Associations between oceanographic processes and humpback whale entanglement in Southeast Queensland shark-control nets

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by

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Abstract

East Australian humpback whales undertake lengthy annual migrations, which require sophisticated navigation abilities. These are likely influenced by the interplay between spatial memory and responses to contemporaneous environmental cues, such as water temperature and ocean currents. The physical oceanography of the Australian east coast is dominated by the East Australian Current (EAC). The EAC's inner boundary is characterised by a sharp temperature gradient, which may serve as a navigational tool for migrating humpbacks. Humpback whales encounter numerous anthropogenic threats along their migratory route, including entanglement in shark-control nets. This study provides a quantitative spatio-temporal analysis of the influence of the EAC on the probability of entanglements in shark-control nets. We use satellite-derived sea-surface temperature (SST), an ocean model, and humpback whale entanglement data from the Queensland Shark Control Program, focusing on entanglements in Southeast Queensland since 2001. We present novel algorithms for detecting the EAC edge and core via Principal Components Analyses (PCA). We investigate correlations between the probability of humpback entanglement and the position of the EAC's edge and core, the maximum environmental gradient (structure) of the edge and core as determined by PCA results, in addition to SST at the shark-control net. We find that likelihood of entanglement increases when the EAC edge is less structured and closer to shore in the vicinity of the corresponding net, and that the first PC of a PCA designed to capture ocean structure explains relatively large amounts of variance. We also found an interaction indicating that more oceanic structure beyond the EAC edge lessens the influence of the edge structure on entanglement probability. Our results support the emerging idea that humpback whales use the edge of the EAC, as a navigation tool. Our findings can improve predictive capacity of future entanglements, and inform the monitoring of shark-control nets.

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of the EAC core relative to the locations of the five-shark-control nets (plotted as filled black circles) were identified as the cell containing the maximum environmental value along an east-west transect between 153.7˚E – 154.6˚E (solid vertical lines) at the latitude of each net location (dotted horizontal lines). Dashed line in all images represents 200-m depth contour.

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Abbreviations and acronyms

AVHRR – Advanced very high-resolution radiometer

BODAS – BlueLink Ocean Data Assimilation System

BRAN3p5 – The Bluelink ReANalysis Version 3.5

E1 – East Australia sub-population of humpback whales

E2 – New Caledonia sub-population of humpback whales

E3 – Tonga sub-population of humpback whales

EAC – East Australian Current

GHRSST – Group for High Resolution Sea Surface Temperature

GLM – Generalised linear model

GLMM – Generalised linear mixed-effects model

IUCN – International Union for Conservation of Nature

IWC – International Whaling Commission

KZNSCP – KwaZulu-Natal Shark Control Program

MUR SST – Merged ultra-high resolution sea-surface temperature

NASA – National Aeronautics and Space Administration

NOAA – National Oceanographic and Atmospheric Administration

NSW – New South Wales

NSW SMP – New South Wales Shark Meshing Program

OFAM3 – Ocean Forecast Australia Model (Version 3)

PCA – Principal components analysis

PC1 – First principle component

PHA – Polyhydroxyalkanoates

QSCP – Queensland Shark Control Program

QLD – Queensland

RSEC – Remote Sensing in Ecology and Conservation

SEQ – Southeast Queensland

SSH – Sea-surface height

SST – Sea-surface temperature

VCUR – Meridional (longitudinal) current velocity

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Author's declaration

This thesis has not been submitted, either in whole or in part, for a degree at this or any other institution. The author has read the university's rules and requirements relating to the awarding of an honours degree and to the thesis, and certify they have complied with these.

The work presented in this thesis was conducted by the author, under the supervision of Dr. Kylie Scales, Assoc. Prof. David Schoeman, and Carme Piza-Roca. Relevant conferences, workshops and events were regularly attended, at which work was often presented.

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- Poster presentation to the National Science Week with Dr Karl event, The University of the Sunshine Coast, Sippy Downs, Australia. August 2018. *"A current affair: Humpback whale entanglement in QLD shark nets".*

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current affair: humpback whale entanglement in Southeast Queensland shark-control nets".

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Signed:

Jessica A. Bolin

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Chapter I: General prelude

Rationale:

East Australian humpback whales migrate along the Australian eastern seaboard each year, from their Antarctic feeding grounds to their tropical breeding grounds. Humpback whales face numerous anthropogenic threats along their migratory route, including entanglement in shark-control nets.

The oceanographic processes influencing the likelihood of humpback whale entanglements in shark-control nets are poorly understood. To further understand the mechanisms underpinning their navigation, and to improve predictive capacity of future entanglements, it is important to identify the effect on humpback entanglements of these oceanographic processes, including patterns of sea-surface temperature and ocean currents.

The major aims of this thesis are:

- to investigate associations between remotely sensed oceanographic data and the likelihood of humpback whale entanglement in Queensland shark-control nets.
- to develop a quantitative method for delineating the inner edge of the East Australian Current.
- to elucidate the association between the position of the inshore edge of the East Australian Current and the likelihood of humpback whale entanglements in Queensland shark-control nets.
- to further understand the finer-scale mechanisms of humpback whale navigation.

Structure:

This thesis has three components:

1. General Prelude (**Chapter I**);

2. Literature Review (**Chapter II– worth 15% of total honours grade**); and

3. Manuscript (**Chapter III – worth 60% of total honours grade**). This will be submitted to Remote Sensing in Ecology and Conservation (RSEC). See Appendix 1 for author guidelines, and Appendix 2 for the required cover letter at submission.

Chapter II: Literature review

Humpback whale migration ecology and interactions with oceanographic processes: a review

1.1 Humpback whale ecology

Baleen whales (*Mysticetes*), a taxon comprising 11 species of highly mobile, migratory, wide-ranging and intellectually complex marine cetaceans (Thomas et al., 2016), are characterised by the presence of baleen plates in their mouths, which act as a filtration system to strain prey from large quantities of seawater (Clapham et al., 1999). Whilst migratory patterns vary between species and local environmental conditions, some populations have recently been found to remain resident in a particular area instead of migrating, depending on biophysical ocean conditions and prey availability (Panigada et al., 2017, Scales et al., 2017). The humpback whale, *Megaptera novaeangliae*, exhibits a near-cosmopolitan distribution across the open ocean, and most populations migrate up to 10 000 km, annually, between summer foraging areas in temperate or polar waters, and winter breeding areas in shallow, tropical waters (Baker et al., 1990). During their migrations, they link different ecosystems and cross international boundaries (Maxwell et al., 2013). Humpback whales are separated into subpopulations, depending on their geographic range. Populations in the Northern Hemisphere are separated by the American and Eurasian landmasses, and individuals from common breeding grounds show strong site fidelity to their distinct foraging grounds (Schmitt et al., 2016).

The primary driver of migration for humpbacks is calf development and survival (Derville et al., 2018). Calves are born with very little blubber, and would be unlikely to survive the cold, if born in their polar foraging grounds, thus requiring mothers to migrate to warm, tropical waters to give birth (Rasmussen et al., 2007). Within the Southern Hemisphere, humpbacks segregate into seven distinct subpopulations or breeding stocks (named A to G; or I to VII) when they undertake their

annual migrations, because their breeding areas are distributed in shallow waters around oceanic islands and coastal continental shelves (Schmitt et al., 2016, Thomas et al., 2016). Their high-latitude feeding grounds in the Southern Ocean are circumpolar, and this absence of continental barriers hindering movement allows humpbacks from different breeding populations to interact. As a result, various studies have found low levels of genetic differentiation between geographically close populations (Baker et al., 1990, Rosenbaum et al., 2009, Schmitt et al., 2016).

Whilst humpback whales, globally, are red-listed as least concern on the International Union for Conservation of Nature (IUCN) Red List, due to current estimates of population size exceeding 110 000 individuals (Reilly et al., 2008, Thomas et al., 2016), the Oceania subpopulation (subpopulations E and F) is separately classified as endangered (Reilly et al., 2008, Bejder et al., 2016). Nevertheless, there is a general consensus that a new assessment of their status is needed, due to the strong rate of population recovery exhibited by this species, and a potential redistribution of animals as they seek more populous mating grounds (Thomas et al., 2016). Also, the potential immigration and emigration of individuals between neighbouring subpopulations is an emerging issue that should be taken into account for reassessment, as seen in a recent study in New Zealand (Franklin et al., 2014, Gibbs et al., 2017, Andrews-Goff et al., 2018). While there is no classified subpopulation for New Zealand, numbers of recent sightings of humpbacks are increasing around the country, most likely due to immigrants from the East Australian breeding stock (Gibbs et al., 2017; Andrews-Goff et al., 2018).

The International Whaling Commission (IWC) has subdivided breeding stock E, or Group V, into three 'substocks', depending on their breeding areas: E1 (eastern Australia), E2 (New Caledonia) and E3 (Tonga) (Burns et al., 2014). Members of substock E1 use the Australian eastern seaboard as their migratory corridor. Pre-whaling estimates of population size were between 16 000 – 23 000 individuals (Schmitt et al., 2016), but their numbers reduced to as few as a 100 individuals in 1963, when whaling ceased (Chittleborough, 1965, Paterson et al., 1994). The E1 substock is now experiencing a population recovery of 10.9% per year, which is among the highest growth rates for any mammalian population (Bruce et al., 2014). Since the 1980s, population estimates were

derived from visual surveys of migrating whales (Noad et al., 2011). In an attempt to gain a more accurate indication of E1 population size, Noad et al. (2017) used acoustic surveys of whale song to measure whale abundance. However, the spatial range over which humpback whales communicate acoustically is poorly understood, and only males sing on their migration and, even then, they do so periodically. It was therefore determined that acoustic surveys are a poor measure of total abundance (Noad et al., 2017). Consequently visual surveys were reinstituted, indicating a current population estimate of maximum absolute abundance of 27 851 individuals in the E1 humpback substock (Noad et al., 2017). This substock is listed as vulnerable under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) (*Environment Protection and Biodiversity Conservation Act 1999,* Cth).

1.2 Migration

Humpbacks' major life functions require specific habitats, so E1 whales migrate between nutrient-rich, cold, feeding grounds in the Southern Ocean, and warm, shallow breeding grounds in the Great Barrier Reef. They characteristically migrate close to the shore, often passing within 10 – 30 km of the coast (Noad et al., 2011, Meynecke and Meager, 2016). It is hypothesised that calves imprint on their mother's migration pathway during their first year of life (Clapham and Mayo, 1987, Baker et al., 1990, Acevedo et al., 2006). This could explain why individual humpbacks display high natal site fidelity, returning to the same feeding and breeding grounds each year (Bruce et al., 2014). Humpbacks travel up to 5000 km (Bruce et al., 2014) to calve, demanding large energy stores to meet the energetic costs of reproduction, locomotion and maintenance (Irvine et al., 2017). Therefore, they target polar feeding grounds in Antarctica, which are highly productive and abundant in krill, which is the humpbacks' main food source (Matthews, 1937).

The exact locations of E1 humpbacks' feeding grounds are poorly known, because research into habitat use and distribution has been constrained by the inaccessibility of the Southern Ocean, and limitations in satellite-tracking technology (Riekkola et al., 2018). The few studies that have been

conducted on the migratory movements of individual humpbacks within the broader Oceania subpopulation used discovery tags and similar methods that provided only endpoint locations (Chittleborough, 1959, Dawbin, 1959, Robbins et al., 2011, Steel et al., 2018), omitting detailed movement information between habitats or sites. The general consensus is that their feeding grounds can span ~4 500 km in the Southern Ocean (Riekkola et al., 2018); however, the majority of foraging ground studies were conducted around the Antarctic Peninsula (Thiele et al., 2004, Friedlaender et al., 2006). Recent satellite tagging studies are starting to provide more detailed insights into preferred foraging locations of E1 humpbacks in the Antarctic. Based on the satellite tracking of 26 humpbacks, the Balleny Islands, a highly productive island chain off Eastern Antarctica, have been identified as a potentially important summer feeding area for E1 individuals (Franklin et al., 2012, Constantine et al., 2014). Moreover, Antarctic foraging habitat has been recently associated with the marginal ice zone (Andrews-Goff et al., 2018). However, there is a clear need for further studies into the locations of E1 humpback foraging grounds, particularly because few studies exist on tagging E1 humpbacks for the duration of their migratory cycle (Gales et al., 2010).

Similarly, the locations of the exact breeding areas of E1 humpbacks is also limited, with most studies suggesting that they disperse throughout the Great Barrier Reef and into the Coral Sea (Burns et al., 2014). E1 whales spend up to two months in the northern quarter of their range during the Austral winter breeding season (Burns et al., 2014). Generally, the species is rarely observed travelling in large groups; instead, a humpback calf will travel with its mother and sometimes an unrelated adult 'escort' whale on its first southern migration (Bruce et al., 2014). The mother is the primary provider of food, care, and life-skills teaching (Bruce et al., 2014).

While knowledge gaps exist regarding the migratory phases of humpback whale life cycles, especially for calves on their first southern migration, mother-calf pairs have been found to show a preference for resting and socialising in warm and shallow waters, particularly in protected bays. They can remain here for days or weeks (Bruce et al., 2014, Burns et al., 2014), in the relative protection from harsh environmental conditions, conspecifics and harassment from predators

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(Bruce et al., 2014). These areas include Hervey Bay (Franklin et al., 2011), the Gold Coast Bay (Meynecke and Meager, 2016), and Jervis Bay (Bruce et al., 2014).

Migration is an energetically costly exercise, and the success of migration is largely dependent on sufficient energy reserves to fuel locomotion (Owen et al., 2015). A recent study on humpback migration found that pregnant females reached a sampling site in the Great Barrier Reef later, and carried larger lipid stores, than humpbacks that arrived earlier, which reflects variation in residence times at their foraging grounds (Irvine et al., 2017). Furthermore, the size of the female plays a role in migratory success, because smaller whales do not accumulate as much energy and are more vulnerable to nutritional stress (Irvine et al., 2017).

