



Ocean productivity

Jenny Huggett and Margareth Kyewalyanga

“Scientists aboard the *Nansen* endeavoured to measure ocean productivity by assessing nutrient concentrations as well as plankton biomass and production.”

Abstract

Plankton forms the base of the marine food web, providing nourishment to higher trophic levels from squid and fish to whales and seabirds. Over the course of 22 surveys between 1975 and 2015, scientists aboard the RV *Dr Fridtjof Nansen* have endeavoured to measure ocean productivity within the Western Indian Ocean, by assessing nutrient concentrations as well as plankton biomass and production. Ecosystem-focussed surveys since 2007 have provided important baseline data and yielded new insights into this largely oligotrophic (low-nutrient) and under-studied region. The monsoon-influenced Somali Current system north of the Equator exhibits the highest productivity of all, with high nutrient concentrations driven by strong upwelling. The most productive areas over the Mozambique shelf are Delagoa Bight in the south, the central Sofala Bank, influenced by seasonal nutrient input from the Zambezi delta, and Angoche in the north. All are influenced to some extent by the southward passage of mesoscale eddies through the Mozambique Channel, which may induce upwelling on the shelf, enhancing local production, or entrain coastal production offshore. These eddies strongly influence the distribution of mesozooplankton biomass in the Mozambique Channel, with significantly greater biomass found in cyclonic eddies compared to anticyclonic eddies. Mesozooplankton biomass was largely concentrated within the upper 100 m layer of water. Off Madagascar, both satellite and *in situ* data indicate enhanced productivity over the southern shelf, particularly around the south-eastern corner, an area characterised by regular blooms of nitrogen-fixing bacteria. Smaller productivity hotspots were observed off Cap St André and Nosy Be on the west coast, and at the northern tip of Madagascar. A survey along the axis of the Mascarene Plateau showed the northern sector (N of 12°S) to be most productive, with fluorescence maxima at 30 to 100 m depth, elevated phytoplankton biomass over the Saya de Malha Bank and at the south-eastern edge of the Seychelles Bank, and an extensive bloom of diatoms along the Amirantes Ridge. Sampling at six seamounts (five along the Southwest Indian Ridge and one on the Madagascar Ridge) showed a latitudinal gradient in phytoplankton biomass (highest at the southernmost seamount) and composition (more dinoflagellates in the tropics, more diatoms in the south). There was no general seamount effect on the phytoplankton, although biomass was enhanced over two seamounts with a relatively shallow summit (<200 m). A coordinated, regional plankton monitoring programme for the Western Indian Ocean is recommended, to provide indicators of ecosystem change.

Previous page: A hotspot of productivity – a whale shark *Rhincodon typus* feeds in a dense patch of the planktonic shrimp *Lucifer hansenii* beneath a bloom of cyanobacteria *Trichodesmium* sp. off Mafia Island, Tanzania. © Chris Rohner

5.1 Introducing the plankton

This chapter is mainly about plankton (Figure 5.1), which refers to the mostly small organisms in the ocean that are incapable of swimming against the currents, but instead are passively transported by them. The name plankton is derived from the Greek *planktos*, which means drifter or wanderer. Plankton includes tiny marine plants (phytoplankton) and animals (zooplankton), as well as even tinier bacteria (bacterioplankton) and viruses (virioplankton). These marine micro-organisms comprise 98 percent of the ocean's living biomass and produce over half the world's oxygen. Larger organisms that can swim against the ambient flow and control their position, such as squid, fish, and marine mammals, are known as nekton. These organisms comprise the remaining 2 percent of the ocean's biomass.

Phytoplankton are the primary producers in marine foodwebs, using energy from the sun and nutrients from the ocean to produce their own food, a process known as photosynthesis. Being dependent on sunlight, phytoplankton are most abundant near the surface of the ocean, and the well-lit surface layer where they thrive is known as the euphotic zone. Primary production, phytoplankton distribution and abundance are influenced by several factors, leading them to vary both seasonally and spatially. Primarily, phytoplankton depend on carbon dioxide, sunlight and nutrients for growth, but other factors such as water depth, water temperature, winds and especially the abundance of grazers play a significant role. Since carbon dioxide and sunlight are abundant, the main limiting factor for primary production is nutrients. The most important nutrients for phytoplankton are nitrate, phosphate and silicate. Silicate is used by diatoms to build their cell walls. Generally in the Western Indian Ocean, nitrate and phosphate are the most limiting nutrients, while silicate is more accessible (Barlow *et al.*, 2007; Kyewalyanga *et al.*, 2007; Leal *et al.*, 2009; Sá *et al.*, 2013).

Numerically, the most important groups of phytoplankton are the diatoms, cyanobacteria and dinoflagellates, although many other groups of algae are

represented. In oligotrophic (low-nutrient) regions, phytoplankton are dominated by small-sized cells, called picoplankton (0.2-2 μm) and nanoplankton (2-20 μm). Phytoplankton use pigments such as chlorophyll *a* (chl *a*) to absorb solar energy and convert carbon dioxide and water into high-energy organic carbon compounds that fuel growth by synthesizing vital components such as amino acids, lipids, protein, polysaccharides, pigments and nucleic acids. Since all phytoplankton contain chl *a*, and the amount of chl *a* pigment in sea water is related to the amount of plant material, chl *a* is used as an index of plant biomass in the ocean.

Most phytoplankton also contain so-called accessory pigments such as chlorophyll *b* and chlorophyll *c*, as well as photosynthetic carotenoids (Kirk, 1994; Barlow *et al.*, 2008). These are different-coloured pigments that are able to use light for photosynthesis at wavelengths that differ from the wavelengths used by chl *a*. Many of these accessory pigments are specific to a group of phytoplankton. Measuring the relative amounts of the different types of pigments in a water sample provides an indication of which major groups of phytoplankton are present in the seawater.

Zooplankton are the secondary producers in marine foodwebs, feeding on phytoplankton as well as smaller zooplankton and bacteria. Some species spend their entire life-cycle in the plankton, and are known as holoplankton, while others, known as meroplankton, spend only a part of their lives in the plankton before graduating to either the nekton or a sessile, benthic existence. Members of the holoplankton include protozoans (e.g. foraminiferans, radiolarians and ciliates), cnidarians (siphonophores and some jellyfish), ctenophores (comb-jellies), crustaceans such as cladocerans, ostracods, copepods, mysids, amphipods and euphausiids, chaetognaths (arrow worms), molluscs such as pteropods, and tunicates such as salps and doliolids. Typical examples of meroplankton are the larval stages of invertebrates such as barnacles, molluscs (gastropods, bivalves and cephalopods), echinoderms, decapods (crabs,

