

REVIEW

Seasonality in East Africa's coastal waters

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ABSTRACT: A review of existing literature and data on seasonal patterns in East Africa's coastal waters indicates distinct seasonality in physical, chemical and biological oceanographic parameters. Seasonal patterns are dictated by the behavior of the Inter-Tropical Convergence Zone (ITCZ) which creates 2 distinct seasons – the northeast and southeast monsoons. SE monsoon (March to October) meteorological parameters are characterized by high cloud cover, rainfall, river discharge, terrestrial runoff and wind energy while solar insolation and temperatures are low; SE monsoon oceanographic parameters are characterized by cool water, a deep thermocline, high water-column mixing and wave energy, fast currents, low salinity and high phosphorus. These parameters are reversed during the NE monsoon. Nitrogen availability and planktonic primary productivity are high along the Somali coast and estuarine and river discharge areas during the southeast monsoons due to nutrient upwelling and terrestrial runoff. In near-shore waters off Tanzania, nitrogen fixation is the major source of nitrogen and is highest during NE monsoons when the water column is stable. Coral reef benthic algal biomass and diversity is greatest during the SE monsoons. Fish catch and reproduction are highest during NE monsoons in Kenya and Tanzania. Transition periods between monsoons may also be important times in determining productivity and reproduction.

INTRODUCTION

Tropical marine ecosystems have been noted for minor seasonal changes or aseasonality (Heinrich 1962, Sournia 1969, Blackburn et al. 1970, Steven & Glombitze 1972) but in East Africa large seasonal changes control many ecological processes. While seasonality of the wet and dry seasons is a well-documented phenomenon for East Africa's terrestrial (Western 1975, Sinclair & Norton-Griffiths 1979) and lacustrine (Melack & Kilham 1974, Melack 1979) environments, seasonality of the marine environment is less understood and studied. Nevertheless, some research has been completed on this subject, focusing on various physical, chemical and biological processes. This paper reviews this literature in an attempt to synthesize and develop an understanding of seasonality in East Africa's coastal waters focusing on the area 10° north and south of the equator constituting the coastlines of Somalia, Kenya and Tanzania (Fig. 1).

METEOROLOGICAL PARAMETERS

Climatic patterns are the single most important factor affecting seasonal changes throughout East Africa, and a good understanding of these factors lends insight into the affected physical, chemical and biological processes. In particular, the Inter-Tropical Convergence Zone (ITCZ) is the single most important climatic phenomenon affecting seasonality, and its annual migration creates the 2 seasons experienced near the equator known in East Africa as the northeast (NE) and southeast (SE) monsoons. Off the Somali coast the easterly air movement during the SE monsoon is over-ridden by a westerly flow towards the Asian continent in the northern hemisphere summer (Fig. 1) and is therefore named the southwest monsoon in some literature. Within the Indian Ocean region the ITCZ shifts further north during the SE monsoon than in most tropical areas due to the low pressure belt created on the Asian continent during the northern hemisphere

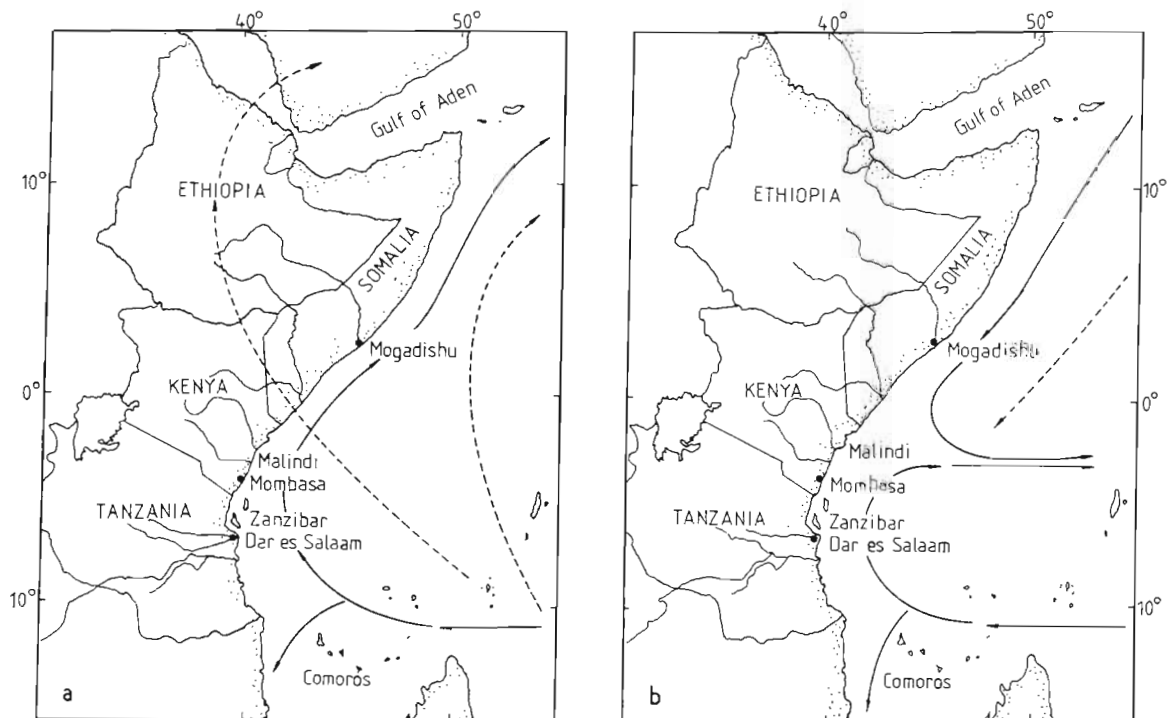


Fig. 1. Current patterns (solid lines) and wind directions (dashed lines) during (a) the SE and (b) the NE monsoons in the East African region

summer. This shift is responsible for the greater seasonality experienced in East Africa and a greater distinction between wet and dry seasons than in many other tropical areas.

