Oceanographic influences on a global whale shark hotspot in southern Mozambique

Coastal aggregations of whale sharks *Rhincodon typus* around the world are generally seasonal and driven by prey availability. At a major aggregation site in southern Mozambique, whale sharks are, somewhat unusually, present and seen feeding throughout the year. We investigated potential oceanographic mechanisms that may regulate prey availability on the narrow regional shelf and hence account for this year-round whale shark hotspot. We used regional aerial surveys to show that the highest density of whale sharks (29 sharks 100 km^{-1}) was near Praia do Tofo (23.85˚S, 35.55˚E). To investigate how the regional oceanography influences the enrichment of shelf waters, we used 5- and 9-year time series of hourly underwater temperature, and 10-year time series of remotely-sensed sea surface temperature, chlorophyll-*a* concentration and sea surface height anomaly data. We found that upwelling of cool, nutrient-rich water was common in the region throughout the year and describe three mechanisms, all of which are likely to stimulate productivity: (1) Shelf-edge upwelling and subsequent elevated plankton biomass in coastal waters north of Praia do Tofo, driven by the interaction of southward-propagating mesoscale eddies with the narrow shelf. *In situ* temperature data show that this interaction frequently leads to intense upwelling, up to 7.5˚C daily amplitude, throughout the year, but is most pronounced in spring/summer. (2) Divergent upwelling south of Praia do Tofo driven by the current flow along the shelf edge as it diverges from the coastline. This upwelling can occur throughout the year and is similar in intensity, but less frequent, than the shelf-edge upwelling. (3) Vortex-driven upwelling by the Delagoa Bight lee-eddy, which may increase phytoplankton biomass in the Bight and also force a northward coastal current that transports recently-upwelled water towards Praia do Tofo. We hypothesise that whale sharks aggregate in coastal waters around Praia do Tofo throughout the year because these upwelling mechanisms contribute to year-round productivity in the region.

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Oceanographic influences on a global whale shark hotspot in southern Mozambique

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INTRODUCTION

Large planktivorous animals aggregate to feed on seasonally abundant, high-density zooplankton patches. In higher latitude systems, baleen whales forage on euphausiids during summer toward the poles (Murase et al., 2002) and basking sharks *Cetorhinus maximus* target dense prey patches in the temperate Atlantic Ocean during summer (Sims & Quayle, 1998). At these latitudes, sunlight and temperature are the major drivers for the regular, seasonal, high zooplankton abundance. In the comparatively nutrient-poor tropics and subtropics, planktivore aggregations are also typically strongly seasonal, generally associated with physical and biological oceanographic features, such as upwelling or thermal fronts, that concentrate productivity. Reef manta rays *Manta alfredi* in the Maldives feed on zooplankton on the downstream side of the atolls and change their location according to the seasonally reversing monsoon currents (Anderson, Shiham & Goes, 2011). Similarly, whale shark aggregations in the tropics and subtropics usually coincide with seasonal biological events, such as fish or crab spawning (Meekan et al., 2009; de la Parra Venegas et al., 2011; Robinson et al., 2013) driven by oceanographic and climatic processes. While the specific drivers of whale shark aggregations vary among sites, well-defined seasonality is a general paradigm.

Unusually, there is one major whale shark aggregation, in southern Mozambique, where whale sharks are found and observed feeding all year round. Similar to other coastal whale shark aggregations, the area off Praia do Tofo in the Inhambane Province is frequented by mostly juvenile males from 3–9.5 m in length (Rohner et al. submitted) that feed on coastal and deep-water zooplankton (Rohner et al., 2013a). Unlike other aggregation sites, there is no seasonality in whale shark sightings here (Rohner et al., 2013b) (Fig. 1). No specific biological event, such as fish spawning, was evident to account for the sharks' presence along this coast, and modelled local-scale bio-physical parameters had a poor explanatory power for whale shark sightings (Rohner et al., 2013b). Whale sharks were observed feeding at the surface throughout the year on ~20% of encounters (n=689, 2008–2010; Haskell et al., 2014) and individual sharks are seen only for 2–3 days before they move elsewhere (SJP unpubl.), indicating that event-scale, short-term drivers might explain their sightings in this region.

Abundant zooplankton as prey for whale sharks off the Inhambane coast is likely to be driven by physical processes. With no significant river inflows within 230 km of Praia do Tofo, upwelling of nutrient-enriched waters could be the key process for planktonic enrichments in this coastal region. We therefore identified and investigated three potential upwelling mechanisms in the southern Mozambique Channel, which can enhance plankton biomass on the shelf and hence account for this whale shark hotspot. We examined the temporal extent of these upwelling mechanisms to see whether they, as the whale shark sightings, were also event-driven with no seasonality. The mechanisms leading to productivity in the area and their seasonality are relatively little studied.

Upwelling in the region is likely to be linked to the hydrodynamics of the Mozambique Channel (MC). This region is governed by highly dynamic flow fields rather than by a characteristic western boundary current (Quartly & Srokosz, 2004; Lutjeharms, 2007). De Ruijter *et al.* (2002) first demonstrated that the flow through the MC mainly comprises large (>300 km diameter) anticyclonic eddies. Each year, 4–5 eddies propagate southwards at a speed of 3–6 km d^{-1} along the Mozambique coast (Schouten et al., 2002; Backeberg & Reason, 2010). Their course is constrained by the bathymetry of the MC, with the mid-channel islands of Bassas da India and Île Europa restricting their paths to the Mozambican side (Ridderinkhof & Ruijter, 2003; Quartly & Srokosz, 2004). In the southern MC, the continental shelf between Bazaruto and Praia do Tofo (Fig. 2) is narrow with a steep slope. The shelf broadens south of Praia do Tofo, in the lee of a major coastline inflection, to form an area of wide continental shelf known as the Delagoa Bight. Anticyclonic eddies in the southern MC are often preceded downstream by smaller cyclonic eddies, thus forming eddy dipoles (Roberts, Ternon & Morris, 2014). Eddies from the MC eventually merge into the Agulhas Current, often triggering a phenomenon known as the Natal Pulse (Schouten et al., 2002).

Much of the oceanographic information on the MC has been derived from case studies during research cruises and from numerical models (Ternon et al., 2014). Long-term observational data are scarce, particularly for coastal areas of the southern MC. Here, we use long-term *in situ* and satellite-derived data to investigate upwelling in this region. We provide evidence for three oceanographic mechanisms in the southern MC region that are likely to lead to high densities of zooplankton prey for whale sharks in coastal waters: (1) Shelf-edge upwelling along the narrow continental shelf to the north of Praia do Tofo; (2) Divergent upwelling where the continental shelf diverges from the coastline south of Praia do Tofo; and (3) Vortex-driven upwelling of the Delagoa Bight lee-eddy that also drives a northward coastal current towards Praia do Tofo. These three event-driven mechanisms occur throughout the year. We hypothesise that they drive intermittent dense concentrations of coastal zooplankton, which in turn explains the unusual year-round presence of whale sharks in this region.