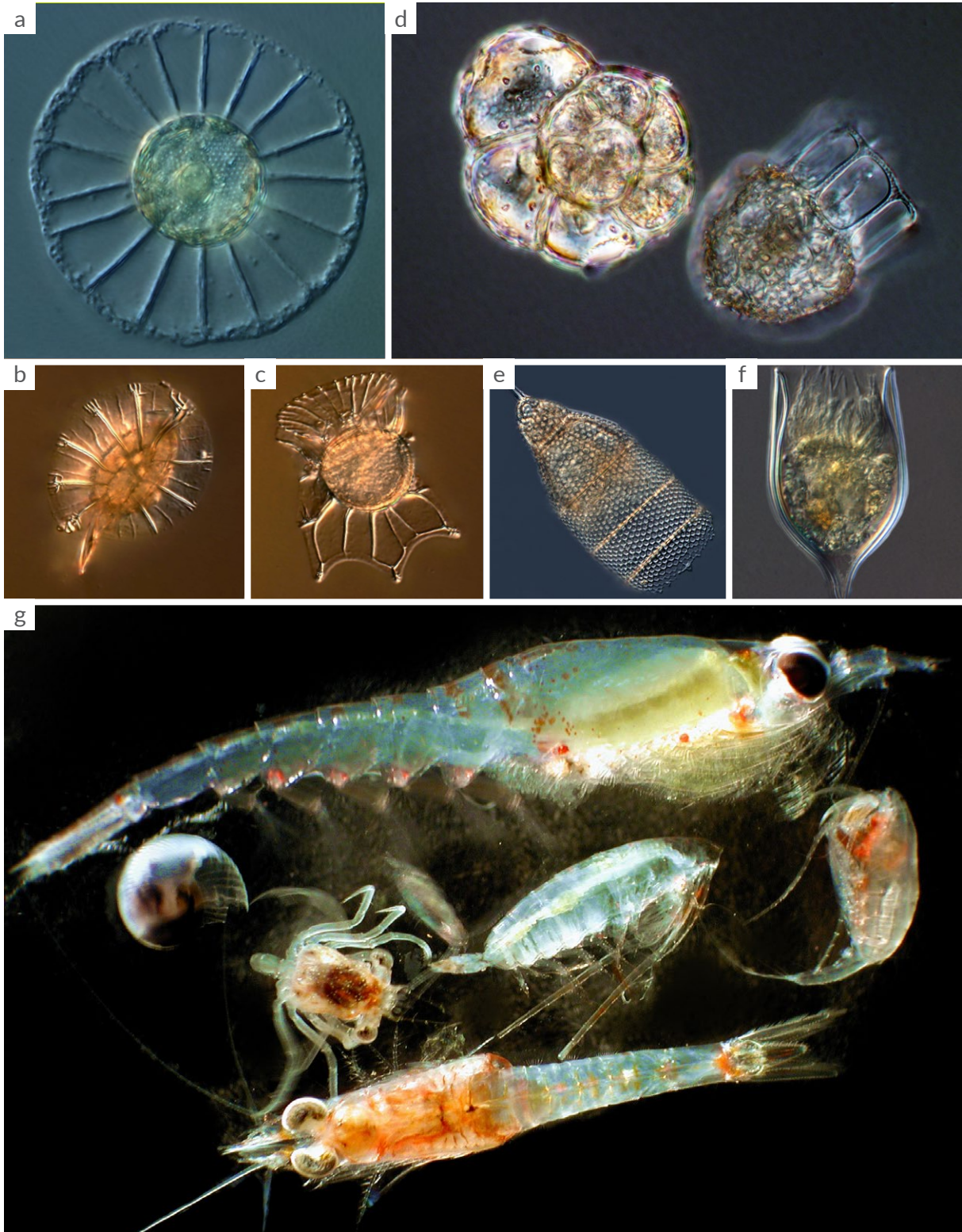


Figure 5.1 Some examples of plankton: a. diatom *Planktoniella* sp.; b. dinoflagellate *Cladopyxis* sp.; c. dinoflagellate *Ornithocercus magnifica*; d. foraminiferan and tintinnid ciliate; e. radiolarian; f. ciliate; g. euphausiid (top), gastropod, crab larva and copepods (middle), and mysid (bottom).

prawns and spiny lobsters), as well as fish larvae. Jellyfish are a special case, as most have alternating generations of sexual reproduction by the pelagic medusae and vegetative propagation by benthic polyps. Crustacean zooplankton are usually much more abundant than the gelatinous forms, with copepods the most numerous of all, forming the biggest source of protein in the oceans.

Although at the mercy of currents, most zooplankton are able to move vertically in the water column. Many zooplankton species perform what is known as diel vertical migration (DVM), a daily pattern whereby the population lives at depth during the day, ascending at dusk to feed in the upper food-rich surface layers at night, then around dawn descending once more to the deeper, darker water layers where the risk of being seen by visual predators is greatly reduced. Such a strategy is most beneficial to larger organisms or those with strong colouration. Although predator avoidance is thought to be the major reason for DVM, organisms may also use the depth-temperature differential to incur metabolic advantages, or use deep and shallow currents to find food patches or to maintain a geographical location (Kerfoot, 1985).

Zooplankton size varies enormously, from tiny protists a few microns wide up to giant jellyfish with a bell diameter of almost 2 metres. To cope with such a vast size range, a size classification revised by Sieburth *et al.*, (1978) is now widely accepted (see the Glossary in Appendix 5.1). There are five size classes for zooplankton: nanoplankton (2–20 μm), microplankton (20–200 μm), mesozooplankton (0.2–20 mm), macro-zooplankton (2–20 cm) and megaloplankton (20–200 cm). The mesozooplankton category corresponds to the size spectrum of traditional zooplankton samples collected with a mesh size of 200–300 μm , which contains the bulk of crustacean zooplankton as well as meroplankton (Harris *et al.*, 2000).

Productivity refers to the rate of production of organic matter, either by phytoplankton through the process of photosynthesis (primary production), or by zooplankton through the processes of body growth and reproduction (secondary

production). Plankton productivity is the foundation of marine food webs and determines energy flow to higher trophic levels such as fish, shellfish, seabirds and marine mammals (Verheye *et al.*, 2016). In a simple food chain, phytoplankton are consumed directly by zooplankton, which are then eaten by fish larvae, and the chain goes on to small fish, larger fish and all the way to top predators such as seals, birds, dolphins and whales. This creates a link between plankton productivity and fisheries production as well as management.

For the purposes of this book, ocean productivity is defined broadly to include nutrient concentrations, chl *a* concentration as well as that of other phytoplankton pigments, phytoplankton species composition, primary production, zooplankton biomass, zooplankton species composition and secondary production.

5.2 Historical background

The most comprehensive study of nutrient concentrations (inorganic nitrate, phosphate and silicate) in the Indian Ocean unfolded during the pioneering International Indian Ocean Expedition (IIOE) of 1959 to 1965 (McGill, 1973), the first cooperative project coordinated by the Intergovernmental Oceanographic Commission (Rao, 1973). The first measurements of primary production in the Indian Ocean using the ^{14}C technique were conducted during an expedition by the *Galathea* (a Danish corvette) in 1950 to 1952, and subsequent measurements were made during the IIOE (Aruga, 1973). Taylor (1973) reported on dinoflagellates collected by the *Anton Bruun* during the IIOE, and chlorophyll concentrations were measured during the IIOE *Discovery* survey (1963–1964).

The earliest zooplankton collections in the Indian Ocean date back to 1857 to 1859 during a circumglobal scientific expedition by the Austro-Hungarian naval frigate *SMS Novara* (Rao, 1973). Subsequent major collections over the next 100 years include those by the Danish RRS *Dana* between 1928 and 1930, and the British RRS *Discovery II* between 1930 and 1938 (Rao, 1973).

However, the most comprehensive study of the planktonic realm took place during the IIOE (Rao, 1973). Most zooplankton samples were collected in the upper 200 m using an Indian Ocean Standard Net, which had a mesh size of 330 µm and a mouth diameter of 130 cm (Currie, 1963).

Subsequent to the IIOE, considerable research effort was concentrated in the productive Arabian Sea, such as the Indian Ocean Experiment (INDEX) in 1979, and in particular during the Joint Global Ocean Flux Study (JGOFS) Process Studies of the Arabian Sea. Expeditions undertaken by Germany, India, Pakistan, United Kingdom and the United States of America focussed on the northern Arabian Sea during 1992/97, while the Netherlands studied the Somali Current system during 1992/93 (Watts *et al.*, 2002). Within the framework of the Netherlands Indian Ocean Programme (NIOP), RV *Tyro* conducted several surveys off the Somali coast and in the Somali Basin, and two surveys off the Kenyan coast, during which data on nutrients, chlorophyll, primary production and zooplankton biomass and species composition were collected (Baars *et al.*, 1998; Heip *et al.*, 1995). The first studies in the Indian Ocean conducted by the RV *Dr Fridtjof Nansen* were also in this region (1975–1976; see Table A5.1; A refers to Tables and Figures in Appendix 5.2 and Appendix 5.3 respectively).

After a lull in offshore oceanographic research in the Western Indian Ocean, a series of oceanographic surveys was undertaken in its southern part from 2002 onwards, during the African Coelacanth Ecosystem Programme (ACEP) in the Delagoa Bight off southern Mozambique and in the KwaZulu-Natal Bight off the east coast of South Africa. Between 2007 and 2010, the *Nansen* undertook a series of surveys with a strong ecosystem focus, many within the ASCLME (Agulhas and Somali Currents Large Marine Ecosystems) and SWIOFP (Southwest Indian Ocean Fisheries Project) frameworks, which are the subject of much of this chapter. Over the same period, several other multidisciplinary surveys were undertaken to study mesoscale eddies in the Mozambique Channel, in addition to one during

the ASCLME project in 2008. Collectively, these surveys in the new millennium have made a fundamental contribution to our understanding of ocean productivity in the Western Indian Ocean, with the *Nansen* unquestionably a key role player.