Until recently, it was accepted that whales mostly relied on Antarctic-derived energy reserves during their migration (Eisenmann et al., 2017), and fed rarely whilst migrating. To feed whilst migrating trades off costs associated with stopping to feed on available prey, which is a consequence of environmental heterogeneity, against benefits of reaching nutrient-rich feeding grounds with an abundance of high-quality prey (Owen et al., 2017). Humpbacks are generalist feeders, and they target various prey types from zooplankton to schooling baitfish, even switching between krill and fish as conditions vary (Cade et al., 2016). Therefore, changes in prey type along the migration route can influence the extent to which whales feed opportunistically (Owen et al., 2017). Humpbacks generally do not feed during their northern migrations, because conditions are not favourable for krill, particularly towards their tropical breeding grounds (Owen et al., 2017). However, recent studies have provided biochemical, satellite-tracking, and observational evidence of humpbacks feeding opportunistically in temperate waters during their southern migration, before reaching their foraging grounds (Silva et al., 2013, Owen et al., 2015, Eisenmann et al., 2017, Owen et al., 2017, Andrews-Goff et al., 2018). For instance, Eden, in south-eastern New South Wales, has highly productive waters, with an abundance of krill (*Nyctiphanes australis*) and small baitfish species, presenting a potentially significant supplemental feeding ground for southward-migrating female and juvenile humpbacks. Indeed, some individuals spend up to 20 days in the same area before continuing their migration (Owen et al., 2015). Such localised feeding grounds

may allow whales to replenish energy reserves depleted by breeding and locomotion (Stamation et al., 2007, Owen et al., 2015, Owen et al., 2016).

On their southern migration, humpbacks have been observed using a lunge-feeding strategy, where they rapidly accelerate to engulf prey-laden water through the expansion of their oral cavity (Owen et al., 2017). Whilst the exact mechanisms underlying this process are poorly understood, it is an energetically costly exercise (Cade et al., 2016). Owen et al. (2016) found that whales lunge feed at a higher rate on krill (49 lunges/hour) compared to fish (5/hour), perhaps because krill have a higher lipid content and are slower than fish, meaning krill can replenish whale fat reserves more quickly (Owen et al., 2017). Therefore, the lipid content and speed of available prey may influence the decision of humpbacks to feed whilst migrating, because the energy expenditure to capture fish may exceed that obtained from their capture (Owen et al., 2017), particularly on their southern migration when energy reserves are already depleted.

1.3 Navigation

Whilst habitat requirements of humpback whales' foraging and breeding grounds are well known (Smith et al., 2012), the mechanisms underlying whale navigation to these areas are less understood. Nevertheless, whales are known to demonstrate well-developed navigational abilities, and it is likely that they rely on a combination of cognitive processes, such as learning and memory, as well as responses to contemporaneous environmental cues (Sequeira et al., 2018).

Humpbacks exhibit high route fidelity, following near-identical routes across open oceans, with high spatial accuracy each migratory cycle (Horton et al., 2017). During this process, they maintain near-constant headings, or direction of travel, and travel in near-straight lines (Horton et al., 2017). The primary mechanism underlying whales' high route fidelity within the oceanic environment remains contentious. The causal links between environmental navigation cues and navigational decisions can be established by integrating experimental testing with satellite tracking. But undertaking experimental studies of a large, live, mobile marine vertebrate that undertakes ocean-

scale movements covering thousands of kilometres, such as the humpback whale, is challenging (Horton et al., 2017). Nevertheless, there are various hypotheses regarding the mechanisms underpinning their broad-scale navigation (Horton et al., 2017).

Horton et al. (2011) tested individual environmental predictors, such as the position of the sun and magnetic inclination for correlation with whale headings. They found no relationship between navigational decisions for the individual predictors, which indicates that whales use a combination of factors for navigation. Some studies have since proposed that whales use a 'map and compass' framework for navigation (Horton et al., 2011, Horton et al., 2017). Magnetic inclination was found to be a significant predictor of high route fidelity among humpbacks, and is associated with orientation and navigation across taxa (Light et al., 1993). The idea is that magnetic inclination is used as a 'compass' to navigate (Wiltschko and Wiltschko, 1972), so learning a 'map' of the Earth's magnetic field enables positional identification (Putman et al., 2011, Horton et al., 2017). However, because the Earth's magnetism varies widely in the ocean, and solar navigation cannot alone explain their navigational abilities, there is now general agreement that humpbacks use a coupled system of the Earth's magnetic field and the sun's orientation, in addition to acoustics, large-scale oceanic currents, and the position of the moon and stars to navigate across vast ocean basins and maintain constant headings (Horton et al., 2011, Trudelle et al., 2016, Horton et al., 2017, Vanselow et al., 2017). Furthermore, humpbacks in New Caledonia were found to actively use seamounts when migrating, which are characterised by shallower water, relative to the surrounding deep ocean. However, the use of seamounts as navigational landmarks might have more to do with associated perturbations of the magnetic field than with shallowness of the water (Garrigue et al., 2015). It may be that the whales use a combination of ocean bathymetry, and oceanic processes such as surface currents to stay in shallower water whilst migrating. But this hypothesis remains to be explored.

A mechanistic understanding of how whales navigate at finer scales (10 – 100 km), within their migratory corridors remains poorly understood, particularly in coastal environments through which whales frequently migrate. At a regional scale, whales seem to align their headings, or direction of

travel, with local current conditions to exploit favourably directed surface currents (Trudelle et al., 2016). However, whales can deviate within their migratory corridors by 150 km (Horton et al., 2017), and the environmental drivers of this finer-scale variability is not known. Nevertheless, habitat structure may predict finer-scale movement (Sequeira et al., 2018).

Habitat structure was found to be a strong driver of movement patterns in marine megafauna globally, so humpbacks may engage in more complex movement patterns close to coasts, especially when they move close to, or over, the continental shelf, where the environment is more structurally complex than in the open ocean (Sequeira et al., 2018). For example, Dransfield et al. (2014) found that the upwelling index is positively correlated with humpback presence. Upwelling fronts are associated with enhanced primary production, and humpbacks are known to use them for foraging (Tynan et al., 2005). Furthermore, humpback whales appeared to be associated with the inshore edge of the coastal upwelling front of the Northern California Current, and in waters near the edge of the continental shelf (Dransfield et al., 2014). However, this study was done in a highly productive eastern boundary current, which is characteristic of intense upwelling (Dransfield et al., 2014), and resultant associations are believed to be driven by feeding activity rather than by navigational utility during a directional migration.

Very few studies exist on humpback whale fine-scale navigation in western boundary currents, particularly the oligotrophic East Australian Current (EAC). E1 humpbacks are unlikely to engage in complex movement patterns close to the coasts due to structural complexity, because they are heading on a north/south axis with a few resting stops. Also, they are unlikely to use fronts and upwelling features for navigation to indicate foraging grounds, because E1 humpbacks rarely engage in opportunistic feeding during their northern migration, and do so on their southern migration only in the vicinity of Eden (Owen et al., 2015).

Mother and calf pairs consistently stay close to the shoreline whilst migrating, and rest in protected, embayments on their return journeys, as evidenced by observations from Australia (Bruce et al., 2014), Madagascar (Rosenbaum et al., 2009), Ecuador (Félix and Botero-Acosta, 2011) and California (Dransfield et al., 2014), especially when waters are shallower than 50 m (Derville et al.,

2018). Visual observations have provided evidence that southward-migrating humpbacks rest in shallow water bays: Hervey Bay, Gold Coast Bay and Jervis Bay (Bruce et al., 2014, Reinke et al., 2016) as well as at a foraging stop in the vicinity of Eden (Owen et al., 2016); but it is not known what environmental cues the whales use to navigate to these areas.

2.1 Anthropogenic threats to humpback whales

Baleen whales were commercially hunted for their blubber during the 19th and 20th centuries, due to the high demand for whale oil. This led to the global depletion of whale populations, resulting in the International Whaling Commission's (IWC) ban on whaling in 1986 (Gibbs et al., 2017). Despite current legal protections, human-related mortality continues, because Norway, Iceland and Japan still engage in commercial or research whaling under objection to the IWC moratorium. Whilst many populations are now in strong recovery from exploitation, including humpback whales and southern right whales (Noad et al., 2011), others remain critically endangered, including the northern Atlantic right whale (Cooke, 2018).

Although whaling has mostly ceased, whales and their associated habitats still face myriad anthropogenic threats (Thomas et al., 2016). At the population level, incidental entanglement in fishing gear, or bycatch, and vessel strikes are the primary threats to baleen whales. This results in high mortality and the immediate removal of whales from the population (Thomas et al., 2016), as demonstrated in the eastern population of northern right whales in eastern North America. Their population recovery has been seriously impaired by ship-collision mortality, and even with the modification of shipping lanes to avoid areas of high use, only an estimated 50 individuals remain (Rolland et al., 2012, Thomas et al., 2016).

Globally, the volume of commercial shipping traffic has increased by a factor of four between 1992 and 2012 (Tournadre, 2014), with a concomitant increase in the frequency and intensity of vessel-whale strike (Thomas et al., 2016). This is especially true in coastal regions, where high maritime traffic density and major shipping routes overlap baleen whale habitat, which is a cause for

conservation concern (Peel et al., 2018). One factor driving the increasing rate of vessel strikes is the fact that modern commercial vessels are increasing in size and speed (Dransfield et al., 2014). While a vessel of any size or type can strike whales, the most severe vessel strikes are caused by ships 80 m or longer, and ships travelling 14 knots or faster. Increased shipping traffic has also resulted in an increase in anthropogenic underwater noise, which is an emerging and pervasive threat, but remains poorly understood (Chion et al., 2017).

Baleen whales have evolved to rely primarily on acoustic signals for communication, and thus communicate with low-frequency sounds that allow contact over large distances, although the exact range remains unknown (Rolland et al., 2012). The propellers and engines of large commercial ships generate low-frequency noise that overlaps the frequency band used by baleen whales. Furthermore, baleen whales actively avoid close approaches to active underwater airguns and seismic arrays, and will change their surface and diving behaviours in response to such equipment (Thomas et al., 2016, Gedamke et al., 2011). The ability of baleen whales to detect and project sound has been jeopardised by elevated anthropogenic sound levels, particularly in coastal environments (Clark et al., 2009), with several studies concluding that acoustic pollution has elicited habitat displacement, behavioural changes and changes in vocalisation patterns (Clark et al., 2009, Ellison et al., 2011, Hatch et al., 2012, Rolland et al., 2012).

Whales also must contend with bioaccumulation of pollutants, namely plastic-derived chemicals from plastic pollution, and exposure to Polyhydroxyalkanoates (PHAs), which are a byproduct of burning fossil fuels. While this has led to cancers in toothed whales, the long-term exposure of plastic-derived pollutants to mysticetes is unknown (Thomas et al., 2016). Incidental entanglement in fishing gear is also a major concern, especially for baleen whales that frequent nearshore areas and along continental shelves (Thomas et al., 2016).

2.2 Entanglements in fisheries gear

Baleen whales are vulnerable to entanglement in gear deployed by commercial, artisanal and recreational fisheries worldwide (Benjamins et al., 2012). The incidental capture of non-target species in fisheries (hereafter referred to as bycatch) is considered the most pertinent management issue affecting baleen whales (Brown et al., 2013). As defined by the IWC, entanglement of whales in fishing gear involves anthropogenic materials becoming tangled around areas of a whale's body (Benjamins et al., 2012). With the rise of global food demand in the past decades, the fisheries industry has boomed. This has resulted in a concomitant increase in bycatch, which is especially prevalent in areas where baleen whale distributions overlap with intense fishing effort (García-Godos et al., 2013). While there remain challenges in describing the global extent of whale bycatch in commercial fisheries, bycatch is a common occurrence in the western North Atlantic, Alaska and the Mediterranean, all of which are important feeding grounds for baleen whales (Mazzuca et al., 1998, Neilson et al., 2009, Groom and Coughran, 2012, Benjamins et al., 2012). Whale entanglements have been documented in gillnet, pot, longline, bottom otter, drift net and pelagic trawl fisheries (Brown et al., 2013, Volep et al., 2017). Each fishery targets different species, necessitating different gear configurations, and therefore some fisheries pose more of a risk to whales than others (Brown et al., 2013).

Bycatch often results in injury to and mortality of individuals (Benjamins et al., 2012). Lines can snag around various parts of the body, including the jaw, pectoral fins, dorsal fin, tailstock and flukes (Benjamins et al., 2012). Entanglement can cause emaciation, skin trauma, restricted movements, increased energetic demands and stress, and reduced reproductive success (Meÿer et al., 2011), all of which are a cause for conservation concern. Baleen whales are long lived, and have low reproductive rates, with several studies agreeing that entanglement limits population recovery potential (Benjamins et al., 2012, Brown et al., 2013, Volep et al., 2017), particularly for populations of the critically endangered North Atlantic right whale, where 71% of individuals have been entangled at least once in fishing gear (Johnson et al., 2005, Volep et al., 2017).

