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PII: S0967-0645(13)00406-2
DOI: http://dx.doi.org/10.1016/j.dsr2.2013.10.012
Reference: DSRII3542

To appear in: *Deep-Sea Research II*

Cite this article as: J.F. Ternon, The Mozambique Channel: From physics to upper trophic levels, *Deep-Sea Research II*, http://dx.doi.org/10.1016/j.dsr2.2013.10.012

The Mozambique Channel: from physics to upper trophic levels

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ABSTRACT

A multidisciplinary programme, MESOBIO (Influence of **meso**scale dynamics on **bio**logical productivity at multiple trophic levels in the Mozambique Channel*)* was undertaken in the Mozambique Channel within the framework of a scientific partnership between France and South Africa. MESOBIO focused on the signature of the highly energetic eddy dynamics in the Mozambique Channel. The Channel, which is known to be one of the most turbulent areas in the world ocean, has a great diversity of marine organisms and is the site of active pelagic fisheries. MESOBIO was mostly based on observations at sea during 12 multidisciplinary cruises between 2002 and 2010. Hydrographic measurements, sampling of biological organisms ranging from phytoplankton to top predators, and experiments on primary production and energy transfer through the food web, were conducted onboard various research vessels. The data were analyzed in relation to eddy field characteristics for the periods of the cruises, including seasonal or inter-annual variability in mesoscale activity. A modeling approach was also developed within MESOBIO for both the circulation in the Channel and the biogeochemical response to eddy forcing. This paper introduces the suite of articles on the MESOBIO investigations by summarizing background knowledge for the different disciplines and the key issues that were addressed within the programme.

Keywords: Mozambique Channel, Mesoscale circulation, Biological production, Physical-biological coupling, Multi-disciplinary approach

1. Introduction

The Mozambique Channel in the southwestern Indian Ocean is bordered by the coast of Mozambique in the west and Madagascar to the east. It is limited by the Comoros archipelago to the north and is connected to the greater Agulhas Current system to the south. Its particular geographic shape and location make the Mozambique Channel very specific in terms of ocean circulation, as it is considered to be one of the most turbulent areas in the world ocean. The Channel also contributes to inter-ocean exchanges due to its connection to the climatologically important Agulhas Current system that interacts between the Indian and Atlantic Oceans. Ecological concerns related to the Mozambique Channel focus particularly on how biodiversity loss might affect many areas (e.g. the Coral Triangle in the north, south and east of Madagascar, the almost undisturbed Iles Eparses) and how mesoscale dynamics impact population connectivity. Furthermore, improved knowledge of the complex ecosystems in the Mozambique Channel are likely to contribute to better management of marine resources exploited by regional and international (European and Asian) fisheries.

The Mozambique Channel is characterized by complex and variable surface and sub-surface circulation (Fig. 1) that is dominated by mesoscale activity (e.g. Biastoch and Krauss, 1999; de Ruijter et al., 2002; Ridderhinkhof and de Ruijter, 2003; Schouten et al., 2003; Lutjeharms, 2006) and related to the large scale circulation in the Indian Ocean (Penven et al., 2006; Palastanga et al., 2006; Ridderinkhof et al., 2010; Backeberg and Reason, 2010). Eddies are generally formed at the channel narrows (~ 16°S) between the northern and central basins and migrate southward mostly along the Mozambique coast (e.g. Schouten et al., 2003). Eddies are also formed at the southern tip of Madagascar, some of them entering the channel northwards along the west coast of Madagascar (Quartly and Srokosz, 2004). Due to the shape of the channel, eddy-eddy or eddy-shelf interactions are common and they contribute to different enhancement processes that are highlighted by sea surface chlorophyll distribution (Quartly and Srokosz, 2004; Tew-Kai and Marsac, 2009; Omta et al., 2009).

Indeed, mesoscale eddies are known to have a strong structuring effect on biological production, firstly at the lowest trophic level (McGillicuddy et al., 1998; Oschlies and Garçon, 1998; Rodriguez et al., 2001; Lévy and Klein, 2004) by the injection of nutrients into the euphotic zone and the resulting phytoplankton blooms. Such processes strongly depend, however, on eddy maturity and advection within property gradients (Bakun, 2006; Siegel et al, 2008), eddy-eddy interaction (Lima et al. 2002; Tew-Kai and Marsac, 2009) or eddy-wind interaction (Gillicuddy et al., 2007). Statistics based on satellite observation of thousands of cyclonic and anticyclonic eddies showed that several mechanisms have generally to be considered for understanding the bio-optical signatures of mesoscale eddies (Siegel et al., 2011; Chelton et al., 2011).

Mesoscale structures are supposed to affect the distribution and behaviour of intermediate and upper trophic levels. Acoustic surveys of micronekton (i.e. small swimming pelagic organisms preyed upon by marine top predators) indicated potential relationships with mesoscale eddies (Sabarros et al., 2009; Drazen et al., 2011; Godo et al, 2012). In turn, the influence of mesoscale structures on forage fauna impacts the presence and catchability of marine top predators (Domokos et al., 2007; Tew-Kai and Marsac, 2010), and the behaviour of seabirds (Nel et al., 2001; Weimerskirch et al., 2004; Tew-Kai and Marsac, 2010) and sea turtles (e.g. Polovina et al, 2004; Luschi et al., 2006). Few programmes have considered the “entire food web”, however, from the physical driving forces to the lower and intermediate trophic levels, to the upper predators at the top of the food chain. A joint research initiative was therefore developed between France and South Africa, with the name of MESOBIO (Influence of **meso**scale dynamics on **bio**logical productivity at multiple trophic levels in the Mozambique Channel*)*. This programme focussed on mesoscale eddies as ecosystem structuring features in the Channel (Fig. 2). New observations at sea (two cruises in 2009 and 2010) complemented previous work within the French ECOTEM programme (Ecologie Trophique en Environnement Marin, 2002-2004), the South African ACEP programme (African Coelacanth Ecosystem Project) with “eddy cruises” in 2005 and 2007, and the more recent ASCLME programme (Agulhas and Somali Currents Large Marine Ecosystem) where a cruises were staged in 2008 and 2009.

This suite of seventeen articles focussed on the different scientific components of the MESOBIO programme. The objective in this introductory article is to (1) to summarize the current knowledge for each discipline and the impact of mesoscale activity on the trophic compartments, (2) present a synopsis of research cruise activities, and (3) summarize the objectives of the research undertaken within MESOBIO. The final article summarizes the major results of the programme and also proposes new avenues of research to expand our knowledge of the functioning of the ecosystem in the Mozambique Channel. One paper in this suite does not result directly from MESOBIO activities, namely the article by Pripp et al., but it naturally fitted with the objectives of the programme.

2. Current knowledge

2.1 Physics

Early studies relying on non synoptic hydrographic observations concluded that circulation was dominated by large and highly variable circulation cells (e.g. Særte and Jorge da Silva, 1984; Donguy and Piton, 1991). Remote sensing observations (e.g. Schouten et al., 2003; Quartly and Srokosz, 2004) and ocean models (Biastoch and Kraus, 1999) indicated the dominance of mesoscale dynamics on the circulation and Schouten et al. (2003) estimated a mean rate of 4-7 eddies a year moving southward through the Channel. More energetic eddies were found in the central Channel (Schouten et al., 2003; Palastanga et al., 2006) particularly due to eddy-eddy interactions. Based on current observations from a set of moorings across the narrows of the Channel at 15°-16°S, Ridderinkhof and de Ruijter (2003) demonstrated that the eddies extended down to 2000 m. Further south, hydrographic sections perpendicular to the coast of Mozambique (ACSEX programme) characterized anticyclonic eddies down to the bottom of the water column (Swart et al., 2010). Measurements over the deployment time of the moorings at 16°S ruled out the existence of a continuous Mozambique Current throughout the year at this latitude (Ridderinkhof and de Ruijter, 2003), although Lutjeharms et al. 2012 alluded to the possibility of such a current for very short periods under particular conditions.

