to East–West (U) and North–South (V) vector components and then averaged on a weekly and monthly basis. The resulting vectors were then re-transformed as wind speed (km h^{-1}) and direction (divided into eight cardinal directions).

Trophic grouping and biomass estimates

Preliminary inspection of relative abundance estimates for individual taxonomic groups (i.e. whales, dolphins, etc.) indicated that the observation data violated statistical assumptions of not conforming to typical Poisson distributions, even after applying transformations. To account for this discrepancy, we used a hierarchical classification scheme similar to those used in other megafauna studies (Davis *et al.* 2002), where animals were grouped on the basis of their predominant dietary components and their trophic level (Pauly *et al.* 1998) to reduce the number of species and maximise sample size for statistical analysis.

The three simplified trophic guilds we used to regroup animals were: (i) krill feeders, (ii) fish/cephalopod feeders, and (iii) other invertebrate/macro-algae feeders. Average group sizes were calculated for each trophic guild. Within each guild, relative biomass was calculated using the observed number of individuals per survey day and the average bodyweights (obtained from the published reports) for each taxonomic class (Spain and Heinsohn 1975; Pai *et al.* 1983; Stevens and Lyle 1989; Stevens and McLoughlin 1991; Lanyon and Marsh 1995; Plotkin 1995; Kohler *et al.* 1996; Marsh *et al.* 1997; Tamura and Ohsumi 2000; Uchida *et al.* 2000; Wintner and Dudley 2000).

Krill feeders included humpback (*Megaptera novaeangliae*), pygmy blue (*Balaenoptera musculus brevicauda*) and minke whales (*B. acutorostrata*) (Preen *et al.* 1997) and filter-feeding whale sharks (*Rhincodon typus*), manta (*Manta birostris*) and mobulid rays (*Mobula eregoodootenkee*). The latter elasmobranchs have been observed feeding on tropical krill around the waters of Ningaloo Reef (Taylor and Grigg 1991; Taylor 1994; Wilson *et al.* 2001). The fish/cephalopod feeders' guild was composed of dolphins, predominantly bottlenose (*Tursiops truncatus*), Indo-Pacific humpback (*Sousa chinensis*), clymene (*Stenella clymene*) and Risso's (*Grampus griseus*) dolphins, and sharks. The latter included hammerheads (*Sphyrna* spp.) and various species of requiem (*Carcharhinus* spp.) sharks. The other invertebrate/macro-algae feeders included turtles, of which most were green (*Chelonia mydas*), with only a small proportion of other species such as the flatback (*Natator depressus*), hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*) and leatherback (*Dermochelys coriacea*) turtles (Prince 1994; Preen *et al.* 1997) and dugongs (*Dugong dugon*). Dugongs are algal and invertebrate feeders that are also common at Ningaloo Reef (Gales *et al.* 2004). Although the present study focuses on spatial and temporal variation in megafauna species, sightings of schools of prey items including anchovies (*Stolephorus indicus*) and tropical krill (*Pseudeuphausia latifrons*) were also recorded to compare relative distributions with their surveyed predators. No attempt

was made to estimate the relative abundance or biomass of particular species of fish or krill.

The classification of different animal taxa into trophic groups was based predominantly on the major diets of the numerically dominant species. Not all species within certain taxonomic groups (e.g. whales, dolphins) adhered to the broad trophic restrictions implied by the guild categorisation; however, they were included in the analysis because relatively few animals could be positively identified to species (see Table 2). For instance, unlike other 'fish-feeding' dolphins and sharks commonly sighted at Ningaloo, Risso's dolphins and tiger sharks are known to have diets composed largely of other prey such as cephalopods (Cockcroft *et al.* 1993; Blanco *et al.* 2006), and turtles, sea snakes and dugongs, respectively (Heithaus 2001; Simpfendorfer *et al.* 2001). Relatively few surveyed animals were positively identified as Risso's dolphins or tiger sharks, so it is possible that other species of dolphins and sharks could have been present and not identified or misidentified. Consequently, a certain degree of generalisation was required in the 'trophic' categorisation. Given that bottlenose dolphins are among the most frequently sighted dolphin species in boat-based surveys (Preen *et al.* 1997) at Ningaloo and the small proportion of sharks, which constitute megafauna in the 'fish/cephalopod feeders' guild, we expect the inclusion of any misclassified (to 'trophic' guild) species to have negligible effects on the results.

Modelling

We used a generalised linear modelling (GLM) approach with the open-source software R Package (Ver.2.2.0, Vienna, Austria) (R Development Core Team 2004) to determine if certain variables or combinations of these could aid in predicting the relative biomass or abundance of different trophic guilds of megafauna. Examination of the residuals for the saturated models showed that the relative biomass data had a statistical error distribution best represented by a gamma distribution with an identity link function. Model selection was based on Akaike's Information Criterion corrected for small samples (AIC_c), (Akaike 1973, 1974; Lebreton *et al.* 1992; Burnham and Anderson 2001). AIC_c values were ranked, with the most parsimonious model(s) having the lowest AIC_c values and highest model weights (Lebreton *et al.* 1992).

From the set of *a priori* models we used a predictive model-averaging procedure to determine the magnitude of the effect of some terms, keeping all other dependent variables constant (Burnham and Anderson 2002). The weights of evidence (w_{+i}) for each variable i were calculated by summing the model AIC_c weights (w_i) over all models in which each term appeared. However, the w_{+i} values are relative, rather than absolute, so they will often be >0 even if the predictor has no contextual explanatory importance (Anderson and Burnham 2002). To determine the predictors that were relevant to the data, a baseline for comparing relative w_{+i} across predictors was required. Following Anderson & Burnham (2002), we randomised the data for each predictor separately, re-calculated w_{+i} , and repeated this procedure 100 times for each predictor. The median of this new randomised w_{+i} distribution for each predictor was taken as the baseline (null) value ($w + 0$). For each term the relative weight of evidence (Δw_{+}) was obtained by subtracting $w + 0$ from w_{+i} . Predictors with Δw_{+} of zero or less have essentially no explanatory power.

We considered five oceanographic variables within the all-subsets model set: SST, SSTg, Chl-*a*, bathymetry (BTH) and bathymetric gradient (BTHg) where the saturated model was:

$$\text{Guild relative biomass}/25 \text{ km}^2 \text{ grid cell} \sim \text{SST} + \text{SSTg} + \text{Chl-}a + \text{BTH} + \text{BTHg} + \epsilon$$

where ϵ represents the error term. All variables were log-transformed before analysis to account for their large range in values. We did not use the complete set of variables available to prevent the loss of too many degrees of freedom that could lead to poor model convergence. In addition, exclusion of variables such as geostrophic currents was necessary owing to their coarse spatial scale (relative to aerial data) and poor coverage (i.e. missing data at coastal boundary zones). We also parameterised the models with a 50% random sub-selection of the data to reduce autocorrelation problems associated with the fact that the count and oceanographic measurements were not temporally or spatially independent (e.g. Bradshaw *et al.* 2004). The relative biomass of humpback whales was large compared with all the other animals (making the distribution of krill-feeder relative biomass bimodal and too skewed to correct with transformation), so these animals were considered in two modelling scenarios: one where humpback counts rather than relative biomass (with single-species models, the 'relative biomass' response was essentially a scalar of the count data, so counts were used instead) were considered alone,

$$\text{Humpback relative abundance per } 25 \text{ km}^2 \text{ grid cell} \sim \text{SST} + \text{SSTg} + \text{Chl-}a + \text{BTH} + \text{BTHg} + \epsilon$$

and one where humpbacks were excluded from the krill feeder guild altogether.

The latter model was likely to hold greater support particularly given that humpback whales are known to be migrating through the region and are unlikely to be feeding (Chittleborough 1965; Jenner *et al.* 2001).