Areas of intense fishing effort are concentrated in coastal areas, which often overlap the distributions and migratory routes of baleen whale populations (Kroodsma et al., 2018), and elevated entanglement rates of humpback whales in coastal fisheries in the Atlantic and South Africa coincide with the whales' annual breeding migrations (Meÿer et al., 2011, Johnson et al., 2005). Furthermore, various studies have concluded that humpback whales are more prone to entanglement in coastal and continental shelf waters compared to the open ocean, due to the higher intensity of fishing effort (Meÿer et al., 2011, Thomas et al., 2016, Figure 1). However, this may be because most studies on humpback entanglements have been conducted in foraging or breeding areas, which overlap areas of intense fishing effort. Nevertheless, some studies of entanglements beyond foraging and breeding areas have been undertaken in Western Australia, Ecuador, and Peru (Groom and Coughran, 2012, Alava et al., 2012, García-Godos et al., 2013), but these exceptions only serve to highlight the significant gap in understanding regarding the drivers of humpback entanglements within their migratory corridors.

Humpbacks are also prone to entanglement because they often get entangled in the vertical buoy and float lines in gillnet and pot fisheries (Johnson et al., 2005, Brown et al., 2013). Gillnets are often used in coastal fisheries, are responsible for the majority of humpback whale bycatch in global commercial fisheries, and pose the greatest risk to humpback whales (Brown et al., 2013, Volep et al., 2017).
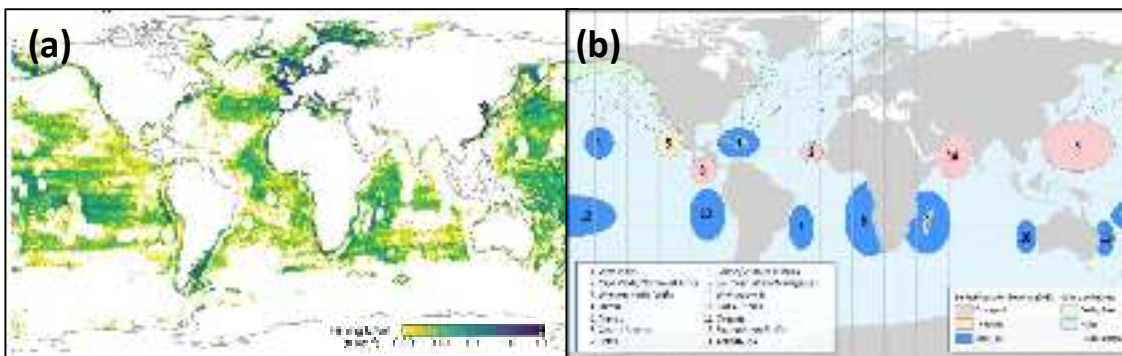
Figure 1. Humpback whale distributions overlap areas of intense fishing effort. (a) Global fishing effort (hours fished per square kilometre) in 2016 (Kroodsma et al., 2018). (b) Global humpback whale population distributions (NOAA Fisheries, 2018).

Due to gillnets' high propensity for bycatch, various bycatch-reduction strategies are currently in use. In some commercial fisheries, national and international law requires observer programs to monitor whale bycatch. However, there is a lack of information on the global extent of whale bycatch, because bycatch events may not be witnessed, and programs are not often mandated in artisanal fisheries of developing countries (Read, 2008, Brown et al., 2013). Full or periodic closures of fisheries have been successful in reducing bycatch, as is the case in the moratorium on Atlantic cod in Canada (Benjamins et al., 2012), but these restrictions have significant impacts on fishers' livelihoods (Groom et al. 2012). Recently developed satellite-derived management tools (eg. WhaleWatch) produce predictive maps of whale densities in near-real-time (Hazen et al., 2016). This can demonstrate the potential overlap between whale habitat and harmful anthropogenic activities, and managers can use this information to reduce entanglements. Other strategies include making the nets more acoustically visible to whales by braiding nets with stainless steel (passively making them more reflective to acoustic signals) or attaching acoustic alarms to gillnets to actively warn whales of the net's presence, a practice common in government-mandated shark-control programs. Unfortunately, neither of these strategies have had much success in reducing humpback whale bycatch (Groom and Coughran, 2012, Pirotta et al., 2016, Volep et al., 2017).

3.1 Shark-control programs

A variety of shark-control methods currently exist or have existed in Australia, New Zealand, South Africa, Brazil, California, Reunion Island, Hong Kong and Hawaii. These include drumlines, drone surveillance, spotter planes, visual surveys from elevated vantage points, and tag/release programs (Wetherbee et al., 1994, Meÿer et al., 2011, Reid et al., 2011, Hazin and Afonso, 2014, Engelbrecht et al., 2017). Shark barriers have recently been found to be effective (O'Connell et al., 2018) and have little environmental impact, because they extend from the surface of the water to the bottom, enclosing a beach with an impenetrable barrier. They are made of plastic or nylon

tubing, which reduces the risk of entanglement by marine animals (O'Connell et al., 2018). Western Australia uses this technique, resulting in enhanced swimmer positivity and reduced mortality of both sharks and non-target species (O'Connell et al., 2018).

However, South Africa and Australia use gillnets in large-scale shark-control programs. These nets are anchored off popular beaches to reduce resident large shark population sizes (Dudley et al., 1998, Cliff and Dudley, 2011). The Queensland Shark Control Program (QSCP), New South Wales Shark Meshing Program (NSW SMP) and KwaZulu-Natal Shark Control Program (KZNSCP) are the three current long-standing shark-control programs (Cliff and Dudley, 2011). These programs were implemented in the mid-1900s, all after a series of fatal shark attacks. Public perception of sharks was negative and little concern existed for the nets' impact on the environment (Cliff and Dudley, 2011).

The KZNSCP commenced at Durban, South Africa in 1952 (Cliff and Dudley, 2011). At the height of the program, in the 1990s, nets existed at 44 beaches, totalling 44 km of netting (Erbe et al., 2016). After the end of apartheid, public perception of the program changed and legislative pressure was placed on the program to reduce bycatch whilst enhancing swimmer safety. This has resulted in the elimination of 7 shark-control nets (Erbe et al., 2016). Furthermore, nets are lifted during the annual 'sardine run' to minimise entanglements of cetaceans (Caputo et al., 2017).

In Australia, shark-control nets are employed in state-wide programs in New South Wales (NSW) and Queensland (QLD). The NSW SMP uses drumlines and bottom-set gillnets at 51 beaches from Wollongong to Newcastle. The nets are fitted with acoustic pingers, or warning devices, to deter cetacean entanglement (Green et al., 2009). Since 1989, nets are removed in the Austral winter, when there are fewer recreational swimmers, to reduce humpback whale entanglement during their annual migration (Reid et al., 2011, Volep et al., 2017).

3.2 Queensland Shark Control Program

The Queensland Shark Control Program has used a combination of drum lines and permanent surface-set gillnets since 1962 (Cliff and Dudley, 2011, Figure 2). Nets consist of three mesh panels stitched together, with the entire structure being 186 m long and generally 6 m deep. Nets are set adjacent to the shoreline at a distance of 400 – 700 m from shore, depending on bathymetric and oceanographic features of the area (Meager and Sumpton, 2016). The structure is anchored to the ocean floor and marked at the surface using a buoy (Taylor et al., 2011). All equipment is checked by independent contractors 15 – 20 days/month (weather permitting), and is replaced with new equipment every 21 days (Taylor et al., 2011). Gillnets are a passive system, entangling anything that swims into them (Sumpton et al., 2011). Over time, the nets' high propensity for indiscriminate bycatch has resulted in public pressure to gradually reduce the number of shark nets, as has their listing by the Australian Fisheries Scientific Committee as a key threatening process (Hazin and Afonso, 2014). There are 26 nets currently in use at Mackay, Rainbow Beach, the Sunshine Coast and the Gold Coast (DAF, 2018), but all nets have been removed from Queensland Marine Protected Areas since May 2017.
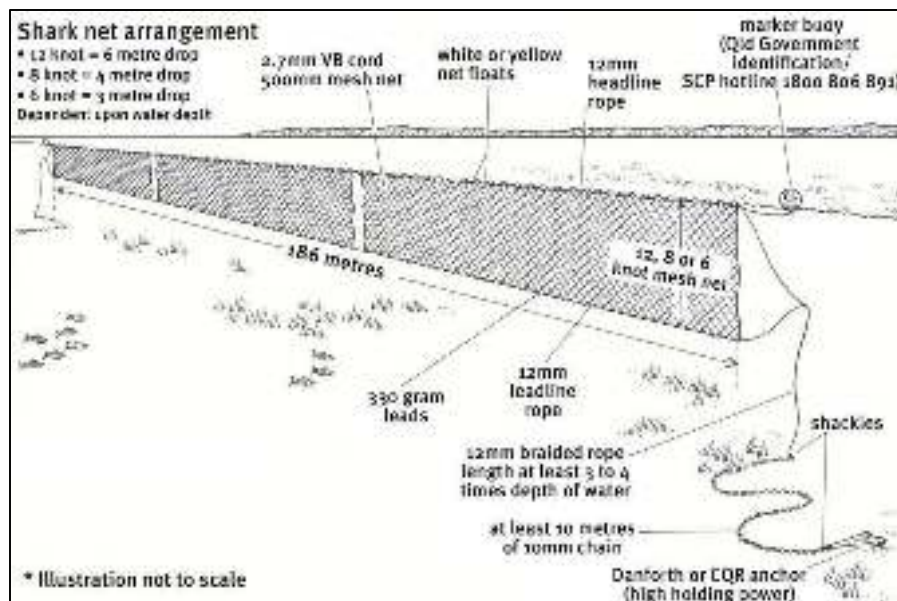
Figure 2. Diagram of Queensland Shark Control Program shark-control net (Department of Agriculture and Fisheries, 2018).

The QSCP uses various mitigation strategies to minimise bycatch. Drumlines, which are baited hooks attached to floats that are anchored to the seabed, are used instead of nets where possible, because drumlines target actively feeding sharks and reduce bycatch (Sumpton et al., 2011). Moreover, Queensland is considering trialling 'Smart drumlines', used with great success in the NSW SMP. These send a text communication to contractors when an animal is caught, enabling a swift response, thereby reducing mortality (Green et al., 2009). Where nets persist, the Marine Animal Release Team is employed to undertake the swift release of primarily cetaceans and marine mammals from nets, especially during the annual humpback migration. The QSCP have also attached permanent high-frequency dolphin pingers to nets throughout the year since 1992, and since 2011, low frequency whale alarms on nets seasonally during the humpback whale migration (DAF, 2018).

There are conflicting results from tests of the effectiveness of humpback whale alarms. While McPherson et al. (2001) found that whales should be able to hear the whale alarms based on their auditory anatomy and the ambient noise budget of the water, recent studies have concluded that migrating humpback whales show no detectable response to the QSCP pingers (Harcourt et al., 2014, Pirotta et al., 2016), suggesting that pingers do not reduce whale bycatch. This result has been attributed to the high levels of ambient noise in the coastal environment from waves, seasonal storms, boats and shipping lanes that might mask the sound of the pingers (Pirotta et al., 2016).

4. East Australian Current

The East Australian Current (EAC) is the western boundary current of the South Pacific sub-tropical gyre, and is the dominant physical oceanographic process of the Australian eastern seaboard. Its source water is from the Coral Sea, which flows from the South Equatorial Current. This is a nutrient-poor water mass, because it has spent 1-2 years flowing across the Pacific close to the equator (Suthers et al., 2011). The EAC is therefore a high-energy oligotrophic western

boundary current, carrying warm water in the core of the current poleward from the equator
(Suthers et al., 2011).

The continental shelf strongly influences the location of the EAC. The core of the EAC is centred
over the continental slope, so the continental shelf and width determines the position of the EAC
(Schaeffer et al., 2013). The current intensifies and strengthens along the coast of Southeast
Queensland and Northern New South Wales (Suthers et al., 2011). Where the continental shelf
narrows 160 – 320 km north of Sydney, the EAC bifurcates into the eastward flowing Tasman
front, forming a sharp front in velocity and temperature (Roughan and Middleton, 2004), and a
southward extending eddy field, known as the EAC extension, reaching northern Tasmania
(Suthers et al., 2011). The strength of the EAC extension has an approximate 10 – 15 year
oscillation (Hill et al., 2008). On shorter timescales, the EAC's strength and temperature range vary
seasonally, being stronger and warmer in summer, and weaker and cooler in winter (Cai, 2006).
Typically, the current is >30 km wide, up to 1.5 km deep, and flows at up to 4 knots (Suthers et al.,
2011). The annual volume of water transported is variable, and is estimated to be 5-fold greater
than the Leeuwin current on the Australian west coast (Suthers et al., 2011).

Generally, the prevailing south-easterly trade winds are upwelling-unfavourable in eastern
Australia (Thompson et al., 2011). Low-intensity coastal upwelling nevertheless occurs with the
presence of sporadic northerly winds, driving pulses of primary production (Brieva et al., 2015).
Between the cooler upwelled waters close to the coast and the warm core of the EAC, thermal
fronts are produced, and are a possible navigation tool for humpback whales (Reinke et al., 2016).

5. Oceanographic predictors of entanglement in shark-control nets

The oceanographic predictors of humpback entanglement in QSCP shark-control nets have only recently begun to be investigated. Volep et al. (2017) conducted an exploratory study of humpback whale entanglements from 2001 – 2012 in QSCP nets on the Gold Coast, representing the first study, globally, to investigate the environmental predictors of humpback entanglement in fishing gear. During this period, it was found that the highest number of humpback entanglements occurred in September each year, with a 95% greater probability of entanglements occurring during the southern migration, spanning August to November. During the southern migration, humpbacks are known to rest in the Gold Coast to conserve energy. A longer residence time would increase their likelihood of entanglement in shark-control nets. Also, entanglements were more frequent when the sea was calm, but less frequent during heavy rainfall events. However, this study also identified that further statistical analyses are required to investigate other environmental conditions, and to substantiate reported results (Volep et al., 2017).

Furthermore, Meynecke and Meager (2016) investigated environmental predictors of humpback strandings in Southeast Queensland, and identified a relationship between a higher number of strandings and strong La Niña events. While it has previously been speculated there is a link between the Southern Oscillation Index and humpback population dynamics (Meynecke and Meager, 2016), the mechanisms underpinning this relationship are not understood.