Inland areas in East Africa experience 2 rainy seasons occurring shortly after equinoxes and 2 dry seasons occurring during solstices. Due to the shape of the African continent and wind direction the greatest amount of rainfall occurs during the SE monsoon when winds pass over the Indian ocean. During the NE monsoon the air mass passes over the drier Somali land mass and therefore coastal areas receive only a small rainfall peak (Fig. 2) that may be attributed to the generation of a local land-sea breeze system. Inland areas receive more rainfall due to the expansion of a wet low pressure area from Central Africa which rarely reaches the coast.

Coastal meteorological measurements from Mombasa (4° S) reflect the described processes (Fig. 2). The division between NE (October to March) and SE monsoons (March to October) indicates 2 distinct coastal seasons compared to 2 wet and 2 dry seasons at similar latitudes inland. SE monsoons are characterized by high cloud cover, rain, wind energy and decreased temperatures and light. This is in contrast to NE monsoons when variables are reversed. These climatic phenomena ultimately affect physical, chemical and

biological oceanographic processes (for fuller meteorological information see Griffiths 1972).

PHYSICAL OCEANOGRAPHIC PROCESSES

Currents along the coast are affected by wind patterns, the continent and the Coriolis force. The major circulation is part of the clockwise current of the northern part of the Indian Ocean (Düing 1970; Fig. 1). The Southern Equatorial Current traverses the Indian Ocean, encounters the coast at Tanzania and moves northward forming the East African Coastal Current. During the SE monsoon (Fig. 1a) this current continues north and leaves the continent at Somalia. During the NE monsoon (Fig. 1b) the changing winds slow the northerly water movement and eventually reverse the movement, forming the Somali Counter Current. This current can reach as far as 4° S during years when it is strong, before leaving the coast (Johnson et al. 1982).

Due to these currents the major downwelling area and associated low nutrient waters are along Tanzania and southern Kenya (Bell 1972). Downwelling occurs throughout the year but is strongest during SE monsoons when current speeds are greatest. Upwelling occurs along northern Somalia during SE monsoons but breaks down during NE monsoons as the current direc-

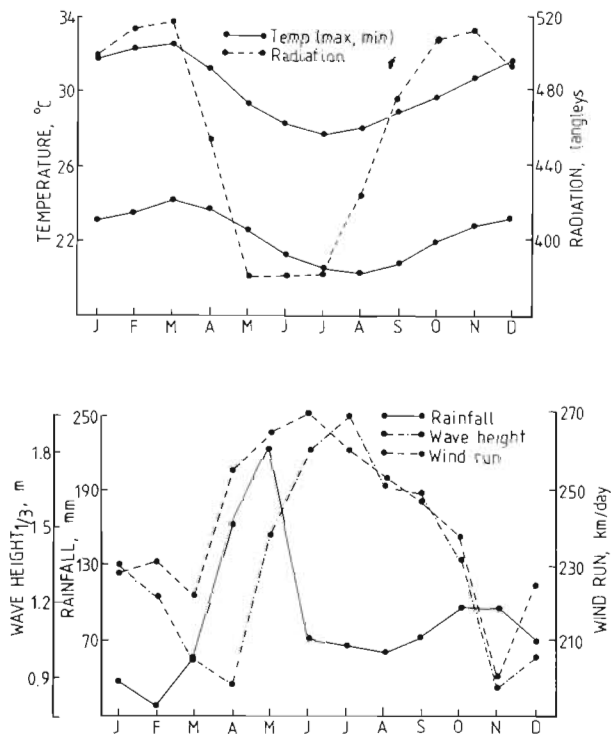


Fig. 2. Meteorological parameters in Mombasa. Monthly (a) air temperature (maximum and minimum, 1946 to 1980) and solar radiation (1963 to 1980); and (b) rainfall (1946 to 1980), wind run (1971 to 1980) and significant sea and swell wave height (height of the 1/3 largest waves). Data from the East African Meteorology Department (1980) and Turyahikayo (in press)

tion switches (Warren 1966, Warren et al. 1966, Düing & Schott 1978, Smith & Codispoti 1980, Leetmaa et al. 1982). During NE monsoons, currents leave the coast from northern Kenya and slight upwelling may occur there (Kabanova 1968).

Differences in currents, up and downwelling, water temperatures and nutrients cause a north-south dichotomy between ecosystems along the coast. The southern section is predominated by coral reefs and benthic productivity associated with low-nutrient warm waters. The northern section has cooler nutrient-rich waters and a greater predominance of planktonic productivity.

Current speed and water column mixing are affected by wind speed and duration. As wind run and speed are greatest during SE monsoons so is water column mixing and an associated deeper thermocline (Newell 1957, 1959, Morgans 1962, Iversen 1984). Wave height off the Kenyan coast (Turahikayo in press) lags slightly behind wind energy and is greatest during the SE monsoons (Fig. 2; Norconsult 1977). Increased cloud cover and decreased air temperatures during SE monsoons lower surface seawater temperatures which lag behind air temperatures (Fig. 3).

