Retrospective Analysis of Plankton Community Structure in the Benguela Current Large Marine Ecosystem (BCLME), to provide an Index of Long-term Changes in the Ecosystem

5TH INTERIM PROGRESS REPORT

(PERIOD: FEBRUARY – JULY 2006)

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Introduction

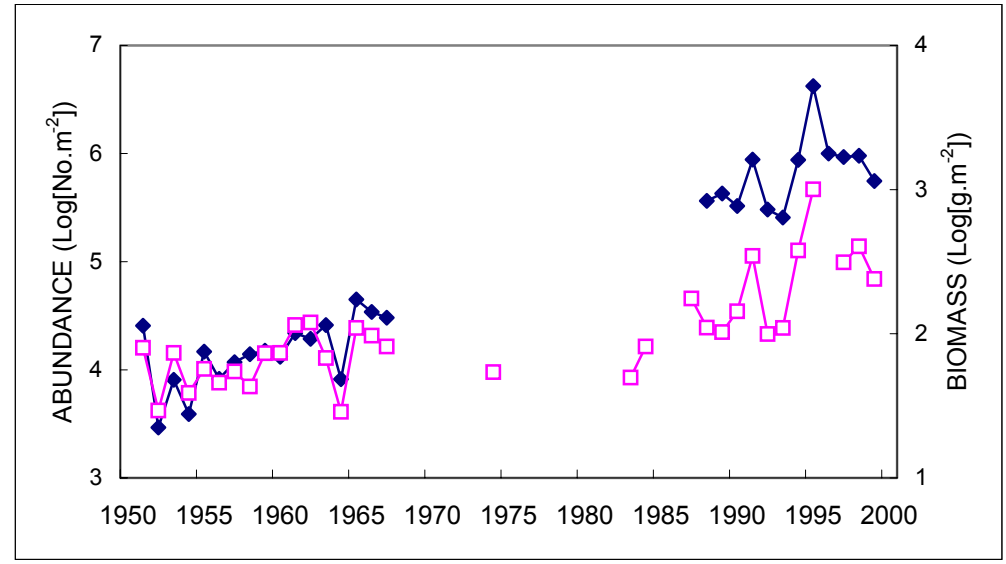
Several of the world's productive upwelling regions of the eastern boundary current systems have experienced substantial, decade-scale food web changes over the past four to five decades. These changes are not only reflected in extensive fluctuations in pelagic fish yields and regime shifts of fish populations (Lluch-Belda *et al*. 1989, 1992, Schwartzlose *et al*. 1999). They are also manifested in long-term variations in the abundance, distribution and species composition of plankton (see Perry *et al*. 2004 and references therein) on which these fish, at one or another stage of their life history, are relying for their successful growth and recruitment.

In the southern part of the BCLME off South Africa, an initial retrospective analysis of plankton samples collected over five decades in the pelagic fish recruitment area of St Helena Bay on the West Coast has shown a significant increase in zooplankton, accompanied by marked changes in its community structure (Fig. 1), which coincided with changes in the recruitment and abundance of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* (Verheye *et al*. 1998, Verheye and Richardson 1998, Verheye 2000).

While extensive plankton collections exist for the central/northern BCLME off Namibia (referred to as the SWAPELS collections – South West African Pelagic Egg and Larval Surveys), to date no equivalent retrospective analysis has been undertaken there. As a consequence, it has not been possible to quantify (suspected) large changes in this part of the ecosystem (but see Hansen *et al.* 2005). A pilot programme of retrospective analysis of zooplankton off Namibia, focussing on a limited number of SWAPELS transects and years has, however, recently been initiated through the BENEFIT Programme (e.g. Tsotsobe *et al.* 2003, 2004; Mainoane 2003).

The overall objective of this BCLME project is therefore to extend and fast-track the abovementioned BENEFIT pilot programme so that changes in the entire BCLME region over the past 50 years can be properly documented and quantified. The provision of such baseline and time-series is crucial in the assessment of natural (climate change) and anthropogenically forced changes (fishing activities) in the ecosystem. Knowledge of such past changes is a prerequisite for sustainable ecosystem management in the future, and forms the subject of several global initiatives such as GLOBEC (Global Ocean Ecosystems Dynamics) and GOOS

(Global Ocean Observing System), the protocols of which are largely followed in the BCLME.



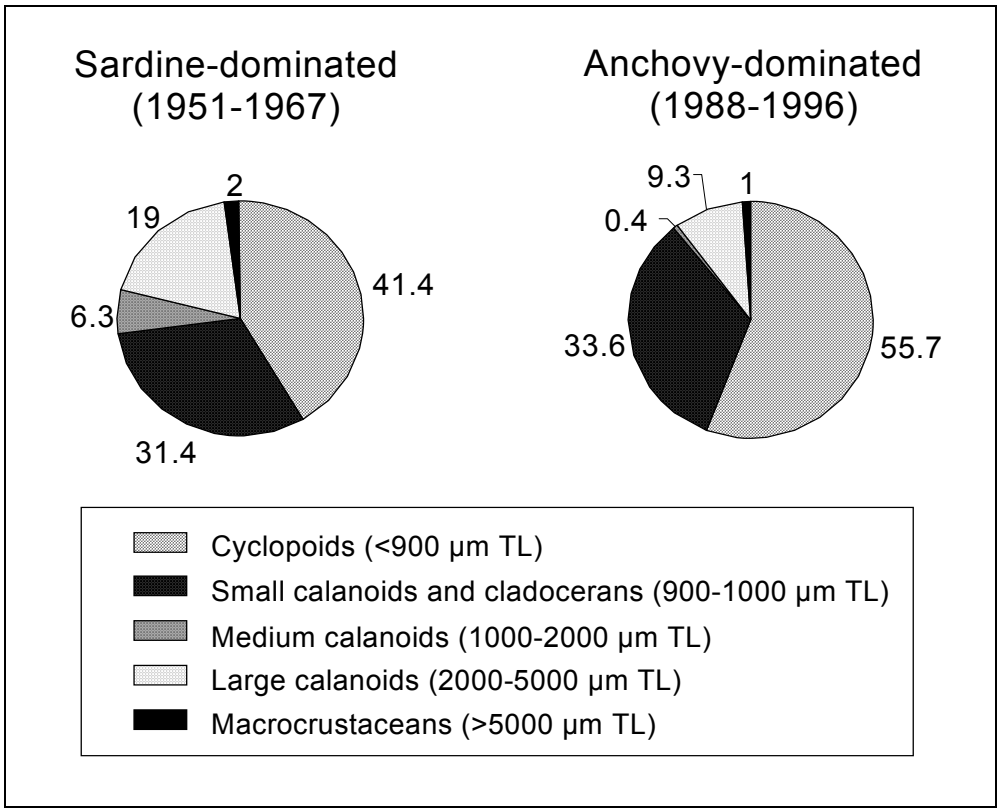


Figure 1. Southern Benguela: (Top) Time-series of copepod abundance (diamonds) and dry mass (squares) in St Helena Bay, 1951-1999; note the logarhitmic scale [$Log_{10}(x+1)$] on both y-axes. (Bottom) Community structure (%) of crustacean zooplankton during periods of sardine and anchovy dominance. Redrawn from Verheye *et al*. (1998) and Verheye and Richardson (1998).