A recent link has been established between humpback whale distribution and cooler waters on the Gold Coast (Reinke et al., 2016), making this area a favourable location for humpback whales. Contrastingly, Volep et al. (2017) found no significant correlation between sea-surface temperature (SST) and incidence of entanglements in shark nets. Therefore, opposed to sea-surface temperature, humpbacks may instead use the position of the EAC as a navigation tool. In the Gold Coast Bay, the EAC meanders close to the shore (Meynecke and Meager, 2016) and as the EAC core moves closer to shore, upwelling events and slope-water intrusion can introduce cooler waters.

Meynecke and Meager (2016) also found that between 1993 and 2007, 89% of humpback whale strandings in Southeast Queensland occurred when the centre of the EAC was closer to shore than average, with a key hotspot occurring at the Gold Coast. Similarly, Volep et al. (2017) found that 72.7% of humpback entanglements in QSCP shark-control nets occurred when the centre of the EAC was west, or shoreward, of its average position. Both of these studies support the hypothesis that the position of the EAC may affect the distribution of humpback whales, particularly in the Gold Coast, where 11 shark-control nets are placed (DAF, 2018).

The inshore boundary of the EAC is characterised by sharp temperature gradients, or fronts, which are strong changes in temperature formed at the border of the warm current and cooler upwelled coastal waters (Reinke et al., 2016). The fronts generated by the EAC generally run parallel to the shore, and may serve as a navigation tool for humpbacks. Humpback whales have recently been found to associate with areas exhibiting a strong temperature gradient in the Gold Coast, indicative of coastal fronts (Reinke et al., 2016). Sensing changes in temperature and current may allow the whales to follow these features, and avoid straying too far from their migratory pathway (Reinke et al., 2016).

If the whales are using thermal gradients to navigate, they might be using the inner edge of the EAC as a navigation tool as opposed to the core of the jet, because the EAC's inner boundary is characterised by a strong temperature gradient (Reinke et al., 2016). This putative use of the edge of the EAC for navigation would mirror humpbacks' use of the southern boundary of the Antarctic Circumpolar current for navigation when crossing the Southern Ocean (Volep et al., 2017), but it remains to be tested. Nevertheless, if this were the case, the tendency of the EAC to meander inshore would cause a nearshore range compression, particularly at the Gold Coast where the continental shelf is narrow (Tran Van et al., 2015). Effectively, humpbacks following the current would be forced into the shallow coastal waters where the risk of entanglement in shark-control nets is highest. No published studies have investigated whether the inshore edge of the EAC influences the likelihood of humpback whale entanglements.

6. Conclusions and recommendations for future work

The tendency for the E1 humpback population to migrate within 10 km of the shore, coupled with its strong recovery from whaling (Harcourt et al., 2014), suggest that interactions with shark-control nets are likely to intensify. Various studies conclude that the largest present threat to whales is entanglement in fishing gear (Benjamins et al., 2012, Brown et al., 2013), therefore it is essential that management strategies are implemented immediately to minimise their risk of future entanglement. However, there are still many knowledge gaps and questions surrounding humpback whale navigation, and this hampers predictions of why the species enters shallow waters where shark-control nets are deployed. While it is assumed humpback whales use a combination of cognitive processes, spatial memory, and responses to environmental cues to navigate during their migrations, there is no agreement within the literature as to what exact mechanisms humpback whales use, when they use them, or in what type of habitat they use them in. Humpback whales are a migratory species travelling through a variety of habitats, including ocean basins and dynamic coastal environments, so a mechanistic understanding of humpback navigation strategies on both of these broad and finer scales must be achieved before effective management strategies can be properly implemented.

Specifically, the lack of quantification of the association between humpback whale navigation and boundary currents means that the relationship between humpback whale migration and the variability of the EAC is poorly understood. No studies have investigated whether the position of the inshore edge of the EAC or warmer sea-surface temperatures are associated with humpback whale entanglements in Queensland shark-control nets, and only one study exists on general oceanographic conditions associated with humpback entanglements in the QSCP (Volep et al., 2017). There is still a clear need for an updated and in-depth analysis of whether the EAC and SST influence humpback whale entanglements in QSCP nets. This knowledge may allow managers to consider innovative shark-control strategies that can reduce future entanglements, and improve conservation outcomes for E1 humpback whales.

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Chapter III: Manuscript

A current affair: Associations between the East Australian Current and humpback whale entanglement in Southeast Queensland shark-control nets

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1. Introduction

Humpback whales, *Megaptera novaenageliae,* are a wide-ranging, migratory marine species that travel through ocean basins, coastal environments, and a variety of political domains (Harrison et al., 2018). Their movement patterns are complex, probably driven by the interplay between intrinsic factors such as spatial memory and breeding cycles, and responses to contemporaneous cues in a heterogeneous environment (Scales et al., 2017, Sequeira et al. 2018). With anthropogenic activities such as commercial fishing and shipping overlapping migratory routes of humpbacks (García-Godos et al., 2013, Peel et al., 2018), effective management and conservation of their populations is challenging.

Globally, humpback whale populations are rapidly recovering from the cessation of commercial whaling, resulting in a concomitant increase in humpback bycatch by fisheries, or unintentional entanglement in fishing gear (Thomas et al., 2016). Humpbacks are particularly vulnerable to gillnets (Thomas et al., 2016), which are also used in shark-control programs. Since 1962, the Queensland Shark Control Program (QSCP) has used permanent surface-set gillnets (hereafter shark-control nets) to reduce the population size of large sharks at popular beaches (Cliff and Dudley, 2011). Shark-control nets are passive devices (Sumpton et al., 2011), known to be a threat to a wide range of species including turtles, finfish, rays, dolphins and humpback whales, especially during the whale migration season (Volep et al., 2017).

East Australian (substock E1) humpback whales undertake predictable annual migrations from their Antarctic feeding grounds to their tropical breeding grounds in the Great Barrier Reef (Bruce et al., 2014). They exhibit well-developed navigational abilities, and display high route fidelity when travelling across the open ocean (Horton et al., 2017); however, whales can deviate from their migratory corridors by as much as 150 km (Horton et al., 2017). Along the Australian east coast, humpbacks have a tendency to pass within 10 – 30 km of shore (Noad et al., 2011, Harcourt et al., 2014), with mother and calf pairs known to rest in shallow, sandy bays during the southward return migration (Meynecke and Meager, 2016). This behaviour exacerbates the risk of

entanglement as whales travel between the shark-control nets and surf zone (McPherson et al., 2001). A (sub-)mesoscale (10 – 100 km) understanding of the mechanisms underlying whale navigation along their migratory corridors remains poorly developed. This presents an issue for understanding the movement patterns of humpbacks that migrate along the highly dynamic coastal ocean of Eastern Australia. Such knowledge is needed for assessment of entanglement risk, and informed management of migrating humpbacks.

The East Australian Current (EAC) is the dominant oceanographic feature of the Australian east coast, manifesting as an oligotrophic western boundary current that closes the South Pacific subtropical gyre, and brings warm, tropical water poleward (Suthers et al., 2011). A characteristic feature of the EAC is its intrinsic variability, exhibiting a strong seasonal cycle in velocity and transport volume (Ridgway and Godfrey 1997). Whilst the core of the EAC generally follows the continental slope, the inner and outer edges of this current frequently meander and stochastically shed (sub-)mesoscale structures, such as fronts, filaments, and eddies (Bull et al., 2017).

Despite its variability, the location of the EAC's inner boundary may be used by humpback whales for navigation along the Australian east coast. For instance, previous research has shown that in the Gold Coast Bay, rates of humpback entanglement increased when the EAC's maximum velocity was shoreward of its average position (i.e., when the current meanders close to the shore, and consequently to the shark-control nets), indicating a relationship between the dynamics of the EAC and humpback navigation (Meynecke and Meager 2016, Volep et al., 2017). The inner boundary of the EAC is characterised by strong temperature gradients, or coastal fronts (Reinke et al., 2016), which generally run parallel to the shore. Humpback whales have recently been found to favour areas with strong temperature gradients (Reinke et al., 2016), and they appear to use the southern boundary of the Antarctic Circumpolar current for navigation across the Southern Ocean (Volep et al., 2017). This suggests that that the fronts associated with the inshore edge of the EAC may represent a potential navigation tool for humpbacks. Being able to sense changes in temperature and current would allow the whales to follow these features, and avoid straying too far from their migratory corridor (Reinke et al., 2016).

Here, we investigate the possibility that humpback whales might be using the inner edge of the EAC, or associated fronts and eddies, as navigation tools. If this is the case, we would expect inshore meanders of the EAC to cause nearshore range compression, particularly at the Gold Coast, where the continental shelf narrows sharply. Such nearshore range displacement is likely to result in an increased risk of entanglement in shark-control nets, which are deployed in shallow waters off popular bathing beaches. To address this issue, we use a data-driven approach that aims to quantify potential effects of sea-surface temperature, the position of the inshore edge of the EAC, and the overall structure of the current, on the probability of humpback whale entanglements in QSCP shark-control nets.

2. Methods

2.1. Study area

2.1.1. Shark-control net locations

We used entanglement data collected since 2001 at 18 shark-control nets along the coastline of South-East Queensland (SEQ), Australia, stretching from Rainbow Beach (~25˚8'9.400''S, 153˚0'9.700''E) to Coolangatta, Gold Coast (~28˚1'5.510''S, 153˚5'3.600''E) (Figure 3). Due to low numbers of entanglement events (58 since 2001), shark-control nets were aggregated to five sites: Rainbow Beach, Noosa, Sunshine Coast, North Stradbroke Island and the Gold Coast (Figure 3). Mackay was also originally considered, but subsequently discarded given that no entanglements were recorded since 2001. Each site comprised 1 – 11 shark-control nets (Table 1). Nets are surface-set 400 – 700 m from the shore, are 186 m in length and vary between 3 – 6 m depth. We used the location of the central net at each site (between the northernmost and southernmost net) to represent the geographical location of the entire site; all environmental variables were therefore derived for these centralised locations.

Table 1. Locations of Queensland Shark Control Program nets used for analysis, number of nets at each location, and places of humpback whale entanglement between 2001 and 2017.

Site	Nets	Places of Entanglement
Rainbow Beach	3	Rainbow Beach
Noosa	2	Main Beach
Sunshine Coast	10	Coolum Beach, Twin Waters Resort, Maroochydore Beach, Mooloolaba Beach
North Stradbroke Island	1	Ocean Beach
Gold Coast	11	Kurrawa Beach, Mermaid Beach, Coolangatta Beach, Tallebudgera Beach, Surfers Paradise Beach, Main Beach, Currumbin Beach, Burleigh Beach, Kirra Beach, Miami Beach, Bilinga Beach

2.1.2. Oceanography

The EAC is a nonlinear western boundary current. Generally, the current is <100 km wide, with its core running ~200 m deep (Zilberman et al., 2018). The EAC comprises four zones: formation, intensification, separation and extension (Ridgway and Dunn, 2003). The study area, SEQ, falls within the intensification zone, where the current accelerates and establishes a seasonally variable poleward flow as the continental shelf progressively narrows.

The EAC plays an important role in the intrinsically dynamic coastal oceanography of SEQ. The inner edge of the EAC is known to stochastically shed eddies, with SEQ recently identified as an eddy-shedding hotspot, where 4 – 5 mesoscale cyclonic eddies are generated per year (Ribbe and Brieva, 2016; Ribbe et al., 2018). Furthermore, the recently discovered Fraser Gyre (Ismail et al., 2017) is a wind-driven, quasi-permanent eddy occurring between southern Fraser Island and Moreton Island from April to August. The outer edge of the gyre is also the inner edge of the EAC.
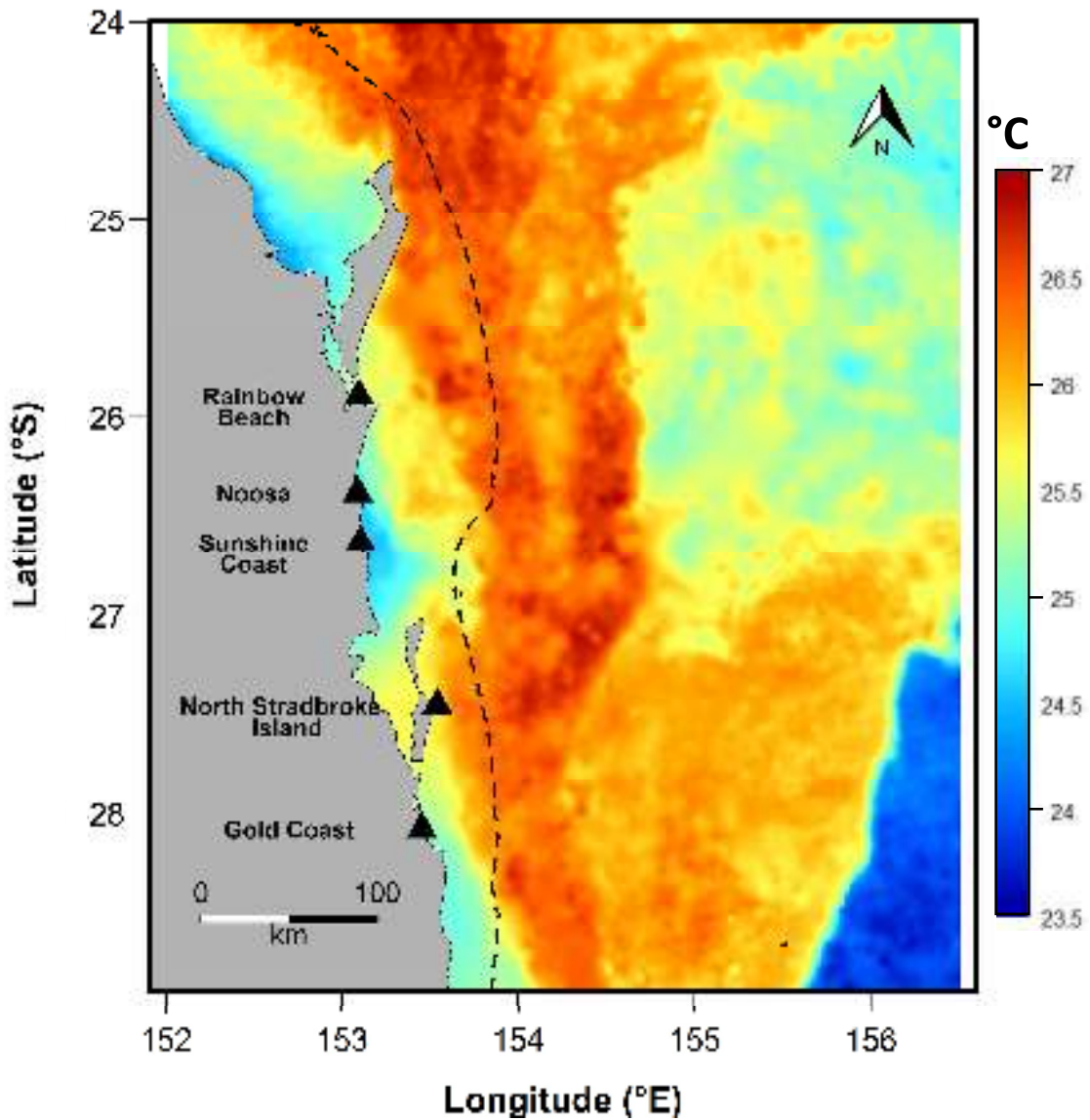
Figure 3. The study area, encompassing Southeast Queensland, overlaid on sea-surface temperature (SST) image for 1st May 2010. Black triangles indicate sites of aggregated net entanglements used for analysis. The dashed line indicates the 200-m depth contour. The map displays Merged Ultra-high Resolution daily SST (MUR SST), generated by the Global High Resolution SST (GHRSST) project and distributed by NOAA Coastwatch (https://coastwatch.pfeg.noaa.gov/erddap/files/jplMURSST41/).

