

METEOR-Berichte 06-5

South East Atlantic 2000

Part 5

Cruise No. 48, Leg 5

13 — 30 October 2000, Walvis Bay — Walvis Bay

Benguela-Planktonproduktion

J. Alheit

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5 METEOR cruise No. 48 Leg 5

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Participating Institutions

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IFMK	Institute for Marine Research, Kiel University, Germany; since 2004:IFM-GEOMAR, Kiel
FIS	Forschungsinstitut Senckenberg, Wattenmeerstation List, Sylt, Germany
US	Universität Stuttgart, Germany
SL	Southampton Laboratory, UK
PML	Plymouth Marine Laboratory, UK
MBA	Marine Biological Association, Plymouth, UK
MCM	Marine and Coastal Management, Cape Town, South Africa
UCT	University of Cape Town, South Africa
NatMIRC	National Marine Information and Research Centre, Swakopmund, Namibia
FH	Fachhochschule Hamburg, Germany
DWD	Deutscher Wetterdienst, Hamburg, Germany

5.2 Research Program

Little is known of plankton and fish production processes in the northern Benguela Current off the Namibian coast. Consequently, the objective of cruise leg 48-5 was for a better understanding of the impact of meso-scale physical structures and processes on zooplankton production with reference to fish recruitment. Studies were carried out within the *Small Pelagic Fishes and Climate Change (SPACC)* programme of *GLOBEC* and the regional *BENEFIT* programme and focussed on four main questions:

1. What is the impact of the nutrients generated by the Lüderitz upwelling cell on primary production and the development of pelagic food webs up to the level of ichthyoplankton in regions north of Lüderitz?

The impact of the nutrients generated by the Lüderitz upwelling cell is not clear. It is hardly known which production processes are initiated further offshore and north by the Lüderitz cell, where these processes are taking place, which final products are generated and what proportion of plankton production finally ends up as fish production. The context of the study will be to see where (how far offshore and north) the Lüderitz nutrients generate the food chain link from phyto- to zooplankton and whether there is any direct impact on the spawning grounds farther north. The focus will be on:

- temporal and spatial shifts of phytoplankton concentration as dependent on the strength of upwelling off Lüderitz
- temporal and spatial development of the pelagic food web (maturation of food web)
- quantification of the spatially decoupled transfer of organic carbon into the spawning areas.

In summary, the aim will be to examine to what extent the Lüderitz upwelling acts as a "fertilizer factory" for pelagic fish production in distant regions.

2. What is the role of the two-cell cross-shelf circulation in the northern Benguela for zooplankton production and survival of fish larvae?

The main spawning centers of anchovy and sardine are outside the upwelling cells off Lüderitz and Cape Frio. It will be examined why these regions offer good survival conditions for fish larvae. Possible reasons include: (i) avoidance of advection into the open sea by the complex cross-shelf circulation (retention), (ii) improved feeding conditions due to the stabilized water column (low turbulence) or (iii) high density of food particles due to concentrations of zooplankton accumulating in the region of the coastal cell.

3. To what effect do physically contrasting environments in the Benguela Current influence plankton production?

The waters off Namibia encompass a wide range of different physical regimes: upwelled, non-upwelled and oceanic waters. Upwelled waters range from newly upwelled to mature upwelled environments. Different water masses are separated by fronts and clines which themselves represent different environments. All these contrasting environments will affect, growth rates and production of plankton in different ways. Special attention was given to determine species composition, distribution, abundance and biomass of zooplankton and to estimate daily production rates of copepods in contrasting environments and to assess the hatching success of copepod eggs produced under contrasting feeding conditions.

4. What is the variability of the bio-optical properties of water masses in the Benguela ecosystem and the impact on ocean colour?

A series of bio-optical measurements was carried out to (i) examine the validity of existing methods to determine chlorophyll *a* from ocean colour sensors including SeaWiFS and MERIS, (ii) validate novel bio-optical models to determine phytoplankton absorption characteristics from ocean colour, (iii) examine the role of photosynthetic and photoprotective pigments in phytoplankton absorption and (iv) assess the logistical feasibility of determining photosynthetic rates from *in situ* Fast Repetition Rate Fluorometry in order to estimate primary production.

The cruise leg also served for training of young scientists and technicians from Namibia, South Africa and Germany in modern methodologies.

Intensive biological measurements and sampling were carried out on 5 transects perpendicular to the Namibian coast (Fig. 5.1) to sample in a range of contrasting environments from newly upwelled to oceanic waters. The location of the transects and the sampling stations were determined using remote sensing and UOR (undulator) data.

SeaWiFS and SST images were transmitted daily to METEOR. Unfortunately, during cruise leg 48/5, the entire region north of Walvis Bay was permanently cloud covered. Thus, remote sensing information could be used in the second part of the cruise only, in waters south of Walvis Bay.

The UOR was towed behind the ship with a speed of about 10 knots and was set to undulate between 5 and 50 m depth. It carried a package of sensors recording depth, temperature, salinity, fluorescence and light attenuation. The data were analysed directly after each tow and yielded a synoptic picture of the biophysical conditions along the transect.

Between 23° and 19° S, a transect was set parallel to the coast following the 200 m isobath. In northern Namibian waters, in the known spawning grounds of anchovy and sardine, 3 transects were laid approximately perpendicular to the coast starting at the coast at about the latitudes 19°, 20° and 21° S. The locations of the transects were selected as representative of the contrasting environments off northern Namibia. Each transect extended from the coast to 100 miles offshore and was first sampled by an UOR tow starting near the coast. On return to the coast, intensive biological sampling for phyto-, zoo- and ichthyoplankton was carried out at stations along the transect selected on the basis of the UOR data. The criteria for selection of these stations were their contrasting characteristics. Another transect perpendicular to the coast was set at 23° S latitude, also extending offshore for 100 miles. Namibian monitoring for physical parameters and plankton is carried out on a monthly basis along this 23° S latitude line. The line was therefore selected so that the METEOR results can be compared with the equivalent Namibian long-term data from this line. A fifth transect was selected at 25° S latitude which extended from the coast to 160 miles offshore. The objective of this transect was to follow an upwelling filament extending offshore originating from the Lüderitz upwelling cell.

Throughout the cruise, ADCP measurements were carried out continuously. At all stations, temperature, salinity, oxygen and chlorophyll *a* were determined by CTD casts.

To determine the relationship between primary production, photosynthetic pigments and light, samples were taken from CTD bottles for the analysis of pigments by HPLC, Gelbstoff and particle absorption. *In-situ* optical measurements were performed with a bio-optical profiler equipped with sensors measuring reflectance at the SeaWiFS and MERIS wavelengths, a fast repetition rate fluorometer to measure photosynthetic parameters, and a CTD to verify alignment of the water samples with the bio-optical profiles.

Water samples were collected at each CTD station to determine the changing nutrient concentrations within the upper 200 m of the water column. The standard colorimetric methods were used to manually analyse the samples for silicate, phosphate, nitrate, nitrite and ammonium content.

Phytoplankton was collected with the micro net of 20 µm mesh size. The samples served to study species composition and to determine indicator species communities for different upwelling scenarios. Taxonomic studies focused on dinoflagellates which have been rarely studied in Namibian waters. Dinoflagellates have different nutritional strategies, some are phototrophic, others are heterotrophic or even parasites. Also, the hypothesis was tested that heterotrophic dinoflagellates show a larger abundance in upwelled waters with a high diatom biomass than in diatom-poor waters where phototrophic species should dominate.

In order to determine species composition, distribution and abundance of zoo- and ichthyoplankton a suite of different multiple opening/closing plankton samplers with differing mesh sizes was deployed. The Multinet of 200 µm mesh size equipped with 5 separate nets was hauled vertically for catching meso-zooplankton and was deployed on each station of the perpendicular transects. The BIOMOC, a modified MOCNESS with 9 nets of 335 µm mesh size, was used to collect ichthyo- and larger zooplankton on oblique hauls. The Longhurst-Hardy-Plankton-Recorder (LHPR) was used to investigate the concurrent fine-scale vertical distribution of microzooplankton (53 µm mesh system) and ichthyoplankton (200 µm mesh system). On the perpendicular transects, BIOMOC and LHPR collections were carried out at selected stations representing different bio-physical regimes.

Daily egg production and moulting rates of copepods were measured in contrasting areas of thermal (inshore *vs* offshore) and food conditions (i.e. low *vs* high Chl *a*, dinoflagellate *vs* diatom assemblages) to estimate secondary production. Hatching success of copepod eggs was assessed under contrasting feeding conditions (diatom-dominated *vs* non-diatom food assemblages) to test the hypothesis whether diatoms have a deleterious effect (toxic or nutritionally insufficient) on hatchability of eggs.

5.3 Narrative of the Cruise

On the night of 12 October 2000, the day before the start of this cruise leg, Cptn. Kull gave a reception for authorities from the Namibian Ministry of Fisheries and Marine Resources and the National Marine Information and Research Centre. The reception was attended by the German Ambassador, U. Nestroy, the Director of the Fisheries Institutes in Swakopmund and Lüderitz, Dr. B. Oelofsen and many Namibian scientists. METEOR left Walvis Bay on the morning of 13 October and headed for the CTD test station. Subsequently, METEOR began its station work along transects. The UOR was towed northwards along a transect which was set parallel to the coast following the 200 m isobath between 23° and 19° S. The most northern station of this transect was reached on 14 October. Next day, a 100 miles transect was laid out perpendicular to

the coast. Station work on the transect lasted until 17 October. METEOR then turned southwards along the previous north-south transect and worked up five additional transects perpendicular to the coast at appr. 20° S (17-19 October), 20°30' S (20-21 October), 23° S (23-25 October), 25°10' S (26-28 October) and 24° S (29 October). METEOR finished station work on 30 October and returned to Walvis Bay the same day.

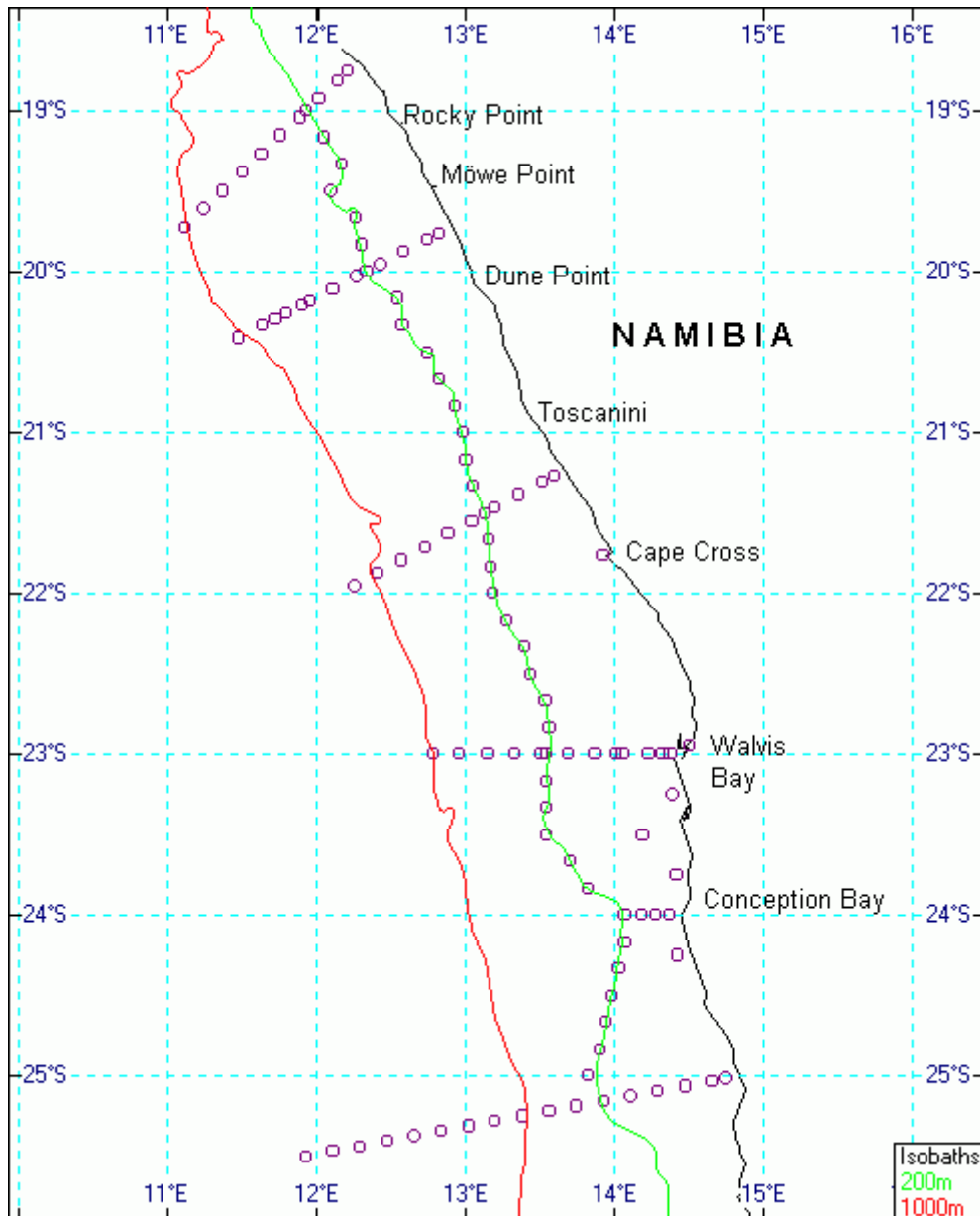


Fig. 5.1: Map with transects and stations.

5.4 Preliminary Results

5.4.1 Physical Measurements

5.4.1.1 CTD

(Rainer Feistel, Aina Iita, Alan Kemp, Craig Risien, Christo Whittle)

Physical CTD measurements on Meteor cruise 48-5 off Namibia have been carried out using a Seabird Electronics SBE 911+ bathysonde, equipped with sensors for pressure, temperature, conductivity, oxygen, and a Haardt fluorometer. Except for one station (93), all casts have recorded profiles not deeper than 500 m.

All CTD data are unvalidated and therefore preliminary ones. Calibration measurements have been carried out regularly along the cruise. While no major changes due to calibration are to be expected for salinity, temperature, and pressure, the oxygen data are likely to be rescaled by a factor of about 2/3, i.e. the figures shown here may exceed the true values even by about 50%.