The primary focus of this BCLME project is on the retrospective analysis of a representative amount of samples collected during the monthly SWAPELS surveys between the Cunene River (17ºS) and Lüderitz (26ºS) off the Namibian coast during the 1970s and 1980s (Fig. 2).

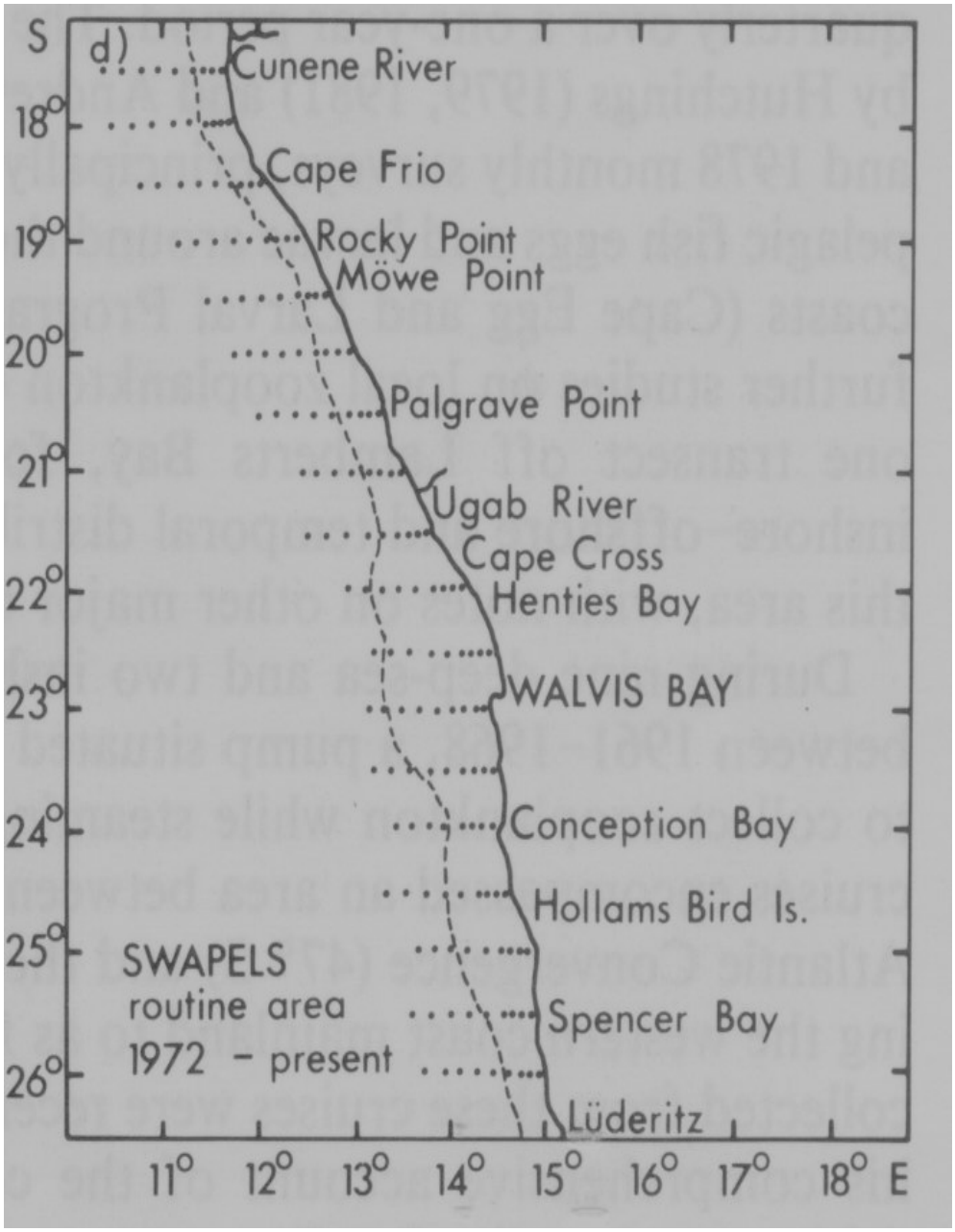


Figure 2. Northern Benguela: Map showing the cross-shelf transects and station positions sampled monthly during the SWAPELS programme, 1972-1989 (from Shannon and Pillar 1986)

The analysis of this enormous collection (in total approx. 20 000 samples were collected; however, an as yet unknown proportion is no longer available), which

is housed at MCM's sample store in Cape Town, involves students pursuing degrees at BSc(Hons), MSc and PhD level, and is backed up by technical assistance of a contracted sample analyst. Cataloguing and curation of this sample collection, for which partial funds were previously obtained from the Envifish and VIBES/IDYLE programmes in recognition of the collection's scientific value, is continued by a contracted sample curator. Ultimately, the SWAPELS long-term time-series data will form an important component of the comprehensive inventory of plankton and ancillary hydrographic and fisheries data archives in the BCLME region, which is to be established by a contracted data manager. This regional database will allow relationships between indices of upwelling and demographic parameters of zooplankton and pelagic fish to be examined, with the primary focus on decade-scale variability and ecosystem change.

Progress to date

1. Administrative update

The agreement between UNOPS and BENEFIT for the execution of this BCLME project was signed on 16 March 2004. The work plan covering the activities for the first year (2004/2005) made provision for a number of tasks, which are listed in Table 1. The status of progress made since then with regard to the recruitment and appointment of human capacity, on which the project relies heavily, is summarized in Table 1.