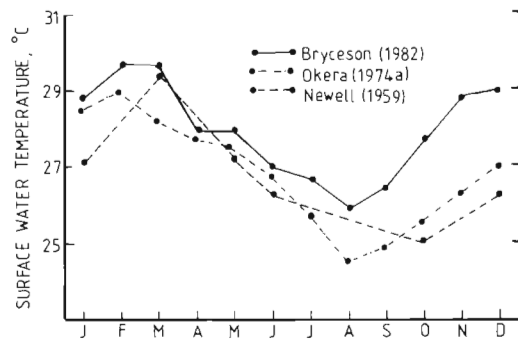


Fig. 3. Monthly surface water temperatures off the Tanzanian coast for 3 sampling periods (1975, 1969, 1955-56)

The tidal range in Kenya is 4 m which is relatively large for a tropical coastline (Brakel 1982). The general tidal pattern in East Africa, as in many equatorial regions, is to have the most extreme tides around equinoxes or intermonsoon periods and lesser extremes during solstices. This affects the number of emersions per lunar month, the duration of emersions and submersions (Brakel 1982) and ultimately the growth of intertidal organisms and their distribution on a seasonal basis. Spring tides and extreme spring tides during intermonsoon times may result in periodic nutrient inputs from estuarine areas on a lunar and annual basis.

CHEMICAL OCEANOGRAPHIC PARAMETERS

Chemical parameters have been measured (single samples) off Tanzania by Newell (1959) in offshore waters (> 500 m deep) 25 km east of the southern end of Zanzibar for a variety of depths, and by Bryceson (1977, 1982) in nearshore (60 m deep, 6°40' S, 39° 17' E) surface waters (0.5 m deep). Chemical parameters also reflect seasonal changes. The main sources of mineral elements such as phosphorus are water column mixing, upwelling, river discharge and runoff. In downwelling areas off Tanzania and southern Kenya the main sources of phosphorus are water-column mixing (Newell 1959, Bryceson 1982), discharge and runoff occurring during rainy seasons. Phosphorus concentrations peak in June (Fig. 4) soon after the initiation of the SE monsoon. Newell (1959) showed that phosphorus concentrations increase with depth. This phosphorus reaches surface waters during the SE monsoon due to water-column mixing. In northern Kenya water-column mixing and river discharge are likely to be important nutrient sources, and upwelling off the Somali coast (McGill 1973, Smith & Codispoti 1980).

Discharge of major rivers is affected by inland rainfall patterns rather than local patterns. Hence, dis-

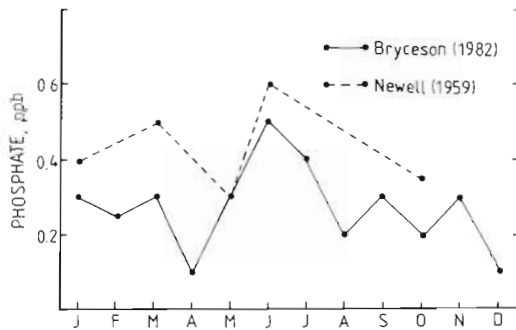


Fig. 4. Seasonal surface water phosphate-phosphorus changes for 2 yr (1975, 1956) off the Tanzania coast. Newell's (1959) data are averages of single samples collected at 0 and 20 m and Bryceson (1982) single samples collected at 0.5 m

charge peaks during NE and SE monsoons occur shortly after the inland rainy season (Fig. 5). Local runoff is greatest during the SE monsoon. The total effect is such that the SE monsoon has the greatest influx of freshwater and terrestrial nutrients. Nutrient concentrations in rivers are quite high due to poor inland soil conservation practices. Measurements from

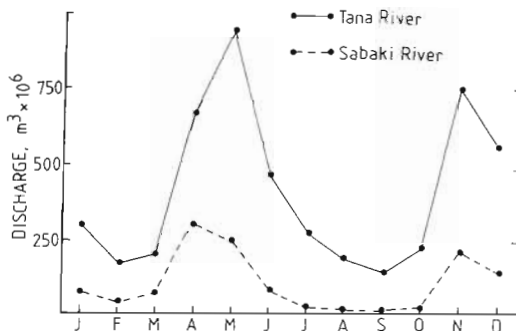


Fig. 5. Average monthly discharge from Kenyan Rivers Tana (1948 to 1979) and Sabaki (1952 to 1979). Data from the Tana River Development Authority (1981)

the Sabaki river (1980-1981) show average phosphorus concentrations of 1300 ppb and nitrates of 165 ppb (Giesen & van de Kerkhof 1984). During SE monsoons current circulation is towards the north as are freshwater inputs (Brakel 1984). NE monsoon discharges are less and current velocities slower to the south keeping discharge effects localized around discharge points (Brakel 1984). The Sabaki and Tana river discharges occur in northern Kenya which further emphasizes the previously mentioned north-south dichotomy.

Lowest salinities occur at the onset of the SE monsoon when discharge, cloud cover and rainfall are high (Fig. 6). Immediately following the rainy season, near-

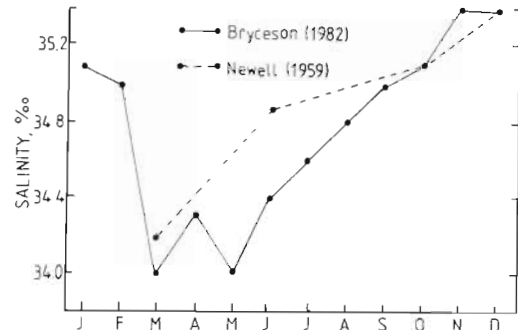


Fig. 6. Salinity changes during 2 yr (1975, 1956) off the Tanzanian coast

shore salinity can drop drastically in nearshore areas and has been measured as low as 26‰ (Mwaiseje 1973). Highest salinities occur during NE monsoons when air temperatures and solar insolation are high and rainfall and discharge low.

