Marine and coastal ecosystems of Madagascar

By Andrew Cooke, 2002

Geophysical setting

Madagascar, with a coastline of over 5000 km and a continental shelf of 117,000 km^2, has the most extensive brackish water, shallow marine, and continental shelf habitats of any Indian Ocean country apart from India. Madagascar spans almost 14^{O} of latitude (11^{O}47' - 25^{O}35' S). While the majority of the coast lies within the southern tropics, the extreme south represents an ecotone of tropical and temperate systems. Mean annual open water surface temperatures range from 22^{O} C in the south to 28^{O} in the north, with local seasonal extremes from 19^{O} to 33 ^{O} C. Anomalously high sea temperatures have occurred in 1998 and 2001,2002,2003 associated with major coral bleaching events on both coasts. A poorly defined thermocline occurs at about 150 m on the west coast which disappears completely between Maintirano (18^{O} S) and Morondava (20^{O} S). On the east coast, the thermocline is very marked and constant at 100 m (Ranaivoson, 1997).

The continental shelf is on average wider in the western sense than the eastern sense, with certain notable exceptions. Between Androka and Andavadoaka, in the south west, the shelf is only a few kilometres wide. Opposite the Onilahy River mouth, the shelf narrows to just a few hundred meters (Battistini et al. 1975).

Major oceanic and atmospheric systems

The principal features of existing atmospheric and oceanic circulation affecting Madagascar were probably established by the Paleocene, although punctuated by numerous episodes of disturbance. Prevailing circulatory patterns have held for at least the last 2 million years (Winter & Martin 1990). However, recent anomalies have occurred, possibly associated with global warming, that have implications for terrestrial climate as well as for marine ecosystems (e.g., Jury et al. 1995; Reason & Lutjeharms 1998).

Ocean surface currents

The surface circulations of subtropical ocean basins are wind-driven, anti-cyclonic and intensify in their western parts to form strong boundary currents. In the South Indian Ocean basin, the situation is complicated by the presence of Madagascar that obstructs the typical flow pattern. As a result the nature of the currents differ markedly from coastline to coastline (Figure 1).

On the east coast of Madagascar the currents are under the direct influence of the northern component of the South Indian Ocean gyre, the South Equatorial Current. The core of this current impinges on the coast at a latitude of about 17° S (Swallow et al., 1988) from where water moves along the coast both in an equatorward and a poleward direction (Figure 1) as the southern and northern limbs of the East Madagascar Current (Lutjeharms et al., 2000). This current is narrow and intense and its velocity seems to increase in both downstream directions. Speeds of 1 m/s are often found along this coastline, but speeds in excess of 1,5 m/s only in the downstream parts of both limbs of the current. The northern limb has a total volume flux of $21 \times 10^6\ m^3/s$ and augments the water movement of the northern part of the wide drift of the South Equatorial Current as it moves westward past Cap d'Ambre. Over most of its length it has speed in excess of 0.6 m/s (Schott et al., 1988) and is about 300 m deep. It exhibits very energetic, but as yet unexplained, transport variations in the temporal band of 40-55 days.

The southern East Madagascar Current is intense, narrow (80 km) and hugs the shelf edge (Lutjeharms et al., 1981). All data to date suggest that its trajectory is very stable (Swallow et al., 1988). The upper 50 m is Tropical Surface Water with a salinity of less than 35 ppt. and a temperature in excess of 23° C. This is in contrast to the ambient surface waters that are Subtropical Surface Water and have a salinity greater than 35.7 ppt. In the East Madagascar Current itself, Subtropical Surface Water is found as a subsurface salinity maximum at a depth of about 200 m. The termination of the southern branch of the East Madagascar Current is also very different to that of its northern counterpart.