Table 1. Overview of project tasks and summary of progress status

TASK	STATUS
1. Sample analysis	
a. recruitment of **1 B.Sc.(Hons) student** (Mr I. Kauvee) b. analysis of ca. 180 samples from 1983 (N and S of Lüderitz) completed, forming the basis for a BSc Honours project on "Observations on the composition of the copepod community either side of the Lüderitz upwelling cell"	Studies at Univ. of the Western Cape completed during 2004; BSc(Hons) degree awarded on 8 April 2005.
c. recruitment of **1 M.Sc. student** (Mr I. Kauvee) d. detailed analysis of all developmental stages of 2 dominant	Student registered at Univ. of Cape Town, Feb. 2005;

copepods (*R. nasutus* and *C. carinatus*) from SWAPELS samples off Walvis Bay, forming the basis for a MSc project on "Population dynamics of the calanoid copepod *Rhincalanus nasutus* (Copepoda: Calanoida) in the northern Benguela".	envisaged graduation: June 2007; MSc project proposal submitted (see 3rd interim progress report); MSc thesis Chapter 1 drafted (see 4th Interim Progress Report); summaries of Chapters 2 and 5 drafted (see **Appendices A and B** – obtainable from PI); analysis of 206 samples near completion.
e. recruitment of **1 Ph.D. student** (Ms F. Cazassus) f. continuation of microscope analysis of several 100s of SWAPELS samples from 2 months of contrasting hydrographic conditions (upwelling vs. quiescence) per year at 3 stations (inshore, mid-shelf, offshore) on 9 transects (at latitudes 17, 19, 20, 21, 22, 23, 24, 25 and 26˚S), forming the basis for a PhD project entitled "Long-term variations of the zooplankton community of the northern Benguela ecosystem".	Student started end Sept. 2005 (>1 year after project started); registered at Univ. of Cape Town, Zoology Dept; 3-yr PhD research proposal completed (see 4th Interim Progress Report); extensive literature review ongoing; thus far good progress made regarding both sample and data analyses (see **Appendix C** – obtainable from PI).
g. recruitment of **1 sample analyst** (Mr F. Kotze) h. analysis of SWAPELS samples from line 70 off Walvis Bay completed, and from line 48 off Palgrave Point nearly completed; data being used by PI and PhD student (see later in this report and **Appendix C** – obtainable from PI).	Analyst appointed on 1 Aug. 2004; contract renewed on 1 Aug. 2005; sample analysis and data entry ongoing.
2. Training	
i. identification of training opportunities: ongoing; Regional zooplankton taxonomy workshop (originally planned for end 2005) postponed until late 2006; additional funds secured from the Sloan Foundation through CMarZ; Automated Sample Analysis Workshop in San Sebastian, Spain attended during November 2005	Various students being trained at different academic levels and institutions: (i) the MSc student completed Biostatistics course at UCT (January-March 2006) 'with flying colours'; attended the 2006 BENEFIT Forum meeting (Swakopmund, 5-8 April 2006) and presented

	oral paper on MSc project. (ii) PhD student currently attending a course in PRIMER at UCT (July-August 2006); (iii) sample curator received in-house hands-on training in the use of spreadsheets (MS Excel) for the electronic transcription of his sample catalogue.
3. Curation of sample collections	
j. recruitment of **1 sample curator** (Mr P.H. de Vos)	Curator appointed 1 August 2004; contract extended on 1 Aug. 2005 for 1 extra year; to date ca. 14 000 zooplankton samples have been curated and catalogued; electronic transcription of hand-written catalogue initiated by curator (terminated due to expiry of his contract on 31 July 2006).
4. Preparation of data archives for transfer to SADCO	
k. recruitment of **1 data manager**	IOI-SA contracted on 14 March 2005 for one year; contract period extended until end September 2006, however without any financial implications; see **Appendix D** for progress made since the 4th interim report.

Mr Ignatius Kauvee, MSc student (by dissertation) at the University of Cape Town (UCT) under supervision by Dr C.L. Moloney (UCT) and Dr H.M. Verheye (MCM), envisages completion of the microscope analysis of 206 SWAPELS samples collected off Walvis Bay by September 2006. His detailed analysis of the abundance and distribution of all developmental stages of his target copepod,

Rhincalanus nasutus, required him first to acquaint himself with the morphological characteristics of this species' ontogenetic stages (6 nauplii and 6 copepodids), whose descriptions are scattered widely in the published literature (Giesbrecht 1892; Sars 1903; Gurney 1934; Gibbons 1936; Bjornberg 1972; Geleten 1976) and not easily accessible. He has nevertheless been able to consolidate the findings of his extensive literature search into a comprehensive, diagnostic identification guide, describing for each stage its body size, shape and segmentation, its sensory, feeding and swimming appendages, and the morphology of the 5th pair of swimming legs in males, which is often extremely modified in copepods in order to perform various copulatory activities. All this information has been tabulated and forms part of Chapter 2 of his MSc dissertation, a summary of which is attached (**Appendix A** – obtainable from PI).

In addition to listing the taxonomic criteria used to identify all developmental stages of *R. nasutus*, this chapter also aims at using *a priori* statistical power analysis in order to select the appropriate sub-sample size for the enumeration of stage-specific abundances of this copepod, as well as of the other target copepod, *Calanoides carinatus*, in the 206 samples that he is analysing.

Mr Kauvee also started with the construction of the model, which forms one of the chapters (Chapter 5) of his dissertation. The model aims to simulate stage-specific development of the two copepod species, *R. nasutus* and *C. carinatus*, at a fine temporal resolution, which is otherwise not attainable with the empirical data collected using conventional zooplankton and hydrographic sampling techniques. The model requires the usage of spreadsheet programming techniques by macros (Excel) written in Visual Basic (Microsoft). Therefore, acquainting himself with these programming techniques has been an additional challenge for Mr Kauvee. A summary of Chapter 5 is appended (**Appendix B** – obtainable from PI).

Besides making good progress with his thesis, Mr Kauvee has also attended classes and tutorials on Biostatistics during the first 2006 semester, which forms part of the taught MSc. course at UCT. He successfully passed the exam in March 2006 and come 2nd of his class having scored >90%, which is a noteworthy achievement!