Stations have been located on the shelf off Namibia between 19°S and 26°S as shown in Fig. 5.1. The net especially includes the standard NatMIRC monitoring transect along the 23°S parallel. The attention was focussed on varying upwelling conditions in both - parallel and perpendicular to the coast - directions. Correspondingly, the transects have been placed either along the 200 m isobath line, or normal to the shelf at 19°S, 20°S, 21°30'S, 23°S, and 25°S from 5 nm to 90 nm offshore. The southernmost transect was extended to even 160 nm offshore following a stationary upwelling filament visible there in a series of satellite SST (sea surface temperature) images. Station spacing was always about 10 nm or less. Some additional stations have been added to this scheme for specific biological samplings near the coast.

Sea surface temperature (SST) is commonly used as indicator for upwelling. Zonally, we have observed - as expected - a general tendency of rising SST with increasing distance from the shore, due to a gradually changing influence of cold upwelled water and warm ocean surface water. Meridionally, the distribution of surface properties is not governed by simple rules but depends on the actual locations of upwelling cells and on further meteorological and climatic factors. Under the conditions of our cruise, we found nearshore SST rising systematically from below 12°C at 25°S to above 14°C at 19°S. This is in agreement with a climatological SST of 14°C in October at 20°S (Janke 1920, Hagen et al. 1981). The upwelling threshold temperature is usually specified as 14°C (Hart and Currie 1960) or 13°C (Hagen and Feistel 2001), so in either case the cruise has passed from upwelling to non-upwelling situations, as it was intended in the cruise objectives.

The northern boundary of Benguela upwelling in October is subject to large interannual fluctuations, it may vary between latitudes of 25.4°S in 1993 and 16.8°S in 1983, as has been shown from satellite images between 1982 and 1997 (Hagen and Feistel 2001). The currently observed 13°C SST isotherm at about 24°S fits into this interval but belongs to the years of rather southern positions of the northern boundary (1993: 25.4°S, 1982: 23.8°S, 1992: 22.8°S).

The almost continuous alongshore SST gradient observed suggested a working hypothesis that the Benguela current waters may exhibit an age succession from „young“ fresh upwelled water in the south to „old“ mature upwelled water in the North. Assuming an average northward current velocity of about 20 cm/s (Hagen et al. 1981), the transport of water from 25°S to 19°S would take roughly 1 month.

To investigate the physical, chemical and biological details of such a possible sequence of stages, an alongshore transect on the mid shelf at 200 m water depth was carried out by CTD casts from 19°S to 25°S every 10' latitude. Due to extended time gaps in between, the transect is depicted here in 4 parts, from 19°S to 20°S, from 20°S to 21°30'S, from 21°30'S to 23°S and from 23°S to 25°S. Note that the last transect was done in northward direction while the other ones have been steamed along southward. North of 22°S, there was a measurement gap of about 8 hours due to an excursion to station 94, located 2 nm off Cape Cross.

Every 1-2 degrees of latitude, a transect perpendicular to the shelf was studied, from 5 nm offshore to 90 nm offshore with 10 nm station spacing. As an example, their rich zonal structures are shown for 19°S (Fig. 5.2a-d). a) stands for the temperature plot, b) for salinity, c) for density, and d) for dissolved oxygen. The 23° transect off Walvis Bay is identical with the monitoring line of the Namibian National Marine Information and Research Center (NatMIRC) at Swakopmund. Some additional casts have been included in these transects due to biological or other reasons, especially the southernmost transect was extended to 160 nm offshore to study a cold SST filament.

The 19°S transect shows typical features of the Benguela upwelling regime in agreement with the general scheme proposed in (Hagen et al. 1981). If we consider the density section (Fig. 5.2c) we see an almost constant vertical density gradient. The pycnocline at about 100 m depth is only weakly pronounced, and so is the thermocline (Fig. 5.2a).

Above the pycnocline, density surfaces rise towards the coast due to weak upwelling. These density gradients are usually geostrophically balanced by a northward current. Farther offshore, density above 100 m shows a maximum due to secondary upwelling, accompanied by a pair of opposite geostrophic currents on both sides of the upwelling front. Below 100 m, density surfaces decline towards to shore, corresponding to extended kernel of a southward undercurrent.

The same up- and downwelling features are visible in the pictures of temperature (5.2a), salinity (5.2b), and oxygen (5.2d). The latter one shows very clearly the extended oxygen minimum in the undercurrent area. There was no hydrogen sulfite detected, however, except for one station at 100 m water depth off Walvis Bay, where a thick mud layer was found and intensive H²S smell.

The 14°C isothermal in Fig. 5.2a is located within the offshore thermocline at 100 m depth and is only upwelled below the mixed surface layer at the coast. The 13°C isothermal is already properly below the offshore thermocline, and it is even downwelled near the shore. We see the the 14° SST criterion for upwelling refers to the limiting case where the thermocline is bent upward to touch the surface, wherever the 13°C SST criterion expresses to stronger condition that water from actually below the pycnocline has been lifted to the surface.

The existence of different upwelling front systems at the surface is most clearly seen in the salinity distribution (Fig. 5.2b), where we find relatively strong lateral salinity gradients persisting even through the wind-stirred mixed layer.

The other transects perpendicular to the shelf show qualitatively analogous features, but deviate from it quantitatively. For instance, we see that the pycnocline varies in depth between 60 m and 100 m, that the 14°C isothermal is located sometimes within, sometimes just below it. It will be the sake of future investigations to further study and evaluate the importance of these differences especially for their biological consequences.

Slightly different is the zonal transect at 25°S, which requires some additional comments. First, it is almost twice as long as the other ones, namely 160 nm, and followed a cold filament detected in the SST satellite images of October 23, 24, and 25. Second, the conditions along the transect changed drastically when we passed 14°E from permanent southerly winds with BF 5-7 to virtually no wind. The SST followed the wind fading very rapidly, indicating that the formerly intense upwelling has broken down. This rapid change becomes evident at station 100, the inshore end of the transect. It was visited twice, first, before the transect started, on 26.10.2000 at 0:31 UTC, where SST [°C]= 11.85 and density [kg/m³]= 1026.55 were found, and second, after the transect was finished, on 27.10.2000 at 17:08 UTC with then SST [°C]= 14.19 and density [kg/m³]= 1026.11. Inspection of the ship's weather and thermosalinograph recording shows that the formerly persistent southerly wind dropped from 6.1 m/s at 7:45 UTC to 0.5 m/s at 8:36 UTC. The low surface temperature started around 10:00 UTC, just 2 hours later, to oscillate heavily between 12.5°C and 14.5°C with a period of roughly 1h. At about 17:00 UTC, oscillations became smaller and more stabilized at around 14°C.

Thus, this transect must be considered differently west and east of 14°E, and we exclude its very inshore part from the following remarks. The 13°C isotherm intersects with the surface at

about 14°E, that is about 50 nm offshore. There is no hint for downwelling nor for an upwelling front along the transect, neither in temperature, nor in density nor in oxygen, as compared with the more northern transects. The southward undercurrent with its isopycnals falling towards the shelf is found at 300 m depth and below. The picture appears as if the usual upwelling zone is extremely stretched, horizontally as well as vertically.

While the surface part above the pycnocline (60 m) is almost unstructured, we find a strong and rather regular wave pattern below it in the distributions of oxygen, salinity, and temperature. The feature is almost barotropic with a wavelength of about 40 nm. Because it is nearly invisible in the density plot, it cannot be accompanied by geostrophic currents as discussed for the alongshore wave discussed below. Rather, different water masses are finger-like merged into each other along surfaces of equal density. The causes for the strength and regularity of the structure need deeper investigations, however.

The transect along the 200 m isobath is well located in the upwelling zone, as we can see in the transversal transects like in Figs. 5.2. The dominant, striking pattern in the density section between 19°S and 29°S is a very regular wave structure with strong amplitudes and an apparent wavelength of about 30 nm (without taking into account time delays between the stations). This meandering of the undercurrent is almost barotropic (excluded the boundary layers at surface and bottom), i.e. it includes the entire water column as a whole. All other water properties follow the same oscillation. If we assume geostrophic currents with these horizontal density gradients, they must significantly exceed the strength of the meridional currents discussed on connection with the transect at 19°S. We may assume, however, that the 19°S transect hit the undercurrent where the density surfaces reached almost their highest location, and that a similar transect taken at 19°20' or even 19°50' might have shown a fairly stronger downwelling below the pycnocline. The existence of an undercurrent meandering due to low-frequency instabilities has already been discussed in (Hagen et al. 1981).

Despite of the wave pattern penetrating from the undercurrent to the surface, surface values show a weak meridional gradient along the 200 m isobath. The wave structures repeat along that isobath going further south, but become more and more superimposed by other features and distortions. For example, at 21°20' between 40 and 120 m depth an eddy-like structure with opposite circulation above and below 90 m can be observed.

Section 19°S Temperature

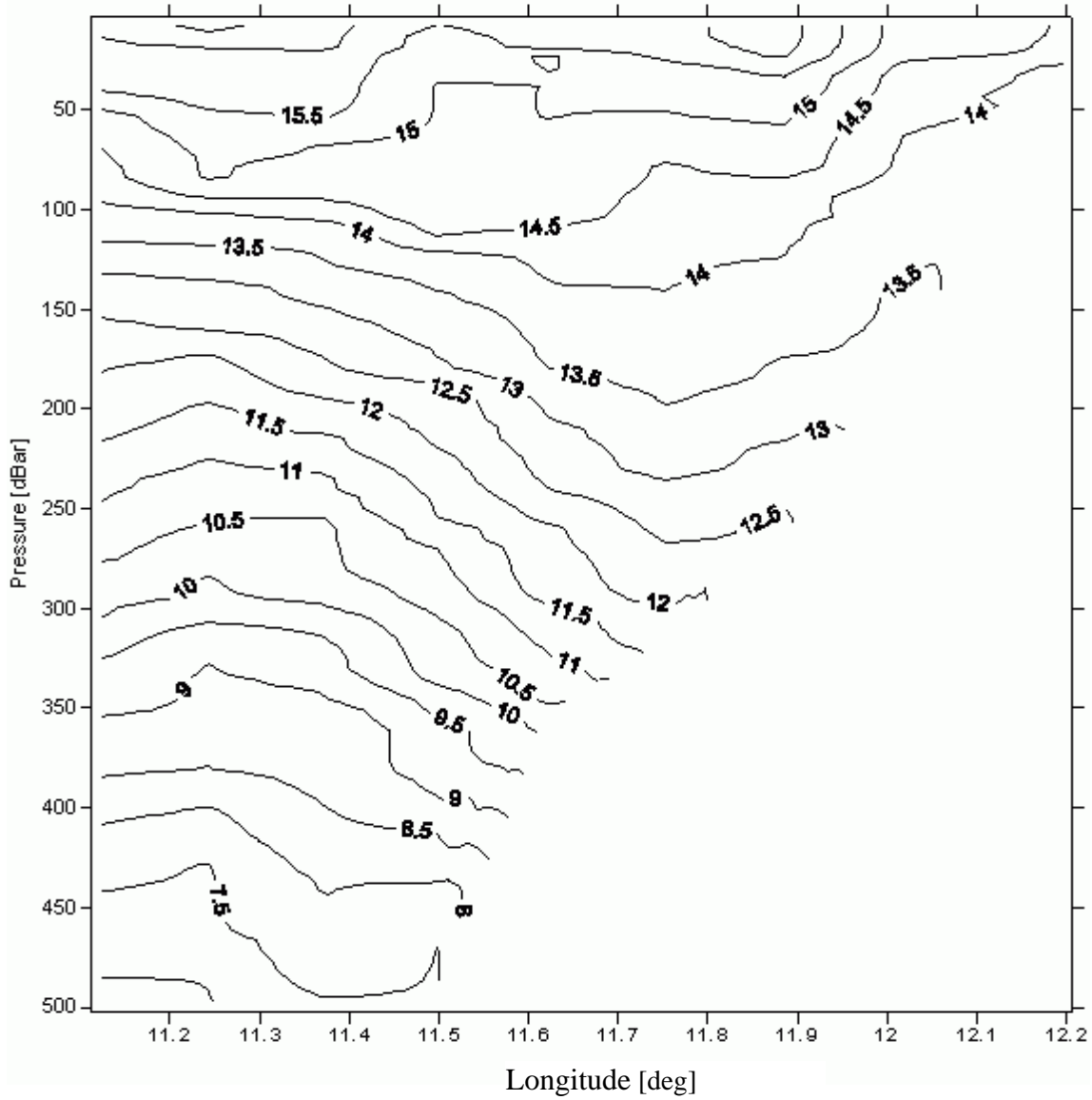


Fig. 5.2a: Temperature distribution on the transect at 19°S.

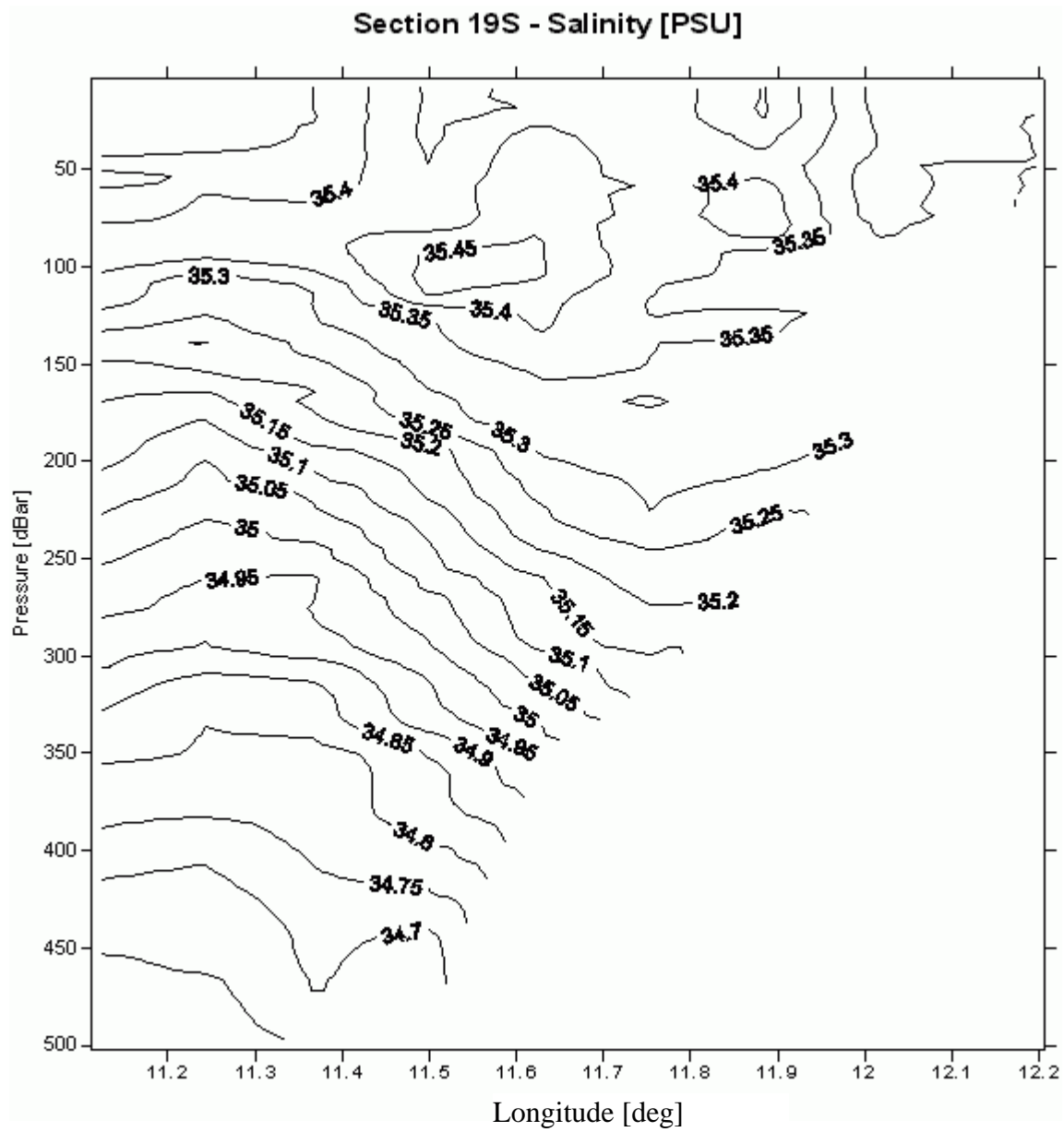


Fig. 5.2b: Salinity distribution on the transect at 19°S.