2.2. Data

2.2.1. QSCP entanglements

Yearly QSCP entanglement records were provided by Queensland Department of Fisheries. Whilst cetacean entanglement records exist from 1968, the analysis was restricted to 2001 – 2017, because before 2001 contractors often did not identify the species entangled. Nets are routinely checked by contractors every two or three days; however, the marine animal release team are called out immediately when a humpback whale entanglement occurs. Therefore, we assumed the dates in the humpback entanglement records reflected the true date of entanglement and not the service runs. Records included 58 humpback whale entanglements. However, three days had multiple incidences of entanglement, resulting in 55 entanglement-positive days. Entanglement events (entanglement-positive days) were used as the response variable to model the likelihood of entanglement.

2.2.2. Environmental Data

We derived the SST daily at each site at a 1-km resolution using NASA Multi-sensor Ultra-high Resolution Sea-Surface Temperature data (MUR SST) between 2002-06-01 and 2017-11-30. Because MUR SST begins in June 2002, and our study included data from 2001, we used SST from the Advanced Very High Resolution Radiometer (AVHRR) from 2001-05-01 to 2002-05-30 at 2-km resolution, provided by the Integrated Marine Observing System (IMOS). To match the resolution of MUR SST, we downscaled the AVHRR data using bilinear interpolation. If there was cloud contamination in the daily IMOS AVHRR data, we used a three-day SST average, centred on the date of interest. To explore variability of circulation in SEQ, we obtained daily ocean reanalysis data from Bluelink Reanalysis version 3.5 (BRAN3p5). This included meridional velocity (VCUR), current speed, and temperature for the top 5 m of the water column, all between 2001 and 2017. BRAN3p5 assimilates altimetry, SST, Argo temperature and salinity data using the BlueLink Ocean Data Assimilation System (BODAS), and has a resolution of 10-km. These data have been used for various oceanography studies in Southeast Queensland (e.g., Brieva et al. 2014, Ismail et al. 2017), which found that BRAN3p5 realistically represents the regional oceanography of the

study area (Ismail et al. 2017). All spatial manipulation and extractions were done in the "raster" package for R (R Core Team, 2016, Hijmans, 2017).

2.3. Mapping the East Australian Current

We used temperature, meridional velocity (VCUR) and current speed derived from BRAN3p5 to create daily maps delineating the position of the inner edge of the EAC (henceforth EAC inner edge). First, we mapped the latitudinal gradients of each daily variable (temperature, meridional velocity and speed) at 10-km resolution by subtracting the value of the cell immediately to the east of the focal cell, for all cells in the raster. To remove the presence of (sub-)mesoscale (~1 km; 10 s – 100 s of km) structures, such as fronts, filaments and eddies, we applied a 30-km moving average over each daily map of gradients. To ensure that gradients of all variables increase at the EAC edge, we multiplied VCUR by -1 so that southwards flow was positive.

The EAC inner edge is characterised by a collection of correlated environmental variables. Given that we wanted to extract the patterns across all of these variables, we ran a principal components analysis (PCA). A PCA was performed on the data for each day, thereby combining daily data for gradients of temperature, VCUR and speed. PCA is a multivariate analysis often used for pattern identification, which transforms a combination of correlated variables into a series of new, independent variables (Hottelling, 1933). Variables were scaled prior to analysis to cover the same range in values, but not centred at the mean, given that we wanted the sign of each gradient's loading to be meaningful (i.e. to correspond to the sign of the particular gradient). We then extracted the first principal component (PC1), which explained the most variance in the correlated input data, relative to the remaining principal components (see *Results*).

Input data (gradients) were configured to increase at the EAC edge, as explained above, so positive loadings of the variables onto PC1 imply that PC1 values increase as the input values increase. Therefore, when variables' loadings on the PC1 were all negative, the values of PC1 were multiplied by -1 to ensure consistency of interpretation. In some cases, however, the signs of the

loadings did not align; in such cases, we recorded the PCA as a "failure" (see *Statistical Analysis*), because it was unable to resolve the EAC on the basis of gradients in the input data.

The EAC inner edge is characterised by strong latitudinal gradients of temperature, VCUR and speed. For this reason, we used the maximum value of PC1, which indicates the maximum latitudinal gradient of combined variables, as a proxy for the location of the inner edge of the EAC. We defined the maximum value of PC1 as the 'maximum environmental gradient'. Given that the EAC inner edge is assumed to generally run close to the continental shelf, we constrained the search for the maximum environmental gradient between 153.45 ˚E and 154. 25 ˚E. From this longitudinal range, the maximum value was extracted at the latitude of each shark-control net, indicating the location of the inner edge of the EAC. These points were also used to calculate the distance of the EAC inner edge from each shark-control net site. Furthermore, we extracted the variance explained by PC1. Finally, the SSTs of the inner edge were also extracted from corresponding MUR SST or AVHRR data layers for each shark-control net location.

The position of the EAC edge has never been quantified explicitly, so we computed three variants of the same analysis and evaluated their performance in detecting the EAC edge. Method 1 computed the PCA for environmental-gradient data over an extent ranging 152.55 – 155.05 ˚E and 25.55 – 28.45 ˚S. Method 2 adjusted this extent to 152.45 – 155.95 ˚E, and 24.25 – 28.85 ˚S, allowing us to test the sensitivity of results to the extent of the study domain. Method 3 used the same extent as Method 1, but instead of using latitudinal gradients of the three environmental variables as input to the PCA, it used raw values and converted the mapped PC1 to a latitudinal gradient. For each method, the position of the EAC inshore edge was extracted as explained above.

Subsequently, the performance of each method was evaluated manually via visual validation. To do this, we mapped temperature, VCUR and speed for 100 random dates, and extracted the coordinates from the location visually identified as the EAC edge. We then calculated the straight-line distance between the locations of the visually identified edge and the PCA-identified edge, and chose the PCA method with the least error. In this way, Method 1 was selected for use in further analyses (Figure 4).

In addition to the inner edge, we also quantified the position of the core of the EAC by running daily PCAs of 30-km east-west moving averages of the raw values (as opposed to gradients) of temperature, VCUR, and speed using the same extent as the EAC inner edge PCA (Method 1) (Figure 5). The EAC core follows the position of the continental shelf, and is constrained to the west of the Tasmantid seamount chain, so we limited searches for its position to between 153.7 ˚ E and 154.6 ˚ E. Between these longitudinal bounds, we extracted the position of the maximum environmental value from a shore-normal transect extending from each shark-control net site, given that we expected the core of the current to be defined by the maximum values of temperature, VCUR (Volep et al., 2017), and speed. We also used these locations to compute distance to the EAC core for each shark-control net, and extracted the corresponding SST of the core, and overall variance explained by PC1.
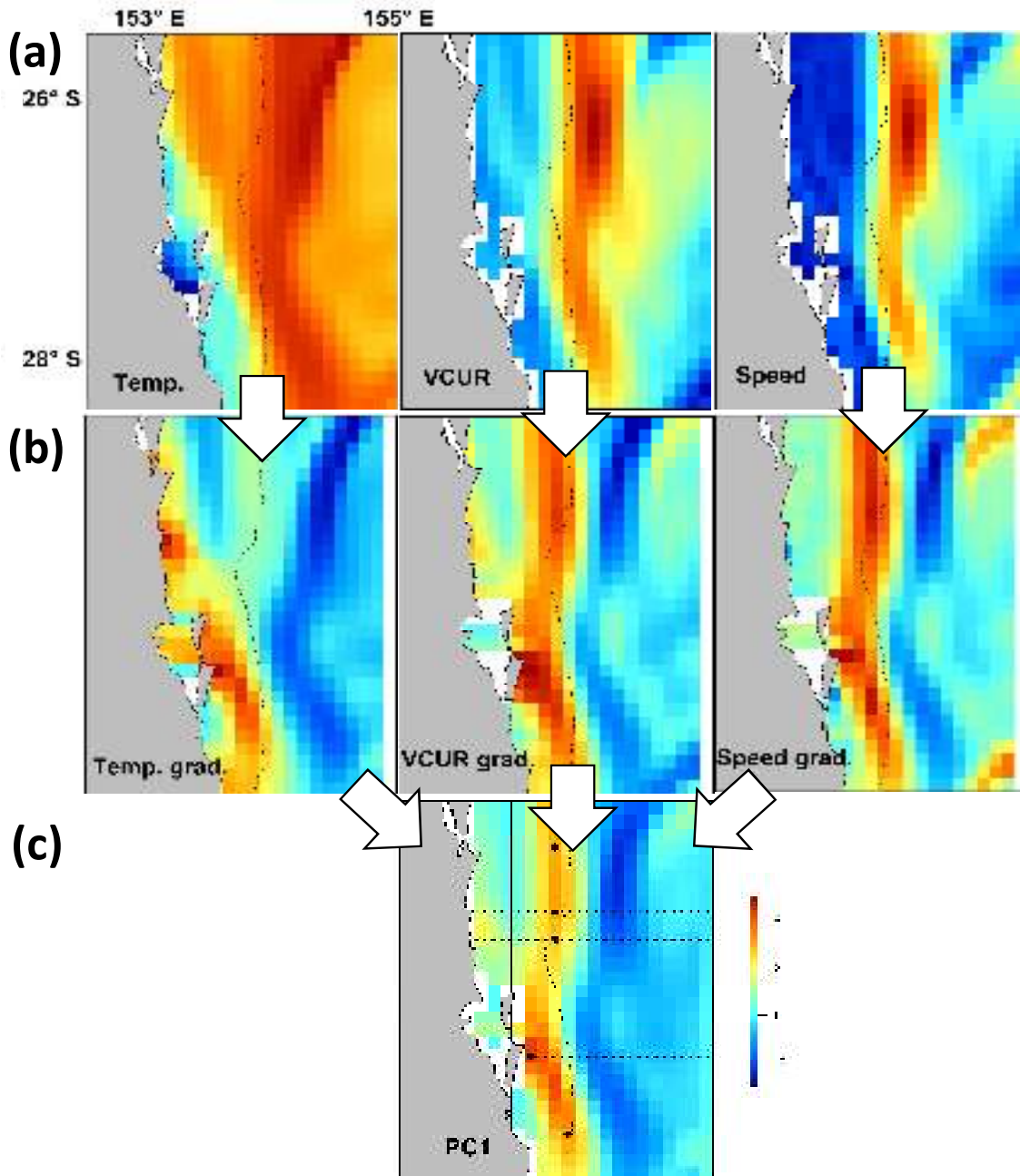
Figure 4. Protocol for mapping the edge of the EAC. (a) Example daily OFAM3 rasters for relative values of (left to right) temperature, VCUR and speed. (b) East-west gradients and 30-km moving average smooth of the rasters in (a). (c) Raster of the first principal component after running a PCA on the three gradients. The positions of the inner edge of the EAC relative to the locations of the five shark-control nets (plotted as black filled circles) were identified as the cell containing the maximum environmental gradient along an east-west transect between 153.45˚E – 154.25˚E (solid vertical lines) at the latitude of each net location (dotted horizontal lines). Dashed line in all images represents 200-m depth contour.
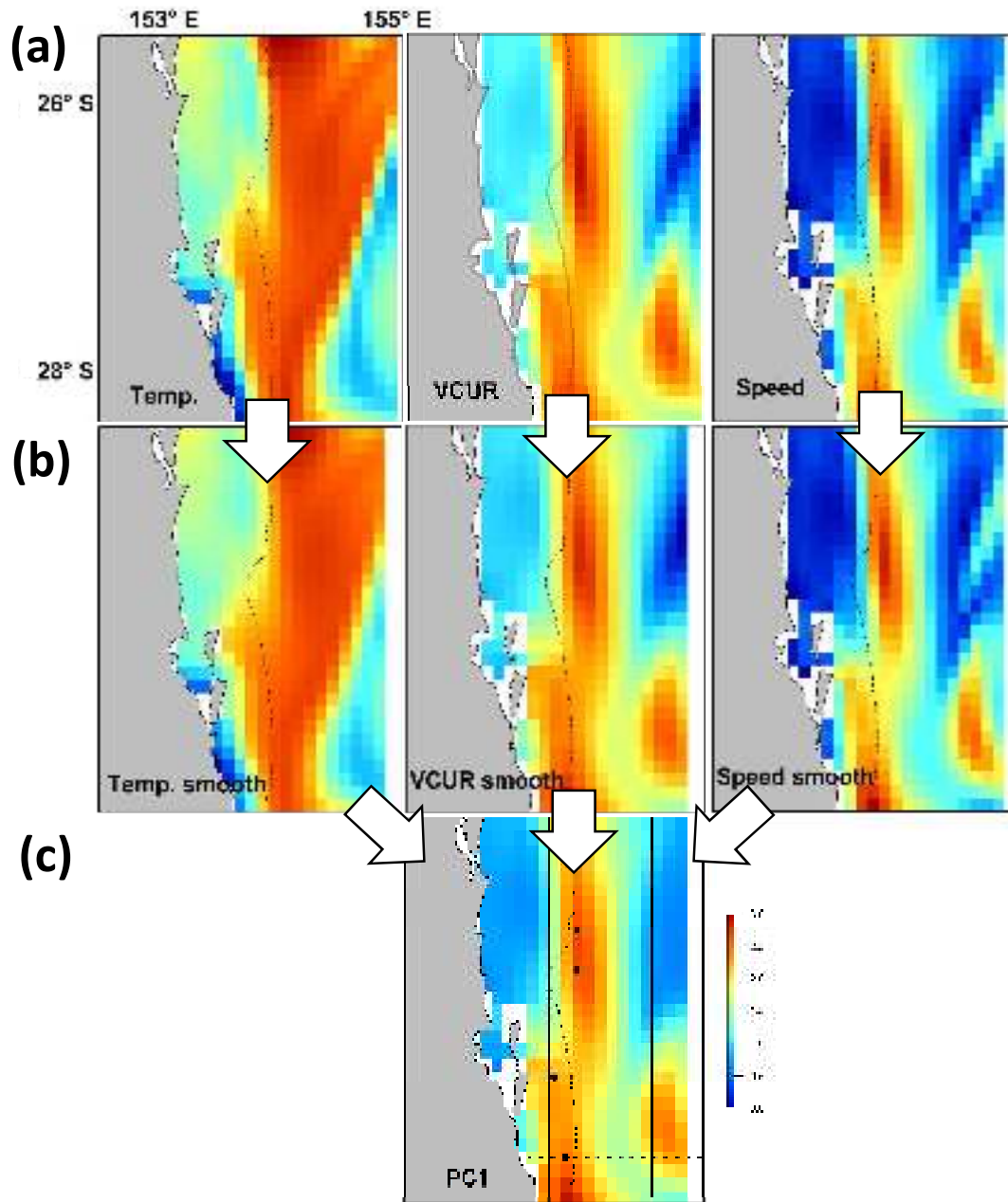
Figure 5. Protocol for mapping the core of the EAC. (a) Example daily OFAM3 rasters for relative values of (left to right) temperature, VCUR, and speed. (b) 30-km moving average smooth rasters of the variables in (a). (c) Raster of the first principal component after running a PCA on the three variables. The positions of the EAC core relative to the locations of the five-shark-control nets (plotted as filled black circles) were identified as the cell containing the maximum environmental value along an east-west transect between 153.7˚E – 154.6˚E (solid vertical lines) at the latitude of each net location (dotted horizontal lines). Dashed line in all images represents 200-m depth contour.