Ms Fabienne Cazassus, PhD student at the University of Cape Town (UCT) also under supervision by Dr C.L. Moloney (UCT) and Dr H.M. Verheye (MCM), has

since her arrival in Cape Town made substantial progress in respect of a comprehensive literature search and intensive data mining pertaining to zooplankton sampling in the northern Benguela Current subsystem. A summary is provided as part of her report (see **Appendix C** – obtainable from PI). Noteworthy here is that the last two (viz. Phase III and Phase IV) of four reports of the Cape Cross Programme, which started in 1970 and preceded the SWAPELS Programme, were obtained from a private source as none are archived at either NatMIRC's (Namibia) or MCM's (South Africa) libraries. In addition, an unpublished manuscript by Rippe and Fernández Tejedor (1999) was recovered, which reports on zooplankton results obtained during a cruise in the vicinity of Walvis Bay in June 1997 (i.e. almost 10 years after conclusion of the SWAPELS surveys and 3 years prior to the initiation by NatMIRC of its current environmental and plankton monitoring programme). Of particular importance here is that the data (in terms of numerical abundances of total copepods and species composition) are tabulated in the manuscript, thus complementing the 'gappy' database for Line 70 in that area. Also of particular importance to the database are the data presented (and tabulated) by Coetzee (1974) in his MSc thesis, which reports on pump samples collected off Walvis Bay during 1972 (April and August only), thus 'closing' somewhat the large hiatus in the present database between 1959 and 1978.

Ms Cazassus has made substantial progress with regard to the microscope analysis of SWAPELS zooplankton samples from three lines to the north of Walvis Bay, viz. line 4 off the Kunene River (17°S), line 16 off Cape Frio (19 °S), and line 38 off Palgrave Point (20.3 °S) (see Fig. 2). Together with data from line 70 off Walvis Bay (23°S) obtained earlier by various students (see earlier interim reports), she has been able to identify some interesting (but preliminary) patterns in the latitudinal variability of zooplankton biomass and copepod abundance through time (1970s and 1980s) and across the shelf (see further in this report and **Appendix C** – obtainable from PI).

In addition, she has consolidated the Walvis Bay line database from 1959 until the present, which spans a much broader time window than for any of the other SWAPELS lines. In her report (see **Appendix C** – obtainable from PI) she presents some of the findings in respect of seasonal and cross-shelf variability of total zooplankton biomass and total copepod abundance (see further in this report), thereby highlighting the need for applying appropriate statistical analysis techniques and examining changes in the zooplankton community structure in addition to these

'bulk' measurements of zooplankton, as well as their relationships with changes in their physical and biological environment.

During the period under review, the contract of the sample curator, Mr Philip de Vos, expired on 31 July 2006. Over the past two years, a total of about 14 000 zooplankton samples, primarily from SWAPELS surveys but also from various South African field sampling programmes, have been adequately curated under the aegis of this BCLME project, thus complementing earlier attempts funded from various other sources including Envifish and VIBES/IDYLE. All these samples were individually checked and their state of preservation and condition of the plankton recorded, and where necessary sample jars were replaced when become brittle, relabelled and/or the preservative (4-5% formalin in seawater) replaced or topped up. Samples were placed in cardboard boxes keeping them dust-free and in the dark, all boxes were numbered and their contents recorded, and stored in chronological order of collection at MCM's FCU sample store in Paarden Eiland, Cape Town.

Throughout his contract, Mr de Vos has maintained a detailed hand-written record in a sample catalogue, which, after receiving some basic training in the use of Excel spreadsheets, he started transcribing electronically. Unfortunately, as mentioned already, his contract expired, which leaves much of his catalogue unfinished, i.e. in paper form instead of computerised. Moreover, as pointed out by Ms Cazassus in her report, there remains an appreciable portion of the sample collection at the FCU store, which originates from 'South West Africa' during the early 1960s and which currently appears not to be reconcilable with information found either in known published papers, or in internal data or cruise reports, or in otherwise documented records. Given the considerable gap in the early decades of the Namibian zooplankton time-series (see Figs 3 and 4), these samples are likely to conceal important information and clues that are crucial for the interpretation of long-term changes in the ecosystem (see e.g. Fig. 5).

Mr Ferdinand Kotze, the contracted sample analyst, undertook to complete the microscope analysis and data capture of all available samples from lines 38, 40 and 42 off Palgrave Point by the due date of this 5th Interim Progress Report. Unfortunately, his efforts were hampered repeatedly during the Koeberg power station's load-shedding episode, followed more recently by ill health. Nevertheless, the data that were partially entered into the database have already been used by Ms Cazassus in a first attempt to examine latitudinal changes in zooplankton biomass

and copepod abundance during the SWAPELS era (see later in this report and in **Appendix C** – obtainable from PI).

2. Training and capacity building progress

The regional zooplankton taxonomy training workshop, which was scheduled to take place at the end of 2005, was postponed owing to time constraints in respect of compiling an adequate budget. The workshop will be rescheduled for later during 2006, and assistance will be sought from BENEFIT's newly appointed Training Officer for the preparation of this important regional event. Through his membership of the Steering Group of the global Census of Marine Zooplankton (CMarZ), which is a project of the global Census of Marine Life (CoML) Programme, the PI of this BCLME project has been successful in securing appreciable financial support from the Alfred P. Sloan Foundation towards this training workshop. According to the CMarZ Science Plan, this workshop will be one of many opportunities for both graduate and professional training envisaged under the umbrella of CMarZ worldwide. Such taxonomically focused workshops address the need for additional technical expertise in the identification of selected zooplankton groups. The workshop will not only serve to disseminate knowledge and skills, but foster collaborative international interactions and ultimately also produce a new generation of taxonomists and parataxonomists.

In the Benguela Current region zooplankton has been collected routinely, usually in support of fisheries research, since the development of the pelagic fishing industry in South Africa in the early 1950s. Although this zooplankton monitoring is still continuing, the region has suffered an enormous loss of expertise in zooplankton taxonomy at an accelerated pace over the past decades, to the extent that the very few experts remaining are on the list of Endangered Species, if not already Extinct. It is hoped that the abovementioned funding from CMarZ toward the organisation of a regional zooplankton taxonomy and identification workshop will attract shared or matching funding from both the BENEFIT and BCLME Programmes.

The use of computer-aided image recognition in the analysis of (zoo)plankton samples (e.g. ZooScan – see 4th Interim Progress Report) has made significant progress in recent years. It is a simple, non-destructive method that allows reliable estimates of biomass (individual numbers, zooplankton biovolume, volume-class

distribution and organic C and N) to be obtained from preserved zooplankton samples. It avoids most of the variability sources owing to sample manipulation when measuring zooplankton volume displacement, or to the presence of particulate material other than zooplankton. Although some software has already been developed to identify 'species' automatically, it is still in its experimental phase and has not been much tested by end-users and for the analysis of large amounts of samples.