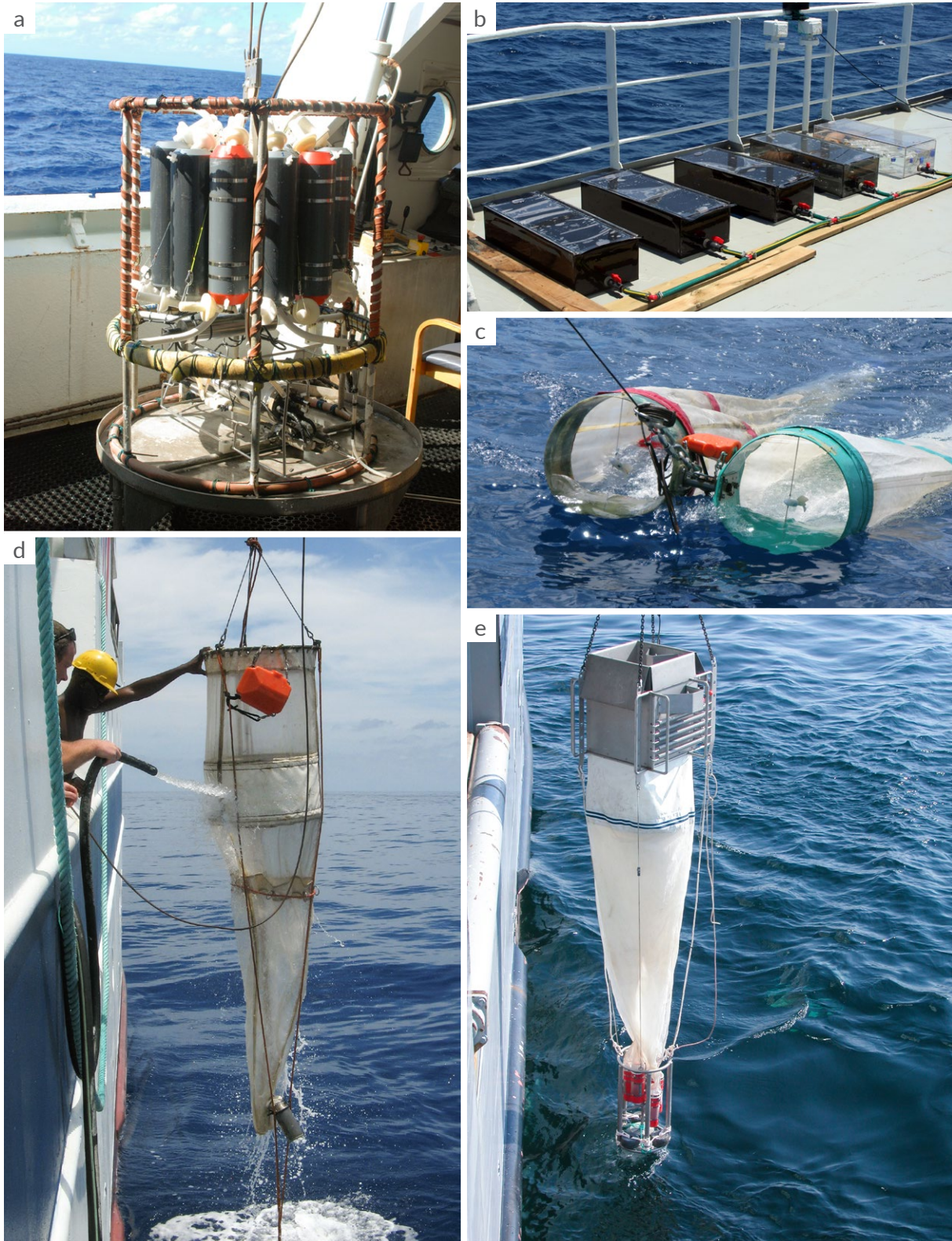
5.3 Sampling methodology

A summary of all the surveys undertaken in the Western Indian Ocean by the *Nansen* is provided in Table A5.1, along with a record of sample collection for all ocean productivity-related parameters mentioned above (see Figure A5.1 for a map of all hydrographic stations where productivity-related sampling was conducted).

Nutrients and phytoplankton

During the first phase of exploratory and descriptive surveys, from 1975 to 1990, the surveys focussed mainly on fish resources, and environmental sampling was restricted to temperature, salinity and dissolved oxygen. There were no measurements of productivity except for the survey of 1980 off Mozambique, when samples were collected for nutrient and chl *a* analysis. During the second survey phase from 2007 onwards, there was a more ecosystem-based approach to sampling, particularly with the advent of the ASCLME programme. For these surveys, sampling for nutrients and phytoplankton followed a standard method through which water samples were collected using Niskin bottles attached to the CTD (Figure 5.2a), the instrument used to determine conductivity, temperature and depth of the ocean. As the CTD was lowered, in addition to profiles of temperature, salinity and oxygen by depth, fluorescence profiles were obtained via a Chelsea Mk III Aquatracka fluorometer and used to detect the depth of maximum fluorescence (fMax).

Some sampling procedures were similar in all the cruises. For example, where the station was deep enough, water samples for nutrient analysis and for calibration of temperature and oxygen sensors were usually collected at 12 standard depths (m): 3 000, 2 500, 1 750, 1 250, 1 000, 800, 500, 300, 100, 85, 50 and surface (4–5 m). For chl *a*



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Figure 5.2 Examples of sampling and experimental equipment: a. CTD rosette sampler; b. primary production incubations; c. Bongo net sampler; d. WP2 net; e. Multinet.

BOX
5.1

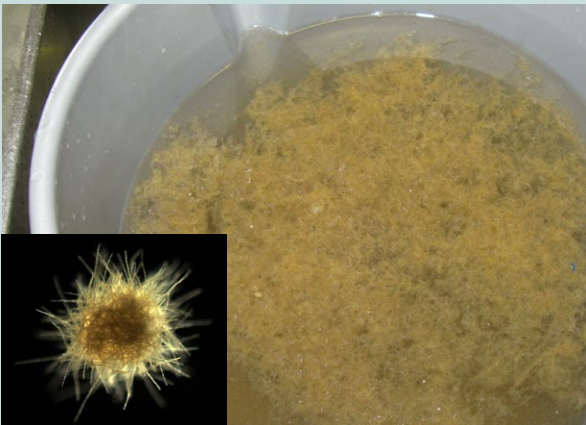
Trichodesmium – a bloom-forming, nitrogen-fixing cyanobacterium

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Streaks of *Trichodesmium* seen from the RV Dr Fridtjof Nansen during a survey in 2008.

© Jenny Huggett; (inset) A. Hynes



Thick *Trichodesmium* “gunge” from a Bongo net haul during the 2008 survey. (Inset) A “puff” colony of *Trichodesmium* sp. as seen under a microscope.

Planktonic marine cyanobacteria of the genus *Trichodesmium* occur throughout the oligotrophic tropical and subtropical oceans, particularly in western boundary currents (Capone *et al.*, 1997). They form large, visible blooms in the surface waters, commonly called “sea saw-dust” because the colonies and large brown blooms were mistaken by seafarers as sandbars in the ocean.

Trichodesmium was first documented in 1770 by Captain James Cook, who observed it in the Coral Sea, outside the Great Barrier Reef, and wrote in his journal: “*The Sea in many places is here cover'd with a kind of a brown scum, such as Sailors generally call spawn; upon our first seeing it, it alarm'd us, thinking we were among Shoals, but we found the same depth of Water were it was as in other places*”. These cyanobacteria can be found as filaments (trichomae) comprised of 10s–100s of cells, or in colonies 1–10 mm in length, aligning either in parallel as fusiform or “tuft” colonies, or radially as “puff” colonies. Colonies can be yellowish-brown to deep red in colour due to their primary light harvesting pigment, phycoerythrin.

The species *T. erythraeum* is endemic to the Indian Ocean, and is responsible for discolouring the Red Sea during blooms. As the major diazotroph (nitrogen fixer) in marine pelagic systems, *Trichodesmium* is an important source of “new” nitrogen in nutrient-poor waters (Siddiqui *et al.*, 1991), and is estimated to produce between 60 and 80 Tg (= 10¹² g) of nitrogen per year (Bergman *et al.*, 2013).

A key characteristic of *Trichodesmium* is the presence of gas vesicles, which enable populations to regulate their buoyancy and move vertically throughout the water column, harvesting nutrients (Siddiqui *et al.*, 1991). Blooms can be traced and tracked using satellite imaging as the highly reflective gas vacuole makes *Trichodesmium* blooms easily detectable from space.

Blooms can form in coastal or oceanic waters, most frequently when the water has been calm for some time and surface temperatures exceed 27°C. Most blooms are several kilometers long and last one to several months (Carpenter and Capone, 1991). Colonies also provide a pseudobenthic substrate for many small oceanic organisms, including bacteria, fungi, diatoms, dinoflagellates, protozoans, hydrozoans, tunicates and copepods (which are their primary predator); in this way, the genus can support complex microenvironments (O'Neil and Roman, 1991).

determination and phytoplankton identification, the common practice was to collect samples from five different depths: one at the surface, one at fMax, one below fMax and two between the surface and fMax. Another common feature was the use of the SBE 21 SeaCAT thermosalinograph, which was run routinely during the survey to obtain measurements of sea surface salinity and relative temperature and fluorescence at 5 m depth, every 10 seconds throughout the survey.

Nutrient samples were frozen at -20 °C and phytoplankton samples for species identification were preserved in 2.5 percent Lugol's solution, both for later analysis. Measurements of other parameters such as particulate organic carbon (POC), nitrate isotopes, pigments, phytoplankton absorption, chl *a* size fractionation and rates of primary production (Figure 5.2b) were made during only some of the surveys. These, together with survey-specific procedures for determination of nutrients, chl *a* and species identification, are highlighted under the respective sub-regions in Appendix 5.4.

Zooplankton

Zooplankton sampling was limited during the first survey phase (1975–1993), but took place during surveys off Somalia (1975), Mozambique (1977/1978), and Seychelles (1978), using a variety of nets and mesh sizes (see Table A5.1). No more zooplankton sampling was conducted until the second phase of ecosystem-based surveys from 2007 onwards, when the Hydrobios Multinet (a multiple net sampler with five nets to enable sampling from five depth strata) and Bongo nets were commonly used. A standard mesh size of 180 µm was used on the Multinet (except for a 405 µm mesh on one survey), whereas Bongo net mesh sizes were more variable, with combinations of 180 + 375 µm, 300 + 500 µm, and 375 + 500 µm used. A Neuston (or Manta) net which samples the surface layer was deployed off Mozambique in 2007 (375 µm mesh) and on the high seas in 2015 (335 µm mesh), and a WP2 net (100 µm mesh) was used during the 2008 Mozambique Channel eddy survey, although the latter was frequently clogged by dense aggregations of *Trichodesmium* (see Box 5.1). Examples of

the nets used are shown in Figure 5.2, and additional details are provided in the sections below.

In the following sections, key results are presented and discussed for each subregion considered in this review: Somali Coast and East Africa Coastal Current subregions, Mozambique (including the Mozambique Channel), Madagascar and Comoros, the Mascarene subregion, and southern seamounts. A summary of nutrient concentrations determined during the various *Nansen* surveys and their corresponding chl *a* values are given in Table A5.2, while a summary of zooplankton biomass from the various surveys is provided in Table A5.3. Detailed results for each survey are given in Appendix 5.4.