Nitrogen has 3 important sources, namely biogenic sources formed from nitrogen fixation, terrestrial runoff and upwelling. In non-upwelling pelagic areas nitrogen fixation is likely to be the main nitrogen source. Bryceson (1982) suggests that nitrates in nearshore waters off Tanzania reflect the breakdown of nitrogenous compounds from nitrogen-fixing algae (Fig. 7). In littoral and estuarine areas nitrogen from terrestrial sources may be more important. A seasonal study of the Tudor creek in Mombasa (Norconsult 1977) showed that nitrate-nitrogen was highest during the SE monsoon suggesting that runoff was the main nitrogen source in these creeks. Data on other nutrients and chemicals except oxygen (Newell 1959, McGill 1973, Bryceson 1982, Iversen 1984) have received no attention but may be a fruitful area of research.

BIOLOGICAL PARAMETERS

Studies of seasonality in biological systems have been restricted to planktonic systems, benthic algae, rocky shores and fisheries. Planktonic systems are variable depending on chemical and physical forces affecting them. Patterns of nitrogen availability are useful in understanding plankton as nitrogen often limits marine primary productivity (Ryther & Dustan 1971, Hecky & Kilham in press). Bryceson (1982) showed that chlorophyll and phytoplankton abundance and diversity are most abundant in Tanzania's nearshore waters during NE monsoons (Fig. 8). He attributed this to calmer conditions which create a shallow stable thermocline which keep phytoplankton at optimal photosynthetic light intensities near the surface. This optimizes conditions for the nitrogen fixing blue-green

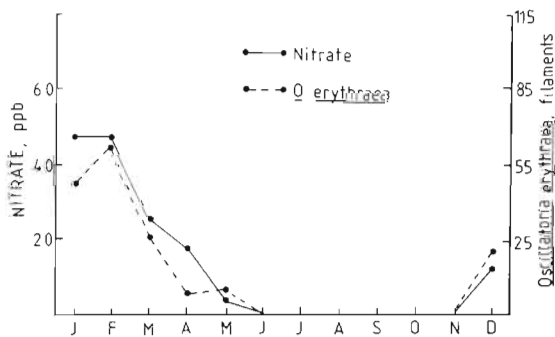


Fig. 7. Seasonal nitrate-nitrogen values and the abundance of a nitrogen-fixing alga from nearshore waters off the Tanzanian coast. Data from Bryceson (1982) collected at 0.5 m during 1965

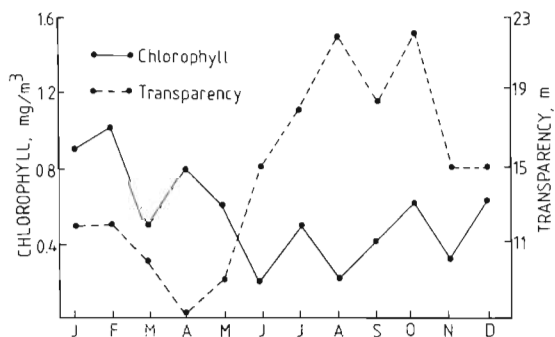


Fig. 8. Seasonal changes in surface-water (1975; 0.5 m) chlorophyll concentrations and turbidity measured by a Secchi disk in nearshore waters off the Tanzanian coast. Data from Bryceson (1982)

algae *Oscillatoria erythroa* which eventually may positively affect other phytoplankton taxa. Okera's (1974a) nearshore zooplankton study (20 m deep, vertical tows at 0.3 m s⁻¹), completed near Bryceson's (1982) site, indicates that zooplankton in Tanzania is most abundant during late NE and early SE monsoons and probably lags somewhat behind phytoplankton peaks (Fig. 9).

In river discharge, estuarine and upwelling areas phytoplankton productivity is greatest during the SE monsoon (Kabanova 1968, Krey 1973, Smith & Codispoti 1980) probably due to increased nitrogen availability from terrestrial sources and upwelling. A zooplankton study of Tudor creek, Mombasa (Kimaro 1986) indicates that zooplankton abundance is greatest 2 to 4 wk after rainfall peaks in March and November although overall creek zooplankton abundance was greatest during the NE monsoon. Bryceson (1977) failed to find planktonic seasonality in Tanzania's estuarine areas.

Moorjani (1978, 1979, 1982) studied seasonal changes in algal biomass on reef platforms of southern Kenya. She found that the richest flora and biomass