METHODS

Whale shark data

To determine where whale sharks were most common along the Mozambique coast, data on their distribution were acquired during aerial survey flights conducted by the KwaZulu-Natal Sharks Board in a top wing aircraft, flown 305 m (1000 ft) above sea level at 184 km h^{-1} (100 knots) (Cliff et al., 2007). Ten flights were conducted between 2004 and 2008, all in either February or March to reduce seasonal influence. Flights extended from the southern border of Mozambique to the Bazaruto Archipelago in the Inhambane Province. Observers recorded time and GPS coordinates for each whale shark within ~750 m of the coast. When large aggregations of multiple sharks were observed, only the start and end GPS position were recorded. Central coordinates were used in these cases. The coastline was divided into 40 km sections for analysis, except for the southern- (260 km long) and northern-most (90 km) sections where few whale sharks were observed (see Results). Sighting rates were standardised by calculating the mean number of whale shark sightings per 100 km flown in each section. No specific approvals were required for the aerial survey.

Oceanographic data

To investigate oceanographic mechanisms that lead to enrichment in the region, we used a combination of data, including *in situ* underwater temperature, and satellite-derived sea surface temperature, chlorophyll-*a* concentration and sea surface height anomaly data.

Underwater temperature

To assess upwelling intensity and frequency, we examined hourly temperature data measured by two *in situ* underwater temperature recorders (UTRs) at Zambia Reef, off Pomene (22.77˚S, 35.58˚E, Fig. 2) and Zàvora (24.48˚S, 35.24˚E, Fig. 2). The Pomene logger at 18 m depth recorded temperatures from 5 August 2002 to 17 May 2011. The Zàvora logger, at a depth of 17 m, recorded temperatures from 22 April 2006 to 26 May 2011. These data sources are the sole long-term *in situ* temperature data records from the region; primary data are available in Appendix 1. Upwelling intensities were classified according to Berkelmans *et al.* (Berkelmans, Weeks &

Steinberg, 2010), where daily amplitudes of 0–0.5˚C was defined as no upwelling; 0.5–1˚C as low-intensity upwelling; 1–2˚C as medium-intensity; and >2˚C as high-intensity upwelling. Seasonality in upwelling intensity was assessed using the climatology of the coefficient of variation (the ratio of the standard deviation to the mean) for daily underwater temperatures. As naturally there is greater variation in daily temperature during summer when temperatures are warmer, we used the coefficient of variation to adjust for the influence of seasonal heating. Weekly anomalies were also used to investigate seasonality in upwelling.

Sea surface temperature

Sea surface temperature (SST) data were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS; http://modis.gsfc.nasa.gov) aboard the NASA Terra and Aqua satellites to produce daily SST time series at 1 km spatial resolution from July 2000 to June 2011. Five-day means and seasonal climatologies were generated from merged day- and night-time data for the southern MC region from 20˚S to 30˚S and 31˚E to 40˚E (Fig. 2). Time series of night-time only data were similarly generated to avoid potential non-representative data caused by intense daytime solar heating of the upper sea surface 'skin' during summer. To quantify the surface expression of upwelling at Zàvora, SST values were extracted for a 3x3 pixel location close to shore (centred at 24.63˚S, 35.21˚E) from the five-day mean night-time time series. To provide an oceanic baseline for comparison to inshore values, night-time SST climatologies were similarly calculated for a location 50 km offshore of Zàvora (centred at 24.63˚S, 35.73˚E). The classification of upwelling intensities was the same as for the UTR data, except that high-intensity upwelling was defined as negative temperature spikes of >1˚C between subsequent five-day means since the surface signal was subdued compared to that at depth.

Sea surface height anomalies

Weekly delayed-time mean sea level anomaly (SSHA) data from the Reference series (Delayed Time-Maps of Sea Level Anomalies "Ref") for July 2000 to July 2011 were used to study the eddy features in the southern MC (Fig. 2; 20˚S–30˚S; 31˚E–40˚E). The dataset has a spatial resolution of 0.25˚ (~27.5 km at the Equator), and is distributed by Archiving, Validation and Interpretation of Satellite Oceanographic data (AVISO; http://www.aviso.oceanobs.com/en/data/products). To determine the number of eddies propagating southward, latitude- and longitude-time averaged Hovmoeller plots were generated along the 37.25˚E (between 22.0˚S–24.75˚S) and the 22.75˚S (between 35.5˚E–40.0˚E) transect lines. Anticyclonic eddies were defined as having a minimum positive core anomaly of +20 cm and cyclonic eddies as having a maximum core height of -20 cm. The proximity of the core of the eddy relative to the coast was determined on the longitude-time Hovmoeller plot.

Chlorophyll-a concentration

To estimate productivity in the region, we used Chlorophyll-*a* concentration (chl-*a*) derived from MODIS Aqua data and generated daily time series at 1 km spatial resolution for July 2002 to June 2011. A latitude-time averaged Hovmoeller plot was generated for chl-*a* on the southern Mozambique inner continental shelf (from the coast out to the 100 m isobath) between 22.0°S and 27.0°S. Bays and shallow waters (<20 m) were excluded to avoid potential terrestrial or coastal riverine contamination. Eight-year means were calculated for the shelf (0–100 m isobath) and off the shelf (200 m isobath to 37˚E) from 22˚S-25˚S.

RESULTS

Whale shark aggregation

Flight observers recorded a total of 202 whale sharks in southern Mozambique during the 10 aerial surveys conducted between 2004 and 2008, with a mean of 3.4 individuals 100 km^{-1}. The hotspot of whale shark sightings was Praia do Tofo, where 29.25 sharks 100 km^{-1} were observed in the adjacent 40 km section of coast (Fig. 3). Here, several large aggregations were observed, with the largest being 51 individuals on 1 March 2005. The southernmost extent of coastal whale shark sightings was Zàvora (24.5˚S) and the northern limit Pomene (22.8˚S).

In situ time series: Underwater temperature

Daily mean *in situ* temperatures at Pomene (18 m depth) and Zàvora (17 m depth) showed seasonal amplitudes of ~8˚C. There were numerous cool-water events at Pomene (daily amplitudes up to 7.5˚C, Fig. 4A) and Zàvora (up to 6.5˚C, Fig. 4B). Stable temperatures with no upwelling were recorded for 33.8% of the total 3206 days at Pomene and for 37.8% of 1860 days at Zàvora. Low intensity upwelling was recorded on 17.8% and 21% of days, and medium-intensity upwelling on 19.5% and 26.7% of days at Pomene and Zàvora, respectively. High-intensity upwelling was experienced on 28.9% and 14.5% of days, respectively. There were pronounced events in all seasons at both locations (Fig. 4A,B), although spring and summer had the most intense upwelling (Fig. 4C).