All presently available evidence suggests that the East Madagascar Current terminates in the general region south of Madagascar in a turbulent flow regime. It sometimes may even retroflect totally (Lutjeharms et al., 1981; Figure 1) with most of its waters subsequently returning eastwards (Lutjeharms, 1988). Where the current moves from a narrow adjacent shelf situation to a wider shelf off Tolagnaro - on the south-eastern corner of the island (Figure 1) - an intense, localised upwelling cell has been identified (Lutjeharms & Machu, 2000; DiMarco et al., 2000) inshore of the current on the continental shelf. This upwelling is evident from noticeably lower temperatures of the coastal surface waters between Tolagnaro and Cape St Marie and by an increase in the chlorophyll in the water. The presence of this upwelling cell seems unrelated to reigning winds and may well be driven by the East Madagascar Current. The retroflection and the attendant coastal upwelling constitute a most unusual configuration and will cause considerable flow variability in the general region south of Madagascar (Cheney et al., 1983). This is substantially increased by the presence of very intense deep-sea eddies (Figure 1).

These anti-cyclonic eddies seem to have their source in the South Equatorial Current whence they drift off towards southern Africa. They form a prominent, but unusual, part of the circulation off the east coast off southern Africa (e.g. Gründlingh et al., 1991). They have high azimuthal speeds of up to 1 m/s and extend to depths exceeding 2000 m. It is not yet known whether these eddies interact with the terminal region of the southern limb of the East Madagascar Current.

The water circulation on the other side of Madagascar, in the Mozambique Channel, is very different. This whole region may be considered to lie in the lee of the island, sheltered from the direct influence of the South Equatorial Current (Figure 1) and not distinctly part of the basin-wide gyre. The South Equatorial Current overshoots the northern tip of Madagascar and passes by the Comoro Islands. Surface water passes southward into the channel only near the coast of Africa. Between the Comoro Islands and Madagascar the circulation on average seems to be anti-cyclonic (Donguy & Piton, 1969) and shallow. The most characteristic part of the circulation in the Mozambique Channel is its extreme complexity (Sætre, 1985; Sætre & Jorge da Silva, 1984) and variability.

Analysis of the variability of the currents for the region as a whole, for example with satellite altimetry (e.g. Cheney et al., 1983), has shown that the western side of the channel - from the narrows poleward - is characterised by extreme levels of mesoscale turbulence. This would not be so if there was a stable westward boundary current, the Mozambique Current, here. Modelling (Biastoch & Krauss, 1999) has indicated that the main circulatory feature may be cyclonic eddies that are predominantly formed just south of the narrows in the channel and that then translate poleward where they eventually leave the Mozambique Channel to join the Agulhas Current. This modelling has subsequently been verified by a research cruise in the region (De Ruijter et al., 2001). Based on this limited data currently at our disposal it must be assumed that the circulation in the western side of the Mozambique Channel is dominated by cyclonic eddies drifting southward. The currents in the eastern side of the channel, along the west coast of Madagascar, are even less clear. Perhaps the only clearly defined feature of the current flow in the Mozambique Channel is the anti-clockwise gyre surrounding the Comoro Islands. It has been postulated that the ecological links created by this gyre system make north west Madagascar an important spawning source for the region (J. Clay, pers. comm. to M. Nicoll).

There is evidence that the flow along the south-western coast of Madagascar can be equatorward on occasion (Sætre & Jorge da Silva, 1984) but there is also evidence to the contrary (Lutjeharms et al., 1981). The only inference possible from existing data is that the currents in the eastern part of the Mozambique Channel are much weaker than elsewhere in the channel and that they exhibit less energetic variability than along the western side (Lutjeharms et al., 2000).

Areas of upwelling and high primary production

The best known upwelling area is opposite Cap St. André near the island of Juan de Nova (Ralison 1991) where elevated nutrient concentrations give rise to high phytoplankton biomass (e.g., chlorophyll *a* counts greater than 4 $mg.m^{-3}$ at 60 m; Citeau et al. 1973). As noted above, there is an area of upwelling between Tolagnaro and Cap Ste. Marie, where waters have high primary productivity (10.5-50 mg C $m^{-2}.d^{-1}$) (Fig. 2) (Marsac 1998). A possible upwelling has been indicated for waters off Cap Masoala, where FAO acoustic surveys in 1983 indicated a high abundance of planktonivorous fishes (Anonymous 1983).