5.4 Findings by subregion

Somali Coast and East Africa Coastal Current subregions

The Somali Current is one of the world's five major upwelling systems, the others being the Benguela, Canary, California and Humboldt Current systems, all of which are characterised by high productivity and rich fisheries. The Somali Current is the only upwelling system that occurs on the western boundary of an ocean, and its marine ecosystem is strongly influenced by seasonal monsoon winds.

The warm Southwest monsoon (SW monsoon) from June to September moves the coastal waters north-eastward, resulting in continuous, strong upwelling along the coast, entraining nitrate into the mixed layer, and resulting in intense, long-lasting, phytoplankton blooms (McCreary *et al.*, 1996). The Northeast monsoon (NE monsoon), which occurs from December to February, causes a reversal of the Somali Current, moving the coastal waters southwest. Cooler air causes the surface water to cool and creates deep mixing, bringing abundant nutrients to the surface (Mann and Lazier, 2006). A composite image of ocean colour from November 2016 (Figure 5.3) depicts the extensive distribution of high phytoplankton biomass off the Somali coast and in the Arabian Sea.

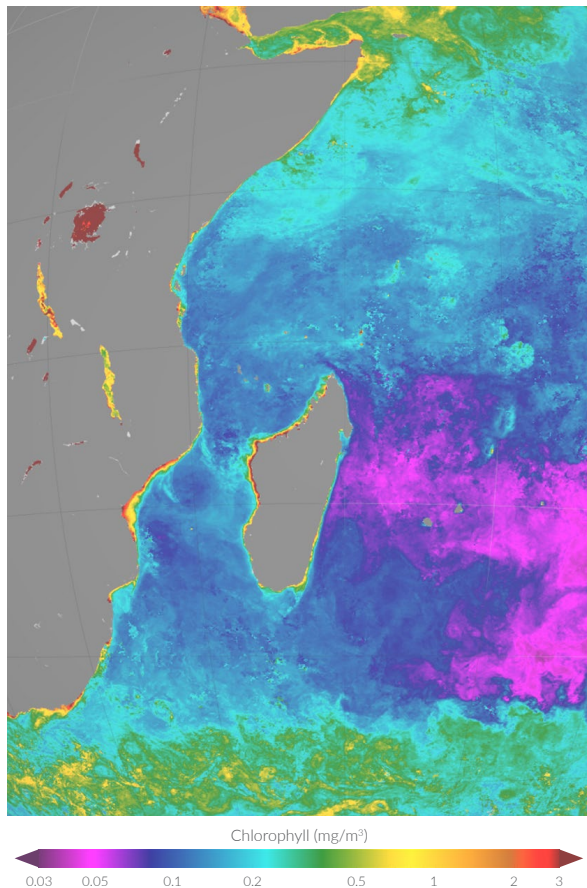


Figure 5.3 Composite image of chlorophyll in the Western Indian Ocean for November 2016 from the VIIRS (Visible Infrared Imaging Radiometer Suite) onboard the Suomi National Polar-Orbiting Partnership (Suomi NPP). Enhanced chlorophyll concentrations are visible in the Arabian Sea, Red Sea and off the Somali Coast, over the Sofala Bank and in the Delagoa Bight off Mozambique, along the northwest and southeast coasts of Madagascar, and along the Subtropical Front. Also evident is offshore entrainment of chlorophyll by eddies in the Mozambique Channel.

The five *Nansen* surveys in this region were conducted during the early phase of the Nansen Programme, when the focus was largely on estimating fisheries resources. Consequently, there was limited sampling of the lower trophic levels. However, the highest zooplankton volumes reported during 1975 (>20 g C m⁻² in the upper 50 m) were the highest recorded from all the *Nansen* surveys conducted in the Western Indian

Ocean (Table A5.3). These high values were recorded off Mogadishu and off the tip of the “horn” at Ras Asir during the SW monsoon (Figure A5.2b), when strong upwelling along the Somali coast leads to primary production of at least 1 g C m⁻² d⁻¹ and high plankton biomass (>1g C m⁻² in the upper 200 m), as was recorded during earlier surveys in the region, including the IIOE (1959–1965), INDEX (1979) and NIOF (1992–1993; Baars *et al.*, 1998). Baars *et al.*, (1998) recorded maximum primary production rates of 2.8 g C m⁻² d⁻¹ during a diatom bloom, compared to 0.9 g in newly upwelled water. Although high for the Western Indian Ocean, these rates are lower than those reported for eastern boundary upwelling systems. In the Benguela Current system, for example, Barlow *et al.*, (2009) measured primary production rates of 0.39–8.83 g C m⁻² d⁻¹ during summer and 0.14–2.26 g during winter. During the NE monsoon, primary productivity along the Somali coast declined to 0.3 g C m⁻² d⁻¹ during the IIOE and INDEX surveys, but zooplankton biomass outside the upwelling season did not decline to the same extent. Mean zooplankton biomass along the Somali coast during the 1975 *Nansen* survey was estimated to be 7.8 g C m⁻² in the upper 50 m. This seems high compared to a mean biomass of 2.5 g in the southern Benguela upwelling system (Huggett *et al.*, 2009; for copepods only, which dominate the zooplankton), but the latter was integrated over a depth of 200 m, so such comparisons should be treated cautiously.

Although the *Nansen* sampled zooplankton off the northern coast of Kenya during surveys in 1975 and 1976, no results were provided (IMR, 1975, 1976, 1977b). Sampling in Kenyan waters aboard RV *Tyro* in 1992, Kromkamp *et al.* (1995) found that the rate of primary production was higher in November/December during the NE monsoon than in June/July during the SW monsoon, and was higher at shallow stations than at deep ones. The gross daily primary production ranged from 0.15–3.0 g C m⁻² d⁻¹ along a transect off the Galana River (3°S), to 0.35–6.0 g off Kiwayuu (2°S). Zooplankton biomass was also higher during the NE monsoon, peaking at 18.6 mg C m⁻³ inshore (50 m) off Gazi (4.36°S; Mwaluma, 1995).

Most international programmes investigating the Arabian Sea focussed on the region further north, such as the US Arabian Sea Expedition of 1994–1996 (Smith *et al.*, 1998; Smith, 2001) and the UK contribution to the JGOFS (Joint Global Ocean Flux Study) Process Studies in the Arabian Sea, ARABESQUE (Burkill, 1995, 1999). More recent planned initiatives in the Somali and East Africa Coastal Current subregions as part of the ASCLME project (2008–2010) were not possible due to pirate activity.

Mozambique subregion

Mozambique has an extensive coastline of some 2 300 km, spanning 16 degrees of latitude. Of the six subregions considered in this study, Mozambique has been the most frequently studied by the *Nansen*, with 14 surveys conducted, nine of which collected samples related to ocean productivity. The most consistently productive areas over the continental shelf (in terms of phytoplankton biomass, at least) seem to be the Delagoa Bight, Sofala Bank, and Angoche regions. Satellite imagery of ocean colour from late 2007 (Figure A5.4a), *in situ* measurements of chl *a* during the 2007 survey (Figure A5.4b) as well as the 2009 and 2014 surveys (Figure A5.5) confirm the elevated productivity. At the Angoche and Delagoa Bight regions, it appears to be partly linked to the frequent passage of eddies, while the Sofala Bank productivity is influenced by the Zambezi delta discharge as well as mesoscale oceanographic features (Leal *et al.*, 2009); this is discussed further below.

Between September and December 2007, the *Nansen* conducted the first multidisciplinary survey of the entire Mozambique continental shelf, which yielded valuable baseline information on nutrients and the phytoplankton community, and which is comprehensively documented by Sá *et al.*, (2013). Both nutrients and phytoplankton changed with region and depth (see Sá *et al.*, 2013, their Figures 3, 4, 5), as shown by other studies in the region (Barlow *et al.*, 2008, 2014). Nutrient results revealed similar phosphate (P) concentrations in all regions (~0.25 μM), with minimum values in the north. Silicate (Si) concentrations generally varied between 6 and 10 μM , except for a peak

of 17.27 μM in the Delagoa Bight, and a few stations south of Bazaruto where results were below detection limit. Nitrate + nitrite (N) concentrations were generally low along the coast, often below detection limit. In contrast, higher concentrations were observed in a few surface samples from the Delagoa Bight and the northern region. No clear trend or differences in nutrient concentrations were observed between surface and fMax samples (Sá *et al.*, 2013).

Pigment analysis via high-performance liquid chromatography (HPLC) allowed determination of phytoplankton biomass and identification of major phytoplankton groups present in Mozambican waters (Sá *et al.*, 2013), in particular *Prochlorophytes* (Divinyl chl *a*), *Haptophytes* (19'Hexanoylofucoxanthin), *Bacillariophytes* (Fucoxanthin), *Cyanophytes* (Zeaxanthin) and *Dinophytes* (Peridinin). Microscopy indicated the diatoms *Chaetoceros* spp., *Proboscia alata*, *Pseudo-nitzschia* spp., *Cylindrotheca closterium* and *Hemiaulus haukii* were the most abundant microphytoplankton taxa, while *Discosphaera tubifera* and *Emiliania huxleyi* were the most abundant coccolithophores, or nanophytoplankton. The smaller picoplankton were associated with warmer northern waters and dominated surface waters, while the larger nano- and microplankton were abundant at the fMax and were mostly associated with the cooler southern and central waters, including north of Angoche to ~15 °S (Sá *et al.*, 2013).