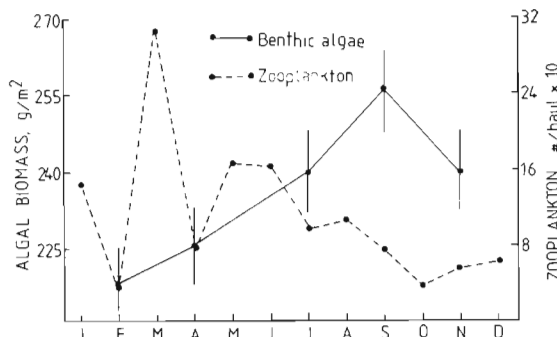


Fig. 9. Seasonal changes in zooplankton abundance in nearshore waters off the Tanzania coast (1969) and average seasonal biomass (1973-74; $\bar{x} \pm 0.5$ SE) of benthic algae from 13 sites on 2 Kenyan reef platforms. Data from Okera (1974a) and Moorjani (1979)

occurred towards the end of the SE monsoon, reaching a peak in September (Fig. 9). Species of Phaeophyta (brown algae) and Rhodophyta (red algae) made their greatest contribution to floral diversity and biomass during this time. During the NE monsoons, Chlorophyta (green algae) and Cyanophyta (bluegreen algae) were relatively more abundant. Moorjani emphasized the physical factors creating this pattern, suggesting that desiccation stress was less severe during the SE monsoons and therefore more favorable to benthic algae. Yet, in tropical areas, herbivory plays an important part in determining algal biomass. It may be that there is reduced herbivory during this time due to lower water temperatures. Herbivory in coral reefs can affect both biomass and taxon-relative abundance (Hay 1984). Additionally, greater water transparency during the SE monsoon (Fig. 8) in southern Kenya and Tanzania may have a positive effect on benthic primary productivity.

During the SE monsoon, many intertidal benthic organisms expand their distribution. This has been observed for benthic algae (Moorjani 1978) and rocky shore gastropods (Ruwa & Jacarrini 1986). Increased wave energy and decreased desiccation factors allow expansion to higher tidal areas. However, seasonal changes in benthic algal biomass failed to show seasonality in a reef-inhabiting algivorous echinoid (Khamala 1971) which may be responding to environmental or biotic factors on a longer time scale (Muthiga & McClanahan 1987).

FISHERIES

Fisheries research in Kenya and Tanzania indicates distinct seasonal changes in finfish catches (Fig. 10). Catch is low during the SE monsoon and high during the NE monsoon with a peak in March at the end of the

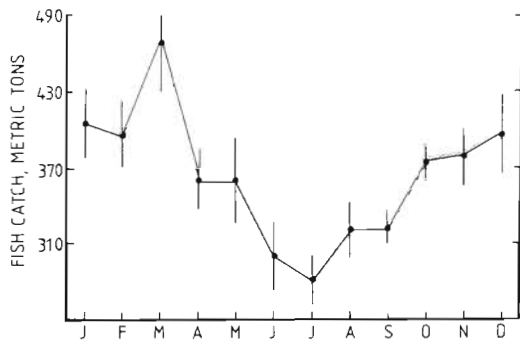


Fig. 10. Kenya's monthly ($\bar{x} \pm SE$) marine fish catch (1968 to 1984 except 1970, 1971 and 1977). Data from the Kenya Fisheries Department (1986)

NE monsoon. It is difficult to determine from existing data the extent that various factors of fishing effort, fish population changes and environmental factors play in these data. Factors affecting observed seasonality include (1) reduced effort by fishermen during the SE monsoon due to rough sea conditions, (2) fish migrations (Williams & Newell 1957) and (3) decreased density and activity due to a deeper thermocline and cooler waters in the SE monsoon (Morgans 1962). Surveys which have measured fishing effort have shown this seasonal pattern to occur when effort was kept constant or catch per unit effort was calculated (Williams 1965, Merrett 1968, Kamanyi 1975, Nhwani 1980a, b). This suggests that the last 2 factors make the greatest contribution to the observed pattern.

Fish reproduction is the most studied topic concerning coastal seasonality. Most studies show that reproduction is highest during the NE monsoon in Kenya and Tanzania for both pelagic (Williams & Newell 1957, Williams 1965, Merrett 1970, 1971, Okera 1974b) and demersal (Talbot 1960, Darracott 1977, Nzioka 1983, 1985) fish (Fig. 11). Yet Rubindamayugi (1983)

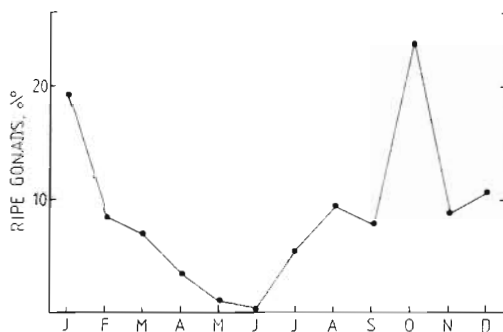


Fig. 11. Percent ripe gonads in fish from 5 families (Serranidae, Lutjanidae, Lethrinidae, Mullidae and Scaridae) along the Kenya and Tanzanian coast (1974–77). Data from Nzioka (1979)

shows a distinct unimodal breeding peak during the SE monsoon for *Leptoscarus vaigiensis* in Tanzania which feeds on seagrass. Some species are aseasonal breeders (Talbot 1960, Nzioka 1979) while others breed during intermonsoon times (Nzioka 1982). Spiny lobsters (Bwathondi 1973) breed throughout the NE monsoon and the important fisheries crab *Scylla serrata* (Bashemererwa 1981) appears to migrate from its mangrove habitat and breeds during the initial part of the NE monsoon between September and December. Many species may be timing their reproduction to high water temperatures associated with the NE monsoon but reproduction should vary according to the species life-histories.