A zone of high productivity is also indicated around Toliara (Marsac 1998), although has not been explained. Fisheries around Toliara have high productivity (Laroche & Ramanarivo 1995; Rakotoarinivo 1998). Madagascar’s only colony of Red-tailed Tropicbird (*Phaethon rubricauda*) at Nosy Ve (Cooke & Randriamanindry 1996) and the large numbers of nesting terns on Nosy Manitse (ZICOMA 1999) indicate a zone of nutrient enrichment.

Winds

The southeastern trade winds and the monsoon affect Madagascar’s coastal seas. The balance between these two systems is determined by shifts in position of the Mascarene anticyclone and a zone of low pressure that appears over the Mozambique Channe*l* in May-July. In general, winds along the east coast are strong and southerly, while on the west coast winds are variable and less strong. Antsiranana, in the extreme north, is the windiest coastal location in Madagascar while Nosy Be, protected by the Tsaratanana Massif, is the least windy.

Tides

Due to the narrowing of the Mozambique Channel, the west coast of Madagascar has some of the largest tidal ranges of the western Indian Ocean region, with mean spring ranges of 3.8 m at Mahajanga and 2.6 m at Toliara. Maximum heights occur along the channel's narrowest section (Cap St. André to Maintirano), where tidal range may exceptionally reach 5 m at sites such as Nosy Chesterfield and Juan de Nova.

The eastern coast tidal range is about 1 m in the northeast, dropping to about 0.5 m in the southeast. Consequently, coral reefs and mangroves cover much larger areas on the west coast than on the east coast (over 90% of all reefs and about 98% of all mangroves are on the west coast). Locally, rising or falling tides engender strong currents that have a marked influence on the distribution of benthic and other biota.

Rainfall and terrestrial hydrological processes

Rainfall effects the distribution of marine and coastal ecosystems and species through the discharge of rivers and deltas. Hydrological processes, notably underground rivers and freshwater springs, influence marine ecosystem development in some areas.

Madagascar's largest rivers drain along the western seaboard, bringing large quantities of fresh water and sediment, reducing salinity, increasing turbidity and adding nutrients and suspended organic matter. At Antsabora, close to the mouth of the Tsiribihina River, salinity varies between 32% in the dry season to 24% in the rainy season (Razafindrainibe et al. 1996). The major estuaries and deltas support vast areas of mangrove.

In the west, tidal salt-water penetration of rivers, high concentrations of dissolved minerals (notably calcium salts), and warm water temperatures, have permitted the development of a diverse euryhaline fauna, with at least 224 euryhaline fish species. Along the east coast, tidal salt water penetration is limited and river waters are acidic, weakly mineralized and cool. Consequently, the euryhaline fauna is less diverse and is restricted to river mouths and brackish lagoons (Kiener 1964). The cyclical presence of freshwater in mangroves is vital to the breeding cycle of several species of shrimp, notably *Paenaus indicus* and *P. monodon*. High catches by the industrial shrimp fishery are associated with years of high rainfall (Lhomme 2000).

At certain locations in the southwestern portion of the island underground rivers and springs discharge mineralized (calcium-rich) water along the littoral fringe, supporting the development of mangroves, influencing coral reef development (Lebigre 1997), and attracting various euryhaline species (Kiener 1964).