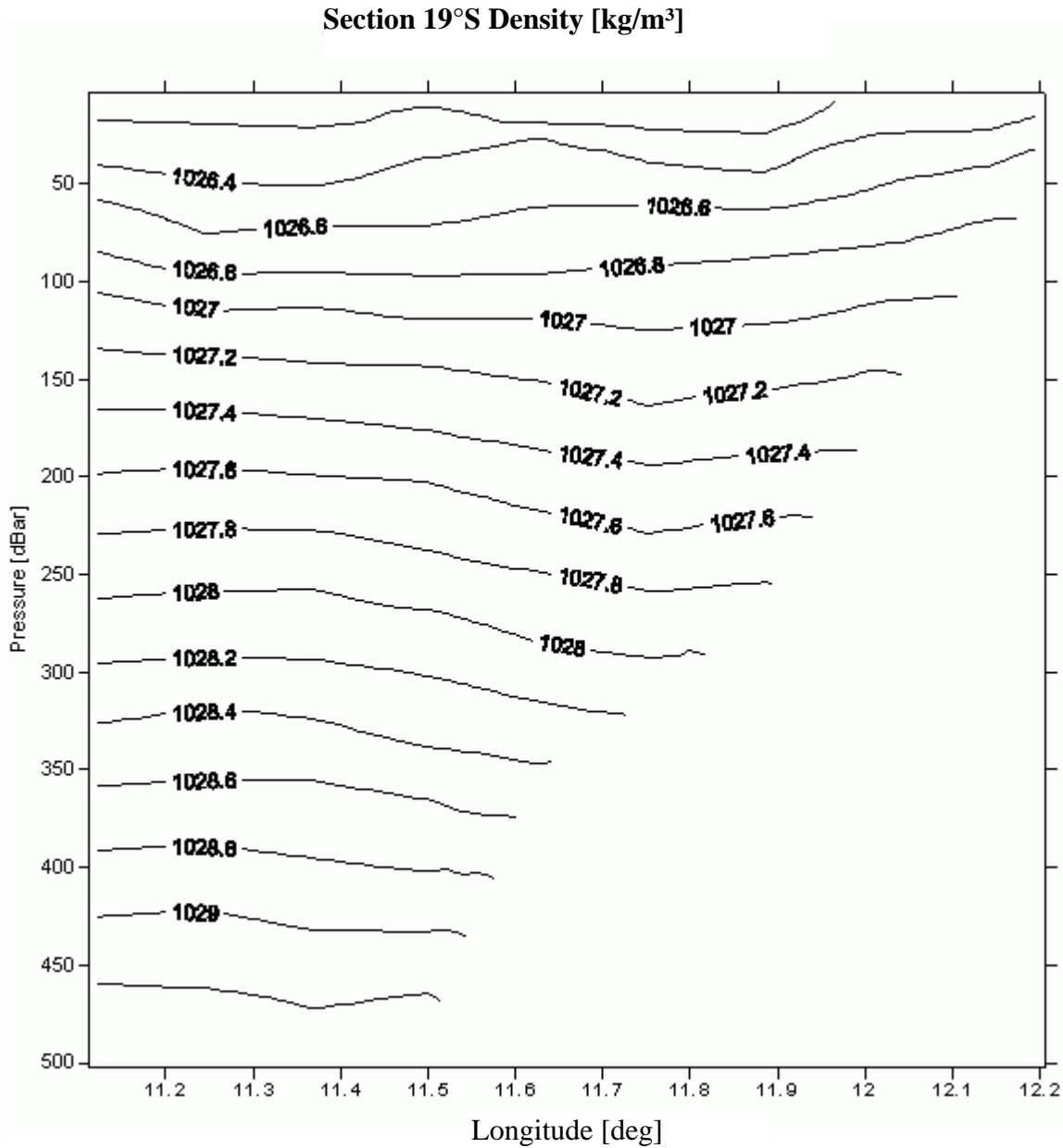


Fig. 5.2c: Density distribution on the transect at 19°S.

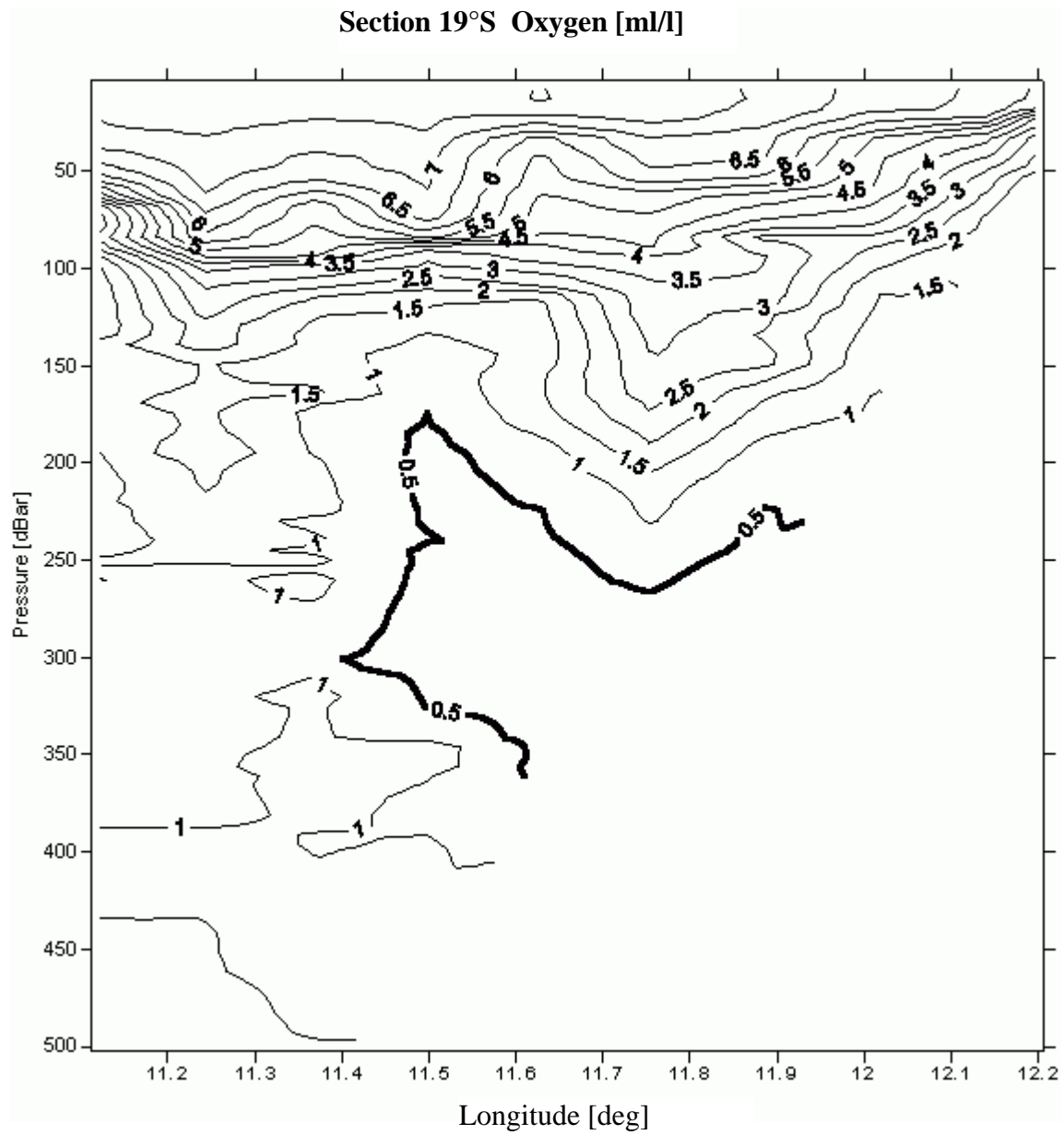


Fig. 5.2d: Oxygen distribution on the transect at 19°S.

5.4.1.2 Undulating Oceanographic Recorder, UOR

(Gerald Moore)

The undulating oceanographic recorder (UOR) developed by the Plymouth Marine Laboratory (Aiken and Bellan 1986) is an autonomous towed vehicle that profiles the surface layer (0-70m) of the ocean. It is ideal for rapid surveys of coastal environments and the euphotic zone, where it can determine biological and frontal features. As an autonomous vehicle it makes low demands on the ship facilities since it does not require special winch facilities. The UOR profiles are controlled by a programmable servo motor system, that is powered by a propeller on the vehicle. The servo system can be programmed to a range of depth, normally with an amplitude of 50 m. On the METEOR leg 48-5 the UOR was programmed to undulate between 5 and 55 m. The UOR was instrumented with a CTD, fluorometer and transmissometer. During daylight tows a Satlantic 7-channel radiance sensor and a tilt and roll sensor were added to provide information on diffuse attenuation and water reflectance. The UOR was used to provide a rapid survey of the transects giving information on biological and physical features that were used to design the station plan and particularly to determine the stations for intense biological sampling.

The UOR was deployed for 10 tows during the leg M48/5. Four tows covered the 200 m isobath northward transect from 23°S to 19°S. These tows were from stations 26-27, 27-28, 28-29 and 29-30. The data from these tows have been combined into a single transect. A further 4 tows were made for the east west transects at 19°S, 20°S, 21° 30'S and 23°S corresponding to stations 31-40, 46-55, 66-75 and 84-93 respectively. The last 25°S transect was covered in two tows between stations 100-105 and 155-116; again these data have been combined into a single tow.

The data presented here are preliminary data without full validation and calibration and thus any absolute numbers for the physical variables should be interpreted with caution. The data has however been checked with the underway thermosalinograph, so trends in temperature, salinity and density are valid. During deployment two instrument problems occurred that have resulted in artefacts in the data. The first is a calibrations shift in the conductivity sensor between the first two tows along the 200 m isobath transect. This results in an error in salinity and density at 22°E (station 27); the second is a temperature / salinity error that occurs in the 23°S transect at 13° 33'S (13.55°S), which results in a false frontal feature appearing.

The attenuation coefficient and the chlorophyll fluorescence are proxies for biological activity. *In-vivo* chlorophyll fluorescence shows a variation in quantum yield that depends on species assemblage, nutrient status and the ambient light history - non-photochemical quenching (Falkowski and Kiefer 1985). The quenching effect is apparent in the 23°S transect, where there is an apparent sub surface maximum between 13.5°E and 12°E, this subsurface maximum in not

observed in the beam attenuation data. The beam attenuation responds to scattering of particles, which depends on the number, size and morphological characteristics of phytoplankton. The data is presented as attenuation, where the attenuation of pure water is around 0.41. The attenuation due to phytoplankton varies as a non-linear relationship of chlorophyll concentration, but is 0.35 for a chlorophyll concentration of 1.0 mg.m^{-3} .

5.4.2 Nutrients

(Benedict Dundee, Matthew Hanghorne, Andrea Laws, Anja van der Plas)

Water samples for nutrient analyses were collected at fixed depths for each CTD cast. In general it can be said that surface levels of nutrients such as nitrate and silicate were low inshore suggesting that there was only weak, if any, coastal upwelling and then restricted to 5 to 10 nm from the coast. Internal data reports from the Ministry of Fisheries & Marine Resources, Namibia, indicate that October can be quite variable in this regard. During some October sampling periods active upwelling can be noted up to 30 nm offshore from the very high nutrient concentrations then measured at the surface. The two-cell upwelling structure noted from the physical oceanographic data may possibly also be inferred from the nutrient profiles. For instance, the phosphate profile of the 19°S transect shows some new upwelling at the coast (5 & 10 nm stations). Between 20 to 30 nm offshore this low-phosphate water seems to be downwelling again. And at around 40nm offshore water from 40-50 m depth is upwelling again to the surface. However, the chemical and physical oceanographic data need to be scrutinised and compared more closely to determine how well they agree.

From 20°S and southward the inshore nitrate levels at the sediment/water interface (5 and 10 nm stations) were very low; in fact at 10nm offshore, 20°S total denitrification had occurred so that both nitrate and nitrite levels were undetectable. The ammonium levels for the bottom samples at the 20-25°S inshore stations were relatively high, as were the phosphate and silicate concentrations. This indicates that regeneration is occurring from the organic-rich sediments. It is expected that oxygen levels at the inshore stations would have been depleted to near anoxic levels (generally $<0.5 \text{ ml/l}$) through the intense regeneration.

The nutrient profiles of the 25°S transect indicate that no coastal upwelling of nutrient-rich deeper waters was occurring at 5-10 nm offshore. However, high nitrate levels at the surface from around 20 nm to 120 nm from the coast suggest that aged upwelled water is being transported offshore here.