The SCOR WG 115 on 'Standards for the Survey and Analysis of Plankton', of which the PI is a Full Member, recognised at its final meeting and mini-symposium held in Plymouth, UK in May 2006, that automated image analysis techniques indeed offer enormous possibilities for the future. However, there is a further step needed in the development process which will allow categorisation of taxa. Systems with this capability are now required to analyse large sample collections produced by time-series surveys. The WG recommended that "… a SCOR WG is established on automated image recognition of plankton. The timeliness of establishing such a Working Group arises because of the decline in taxonomists and the rapid increase in technological capabilities in this field". A proposal for this new working group, to which the PI of this BCLME project was invited to serve as a Full Member, has been submitted to SCOR for funding in May 2006 and is currently being reviewed by the national SCOR committees. SCOR WG 115 further recommended that "Taxonomy and training of taxonomists must be funded as they will be essential in the development and calibration of automated analysis systems for the foreseeable future".

3. Data management progress

Dr Kim Prochazka's (Director of IOI-SA) progress report on activities related to data management is attached (**Appendix D**). The report describes the architecture of a simple 'Benguela Plankton Portal', comprising the Metadata and Metadata Directory, the Database itself, and the Bibliography. The portal was designed in order not to fragment any of the inventory's aspects. It is accessible from BENEFIT's home page.

Once the portal structure is complete, training sessions will be set up in the three BCLME countries to facilitate metadata entry using MATT (Metadata Authoring

Tool). Besides these countries' respective institutional datasets, some additional datasets that have no clear institutional home have been acquired (and others are still being sourced), which will be incorporated into the portal as Excel files. The bibliography is still under construction, and contains currently 305 Benguela plankton publications, which have been keyworded.

The target date for completion of the 'Benguela Plankton Portal' is end September 2006. However, thereafter, as more historical data are 'uncovered' (especially pertaining to Angolan waters) and new data become available, their capturing into the portal will likely become the responsibility of BENEFIT, the regional organisation that currently has an existing hosting and web administration agreement with IOI-SA.

4. Scientific progress

Figure 3a shows a multi-decade time-series (1931-2005) of annual guano yields at Bird Rock, in the vicinity of Walvis Bay, Namibia; the data were taken from a slide presented by Dr RJM Crawford (MCM) in a paper on 'Seabirds, Sardine, Sustainability and the System' at the Angola-Benguela Front Workshop (Swakopmund, Namibia 2-4 April 2006). It shows a sequence of two decade-scale cycles of increasing and declining guano yields. If the guano yields at Bird Rock were a good proxy for pelagic fish stocks off central Namibia in the northern Benguela, the guano time-series reveals an initial increase in fish biomass from the 1930s until the late 1950s, followed by a first decline during the 1960s, increasing again during the 1970s until about the mid-1980s when the trend reversed again and fish biomass shows a second decline, which continues until the present.

In contrast, there appears to be an inverse pattern of increasing and declining trends in the zooplankton time-series, as inferred from the available dataset of annual mean zooplankton biomass (expressed as biovolume per m^2, measured as settled volume) collected off Walvis Bay during the period 1959-present (Fig. 3b). It was speculated during the BENEFIT Forum (Swakopmund, Namibia 5-7 April 2006), when progress with the retrospective analysis of northern Benguela zooplankton archives was reported (Verheye 2006a), that although settled volume is a crude estimate of biomass and despite the presence of large gaps in the dataset, such inverse relationship between the time-series of pelagic fish biomass (proxied by

guano yields) and zooplankton biomass (proxied by settled volume) suggests long-term top-down control (via predator-prey interactions) of zooplankton (prey) by pelagic fish (predator). However, effects by other potential predators (e.g. among the gelatinous zooplankton community) as well as bottom-up processes, for which historical data are currently being mined, are not discounted and will also be investigated.

Results from zooplankton data mining and preliminary analyses – by Ms Cazassus – of seasonal and cross-shelf variability in the Walvis Bay dataset (Figs 4 and 5, see also **Appendix C** – obtainable from PI) have been valuable in support of the above speculation. Unlike the annual mean biovolume data presented in Figure 3b, the dataset for Line 70 off Walvis Bay that was consolidated by Ms Cazassus subsequent to the BENEFIT Forum in April 2006 has two important, additional data points: (i) one for 1972 (April and August) in terms of total copepod abundance only (shown in Fig. 5a and c as March and September respectively); these data were extracted from Coetzee's MSc thesis (Coetzee 1974), and (ii) the other for 1997 (June) in terms of both zooplankton biovolume (see Fig. 4b) and total copepod abundance (see Fig. 5b); these data were extracted from an unpublished manuscript by Rippe and Fernández Tejedor (1999).

Despite seasonal and interdecadal differences in data density, there is evidence to suggest – particularly during spring and summer (Fig. 4c, d) – a gradual increase in zooplankton biomass from the late 1970s to the early 1980s, followed by a decrease until the late 1980s. Thereafter, based on the winter (June) 1997 data and all the 2000-2004 data (Fig. 4b), zooplankton biomass increased again. Thus, the June 1997 data add an important data point to the long-term time-series, confirming the gradual increase in zooplankton biomass after 1989, the last SWAPELS year.

In terms of total copepod abundance, the alternation of these increasing and decreasing trends may not always seem that clear, especially in the absence of abundance data for 1959, for which only biovolumes are available (see Kolmer 1963). However, the few extra data for autumn and spring 1972 (from Coetzee 1974) provide a valuable clue suggesting an increase from around the late 1950s/early 1960s (inferred from biovolume data) to around the late 1960s/early 1970s, followed by a decline through the late 1970s/early 1980s until at least the late 1980s, after

which, at some point during the 1990s copepod abundance increased again to the elevated levels observed today (Fig. 5a, c).