A Poisson error distribution with a log link function was used in the humpback count model. A Spearman's correlation was calculated for each set of variables in each model set. Highly correlated ($r^2 > 0.8$) variables were not included in the same model set. The percentage of deviance explained (%DE) was also calculated for each model as a functional goodness-of-fit measure.

Results

Broad-scale oceanographic/climatic patterns

There were consistent seasonal patterns in SST during the study period with low variability at daily and weekly scales as indicated by the small standard errors in Fig. 2. SST gradually declined to a low in September 2000 and 2001 then increased to a peak during March 2001 and February 2002. Average Chl-*a* concentrations in surface waters were generally higher throughout most of 2000 compared with 2001 (Fig. 2). Concentrations began to rise from a low in August 2000 to a peak in November, and then gradually declined until March 2001. Chl-*a* concentrations peaked during May 2001, although there were large monthly fluctuations between October 2001 and March 2002.

North-easterly winds prevailed throughout most weeks and months (particularly in January and February). Southerly winds rarely lasted longer than 24 h and generally occurred around

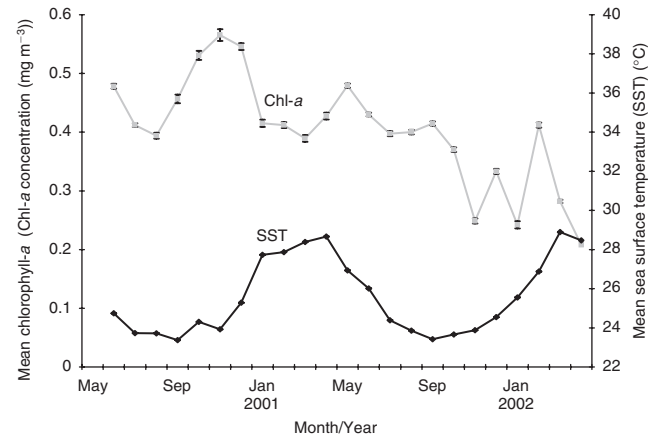


Fig. 2. Average monthly (\pm s.e.) Chl-*a* concentration and sea surface temperature (SST) across the survey region of Ningaloo Reef, Western Australia.

the beginning of April, towards the end of July and the beginning of August in 2000 and 2001. These winds typically blew at speeds greater than 2.6 km h^{-1} , with the highest speeds reaching 16.6 km h^{-1} in August 2001 and 12 km h^{-1} at the beginning of December 2001. On a weekly basis, we observed brief ($< 12 \text{ h}$) and intermittent periods of moderate ($< 2.7 \text{ km h}^{-1}$) southerly winds throughout April 2001, which corresponded with the peak in Chl-*a* concentrations in the Ningaloo region in 2001. Increases in Chl-*a* concentrations also corresponded to changes in intensity of southerly wind speeds from moderate ($< 4.3 \text{ km h}^{-1}$) in November to strong ($< 12 \text{ km h}^{-1}$) in December.

Broad temporal and spatial trends in megafauna sighting occurrence

Krill feeders

Small groups or individual blue whales (mean group size \pm s.e. = 1.5 ± 0.2) were observed along Ningaloo Reef from June to October and in November 2001, and in April and May 2002 (Fig. 3a). The number of blue whale sightings peaked between October and November 2001 when average Chl-*a* concentrations were peaking and SST was rising slowly (Fig. 3a). Humpback whales occurred in the survey region from June to November in both 2000 and 2001, with most sightings in August (Fig. 3b). Fewer were observed in 2001 than in 2000. The humpback whales had the highest sighting occurrence $\sim 5 \text{ km}$ west of Tantabiddi and 30 km north of the Murion Islands (Fig. 4a; see Fig. 1 for map of Ningaloo with place names). Minke whales (mean group size = 1.03 ± 0.3) were most abundant in June 2001 and displayed little seasonality in sighting occurrence during the study (Fig. 3c).

Manta rays (mean group size = 1.97 ± 0.24) were observed in most months of the study, with peak abundance occurring in May 2001 (Fig. 3d). The highest sighting occurrence of manta rays corresponded with fish/krill schools, offshore (South-West) from Yardie Creek and west of Norwegian Bay (Fig. 4b, f). Relatively few whale sharks (mean group size = 1.05 ± 0.05) were observed, and those animals that were detected were seen at the same times of the year (January, March and April) in 2001 and 2002 (Fig. 3e).

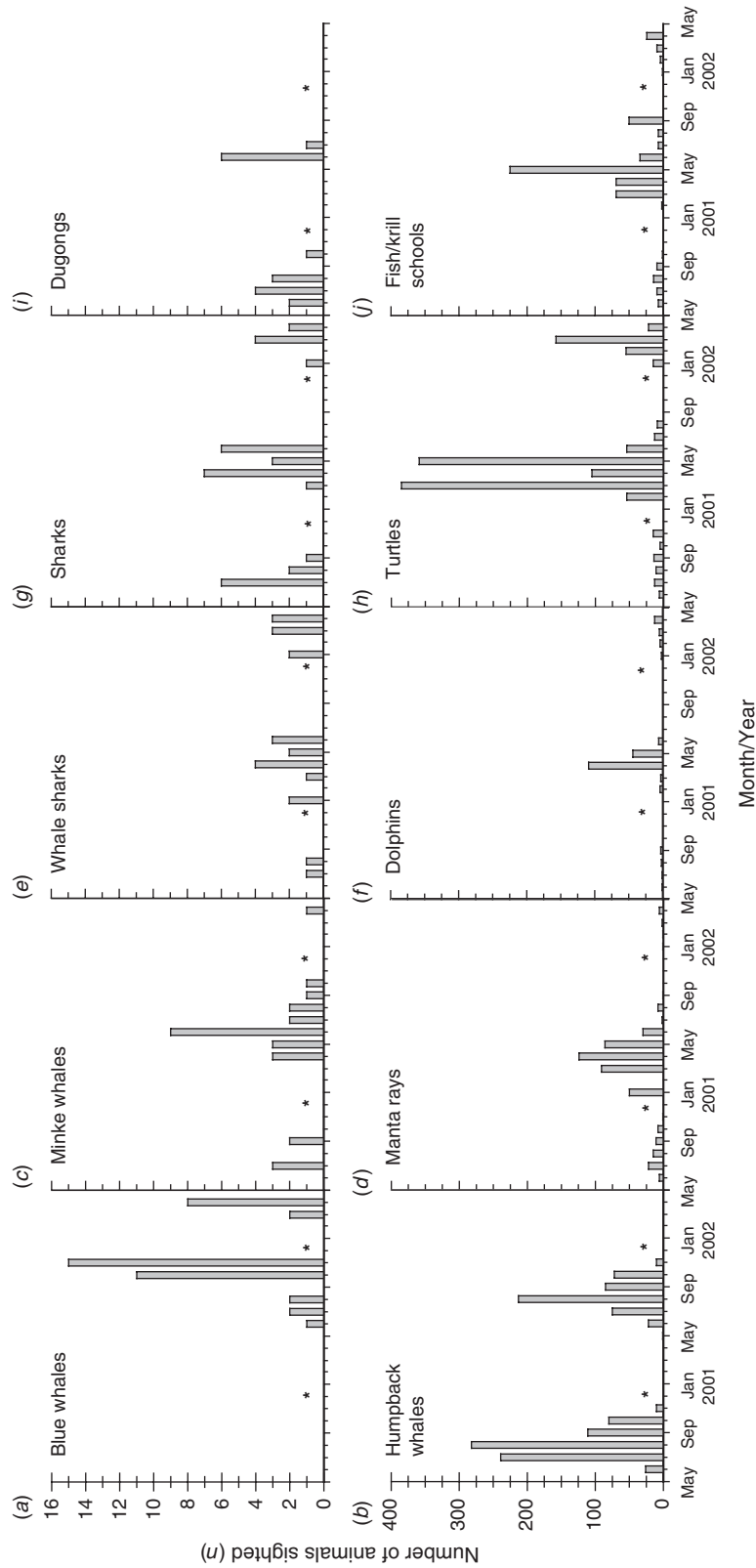


Fig. 3. Monthly sighting occurrence of (a) blue whales, (b) humpback whales, (c) minke whales, (d) manta rays, (e) whale sharks, (f) dolphins, (g) sharks, (h) turtles, (i) dugongs and (j) fish/krill schools throughout the survey period June 2000–April 2002 (*no surveys in December 2000–2001).