The phosphate and nitrate profiles of the 200 m isobath transects also exhibit an alongshore wavelike pattern, such as was noted from the physical data. But it must be emphasised that the nutrient analyses are still preliminary. The 200 m isobath transects, as well as the transects perpendicular to the coast, need to be looked at more closely, unique features identified and compared to the physical and biological findings before further conclusions can be made.

5.4.3 Bio-optics (incl. Pigment Studies and Remote Sensing)

(Ray Barlow, Janet Botha, Gerald Moore, Scarla Weeks)

5.4.3.1 Bio-optics

Solar-powered biological production drives all the processes in the ocean. These processes relate to natural resources, fisheries and the air-sea exchange of biogenic gases, which are implicated in the role of the oceans in the natural and anthropogenically forced greenhouse effect and global climate change. Coupling large-area satellite remotely sensed data of the marine environment with oceanographic measurements of process rates can provide data to model and predict the effects of pelagic primary production on the global biosphere and the responses of oceanic ecosystems to climate change.

Recently, new ocean colour sensors (MOS and OCTS, 1996; SeaWiFS, 1997; MODIS, 1999 and MERIS, due 2001) have provided far superior performance to CZCS: better spectral and radiometric resolution, potentially stable calibration, more spectral bands providing higher precision atmospheric correction and better interpretation algorithms, and daily operational capability. With this performance, there needs to be a consequential improvement of precise quantitative interpretation of colour data, in terms of primary production and bio-diversity. In terms of the determination of secondary production ocean colour can provide information on community and water mass type, and give methods of analysis that are neither site nor season specific, but can provide information on integrated production.

The measurements taken this cruise were planned to validate a new generation of bio-optical models that use analytical rather than empirical approaches. Water reflectance (ocean colour) relates directly to the backscatter from particles (biogenic and inorganic) and inversely to the absorption by particles and dissolved compounds, and so the primary interpretation of ocean colour data should be in terms of backscatter and absorption. Subsequently these can be related directly to the water constituents, and provide accurate data on the biological variables, which are needed to assess water quality and ocean productivity. With the exception of backscatter

measurements, the measurements taken on this cruise will be used to parameterise and validate a bio-optical radiative transfer and inverse model.

Optical measurements of upwelling radiance and downwelling irradiance were taken with sensors attached to a cross bar optical profiler deployed 7 m clear of the aft starboard quarter (Fig. 5.3). This distance is sufficient to avoid ship shadow in more turbid (high chlorophyll waters). Downwelling surface irradiance was measured from a sensor on the ship main mast free of any shadow. The rig was fitted with a tilt and roll sensor to ensure that the measurements were taken within the recommended limits for the SeaWiFS protocols (Mueller and Austin 1995). The sensors were positioned so that there was no shading of the radiance sensor, and that the shading of the irradiance sensor was only by the bridle (5mm steel wire) and by the cable (9 mm steel wire).

The sensors were Satlantic 7 band sensors, with the first six bands chosen to match the SeaWiFS satellite sensor (412 nm, 443 nm, 490 nm, 510 nm, 555 nm & 665 nm), the seventh band was at 620nm corresponding to band 6 of the ESA MERIS sensor on ENVISAT. The sensors were calibrated at PML prior to the M48/5 cruise with a lamp traceable to NIST through the SIRREX intercalibration experiment. The sensors will be calibrated post cruise to correct for any instrumental drift. In addition to the optical sensors the rig was fitted with a CTD, conventional saturating flash fluorometer, transmissometer, and a fast repetition rate fluorometer (FRRF) with integral PAR sensor (Kolber and Falkowski 1993). The FRRF can measure the rate parameters of photosystem II, and can be used to derive instantaneous primary productivity of the water column. In addition to the profiled measurements, determinations of upwelling radiance were taken using the UOR, together with tilt and roll measurements. One of these tows was under clear sky conditions with concurrent SeaWiFS imagery.

In total there were 29 successful optical casts, of which seven were under clear sky conditions, the remainder were under diffuse cloud illumination. Although there were no on board determination of chlorophyll, it is estimated from the diffuse attenuation data that the chlorophyll values ranged from 0.1 to 10 mg.m⁻³, giving two orders of magnitude of variation for the testing and validation of models. The final analysis and development of models from these data require integration of the full sensor data suite and the analysis of the samples from HPLC pigments, gelbstoff and particle absorption.

In terms of the quality and range of data obtained this has been a highly successful cruise.

5.4.3.2 Phytoplankton Pigments and Absorption

Pigments in phytoplankton serve a fundamental role in harvesting light for photosynthesis. Chlorophyll *a* (Chl *a*) is the major, ubiquitous pigment, but it is rarely more than 50% of the total pigment in most marine ecosystems. It absorbs light in the blue spectral region (400-470 nm), with a secondary narrow absorption peak at 670 nm, so it has a restricted influence on ocean colour spectra (400-700 nm). The other major phytoplankton pigments are the chlorophylls-*b*, -*c*, and the carotenoids, some of which are photosynthetic (PSCs) and others that have a photoprotective function (PPCs). The PPCs absorb excess high light in the surface layers of the ocean that may potentially be damaging to the photosynthetic apparatus in the cells and are therefore not directly involved in the photosynthetic process. All these pigments co-exist, co-vary and are highly correlated with Chl *a* (typically $R^2 = 0.85$ over many ecosystems). All absorb light across the blue-green spectral region (400-550 nm) overlapping with the Chl *a* absorption. This makes the interpretation of ocean colour spectra quite complicated. As an integral part of the bio-optical studies on the cruise, samples for pigment and absorption analysis were collected at various localities coinciding with optical profiling measurements.

Sea water was collected from various depths using a CTD rosette system on station and filtered through 25 mm GFF filters to harvest the phytoplankton. Filters were stored frozen in liquid nitrogen and transported to Cape Town for analysis.

Analysis for pigments will be conducted by high pressure liquid chromatography following the method of (Barlow et al. 1997). A range of chlorophyll and carotenoid pigments are separated and quantified using a 3 mm Hypersil MOS2 C8 column in a Thermo Separations HPLC system. Pigments are detected by absorbance at 440 nm and identified by retention time and on-line diode array spectroscopy. Chlorophyll *a* standard is obtained from Sigma chemical Co. and the other standards from the DHI Institute for Water and Environment, Denmark.

Light absorption by phytoplankton will be determined on thawed GFF filters by the method of (Tasser and Ferrari 1995). Absorption is measured relative to a blank filter saturated with seawater in a dual-beam Shimadzu scanning spectrophotometer equipped with an integrating sphere. Correction for absorption by the detrital component is then measured after extraction of the pigments with sodium hypochloride.

Absorption by dissolved organic compounds between 350 and 500 nm was measured on selected samples using a Shimadzu spectrophotometer on board the Meteor.

No results are presently available since analysis has to be completed at the Marine & Coastal Management laboratories in Cape Town. Some 15 chlorophyll and carotenoid pigments will be

quantified and characterised as photosynthetic or photoprotective pigments. Pigment absorption properties will be determined using a reconstruction technique and compared with the phytoplankton community absorption to determine the contribution of each pigment group to photosynthetic absorption.

5.4.3.3. Remote Sensing

Remote sensing images of sea surface temperature (SST) and ocean colour (SeaWiFS) were relayed to the Meteor each day during the cruise. SST images were provided by OceanSpace CC, Cape Town, while arrangements were made with NASA, USA, for SeaWiFS images. It was intended to use the temperature and chlorophyll features displayed in the images to assist in planning the location of the offshore transect lines for the biological and optical work. Unfortunately, there was extensive cloud cover during most of the cruise in the sector to the north of Walvis Bay and so the images were not useful here. However, clear, sunny weather was encountered for a few days to the south of Walvis Bay and the SST and SeaWiFS images were then useful in planning the 25°S transect line. SST and SeaWiFS images for 26 October are provided to show the detailed features of the changes in temperature and chlorophyll at the surface from the coast to 12°E longitude.

5.4.3.4 Fluorometric Chlorophyll *a*

A range of phytoplankton samples were collected at stations on the offshore transects for the analysis of chlorophyll *a* by fluorometry. This chlorophyll data is useful for the Namibian Ministry of Fisheries to assess the distribution and abundance of phytoplankton between 19°S and 25°S. Sea water was collected from various depths using a CTD rosette system on station and the phytoplankton harvested by filtration onto GFF filters and stored frozen in liquid nitrogen or a –80°C freezer for later analysis at the NATMIRC laboratory in Swakopmund. Filters will be extracted in acetone at –20°C for 24 hours and the fluorescence determined using a Turner Designs 10-AU fluorometer following the modified Welschmeyer procedure. Chlorophyll *a* concentrations will be estimated from the fluorescence data and appropriate chlorophyll calibrations. Chlorophyll *a* standard is purchased from Sigma Chemical Co. and a stock standard solution is made up in 100 % acetone. Appropriate standards over a range of concentrations are then prepared in 90 % acetone for calibration of the fluorometer. No results are presently available, but it is anticipated that high chlorophyll levels will be determined for the inshore localities with a progressive decline in concentration to the offshore stations.

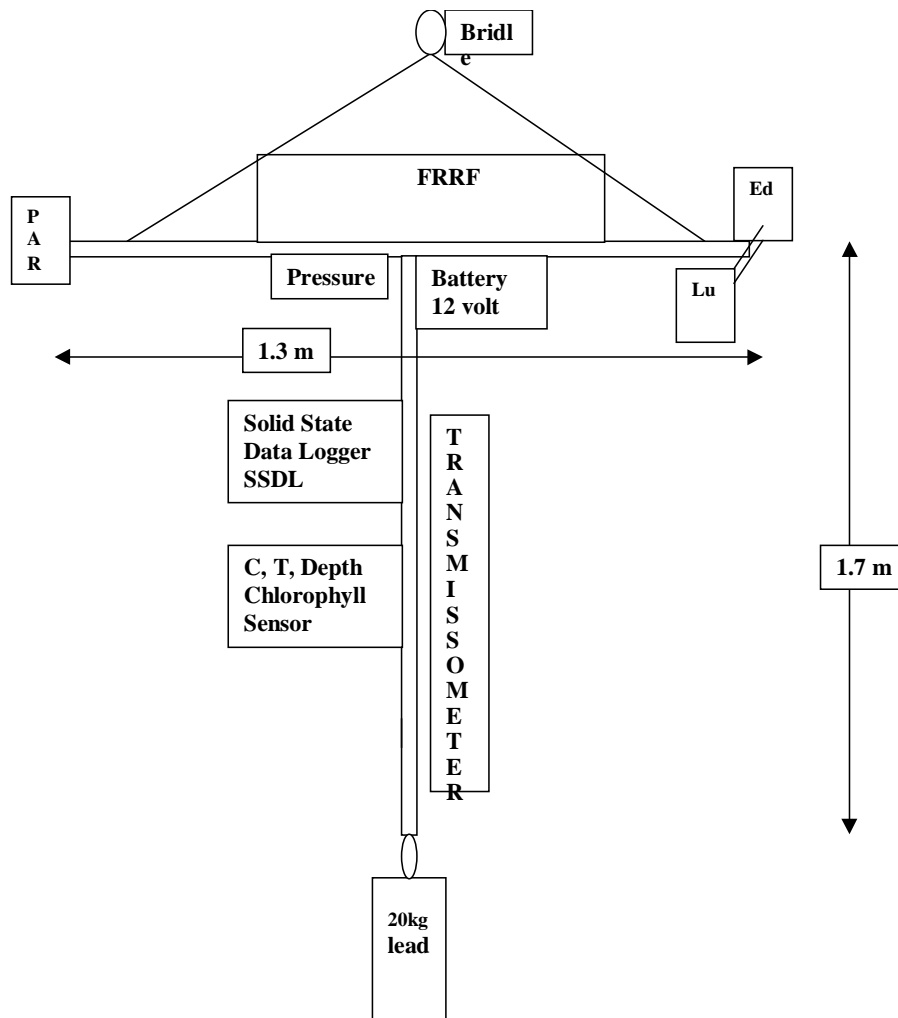


Fig. 5.3: Schematic diagram of optic rig.

5.4.4 Phytoplankton

(Malte Elbrächter, Michael Schweikert)

Phytoplankton species are the main food for copepods and other zooplankton species which in turn are used as food by fish larvae. Therefore phytoplankton is a key component for understanding the dynamic processes in the food web of the upwelling region. As phytoplankton species have a mean reproduction period of 1 to 4 divisions per day they can react very quickly on changes in the environment and make them an ideal indicator of upwelling conditions, where environmental factors as temperature and nutrient supply may change in short time and space intervals. So far the phytoplankton species composition in Namibian waters is not well known. The samples will be used to determine phytoplankton species assemblages which can be used as indicator for upwelling regimes.

The main focus during the present study on board the ship were the taxonomy and nutritional strategies of dinoflagellates. Dinoflagellates are on the borderline between phytoplankton and zooplankton. Many of them are phototroph, having chloroplasts which fluoresce brightly if viewed with an epifluorescence microscope. Others are obligate heterotrophic, feeding on other organisms, mainly diatoms and a small percentage are parasites of diatoms, copepod eggs or even fish eggs. During this cruise we wanted to test the hypothesis we postulated during SONNE cruise 113, that heterotrophic species are dominant in diatom rich (upwelled) waters, whereas in diatom poor waters phototrophic species dominate. In very oligotrophic waters species with an obligate endosymbiosis between heterotrophic dinoflagellates with phototrophic cyanobacteria are expected. To prove this, species believed to have such an endosymbiosis were prepared for later studies with the Transmission Electron Microscope (TEM).

During leg M 48-5 phytoplankton was collected at 88 stations with the micronet (20 m to surface tows). In a subsample the species were analysed immediately alive under the microscope with water immersion lenses with an up to 400x magnification, the other part of the sample was fixed with formaldehyde for later analysis at home. At 75 stations 328 water samples from several depth were fixed for later quantitative analysis. In addition at 66 stations 175 water samples were filtered on membrane filters of 0.45 µm pore size in order to analyse the species composition of the coccolithophorids with the Scanning Electron Microscope at home. In addition, 103 single cells isolated from the living samples have been prepared and embedded for later studies with the TEM.

Preliminary results show, that diatom abundance increases from offshore to inshore waters. At several stations, large diatoms *Coscinodiscus wailesii* (mainly north of Walvisbay) and *C. gigas* (mainly south of Walvis Bay) showed high cell numbers in water layers of 50 or even 150 m whereas at the surface these diatoms were missing. At each station a preliminary species list was established with the dominant organisms in the net samples which was provided to the other working groups.