There was a latitudinal gradient in phytoplankton biomass (as with temperature and salinity), with chl *a* increasing from north to south (Sá *et al.*, 2013), and for all regions surface chl *a* values were lower than those at the fMax (Table A5.2). An exception was for the southern region (with cool, nutrient-rich waters) where values at the surface were similar to those at the fMax, reaching a maximum of 1.62 mg m^{-3} . In the less-productive central and northern regions, maximum chl *a* concentration ranged from 0.37 to 0.53 mg m^{-3} at the surface, and from 0.31 to 0.95 mg m^{-3} at the fMax (Table A5.2). Measurements of mesozooplankton biovolume (>180 μm) during later surveys in 2009 and 2014 also indicated higher biomass in

the southern and central regions (south of 18 °S) compared to the northern region (Table A5.3), but there was no apparent latitudinal gradient in macrozooplankton (>500 µm) biomass during quarterly surveys along the Mozambique coast during 1977–1978 (Table A5.3; Figure 5.4).

The Mozambique Channel has been of particular interest due to its dynamic nature, caused by the passage of mesoscale eddies that affect current dynamics and upwelling, with a consequent impact on biological productivity (Lutjeharms and Da Silva, 1988; Lutjeharms, 2006; Lamont *et al.*, 2010). A *Nansen* survey in 2008 was an important component of a multidisciplinary programme to explore the influence of mesoscale dynamics on biological productivity at multiple trophic levels in the channel (Ternon *et al.*, 2014). During this survey, as in several others in this region, the interaction of mesoscale eddies with the continental slope on the western side of the channel caused upwelling of cooler, nutrient-rich water, which resulted in elevated phytoplankton biomass in the shelf regions (Lamont *et al.*, 2014, their Figure 10). Strong currents at the perimeters of these eddies interacted with the shelf, resulting in

entrainment of high coastal biomass by eddies into frontal regions and further offshore (Lamont *et al.*, 2014). The passage of mesoscale eddies through the Mozambique Channel also has a strong influence on the distribution of mesozooplankton, as biovolume in the cyclonic (cold-core) eddies was on average 55 percent greater than in the anticyclonic (warm-core) eddies sampled during four surveys (Huggett, 2014). This is likely due to upwelling in the cores of the cyclonic eddies, resulting in enhanced nutrients, primary production and hence secondary production, which is supported by the higher abundance of copepod and euphausiid nauplii observed in the cyclonic eddies compared to the anticyclonic eddies.

Multinet sampling during the eddy surveys showed that mesozooplankton biomass in the Mozambique Channel was largely concentrated within the upper 100 m (Huggett, 2014). Multifrequency acoustic profiling at high vertical resolution (1 m intervals) during two surveys showed size-related differences in zooplankton depth distribution, with the smallest zooplankton (<0.2 mm) concentrated in the upper 50 m, within the upper mixed layer, while the largest size fraction (1–3 mm) extended deeper in the water column. In the cyclonic eddies peak concentrations coincided with the fluorescence maximum (Lebourges-Dhaussy *et al.*, 2014). Neither sampling method revealed any clear evidence of diel vertical migration within the mesozooplankton.

Eddies along the Mozambique shelf were documented in a number of other *Nansen* surveys. During September 1977 a cyclonic eddy was detected off Angoche, with its centre about 100 km from the coast, and there was also a suspected eddy in this region during November 1977 (Sætre and Paula e Silva, 1979). Malauene *et al.* (2014) investigated these

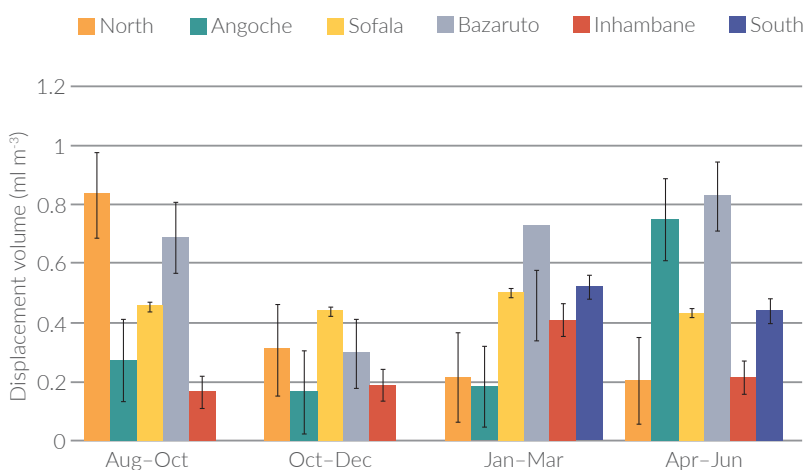


Figure 5.4 Seasonal pattern of mean zooplankton displacement volume (ml m^{-3}) collected with a Juday net (500 µm mesh, upper 100 m) along six transects during quarterly surveys off Mozambique from 1977–1978. Recalculated using displacement volumes (ml) from Sætre and Paula e Silva (1979) and Nansis data on bottom depths to estimate sampling depths (maximum of 100 m or 5 m from the bottom if shallower).

phenomena and describe intermittent periods of relatively cool surface water and elevated chl *a* signatures indicative of upwelling near Angoche between August and March. They suggest that these conditions are primed and formed by wind-driven coastal upwelling, in response to the along-shore north-easterly monsoon winds that prevail during this period. The waters are enriched in chl *a* and advected further offshore by the interaction of anti-cyclonic/ cyclonic eddy pairs with the shelf. Cyclonic eddies were also observed off Inhambane during surveys in November 1977 and March 1978 (Sætre and Paula e Silva, 1979), as well as slightly north of Inhambane in October 2007. The passage of cyclonic eddies in this region has been found to influence the water masses of the Delagoa Bight through upwelling onto the shelf, resulting in enhanced productivity (Quartly and Srokosz, 2004; Kyewalyanga *et al.*, 2007; Lamont *et al.*, 2010). Kyewalyanga *et al.*, (2007) recorded high chl *a* and primary production values in the northern part of the Delagoa Bight, and intermittent acoustic recordings of pelagic fish, mostly round herring (*Etrumeus teres*), were noted here during the survey in Oct/Nov 1980 (Brinca *et al.*, 1981).

The cyclonic eddy observed in 2007 was bounded by a large anticyclonic eddy to the north, and high chlorophyll concentrations at the fMax along a transect between Bazaruto and Inhambane were presumed to be associated with a frontal zone between the two counter-rotating eddies (Johnsen *et al.*, 2007). This would have resulted in coastal biomass being advected offshore by strong currents between these eddies, as observed by Lamont *et al.* (2014). An inshore northward coastal current is also commonly observed in the Delagoa Bight, which may cause upwelling depending on the interaction of eddies with the topography of the shelf and slope (Lamont *et al.*, 2010).

The Sofala Bank is one of the more productive regions off the Mozambican coast (Sá *et al.*, 2013); it is markedly influenced by the Zambezi River, being characterised by strong tidal currents and estuarine runoff that determines hydrological features (Lutjeharms, 2006), with river discharges

relatively rich in nutrients. The region is also influenced by the passage of mesoscale eddies, and interactions of eddies with the shelf are likely to bring nutrients into the region, thereby enhancing productivity. However, during an intensive study off the Zambezi River mouth during 2007, phytoplankton biomass was very low, between 0.003 and 0.202 mg m⁻³, and the community was dominated by microflagellates, specifically Haptophytes (coccolithophorids; Leal *et al.*, 2009). This study was conducted in December, at the end of the dry season, and before the onset of the rainy season (Leal *et al.*, 2009). Salinity near the coast was around 35, which is considerably higher than salinity values of around 20, as described by Lutjeharms (2006) for the Sofala Bank region during the wet season, indicating minor estuarine runoff. Nutrient ratios were strongly influenced by depleted nitrate + nitrite concentrations, indicating low estuarine discharges typical of the dry season. The very low N:P ratio obtained (0–0.9) suggests the phytoplankton communities were strongly nitrogen limited, supporting the low phytoplankton abundance observed. The influence of seasonal river discharge on productivity in this region is highlighted by results from surveys over the Sofala Bank in 1977–1978, when zooplankton biovolume was roughly three times higher in January to March 1978, during the wet season, than in October to December 1977 (Sætre and Paula e Silva, 1979).

The Sofala Bank area off Beira and the shelf area off the Zambezi River have also been noted as the most important distribution areas for pelagic fish such as buccaneer anchovy (*Encrasicholina punctifer*; Sætre and Paula e Silva, 1979).

Trichodesmium is an important diazotroph (nitrogen fixer) in nutrient-poor tropical and subtropical oceans. Dense *Trichodesmium* blooms were observed at least twice during Nansen surveys off Mozambique. The first time was north of Beira in autumn 1977 (IMR, 1977a) and the second time was in December 2008, while sampling in a cyclonic eddy also north of Beira (see stations forming a cross in Figure A5.3). The bloom was visible as broad streaks at the ocean surface (see Box 5.1 for more details).