Upwelling, eddies and the coastal current: Sea surface temperature from satellite

Subsurface upwelling did not always reach the surface, but when it did, the expression was most apparent in the Zàvora area. There, the spatial extent of the upwelling signal varied, but usually extended southwards from Zàvora out to the 100 m bathymetric contour (Fig. 5A). Further, the surface expression of a cyclonic eddy feature in the Delagoa Bight was frequently apparent in SST images, as shown by the example for 26–30 May 2007 (Fig. 5B). Both the Delagoa Bight eddy signal and that of the associated northward coastal current were clearly evident even in the long-term mean temperature distributions (e.g. 11-year winter climatology in Fig. 5C). Seasonal SST climatologies showed cool water extending along the coast of the Delagoa Bight, with the northern extent of this cool band extending beyond Zàvora towards Praia do Tofo.

Spatial and temporal variation in eddies: Sea surface height anomaly

The number of anticyclonic eddies propagating southward between the coast and 40˚E decreased from north to south (Fig. 6A). At the northern limit of the study region (22.00˚S), 36 anticyclones were identified over the 11-year study period, 34 off Pomene (22.77˚S), and 27 off Praia do Tofo (23.85˚S). The inter-annual variation was large off Pomene, ranging from no anticyclones in 2001 to 6 in 2006. More anticyclones were detected in warmer than in colder months ($t = 2.2779$, $df = 21.806$, $p = 0.03$), with 11 anticyclones in spring and 11 in summer, while 7 were detected in autumn and 5 in winter. The proximity of the centre of the anticyclonic eddies to the Pomene coast varied mostly between 36.5˚E and 38˚E, or a distance of ~100–250 km (Fig. 6B).

Productivity in the region: Chlorophyll-a concentration

The highest chl-*a* on the inner continental shelf was identified directly offshore and slightly to the north of Zàvora (Fig. 7). There, the maximum monthly mean chl-*a* concentration was ~8 mg m^{-3}. Chl-*a* was seasonal and most pronounced at Zàvora, where chl-*a* peaked in late austral winter, during August and September (Fig. 7). We found no strong or seasonal chl-*a* signal directly off Praia do Tofo. The long-term mean chl-*a* on the inner shelf (0–100 m depth) between Bazaruto and Zàvora was 0.6 mg m^{-3} compared to 0.14 mg m^{-3} off the shelf (200 m depth to 37˚E).

DISCUSSION

The highest density of whale sharks in the coastal waters of southern Mozambique was in the Praia do Tofo area. Whale sharks are sighted here throughout the year, indicating that no seasonal, well-defined biological enrichment event, such as fish spawning, was responsible for whale sharks frequenting the area, as observed at other whale shark aggregation sites. We describe three regional, event-driven, aperiodic upwelling mechanisms that enhance plankton biomass in this region (Table I), and thus drive the high productivity that could explain the lack of seasonality in whale shark presence.

Whale shark aggregation

Aerial surveys showed that whale sharks in southern Mozambique are concentrated along a 200 km stretch of coast from Zàvora to Pomene, with the highest observed density around the centre at Praia do Tofo. The mean density of whale shark sightings of 29.3 sharks 100 km^{-1} around Praia do Tofo was similar to the highest monthly value recorded from aerial surveys at Mahé Island in the Seychelles of ~20 sharks 100 km^{-1} [14.4 h^{-1}, at 70 km h^{-1} flying speed; 29]. There were many more whale sharks in southern Mozambique than observed from aerial surveys in the northern part of South Africa (0.5 sharks 100 km^{-1}) or the summer peak in the far northern section of KwaZulu-Natal [1.1 sharks 100 km^{-1}; 27]. The southern Mozambican coastline also hosts large aggregations of reef (*Manta alfredi*) and giant manta rays (*M. birostris*) (Marshall, Compagno & Bennett, 2009; Marshall, Dudgeon & Bennett, 2011), indicating that it provides suitable habitat for high densities of large planktivores.

Although our aerial surveys were temporally biased by only being conducted in February/March, and over a short five-year timeframe, anecdotal reports from dive centres along this coast indicate that there are whale shark aggregations at various locations between Zàvora and Bazaruto throughout the year. Increased aerial survey effort and electronic tracking of individual sharks (Brunnschweiler et al., 2009) can be used to investigate this further.

We identified three oceanographic mechanisms that are event-based and that exhibit relatively little seasonality, which may explain the lack of seasonality and high temporal variability in whale shark sightings at Praia do Tofo (Rohner et al., 2013b).

1. Shelf-edge upwelling

The frequency of high-intensity upwelling on the narrow northern shelf at Pomene was high and double that found further south at Zàvora (i.e. 28.9% vs. 14.5% of days). This suggests that this shelf region is particularly dynamic compared with other regions. Only ~1% of observations exhibited high-intensity upwelling along the central Great Barrier Reef (Australia), a tropical system influenced by the East Australian Current, an analogous western boundary current system (Berkelmans et al., 2010). In the present study, the seasonal increase in upwelling intensity in spring and summer coincided with a seasonal increase in eddy frequency and intensity, suggesting that upwelling along the narrow shelf is mainly driven by eddies. This corroborates work by Roberts *et al.* (2014) which describes dipole-driven shelf-edge upwelling in this region. These authors, based on a case study from April–May 2005, suggested that regional upwelling was linked to the leading edge of anticyclones, to eddy dipoles, and to the trailing edge of cyclonic eddies.

Our long-term SSHA and temperature logger datasets show that this shelf-edge upwelling mechanism operates frequently and is the likely driver for enhancing plankton availability on the narrow shelf off Pomene. From July 2000 to July 2011, we identified 34 anticyclonic eddies moving along this narrow shelf. However, upwelling was also observed in the absence of anticyclones, perhaps driven by cyclonic eddies (Roberts et al., 2014) or by weak anticyclones not detected in our analyses. We focused on anticyclones for the SSHA analysis as eddies in southern Mozambique often propagate as dipoles, and the smaller cyclones can dissipate, or track closer to shore, and are thus not as readily detectable in altimetry data (Halo et al., 2013; Roberts et al., 2014). Similar to our study, Schouten *et al.* (2003) found a north-south decrease in eddy numbers over a larger region spanning the whole MC and suggested that some eddies dissipated or merged with others at ~20˚S. This may explain why we found ~3 eddies per year in our study area in the southern MC compared to 4–5 per year previously described for the whole MC (de Ruijter et al., 2002; Schouten et al., 2003). Previous studies did not report their SSHA definitions of an anticyclone, which may lead to different counts and highlights the need for reporting the SSHA definitions in use. Our limit of +20 cm was selected based on visual assessment of SSHA time series in the region, operating under the assumption that weak eddies are unlikely to have a significant influence on the whale shark aggregation. Some weak anticyclonic eddies were therefore excluded, especially in colder months, due to our strict classification. The seasonality in eddy intensity, as measured by their core height, can explain the seasonal trend towards more intense coastal upwelling in spring and summer.