Long time series of both remote sensing data (sea surface topography, ocean colour) and in situ data (LOCO programme, de Ruijter et al, 2006) improved the understanding of the formation and dynamics of anticyclonic eddies in the Channel (Harlander et al., 2009), and the remote control of the system in terms of inter-annual variability (Palastanga et al., 2006; Ridderinkhof et al., 2010). The latter study linked basin scale anomalies (i.e. the Indian Ocean Dipole, Saji et al., 1999) and the related variation in the strength of the SEC, to the variability of the southward flow through the Channel.

2.2 Phytoplankton

Investigations of phytoplankton in the Mozambique Channel have been quite limited. Following the International Indian Ocean Expedition (1959-1965), Sournia (1970) collated taxonomic data on planktonic diatoms and dinoflagellates in different areas of the Mozambique Channel. Ryther et al., (1966) measured primary production and found rates of 0.26-0.5 g C m^{-2} d^{-1} in the central part of the channel, but more elevated production of 1-3 g C m^{-2} d^{-1} in the shelf ecosystems of the Sofala Banks and Delagoa Bight. Variability in chlorophyll *a* on the Mozambican shelf was investigated by Mordasova (1980) in the late 1970's but no measurements were reported for offshore waters. A flow cytometric and satellite study of surface waters along a transect indicated chlorophyll *a* variability of 0.1-0.3 mg m^{-3}, where low concentrations occurred in mid-channel and the higher levels in the southwest near Mozambique and in the northeast close to Madagascar (Zubkov and Quartly, 2003). *Prochlorococcus* was determined to be the dominant component of these surface communities and *Synechococcus* and picoeukaryotes were present in lower abundance. Later studies using satellite climatology demonstrated a seasonal cycle in surface chlorophyll *a*, with a maximum in winter and a summer minimum, with concentrations varying from 0.15-0.3 mg m^{-3} (Lévy et al., 2007). These winter maxima and summer minima were confirmed by a modeling and satellite study by Omta et al., (2009), although the data revealed considerable interannual variability in chlorophyll *a* during a 1998-2007 time series. Tew-Kai and Marsac (2009) demonstrated that chlorophyll *a* was below normal levels when anticyclones were prevalent in mid-channel, but chlorophyll was enhanced when cyclonic eddies were dominant. Furthermore, chlorophyll *a* tended to be higher on the western side of the channel as the movement of eddies followed a southwestward trajectory offshore from the Mozambique coast.

2.3 Zooplankton

Information on zooplankton in the Mozambique Channel is relatively scarce. Broad scale sampling in the region was initiated during the International Indian Ocean Expedition (IIOE) of 1959-1965, but coverage in the Mozambique Channel was relatively poor (Rao, 1973). Zooplankton biovolume in the southwest Indian Ocean was generally low compared to the strongly monsoon driven northern Indian Ocean. Binet and Dessier (1965) extensively sampled an area (coastal, shelf and open ocean) up to 90 km from Nosy Bé off Madagascar and provided systematic classification and ecological information on zooplankton. Sampling of macrozooplankton (>500µm) off the Mozambique coast during 4 fisheries surveys on the RV *Dr Fridtjof Nansen* during 1977-1978 yielded displacement volumes of mostly <0.5 ml m^{-3} in the upper 100 m, with highest values on the Sofala Bank during late summer (Sætre and de Paula e Silva, 1979). Plankton sampling during a more comprehensive survey in the western Mozambique Channel during February/March 1980 on the RV *Alexander von Humboldt* indicated higher mesozooplankton (>200µm) biomass inshore compared to offshore, and higher biomass in the southern sector of the western Channel (south of 18°S) compared to the oligotrophic northern region (Nehring et al., 1987). Very high biomass, suggesting high productivity, was associated with the southern inshore edge of a strong cyclonic eddy located south of Angoche. Other productive areas during this cruise were the Sofala Bank and southern inshore regions (Bazaruto and Delagoa Bight). A recent study of the Delagoa Bight region indicated a high degree of homogeneity within the mesozooplankton community, dominated by the same group of five zooplankton taxa (Paracalanidae, Oithonidae, Oncaeidae, Chaetognatha and Oikopleuridae) irrespective of season, year or distance offshore (Huggett, unpublished data).

2.4 Micronekton

Micronekton organisms are small actively swimming fishes, crustaceans or cephalopods, and are the trophic link between zooplankton and top predators in open-sea ecosystems. In spite of its importance, the micronekton fauna of the Indian Ocean is poorly documented. Early cruises during the International Indian Ocean Expedition led to investigations on systematics of myctophids collected along 60°E and 65°E (Nafpaktitis and Nafpaktitis, 1969), and further information on the genera *Lobianchia* and *Diaphus* was published by Nafpaktitis (1978). Cruises conducted in 1975-1983 on the RV *Fridtjof Nansen* produced only a small collection of micronekton samples, and species composition and some biological observations were carried out occasionally during two cruises in 1978 (Sætre and de Paula e Silva, 1979). In contrast, mesopelagic fishes of the Arabian Sea have been fairly intensively studied (Gjøsaeter 1984), and abundance estimates by acoustics were much lower in the Mozambique Channel than those recorded in the Arabian Sea. Recent studies conducted in the western Indian Ocean (including the Mozambique Channel) used large fish predators as biological samplers of micronekton organisms (Potier et al., 2007, Ménard et al., in press). The prey composition of the stomach contents provided information on the diversity of the micronekton fauna occurring within predator foraging ranges. Sabarros et al. (2009) investigated the effect of eddies on micronekton organisms in the Mozambique Channel using acoustic surveys and satellite altimetry, and showed that large aggregations of micronekton occurred mainly in areas where the local horizontal gradient of sea level anomalies was strong, i.e. at the periphery of eddies.

2.5 Top predator pelagic fisheries

Tunas and billfish have been harvested in the Mozambique Channel by industrial fisheries since 1955 when the longline fleets started to expand their activities in the Indian Ocean. Japan was the first fleet to operate in the region, followed in 1968 by Taiwan and China. European longliners (French, Spanish and Portugese) entered the fishery in the mid 1990s. During 1960-1970, the total catch averaged 4500 tons y^{-1}, then declined substantially until 1993 (600 tons annually) when the fleets shifted to other fishing grounds in the Indian Ocean. The trend reverted in 1994 when longline fishing efforts intensified Yield increased dramatically to an average 6000 tons y^{-1} during 1994-2010, with a peak catch recorded in 2006-2007). Although several large pelagic species are caught in the Mozambique Channel (temperate and tropical tunas, swordfish and sharks), the area is mostly considered to be a yellowfin (*Thunnus albacares*) fishing ground for longliners, representing 60% of the total catch (average 1955-2010) and 4% of the yellowfin longline catch in the whole

Indian Ocean (average 1994-2010). Longliners operate throughout the year in the entire Mozambique Channel and catches peak from December to March.

Purse seine tuna catches are seasonal and have been variable for the period 1991-2011, with a range of 4000–47000 tons and an average catch during 2005-2011 of ~ 30,000 tons (Fonteneau, 2010). The fishery operates in February-June, peaking from March to May, with bulk of catches north of 16°S. In some years, the fishery expands southwards to 20°S (Tew Kai and Marsac, 2010) and the main species caught are the skipjack (*Katsuwonus pelamis*, 69%) and yellowfin tuna (26%). Pelagic fisheries by local fleets of the two countries bordering the Mozambique Channel remain limited compared to the production by the industrial fisheries. National statistics for Mozambique report 7 tons per annum caught through sport fishery which is composed of marlins, tunas and tuna like species such as kingfish and wahoo. No reliable estimate is available for the artisanal fisheries, although it is known that large pelagic fish are taken with artisanal gear (Palha de Sousa, 2012, Fanazava et al., 2012). Madagascar longliners mostly operate to the east of Madagascar and a very minor proportion of the 500 tons reported annually in this country are taken in the Mozambique Channel (Fanazava et al., 2012).

2.6 Seabirds

Sixteen species of seabird, totaling more than 3 million pairs, breed annually in the Mozambique Channel. Three species are inshore feeders that forage over coral reefs; all others are oceanic foragers. Although numerous seabird colonies exist along the coast of East Africa and Madagascar, three offshore islands, namely Europa, Juan de Nova and Lys Island in the Glorioso Archipelago, host 99% of the breeding populations (Le Corre and Jaquemet, 2005). One species, the sooty tern *Onychoprion fuscata*, accounts for more than 99% of the number of breeding birds (Le Corre and Jaquemet, 2005; Feare et al., 2007). Anthropogenic perturbations such as poaching by local populations seems to be the main cause for the very low abundance of seabirds along both the coastline of East Africa and Madagascar (Le Corre and Jaquemet, 2005; Le Corre and Bemanaja, 2009).