An analysis of latitudinal changes in zooplankton biomass and copepod abundance has been initiated by Ms Cazassus (see **Appendix C** – obtainable from PI). Thus far, samples from four SWAPELS lines at fairly widely spaced latitudes collected during six consecutive years (1978-1983) have been analysed (albeit partially at this stage): line 4 off the Kunene River (17°S), line 16 off Cape Frio (19 °S), line 38 off Palgrave Point (20.3 °S), and line 70 off Walvis Bay (23.3°S). For reasons of data availability, only data from spring (September) were assembled. Although the results here, too, are still preliminary, it is noteworthy that levels of zooplankton appear to be more elevated (possibly by as much as one order of magnitude!), both in terms of biomass and abundance, in the south, off Walvis Bay, compared with the area further north (see Fig. 6). In addition, whereas September trends observed on the three northerly lines appear to be fairly stable over the six years examined thus far (except inshore; Fig. 6a-c), there is a clearly declining trend in copepod abundance evident at all stations off Walvis Bay over the two-decade period (1970s-1980s), for which data are available here – note that there are two additional data points (1972 and 1987) for that transect (Fig. 6d).

At this stage of the project, only 'bulk' measurements of zooplankton, i.e. total zooplankton biomass and total copepod abundance, have been reported on. These data do provide a fairly good indication of temporal (seasonal, interannual and interdecadal) and spatial (cross-shelf and latitudinal) variability of zooplankton and copepods in the northern Benguela and may even allow for some speculations to be made or hypotheses to be formulated, as illustrated above. However, it is essential now to refine these 'crude indicators', and this forms an integral part of Ms Cazassus' PhD work through detailed analyses of species composition in order to examine changes over time in terms of zooplankton community structure, together with investigations of fluctuations in environmental parameters and biological interactions between zooplankton, their prey/food and their predators/competitors.

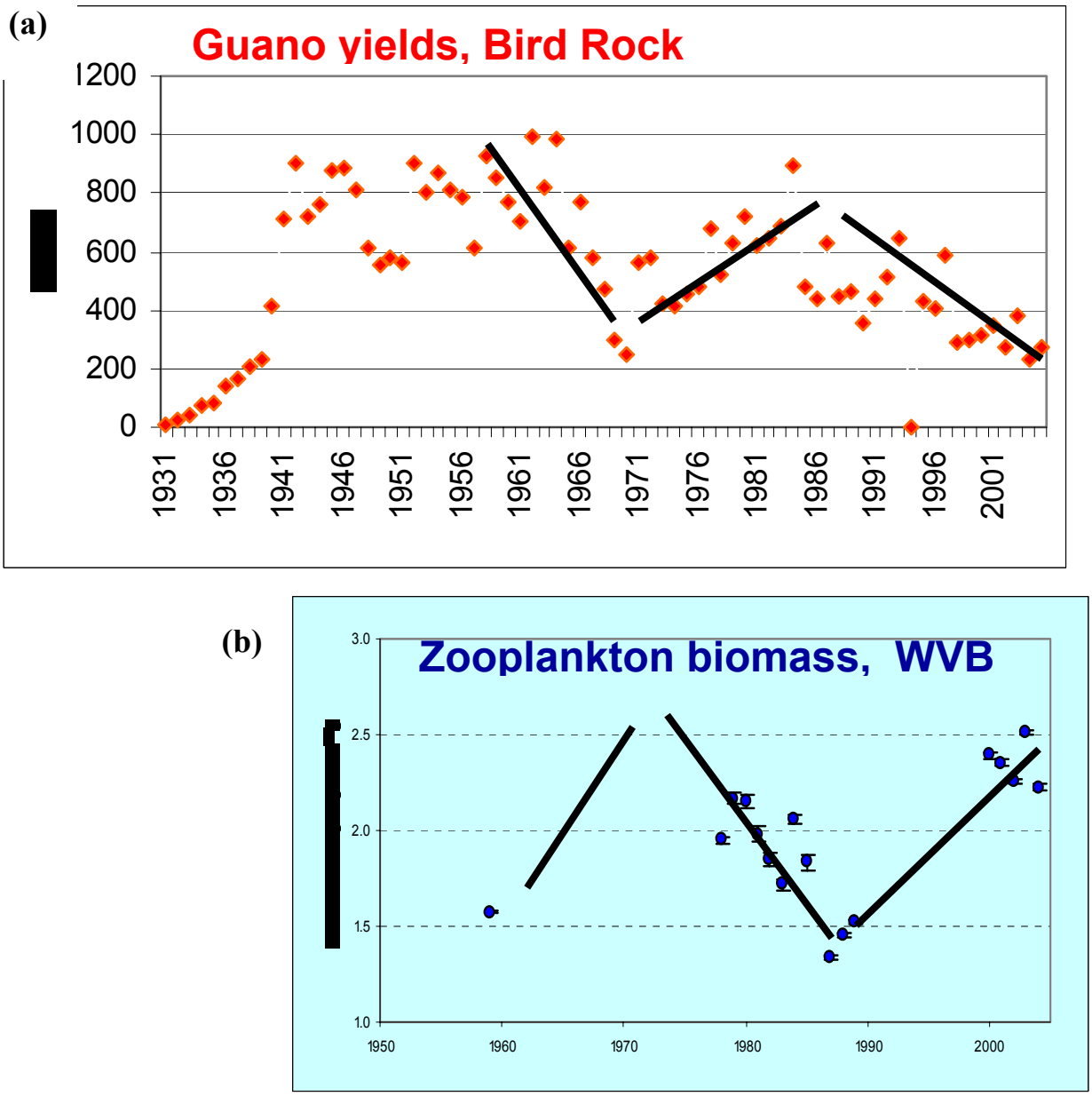


Figure 3. Time-series of (a) annual guano yields (tons) from the platform at Bird Rock, Namibia, during the period 1931-2005 (courtesy RJM Crawford, MCM) and (b) total zooplankton biomass (Log_{10} Biovolume in ml m^{-2}) averaged (± 1s.e.) per year over all stations on SWAPELS line 70 off Walvis Bay, Namibia, during the period 1959-2004 (updated from 3rd and 4th Interim Progress Reports). The trend lines were hand-drawn and indicate opposing cycles of increases and decreases in both time-series, indicative of a fluctuating predator-prey relationship between planktivorous pelagic fish stocks (proxied by guano yields) and their zooplankton prey (proxied by total zooplankton biovolume) (according to Verheye 2006a and 2006b).