Shelf-edge upwelling along the narrow shelf is likely to play a major role in increasing prey availability for whale sharks at Praia do Tofo. Nutrient enrichment and the associated phytoplankton biomass increase are direct responses to shelf-edge upwelling here (Roberts et al., 2014) and are likely to lead to subsequent zooplankton abundance increase downstream (Flagg, Wirick & Smith, 1994). Such presumed links between upwelling, zooplankton abundance and planktivorous megafauna have also been indicated by others in different regions (Squire, 1990; Taylor & Pearce, 1999).

2. Divergent upwelling

The numerous upwelling events at Zàvora, south of Praia do Tofo, support our hypothesis that divergent upwelling is a key driver of increased plankton biomass in this region. The southward flow in the south-western MC has previously been suggested to follow the continental shelf edge (Lutjeharms, 2007), maintaining its path along the shelf edge where the coastline diverges and the shelf broadens at ~24˚S, advecting surface waters offshore. These waters would be replenished with cold, nutrient-rich water from beneath the thermocline, forced onto the continental shelf (Bakun, 1996). Similar scenarios, where the main current trajectory moves along a widening shelf resulting in upwelling, have been described for the Agulhas Current near Cape St Lucia, South Africa (Lutjeharms, Cooper & Roberts, 2000), and the East Madagascar Current (Lutjeharms & Machu, 2000). Because the flow in the MC is dominated by mesoscale eddies rather than a well-defined western boundary current, the divergent upwelling at Zàvora is likely to be event-driven. When anticyclonic eddies are embedded in the flow, divergent upwelling is likely to be enhanced by an intensified flow along the shelf edge. Although no current meter data are available for the area, temperature logger data from Zàvora support such an event-driven nature of this upwelling mechanism.

High-intensity upwelling events were apparent in both the UTR and SST data, but the surface expression of upwelling was less pronounced than the daily amplitudes at depth. Similar differences between *in situ* and SST upwelling signatures have been found in northern Mozambique (Malauene et al., 2014) and off Port Alfred at the inshore edge of the Agulhas Current (Lutjeharms et al., 2000). Only pronounced upwelling events lead to a surface expression. Less intense events might not reach the surface, high solar insolation may result in thermal capping of some waters during weak upwelling especially under low wind conditions, or the surface signal may be masked as a result of compositing SST data into 5-day means.

The seasonality in upwelling intensity at Zàvora was similar to that at Pomene, hence this location may also be influenced by seasonally intensified eddies. Our SSHA analysis shows a trend towards more eddies propagating through the southern MC during spring and summer. These would provide a seasonal influence on the divergent upwelling observed in the UTR and SST data. Chl-*a*, however, peaked in late winter irrespective of upwelling activity at Zàvora, suggesting that temperature data may provide a better measure of upwelling here than chl-*a* data. This is likely because winter is often associated with stronger winds, leading to increased vertical mixing of the shallow shelf waters and hence an increased chl-*a* signal. Other drivers of high chl-*a* at Zàvora may include transport of chlorophyll-rich water by the coastal northward current (Lutjeharms & da Silva, 1988) or direct leaching of nutrients from coastal lakes.

For divergent upwelling at Zàvora to influence plankton densities and whale sharks at Praia do Tofo, upwelled water must be transported northward by a coastal current. As such, prey for whale sharks will be concentrated on the narrow shelf north of Zàvora rather than in the upwelling cell itself, because of the temporal and spatial displacement between upwelling, phyto- and zooplankton (Flagg et al., 1994). This northward coastal current in the Delagoa Bight is driven by the cyclonic eddy [42].

3. Delagoa Bight upwelling

The Delagoa Bight cyclonic lee-eddy was evident in the SST and chl-*a* signals, both on an event-scale and in long-term climatologies. That the signal is evident even in our 11-year climatologies indicates that this eddy is frequently present. Case studies have suggested this eddy is a result of the coastline divergence from the continental shelf edge (Lutjeharms & da Silva, 1988). A boundary flow along the shelf slope, as a result of lateral stress, will spin up a cyclonic eddy in the Bight. This will invoke an upward doming of the thermocline in the eddy centre, moving cool, nutrient-rich water into the photic zone (Lamont et al., 2010; Weeks et al., 2010). This nutrient enrichment of surface waters increases phytoplankton concentrations in the Bight (Barlow et al., 2008).

Satellite SST, SSHA and Chl-*a* indicate that the cyclonic nature of the lee-eddy forces a north-eastward coastal current along the entire northern margin of the Bight towards Praia do Tofo. Short-term *in situ* case studies corroborate this (Lamont et al., 2010). Similar to the two upwelling mechanisms described previously, the Delagoa Bight eddy is driven by infrequent anticyclonic eddies propagating southward along the shelf edge (Quartly & Srokosz, 2004; Lamont et al., 2010). This implies that the production transported to Praia do Tofo will be intermittent and vary in concentration depending on the intensity of the boundary southward flow.

The Delagoa Bight eddy may strongly influence the whale shark aggregation at Praia do Tofo by enhancing the regional phytoplankton (and hence zooplankton) concentrations (Kyewalyanga et al., 2007) and, importantly, forcing the northward coastal current on the shelf. This current may be responsible for transporting phytoplankton-rich water from the Bight and the Zàvora upwelling cell towards Praia do Tofo (Lutjeharms & da Silva, 1988). A case study previously confirmed that this current can contribute to the cool, high chl-*a* water at the northern extent of the Bight (Lamont et al., 2010). Our SST climatologies suggested that the northernmost extent of the coastal current varied, but continued well past Zàvora and may reach Praia do Tofo. Climatology data also support the presence of the coastal northward current along the Delagoa Bight coast throughout the year. Although a northward current was only rarely recorded by SCUBA divers at Praia do Tofo itself (6.5%, n=760; A. Marshall, personal communication), this current is likely to be more persistent on the shelf below the 20–30 m depth commonly reached by divers (Lamont et al., 2010).