From the data presented it is clear that seasonality is a major factor affecting biological processes on a yearly basis, but it should also be appreciated that the severity of meteorological and oceanographic conditions changes between years as well as within years. Observations on Kenyan fish catches over the past 17 yr show marked variation between years and no overall upward or downward trend that might be expected from changes in fishing effort or overfishing (Fig. 12). In fact, Martin (1973) has observed that fishing effort has been fairly constant in Malindi since the introduction of modern fishing gear before 1958. Correlating Kenyan fish catch with Tana river discharge (Garissa station) and coastal rainfall (Mombasa station) for lag times between 1 and 5 yr shows a positive association increasing up to the fourth year for both river discharge ($t + 1$ to 5, $r = -0.06, 0.29, 0.46, 0.62, 0.43$) and rainfall ($t + 1$ to 5, $r = 0.01, 0.32, 0.43, 0.65, 0.38$) but both variables are statistically significant ($p < 0.01$) only at the 4 yr lag time. Nutrient inputs associated with discharge may eventually result in increased recruitment and growth (Sutcliffe 1972).

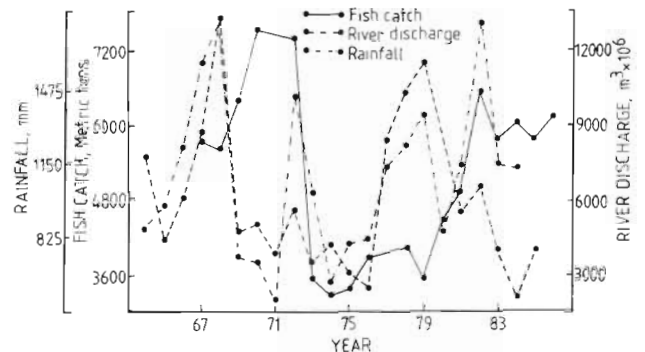


Fig. 12. Total Kenyan marine fish catch (1967 to 1984, except 1971 and 1977), Mombasa annual rainfall (1964 to 1984) and Tana river flow (Garissa, 1964 to 1985, except 1980). Data from Kenya Fisheries Department (1986), East African Meteorological Department (1980), Tana River Development Authority (1981) and Kenya Ministry of Water Development (1986)

River discharge and runoff may have some initial negative effects due to increased sediment, reduced light penetration or large changes in salinity. These negative effects are probably localized close to discharge points and the total effect, on a larger spatial scale, is one of increased productivity. Discharge areas such as the Tana and Sabaki rivers have long been known as areas of good fishing and high productivity for tropical waters (Morgans 1959, Wickstead 1961, Iversen 1984, Venema 1984) and this is undoubtedly due to river discharge inputs and discharge-induced upwelling. There is no evidence to suggest that poor inland soil conservation practices are having a negative effect on fisheries or on coral reefs south of Malindi (Giesen & van de Kerkhof 1984), but a thorough study has yet to be completed. River discharges within this region have existed north of 3° S since the formation of the Rift Valley (approximately 30 million yr ago) and most extensive coral reefs have developed at sufficient distances from these discharge points to avoid their detrimental effects. The present anthropogenic changes in discharge are probably not beyond the historical variation experienced in recent geological time due to climatic changes. Poor soil conservation practices cause a shift in productivity from high potential terrestrial productivity to the lower potential productivity of marine plankton and benthic ecosystems. The major environmental problem is not the loss to fisheries or coral reefs but the lost potential productivity of the terrestrial environment.

CONCLUSION

It is apparent that seasonality is a major factor affecting annual patterns of physical, chemical and biological processes along the East African coast. Factors affecting seasonality are different from temperate regions. Rather than large solar radiation and temperature changes, characteristic of temperate regions, smaller changes in solar radiation result in the shifting ITCZ and associated meteorological and oceanographic changes. Research to date has often been descriptive and of poor temporal and spatial resolution. Future research needs to closely examine the causes of observed patterns with improved spatial and temporal resolution. This includes the need to study spatial and temporal patterns of primary and secondary productivity and annual fish migrations. Also, there is a complete lack of information on many of the major ecosystems including mangroves, seagrass beds, coral reefs and their response as species and ecosystems to seasonal changes. Further, fisheries data needs to be improved for its relevance to statistical analysis in order to make informed management decisions. This region offers the

potential to understand tropical seasonality and should receive further research efforts.

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LITERATURE CITED

- Bashemerwa, V. (1981). Some aspects of the biology of *Scylla serrata* (Forsk.) (Crustacea: Portunidae) in Dar es Salaam area. M. Sc. thesis, University of Dar es Salaam
- Bell, B. E. (1972). Marine fisheries. In: Morgan, W. T. W. (ed.) East Africa: its people and resources. Oxford University Press, London, p. 243–254
- Blackburn, M., Laurs, R. M., Owen, R. W., Zeitzschel, B. (1970). Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. *Mar. Biol.* 7: 14–31
- Brakel, W. H. (1982). Tidal patterns on the East African coast and their implications for the littoral biota. *Proc. Symp. Coastal & Mar. Envir. Red Sea, Gulf of Aden and Trop. West. Indian Ocean*, Vol. 2. ALESCO/UNESCO, Khar-toum, p. 403–418
- Brakel, W. H. (1984). Seasonal dynamics of suspended-sediment plumes from the Tana and Sabaki Rivers, Kenya: analysis of Landsat Imagery. *Remote Sensing Environ.* 16: 165–173
- Bryceson, I. (1977). An ecological study of the phytoplankton of the coastal waters of Dar es Salaam. Ph. D. thesis, University of Dar es Salaam
- Bryceson, I. (1982). Seasonality of oceanographic conditions and phytoplankton in Dar es Salaam waters. *Univ. Sci. J. (Dar Univ.)* 8: 66–76
- Bwathondi, P.O.J. (1973). The biology and fishery potential of *Palanurid* lobsters in Tanzania. M. Sc. thesis, University of Dar es Salaam
- Darracott, S. (1977). Availability, morphometrics, feeding and breeding activity in multi-species, demersal fish stock of the Western Indian Ocean. *J. Fish Biol.* 10: 1–16
- Düing, W. (1970). The monsoon regime of the currents in the Indian Ocean. East-West Center Press, Honolulu
- Düing, W., Schott, F. (1978). Measurements in the source region of the Somali current during monsoon reversal. *J. phys. Oceanogr.* 8: 278–289
- East African Meteorological Department (1980). Climatological statistics for East Africa. Nairobi
- Giesen, W., van de Kerkhof, K. (1984). The impact of river discharge on a Kenya coral reef ecosystem – the physical processes. II. Effect on the Malindi-Watamu coastal environment. Report to the Kenyan Office of the President, Nairobi
- Griffiths, J. F. (1972). *Climates of Africa*. Elsevier, New York
- Hay, M. E. (1984). Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? *Oecologia (Berl.)* 64: 396–407
- Hecky, R. E., Kilham, P. (in press). Nutrient limitations of phytoplankton in freshwater and marine environments: a