More or less on all stations potential toxic algae were found known to produce paralytic shellfish poisoning (PSP), diarrhetic shellfish poisoning (DSP) or amnesic shellfish poisoning (ASP). They belong to the dinoflagellate genera *Alexandrium* (PSP), *Dinophysis* (DSP) and the diatom genus *Pseudo-nitzschia* (ASP). From several stations special phytoplankton samples have been taken in order to make toxin analysis at the University of Jena in Germany.

The dinoflagellate species were characterised as phototrophic or heterotrophic-parasitic. Some of the species show a brilliant fluorescence of phycobilins, a pigment characteristic for cyanobacteria and cryptophytes. These species are conspicuous for having either fed on cryptophytes or cyanobacteria or they may have a permanent endosymbiosis. This has been established earlier for some species of the genus *Dinophysis*. During the present cruise, we found

a new candidate, the rarely observed *Achradina pulchra* which has been embedded for later TEM studies.

Some heterotrophic dinoflagellates show a brilliant autofluorescence, either green or blue if analysed with the epifluorescence microscope. These stable characters of the different species are also listed in the species list, if available. The species list of the dinoflagellates has to be revised in respect to nomenclature and will be after correction the most extensive species list for dinoflagellates of Namibian waters.

Although the micronet is far from being suited for studies on picoplankton, the samples showed marked differences in the presence of cyanobacteria of about 1 μm in diameter. In offshore stations poor in diatoms and rich in zooplankton many of these brilliant orange fluorescent organisms were seen. It was obvious, that many of these cyanobacteria were abundant in the gut of copepods. Fecal pellets of zooplankton contained quite high number of these cyanobacteria, apparently not effected by the gut passage. It is speculated that the cyanobacteria perform photosynthesis in the fecal pellet, thus enhancing their food value for coprophagic zooplankton. A sample of about 1000 fecal pellets picked out of a sample was filtered and the pigment content and composition will be analysed by the colleagues of South Africa, working-group biooptics.

5.4.5 Zooplankton and Fish Larvae

5.4.5.1 Collections with the Multinetz

(Rudi Cloete, Frank Hansen, Ekkehard Klingelhoefter, Ulrike Schütz)

In order to study the vertical distribution and abundance of mesozooplankton, vertical plankton tows were carried out using the Multiple-Closing-Net (Multischliessnetz, MSN) manufactured by HYDROBIOS, Kiel, Germany. The MSN has a net opening area of 0.25 m² and was equipped with 5 nets of 200 μm mesh-size and with a depth sensor. In addition to the online electronic flowmeter in the opening area of the MSN, mechanical flowmeters were placed in each of the nets to measure the filtered volumes. If water depth was permitting, samples were collected from 5 different depth ranges: 0-25 m, 25-50 m, 50-100 m, 100-150 m and 150-200 meters. At stations shallower than 200 m, sampling started at about 10 meters above the bottom. The MSN was run with the W3 winch, winch speeds were 0.7 m/s down and 0.5 m/s up. The collected plankton was preserved in buffered freshwater-formalin (in order to keep the osmotic pressure) of 4% final concentration. Prior to fixation, large jellyfish were removed from the sample and their presence was noted in the protocols. Between 15. and 29. October, 197 samples were taken with the MSN. Main sampling was done at 59 stations on the 5 transects at approximately 19° S, 20° S, 22° S, 23° S and 25° S latitude. In addition, samples were taken at 11 stations situated between the transects. In order to get a brief, semi-quantitative overview of the samples during the cruise, the samples were characterized by noting the estimated volume of the plankton,

discolouration of the sample, the amount of diatoms and the presence of larger copepods and makrozooplankton taxa as it could be seen with the naked eye.

The samples of the 19 degrees South transect are characterized by small plankton volumes with small jellyfish at the offshore stations and progressively larger volumes with more diatoms at the inshore stations. Notably, maximum volumes were found in a depth range from 50 to 100 meters. The samples of the 20 degrees South transect showed the same offshore-inshore trends, with even higher volumes of diatoms inshore, also in the upper 50 m layer. At offshore stations, numerous veliger larvae were present, whereas some larger jellyfish medusae occurred inshore. The 22 degrees South transect samples differ from the previous two in containing more gelatinous plankton. At offshore stations, many salps occurred, but at midshore stations numerous small jellies occurred and inshore, large jellyfish medusae were found. The 23 degrees South transect samples exhibit little plankton volumes offshore. Compared with the former three transects, more mesozooplankton, mainly copepods were found at the midshore and inshore stations. At the inshore stations, some nets were clogged by large jellyfish medusae. A large amount of diatoms only occurred at the most inshore station in the upper 25 m layer. The transect at 25 degrees South was longer than all previous transects and extended up to 160 nautical miles offshore. The samples taken most offshore contained small plankton volumes with mainly copepods, chaetognaths and euphausiids. Occasionally, salps and veliger-larvae from gastropods were found. At midshore stations, plankton volumes were higher and contained also small jellyfish, comb-jellies and fish larvae. The inshore stations were characterized by large plankton volumes, containing mainly diatoms, copepods and large jellyfish medusae.

5.4.5.2 Collections with the BIOMOC

(Rabea Dieckmann, Dirk Jarosch, Gerd Kraus, Christian Möllmann)

The aim of this part of the study was to quantitatively describe the spatial distribution of ichthyo- and zooplankton by vertically stratified sampling along transects perpendicular to the coast. Thereby we followed a gradient along upwelling intensity and intended to investigate the fate of the upwelled water and resulting primary production and its effects on secondary and fish production. By following this approach we confronted different abiotic and biotic environments (nutrient rich and productive upwelling water vs. nutrient poor oceanic water.) and their varying effects on ichthyo- and zooplankton populations.

The Biomoc is a modified MOCNESS (Multiple Opening Closing Environmental Sensing System) analogous to the BIONESS with a 1 m² wide opening rack. Via an electronic control panel on board nine different nets (mesh size 335 mm) can successively be used. Additionally 50 mm liners to sample microzooplankton with an opening size of 40 mm are applied in the centre

of each net. The BIOMOC collects samples from distinct water depths and measures concurrently hydrographic data and the filtered volume of water. The gear is towed with a ship cruising speed of 3 knots and the maximum hauling speed was 0.5 m/s.

Samples were taken at selected stations along transects perpendicular to the coast and in total 35 hauls were conducted. The gear is lowered to 200 m (on selected stations close to shelf edge to 350 m) and afterwards the following depth horizons were covered: 200-175 m, 175-150 m, 150-125 m, 125-100 m, 100-75 m, 75-50 m, 50-25 m, 25-0 m. Trawling time per 25 m depth range varied between 2 and 6 min. Samples were preserved in 4% buffered formalin/freshwater solution.

335 mm samples were roughly inspected by eye. Biovolumes as an rough index of biomass and proportions of phytoplankton, euphausiids as well as other zooplankton were estimated and related to the filtered volume.

As a first step biovolumes of the samples divided by estimated proportions of phytoplankton (mainly *Coscinodiscus*, Diatomeae), euphausiids and other zooplankton organisms have been analysed on board. Jellyfish of the phylum Cnidaria were not preserved and thus, not considered in the biovolume estimations; other gelatinous plankton was included in the zooplankton fraction.

Transect 1: Depth on stations of the 1st transect ranged between 664 m and 209 m. All 3 major groups were regularly observed in the samples (Figure 5.4). Maximum biovolumes of phytoplankton (*Coscinodiscus*) were found on stations 494/37 and 496/35. Euphausiids constituted in almost all samples the largest proportion of the biovolume and had a tendency to a shallower distribution at daylight (e.g station 498/33) compared to the nighttime (e.g station 495/36). No clear trends were obvious for the mixed zooplankton-group.

Transect 2: Water depth of the second transect ranged between 89 m and 1077 m. Phytoplankton (*Coscinodiscus*) was only observed on the two near coast stations (89 m and 137 m water depth) with the highest displacement volume on the shallowest station (Figure 5.5). Sample composition of the other four stations covered mainly consisted of zooplankton with relatively low abundances of euphausiids. No clear trends in the depth distribution of euphausiids and other zooplankton could be observed.

Transect 3: The third transect covered a depth range from 90 m to 1314 m (Figure 5.6). Phytoplankton was only observed on stations 534/73 displaying very low biovolumes. In contrast to transects 1 and 2 station 535/72 showed despite phyto- and zooplankton a low abundance of radiolarians (included in the phytoplankton column of Figure 5.6). A considerable proportion of euphausiids within the zooplankton was only found on station 534/73. On the average biovolumes were highest in the upper water layers.

Station 545/94: One biomoc haul was done apart from the transects, in shallow water (50 m depth) near to Cape Cross (graph not shown). 10 m depth strata were sampled to in maximum 40

m. Very high displacement volumes were measured, especially in the near bottom layers (more than 2800 units). No euphausiids and hardly any phytoplankton were found.

Transect 4: Six Biomoc stations were performed on this transect covering a depth range from 919 m to 98 m (Figure 5.7). Biovolumes were not estimated on station 560/87 because nets were clogged with jellyfish of the genera *Aequorea* and *Chrysaora*. Displacement volumes were low in the oceanic stations, but reached high values at the station near the shore (St. 563/84). The abundance of euphausiids on this station was the highest observed in all samples. Phytoplankton, i.e. *Coscinodiscus*, did not appear in remarkable quantities on the whole transect.

Transect 5: Stations on transect 5 covered a depth range between 71.8 and 3684 m (Figure 5.8). Phytoplankton was only found on station 578/110 in deeper depth strata. Regularly zooplankton constituted the main fraction of the samples, whereas euphausiids were especially found in the middle of the transect.

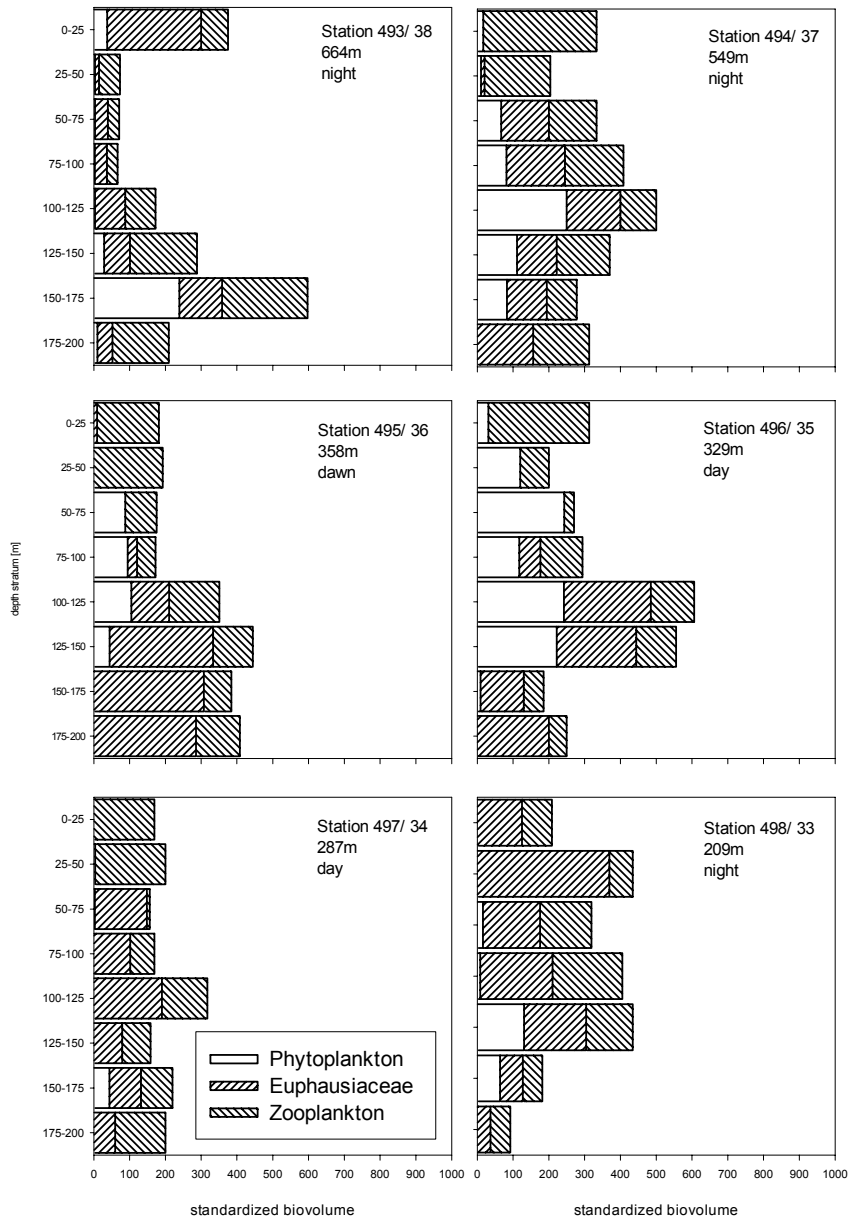


Fig. 5.4: Rough taxonomic composition and vertical distribution of plankton at stations of transect 1.