Conclusion

Our analyses advance our understanding of the influence of mesoscale features on coastal upwelling in the dynamic MC, and their potential influence on whale shark presence in the region. This study showed that whale shark sightings are high along the coast from Zàvora to Pomene, with the hotspot at Praia do Tofo. At this location, whale sharks are found feeding all year round. The three oceanographic mechanisms described here create intense and frequent upwelling on the shelf in this region and regularly stimulate phytoplankton biomass and thus create favourable conditions for zooplankton populations for whale sharks to feed upon. These event-based upwelling mechanisms that are found throughout the year are all likely to contribute to the productivity at Praia do Tofo and thus explain the unusual year-round shark sightings and feeding.

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Figure legends

Fig. 1. Whale shark sightings off Praia do Tofo. (A) Sightings over 720 trips between 2005 and 2011; (B) mean monthly sightings per observation trip with SD error bars (adapted from Rohner et al., 2013b).

Fig. 2. The study region in southern Mozambique, showing locations, underwater temperature recorders, oceanographic features and the 200 m (solid black contour) and 1000 m isobaths (solid grey contour).

Fig. 3. Density of whale sharks (individuals km^{-1}) along the coast of southern Mozambique as estimated from aerial survey flights in February and March from 2004–2008. Each sector was 40 km long, except ([a]) from 22.67 – 22.02˚S at 90 km and ([b]) 25.96 to 24.62˚S at 260 km.

Fig. 4. Daily mean *in situ* (UTR) temperatures at (A) Pomene and (B) at Zàvora showing the seasonal cycle as well as pronounced temperature fluctuations throughout the year (note different temperature scales). (C) Climatology of daily coefficients of variation in UTR data (black = Pomene, blue = Zàvora), showing seasonality in upwelling intensity.

Fig. 5. (A) Three-day mean SST image from 30 January to 1 February 2007, showing the spatial extent in the surface expression of a pronounced upwelling event at Zàvora. (B) The Delagoa Bight lee-eddy seen in five-day mean night-time only SST images for 26-30 May 20. (C) Three-monthly mean SST night-time only climatology for southern Mozambique during winter (July–September, 2000-11), suggesting a coastal northward current extending past Zàvora.

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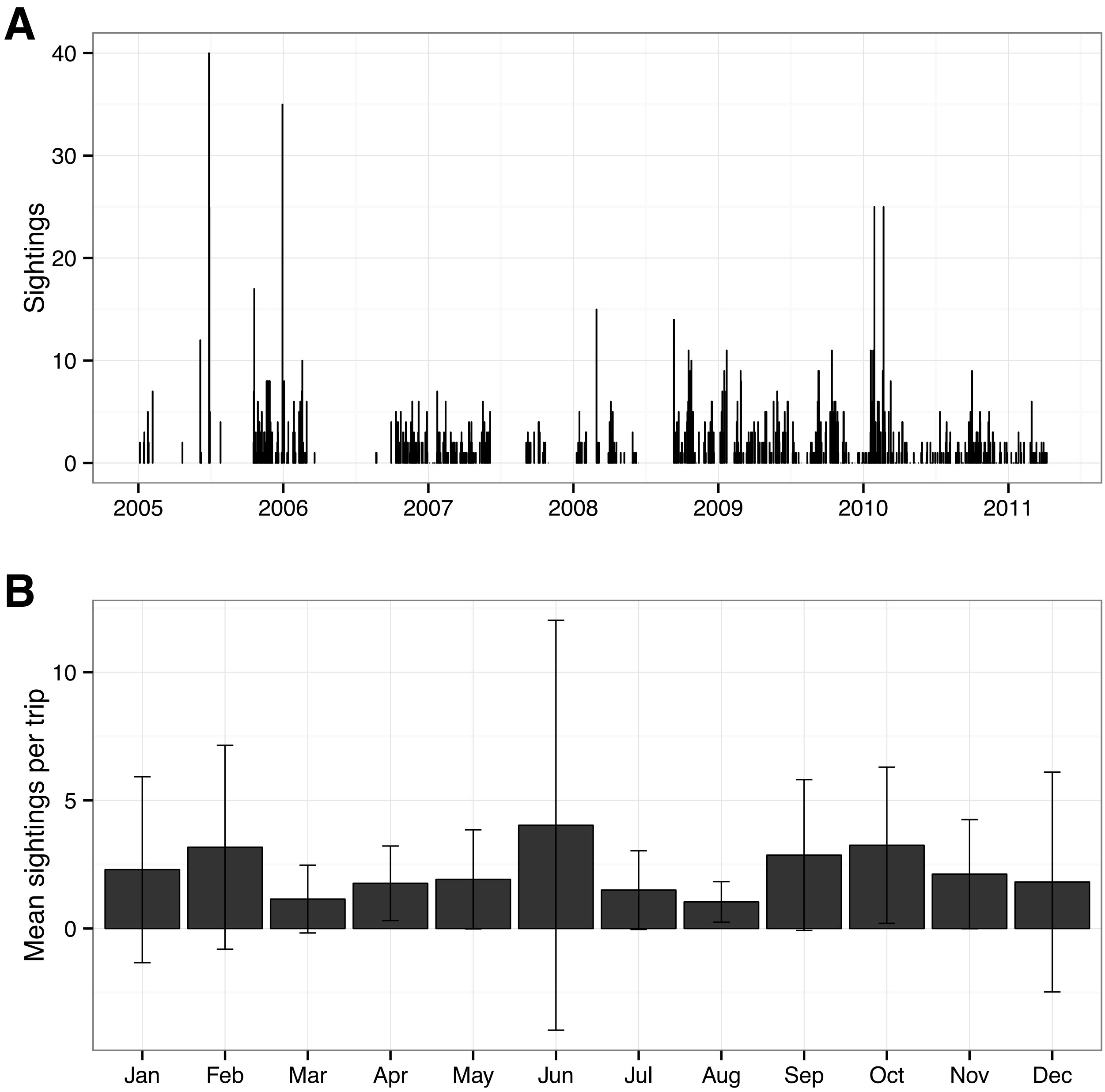