Erosion of watersheds

The erosion of watersheds has a marked effect on near shore ecosystems, especially along the west coast. There is abundant evidence for hyper-sedimentation, especially over the last 15-25 years (e.g., Vasseur 1997; Rabarison et al. 2000), and for locally extreme turbidity during periods of peak river discharge along the west coast (Cockroft & Young, 1998). The impacts of sedimentation have not been systematically evaluated. Randriamanantsoa (1997) reports that terrigenous sediments make up just 1-1.5% of sediments of the lagoon floor at Toliara, while sedimentation of reefs north of Toliara due to the Fiherenana River is extreme, with considerable areas of reef and mangrove smothered by alluvial sands (e.g., Vasseur 1997). River discharges contribute nutrients to coastal waters that are readily observable in satellite images as zones of raised chlorophyll concentration extending several km from the major river mouths.

The principal marine and coastal ecosystems

Pelagic waters

Pelagic waters (those over the continental shelf) are more productive than oceanic waters, due to higher temperature, the influence of river discharge, and vertical transfer of nutrients from bottom sediments. Madagascar's pelagic areas have considerable potential for fisheries, notably for benthic lobster, deep-water shrimp, and demersal fish (Andrianaivojaona et al. 1992).

On the east coast, surface waters are oligotrophic, with moderate primary productivity (2-5 mg C $m^{-2}.d^{-1}$ in summer). On the west coast, productivity is moderate as far north as Maintirano (with the exception of the Toliara "hotspot"), but higher in the northwest from Cap St. André to Cap d'Ambre (5.1-10 mg C $m^{-2}.d^{-1}$ in summer) (Marsac 1998).

Oceanic banks and shoals

A number of oceanic banks occur close to the edge of Madagascar's continental shelf. The largest of these is the Banc de Leven (with the associated Banc de Castor), some 40 km west-northwest of the Mitsio Island group, which covers an area of about 2500 km^2 and effectively constitutes an extension to Madagascar's continental shelf. To the west of Leven lies Banc de Geyser, likewise part of the Comoro Islands volcanic chain. About 150 km due west of Cap St. André is a pair of seamounts, former atolls, rising to within 30 m of the surface. Ile Juan de Nova (17^{O}03'S, 42 ^{O}43'E) is the only fully exposed atoll, with an extensive coral reef. To the south of Juan de Nova are three further banks (Taunton Castle, Estaign, and Vines). Oceanic banks are absent along the southwest coast. About 80 km south of Cap Ste Marie lies the Banc de Tabinta, separated from the continental shelf by a small gap. South of Tabinta the ocean floor, at around 2000 m, includes a number of mounts rising to within 500 m of the surface and several holes descending to over 3 km. Oceanic banks are absent along the east coast of Madagascar.

Oceanic banks do not necessarily escape from fishing pressure. Of the 23 oceanic reefs visited by Polunin & Frazier (1974) in April-July 1973, they reported Banc de Geyser as the only oceanic site to be substantially free of human impact, judged on the presence of large predators and tameness of the fish. However, even this site is now quite heavily fished (Quod et al. 2000).

Abyssal zone

The abyssal habitats of Madagascar are virtually unstudied. A review of scattered deep-sea fisheries research might yield insights into the ecology of the abyssal zones around Madagascar. At St. Augustin the sub-marine canyon of the Onilahy River, which drops to 1500 m close to the coast (Battistini et al. 1975; Salomon 1986), supports a population of the coelacanth *Latimeria chalumnae*, of which specimens were caught in 1996 and 1998 (see below).

Intertidal and shallow marine ecosystems

The length of Madagascar's coast is officially set by Foiben Taosarintanin'i Madagasikara (FTM) at 5,603 km, including the principal inhabited islands. The principal shallow water marine and coastal habitats are mangroves, estuarine mud flats, rocky foreshore, beaches, coral reefs, and seagrass beds. Coral reefs, mangroves, seagrass beds, and mud flats are the dominant habitats along the shallow sloping west coast, whereas steeply shelving beach and rocky shoreline predominate on the east coast.