The breeding activity is seasonal for most of the species and is related to oceanic conditions (Le Corre, 2001; Jaquemet et al., 2007) or to the availability of prey (Le Corre et al., 2003).Some species have developed specific foraging strategies. Sooty terns leave colonies grouped, and progressively spin a net of foragers that scan large oceanic areas for feeding opportunities (Jaquemet et al., 2005). Great Frigatebirds (*Fregata minor*) exhibited long travel distances when foraging to reach the most productive areas in the southwest Channel characterized by active mesoscale activity (Weimerskirch et al., 2004) and they also use eddies for traveling (Tew-Kai et al., 2009). Red-footed boobies (*Sula sula*) feed actively at the most distant part of the foraging trip, which is greatly favored by the presence of sub-surface predators (Le Corre, 1997). Red-tailed tropicbirds (*Phaethon rubricauda*) from Europa prey on juvenile dolphinfish (*Coryphaena* spp.) in summer to feed their chicks (Le Corre et al., 2003). For most of other species, however, virtually nothing is known of their foraging ecology and distribution at sea in the Mozambique Channel.

2.7 Modeling

Numerical ocean models designed specifically for the Mozambique Channel are rare. The first regional model of the greater Agulhas Current based on MOM2 at 1/3° resolution (AGAPE) produced a circulation dominated by a train of anticyclonic eddies that propagated southward along the western side of the channel (Biastoch and Krauss, 1999; Hermes et al.. 2007). These eddies were generated by barotropic instabilities at a rate of 4-6 per year, but did not penetrate deeper than 400 m, in contrast to observations (Biastoch and Krauss, 1999; Hermes et al. 2007). These early simulations showed an annual cycle in eddy variability (Hermes et al. 2007) and in volume transport (Biastoch et al., 1999), with transport also being observed in eddy simulations of the global Ocean at 1/4° resolution (Matano et al., 2002). Process oriented simulations have highlighted the role of Madagascar in the generation of Mozambique Channel eddies and their subsequent effects on the timing of spawning of Agulhas rings (Penven et al., 2006).

More recent eddy resolving global ocean models are able to represent the mesoscale variability in the Mozambique Channel (van der Werf et al., 2010). These high resolution models improve the simulation of the vertical structure of Channel eddies, but they display discrepancies in eddy generation mechanisms and in the dominance of the seasonal cycle (van der Werf et al., 2010). This emphasizes the need for dedicated regional experiments. In a regional model based on HYCOM at 1/10° resolution, Backeberg and Reason (2010) demonstrated the link between bursts in the South Equatorial Current and the generation of Mozambique Channel eddies, and they reproduced the increase of anticyclonic vorticity in the eddies during their southward propagation in the Channel. In relation to biogeochemical and ecosystem modelling, it appears that no such modelling has been undertaken for the Mozambique Channel prior to the MESOBIO programme.

3. Research cruises

Four ECOTEM cruises (Table 1) were undertaken in the Mozambique Channel during different seasons (Fig. 3a-d). These cruises focused on the spatial and temporal variability of biomass and specific diversity of the prey related to marine top predators (forage fauna of tunas, swordfish and sharks) and included hydrographic profiling, acoustic surveys and seabird observations. Biological sampling was conducted using mesopelagic trawling (MC02) and longline fishing (MC03, MC04A, MC04B). The MC02 cruise followed a south to north transect, while the other three cruises focused on the ecosystems around Mozambique Channel Islands (Fig. 3).

In April 2005 and September 2007 (Table 1), two cruises of the South African ACEP programme (African Coelacanth Ecosystem Project) focussed specifically on eddy pairs, the first off southeast Mozambique (MC05, 24°-26°S) and the other off the Sofala Banks (MC07, 18°-23°S) (Fig. 4a-b). Shipboard activities included along track ADCP current measurements, hydrographic profiling (CTD and water sampling), phytoplankton and zooplankton sampling, and seabird observations during MC07 only.

Leg 4 of the 2008 ASCLME cruise (MC08A, Table 1; Fig. 5a) focussed on the “biological” components for the various trophic levels (phyto- and zooplankton, micronekton, pelagic fish and seabirds). A succession of eddies were investigated between 14°S and 23°S and hydrographic profiling (CTD and water sampling), phytoplankton and zooplankton sampling, and mesopelagic trawling were undertaken. In addition, multi-frequency bio-acoustic surveys and ADCP current measurements were performed along the cruise track. Large pelagic fish were sampled from a commercial longliner that operated in association with the research vessel (MC08B, Table 1, Fig. 5b). During another ASCLME cruise in 2009, a hydrographic survey was undertaken off the northeast coast of Mozambique in the vicinity of 14°S (MC09A, Table 1).

Two MESOBIO cruises were conducted in October 2009 off southeast Mozambique (MC09B, 22°-25°S, Table 1, Fig. 6), and in April 2010 in the central and eastern Channel (MC10A, Table 1, Fig. 7). In 2010, leg 1 focused mostly on the mid and top trophic levels, and a commercial longliner was leased in order to sample large pelagic fish (MC10B, Table 1, Fig. 7c). Leg 2 focussed more specifically on the assessment of productivity in different locations of the eddy field (Fig. 7b). Hydrographic profiling, phyto- and zooplankton sampling, seabird observations, as well as a multi-frequency bio-acoustic survey and ADCP current measurements were performed along the cruise track. A dedicated acoustic profiler (TAPS) was also used to study the vertical distribution and size classes of zooplankton.

4. Objectives

4.1 Physical and biogeochemical dynamics

Questions addressed during MESOBIO using in situ data and satellite imagery, concerned the occurrence of eddy (cyclonic) induced upwelling, the offshore entrainment of shelf biomass due to eddy-shelf or eddy-eddy interactions, the occurrence and origin of coastal upwelling, and the potential dispersal corridors for larval and juvenile fish species offered by eddy field dynamics within the Mozambique Channel. Modeling experiments on eddy dynamics were also undertaken using a high resolution regional model (ROMS) set up for the Mozambique Channel, and biogeochemical modeling (PISCES) was used to investigate the phytoplankton response to eddy characteristics.

4.2 Phytoplankton and zooplankton

Ecosystem functioning in the Mozambique Channel appears to be constrained by the pattern of eddies as they migrate through the channel and knowledge of phytoplankton communities and adaptation strategies by these populations is poorly understood. Studies were therefore initiated to elucidate community structure, while pigment and absorption measurements were undertaken to examine the adaptation of phytoplankton to various eddy features, and also between the surface and the deep chlorophyll maximum.

The physical and biological processes shaping zooplankton dynamics in mesoscale features were investigated by studying the distribution, abundance and composition of zooplankton communities along eddy gradients using standard sampling techniques such as Multinet® and Bongo nets, and dedicated acoustics profiling (TAPS). Questions on the zooplankton biomass relative to the location within the eddy field, and the relation between zooplankton and phytoplankton, were addressed.

4.3 Forage fauna and top predators

Field investigations on micronekton were combined with hydro-acoustic transects across eddies, pelagic trawls to estimate species composition and densities, diet analyses of large pelagic fish, and isotopic signatures of a large assemblage of micronekton organisms. Observational transects (for birds, cetaceans and surface schools of tunas) and longlining (for swordfish and tuna-like species) were used to address specific issues regarding the top predator feeding strategies (seabirds) and their distribution and catchability (marine species) related to the mesoscale environment.

4.4 MESOBIO

In summary, the programme focussed on the imprint of mesoscale dynamics on components of the ecosystems in the Mozambique Channel including primary and secondary producers, intermediate trophic levels and top predators. The specific objectives were to (1) identify how eddies enhance nutrient sources, production and biomass of primary producers, (2) assess the relative importance of nutrient and energy sources (e.g. shelf, pelagic, upwelled) to the upper consumers in the region, (3) investigate the importance of eddy induced transport processes in the spatial distribution of zooplankton that in turn attract foraging higher-order predators, and (4) examine the effect of eddy driven physical and biological processes on the distribution and abundance of ecologically and/or economically important top predators.