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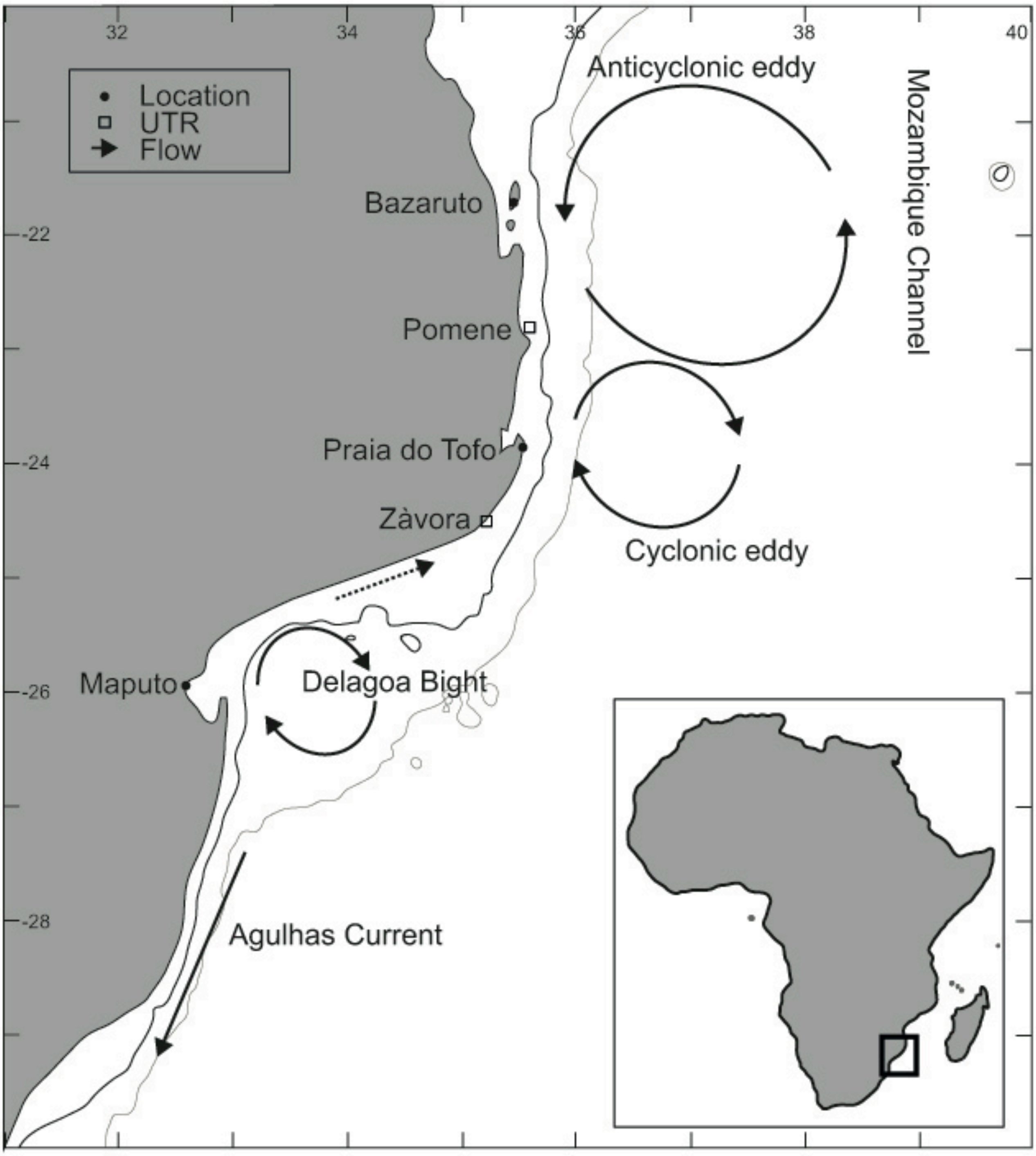

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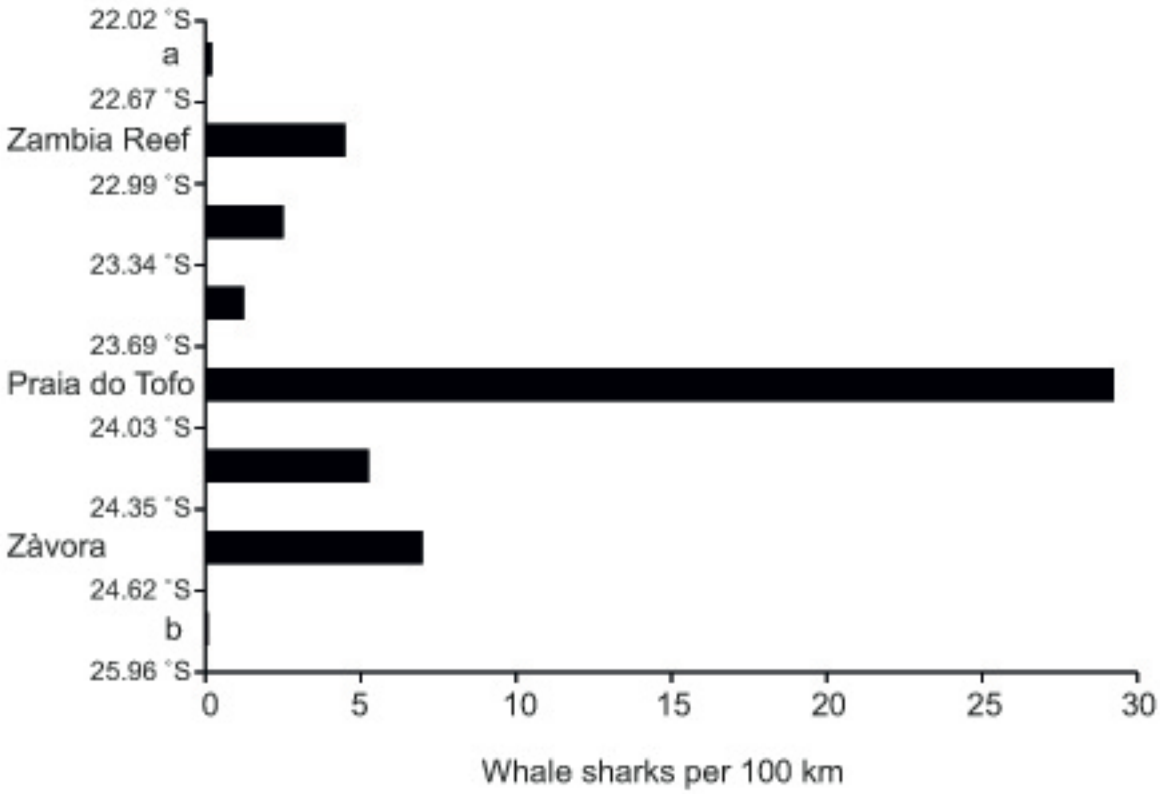