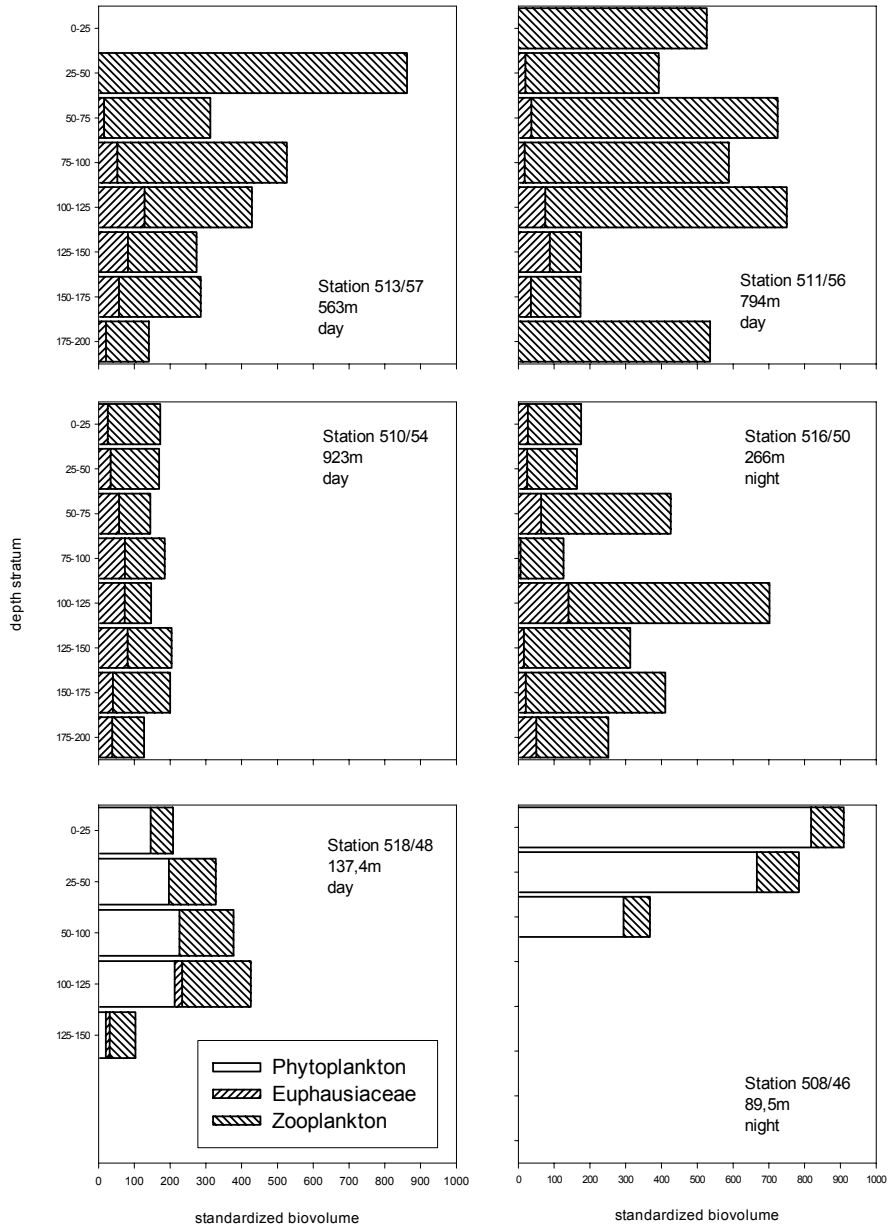


Fig. 5.5: Rough taxonomic composition and vertical distribution of plankton at stations of transect 2

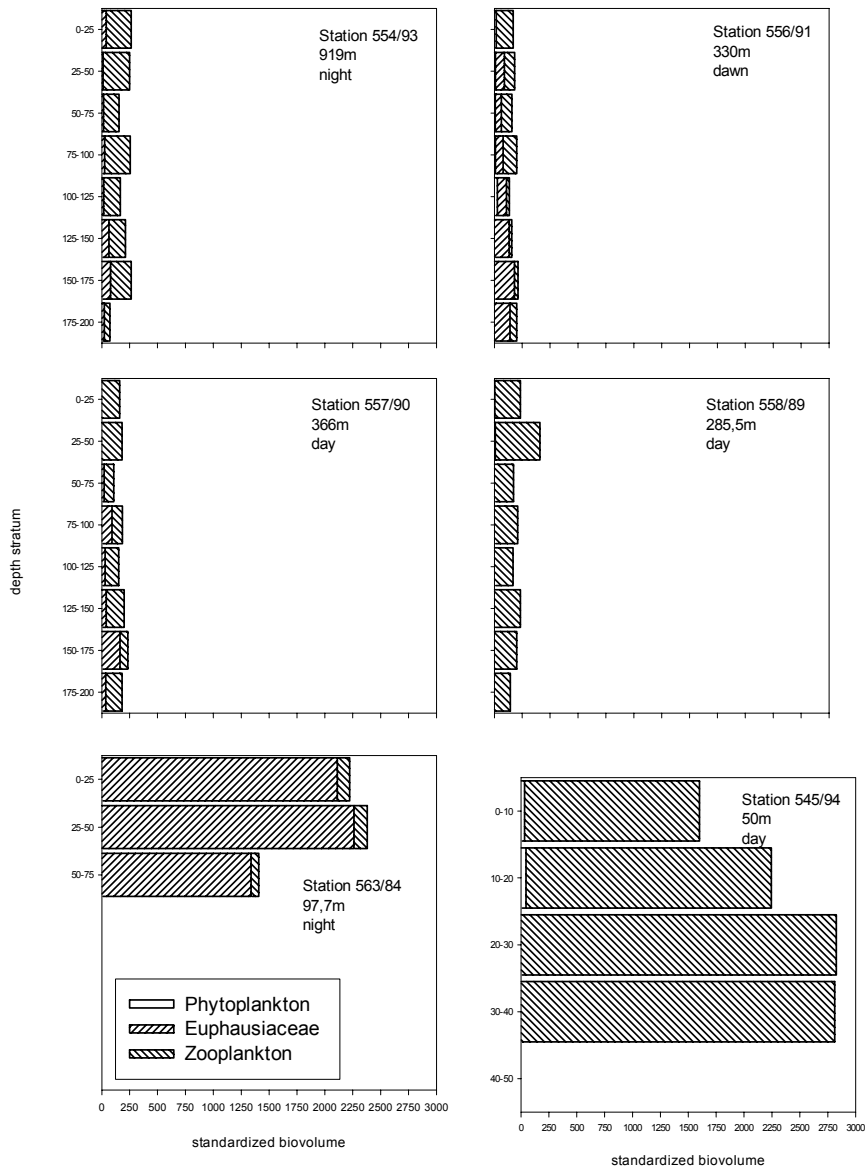


Fig. 5.6: Rough taxonomic composition and vertical distribution of plankton at stations of transect 3.

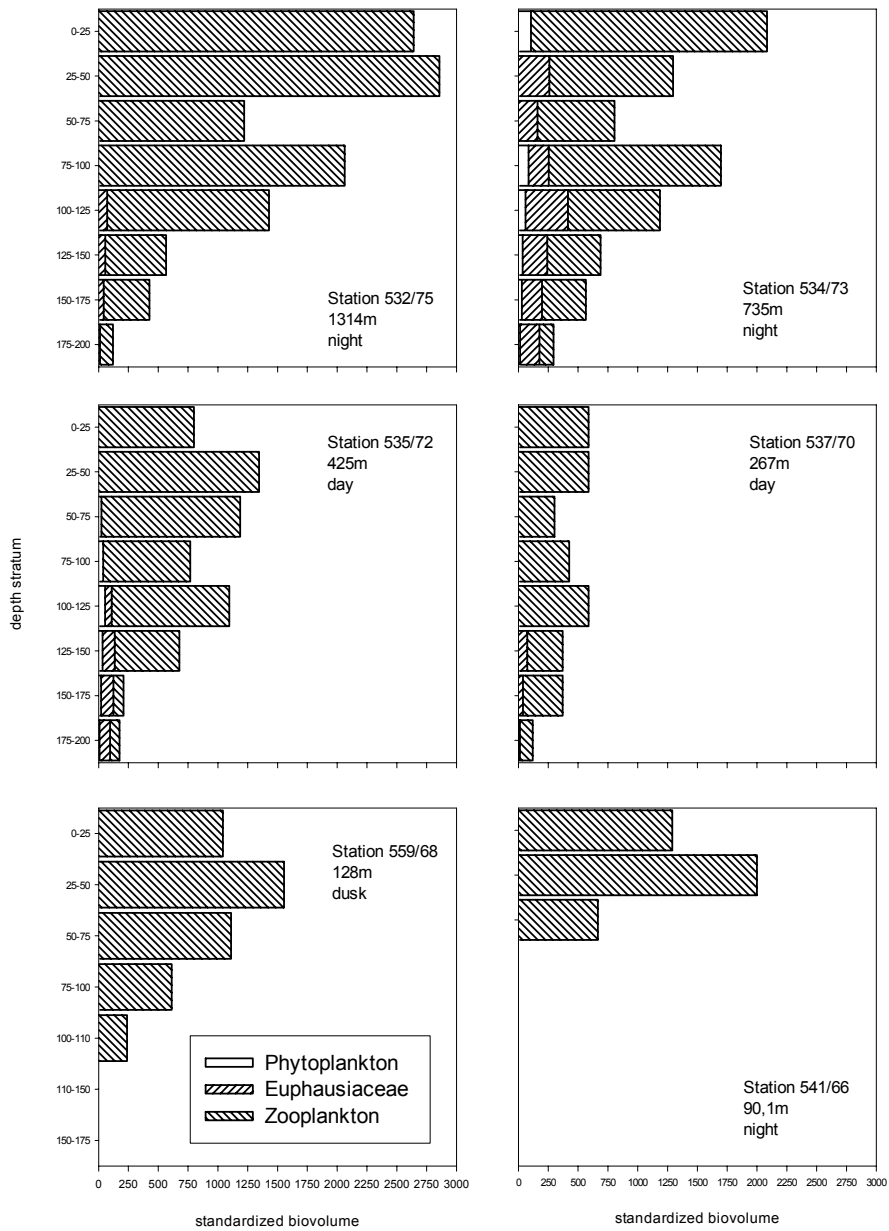


Fig. 5.7: Rough taxonomic composition and vertical distribution of plankton at stations of transect 4.

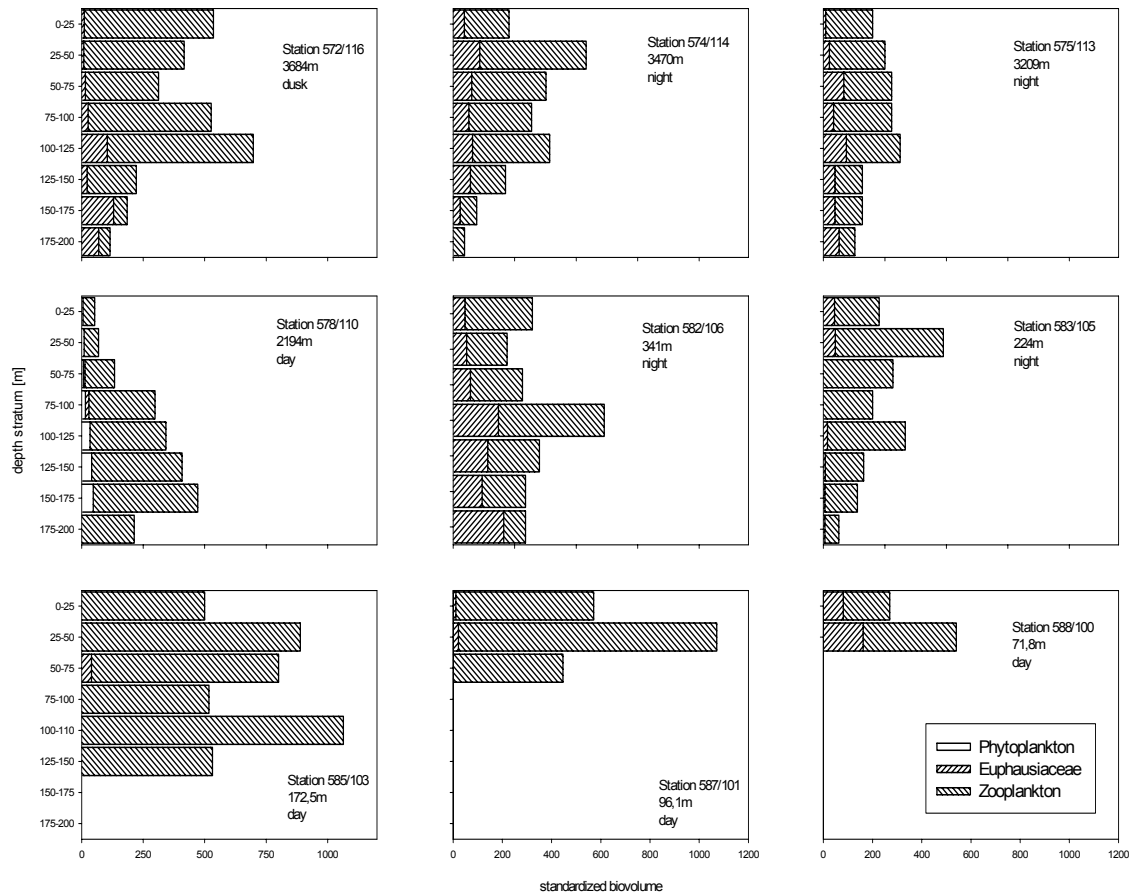


Fig. 5.8: Rough taxonomic composition and vertical distribution of plankton at stations of transect 5.

5.4.5.3 Collections with the Longhurst-Hardy-Plankton-Recorder (LHPR)

(Steve Coombs, Tembaletu Tanci)

Vertical distribution plankton sampling was carried out using the LHPR (Longhurst-Hardy Plankton Recorder) to take a series of fine (53 μm) and coarse (200 μm) net plankton samples on each haul (Table LH1). Real-time data on the depth at which the samples were taken together with temperature and salinity profiles were relayed via cored towing cable for onboard PC display. The volume of water filtered per sample was adjusted according to ambient plankton concentration by changes to the sampling interval (1 and 2 minute intervals), tow speed (2-4.5 knots) and nose cone inlet diameter (35 and 20.5 cm diameter for the coarse mesh net, and 30, 50 and 70 mm diameter for the fine). An Example of the LHPR-display during a haul is given in Fig. 5.9.

A total of 20 hauls were taken over the survey area (Table LH1) providing 666 samples at a depth resolution of around 5-15 m. No faults were encountered with the LHPR system function. Some problems were experienced on Transects 1 and 2 with overloading of samples with *Coscinodiscus* and other phytoplankton and also on Transect 2 with salps and coelenterates. Preservation of the samples was in 4% fresh water formalin for subsequent analysis.

Five hauls were taken at alternate stations along Transect 1. The samples became progressively more heavily loaded with phytoplankton (*Coscinodiscus*) at station positions towards the coast; at stations 36 and 32 the coarse mesh samples were discarded since it was not possible to distinguish individual samples due to the overwhelming quantities of *Coscinodiscus*. All hauls provided valid fine mesh samples. Zooplankton abundance was consistently low.

Three hauls were taken along Transect 2, the LHPR stations being selected as representative of deep oceanic, shelf-edge and shelf regimes. Heavy loading of *Coscinodiscus* was a problem at the inshore shelf station only. All samples, both fine and coarse provided valid samples. Zooplankton abundance was consistently low.

Along Transect 3, sampling was designed to give higher resolution discrimination in the upper 125 m of the water column where the most intensive changes in biological and physical structure were observed on the preliminary Undulator run along the transect. Four hauls were taken along this transect, all of which provided valid fine and coarse mesh samples. Fairly heavy presence of salps at the oceanic stations and of coelenterates at the more inshore stations invalidated some samples.