Acknowledgements

MESOBIO (2009-2011) was funded by the MASMA programme of the WIOMSA (West Indian Ocean Marine Association) and supported by both the ASCLME (Agulhas Somali Current Large Marine Ecosystem) and SWIOFP (South West Indian Ocean Fisheries Project) programmes. Other contributing programmes included ECOTEM (2002-2004) funded by IRD (Institut de Recherche pour le Développement) and the South African ACEP programme (African Coelacanth Ecosystem Project). We are grateful to the officers and crews of the research and fishing vessels for their contribution to the success of the research cruises.

References

Backeberg, B.C., Reason, C., 2010. A connection between the South Equatorial Current north of Madagascar and Mozambique Channel eddies. Geophys. Res. Lett. 37, L04604.

Bakun, A., 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: Opportunitiy, adaptative response and competitive advantage. Sci. Mar. 70, 105-122.

Biastoch, A., Krauss, W., 1999. The role of mesoscale eddies in the source regions of the Agulhas Current. J. Phys. Oceanogr. 29, 2303-2317.

Biastoch, A., Reason, C.J.C., Lutjeharms, J.R.E., Boebel O., 1999. The importance of flow in the Mozambique Channel to seasonality in the Greater Agulhas Current System. Geophys. Res. Lett. 26, 3321-3324.

Binet, D., Dessier, A., 1965. Zooplancton dans la région de Nosy-Bé : III Premières données sur les copépodes. Cah. ORSTOM Ser. Océanogr. 6, 3-26.

Chelton, D., Schlax, M., Samelson, R., 2011. Global observations of nonlinear mesoscale eddies. Prog. Oceanogr. 91, 167–216.

De Ruijter, W.P.M., Ridderinkhof, H., Lutjeharms, J.R.E., Schouten, M.W., Veth, C., 2002. Observations of the flow in the Mozambique Channel. Geophys. Res. Lett. 29, 1502.

De Ruijter, W.P.M., Brummer, G.-J.A., Drijfhout, S.S., Lutjeharms, J.R.E, Peeters, F., Ridderinkhof, H., Van Aken, H., Van Leeuwen, P.J., 2006. Observations of the inter-ocean exchange around South Africa, EOS Trans. AGU 87, 97-101.

Domokos, R., Seki, M.P., Polovina, J.J., Hawn, R.H., 2007. Oceanographic investigation of the American Samoa albacore (*Thunnus alalunga*) habitat and longline fishing grounds. Fish. Oceanogr. 16:6, 555-572.

Donguy, J.R., Piton, B., 1991. The Mozambique Channel revisited. Oceanol. Acta 14, 549-558.

Drazen, D.C., de Forest, L.G., Domokos, R., 2011. Micronekton abundance and biomass in Hawaiian waters as influenced by seamounts, eddies and the moon. Deep Sea Res. I 58, 557-566.

Fanazava, R., Rasolonjatovo, H., Rahombanjanahary, D.M., Ratsimanarisoa, N, 2012. Madagascar national report to the Scientific Committee of the Indian Ocean Tuna Commission, 2012. IOTC-2012-SC15-NR15. Report of the Fifteen Session of the IOTC Scientific Committee, Mahe, Seychelles, 10-15 December 2012.

Feare, C.J., Jaquemet, S., Le Corre, M., 2007. An inventory of Sooty Terns (*Sterna fuscata*) in the western Indian Ocean with special reference to threats and trends. Ostrich 78, 423-434.

Fonteneau, A., 2010. Atlas des pêcheries thonières de l'Océan Indien. Atlas of Indian Ocean tuna fisheries. IRD Editions.

Gjøsaeter, J., 1984. Mesopelagic fish, a large potential resources in the Arabian Sea. Deep-Sea Res. 31, 1019–1035.

Godø, O.R., Samuelsen, A., Macaulay, G.J., Patel, R., Hjøllo, S.S., Horne, J., Kaartvedt, S., Johannessen, J.A., 2012. Mesoscale eddies are oases for higher trophic marine life. PLoS ONE 7(1):e30161. Doi:10.1371/journal.pone.0030161.

Harlander, U., Ridderinkhof, H., Schouten, M.W., De Ruijter, W.P.M., 2009. Long-term observations of transport, eddies, and Rossby waves in the Mozambique Channel. J. Geophys. Res. 114, C02003.

Hermes, J.C., Reason, C.J.C., Lutjeharms, J.R.E., 2007. Modeling the variability of the greater Agulhas Current System. J. Clim. 20, 3131-3146.

Jaquemet, S., Le Corre, M., Marsac, F., Potier, M., Weimerskirch, H., 2005. Foraging habitats of the seabird community of Europa Island (Mozambique Channel). Mar. Biol. 147, 573-582.

Jaquemet, S., Le Corre, M., Quartly, G.D., 2007. Ocean control of the breeding regime of the sooty tern in the southwest Indian Ocean. Deep-Sea Res. I 54, 130-142.

Le Corre, M., 1997. Diving depths of two tropical Pelecaniformes: the red-tailed tropicbird and the red-footed booby. Condor 99, 1004-1007.

Le Corre, M., 2001. Breeding seasons of seabirds of Europa Island (southern Mozambique Channel) in relation to seasonal changes in the marine environment. J. Zool. 254, 239-249.

Le Corre, M., Cherel, Y., Lagarde, F., Lormée, H., Jouventin, P., 2003. Seasonal and inter-annual variation in the feeding ecology of a tropical oceanic seabird, the red-tailed tropicbird (*Phaethon rubricauda*). Mar. Ecol. Prog. Ser. 255, 289-301.

Le Corre, M., Jaquemet, S., 2005. Assessment of the seabird community of the Mozambique Channel and its potential use as an indicator of tuna abundance. Est. Coast. Shelf. Sci. 63, 421-428.

Le Corre, M., Bemanaja, E., 2009. Discovery of two major seabird colonies in Madagascar. Mar. Ornithol. 37, 153-158.

Lévy, M., Klein, P., 2004. Does the low frequency variability of mesoscale dynamics explain part of the phytoplankton and zooplankton spectral variability? Proc. Roy. Soc. London Ser. A 460-2046, 1673-1683.

Lévy, M., Shankar, D., Andre, J-M., Shenoi, S.S., Durand, F., de Boyer Montegut, C., 2007. Basin-wide seasonal evolution of the Indian Ocean's phytoplankton blooms. J. Geophys. Res. 112, C12014.

Lima, I.D., Olson, D.B., Doney, S.C., 2002. Biological response to frontal dynamics and mesoscale variability in oligotrophic environments: Biological production and community structure. J. Geophys. Res. 107 (C8).

Luschi, P., Lutjeharms, J.R.E., Lambardi, P., Mecacci, R., Hughes, G.R., Hays, G.C., 2006. A review of migratory behaviour of sea turtles off southeastern Africa. S. Afr. J. Sci. 102, 51-58.

Lutjeharms, J.R.E., 2006. The coastal oceans of south-eastern Africa, in: Robinson A.R., Brink, K.H. (Eds.), The Sea, Volume 14B. JohnWiley, NewYork, pp. 781-832.

Lutjeharms, J.R.E., Biastoch, A., van der Werf, P.A.; Ridderhinkhof, H., de Ruijter, W.P.M., 2012. On the discontinuous nature of the Mozambique Current. S. Afr. J. Sci. 108 (http://dx.doi.org/10.4102/sajs.v108i1/2.428).

Matano, R.P., Beier, E.J., Strub, P.T., Tokmakian, R., 2002. Large-scale forcing of the Agulhas variability: The seasonal cycle. J. Phys. Oceanogr. 32, 1228-1241.

McGillicuddy, D.J., Robinson, A.R., Siegel, D.A., Jannasch, H.F., Johnson, R., Dickey, T.D., McNeil, J., Michaels, A.F., Knap, A.H., 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. Nature 394, 263-266.