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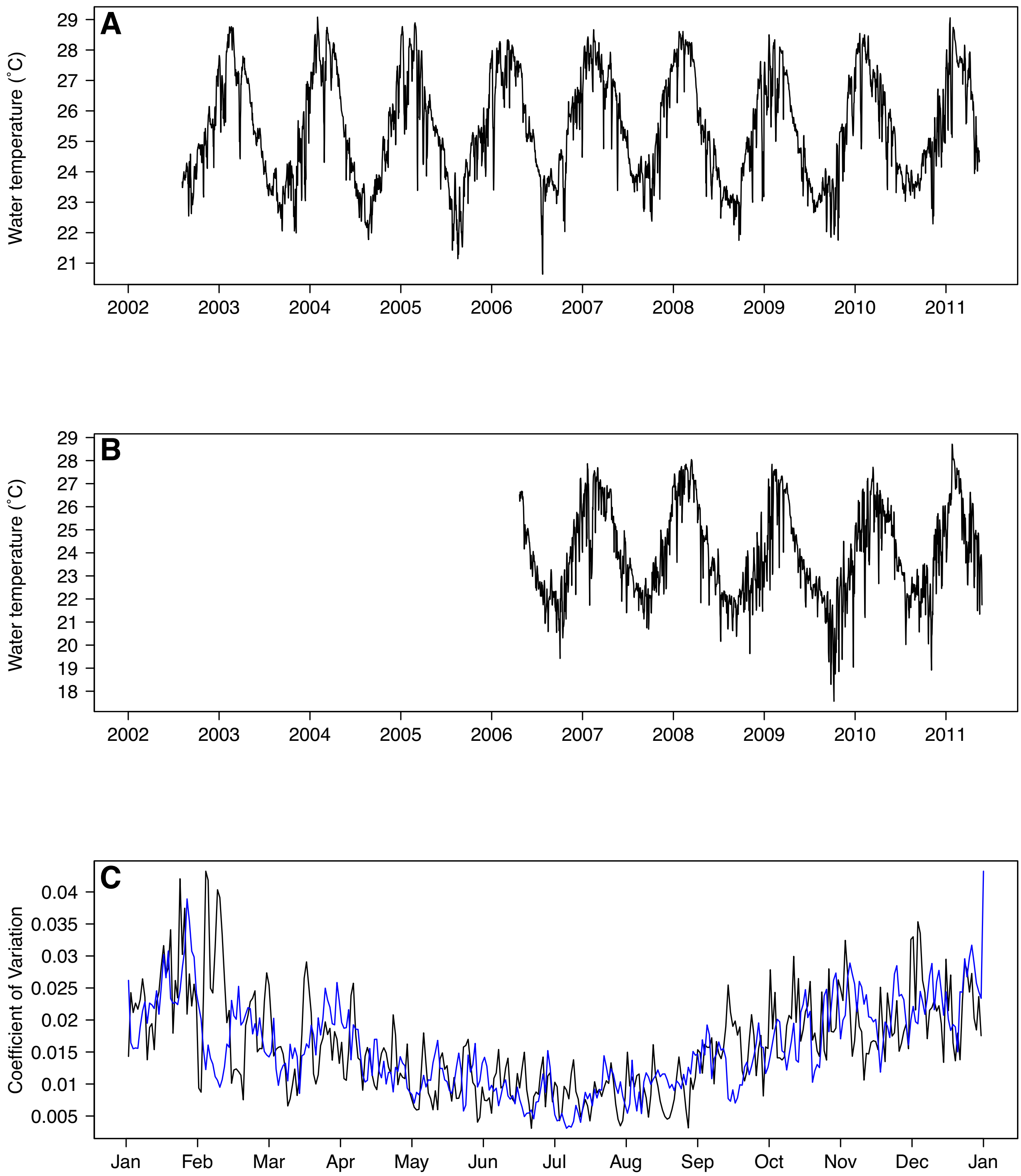

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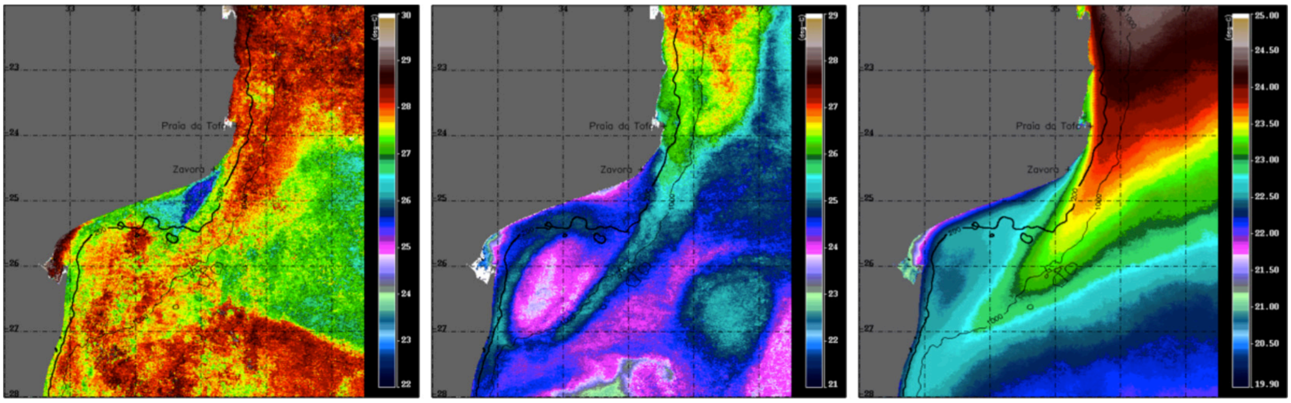