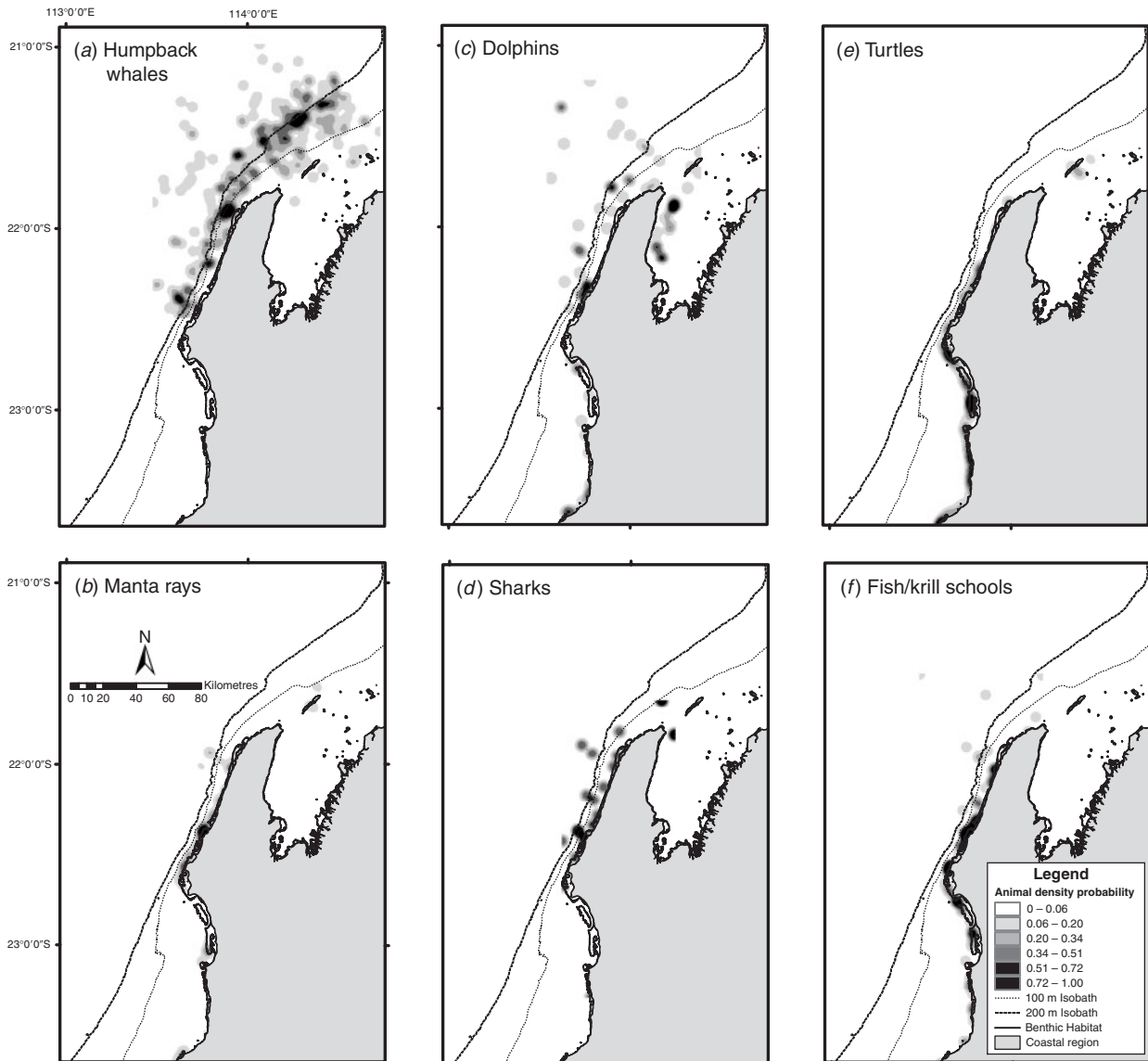


Fig. 4. Sighting distribution maps (5 km neighbourhood kernel) for truncated aerial survey observations of (a) humpback whales, (b) manta rays, (c) dolphins, (d) sharks, (e) and turtles and (f) krill/fish schools.

Fish/cephalopod feeders

Dolphins (mean group size = 2.9 ± 0.5) were observed throughout most of the year, with the largest number sighted between March and May 2001 (Fig. 3f). Dolphin sightings were relatively well distributed in the Ningaloo region, with most sighted in the Gulf of Exmouth (10 km east of Bundegi) and 5 km west from Yardie Creek on Ningaloo Reef (Fig. 4c). Sharks (mean group size = 1.06 ± 0.04) were observed in greatest numbers in July in 2000 and in April–June 2001 (Fig. 3g). The highest sightings of sharks occurred 10 km south-west of Yardie Creek, directly off Bundegi and 15 km north of the tip of North West Cape (Fig. 4d).

Other invertebrate/macroalgae feeders

Turtles (mean group size = 1.31 ± 0.03) occurred in almost every month of the study (with the exception of January and

September–November 2001) and sightings peaked in March and May 2001, corresponding to a peak in SST and Chl-*a* concentrations (Fig. 3h). The greatest density of turtles occurred adjacent to Point Cloates and 10 km west of Bruboodjoo Point (Fig. 4e). Dugongs (mean group size = 1) were observed in June and July in both 2000 and 2001, with largest numbers sighted in June 2001 (Fig. 3i). Fish/krill schools were sighted in greatest numbers during April and May 2001 (Fig. 3j) and sighting occurrence tended to correspond in distribution with that of manta rays (Fig. 4f).

Fine-scale trends in megafauna sighting occurrence and biophysical variables

Krill feeders

Overall, more than 55% of blue whales observed were seen in water between 25°C and 27°C (Fig. 5a). Blue whales