Madagascar and Comoros subregion

Although the *Nansen* surveyed 22 transects around Madagascar in 2008 and 2009, and ten transects in the Comoros gyre during 2009 (Figure A5.6), quantitative data on ocean productivity in this subregion remain limited, particularly for zooplankton. Composite maps of near-surface (5 m) temperature and fluorescence from 2008 and 2009 (Figure A5.7a, b) indicate considerable spatial variation in chl *a*, but mostly low concentrations ($\leq 0.2 \text{ mg m}^{-3}$). There was evidence of upwelling and offshore surface flow off south-east Madagascar near Fort Dauphin in 2008, supported by relatively high chlorophyll concentrations there (a maximum of 1.1 mg m^{-3}) and to the immediate north. A cyclonic eddy with a diameter of approximately 250 km was observed off the southern tip of Madagascar, to the lee side, and similar observations of eddies in this region have been associated with high productivity (Quartly and Srokosz, 2004). Furthermore, studies off southern Madagascar have shown a large phytoplankton bloom most years in late austral summer (February–April), which propagates to the east, away from Madagascar (Poulton *et al.*, 2009; Srokosz and Quartly, 2013; Srokosz *et al.*, 2015). The bloom to the south of Madagascar in 2005 comprised the nitrogen-fixing cyanobacteria (*Trichodesmium*), while diazotrophic diatoms (*Rhizosolenia* spp., harbouring the extracellular endosymbiont cyanobacterium *Richelia intracellularis*, which also fixes nitrogen, in a symbiotic relationship) were observed to the east of Madagascar (Poulton *et al.*, 2009). These authors calculated nitrogen fixation rates in the order of $1 \text{ to } 5 \text{ mM N m}^{-2} \text{ d}^{-1}$ and $0.24 \text{ to } 2.4 \text{ mM N m}^{-2} \text{ d}^{-1}$, off the south and east coasts respectively. The presence of these nitrogen fixers as nitrogen sources (ammonia or dissolved nitrogen) is likely to enhance productivity along the southeast coast of Madagascar, a region characterised by elevated net primary production (NPP) in 2009 (Pripp *et al.*, 2014).

In 2009, Pripp *et al.* (2014) identified three upwelling regions off Madagascar – along the southern coast, near Cap St André at approximately 16°S , and a small area north of Nosy Be Island at 13°S . All upwelling cells were associated with

elevated surface chl *a*, but low concentrations were observed along the central west coast. Chl *a* and NPP (Pripp *et al.*, 2014, their Figure 2) displayed similar patterns, except in the central region where NPP was high near the coast but there was no ship-track to monitor the chl *a*. Both total copepod abundance and copepod species diversity appeared to be greatest in samples collected off Cap St Marie in the south, compared to samples collected from transects along the west coast (Remanevy, 2014). Moving up the food chain, acoustic estimates, trawling and whale observations indicated high biological productivity in the three upwelling regions, whereas such estimates for the entire western coast were low, typical for tropical waters (Pripp *et al.*, 2014).

The Comoros basin was characterised by warm water in 2009, suggesting low nutrient concentrations. Near-surface fluorescence indicated low chl *a* concentrations ($< 0.1 \text{ } \mu\text{g m}^{-3}$; Figure A5.7b), implying low surface productivity at the time of sampling. Zooplankton dry biomass ($> 375 \text{ } \mu\text{m}$, upper 200 m) ranged from $0.17 \text{ to } 1.42 \text{ g m}^{-2}$ (Table A5.3). The larger ($> 2 \text{ mm}$) size fraction tended to make up a large proportion of the biomass at night, when the larger euphausiids and decapods were most abundant (Roman *et al.*, 2009). Spatially, biomass was highly variable, but was greatest southeast of the Comoros Islands and lowest to the southwest (Figure A5.8). This pattern coincided closely with the locations of a cyclonic (cold-core) eddy and an anticyclonic (warm-core) eddy respectively, supporting previous observations from this region that warm-core eddies contain less zooplankton compared to cold-core eddies and frontal boundary regions (Kolasinski *et al.*, 2012; Huggett, 2014).

Mascarene subregion

The Mascarene Plateau is a crescent-shaped ridge approximately 2 200 km in length, running from the Seychelles Bank in the north (4°S) to the island of Mauritius in the south (20°S). It forms a partial barrier to the predominantly westward flowing South Equatorial Current (SEC; Gallienne *et al.*, 2004). It has been suggested that divergence on the leeward (western) side of the plateau might

BOX
5.2

Isotopic investigations of POM over the Mascarene Plateau

Particulate organic matter (POM) suspended in the water column plays a key role in the regulation of recycling and export of organic materials into and out of the euphotic zone and is particularly important in oceanic biogeochemical cycles (Volkman and Tanoue, 2002). It is a principal component of many food webs, both in open-ocean and coastal communities and may contain variable proportions of phytoplankton, bacteria and detritus, among others (Savoie *et al.*, 2003; Miller *et al.*, 2013).

Stable isotope signatures of POM can be useful for investigating nitrogen (N) and carbon (C) sources driving primary production, which ultimately supports multiple food webs. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of POM collected at the surface and fluorescence maximum (fMax) of the water column across the Mascarene Plateau during an ASCLME survey in 2008 provided some insight into nutrient dynamics and sources in this otherwise oligotrophic region of the Western Indian Ocean.

Substantial concentrations of both N and C in surface water (Figure A5.11) were shown across the entire plateau, particularly on the southeastern plateau shelf (Saya de Malha), with concentrations at fMax on a much lower scale. The range of $\delta^{13}\text{C}$ signatures of POM were similar at both the surface and fMax, suggesting that C sources (and contributions) to POM in the water column were likely comparable across all sections of the plateau. However, at fMax, POM from the open ocean region between the two main shelves of the plateau was slightly more enriched in $\delta^{13}\text{C}$, most likely reflecting changes in either C source or composition at the fMax. This trend was not evident in surface POM and suggests

that C sources at the surface are routinely transported between shelf sections of the plateau, which is also supported by the variability in $\delta^{15}\text{N}$ values in surface POM. Furthermore, high variability in $\delta^{15}\text{N}$ suggests a dynamic mix of N sources included in surface POM composition. $\delta^{15}\text{N}$ POM signatures at the fMax on the plateau shelves were more enriched relative to those between the shelves in the open ocean.

Higher $\delta^{15}\text{N}$ is usually associated with greater proportions of re-suspended detritus and likely also with phytoplankton species associated with shelf communities, while the depleted, lower $\delta^{15}\text{N}$ values are clearly indicative of N generated via nitrogen-fixation at depth.

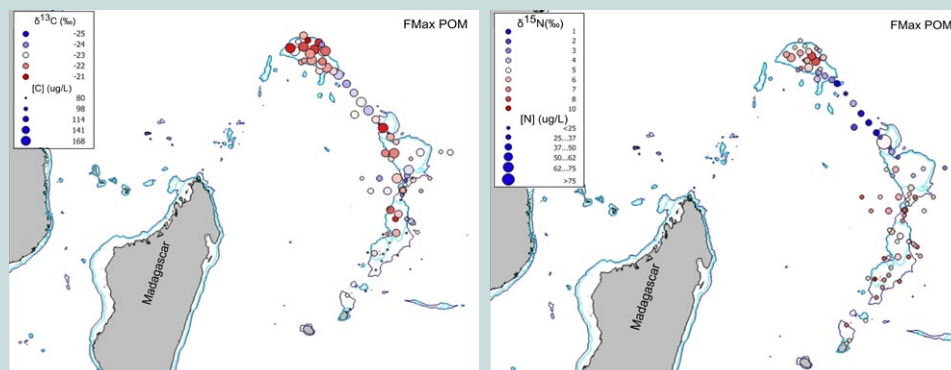
The apparent differences in isotopic values between surface and fMax, and clear changes in C and N signatures between shelf and open ocean regions of the plateau at the fMax, likely reflect dynamic and shifting nutrient pools, which will ultimately influence trophic subsidies to higher trophic-level fauna.

Contributed by: Jaclyn Hill¹ and Sven Kaehler²

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Pictured below: Dr Sven Kaehler, the principal isotope ecologist on this project, died in September 2014 and is sorely missed.



Stable isotopic values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) from particulate organic matter (POM) collected from the fluorescence maximum (fMax) of the water column, across the Mascarene Plateau on the ASCLME survey on the RV Dr Fridtjof Nansen in 2008.



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result in upwelling, with nutrient enrichment and enhanced chlorophyll and secondary production levels downstream (Gallienne and Smythe-Wright, 2005). This followed the observation in 2001 of ten times greater mesozooplankton biomass downstream from the plateau, north of 13 °S, compared to the region away from the influence of the Mascarene ridge (Gallienne *et al.*, 2004).

A subsequent survey in 2002 found contrasting results, with little evidence of topographically induced upwelling enhancing primary and secondary production north of 13 °S. Nevertheless, there was some enhancement of phytoplankton and zooplankton biomass downstream of the plateau, south of 13 °S, possibly associated with turbulent mixing as water passed through the large gaps in the plateau (Gallienne and Smythe-Wright, 2005).