2.4. Statistical Analysis

First, we wanted to know whether the variance explained and the relative directions of variables' loadings of PC1 were correlated with risk of entanglements. If the direction (sign) of the loadings of variables onto PC1 were different, and the variance explained by PC1 was low, we concluded that PC1 was a "failure" and unable to resolve the EAC, a situation that might arise when surface-layers of the ocean are mixed and the EAC is ill-defined (at least at the surface). By contrast, when the loadings of variables onto PC1 were the same direction, and the variance explained by PC1 was high, we concluded that PC1 had greater skill in resolving the EAC because the EAC was well defined for that day. Therefore, for each PCA, we recorded the variance explained by PC1 and whether the loadings of variables onto PC1 were consistent in direction, or contrasting. We then modelled entanglement (yes/no) as a function of variance explained by PC1 (continuous) and direction of the loadings (factor: consistent/contrasting) using a binomial generalised linear model. Humpback entanglements are rare (n = 55), so data were severely zero inflated. We accounted for this using a bootstrap resampling approach with 1000 iterations. At each iteration, we selected from the empirical dataset all 55 entanglement dates, in addition to 220 random non-entanglement dates (with replacement) from the same month/year combinations as the entanglement dates. This ensured we had similar general environmental conditions for days on which entanglements were recorded or not, thereby accounting for seasonality in the data. Duplicate non-entanglement dates (1.36 to 9.54% of the 220 random days) were removed prior to analysis in each iteration. After each iteration, we extracted model coefficients (and their standard errors) and used their distributions over the 1000 iterations to assess significance of predictors. For these analyses, significance of predictors were assessed by the 2.5^{th} to 97.5^{th} percentile range (i.e., the empirical 95% confidence interval) of the distribution of their coefficients across 1000 bootstrapped iterations of the analysis. Where confidence intervals overlapped zero, coefficients were considered non-significant, but where they did not overlap zero, they were considered significant ($\alpha = 0.05$).

In order to determine whether entanglements of humpback whales were related to the position and characteristics of the EAC edge, a regression-based approach was used. We used the same

bootstrap resampling approach outlined above, except that non-entanglement dates were resampled using the same month/year/site combinations as the entanglement dates from the empirical dataset. All environmental predictors, including distance to shark net, maximum environmental gradient (at edge), variance explained, and SST of the edge were scaled to a mean of zero and unit variance to ensure comparability of coefficient estimates. These variables (and all two-way interactions) were used as predictors in a binomial generalised linear mixed-effects model (GLMM, lme4 package for R, Bates et al., 2014) of entanglements (yes/no), with site as a random effect, again using a resampling method with 1000 iterations following the protocol outlined above. To investigate whether the differing number of shark-control nets at each site (Table 1) would impact the probability of entanglement, we also included the number of nets (scaled to a mean of zero and unit variance) as a fixed predictor in the models, together with all two-way interactions with the other predictors. However, given that number of nets and its interactions with other predictors were non-significant across model iterations, we excluded this variable from our final model. We used the same modelling approach to quantify the relationship between the EAC core and entanglement probability, using distance to the shark net, SST of the core, variance explained, and the maximum environmental value as predictors, together with SST of the site. Finally, we used Pearson's correlation to determine whether the results from the EAC core and results from the EAC edge were correlated.

3. Results

3.1. PCA methodology

Among the three candidate PCA methods tested for identification of the EAC edge, Method 1 (PCA of 30-km smoothed gradients of temperature, VCUR and speed over the extent (152.55 – 155.05° E, 25.55 – 28.45° S) performed best on all criteria (Table 2). This method was therefore selected for use in subsequent analyses, including detecting the EAC core, albeit that it performed slightly worse in this respect (Table 2). Entanglements on 2004-07-19 and 2009-10-08 corresponded with "failure" PCAs for detection of the EAC core, representing 3.6% of total entanglements. The ratios of entanglements against non-entanglements for Method 1 were not dependent on the variance explained by PC1, or the direction of the loading coefficients, as indicated by coefficient distributions showing overlap with zero and high variability (Figure 6). These results indicate the failure rate of the PCA methods does not significantly affect probability of entanglement.

Table 2. Accuracy of the separate PCA approaches to characterise the EAC edge and core. Variance explained by PC1 (mean ± standard deviation), number of failure PCAs (i.e., PCAs in which loadings of variables on PC1 had contrasting signs), percentage of failure PCAs, and average absolute error from visual validation. Only one approach to PCA was used to characterise the EAC core, hence no error value. * indicates chosen approaches to characterise the EAC.

PCA approach	Variance explained	Failures	Failures (%)	Error (km)
* Method 1	0.697 ± 0.094	106	2.91	8.18
Method 2	0.62 ± 0.087	137	3.76	8.24
Method 3	0.849 ± 0.081	160	4.39	8.89
* EAC core	0.868 ± 0.079	142	3.9	N/A
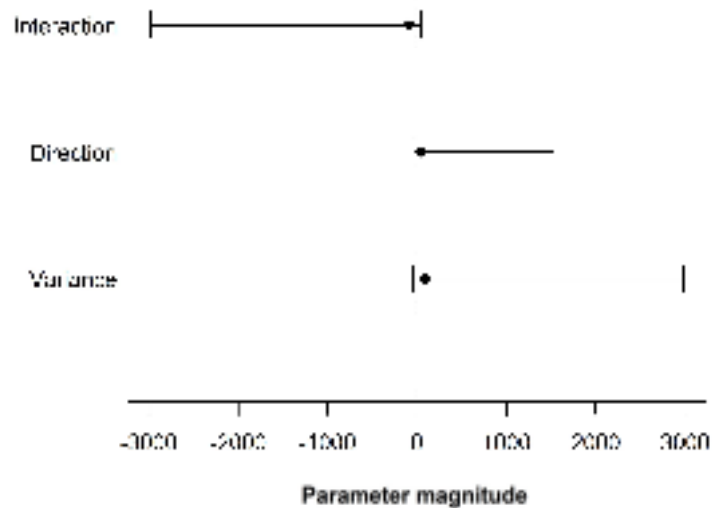
Figure 6. Distributions of parameter estimates from 1000 models fit to subsets of data comprising all observed entanglements, and a random sub-sample of ~220 days on which entanglements were not observed for variance explained by PC1 (*Variance*), all loadings' signs in the same direction (*Direction*), and the interaction between the two (*Interaction*). Filled circles indicate medians of estimates, and 95% confidence intervals are shown as horizontal lines.

3.2. SST of shark-control net

The SST of the shark-control net, when accounting for site, did not significantly influence the probability of humpback whale entanglement. The 95% confidence intervals of regression coefficients for SST of the shark-control net included zero, indicating little explanatory significance (Figure 7a, Table 3a).

3.3. East Australian Current

The maximum environmental gradient at the EAC edge, the distance of the inner edge to the shark-control net, variance explained by the first principle component of PCA Method 1, and the interaction between variance and maximum environmental gradient at the EAC edge were significant predictors of humpback whale entanglement because confidence intervals did not

overlap zero (Figure 7b, Table 3b). Entanglements were more likely to occur when the maximum environmental gradient at the EAC edge was smaller (when controlling variance explained at its average), when variance explained by Method 1 was higher (when controlling maximum environmental gradient at its average), and when the EAC edge was closer to the shark-control net (Figure 8a, 8b, 8c). The positive significant interaction between the maximum environmental gradient and variance explained indicates that the negative effect (the slope) of the maximum environmental gradient on entanglement probability decreases as variance explained increases. Similarly, the positive effect of variance explained on entanglement probability decreases when the maximum environmental gradient increases (Figure 7b, Figure 9). The confidence intervals for SST of the EAC edge overlapped zero, indicating non-significance (Figure 7b).