McGillicuddy, D.J., Anderson, L.A., Bates, N.R., Bibby, T., Buesseler, K.O., Carlson, C.A., Davis, C.S., Ewart, C., Falkowski, P.G., Goldthwait, S.A., Hansell, D.A., Jenkins, W.J., Johnson, R., Kosnyrev, V.K., Ledwell, J.R., Li, Q.P., Siegel, D.A., Szteinberg, D.K., 2007. Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms. Science 316, 1021-1026.

Ménard, F., Potier, M., Jaquemet, S., Romanov, E., Sabatié, R., Cherel, Y., in press. Pelagic cephalopods in the western Indian Ocean: new information from diets of top predators. Deep Sea Res. II (http://dx.doi.org/10.1016/j.dsr2.2012.08.022).

Mordasova, N.V., 1980. Chlorophyll in the southwestern Indian Ocean in relation to hydrologic conditions. Oceanology 20, 75-79.

Nafpaktitis, B.G., 1978. Systematics and distribution of lanternfishes of the genera *Lobianchia* and *Diaphus* (Myctophydae) in the Indian Ocean. Nat. Hist. Mus. Los Ang. Cty. Sci. Bull. 30, 1-92.

Nafpaktitis, B.G., Nafpaktitis M., 1969. Lanternfishes (Family Myctophidae) collected during cruises 3 and 6 of the R.V. *Anton Brunn* in the Indian Ocean. Nat. Hist. Mus. Los Ang. Cty. Sci. Bull. 5, 1–79.

Nel, D., Lutjeharms, J.R.E., Pakhomov, E.A., Ansorge, I.J., Ryan, P.G., Klages, N.T.W., 2001. Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. Mar. Ecol. Prog. Ser. 217, 15-26.

Nehring, D., Hagen, E., Jorge da Silva, A., Schemainda, R., Wolf, G., Michelchen, N., Kaiser; W., Postel, L., Gosselck, F., Brenning, U., Kühner, E., Arlt, G., Siegel, H., Gohs, L., Bublitz, G., 1987. Results of oceanological studies in the Mozambique Channel in February-March 1980. Beiträge zur Meereskunde, Berlin 56, 51-63.

Omta, A.W., Llido, J., Garcon, V., Kooijman, S.A., Dijkstra, H.A., 2009. The interpretation of satellite chlorophyll observations: The case of the Mozambique Channel. Deep-Sea Res. I 56, 974-988.

Oschlies, A., Garçon, V., 1998. Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean. Nature, 394, 266-269.

Palastanga, V., van Leeuwen, P.J., de Ruijter, W.P.M., 2006. A link between low-frequency mesoscale eddy variability around Madagascar and the large-scale Indian Ocean variability. J. Geophys. Res. III, C09029.

Palha de Sousa, B. 2012. Mozambique national report to the Scientific Committee of the Indian Ocean Tuna Commission, 2012. IOTC-2012-SC15-NR19. Report of the Fifteen Session of the IOTC Scientific Committee, Mahe, Seychelles, 10-15 December 2012.

Penven, P., Lutjeharms, J.R.E., Florenchie, P., 2006. Madagascar: a pacemaker for the Agulhas Current system? Geophys. Res. Lett. 110, C10021.

Polovina, J.J., Balazs, G.S., Howell, E.A., Parker, D.M., Seki, M.P., Dutton, P.H., 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. Fish. Oceanogr. 13, 36–51.

Potier, M., Marsac, F., Cherel, Y., Lucas, V., Sabatié, R., Maury, O., Ménard, F., 2007. Forage fauna in the diet of three large pelagic fish (lancetfish, swordfish, and yellowfin tuna) in the western equatorial Indian Ocean. Fish. Res. 83, 60-72.

Quartly, G.D., Srokosz, M.A., 2004. Eddies in the southern Mozambique Channel. Deep Sea Res. II 51, 69-83.

Rao, T.S.S., 1973. Zooplankton studies in the Indian Ocean, in: Zeitschel, B. (Ed.), The Biology of the Indian Ocean. Springer, Berlin, pp. 243-255.

Ridderinkhof, H., De Ruijter W.P.M., 2003. Moored current observations in the Mozambique Channel. Deep-Sea Res. II 50, 1933-1955.

Ridderinkhof, H., Van der Werf, P.M., Ullgren, J.E., Van Aken, H.M., Van Leeuwen, P.J., De Ruijter, W.P.M., 2010. Seasonal and interannual variability in the Mozambique Channel from moored current observations. J. Geophys. Res. 115, C06010.

Rodriguez, J., Tintoré, J., Allen J.T., Blanco, J.M., Gomis, D., Reul, A., Ruiz., J., Rodriguez, V., Echevarria, F., Jiménz-Gómez, F., 2001. Mesoscale vertical motion and the size structure of phytoplankton in the ocean. Nature 410, 360-363.

Ryther, J.H., Hall, J.R., Pease, A.K., Bakun, A., Jones, M.M., 1966. Primary organic production in relation to the chemistry and hydrography of the western Indian Ocean. Limnol. Oceanogr. 11, 371-380.

Sabarros, P.S., Ménard, F., Lévénez, J.J., Tew-Kai, E., Ternon, J.F., 2009. Mesoscale eddies influence distribution and aggregation patterns of micronekton in the Mozambique Channel. Mar. Ecol. Prog. Ser. 395, 101–107.

Saetre, R., de Paula e Silva, R., 1979. The Marine Fish Resources of Mozambique. (www.fao.org/WAIRDOCS/FNS/FN130E).

Saerte, R., Jorge da Silva,A., 1984. The circulation of the Mozambique Channel. Deep-Sea Res. 31, 485-508.

Saji, N.H., Goswami, B.M., Vinayanchandran, P.N., 1999. A dipole mode in the tropical Indian Ocean. Nature 401, 360-363.

Schouten, M.W., De Ruijter, W.P.M., Van Leeuwen, P.J., Ridderinkhof, H., 2003. Eddies and variability in the Mozambique Channel. Deep-Sea Res. II 50, 1987-2003.

Siegel, D.A., Court, D.B., Menzies, D.W., Peterson, P., Maritorena, S., Nelson, N.B., 2008. The satellite and in situ observations of the bio-optical signatures of two mesoscale eddies in the Sargasso Sea. Deep-Sea Res. II 55, 1218-1230.

Siegel, D.A., Peterson, P., McGillicuddy, D.J. Jr., Maritorena, S., Nelson, N.B., 2011. Bio-optical footprints created by mesoscale eddies in the Sargasso Sea. Geophys. Res. Lett. 38, 1–6.

Sournia, A., 1970. A checklist of planktonic diatoms and dinoflagellates from the Mozambique Channel. Bull. Mar. Sci. 20, 678-696.

Swart, N.C., Lutjeharms, J.R.E., Ridderinkhof, H., de Ruijter, W.P.M., 2010. Observed characteristics of Mozambique Channel eddies. J. Geophys. Res. 115, C09006.

Tew Kai, E., Marsac, F., 2009. Patterns of variability of sea surface chlorophyll in the Mozambique Channel: a quantitative approach. J. Mar. Syst. 77, 77-88.

Tew-Kai, E., Marsac, F., 2010. Influence of mesoscale eddies on spatial structuring of top predator's communities in the Mozambique Channel. Prog. Oceanogr. 86, 214-223.

van der Werf, P.M., van Leeuwen, P.J. Ridderinkhof, H., de Ruijter W.P.M., 2010. Comparison between observations and models of the Mozambique Channel transport: Seasonal cycle and eddy frequencies. J. Geophys. Res. 115, C02002.

Weimerskirch, H., Le Corre, M., Jaquemet, S., Potier, M., Marsac, F., 2004. Foraging strategy of a top predator in tropical waters: great frigate birds in the Mozambique Channel. Mar. Ecol. Prog. Ser. 275, 297-308.

Zubkov, M.V., Quartly, G.D., 2003. Ultraplankton distribution in surface waters of the Mozambique Channel – flow cytometry and satellite imagery. Aquat. Microb. Ecol. 33, 155-161.

Table 1: Codes, dates and research vessels for research cruises in the Mozambique Channel related to the MESOBIO programme (RV: research vessel; FV: fishing vessel).