Mangroves

Madagascar possesses over 425,000 ha of tidal marshes, of which an estimated 327,000 are covered by mangroves. Due to the greater tidal range (2.10-4.5 meters), most (98%) of Madagascar's mangroves are on the west coast, with just 2% on the east coast. On the west coast, over 95% of mangroves are distributed between the Mangoky delta (21^{O}S) and the Mahavavy estuary (13^{O}S). Between Morombe (21.5^{O}S) and Androka (25^{O}S), a region important for its coral reefs, are about 1000 ha of mangroves. Most (70%) of western mangroves are in large stands exceeding 500 ha. Very large stands of over 20,000 ha occur in the estuaries of Mangoky, Tsiribihina, Ranobe (Besalampy), Betsiboka, Mahajamba and Mahavavy (Baie d'Ambaro). The principal concentrations of mangrove on the east coast are between Cap d'Ambre and Iharana (13^{O}S), Masoala peninsular (15-16^{O}S), Mananara/Antanambe (16-16.5^{O}S), Toamasina and north of Tolagnaro (Manantenina, Ste Luce, Evatraha). Mangroves are virtually absent between Toamasina and Manantenina). While of much smaller surface area, east coast mangroves are typically dense with dark soils and are presumably locally in coastal ecology and defense (Kiener 1972; Lebigre 1990*)*.

Mangroves on the west coast are important as breeding areas for several commercial fish species, such as mullet (Mugilidae), sicklefish (Drepanidae), and ponyfish (Leignathidae) (Andrianjohany 1992). Temporal patterns of fish assemblages in Toliara mangroves have been documented by Laroche et al. (1997). Large stands of mangrove are associated with a high proportion of organic material in bottom sediments and high productivity of the shrimp *Penaeus indicus* (Razafindrainibe et al. 1996). Catches of the industrial shrimp fishery correlate positively with mangrove area (Lhomme 2000).

Madagascar's mangroves are similar to those of East Africa in species composition and diversity, being much less diverse than those of India and Pacific-Asian countries. Jenkins (1987) reports nine species in six families: Rhizophoracae (*Rhizophora mucronata, Bruguiera gymnorrhiza, Ceriops tagal*); Avicenniaceae (*Avicennia marina*); Sonneratiaceae (*Sonneratia alba*); Combretaceae (*Lumnitzera racemosa*); Meliaceae (*Xylocarpus granatum, X. molllucensis*); Sterculiaceae (*Heritiera littoralis*) noting that *Ceriops* is sometimes considered to be represented by an endemic species *Ceriops boviniana*.

Coral reefs

The coral reefs of Madagascar have been described by Battistini (1972) and Pichon (1972). Reefs occur as emergent fringing and barrier reefs, patch reefs, and as submerged coral banks and shoals. While Madagascar is particularly known for the spectacular barrier reefs of the Toliara region, equally impressive is the existence of an ancient submerged barrier reef parallel to the western and northwestern continental shelf. The ancient reef is manifested as a string of banks and shoals, sometimes broken by passes, at a general depth of 15 to 30 m with frequent peaks to 10 m or less. Sea levels rose rapidly about 6,000 years ago by about 20 m (Wilkinson and Buddermeier, 1994). Assuming a tidal variation of up to 5 m, this formation was probably emergent along much of its length 6,000 years ago. Coral cover for the submerged reef is low (about 10% on average), indicating that this reef is no longer growing (Jenkins 1987).

Several authors (e.g., Gabrié et al. 2000) have estimated the length of coral reefs in Madagascar. Inspection of marine charts indicates 1130 km of fringing reef, 557 km of reef around islets and islands or patch reefs, 52 km of true barrier reef (all in the Toliara region), and 1711 km of submerged coral banks and shoals, or a total of 3540 km of coral formations.

The principal concentrations of emergent reefs are in the northeast (Cap d'Ambre to Toamasina – 417 km), southwest (Androka to Morombe – 458 km), and the northwest (Mahajanga to Cap d'Ambre (578 km). The principal zone of submerged reef is 1418 km long and runs from Morombe to Cap d'Ambre (Cooke et al. 2000).