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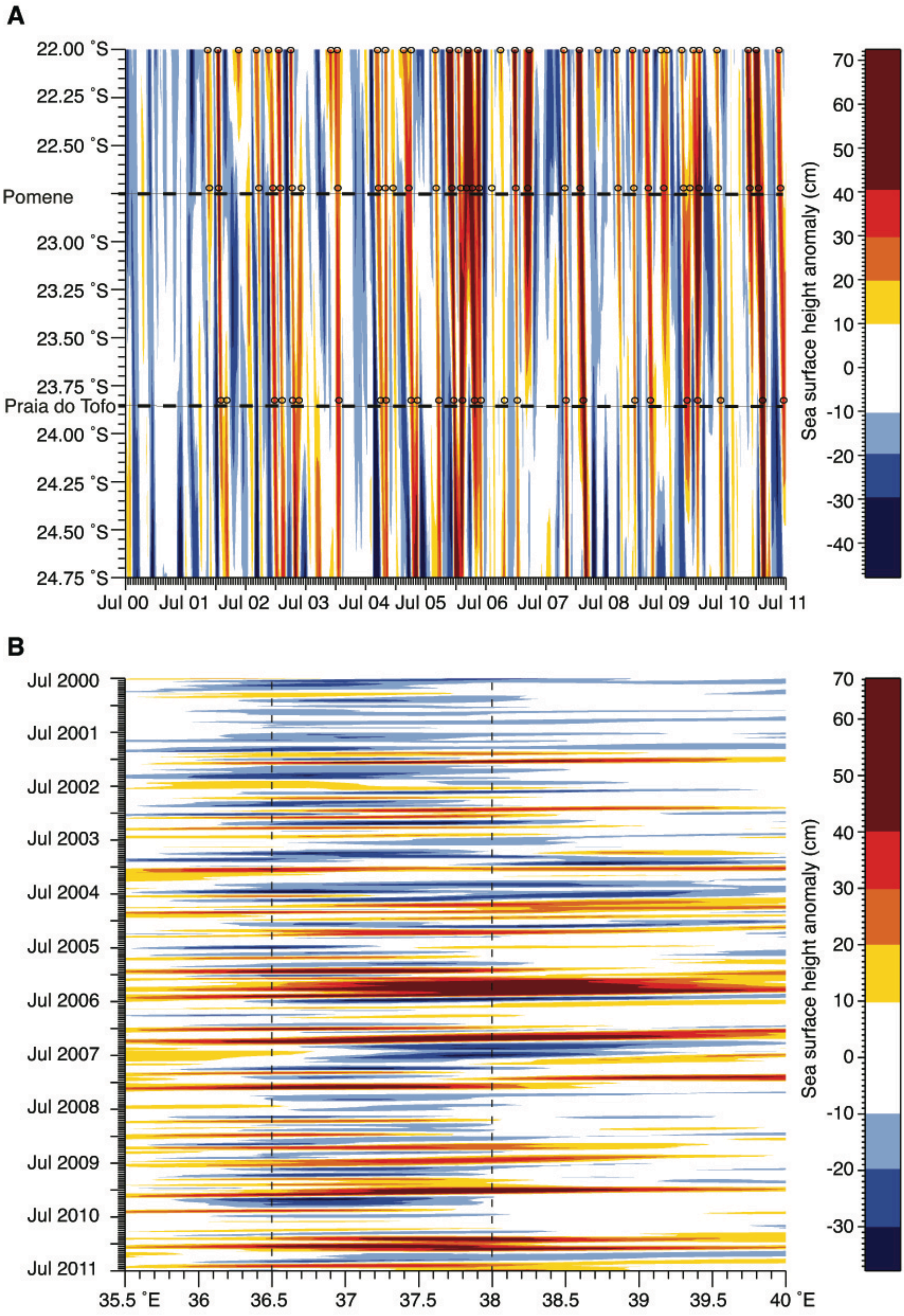
A
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Praia do Tofo
24.00 ˚S
24.25 ˚S
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Sea surface height anomaly (cm)
70 60 50 40 30 20 10 0 -10 -20 -30 -40
B
Jul 2000
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Jul 2011
35.5 ˚E 36 36.5 37 37.5 38 38.5 39 39.5 40 ˚E
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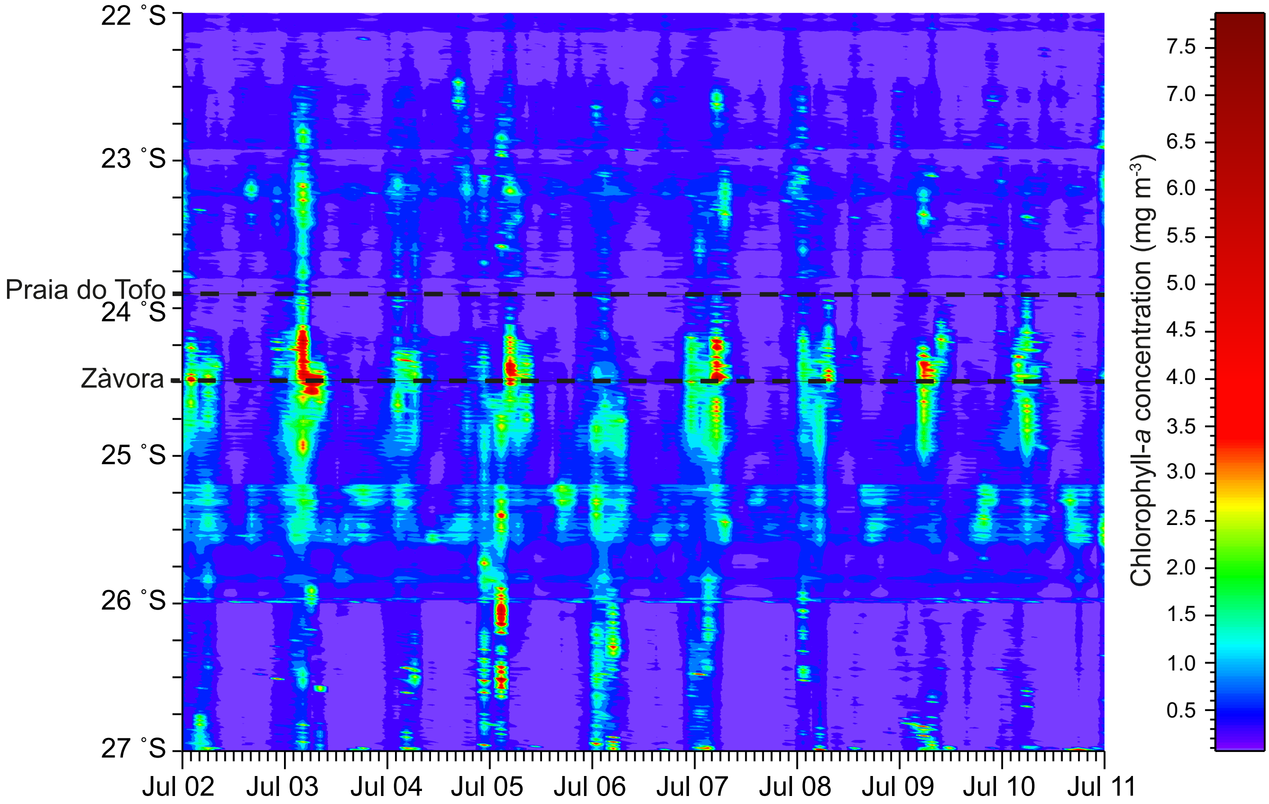

Table I. Description of upwelling mechanisms in the southern Mozambique Channel. *Indicates that no in situ temperature data were available.

Upwelling	Oceanographic mechanism	Frequency of intense upwelling (daily amplitude >2˚C)	Occurrence	Seasonal peak	Proposed by	Type
1. Shelf-edge	Mesoscale eddies interact with the narrow shelf and advect surface waters offshore	29%	Event-driven, year-round	Spring/summer	[26]	Case study
2. Divergent	Flow along shelf edge, where the shelf broadens, advects surface waters offshore. Flow is intensified by southward-propagating mesoscale eddies	15%	Event-driven, year-round	Spring/summer	This study	Long-term data
3. Delagoa Bight	Vortex-driven upwelling in the centre of a cyclonic eddy in the lee of a major coastal inflection	*	Semi-permanent	None, all year	[41]	Case studies