Code	Vessel	Cruise name	Year	Start date	End date
MC02	RV *La Curieuse*	ECOTEM 5	2002	12/09/2002	08/10/2002
MC03	FV *Cap Morgane*	ECOTEM 9	2003	02/09/2003	25/09/2003
MC04A	FV *Cap Morgane*	ECOTEM 6	2004	02/05/2004	20/05/2004
MCO4B	FV *Cap Morgane*	ECOTEM 7	2004	10/11/2004	29/11/2004
MC05	RV *Algoa*	ACEP 2005	2005	08/04/2005	02/05/2005
MC07	RV *Algoa*	ACEP 2007	2007	10/09/2007	23/09/2007
MC08A	RV *Fridtjof Nansen*	NANSEN 2008	2008	28/11/2008	17/12/2008
MC08B	FV *Manohal*	MANOHAL	2008	27/11/2008	18/12/2008
MC09A	RV *Fridtjof Nansen*	NANSEN 2009	2009	09/08/2009	16/08/2009
MC09B	RV *Antea*	MESOP 2009	2009	27/10/2009	24/11/2009
MC10A	RV *Antea*	MESOP 2010	2010	07/04/2010	08/05/2010
MC10B	FV *Brahma*	BRAHMA	2010	02/04/2010	17/04/2010

Figure legends

Fig. 1. Surface circulation in and around the Mozambique Channel and the greater Agulhas Current system (after Lutjerharms, 2006).

Fig. 2. Schematic of the multi-disciplinary science plan developed for the MESOBIO programme between French and South African research teams.

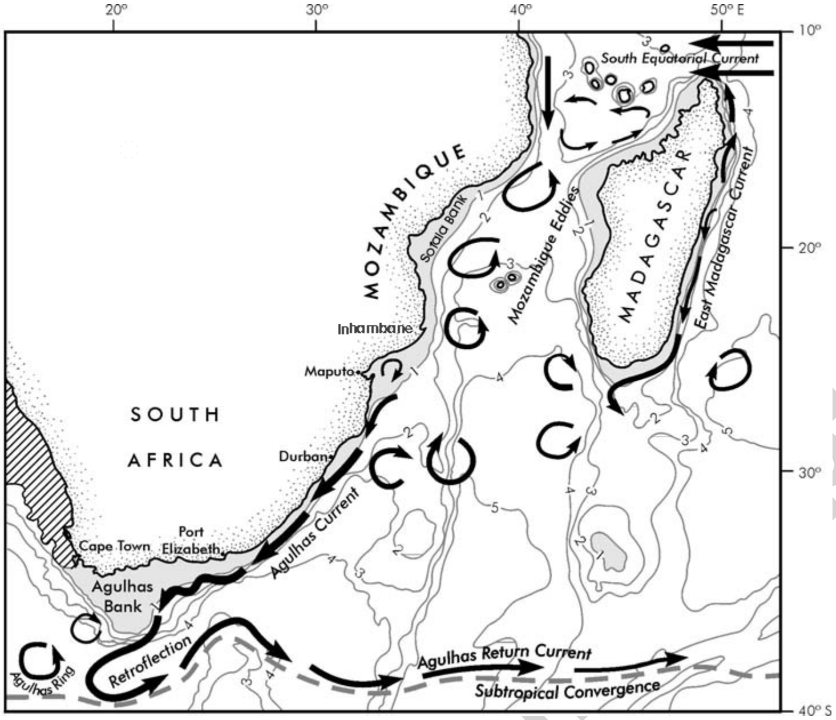
Fig. 3. Cruise tracks for the four ECOTEM cruises superimposed on the eddy field for a specific date: (a) cruise MC02 in September 2002; (b) cruise MC03 in September 2003; (c) cruise MC04A in May 2004; (d) cruise MC04B in November 2004. Grey scale indicates sea level anomaly (cm).

Fig. 4. Cruise tracks for the two ACEP cruises superimposed on the eddy field for a specific date: (a) cruise MC05 in April 2005; (b) cruise MC07 in September 2007. Grey scale indicates sea level anomaly (cm).

Fig. 5. Cruise tracks for the 2008 ASCLME and longliner cruises superimposed on the eddy field for a specific date: (a) cruise MC08A in December 2008 on RV *Fridtjof Nansen*; (b) cruise MCO8B in December 2008 on FV *Manohal* (black stars depict fishing sites). Grey scale indicates sea level anomaly (cm).

Fig. 6. Cruise tracks for the MESOP cruise in November 2009 superimposed on the eddy field for a specific date: (a) leg 1 of cruise MC09B; (b) leg 2 of cruise MC09B. Grey scale indicates sea level anomaly (cm).

Fig. 7. Cruise tracks for the MESOP and longliner cruises in April-May 2010 superimposed on the eddy field for a specific date: (a) leg 1 of cruise MC10A on RV *Antea*; (b) leg 2 of cruise MC10A on RV *Antea*; (c) cruise MC10B on FV *Brahma* (black stars depict fishing sites). Grey scale indicates sea level anomaly (cm).



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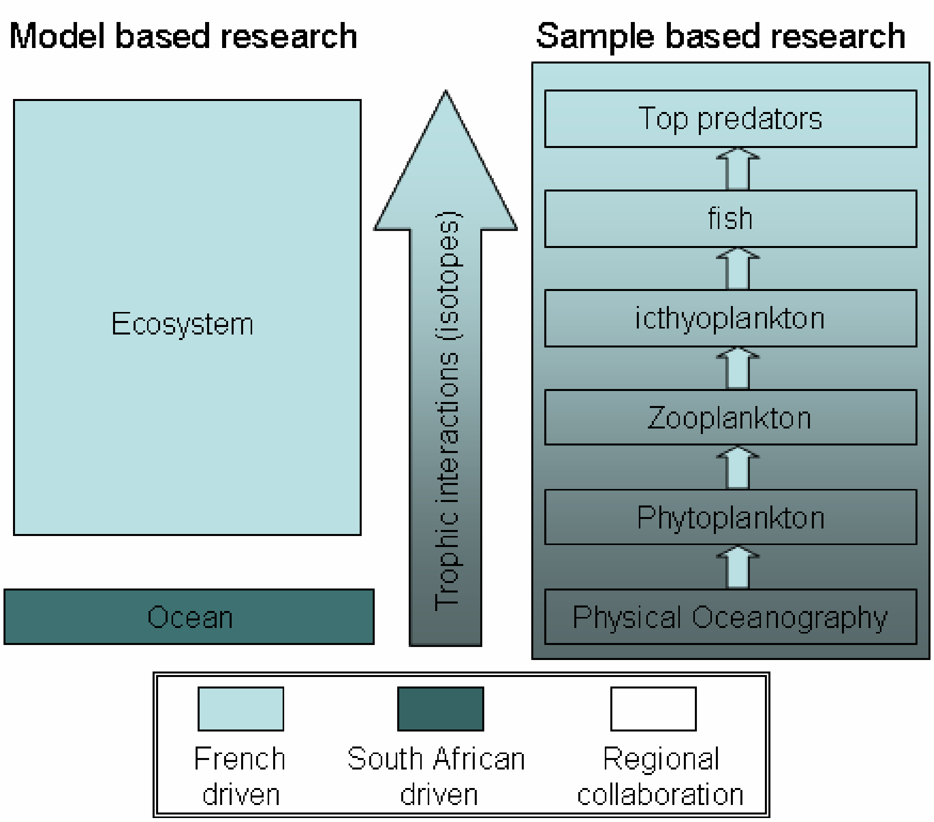