During three consecutive surveys by the *Nansen* in 2008, sampling was conducted along the axis of the Mascarene Plateau (Figure A5.9), in order to assess the productivity, biodiversity and biomass of the pelagic ecosystem. Whether primary production may be enhanced through upwelling along the leeward edge and in the three main gaps through the plateau, was also assessed (Strømme *et al.*, 2009). Mean chl *a* concentration across the plateau was 0.26 mg m⁻³ near the surface and 0.96 mg m⁻³ at the depth of maximum fluorescence (Figure A5.10a, b), which varied between 30 and 100 m (Figure A5.10c). Microplankton (2–20 µm) dominated the biomass, with nano- and picoplankton biomass rarely exceeding 1 mg m⁻³. No indication of upwelling was discovered, except for the Amirantes Ridge, where chl *a* biomass exceeded 30 mg m⁻³. The highest phytoplankton biomass between Mauritius and Seychelles was recorded on the Saya da Malha Bank (Figure A5.10b, c). The phytoplankton bloom along the Amirantes Ridge (Figure A5.10b) consisted of chain-forming diatoms (Strømme *et al.*, 2009). The most important outcomes from these particular surveys are higher phytoplankton biomass in the northern part of the plateau (north of 12 °S), higher biomass at depth (30–100 m; also see Box 5.2), and no evidence of leeward or gap-related enhancement of production.

During the *Nansen* surveys of Oct/Nov 2008, zooplankton biomass was also observed to increase towards the north of the plateau, with highest mean biomass measured over the Seychelles Bank (0.25 ml m⁻³ in the upper 50 m; Table A5.3). Euphausiid species diversity increased northwards too, although abundance increased towards the southeast of the plateau (Box 5.3). Biomass over the Seychelles Bank in July 1978, during the first *Nansen* survey in this region, was approximately four times higher over the same depth range, which points to either high variability for the region or a strong seasonal effect (or both). Given that chlorophyll biomass was consistently highest in subsurface waters over the plateau, seasonal and interannual patterns in productivity are unlikely to be discerned from satellite observations of ocean colour, but will require more frequent *in situ* sampling in the region. Nonetheless, these studies highlight the importance of the Mascarene Plateau to enhanced productivity in the Mascarene Basin, and the need for more sampling to discern both broad- and fine-scale variability in productivity in relation to remote and local forcing.

Seamounts subregion

Seamounts are isolated topographic features, rising steeply from the deep-sea floor, and are thought to be hotspots of biological biodiversity and productivity (Read and Pollard, 2017). In 2009, the *Nansen* explored six seamounts in the Southwest Indian Ocean to determine whether they were centres of enhanced biological productivity – Atlantis Bank, Sapmer Seamount, Middle of What Seamount, Melville Bank and Coral Seamount along the Southwest Indian Ridge, and an un-named seamount north of Walters Shoals on the Madagascar Ridge (Figure A5.13). The seamounts cover a large area, spanning over 10° of latitude and longitude, with a correspondingly wide range in SST, from as high as 27 °C in the north to as low as 8 °C in the south, the largest difference occurring across the Subtropical Front and the Agulhas Return Current (Read and Pollard, 2017). In the vicinity of each seamount, mesoscale eddies dominated the flow, with mean speeds ranging from 15 to 25 cm s⁻¹, which was associated with generation of internal tides interacting

with seamount crests (Read and Pollard, 2017). Such dynamics may influence the associated biology over the seamounts.

The maximum chl *a* concentration for this survey was 15.67 mg m⁻³, located in subsurface waters between the Subtropical Front and the Subantarctic Front, whereas the highest value of chl *a* over any of the seamounts was 0.65 mg m⁻³ at the Coral Seamount (Table A5.2; Pollard and Read, 2017). Sonnekus *et al.* (2017) found an increase in phytoplankton biomass with increasing latitude, with Coral Seamount having significantly higher biomass than Atlantis Bank (max 0.18 mg m⁻³) and north of Walters Shoals (max 0.29 mg m⁻³; Table A5.2). Nitrate was limiting to phytoplankton growth at all the seamounts except for Coral Seamount, which was silicate-limited.

The chlorophyll *a* maximum became shallower at higher latitudes, changing from a depth of ~85 m in the subtropics to ~35 m, further south, over the seamounts and in the Subtropical Convergence Zone.

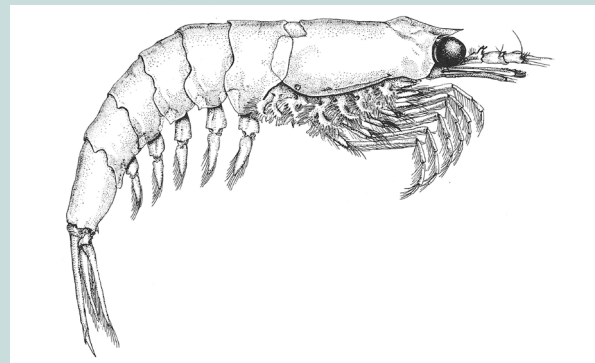
The phytoplankton community also showed a latitudinal gradient with decreasing diversity and a change in dominance from dinoflagellates in the tropics to diatoms towards the Subtropical Convergence Zone (see Sonnekus *et al.*, 2017, their Figure 13 for community composition at each study site). Three communities were observed: subtropical seamount phytoplankton (Atlantis Seamount, Walters Shoals and off-mount samples), phytoplankton of the waters north of the Agulhas Return Current (Melville Bank, Sapmer Bank, Middle of What Seamount) and phytoplankton

BOX 5.3

Euphausiids of the Western Indian Ocean

Euphausiids are comparatively large (1-15 mm body length) members of the holo-zooplankton and are important food items in the diet of a number of fishes, birds and marine mammals. In comparison with copepods, their diversity is low and a total of only 86 species is recognised globally. Multinet and Bongo net samples were examined for euphausiids during two surveys by the RV *Dr Fridtjof Nansen* in the Western Indian Ocean in 2008, off East Madagascar and the Mascarene Plateau. Few euphausiids were found in the vertically stratified net samples, but more than 40 species were found in just 48 Bongo net samples. This is greater than the number of species observed previously in the region, which makes this part of the world something of a diversity hotspot for the taxon.

The most commonly found species was *Euphausia diomedea*, although species of *Nematoscelis* were also widely distributed. Ten species were recovered from single samples, indicating that many species of euphausiid occur at low abundance and are patchily distributed. Over the Mascarene Plateau, diversity increased northwards and into oceanic waters, whilst abundance increased towards the southeast, linked to cooler temperatures (perhaps associated with localised upwelling), slightly lower salinities and elevated chlorophyll. Euphausiids elsewhere in the world are



The most common and widely distributed species of euphausiid recovered in zooplankton samples collected by RV *Dr Fridtjof Nansen* in the Western Indian Ocean during 2008 was *Euphausia diomedea* (10–18 mm in length).

found abundantly only where productivity is high – typically upwelling areas and at high latitudes – and the results generated to date in the Western Indian Ocean are in agreement with those observations.

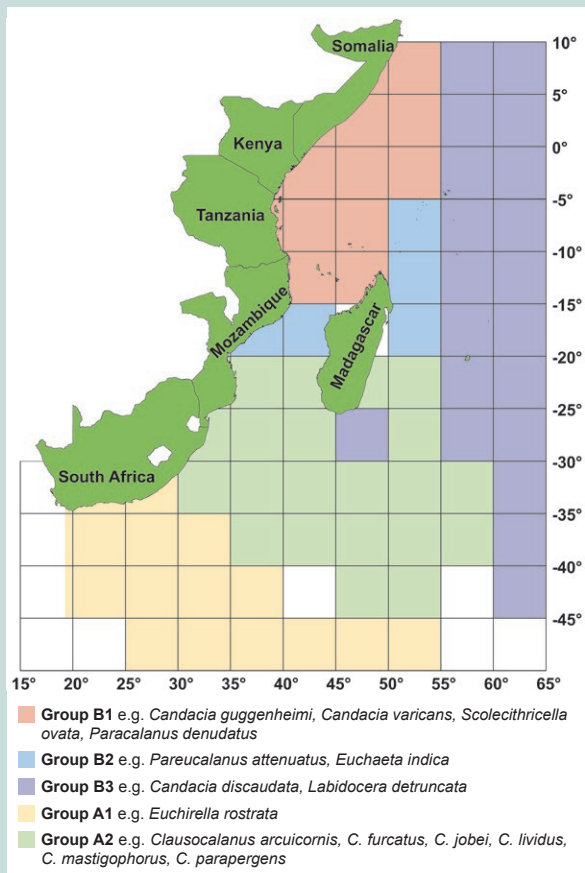
Contributed by: Siyabonga Biyase, Riaan Cedras and Mark J Gibbons
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south of the Agulhas Return Current (Coral Seamount, Subtropical Convergence Zone 1) characterised by a bloom of *Phaeocystis antarctica*. The dominant diatom genus of the survey (>50 percent of the cell counts) was *Pseudo-nitzschia*. Although a general seamount effect in phytoplankton biomass or community composition was not found, phytoplankton biomass appeared to be enhanced over the shallow (<200 m) summits of Coral Seamount and Melville Bank. Strong vertical mixing at these seamounts may have enhanced delivery of nutrients from deeper water into the euphotic zone (Rogers, 2017).