- review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.*
- Heinrich, A. K. (1962). The life histories of plankton animals and seasonal cycles of plankton communities in the oceans. *J. Cons. int. Explor. Mer* 27: 15–24
- Iversen, S. A. (1984). Kenyan marine resources in waters deeper than 10 m investigated by R/V 'Dr. Fridtjof Nansen' In: Iversen, S. A., Myklevoll, S. (eds.) Proceedings of the Norad-Kenya Seminar to Review the Marine Fish Stocks and Fisheries in Kenya. Institute of Marine Research, Bergen, Norway, p. 33–60
- Johnson, D. R., Mutua Nguli, M., Kimani, E. J. (1982). Response to annually reversing monsoon winds at the southern boundary of the Somali Current. *Deep Sea Res.* 29: 1217–1227
- Kabanova, J. G. (1968). Primary production in the northern part of the Indian Ocean. *Oceanology* 8: 214–255
- Kamanyi, J. R. (1975). Biological observations of Indian mackerel *Rastelliger kanagurta* (Cuvier) 1816 (Pisces: Scombridae) from East African waters. *Afr. J. Trop. Hydrobiol. Fish.* 4: 61–78
- Kenya Fisheries Department (1986). Marine fisheries data. Nairobi
- Kenya Ministry of Water Development (1986). Kenyan river discharge data. Hydrology Section, Nairobi
- Khamala, C. P. M. (1971). Ecology of *Echinometra mathaei* (Echinoidea: Echinodermata) at Diani Beach, Kenya. *Mar Biol.* 2: 167–172
- Kimaro, M. M. (1986). The composition and abundance of near-surface zooplankton in Tudor Creek, Mombasa, Kenya. M. Sc. thesis, University of Nairobi
- Krey, J. (1973). Primary production in the Indian Ocean I. In: Zeitschel, B., Gerlach, S. A. (eds.) *Biology of the Indian Ocean*. Springer-Verlag, Berlin, p. 115–126
- Leetmaa, A., Quadfasel, D. R., Wilson, D. (1982). Development of the flow field during the onset of the Somali current, 1979. *J. phys. Oceanogr.* 12: 1325–1342
- Martin, E. B. (1973). The history of Malindi: a geographical analysis of an East African coastal town from the Portuguese period to the present. East African Literature Bureau, Nairobi
- McGill, D. A. (1973). Light and nutrients in the Indian Ocean. In: Zeitschel, B., Gerlach, S. A. (eds.) *The biology of the Indian Ocean*, Vol. 3. Springer Verlag, Berlin, p. 53–102
- Melack, J. M. (1979). Temporal variability of phytoplankton in tropical lakes. *Oecologia (Berl.)* 44: 1–7
- Melack, J. M., Kilham, P. (1974). Photosynthetic rates of phytoplankton in East African alkaline, saline lakes. *Limnol. Oceanogr.* 19: 743–755
- Merret, N. R. (1968). Tuna longline survey in the equatorial western Indian Ocean. *E. Afr. agric. For. J.* 34: 17–65
- Merret, N. R. (1970). Gonad development in billfish (Istiophoridae) from the Indian Ocean. *J. Zool., Lond.* 1: 350–370
- Merret, N. R. (1971). Aspects of the biology of billfish (Istiophoridae) from the equatorial western Indian Ocean. *J. Zool., Lond.* 163: 351–395
- Moorjani, S. A. (1978). The ecology of marine algae of the Kenya coast. Ph. D. thesis, University of Nairobi
- Moorjani, S. A. (1979). Seasonal changes in the marine algal flora of the Kenya coast. *Int. Symp. Mar. Algae Indian Ocean Region*, Bhavnagar, India
- Moorjani, S. A. (1982). Rocky shore zonation in Kenya: horizontal and vertical distribution patterns in the marine flora. *Proc. Symp. Coast. & Mar. Envir. Red Sea, Gulf of Aden and Trop. West. Indian Ocean*, Vol. 2. ALESCO/UNESCO, Kartoum
- Morgans, J. F. C. (1959). The north Kenya banks. *Nature, Lond.* 184: 259–260
- Morgans, J. F. C. (1962). Ecological aspects of demersal tropical fishes off East Africa. *Nature, Lond.* 193: 86–87
- Muthiga, N. A., McClanahan, T. R. (1987). Population changes in the sea urchin (*Echinometra mathaei*) on an exploited fringing reef. *Afr. J. Ecol.* 25: 1–8
- Mwaiseje, B. (1973). Some aspects of the ecology of sandy/muddy inter-tidal zone in Dar es Salaam area. M. Sc. thesis, University of Dar es Salaam
- Newell, B. S. (1957). A preliminary survey of the hydrography of the British East African coastal waters. *Fish. Publ. Lond.* 9: 1–21
- Newell, B. S. (1959). The hydrography of British East African coastal waters. II. *Fish. Publ. Lond.* 12: 1–18
- Nhwani, L. B. (1980a). A gillnetting survey of an inshore fish stock off Mombasa coast. *Univ. Sci. J. (Dar Univ.)* 6: 29–45
- Nhwani, L. B. (1980b). Some aspects of the fishery and biology of the garfish *Tylosurus melanotus* (Bleeker 1850) in the coastal water of Mombasa, Kenya. *Univ. Sci. J. (Dar Univ.)* 6: 47–59
- Norconsult A. S. (1977). Mombasa water pollution and waste disposal study: report to the Ministry of Local Government (Kenya), Marine Investigations 6. Nairobi
- Nzioka, R. M. (1979). Observations on the spawning seasons of East African reef fishes. *J. Fish Biol.* 14: 329–342
- Nzioka, R. M. (1982). Biology of the smallspotted grunt *Pomadasy opercularis* (Playfair 1866) (Pisces: Pomadasyidae) around Malindi in Kenya. *Kenya J. Sci. Tech. (B)* 3: 69–81
- Nzioka, R. M. (1983). Some biological aspects of (*Scolopsis ghanam* [Forsk.] Perciformes: Scolopsidae) in Zanzibar channel. *E. Afr. agric. For. J.* 48: 69–73
- Nzioka, R. M. (1985). Aspects of the biology of the reef fish *Scolopsis bimaculatus* (Ruppell) in Kenya. I: Reproduction, feeding, and length weight relationships, *Kenya J. Sci. Tech. (B)* 6: 13–28
- Okeru, W. (1974a). The zooplankton of the inshore waters of Dar es Salaam (Tanzania, S. E. Africa) with observations on reactions to artificial light. *Mar. Biol.* 26: 13–26
- Okeru, W. (1974b). Morphometrics, 'condition' and gonad development of the East African *Sardinella gibbosa* (Blecker) and *Sardinella albella* (Valenciennes). *J. Fish Biol.* 6: 801–802
- Rubindamayugi, M. S. T. (1983). The biology of the blue-speckled parrotfish *Leptoscarus vaigiensis* (Family: Scaridae) occurring along the coast of Tanzania. M. Sc. thesis, University of Dar es Salaam
- Ruwa, R. K., Jaccarini, V. (1986). Dynamic zonation of *Nerita plicata*, *N. undata* and *N. textilis* (Prosobranchia: Neritacea) populations on a rocky shore in Kenya. *Mar. Biol.* 92: 425–430
- Ryther, J. H., Dustan, W. M. (1971). Nitrogen, phosphorus, and eutrophication in the coastal marine environment. *Science* 171: 1008–1013
- Sinclair, A. R. E., Norton-Griffiths, M. (1979). Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago
- Smith, S. L., Codispoti, L. A. (1980). Southwest monsoon of 1979: chemical and biological response of Somali coastal waters. *Science* 209: 597–600
- Sournia, M. A. (1969). Cycle annuel du phytoplancton et de la production primaire dans les mers tropicales. *Mar. Biol.* 3: 287–303
- Steven, D. M., Glombitza, R. (1972). Oscillatory variation of a phytoplankton population in a tropical ocean. *Nature, Lond.* 237: 105–107