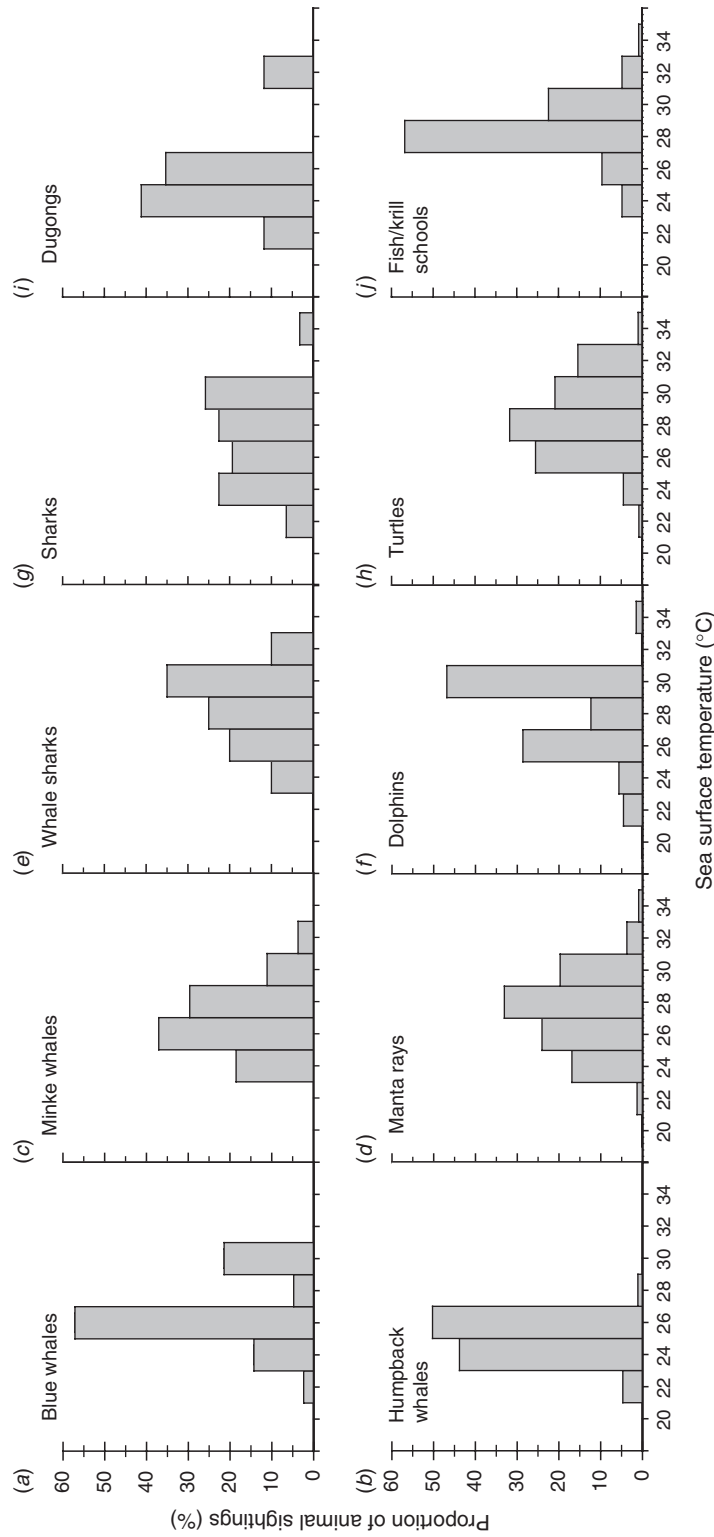


Fig. 5. Histograms showing the proportions of (a) blue whales, (b) humpback whales, (c) minke whales, (d) manta rays, (e) whale sharks, (f) dolphins, (g) sharks, (h) turtles, (i) dugongs and (j) fish/krill schools in relation to surface water temperatures.

occurred in a restricted range of relatively low surface Chl-*a* concentrations, with 65% found in concentrations of 0.125–0.25 mg m⁻³ (Fig. 6a). Blue whales were recorded in a large range of depths (Fig. 7a). Compared with other taxa, humpbacks generally occurred in the narrowest temperature range (Fig. 5b). Approximately 70% of humpbacks were recorded in waters with moderate to high surface Chl-*a* concentrations of 0.25–1.00 mg m⁻³ (Fig. 6b) and tended to be spotted in waters with depths >200 m (Fig. 7b). Almost 70% of minke whales occurred in warm SST between 25°C and 29°C (Fig. 5c) and over 55% occurred in waters with medium to high 0.25–0.50 mg m⁻³ Chl-*a* (Fig. 6c).

Most of the manta rays and whale sharks (>60%) occurred in relatively warm waters between 27°C and 31°C (Fig. 5d, e). Most of the manta rays observed during the surveys were in Chl-*a*-rich waters, with concentrations of 1.0–4.0 mg m⁻³ (Fig. 6d).

Although the average Chl-*a* concentration is low in the Ningaloo region during the period when whale sharks were observed, ~70% of whale sharks were found in high Chl-*a* of 0.5–2.0 mg m⁻³ (Fig. 6e).

Manta rays (Fig. 7d) and whale sharks (Fig. 7e) were found in a range of water depths, but were mainly sighted in shallow waters (<100 m).

Fish/cephalopod feeders

Dolphins occurred in a wide range of SSTs, although >55% were found in warm waters (27–31°C, Fig. 5d). More than 75% of dolphins occurred in moderate Chl-*a* concentrations of 0.125–0.50 mg m⁻³ (Fig. 6f). Dolphins were spotted in waters of varying depths, with around 40% of those sighted occurring in shallow inshore areas (<100 m, Fig. 7f). Sharks occurred in a large range of SSTs (Fig. 5g) with over 75% of sharks sighted being found in high surface Chl-*a* of 0.50–2.00 mg m⁻³ (Fig. 6g). Sharks were observed in a broad range of depths, but most were in shallower waters (<100 m, Fig. 7g).

Other invertebrate/macroalgae feeders

Turtles were observed in the widest range of SSTs, with more than 70% of individuals sighted in waters at 25–33°C (Fig. 5h). Although turtles occurred in a range of Chl-*a* concentrations, more than 70% were found in areas of high Chl-*a* (0.5–2.0 mg m⁻³, Fig. 6h). Most turtles were also found in shallow waters (<100 m, Fig. 7h). Dugongs were generally found in water with intermediate to low temperature ranges (21–27°C) (Fig. 5i). Most dugongs were also found in areas of high surface Chl-*a* (Fig. 6i). All dugongs were only sighted in shallow waters (<100 m, Fig. 7i). Over 57% of fish/krill schools were found in moderate to high SSTs between 27°C and 29°C (Fig. 5j). Most fish/krill schools were observed in high surface Chl-*a* waters (Fig. 6j). Fish/krill schools occurred in a range of water depths, with most in shallow waters (<100 m, Fig. 7j).

Generalised linear models

Krill feeders

The best-supported model for the krill feeding guild (excluding humpback whales) included SST, Chl-*a* and BTH (AIC_c weight = 0.45) and explained a relatively high proportion of the variation in relative biomass (%DE = 32.3%). Models

including SSTg and BTHg also had moderate levels of support (AIC_c weights = 0.16). However, the weights of evidence analysis demonstrated model-averaged support only for BTH ($\Delta w+ = 0.70$), indicating that most of the %DE in the best model was explained by variation in BTH alone (all other terms had $\Delta w+ < 0$) so that there was a greater relative biomass of krill-feeding species observed in deeper water. The Poisson-distributed count model failed to explain much of the variation in sighting occurrence of humpback whales (top model with AIC_c weight = 0.17 and %DE = 1.8%), and none of the explanatory variables had any model-averaged support according to the weights of evidence analysis (all $\Delta w+ \cong 0$).

Fish/cephalopod feeders

For the fish/cephalopod feeders, the best model (AIC_c weight = 0.32) included SST and Chl-*a* and explained 9.4% of the deviance (%DE) in relative biomass. Although the less-supported models had other terms including BTH, SSTg and BTHg (AIC_c weights = 0.14, 0.12 and 0.10, respectively), the weights of evidence analysis indicated that only SST had reasonable model-averaged support ($\Delta w+ = 0.44$). The model suggested that larger relative biomasses of fish/cephalopod feeders were found in warmer compared with cooler surface waters.

Other invertebrate/macroalgae feeders

Models of relative biomass distributions of invertebrate/macroalgae feeders included all oceanographic variables except SSTg (AIC_c weight = 0.50), and explained 8.4% of the deviance (%DE). However, the weights of evidence analysis only demonstrated support for BTHg ($\Delta w+ = 0.46$), indicating that larger relative biomasses of species within this guild were observed in waters over steeper bathymetric slopes.

Discussion

The foraging and distribution patterns of many predatory marine species such as whales, seals and seabirds are often correlated with the physical and biological properties of surface waters (Bradshaw *et al.* 2004; Littaye *et al.* 2004; Polovina *et al.* 2004; Ainley *et al.* 2005). Although the relationship between marine animal distributions and oceanographic conditions can be strong in some circumstances, it is often difficult to establish the relative contribution of different variables (e.g. SST, Chl-*a*, etc.) to variation in distribution patterns (Polovina *et al.* 2004; Piatt *et al.* 2006). These problems arise because models cannot accommodate the complexity of predator behaviour when coupled with factors that can influence primary or first-order secondary production (Horne and Schneider 1994; Agenbag *et al.* 2003; Gende and Sigler 2006).