Analysis of particulate organic carbon (POC) and the microbial community on four seamounts (Atlantis Bank, Sapmer, Middle of What, and Coral) during a survey in 2011 by the RRS *James Cook* also indicated a latitudinal gradient in abundance and composition (Djurhuus *et al.*, 2017). More than 50 percent of POC was attributed to the micro-organisms. Although the highest abundance of microbial cells and POC was found on Coral Seamount (the southernmost one), which was the richest in nutrient concentrations, the distribution of *Prochlorococcus* and *Synechococcus* showed the opposite trend, with *Prochlorococcus* most

BOX
5.4

Biogeography of Western Indian Ocean epipelagic copepods



The distribution of calanoid copepods can be used to define the epipelagic (water from the surface to 200 m depth) zoogeography of the Western Indian Ocean, from Somalia (10°N) to the Cape of Good Hope, South Africa and eastwards to 65°E. Published data have been consolidated with new information from the Southwest Indian Ridge samples, collected by the RV *Dr Fridtjof Nansen*, and records scored as “present” or “absent” in each of 85 5-degree grid squares corresponding to five of Longhurst’s (1998) oceanic biogeographical provinces. In total, 497 calanoid copepod species have been documented, distributed across all five epipelagic regions. These are broadly consistent with the major water masses, and can be delineated into cold- and warm-temperate and subtropical and tropical groupings, within which there are generally strong subgroupings based on latitude and longitude. A fairly good agreement was found between the biogeography, as determined using calanoids, and Longhurst’s (1998) biogeographical provinces. However, some differences were noted, which may be ascribed to variation in sampling effort across the region and to the semi-quantitative nature of the analyses. More data are needed, especially to delineate the ‘missing’ Indian South Subtropical Gyre Province (Longhurst, 1998).

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University of the Western Cape, South Africa

Epipelagic biogeographical provinces identified by an analysis of similarity amongst the calanoid copepod species composition of 5° squares in the Western Indian Ocean. Groups A and B are 10 percent similar to each other, subgroups are similar at a level of 14 percent.

abundant in the northwest while *Synechococcus* dominated in the southeast. Djurhuus *et al.* (2017) attributed these patterns to differences in the water masses that formed three biological regimes: north of the Subtropical Front, the central convergence zone, and south of the Subtropical Front. Overall, more POC was found in the southwest and within the convergence zone than in the northeast, implying that more nutrients were available there, probably caused by upwelling due to ocean currents, thereby supporting high primary productivity (Djurhuus *et al.*, 2017).

A study on pelagic backscatter also pointed to the fronts as being foraging hotspots for top predators in the Southwest Indian Ocean (Boersch-Supan *et al.*, 2017). Structurally distinct scattering layer regimes were found across the Subantarctic Front, which corresponded to the boundary regions of the distinct communities identified for phytoplankton, microbial plankton and cephalopods (Djurhuus *et al.*, 2017; Laptikhovskiy *et al.*, 2017; Sonnekus *et al.*, 2017). This implies that acoustic observations could be used to delineate biogeographical regions (Boersch-Supan *et al.*, 2017). Similarly, the presence or absence of copepod species in samples collected during the 2011 seamount survey were used to refine the oceanic biogeographical provinces proposed by Longhurst (1998; Box 5.4).

5.5 Regional synthesis

Results from the many surveys (spanning 40 years, from 1975 to 2015; Table A5.1) conducted in the Western Indian Ocean by the *Nansen* have contributed significantly to regional knowledge, through enhanced understanding of distribution and abundance of phytoplankton and zooplankton biomass and productivity. These variables are controlled by hydrodynamics, which in turn is influenced by winds, currents, tides as well as sea bottom topography.

As primary production is mainly influenced by light and nutrient availability, water movements that bring nutrients to the ocean layers, which are

adequately illuminated, stimulate production. The main mechanisms which act in the Western Indian Ocean to control biomass, abundance and distribution were shown to be upwelling, mesoscale eddy circulation, frontal systems, riverine flow, and monsoon winds causing turbulence (strong, mixing) or stratification (calm, and associated consequences such as blooms of *Trichodesmium* that fix nitrogen).

In general, high chl *a* concentration was also associated with high zooplankton biomass, although this was not always the case. Organisms at higher trophic levels were also found to follow this trend, for example off Mozambique and in the Southern Seamounts subregion. The Western Indian Ocean is relatively low in terms of productivity, especially in surface waters, where chlorophyll concentrations were generally lower than in the sub-surface layers. Exceptions were coastal embayments, such as around Madagascar, and productive continental shelves, such as Delagoa Bight. Nutrients were also relatively low in surface concentrations, but increased with depth in deeper waters. This was mostly true for nitrate, nitrite, ammonia and phosphate, while silicate was non-limiting in surface waters.

Highest zooplankton biomass was measured off the Somali Coast, reaching approximately double the highest biomass found elsewhere in the region. The second highest biomass was recorded over the Sofala Bank during the rainy season, followed by the Seychelles Bank, but these were all for relatively shallow depths (40–50 m) where biomass is more concentrated. In addition to variability in sampling depths (40–500 m), regional comparisons are complicated by the use of different mesh sizes (180–500 μm), particularly during the early surveys.

During the ecosystem surveys there was an effort to standardise methods, and for all surveys from 2008 onwards the use of a Multinet (180 μm mesh) enabled an equitable comparison of biomass in the upper 200 m for the Mozambique, Mascarene and Seamount subregions. Using this methodology, highest mean biovolumes were associated

with eddies in the Mozambique channels (0.4 ml m^{-3}), and lowest mean biovolumes were recorded over the southern Mascarene Ridge (0.05 ml m^{-3}). Intermediate mean biovolumes of $0.1\text{--}0.3 \text{ ml m}^{-3}$ were recorded around the seamounts, supporting the hypothesis that these are often hotspots of productivity in an otherwise oligotrophic ocean.

5.6 Conclusions and recommendations

The ecosystem surveys since 2007 have made a significant contribution to improving our knowledge of ocean productivity in the Southwest Indian Ocean, in particular. In terms of regional coverage, knowledge gained has been greatest for the Mozambique shelf, followed by the Mascarene subregion. The East Africa Coastal Current subregion remains to be explored, and effort expended in the Madagascar and Comoros subregion far exceeds the outputs. In terms of discipline, knowledge gained has been greatest for phytoplankton and zooplankton biomass, to a moderate degree in terms of species composition, and minimally in terms of primary and secondary production measurements. Whilst the collection and processing of nutrient samples have been extensive, analyses using these data are scarce.

From a technical perspective, the *Nansen* has proven to be an excellent platform for multidisciplinary sampling, which facilitated capacity development such as during the ASCLME surveys. Each survey included local scientists and students from the country or region under investigation, as well as more experienced scientists from other countries, thus providing an ideal mentoring environment.

Some of the practical problems typically encountered with plankton sampling during the surveys were comprehensively summarised by Rogers *et al.* (2009). They include poor condition of the nets, damage to nets due to contact with the other cod-ends and the cod-end frames (with the suggestion that the cod-end frame design be modified), loose-fitting cod-ends resulting in the loss of

cod-end contents, lack of spares for survey equipment, and provision of a full equipment list well in advance of a survey.

An important concern has been the inadequate record-keeping of plankton samples sometimes, as well as oversight of their off-loading subsequent to a survey, including who the responsible agent(s) will be for sample curation and analysis. This should be clearly documented, and should ideally be available in an online metadatabase. Linked to this is the issue of data archiving and access. It has been a difficult task to establish exactly what samples and data have been analysed for some surveys. The survey reports have been of varying quality and content, proving invaluable in some cases, and frustratingly thin in others.

A real challenge encountered during post-2007 surveys was that although considerable expense was put to facilitating regional participants in the numerous surveys, there were no funds allocated for sample analysis after the surveys. While analysis of physical data from CTD casts, for example, is a relatively rapid process, analysis of biological samples such as phytoplankton and zooplankton (particularly for taxonomic identification) can be extremely time-consuming and requires scarce taxonomic skills. The end result has been far fewer outputs, as well as a much longer time to eventual publication, than should be expected. For future large programmes, such as may ensue in support of the IIOE-2, it is recommended that bursaries are made available for students to facilitate the timely analysis of samples.

As plankton are ideal indicators of ecosystem change, transboundary and basin-scale monitoring of their communities is recommended. The *Nansen* could assist with a coordinated monitoring programme, by including previously sampled transects when revisiting an area, and by towing a Continuous Plankton Recorder (CPR) during long transits. The CPR collects phytoplankton and zooplankton abundance and community structured data over large temporal and spatial scales (Verheye *et al.*, 2016). It is a robust, tried and tested, cost-effective plankton sampling

device deployed at high speeds (>20 knots) from commercial ships-of-opportunity on their normal trading routes, although it can also be towed behind research vessels at a minimum speed of 10 knots. Such a programme would ultimately provide a suite of plankton indicators for a number of marine environmental management issues: climate change (for example, distributional shifts and range expansions of plankton populations), ocean acidification (impacts on calcifying species), eutrophication (algal blooms and consequential “dead zones” of bloom decay), productivity supporting fisheries (plankton hotspots, fish dependence on biomass, composition and timing of their plankton prey), invasive species (invertebrates via their planktonic stages), ecosystem health (HABs – harmful/toxic algal blooms, marine pathogens) and biodiversity (community changes, unusual species records; pers. comm. H. Verheyen). There is currently no coordinated CPR survey active in the Western Indian Ocean, although two CPR tows were recently undertaken between South Africa and Madagascar, on the RV *Algoa* in 2013 and the *Nansen* in 2015. Such a programme would require access to a centre with expertise in the enumeration and identification of CPR-collected plankton, which is currently lacking in the region. ■

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