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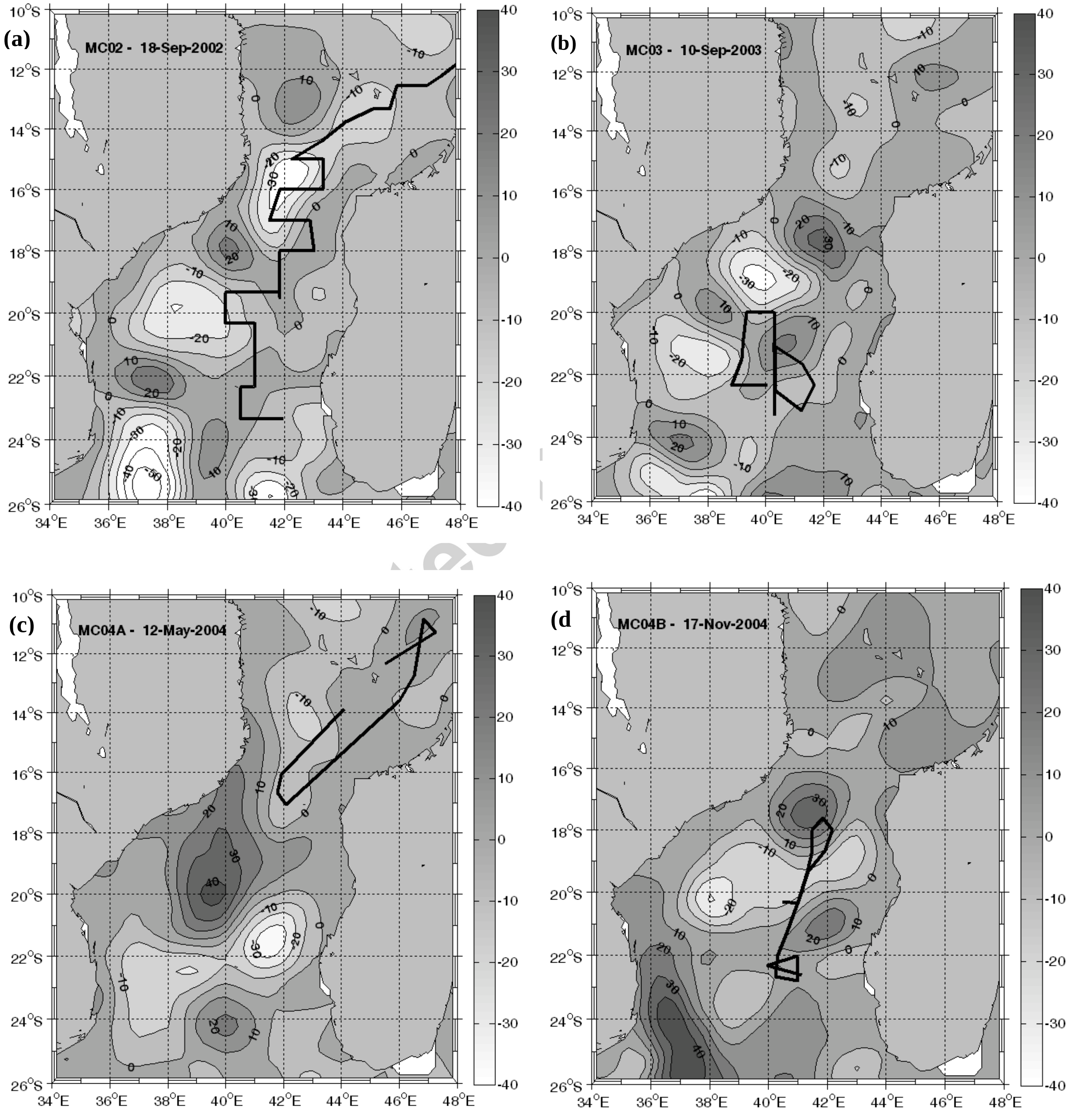

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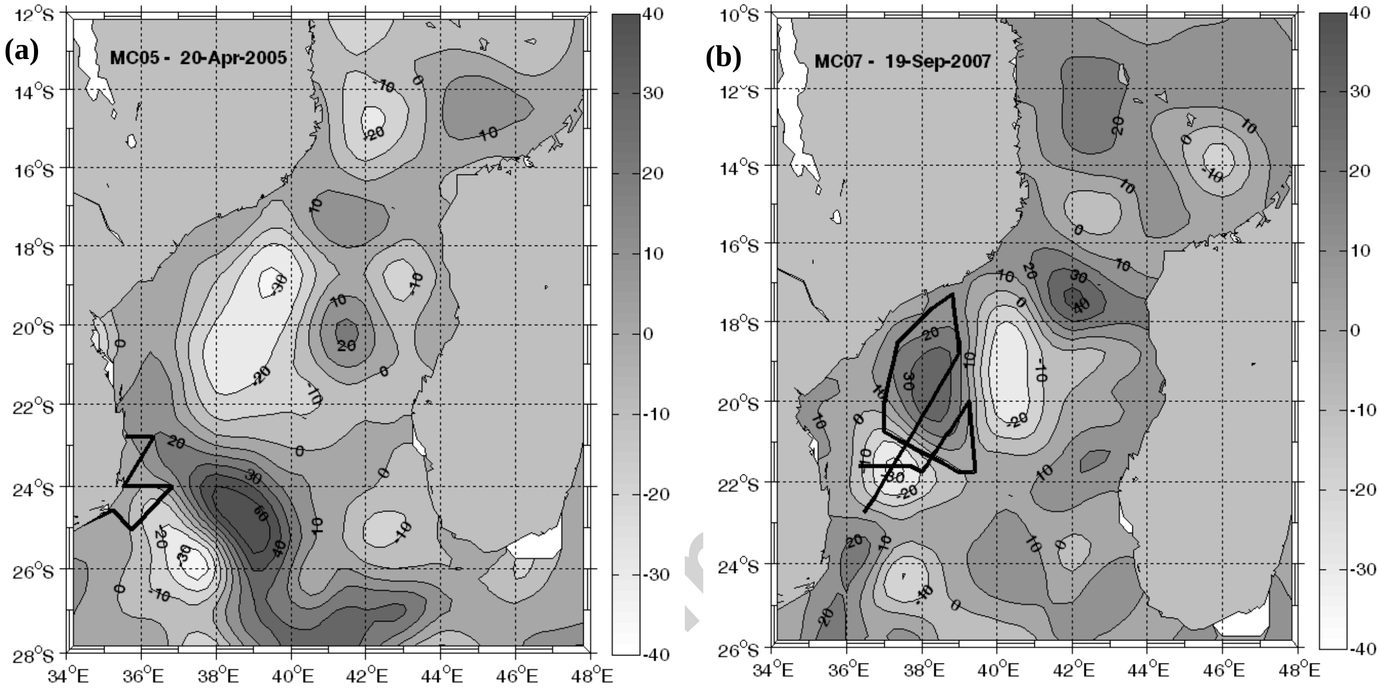

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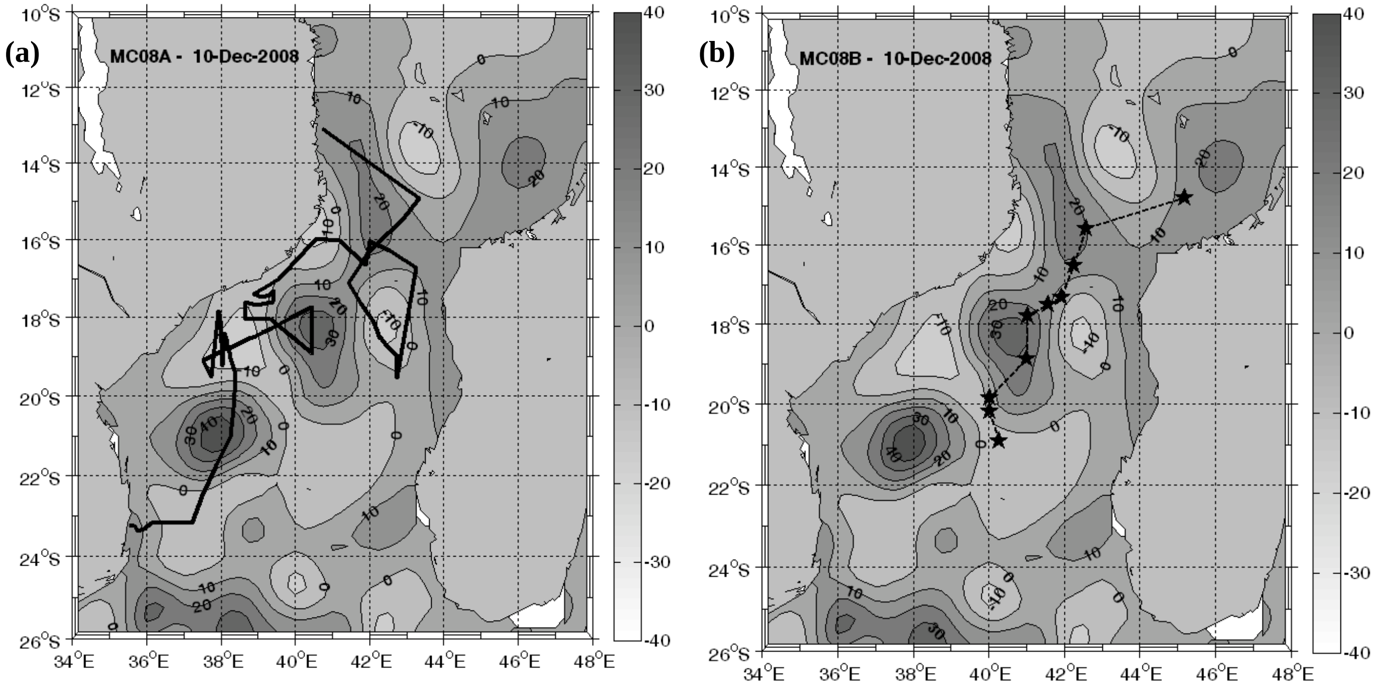