We found that the distributions of krill-feeding animals (not including humpback whales) were largely predicted by variation in bathymetry. This outcome suggests that krill feeders may experience greater foraging success when in deeper waters (assuming krill feeders were mainly observed when foraging) and that they may target increased abundances of krill in areas with greater variation in depth (i.e. for vertical migration or wider resource use) (Wilson *et al.* 2002; Wilson *et al.* 2003). Alternatively, this pattern may relate to the potential distribution of predators (i.e. killer whales) in shallow waters. Killer whales

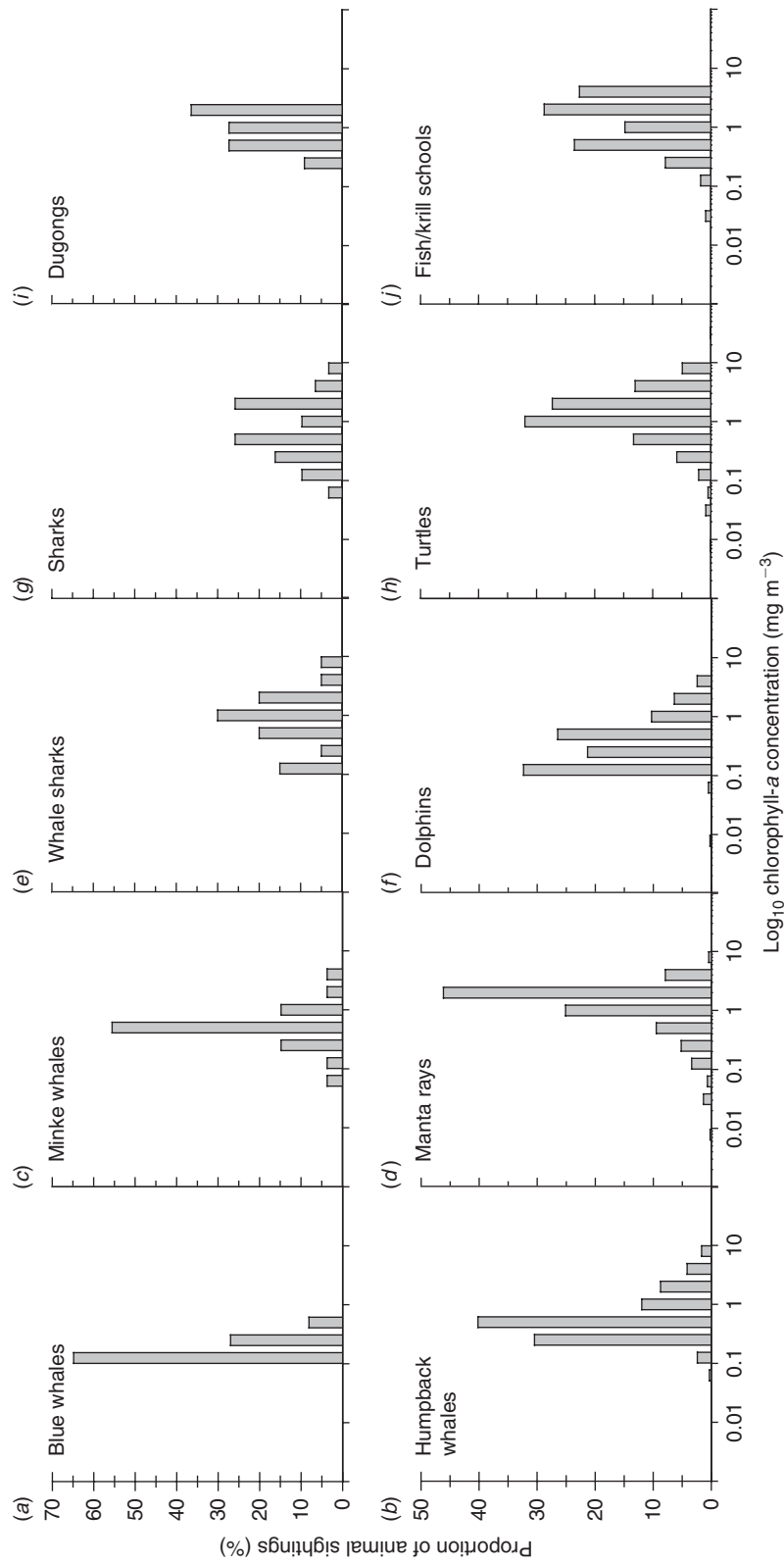


Fig. 6. Histograms showing the proportions of (a) blue whales, (b) humpback whales, (c) minke whales, (d) manta rays, (e) whale sharks, (f) dolphins, (g) sharks, (h) turtles, (i) dugongs and (j) fish/krill schools in relation to chlorophyll-*a* (Chl-*a*) concentrations.