The maximum environmental value at the EAC core and variance explained by PC1 for the core method were also significant predictors of entanglement (Figure 7c, Figure 8d, 8e, Table 3c). Entanglements were more likely to occur when the maximum environmental value was lower, and when there was more variance explained by PC1 over the study area (Figure 8d, 8e). In contrast, distance from the core to the shark-control net and SST of the core were not significant predictors of entanglement, as distributions of regression-coefficient confidence intervals overlapped zero (Figure 7c, Table 3c). Furthermore, both maximum environmental gradient for Method 1 and maximum environmental value for the core method were found to be moderately to strongly positively correlated, with a Pearson's correlation coefficient of 0.665 ($p = >0.001$).
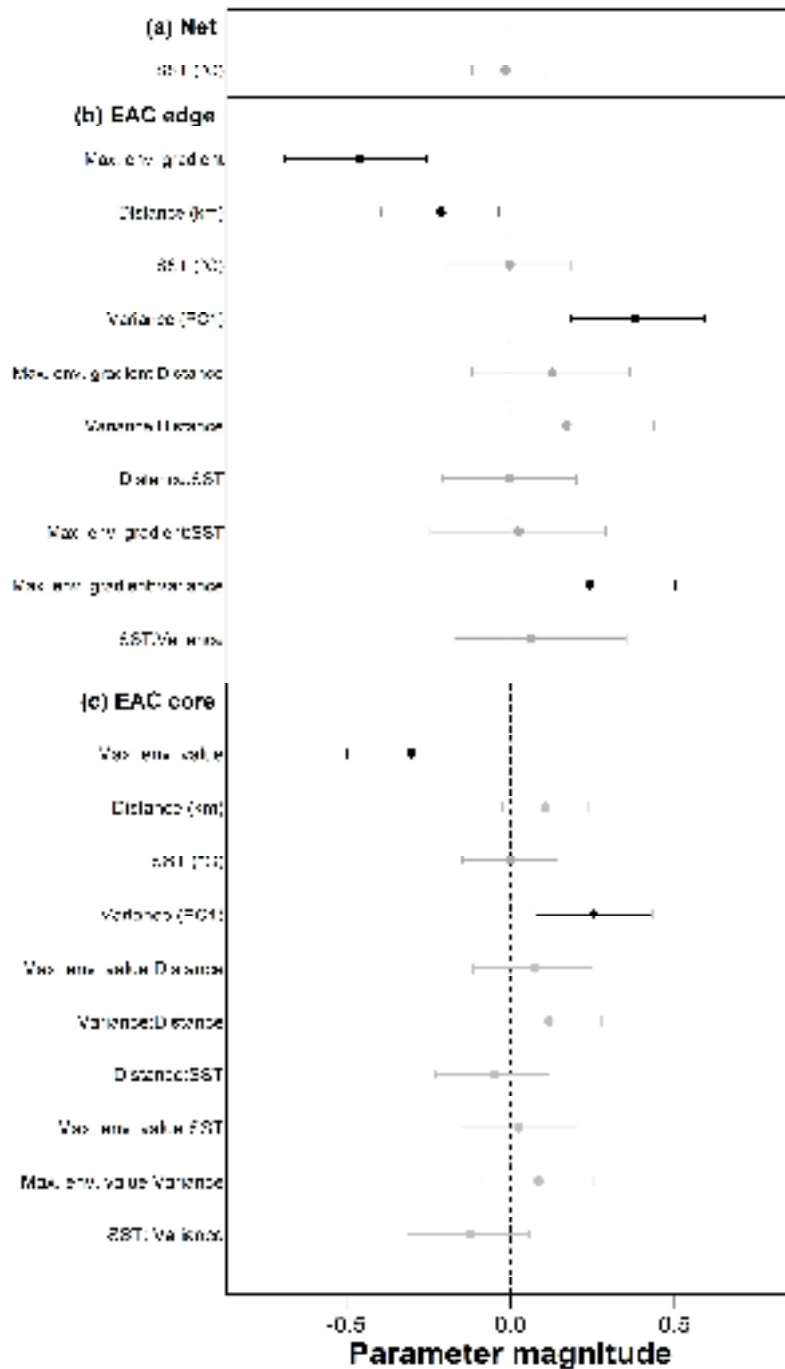
Figure 7. Distributions of parameter estimates from 1000 models fit to subsets of data comprising all observed entanglements, and a random sub-sample of ~220 days on which entanglements were not observed. Metrics relating to (a) the shark-control net, (b) the EAC edge, and (c) the EAC core. To ensure comparability of the magnitudes of parameter estimates, all predictors were scaled to a mean of zero and unit variance prior to analysis. Filled circles indicate medians of estimates, and 95% confidence intervals are shown as horizontal lines. Non-significant parameter distributions are coloured in grey.
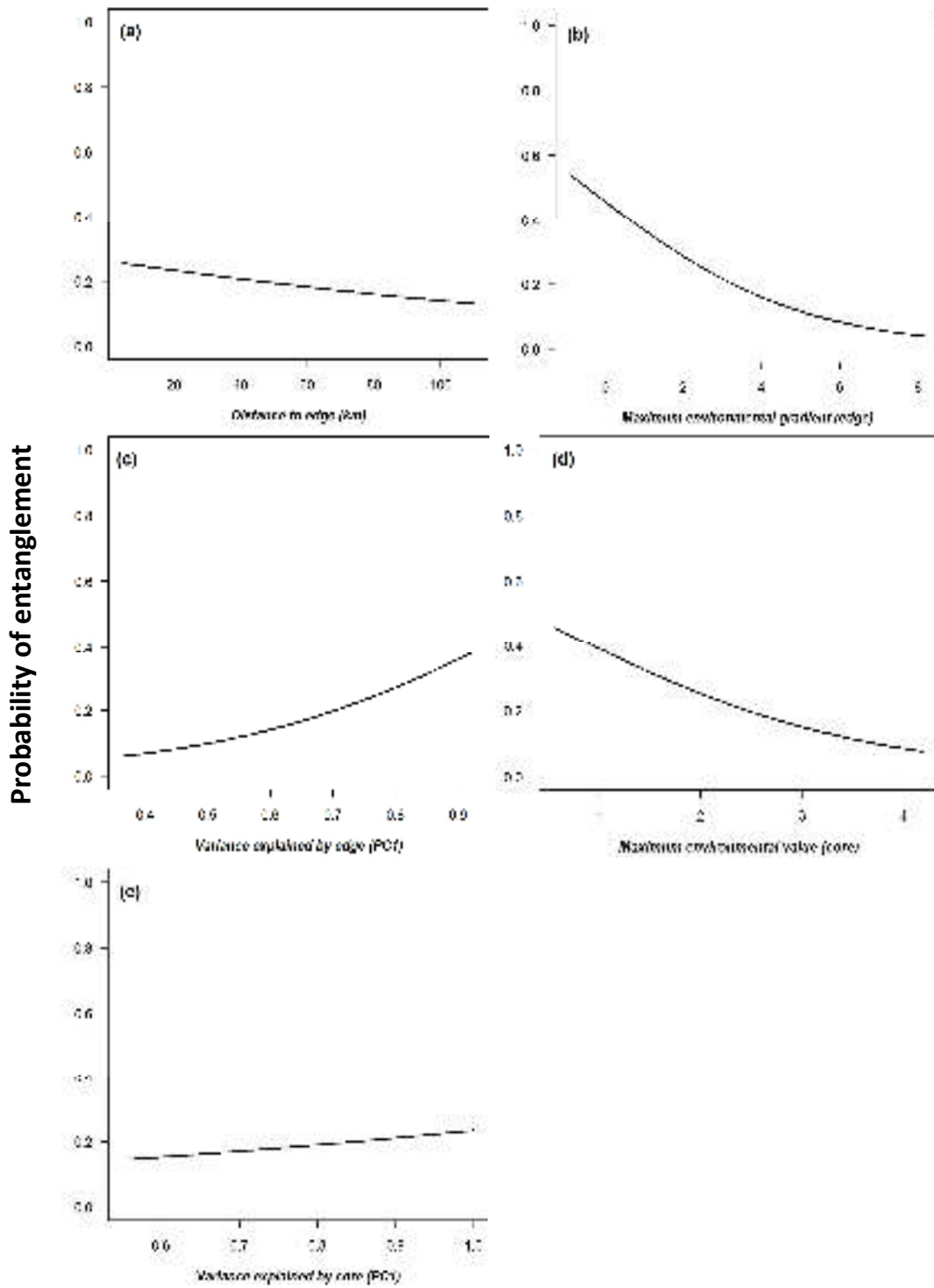
**Figure 8.** Modelling the influence of significant single predictors on humpback whale entanglement. (a-e) Mean effects of distance from the EAC edge to the shark-control net, edge maximum environmental gradient (maximum value of PC1), variance explained by Method 1 PC1, core maximum environmental value (maximum value of PC1), and variance explained by core method PC1 over 1000 model iterations.

Table 3. Modelling the influence of the EAC on entanglement. Model coefficients (median ± standard deviation, and 95% confidence limits) for relationships between metrics corresponding to (a) SST of shark-control net, (b) EAC edge, and (c) EAC core on probability of whale entanglement. All estimates are medians of 1000 models fit to subsets of data comprising all observed entanglements and a random sub-sample of ~220 days on which entanglements were not observed. All predictors were standardised before modelling (binomial GLMM), to ensure comparability of magnitudes among coefficient estimates, but these values were subsequently back-transformed and reported on their original scales.

Predictor (standardised)	Median of 1000 regression coefficients	Median of 1000 standard errors
a. SST of shark-control net metrics *entanglement (0 / 1) ~ SST of net + (1 | site)*		
SST of net (˚C)	-0.015 ± 0.048 (-0.116 – 0.099)	0.127 ± 0.004 (0.113 – 0.137)
b. EAC edge metrics *entanglement (0 /1) ~ distance to edge + SST of edge + maximum environmental gradient + variance + all combinations of two-way interactions + (1 | site)*		
Distance to edge (km)	-0.212 ± 0.077 (-0.391 – -0.037)	0.213 ± 0.007 (0.19 – 0.233)
SST of edge (˚C)	-0.001 ± 0.086 (-0.203 – 0.182)	0.202 ± 0.006 (0.184 – 0.219)
Maximum environmental gradient	-0.456 ± 0.092 (-0.685 – -0.253)	0.197 ± 0.007 (0.176 – 0.215)
Variance (variance explained by first principle component)	0.378 ± 0.087 (0.184 – 0.59)	0.203 ± 0.007 (0.185 – 0.225)
Distance : Max. environmental gradient	0.126 ± 0.104 (-0.118 – 0.363)	0.22 ± 0.013 (0.192 – 0.255)
Distance : Variance	0.169 ± 0.107 (-0.056 – 0.438)	0.231 ± 0.013 (0.206 – 0.265)
Distance : SST	-0.003 ± 0.091 (-0.208 – 0.2)	0.209 ± 0.012 (0.183 – 0.239)
Max. environmental gradient : SST	0.024 ± 0.113 (-0.244 – 0.29)	0.223 ± 0.015 (0.19 – 0.261)
Max. environmental gradient: Variance	0.241 ± 0.017 (0.19 – 0.287)	0.190 ± 0.011 (0.164 – 0.213)

SST : Variance	0.063 ± 0.111 (-0.17 – 0.353)	0.22 ± 0.01 (0.184 – 0.264)

c. EAC core metrics
entanglement (0/1) ~ distance to core + SST of core + maximum environmental value + variance + all combinations of two-way interactions + (1 | site)

Distance to core (km)	0.106 ± 0.056 (-0.023 – 0.234)	0.169 ± 0.002 (0.165 – 0.178)
SST of core (˚C)	0.002 ± 0.066 (-0.145 – 0.144)	0.169 ± 0.003 (0.16 – 0.18)
Maximum environmental value	-0.301 ± 0.082 (-0.497 – -0.126)	0.182 ± 0.006 (0.165 – 0.199)
Variance (variance explained by first principle component)	0.253 ± 0.078 (0.076 – 0.43)	0.212 – 0.009 (0.188 – 0.233)
Distance : Max. environmental value	0.073 ± 0.079 (-0.115 – 0.248)	0.163 ± 0.009 (0.144 – 0.188)
Distance : Variance	0.116 ± 0.072 (-0.051 – 0.279)	0.164 ± 0.008 (0.145 – 0.184)
Distance : SST	-0.046 ± 0.077 (-0.227 – 0.116)	0.178 ± 0.007 (0.164 – 0.195)
Max. environmental value : SST	0.023 ± 0.078 (-0.149 – 0.2)	0.168 ± 0.01 (0.147 – 0.193)
Max. environmental value : Variance	0.084 ± 0.078 (-0.091 – 0.255)	0.182 ± 0.01 (0.158 – 0.205)
SST : Variance	-0.123 ± 0.079 (-0.312 – 0.058)	0.191 ± 0.011 (0.167 – 0.219)
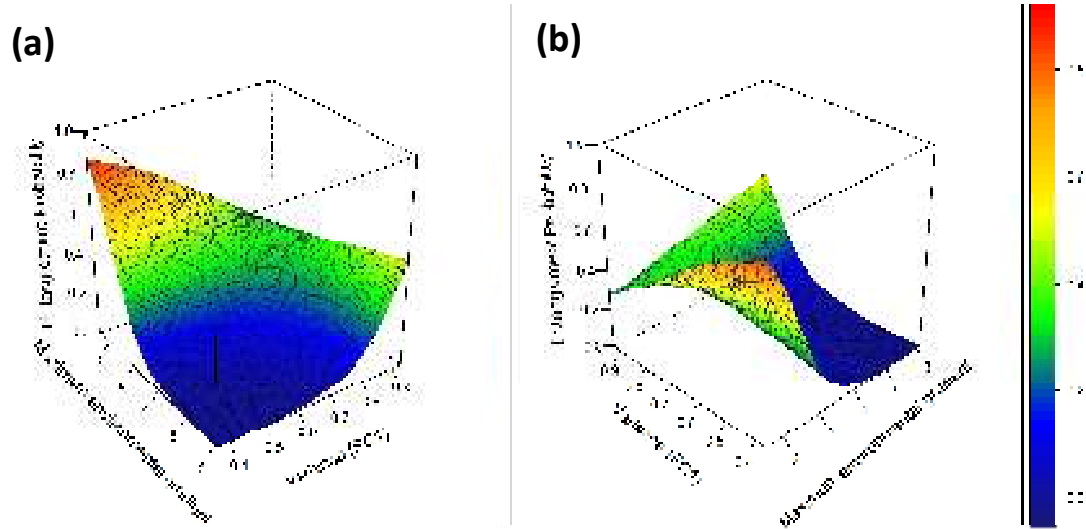
Figure 9. (a) Illustration of the interactive effect for variance explained (*Variance (PC1)*) and maximum environmental gradient on the probability of humpback whale entanglement, from Method 1. Values are coloured according to entanglement probability, indicated by the colour scale. (b) Same illustration, but rotated 90 degrees anticlockwise.

4. Discussion

Previous studies of humpback whale entanglements in SEQ have used *in-situ* data to infer correlations between environmental conditions and entanglements (Meynecke and Meager, 2016), or have used ocean reanalysis velocity data (Volep et al. 2017) to map the position of the EAC core and its relationship with entanglements. These methods have advantages, particularly for beginning to understand the effect of the position of the EAC core on humpback whale movements, but could not directly address the emerging idea that humpbacks use temperature gradients, or fronts, as a navigation tool (Reinke et al. 2016). Here, we introduce a novel, multivariate, data-driven approach to identify the positions of both the inner edge and core of the EAC on a daily basis from 2001 to 2017. This allows us to more directly resolve the relationship between humpback entanglements in SEQ shark-control nets and characteristics of the EAC. To our knowledge, this is the first study, globally, to interface satellite data, ocean reanalysis data and entanglement records to quantify linkages between oceanography and entanglements in shark-control nets.