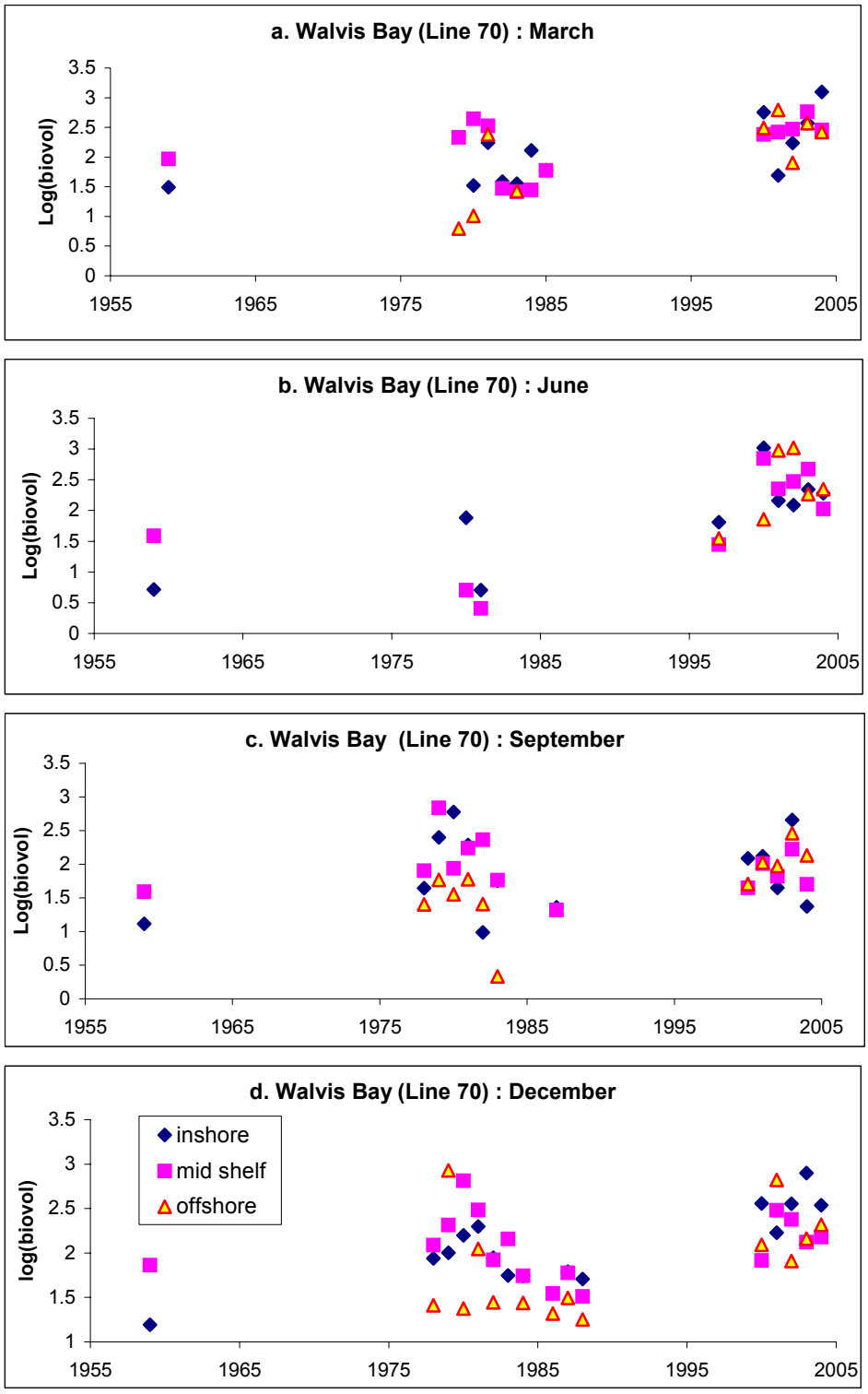


Figure 4. Time-series of zooplankton biovolume at three stations (inshore, mid-shelf and offshore) along the Walvis Bay line during (a) autumn (March), (b) winter (June), (c) spring (September) and (d) summer (December) over the period 1959-2004.