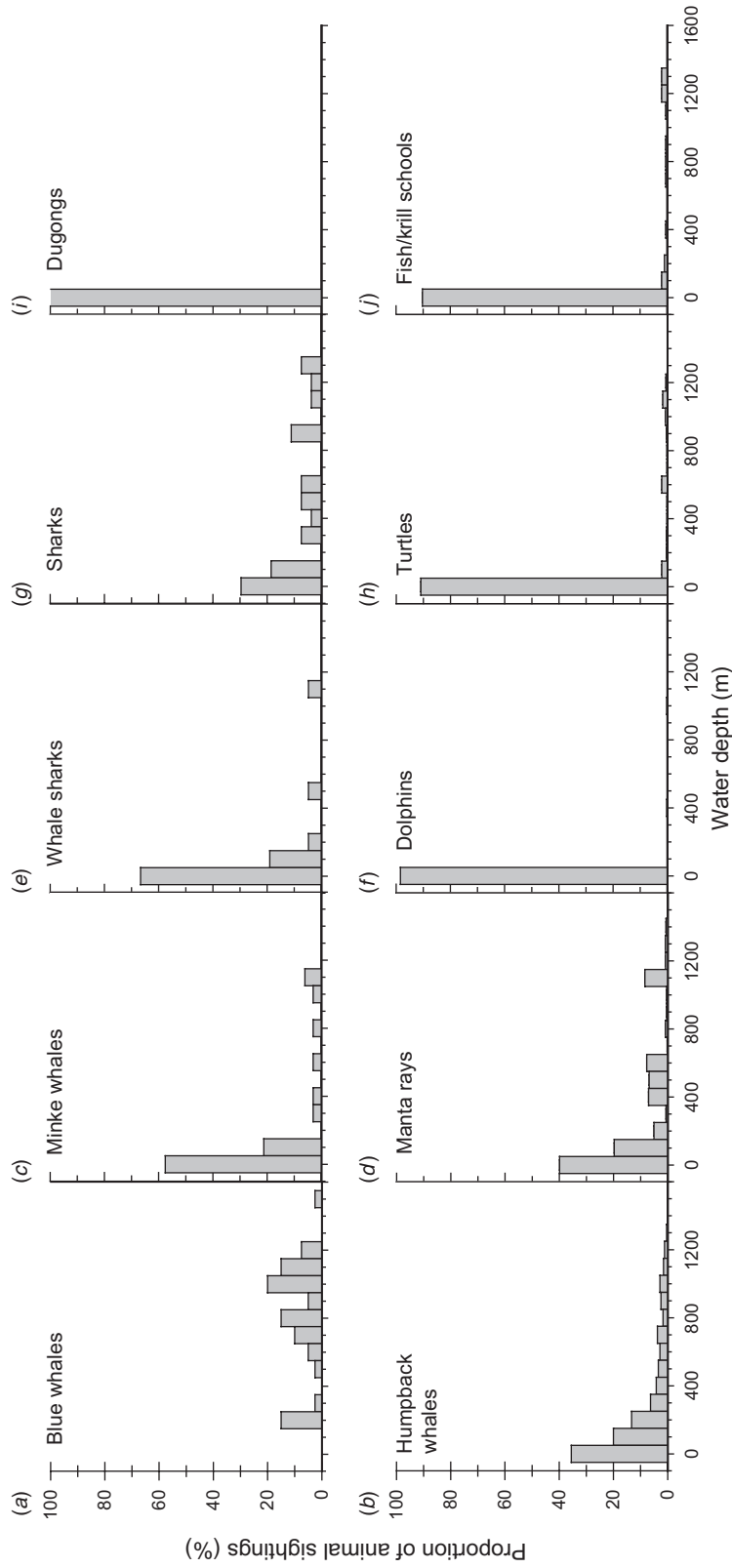


Fig. 7. Histograms showing the proportions of (a) blue whales, (b) humpback whales, (c) minke whales, (d) manta rays, (e) whale sharks, (f) dolphins, (g) sharks, (h) turtles, (i) dugongs and (j) fish/krill schools in relation to water depth.

(*Orcinus orca*) have been known to target krill feeders such as baleen whales as calves or juveniles, when in their high latitude breeding grounds (rather than in their feeding grounds), as evidenced by flesh wounds that resemble the teeth marks of killer whales (Chittleborough 1965; Mehta *et al.* submitted).

If the patterns we observed in the distribution of krill feeders are related to increased abundance of prey, we might expect to see a greater incidence of krill schools in areas with deeper water, yet most of the schools observed in the aerial surveys were sighted in shallow areas (Fig. 4e). Consequently, we can assume that either krill feeders have a foraging advantage in deeper water, or that insufficient data were collected to understand the underlying mechanism. For instance, the observed patterns in krill/fish school distributions may be an artefact of clumping fish/krill into the same taxonomic category or may relate to observer bias issues of omission (i.e. not seeing krill schools in deeper waters as a result of reduced visibility).

The primary and secondary sources of productivity exploited by feeding guilds such as fish/cephalopod and invertebrate/macroalgae feeders were likely to have been influenced by a complex suite of other factors, given that we found a general pattern of weak correspondence between their distributions and the surrounding oceanography and bathymetry. Bathymetry gradient was weakly related to the relative biomass of invertebrate/macroalgae feeders, with these species being more abundant where there was a steep change in depth contours. Such slopes may provide a more suitable habitat for macroalgae and associated benthic fauna with appropriate light, nutrient and dispersal enhancement mechanisms (Kendrick *et al.* 1998). Thus, our results provide little evidence to reject the hypothesis of Gende and Sigler (2006) that the distribution of species feeding on lower trophic-level prey species were not more closely correlated with variables such as SST and Chl-*a* than the distributions of higher trophic-level species (Gende and Sigler 2006).

The patterns in relative biomass of fish/cephalopod feeders were explained to some extent by SST, possibly indicating that warmer currents provide the conditions necessary for the prey species of sharks and dolphins. Similar patterns in distributions of predatory fishes such as tuna have been observed with increasing SST or higher SST ranges (Myers and Hick 1990; Schick *et al.* 2004). We observed peaks in SST in the Ningaloo region around April 2001 and March 2002. This reflects the gradual water surface heating as a result of high summer temperatures from November through to March and an absence or diminished flow of the Ningaloo Current as a result of changes in seasonal wind and weather patterns (Woo *et al.* 2006a).

Krill feeders such as humpback whales were present at Ningaloo during the peaks in Chl-*a* in both 2000 and 2001, yet despite their high sighting occurrence, it is likely that little foraging was occurring during their migration north to warmer waters for calving around July–August and the subsequent return south to the Antarctic in September–October (Chittleborough 1965; Jenner *et al.* 2001; Jenner and Jenner 2002). As such, the lack of association with any oceanographic variables we examined was expected. Other krill feeders such as whale sharks were observed in low numbers, but appeared consistently towards the end of summer (April–May) when ocean productivity was highest. This periodicity likely reflects the availability of major prey items such as the tropical krill, *Pseudeuphausia latifrons*, although

krill distributions may have little direct association with ocean surface properties (Wilson *et al.* 2002, 2003).

Conclusion

Our study illustrates some of the difficulties involved in predicting habitat associations or trophic distributions of marine megafauna from aerial counts and remotely sensed data alone. The prediction of spatio-temporal animal distributions relies on information on the behaviour of individuals in relation to their surrounding environment at the time of the survey, in addition to information on migration patterns, diet and relative habitat selection (e.g. dugongs and seagrass beds; sharks and reefs). Resolving issues associated with food web interactions between taxa and environmental limitations of prey items is important when attempting to understand the expected degree of correlation between trophic groups and biophysical processes. To help further identify mechanisms dictating spatial and temporal patterns in marine megafauna distributions, we require: (1) oceanographic data with higher spatial and temporal resolution, and (2) longer-term sampling of specific species incorporating behavioural information about their habitat use and feeding habits.

Acknowledgements

We are grateful to Woodside Energy Ltd, for authorising the use of the aerial survey data originally collected for the WA-271-P Field Development Environmental Impact Statement. We thank the Australian Institute of Marine Science for providing the Milyering weather station data, NASA Goddard Space Flight Center for the remotely sensed ocean colour and SST data, AVISO for altimetry data and National Oceans Office of Australia for bathymetry data. We thank three anonymous reviewers for helpful comments to improve the manuscript.

References

- Agenbag, J. J., Richardson, A. J., Demarcq, H., Freon, P., Weeks, S., and Shillington, F. A. (2003). Estimating environmental preferences of South African pelagic fish species using catch size and remote sensing data. *Progress in Oceanography* **59**, 275–300. doi:10.1016/J.POCEAN.2003.07.004
- Ainley, D. G., Speara, L. B., Tynanb, C. T., Barthe, J. A., Piercec, S. D., Fordd, R. G., and Cowles, T. J. (2005). Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. *Deep-Sea Research. Part II, Topical Studies in Oceanography* **52**, 123–143. doi:10.1016/J.DSR2.2004.08.016
- Akaike, H. (1973). Information theory as an extension of the maximum likelihood principle. In 'Second International Symposium on Information Theory'. (Eds B. N. Petrov and F. Csaki.) pp. 267–281. (Akademiai Kiado: Budapest.)
- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**, 716–723. doi:10.1109/TAC.1974.1100705
- Anderson, D. R., and Burnham, K. P. (2002). Avoiding pitfalls when using Information-Theoretic methods. *The Journal of Wildlife Management* **66**, 912–918. doi:10.2307/3803155
- Blanco, C., Raduan, M. A., and Raga, J. A. (2006). Diet of Risso's dolphin (*Grampus griseus*) in the western Mediterranean Sea. *Scientia Marina* **70**, 407–411.
- Bradshaw, J. A., Higgins, J., Michael, K., Wotherspoon, S. J., and Hindell, M. A. (2004). At-sea distribution of female southern elephant seals relative to variation in ocean surface properties. *ICES Journal of Marine Science* **61**, 1014–1027. doi:10.1016/J.ICESJMS.2004.07.012