Sampling along the Walvis Bay transect (Transect 4) was reduced to three station positions because of the high concentrations of coelenterates at the more inshore stations (noted in the other plankton sampling), although the single inshore station sampled (station 86) was conducted with negligible coelenterate contamination, a coarse mesh protective net being fitted between the nose cone and the coarse mesh filtering net for this and all subsequent hauls. Valid fine and coarse samples were taken on all hauls. Sardine eggs were noted in the coarse mesh samples at station 91 and hake larvae at station 89. At this latter station, sampling was to within 2 m of the bottom to check for near bottom occurrence of hake eggs (a single hake egg was found in a 0-100 m WP2 net haul at the same station).

Along the final transect (Transect 5), 5 station positions were sampled, two in deep water, one over the shelf slope and two at more inshore positions. Essentially valid samples were taken on all of these hauls. Appreciable numbers of myctophid larvae were taken at the outer two stations; high concentrations of plankton were encountered at the inner two stations (103 and 101).

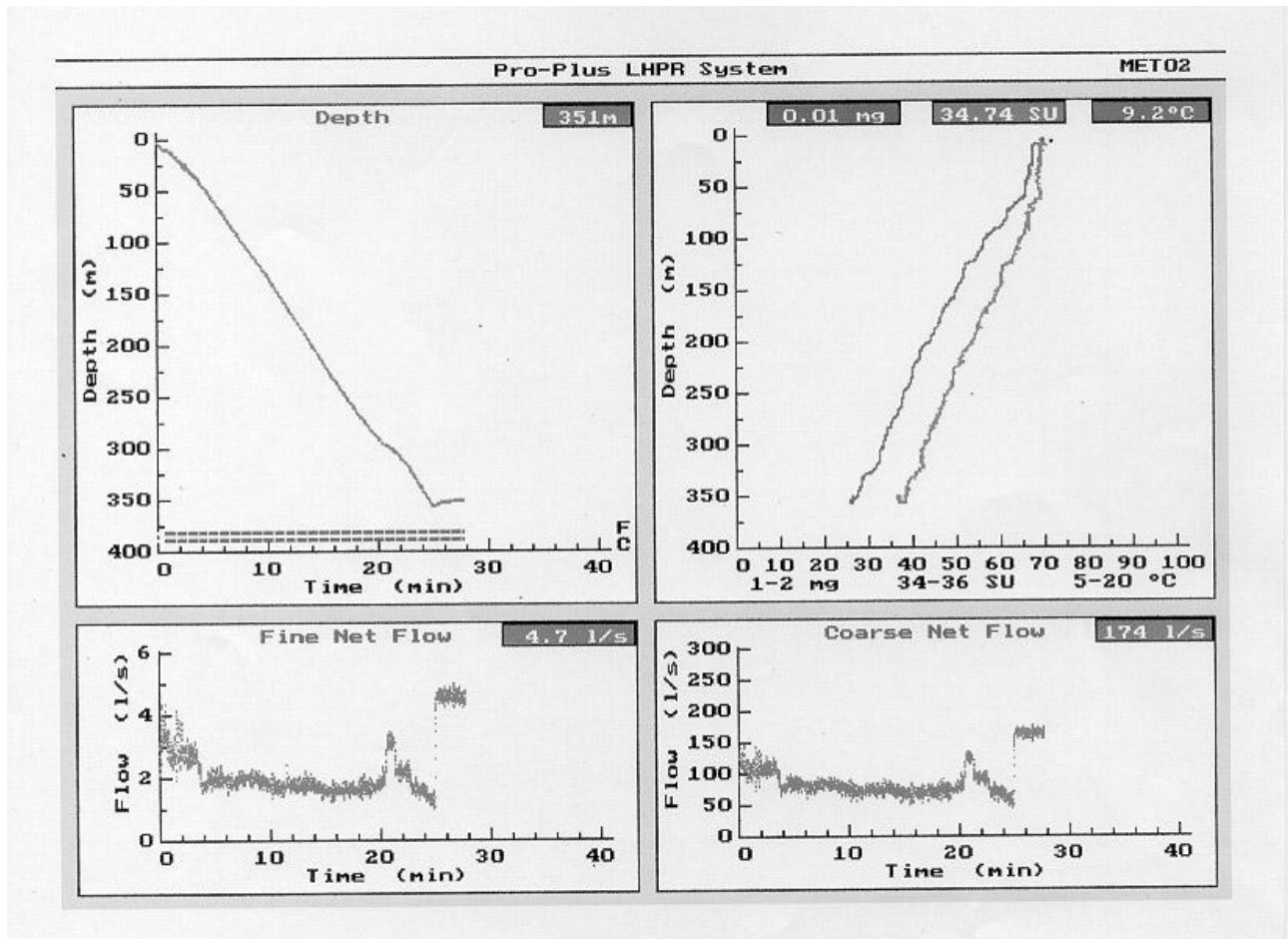


Fig. 5.9: Example of LHPR-display during a haul.

5.4.5.4 Zooplankton Secondary Production

(Xabier Irigoien, Hans Verheye)

In contrast to primary production, which has been measured in aquatic systems for several decades, the measurement of productivity by zooplankton, especially in marine environments, is a comparatively new field of research. It has been argued that the only way to measure zooplankton production accurately is by estimation of species-specific growth rates. Field-based research on the growth rate of copepods has focussed on female egg production, rather than juvenile growth, because of its ease of measurement using bottle incubations.

Identifying factors that control growth of copepods is essential to understand nutrient and carbon fluxes in the marine environment. There has been considerable debate in the literature about the relative importance of the two main factors that control copepod growth, viz. temperature and food. On the one hand, copepods grow at maximum rates in the sea, with an exponential increase in growth rate with temperature over a wide range of habitats (Huntley & Lopez 1992). On the other hand, copepod growth has been found to be more related to food (in

terms of both quantity and quality, i.e. nutritional value and particle size of the phytoplankton) rather than temperature, and in the southern Benguela region, the lack of dependence of growth on temperature was attributed to slower growth at warm (18-22°C) temperatures (Richardson & Verheye 1998), a consequence of very low (usually $<2 \text{ mg Chl.m}^{-3}$) food concentrations at these temperatures. Moreover, it has been suggested that food may also be limited in a body-size dependent way, with larger individuals being more food limited (Hist & Sheader 1997, Richardson & Verheye 1999, Richardson *et al.* 2001).

Recent laboratory experiments have shown that diatoms have a deleterious effect on the hatching success of copepod eggs (Ban *et al.* 1997). This effect has been attributed to the toxicity of some amino compounds produced by diatoms (Miralto *et al.* 1999) but controversy remains on whether diatoms are really toxic or just nutritionally insufficient (Jonasdottir *et al.* 1998). The suggested toxic effect being concentration dependent, the distinction between toxicity or insufficiency is extremely important in upwelling areas where the diatoms can reach very high biomasses. If diatoms were nutritionally insufficient, alternative food sources such as microzooplankton can provide the necessary basic compounds (aminoacids or lipids) for copepods. However, if diatoms were toxic, our basic understanding of the trophic energy flow in upwelling systems, viz. diatom \rightarrow copepod \rightarrow fish, is flawed and a new interpretation of the productivity transfer from diatoms to fish will be required.

The objectives of this project, as part of the zooplankton studies conducted during RV *Meteor* cruise M48-5 in the northern Benguela region (13-31 October 2000), are twofold:

1. to estimate daily egg production and moulting rates of a number of common copepod species (over an as wide as possible range of body size) in contrasting areas of thermal (inshore *vs* offshore) and food conditions (e.g. low *vs* high Chl *a*, small-cell (dinoflagellates) *vs* large-cell (diatoms) dominated assemblages), and
2. to assess the hatching success of copepod eggs produced under contrasting feeding conditions (diatom-dominated *vs* non-diatom food assemblages).

Copepod production

Daily production (P ; grams per m^2 per day) of copepods is the product of copepod biomass (B , grams per m^2 ; to be obtained from various zooplankton samplers such as the MultiNet) and daily growth rate (g , per day; obtained from incubation experiments on board):

$$P = B \times g$$

Daily growth rates of copepods were derived from daily rates of egg production of adult females (= reproductive growth) and daily moulting rates of juvenile stages (= somatic growth) estimated using simple, but laborious (!) bottle incubation techniques. Copepods were collected

using a 300- μm mesh drift net, fitted with a 2-litre plastic bottle as a cod-end and allowed to drift for 5 minutes at a depth usually between 5 and 10 m. Alternatively, a WP-2 net (500 μm), hauled at a very slow rate through the upper 100 m of the water column, was also used for collections of copepods from deeper water layers. Upon retrieval the sample was transferred into a bucket of ambient surface water. Copepods were gently removed from this bucket using a sieve and washed into a petri dish, and lively and undamaged specimens of dominant species were selected with a wide-mouthed dropper under a dissecting microscope.

For egg production experiments, usually 1-2 females per species were placed in a 1-litre bottle (usually 5 replicates per station) containing 80- μm filtered seawater from the surface and incubated in a plankton wheel (0.2 rpm) in a temperature-controlled room (14-16 °C) for 24 hours. After 24 hours, the contents of each incubation bottle were poured through a 37(or 50) μm mesh, the condition of the females checked and the eggs and hatched nauplii enumerated (N_e). Experiments with dead or moribund females were discarded from further analyses. Where eggs were spawned in sufficient numbers, they were re-incubated for subsequent assessment of their hatchability (see below). Daily egg production (E ; eggs per female per day) over the incubation time (T) was calculated as:

$$E = N_e \times 24/T$$

To enable direct comparison of female growth rates of different species, instantaneous weight-specific female growth rates (g_f , per day) were calculated, from published data of female body mass (W_f) and egg mass (W_e), and the number of eggs (E) spawned per female during the 24-hour incubation experiments as:

$$g_f = (E \times W_e)/W_f$$

For moulting rate experiments (mainly using the dominant copepod *Calanoides carinatus* – cf. ease of recognition of its juvenile stages amongst those of other species), at least 15 individuals of a particular stage i were incubated in a 2-litre bottle filled with 80- μm filtered ambient surface water. After 24 hours, the contents of the incubation bottle were preserved and the number of individuals that had moulted (N_{i+1}) and not moulted (N_i) to the next stage $i+1$ were counted. The moulting ratio (MR_i) of each juvenile stage i was calculated as:

$$MR_i = N_{i+1}/(N_i + N_{i+1})$$

Exoskeletons were also counted and experiments were excluded from analyses if the difference between the moulting ratio calculated from the exoskeletons and that from the animals themselves was >10%. The daily stage-specific growth rate (g_i ; per day) was calculated from the

moulting ratio using published average body masses. W_i and W_{i+1} of successive developmental stages. i and $i+1$ respectively, as:

$$g_i = \ln(W_{i+1}/W_i) \times MR_i \times 24/T$$

At each station, the concentration of Chl *a* in the surface water (but screened through a 80- μ m mesh), which was used for the incubations, was considered as a measure of ambient food availability for the copepods. Samples for future detailed taxonomic and quantitative analysis of the ambient phytoplankton assemblage were also collected from selected depths of the CTD Rosette cast.

Hatching success of copepod eggs

In addition to the eggs harvested from the above egg production incubation experiments, eggs were also obtained from 24-hour incubations containing 20-40 females of dominant species. These were placed in 1-litre beakers with a built-in 500- μ m screen which separates the females from their eggs produced, thus preventing possible egg cannibalism under high densities of female copepods.

All eggs thus harvested were then isolated in batches of up to 100 individuals and incubated in filtered seawater for a further 24- or 48-hour period. At the end of these experiments, unhatched eggs and nauplii were preserved. The proportion of the number of eggs hatched (i.e. nauplii) to that of the total number of eggs incubated is an index of the hatchability or hatching success of the eggs. This index will be determined during the post-cruise workshop held at NatMIRC in Swakopmund, Namibia.

In total, 281 incubation experiments were performed with 1 462 females of dominant copepod species including *Calanoides carinatus*, *Rhincalanus nasutus*, *Metridia lucens*, *Centropages brachiatus*, *Nannocalanus minor*, *Eucalanus elongatus/hyalinus*, *Pleuromamma robusta*, *Pleuromamma* sp., *Aetideus* sp., in addition to a few as yet unidentified species. These yielded a total of 12 247 eggs, most of which were subsequently incubated for 24-48 hours to establish hatching success (i.e. 107 hatching experiments in total)..

The results of onboard analyses of daily egg production thus far obtained indicate a clear inshore-offshore trend (Fig. 5.10), with increased rates near the coast, associated with dense blooms of diatoms (e.g. *Skeletonema*, *Chaetoceros*, *Coscinodiscus*), whereas rates were near-zero at the offshore extent of the transects, where dinoflagellates predominated.

Samples for the estimation of hatching rate of copepod eggs were analysed in the NatMIRC laboratory in Swakopmund. The results clearly show that hatching success varied between 80 and 100 % and was not affected by the diatom concentration (Fig. 5.11). Samples for taxonomic

composition of the ambient and experimental phytoplankton communities still need to be analysed.

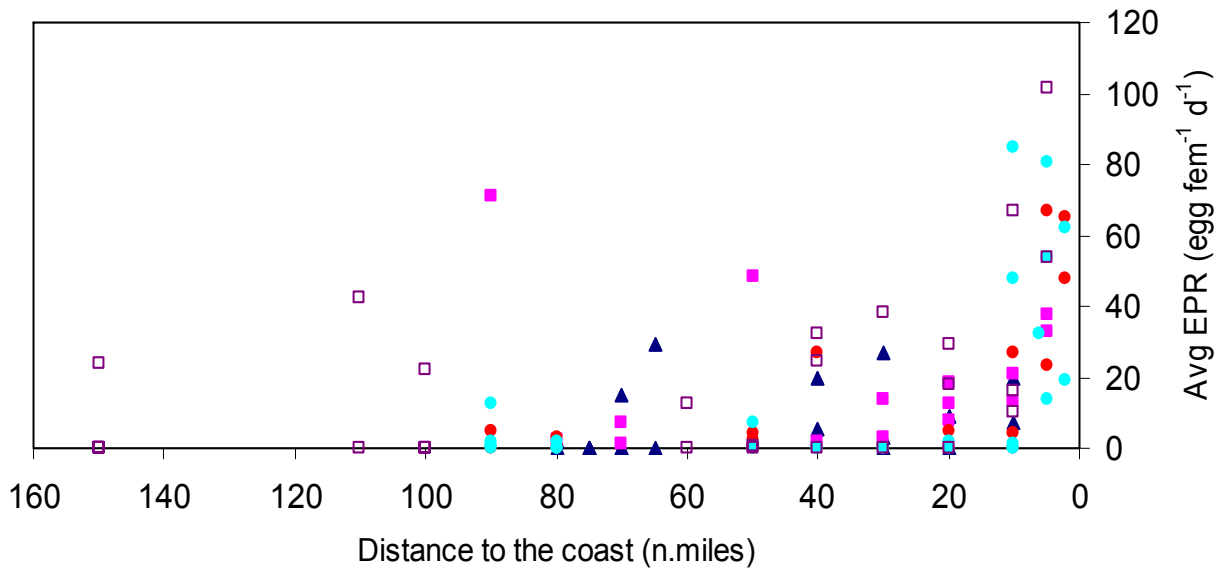


Fig. 5.10: Cross-shelf distribution of daily egg production determined from bottle incubation experiments (all species and 5 transects combined).