4.1. Effectiveness of the EAC mapping algorithms

The low failure rates and relatively high accuracy (errors are smaller than the resolution of the environmental data) of our selected approach to PCA for both the EAC edge and core suggest that our method is suitable for characterising the large-scale oceanography of Southeast Queensland, and for delineating the inner edge and core of the EAC. Whilst our method is both accurate and accessible, we acknowledge that the resolution of OFAM3 is a limiting factor, and might subsume (sub-)mesoscale features such as fronts, filaments, and eddies that may break off the inner edge of the EAC. This could potentially skew our results if whales use these finer-scale structures for navigation (Reinke et al., 2016). Other methods can be used in an attempt to better characterise the oceanography of the study area, such as single-image edge detection (Cayula & Cornillon 1992), composite front mapping (Miller, 2009, Scales et al. 2014), and self-organising maps (Richardson et al., 2003), which have all been previously used to identify dynamic ocean features using remote sensing imagery. Whilst our data are spatially coarse, they have fine temporal resolution, allowing

us to resolve the position of the EAC on a daily basis. This is important given that using contemporaneous environmental data is preferable for fitting habitat-preference models on coarse-scale fields, especially in highly dynamic areas (Scales et al., 2017).

A possible caveat to this study is the use of surface data (within the top 5 m of the water column) to characterise the EAC, given that the EAC is a three-dimensional system that extends up to depths of 1.5 km (Zilberman et al. 2018). A recent study integrated subsurface habitat metrics into species distribution models to provide resolution of the vertical structure of the ocean, which greatly improved model predictive performance (Brodie et al., 2018). We suggest that a future extension of this study could adopt a similar approach, and integrate subsurface metrics of temperature, meridional velocity and speed from OFAM3 to capture the three-dimensional variability of the EAC edge and core. This is especially pertinent if applying our method to other commonly entangled taxa that migrate vertically through the water column (Scales et al., 2018). Nevertheless, our method is suitable for analysing humpback whale entanglements, because whales generally migrate at or close to the surface, and become entangled in nets in shallow (surface) waters. Moreover, because OFAM3 is driven by assimilating satellite data with *in-situ* observations at depth, surface data are likely best characterised by this ocean model, and therefore most reliable in this sort of analysis.

4.2. The East Australian Current as a navigation tool

Recent findings (Volep et al., 2017) suggest that humpback whale entanglements are more likely on the Gold Coast when the EAC core, as defined by maximum velocity, is shoreward of its average position. Our results provide greater insight by demonstrating that the risk of entanglement is better explained by the position of the EAC inshore edge (defined by multiple variables) than by the position of its core. Although the positions of the core and edge of the EAC will be correlated over large scales, our results demonstrate that at finer scales, humpback whales are likely following the inshore edge of the EAC, as opposed to the core of the current. Because we defined the EAC edge as the maximum gradient in temperature, meridional velocity and speed, we can infer that humpbacks use these frontal structures as a navigation tool. This conclusion is supported by

observations from the Gold Coast, where humpback whales were recently found to associate with strong temperature gradients, and were hypothesised to use coastal fronts for navigation (Reinke et al., 2016). Together, these results support the idea of a nearshore range compression, where the whales' range is essentially compressed by an inshore encroachment of the EAC edge (Meynecke and Meager, 2016), forcing them into shallow water and increasing their likelihood of entanglement.

Entanglement probability also decreased on days when the maximum environmental gradient for the edge and maximum environmental value for the core were higher. This suggests that when the EAC edge and core are well defined at the latitudes of the shark-control nets, there is a lower probability of entanglement, further supporting the idea whales are following strong environmental gradients for navigation (Rienke et al., 2016). Humpbacks have been associated with the inner edge of the coastal front in the Northern California Current System (Tynan et al., 2005), and the boundary of the Antarctic Circumpolar Current (Volep et al., 2017). More recently, humpbacks have been found to associate with (sub-)mesoscale thermal fronts in coastal British Columbia (Dalla Rosa et al., 2012), and on the Gold Coast (Reinke et al., 2016). More broadly, marine predators across taxa and spatial scales target fronts for navigation (Miller et al., 2015, Scales et al., 2015, Scales et al., 2018). It may be that when the whales have a well-defined front to follow, they do so. When the surface water starts to mix, and the edge starts to meander, these fronts weaken. Humpback whales may have therefore lost their navigation tool, potentially causing them to drift closer to the coast to reorient themselves, for instance with using the axis of the coastline, thereby increasing risk of entanglement.

Probability of entanglement increased when variance explained by both gradients (Method 1) and raw values of environmental variables (core method) increased. This is a caveat to our study that requires further investigation. It should be noted that our study domain was relatively large, so a potential explanation would be that high variance explained indicates a well-defined EAC near K'gari (Fraser Island), which might progressively become less-well defined near the Gold Coast, where most entanglements occurred.

Furthermore, we found a positive significant interaction between the maximum environmental gradient for the edge method and total variance explained. When the EAC edge is poorly defined locally, as indicated by a low maximum environmental gradient, and when the EAC edge and oceanography of Southeast Queensland is less spatially structured, as indicated by a low variance explained by PC1, entanglement probability is highest. A possible explanation is that the whales may have lost their navigation cue, and move into the nearshore to reorient themselves, increasing their risk of entanglement. Contrastingly, when the EAC edge and oceanography of Southeast Queensland is less spatially structured, but the EAC edge is well defined locally as indicated by a high maximum gradient, entanglement probability decreases. This further supports the idea of humpbacks using the EAC edge as a navigation tool.

An unexpected finding was the non-significance of SST of the EAC edge as a predictor of entanglement probability. On the Gold Coast, humpback whales have shown an apparent preference for cooler water (Reinke et al., 2016). Contrastingly, our study supports the findings from Volep et al. (2017), who found no relationship between humpback whale entanglements and SST on the Gold Coast between 2001 and 2012. We speculate that whales may target cooler water for opportunistic feeding opportunities further south (Reinke et al., 2016). However, given that we identified the EAC inner edge by a combination of environmental gradients, and not solely by SST, our method would not capture this preference.

We recommend that future research adopts a finer-scale approach than our study to investigate the effect of (sub-)mesoscale dynamic structures on entanglements. An emerging technique used to identify these features is using backwards-in-time Finite-Size Lynapunov Exponents. This could resolve any potential links between the seasonally occurring Fraser Gyre (Ismail et al. 2017), the 4 – 5 cyclonic eddies generated by the inner edge of the EAC in SEQ each year (Ribbe and Brieva 2016), and stochastic structures occurring in the nearshore coastal ocean.

4.3. Management applications and future directions

Our results provide valuable insight that could be used to inform management practices within the Queensland Shark Control Program. Currently, the program uses a reactive management strategy

for humpback whale entanglements, whereby the entanglement of a whale in a net triggers the dispatch of the marine animal release team. We suggest that management techniques should shift to a proactive approach under the paradigm of dynamic ocean management, defined as management that changes in space and time in response to changes in environmental conditions (Maxwell et al., 2015). Recently developed predictive tools under dynamic ocean management include WhaleWatch (Hazen et al., 2016) and EcoCast (Hazen et al., 2018), both of which predict species distributions using real-time remote-sensing data. Our results open the door to the development of a similar predictive tool capable of near-casting whale entanglements using real-time data, in the face of changing ocean conditions. This is important because it could allow us to respond to uncertainty in whale behaviour and navigation as conditions change.

On longer time scales, the EAC is predicted to strengthen, warm and intensify under climate change (Cai et al., 2005), with unknown effects on whale navigation cues and therefore unknown changes in risk of entanglement. Continuous, near-real time satellite and ocean model monitoring of the East Australian Current could inform managers of periods of increased risk of entanglement, allowing the monitoring or removal of shark-control nets to reduce whale entanglement, thereby improving conservation outcomes for humpback whales.

5. Acknowledgements

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7. Appendix

Appendix 1. RSEC Author Guidelines

Remote Sensing in Ecology and Conservation – Steps to Publication

Original research articles – maximum of **5000 words,** excluding acknowledgements, references, tables, and figure and table legends

GENERAL INSTRUCTIONS

Author declaration

Remote Sensing in Ecology and Conservation requires a declaration that all authors on the paper have seen and approved the submitted version of the manuscript, that all authors have substantially contributed to the work, and that all persons entitled to co-authorship have been included.

Authors must also confirm that the manuscript has been submitted solely to *Remote Sensing in Ecology and Conservation* and that it has not been published elsewhere, either in part or whole, nor is it in press or under consideration for publication in another journal.

Manuscript preparation

Manuscripts must be submitted in grammatically correct English. Manuscripts that do not meet this standard cannot be reviewed. Authors for whom English is a second language may wish to consult an English-speaking colleague or consider having their manuscript professionally edited before submission to improve the English. A list of independent suppliers of editing services can be found at http://authorservices.wiley.com/bauthor/english_language.asp. All services are paid for and arranged by the author, and use of one of these services does not guarantee acceptance or preference for publication.

We place very few restrictions on the way in which you prepare your article, and it is not necessary to try to replicate the layout of the journal in your submission. We ask only that you consider your reviewers by supplying your manuscript in a clear, generic and readable layout, and ensure that all relevant sections are included. Our production process will take care of all aspects of formatting and style. The list below can be used as a checklist to ensure that the manuscript has all the information necessary for successful publication.

- Title page, including a concise and informative title, authors' names, authors' affiliations, and contact information*
- Running title not exceeding 45 characters
- Word count of the entire paper broken down into main text, acknowledgements, references, tables and figure legends
- Number of tables and figures
- Abstract (maximum 300 words) and 4–6 keywords
- Cover letter detailing the key findings, the novelty of the work and how the manuscript fits the aims and scope of the journal
- Text (Introduction, Materials and Methods, Results, Discussion)
- Acknowledgements, including details of funding bodies with grant numbers
- Data accessibility
- Literature cited (see below for tips on references)

- Figure legends
- Tables (may be sent as a separate file if necessary)
- Figures

*You will be asked to provide the full address information for the corresponding author. Please be sure to do this, as the processing of your manuscript may be delayed without complete address information for the corresponding author.

Abstract (maximum 300 words) should outline the purpose of the paper and the main results and conclusions, using clear and factual statements. Abstracts are expected to set the context and need for the work; indicate the approach and methods used; outline the main results; and identify the wider implications (including, if adequate, the relevance to management or policy).

Keywords (4-6) should include the central terms and concepts of your work that enable your target audience to discover your paper.

Introduction should introduce the reader to the aims and context for the work described.

Materials and Methods should be sufficient to allow the work to be replicated, but should not repeat information described fully elsewhere.

Results should be restricted to a factual account of the findings obtained; the text must not duplicate information given in Tables and Figures.

Discussion should point out the importance of the results and place them in the context of previous knowledge. This section should highlight the wider implications of the key findings; it can also include clear recommendations for management or policy.

References

As with the main body of text, the completeness and content of your reference list is more important than the format chosen. A clear and consistent, generic style will assist the accuracy of our production processes and produce the highest quality published work, but it is not necessary to try to replicate the journal's own style, which is applied during the production process. If you use bibliographic software to generate your reference list, select a standard output style, and check that it produces full and comprehensive reference listings.

Online resources

References to online research articles should always include a DOI, where available. When referring to other web pages, it is useful to include a date on which the resource was accessed.

Tables & Figures

All tables and figures must be cited in the text in the order that they should appear.

Metric system

The metric system should be used for all measurements, weights, etc. Temperatures should be expressed in degrees Celsius (centigrade).

Appendix 2. RSEC cover letter

<div align="right">

Jessica Bolin
Global Change Ecology Research Group
90 Sippy Downs Drive, University of the Sunshine Coast,
Sippy Downs, QLD, Australia 4556

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23rd October 2018

Dear Dr. Nathalie Pettorelli,

We wish to submit our original research article entitled "A current affair: Associations between the East Australian Current and humpback whale entanglement in Southeast Queensland shark-control nets" for consideration by *Remote Sensing in Ecology and Conservation*.

In this paper, we present a novel, multivariate, data-driven approach to delineate the position of the inshore edge and core of the East Australian Current (EAC) on a daily basis, and investigate associations between characteristics of the EAC and probability of whale entanglements in shark-control nets. We show that humpback whale entanglement probability increases when the EAC edge is less structured and closer to shore in the vicinity of the corresponding shark-control net, when the EAC core is less structured, and when our model algorithms explain large amounts of variance, indicating defined oceanic structure in the study area. We also report an interaction indicating that more oceanic structure beyond the EAC edge lessens the influence of the edge structure on entanglement probability.

These are important findings, because they support the emerging idea that humpback whales may use the edge of the EAC, and by extension, fronts and temperature gradients, as a navigation tool, providing valuable insight that may be used to inform management practices within the Queensland Shark Control Program.

We believe that this manuscript is appropriate for publication by *Remote Sensing in Ecology and Conservation* because, to our knowledge, this is the first study globally to interface satellite data, ocean reanalysis data and entanglement records to quantify linkages between oceanography and entanglements in shark-control nets. Our remote-sensing based algorithms are relevant for understanding drivers of humpback whale entanglements, thus opening the door to the development of a predictive tool capable of near-casting whale entanglements using real-time remote sensing data, in the face of changing ocean conditions. Our methods may also be extended for use in other marine species and oceanographic domains.

We confirm that this work is original and has not been published elsewhere, nor is it currently under consideration for publication elsewhere.

Please address all correspondence concerning this manuscript to me at jab055@student.usc.edu.au.

Thank you for your consideration of this manuscript.

Sincerely,

Jessica Bolin