- Sutcliffe, W. H. Jr (1972). Some relations of land drainage, nutrients, particulate material, and fish catch in two eastern Canadian bays. *J. Fish. Res. Bd Can.* 29: 357–362
- Talbot, F. H. (1960). Notes on the biology of the Lutjanidae (Pisces) of the East African coast, with special reference to *L. bohar* (Forskål). *Ann. S. Afr. Mus.* 45: 549–573
- Tana River Development Authority (1981). Athi River pre-investment study. Annexes 1–11. Nairobi
- Turyahikayo, G. R. (in press). Wave characteristics off the East African Coast. *Kenya J. Sci. Tech.* (B)
- Venema, S. C. (1984). Review of marine resource surveys in Kenyan waters. In: Iversen, S. A., Myklevoll, S. (eds.) *Proceedings of the Norad-Kenya Seminar to Review the Marine Stocks and Fisheries in Kenya*. Institute of Marine Research, Bergen, Norway, p. 61–82
- Warren, J. A. (1966). Medieval Arab references to the seasonally reversing currents of the North Indian Ocean. *Deep Sea Res.* 13: 167–171
- Warren, B., Stommel, H., Swallow, J. C. (1966). Water masses and patterns of flow in the Somali Basin during the southwest monsoon of 1964. *Deep Sea Res.* 13: 825–860
- Western, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East Afr. Wildl. J.* 13: 265–286
- Wickstead, J. H. (1961). Plankton on the north Kenya banks. *Nature, Lond.* 192: 890–891
- Williams, F. (1965). Further notes on the biology of East African pelagic fishes of the families Carangidae and Sphyraenidae. *E. Afr. agric. For. J.* 35: 141–167
- Williams, F., Newell, B. S. (1957). Notes on the dorade or dolphin-fish (*Coryphaena hippurus*) in East African waters. *E. Afr. agric. For. J.* 23: 113–118

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