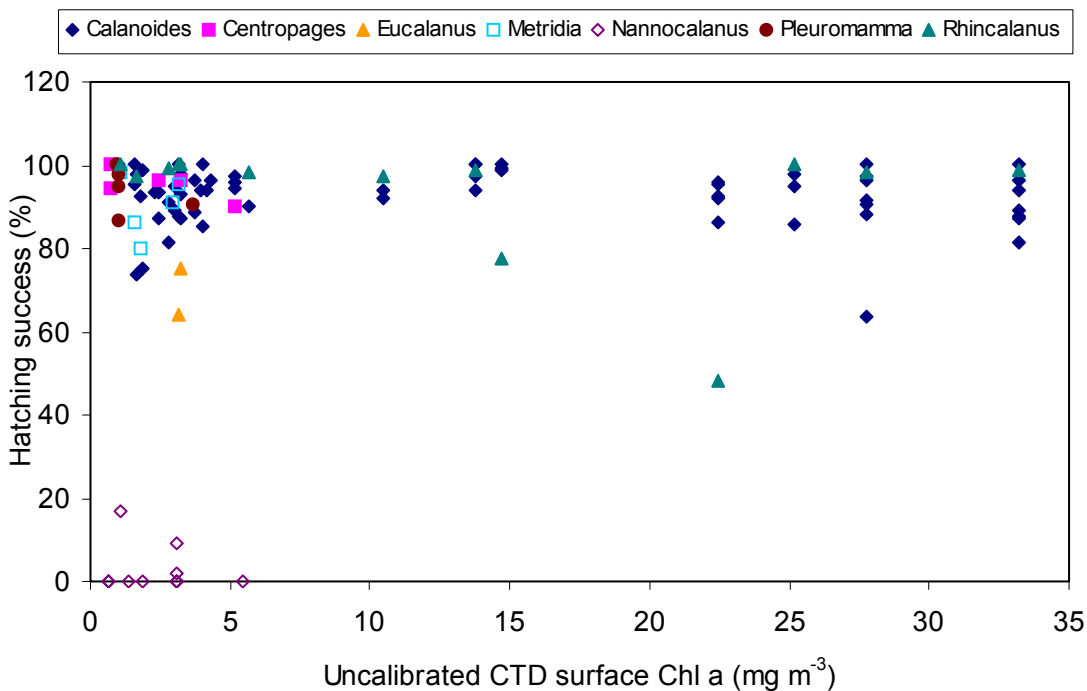


Fig. 5.11: Hatching success as a function of the uncalibrated surface Chl a (CTD fluorometer).

5.5 Ship's Meteorological Station

(Gerhard Kahl, Wolf-Thilo Ochsenhirt)

When METEOR began her Cruise on October 13th, 2000, there were light southerly winds when she left Walvis Bay. However, winds increased to 6 Bft in the afternoon, thus reaching normal Trade Wind force. The South Atlantic subtropical high of over 1030 was situated at about 32°S 15°W. The vessel headed north, reaching 19°S by October 16th. There, the most northerly transect was carried out. While on her way, the METEOR passed a coastal low that emerged and dissipated in about 36 hours and a line of convergence that extended from continental areas out into the ocean in a northwesterly direction. While those systems were passed, winds were light to moderate and variable. The Subtropical High had migrated to 32°S 10°E, weakening to 1025 while on its way. It was followed by a cold front extending from Antarctic waters to about 25°S 15°W on October 16th.

The next anticyclone to become a subtropical high had entered the synoptic chart already on October 14th, lying east of the La Plata with an intensity of 1030 on that day. Two days later, it was to be found near 28°S 25°W with a slight increase in intensity.

From then on, the METEOR made her way southward along the Namibian coast down to 25°S where the last transect was carried out, leaving only a few probing positions to be visited during the last few days of the cruise.

The anticyclone that represented the subtropical high up to October 16th moved into the Indik, thereby weakening temporarily, while the already mentioned high was strengthening to about 1038 at 30°S 15°W on October 18th. For the METEOR this meant that Southeast 6 Bft was observed again except when working adjacent to Namibia's shore line when the Trades were transformed to South 4 Bft.

The high weakened to still over 1030 and elongated south to reach from 30°S to 40°S along the Greenwich Meridian on October 20th while a coastal low very much like that mentioned above developed between Walvis Bay and Luederitz. Consequently METEOR experienced northwesterly winds of 4 Bft.

From the experience of the meteorological personnel at least during the cruises M48/2 to M48/5 it may be said that this coastal low develops every time the subtropical high is weak or is lying too far to the west so that the pressure gradient to the Kalahari static low, the continental heat low, is weak.

Coastal configuration seems to be responsible for the fact that the coastal low is developing always in the same area when conditions are favourable for its formation. This would fit to the fact that upwelling of water masses is observed constantly seaward of Luederitz and at times only seaward of Walvis Bay and for some distance to the north of it. When the coastal low is there, Walvis Bay reports winds from westerly directions thus impeding upwelling.

Trade winds were restored in METEOR's probing area on October 23/24th. The subtropical high had migrated southeastward to lie southwest of Cape Town, but a low developing in the area of Tristan Da Cunha indicated that the wedge stretching northwest from the high's position was strengthened, thereby being pushed eastward.

The coastal low once again was responsible for northerly winds of 4 Bft on October 25 while the next day Southeast 6 Bft was recorded at the research vessel's position. Once again the wedge of high pressure had been strengthened.

October 26th also saw the introduction of the last prominent feature of the synoptic chart we had to deal with during our cruise: a high of 1025 at 40°S 35°W that migrated northeast, then east, and swinging southeastern October 29th. Strength was up to 1041 so that the southeasterly trades were up to 7 Bft, but when Walvis Bay roads was reached on October 30th, the high was weakening, the occurrence of the coastal low was being anticipated, and northwesterly winds of 3 Bft were recorded. The ship berthed in Walvis Bay harbour on October 31th, 2000.

5.6 List of Stations

Station Label	Station Nr.	Date	Latitude	Longitude
0	484	13.10.2000	22°60.00'	13°60.00'
26	485	13.10.2000	22°59.88'	13°30.90'
27	486	14.10.2000	21°59.97'	13°10.42'
28	487	14.10.2000	21°00.04'	12°56.72'
29	488	14.10.2000	19°59.98'	12°20.00'
30	489	14.10.2000	18°59.80'	12°00.13'
31	490	15.10.2000	18°45.29'	12°12.42'
40	491	15.10.2000	19°43.56'	11°06.70'
39	492	15.10.2000	19°36.57'	11°14.49'
38	493	15.10.2000	-19°29.82'	11°22.21'
37	494	16.10.2000	-19°22.98'	11°29.93'
36	495	16.10.2000	-19°16.00'	11°37.58'
35	496	16.10.2000	-19°09.28'	11°45.35'
34	497	16.10.2000	-19°02.44'	11°52.98'
33	498	16.10.2000	-18°55.54'	12°00.80'
32	499	16.10.2000	-18°48.75'	12°08.56'
31	500	16.10.2000	-18°45.26'	12°12.38'
30	501	17.10.2000	-18°59.97'	12°00.91'
41	502	17.10.2000	-19°10.00'	12°06.61'
42	503	17.10.2000	-19°20.08'	12°10.95'
43	504	17.10.2000	-19°29.99'	12°14.23'
44	505	17.10.2000	-19°40.02'	12°16.43'
45	506	17.10.2000	-19°49.97'	12°18.75'
29	507	17.10.2000	-20°00.01'	12°23.41'
46	508	17.10.2000	-19°45.23'	12°50.33'
55	509	18.10.2000	-20°24.56'	11°28.43'
54	510	18.10.2000	-20°19.98'	11°37.88'

Station Label	Station Nr.	Date	Latitude	Longitude
56	511	18.10.2000	-20°17.71'	11°43.14'
53	512	18.10.2000	-20°15.43'	11°47.48'
57	513	18.10.2000	-20°12.57'	11°54.05'
52	514	18.10.2000	-20°10.89'	11°57.00'
51	515	18.10.2000	-20°06.38'	12°06.62'
50	516	19.10.2000	-20°01.73'	12°16.20'
49	517	19.10.2000	-19°57.15'	12°25.56'
48	518	19.10.2000	-19°52.61'	12°35.03'
47	519	19.10.2000	-19°48.06'	12°44.49'
46	520	19.10.2000	-19°45.18'	12°50.28'
29	521	19.10.2000	-19°59.95'	12°23.73'
58	522	19.10.2000	-20°10.00'	12°30.42'
59	523	19.10.2000	-20°19.96'	12°35.74'
60	524	19.10.2000	-20°30.03'	12°42.93'
61	525	19.10.2000	-20°40.01'	12°48.32'
62	526	20.10.2000	-20°50.04'	12°52.64'
28	527	20.10.2000	-21°00.02'	12°57.26'
63	528	20.10.2000	-21°10.00'	13°00.04'
64	529	20.10.2000	-21°19.99'	13°01.92'
65	530	20.10.2000	-21°30.06'	13°05.14'
66	531	20.10.2000	-21°15.89'	13°35.30'
75	532	20.10.2000	-21°57.21'	12°15.12'
74	533	21.10.2000	-21°52.31'	12°24.48'
73	534	21.10.2000	-21°47.54'	12°33.90'
72	535	21.10.2000	-21°42.71'	12°43.32'
71	536	21.10.2000	-21°37.80'	12°52.91'
70	537	21.10.2000	-21°32.98'	13°02.25'
69	538	21.10.2000	-21°28.14'	13°11.70'
68	539	21.10.2000	-21°23.33'	13°21.13'
67	540	21.10.2000	-21°18.49'	13°30.72'
66	541	21.10.2000	-21°15.91'	13°35.23'
65	542	22.10.2000	-21°30.00'	13°05.20'
76	543	22.10.2000	-21°40.01'	13°07.52'
77	544	22.10.2000	-21°50.02'	13°08.20'
94	545	22.10.2000	-21°45.36'	13°54.78'
27	546	22.10.2000	-21°60.00'	13°10.84'
78	547	22.10.2000	-21°60.00'	13°10.84'
79	548	22.10.2000	-22°19.98'	13°23.45'
80	549	22.10.2000	-22°29.86'	13°27.31'
81	550	23.10.2000	-22°39.88'	13°30.33'
82	551	23.10.2000	-22°49.96'	13°31.18'
26	552	23.10.2000	-22°59.99'	13°32.10'
83	553	23.10.2000	-23°00.01'	14°22.19'
93	554	23.10.2000	-22°59.95'	12°46.74'
92	555	24.10.2000	-22°59.98'	12°57.25'
91	556	24.10.2000	-22°59.95'	13°08.59'
90	557	24.10.2000	-22°59.93'	13°19.62'
89	558	24.10.2000	-22°59.96'	13°30.23'
88	559	24.10.2000	-22°59.99'	13°41.18'

Station Label	Station Nr.	Date	Latitude	Longitude
87	560	24.10.2000	-23°00.04'	13°52.05'
86	561	24.10.2000	-22°59.99'	14°03.05'
85	562	25.10.2000	-22°59.97'	14°13.52'
84	563	25.10.2000	-23°00.02'	14°18.95'
83	564	25.10.2000	-23°00.04'	14°22.17'
95	565	25.10.2000	-23°14.96'	14°22.10'
96	566	25.10.2000	-23°30.02'	14°10.91'
97	567	25.10.2000	-23°44.99'	14°24.76'
98	568	25.10.2000	-24°00.05'	14°10.56'
99	569	25.10.2000	-24°15.03'	14°19.72'
100	570	26.10.2000	-25°00.88'	14°44.60'
106	571	26.10.2000	-25°11.21'	13°44.44'
116	572	26.10.2000	-25°29.97'	11°55.31'
115	573	26.10.2000	-25°28.07'	12°06.28'
114	574	27.10.2000	-25°26.12'	12°17.20'
113	575	27.10.2000	-25°24.30'	12°28.06'
112	576	27.10.2000	-25°22.39'	12°39.00'
111	577	27.10.2000	-25°20.53'	12°49.98'
110	578	27.10.2000	-25°18.69'	13°00.70'
109	579	27.10.2000	-25°16.83'	13°11.70'
108	580	27.10.2000	-25°15.01'	13°22.62'
107	581	27.10.2000	-25°13.17'	13°33.62'
106	582	27.10.2000	-25°11.51'	13°44.74'
105	583	28.10.2000	-25°09.37'	13°55.47'
104	584	28.10.2000	-25°07.50'	14°06.33'
103	585	28.10.2000	-25°05.74'	14°17.31'
102	586	28.10.2000	-25°03.74'	14°28.18'
101	587	28.10.2000	-25°01.86'	14°39.12'
100	588	28.10.2000	-25°00.95'	14°44.55'
105	589	28.10.2000	-25°09.32'	13°57.00'
4	590	28.10.2000	-24°59.89'	13°52.29'
5	591	28.10.2000	-24°49.94'	13°54.55'
6	592	29.10.2000	-24°39.94'	13°56.72'
7	593	29.10.2000	-24°29.94'	13°57.56'
8	594	29.10.2000	-24°19.95'	14°00.61'
9	595	29.10.2000	-24°10.00'	14°01.48'
10	596	29.10.2000	-23°59.97'	14°01.60'
98	597	29.10.2000	-24°00.02'	14°10.59'
117	598	29.10.2000	-24°00.02'	14°16.24'
118	599	29.10.2000	-23°59.97'	14°21.72'
10	600	29.10.2000	-23°59.91'	14°01.70'
11	601	29.10.2000	-23°50.01'	13°55.28'
12	602	29.10.2000	-23°40.05'	13°44.25'
13	603	29.10.2000	-23°30.02'	13°35.42'
14	604	29.10.2000	-23°20.02'	13°32.52'
15	605	29.10.2000	-23°09.95'	13°32.38'
89	606	30.10.2000	-22°59.94'	13°32.07'

5.7 Concluding Remarks

The cruise M48/5 was supported by the Sonderforschungsprogramm Meteorfahrten of the Deutsche Forschungsgemeinschaft.

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