- Burnham, K. P., and Anderson, D. R. (2001). Kullback–Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* **28**, 111–119. doi:10.1071/WR99107
- CALM (2005) Management plan for the Ningaloo Marine Park and Muiron Islands marine management area 2005–2015. Department of Conservation and Land Management, Management Plan Number 52, Perth, Western Australia.
- Caputi, N., Fletcher, W. J., Pearce, A. F., and Chubb, L. J. V. (1996). Effects of the Leeuwin Current on the recruitment of fish and invertebrates along the Western Australian coast. *Marine and Freshwater Research* **47**, 147–155. doi:10.1071/MF9960147
- Chaloupka, M., and Osmond, M. (1999). Spatial and seasonal distribution of Humpback whales in the Great Barrier Reef region. *American Fisheries Society Symposium* **23**, 89–106.
- Chittleborough, R. G. (1965). Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Australian Journal of Marine and Freshwater Research* **16**, 33–128. doi:10.1071/MF9650033
- Cockcroft, V. G., Haschick, S. L., and Klages, N. T. W. (1993). The diet of Risso's dolphin *Grampus griseus* (Cuvier, 1812), from the east coast of South Africa. *Zeitschrift fuer Saeugetierkunde* **58**, 286–293.
- Davis, D. (1998). Whale shark tourism in Ningaloo marine park, Australia. *Anthrozoos* **11**, 5–11.
- Davis, D., Banks, S., Birtles, A., Valentine, P., and Cuthill, M. (1997). Whale sharks in Ningaloo marine park – managing tourism in an Australian marine protected area. *Tourism Management* **18**, 259–271. doi:10.1016/S0261-5177(97)00015-0
- Davis, R. W., Ortega-Ortiz, J. G., Ribic, C. A., Evans, W. E., Biggs, D. C., Ressler, P. H., Cady, R. B., Leben, R. R., Mullin, K. D., and Würsig, B. (2002). Cetacean habitat in the northern oceanic Gulf of Mexico. *Deep-sea Research. Part I, Oceanographic Research Papers* **49**, 121–142. doi:10.1016/S0967-0637(01)00035-8
- El-Sayed, S. Z. (1988). Productivity of the Southern Ocean: a closer look. *Comparative Biochemistry and Physiology* **90B**, 489–498.
- Evans, P. G. H., and Hammond, P. S. (2004). Monitoring cetaceans in European waters. *Mammal Review* **34**, 131–156. doi:10.1046/J.0305-1838.2003.00027.X
- Gales, N., McCauley, R. D., Lanyon, J., and Holley, D. (2004). Change in abundance of dugongs in Shark Bay, Ningaloo and Exmouth Gulf, Western Australia: evidence for large-scale migration. *Wildlife Research* **31**, 283–290. doi:10.1071/WR02073
- Gende, S. M., and Sigler, M. F. (2006). Persistence of forage fish 'hot spots' and its association with foraging Steller sea lions (*Eumetopias jubatus*) in southeast Alaska. *Deep-Sea Research. Part II, Topical Studies in Oceanography* **53**, 432–441. doi:10.1016/J.DSR2.2006.01.005
- Gersbach, G. H. (1999). Coastal upwelling off Western Australia. PhD Thesis, University of Western Australia, Crawley.
- Godfrey, J. S., and Ridgeway, K. R. (1985). The large-scale environment of the poleward-flowing Leeuwin Current, Western Australia: longshore steric height gradients, wind stresses and geostrophic flow. *Journal of Physical Oceanography* **15**, 481–495. doi:10.1175/1520-0485(1985)015<0481:TLSEOT>2.0.CO;2
- Guinet, C., Dubroca, L., Lea, M. A., Goldsworthy, S., Cherel, Y., Duhamel, G., Bonadonna, F., and Donnay, J. P. (2001). Spatial distribution of the foraging activity of Antarctic fur seal *Arctocephalus gazella* females in relation to oceanographic factors: a scale-dependent approach using geographic information systems. *Marine Ecology Progress Series* **219**, 251–264.
- Hanson, C. E., Pattiaratchi, C., and Waite, A. M. (2005). Continental shelf dynamics off the Gascoyne region, Western Australia: Physical and chemical controls on phytoplankton biomass and productivity. *Continental Shelf Research* **25**, 1561–1582. doi:10.1016/J.CSR.2005.04.003
- Hays, G. C., Houghton, J. D. R., and Myers, E. H. (2004). Endangered species: pan-Atlantic leatherback turtle movements. *Nature* **429**, 522. doi:10.1038/429522A
- Heithaus, M. R. (2001). The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. *Environmental Biology of Fishes* **61**, 25–36. doi:10.1023/A:1011021210685
- Horne, J. K., and Schneider, D. C. (1994). Lack of spatial coherence of predators with prey – a bioenergetic explanation for Atlantic cod feeding on capelin. *Journal of Fish Biology* **45**, 191–207.
- Jaquet, N., and Whitehead, H. (1996). Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. *Marine Ecology Progress Series* **135**, 1–9.
- Jenner, C., and Jenner, M. (2002). 'Humpback Whale and Mega Fauna Survey 2000/2001 Report North West Cape Western Australia.' (Centre for Whale Research (Western Australia) Inc.: Fremantle.)
- Jenner, K. C. S., Jenner, M.-N. M., and McCabe, K. A. (2001). Geographic and temporal movements of humpback whales in Western Australian waters. *Australian Petroleum Production and Exploration Association (APPEA) Journal* **41**, 749–765.
- Kasamatsu, F., Ensor, P., Joyce, G. G., and Kimura, N. (2000). Distribution of minke whales in the Bellingshausen and Amundsen Seas (60 degrees W–120 degrees W), with special reference to environmental/physiographic variables. *Fisheries Oceanography* **9**, 214–223. doi:10.1046/J.1365-2419.2000.00137.X
- Kendrick, G. A., Langtry, S., Fitzpatrick, J., Griffiths, R., and Jacoby, C. A. (1998). Benthic microalgae and nutrient dynamics in wave-disturbed environments in Marmion Lagoon, Western Australia, compared with less disturbed mesocosms. *Journal of Experimental Marine Biology and Ecology* **228**, 83–105. doi:10.1016/S0022-0981(98)00011-2
- Kideys, A. E., Kovalev, A. V., Shulman, G., Gordina, A., and Bingel, F. (2000). A review of zooplankton investigations of the Black Sea over the last decade. *Journal of Marine Systems* **24**, 355–371. doi:10.1016/S0924-7963(99)00095-0
- Kohler, N., Casey, J. G., and Turner, P. A. (1996). 'Length–Length and Length–Weight Relationships for 13 Shark Species from the Western North Atlantic.' National Oceanic and Atmospheric Administration (NOAA) Technical Memorandum NMFS-NE-110. (NOAA: Washington, DC.)
- Lanyon, J. M., and Marsh, H. (1995). Digesta passage times in the dugong. *Australian Journal of Zoology* **43**, 119–127. doi:10.1071/ZO9950119
- Lebreton, J. D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67–118. doi:10.2307/2937171
- Limpus, C. J., Carter, D., and Hamann, M. (2001). The Green Turtle, *Chelonia mydas*, in Queensland, Australia: the Bramble Cay Rookery in the 1979–1980 Breeding Season. *Chelonian Conservation and Biology* **4**, 34–46.
- Littaye, A., Gannier, A., Laran, S., and Wilson, J. P. F. (2004). The relationship between summer aggregation of fin whales and satellite-derived environmental conditions in the northwestern Mediterranean Sea. *Remote Sensing of Environment* **90**, 44–52. doi:10.1016/J.RSE.2003.11.017
- Marsh, H., Harris, A. N. M., and Lawler, I. R. (1997). The Sustainability of Indigenous Dugong Fishery in Torres Strait, Australia/Papua New Guinea. *Conservation Biology* **11**, 1375–1387. doi:10.1046/J.1523-1739.1997.95309.X
- Marsh, H., and Sinclair, F. (1989). An experimental evaluation of dugong and sea turtle aerial survey techniques. *Australian Wildlife Research* **16**, 639–650. doi:10.1071/WR9890639
- Mate, B. R., Nieukirk, S. L., and Kraus, S. D. (1997). Satellite-monitored movements of the northern right whale. *Journal of Wildlife Management* **61**, 1393–1405. doi:10.2307/3802143
- Mehta, A. V., Allen, J., Constantine, R., Garrigue, C., Gill, P., Jann, B., Jenner, C., Marx, M., Matkin, C., Mattila, D. K., Minton, G., Mizroch, S. A., Olavarria, C., Robbins, J., Russel, K. G., Seton, R. E., Steiger, G. H., Vikingsson, G. A., Wade, P. R., Witteveen, B. H., and