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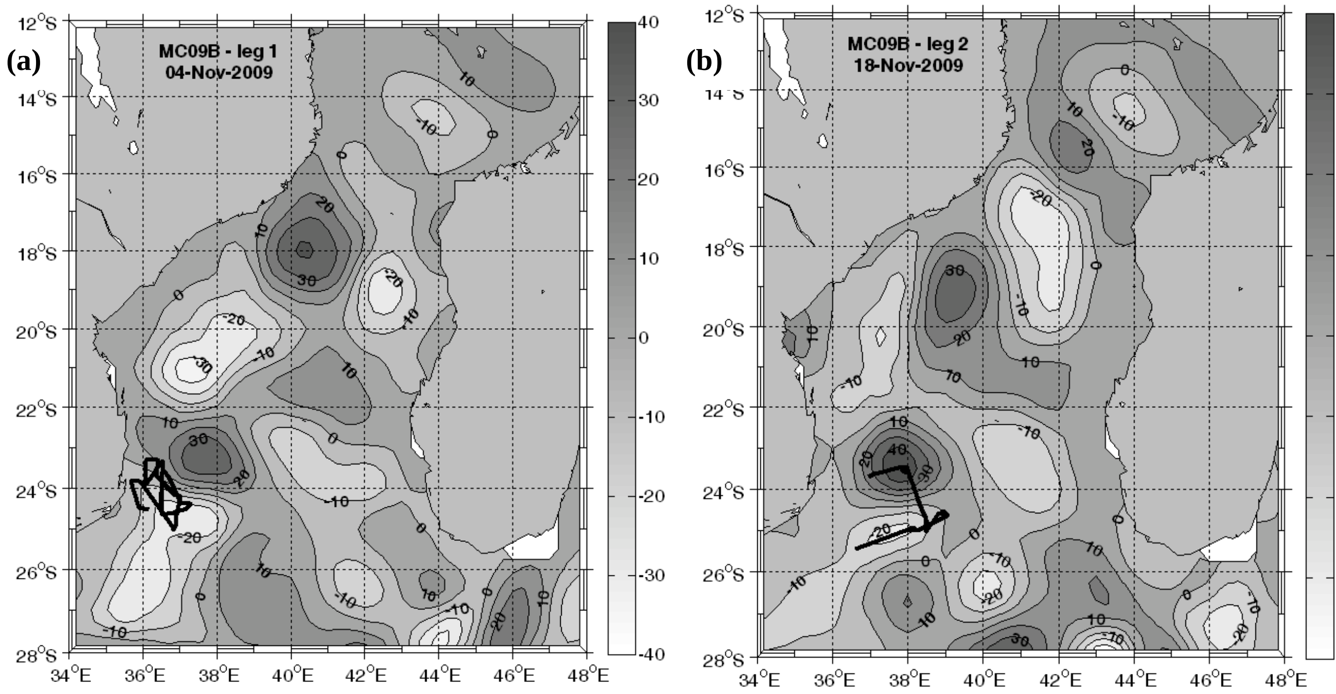
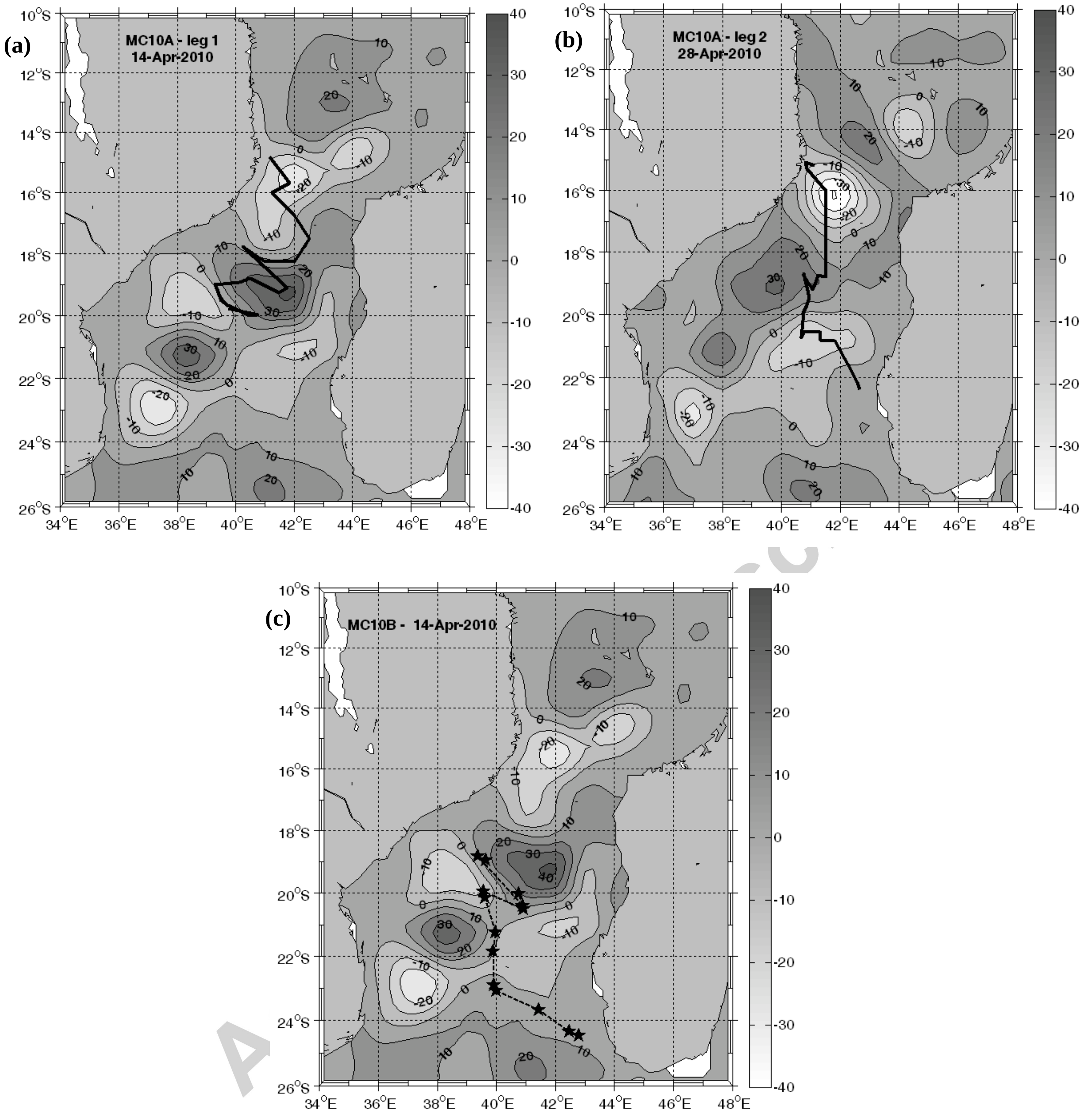


Fig. 6. Cruise tracks for the MESOP cruise in November 2009 superimposed on the eddy field for a specific date: (a) leg 1 of cruise MC09B; (b) leg 2 of cruise MC09B. Grey scale indicates sea level anomaly (cm).



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