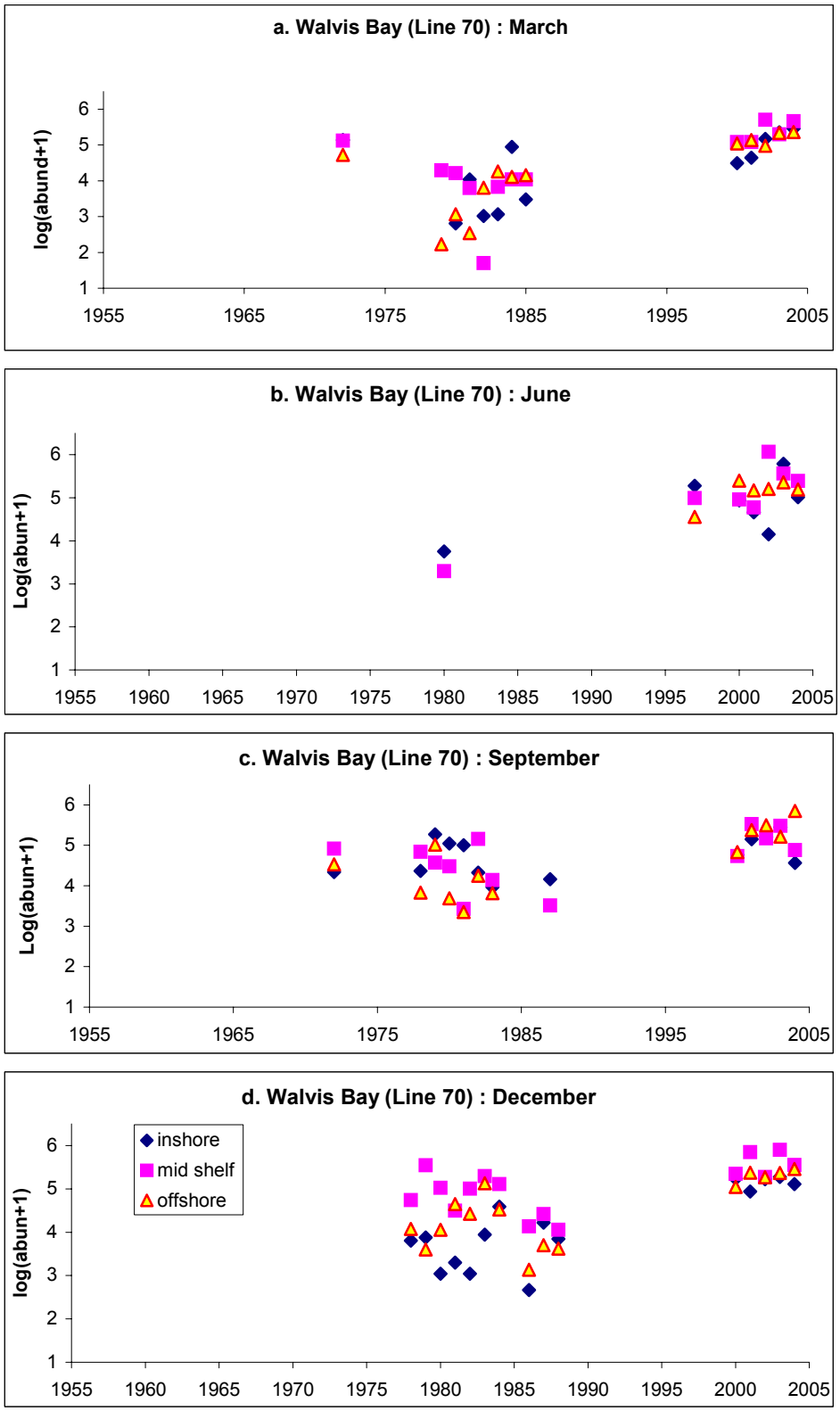


Figure 5 Time-series of total copepod abundance at three stations (inshore, mid-shelf and offshore) along the Walvis Bay line in (a) autumn, (b) winter, (c) spring and (d) summer over the period 1959 -2004.

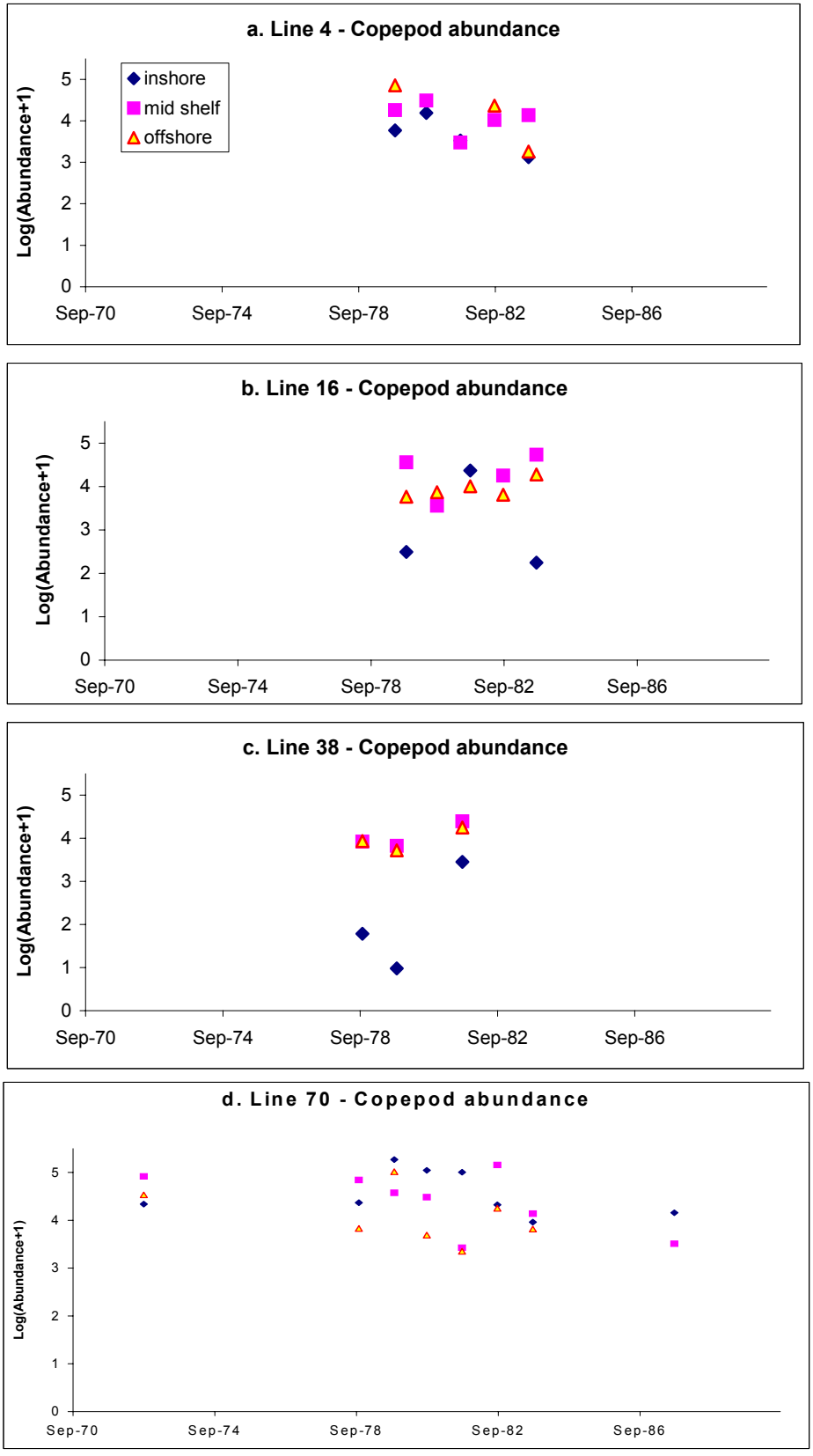


Figure 6. Latitudinal variability of total copepod abundance (1970-1987) at 3 stations (inshore, mid-shelf and offshore) in September (spring) at four latitudes: (a) Line 4 – Kunene River, (b) Line 16 – Cape Frio, (c) Line 38 – Palgrave Point and (d) Line 70 – W alvis Bay.

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APPENDICES

Appendix A.

Kauvee, I.K.V. – Population dynamics of the calanoid copepod *Rhincalanus nasutus* (Coeppoda: Calanoida) in the northern Benguela: Summary of Chapter 2 (Methods and Identification guide), 4 pp.

Appendix B.

Kauvee, I.K.V. – Population dynamics of the calanoid copepod *Rhincalanus nasutus* (Coeppoda: Calanoida) in the northern Benguela: Summary of Chapter 5 (The model), 3 pp.

Appendix C.

Cazassus, F. – Long-term variations of the zooplankton community of the northern Benguela ecosystem: Progress Report No. 2 (July 2006), 11 pp.

Appendix D.

Prochazka, K. – Progress report of the Data Manager on development of the inventory and database for plankton data in the Benguela Current, submitted by the International Ocean Institute, Southern Africa (July 2006), 7 pp.