- Clapham, P. J. (in press). Baleen whales are not important as prey for killer whales *Orcinus orca* in high latitudes. *Marine Ecology Progress Series*.
- Mennis, J., Tomlin, C. D., and Viger, R. (2005). Cubic map algebra functions for spatio-temporal analysis. *Cartography and Geographic Information Science* **32**, 17–32. doi:10.1559/1523040053270765
- Myers, D. G., and Hick, P. T. (1990). An application of satellite-derived sea-surface temperature data to the Australian fishing industry in near real-time. *International Journal of Remote Sensing* **11**, 2103–2112.
- Pai, M. V., Nandakumar, G., and Telang, K. Y. (1983). On a whale shark, *Rhincodon typus* Smith landed off Karwar, Karnataka. *Indian Journal of Fisheries* **30**, 157–160.
- Pauly, D., Trites, A. W., Capuli, E., and Christensen, V. (1998). Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* **55**, 467–481. doi:10.1006/JMSC.1997.0280
- Piatt, J. F., Wetzel, J., Bell, K., DeGange, A. R., Balogh, G. R., Drew, G. S., Geernaert, T., Ladd, C., and Byrd, G. V. (2006). Predictable hotspots and foraging habitat of the endangered short-tailed albatross (*Phoebastria albatrus*) in the North Pacific: Implications for conservation. *Deep-Sea Research. Part II, Topical Studies in Oceanography* **53**, 387–398. doi:10.1016/J.DSR2.2006.01.008
- Plotkin, P. T. (1995). 'National Marine Fisheries Service and U.S. Fish and Wildlife Service Status Reviews for Turtles Listed under the Endangered Species Act of 1973.' (National Marine Fisheries Service: Silver Spring, MA.)
- Polovina, J. J., Balazs, G. H., Howell, E. A., Parker, D. M., Seki, M. P., and Dutton, P. H. (2004). Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fisheries Oceanography* **13**, 36–51. doi:10.1046/J.1365-2419.2003.00270.X
- Preen, A. R., Marsh, H., Lawler, I. R., Prince, R. I. T., and Shepherd, R. (1997). Distribution and abundance of dugongs, turtles, dolphins and other megafauna in Shark Bay, Ningaloo Reef and Exmouth Gulf, Western Australia. *Wildlife Research* **24**, 185–208. doi:10.1071/WR95078
- Prince, R. I. T. (1994). Update: sea turtles in Western Australia. *Marine Turtle Newsletter* **67**, 5–6.
- R Development Core Team (2004). 'R: A Language and Environment for Statistical Computing.' (R Foundation for Statistical Computing: Vienna, Austria.)
- Schick, R. S., Goldstein, J., and Lutcavage, M. E. (2004). Bluefin tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994–96). *Fisheries Oceanography* **13**, 225–238. doi:10.1111/J.1365-2419.2004.00290.X
- Simpfendorfer, C. A., Goodreid, A. B., and McAuley, R. B. (2001). Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. *Environmental Biology of Fishes* **61**, 37–46. doi:10.1023/A:1011021710183
- Spain, A. V., and Heinsohn, G. E. (1975). Size and weight allometry in a north Queensland population of *Dugong dugon* (Muller) (Mammalia: Sirenia). *Australian Journal of Zoology* **23**, 159–168. doi:10.1071/ZO9750159
- Spalding, M. D., Ravilious, C., and Green, E. P. (2001). 'World Atlas of Coral Reefs.' (University of California Press: Berkeley.)
- Stevens, J. D., and Lyle, J. M. (1989). Biology of three Hammerhead sharks (*Eusphyra blochii*, *Sphyrna mokarran* and *S. lewini*) from Northern Australia. *Australian Journal of Marine and Freshwater Research* **40**, 129–146. doi:10.1071/MF9890129
- Stevens, J. D., and McLoughlin, K. J. (1991). Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. *Australian Journal of Marine and Freshwater Research* **42**, 151–199. doi:10.1071/MF9910151
- Sugimoto, T., and Tadokoro, K. (1998). Interdecadal variations of plankton biomass and physical environment in the North Pacific. *Fisheries Oceanography* **7**, 289–299. doi:10.1046/J.1365-2419.1998.00070.X
- Tamura, T., and Ohsumi, S. (2000). 'Regional Assessments of Prey Consumption by Marine Cetaceans in the World.' International Whaling Commission document SC/52/E6. (International Whaling Commission: Cambridge, UK.)
- Taylor, G. (1994). 'Whale Sharks: the Giants of Ningaloo Reef.' (Angus and Robertson: Sydney.)
- Taylor, G., and Grigg, G. (1991). 'Whale Sharks of Ningaloo Reef.' (Australian National Parks and Wildlife Service: Canberra.)
- Taylor, J. G., and Pearce, A. F. (1999). Ningaloo Reef currents: implications for coral spawn dispersal, zooplankton and whale shark abundance. *Journal of the Royal Society of Western Australia* **82**, 57–65.
- Uchida, S., Toda, M., Kamei, Y., and Teruya, H. (2000). The husbandry of 16 whale sharks *Rhincodon typus*, from 1980 to 1998 at the Okinawa expo aquarium. In 'American Elasmobranch Society 16th Annual Meeting, June 14–20, 2000'. La Paz, B.C.S., México.
- Wilson, S. G., Meekan, M. G., Carleton, J. H., Stewart, T. C., and Knott, B. (2003). Distribution, abundance and reproductive biology of *Pseudophausia latifrons* and other euphausiids on the southern North West Shelf, Western Australia. *Marine Biology* **142**, 369–379.
- Wilson, S. G., Pauly, T., and Meekan, M. G. (2002). Distribution of zooplankton inferred from hydroacoustic backscatter data in coastal waters off Ningaloo Reef, Western Australia. *Marine and Freshwater Research* **53**, 1005–1015. doi:10.1071/MF01229
- Wilson, S. G., Polovina, J. J., Stewart, B. S., and Meekan, M. G. (2006). Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. *Marine Biology* **148**, 1157–1166. doi:10.1007/S00227-005-0153-8
- Wilson, S. G., Taylor, J. G., and Pearce, A. F. (2001). The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Niño/Southern Oscillation. *Environmental Biology of Fishes* **61**, 1–11. doi:10.1023/A:1011069914753
- Wintner, S. P., and Dudley, S. F. J. (2000). Age and growth estimates for the tiger shark, *Galeocerdo cuvier*, from the east coast of South Africa. *Marine and Freshwater Research* **51**, 43–53. doi:10.1071/MF99077
- Woo, M., Pattiaratchi, C., and Schroeder, W. (2006a). Dynamics of the Ningaloo Current off Point Cloates Western Australia. *Marine and Freshwater Research* **57**, 291–301. doi:10.1071/MF05106
- Woo, M., Pattiaratchi, C., and Schroeder, W. (2006b). Summer surface circulation along the Gascoyne continental shelf, Western Australia. *Continental Shelf Research* **26**, 132–152. doi:10.1016/J.CSR.2005.07.007
- Woodside (2003). 'WA-271-P Field Development, Draft Environmental Impact Statement and WA-271-P Field Development, Final Environmental Impact Statement, July 2003.' Summary available at <http://www.woodside.com.au/NR/rdonlyres/B05E20B7-6D17-449F-B643-2DCA8E0296A2/3663/ExecutiveSummary.pdf> [accessed 18 June 2007].

Manuscript received 8 November 2006, accepted 22 May 2007