

## VIDEO OBSERVATIONS ON THE HABITAT ASSOCIATION OF DEMERSAL NEKTON IN THE MIDSHELF BENTHIC ENVIRONMENT OFF THE ORANGE RIVER, NAMIBIA

M. J. GIBBONS\*, A. SULAIMAN†, K. HISSMAN‡, J. SCHAUER‡, I. McMILLAN§  
and P. A. WICKENS§

A semi-quantitative assessment is made of the animals observed in archived videotapes taken from the research submersible *Jago*, during diamond mining and exploratory surveys off the mouth of the Orange River on the west coast of southern Africa (28°15'S, 29°11'S) in November 1996. The seabed environment is described and nekton associations with substratum features are identified. The area is characterized by heterogeneity to its physical and biological structure. The variety of observed nekton is low, and communities are dominated by goby *Sufflogobius bibarbatus*, juvenile hake *Merluccius* spp. and cuttlefish *Sepia* spp. (on soft substrata), as well as false jacobever *Sebastes capensis* and kingklip *Genypterus capensis* (on rocky substrata).

The waters of the Benguela system are among the most productive in the world (Cushing 1971), and support several commercially valuable pelagic and demersal fisheries (Stuttaford 1998). Although the pelagic environment along the west coast of southern Africa is fairly well researched, the demersal environment has not been studied to the same degree (Payne *et al.* 1987, 1992). The abundance and distribution of demersal fish has generally been determined using bottom trawl surveys, and associations between fish and their environment have been deduced from superimpositions of catch data onto geological, bathymetric and sedimentary charts. Such studies, in both Namibian (Macpherson and Roel 1987, Macpherson and Gordoia 1992) and South African waters (Roel 1987, Smale *et al.* 1993) have resulted in a division of the fish fauna into assemblages associated with the neritic zone, the continental shelf and the slope.

An alternative way to sample the biological environment is by direct observation from a submersible. The technique allows for the simultaneous collection of information on the fish, as well as the physical features of the environment. Elsewhere, submersibles have been used to describe the physical and biological environment of benthic communities (Sibuet *et al.* 1988), to determine habitat use by nekton (Felley and Vecchione 1995) and in data collection for stock assessment (Giguère and Brulotte 1994).

At the end of 1996, the diamond mining and exploration company De Beers Marine (Pty) Ltd commissioned the two-person, research submersible *Jago* to examine offshore concession areas near the mouth of

the Orange River, Namibia. Much biological information is contained within the underway video recordings that were made. This paper describes the benthic environment off the Orange River from analysis of these videotapes, and comments on habitat associations of the dominant nekton.

### MATERIAL AND METHODS

#### Field sampling

The study area lies north of the Orange River submarine delta, near the 130-m isobath (Fig. 1). The videotapes from 15 diving sites were analysed in the area between 28°15'S and 29°40'S. All surveys were conducted at depths of 100–140 m in the middle reaches of the continental shelf (Fig. 1).

The submersible was launched from the geosurvey ship M.V. *Zealous* and towed on the surface by inflatable dinghy to the first way-point of each dive survey. A hydrophone was lowered into the water to communicate with the submersible, the position of which was tracked every 31 seconds using an acoustic transponder array with an accuracy of approximately 5 m.

The videotapes were recorded using a Hi-8 video camera as the submersible cruised along the seabed (generally at speeds of 0.25 knots). The camera usually faced forwards and downwards through the front acrylic dome window and was only occasionally

\* Zoology Department, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa. E-mail: mgibbons@uwc.ac.za

† Botany Department, University of the Western Cape

‡ Max-Planck-Institut für Verhaltensphysiologie, D-82319 Seewiesen, Germany

§ De Beers Marine (Pty) Ltd, P.O. Box 87, Cape Town 8000, South Africa

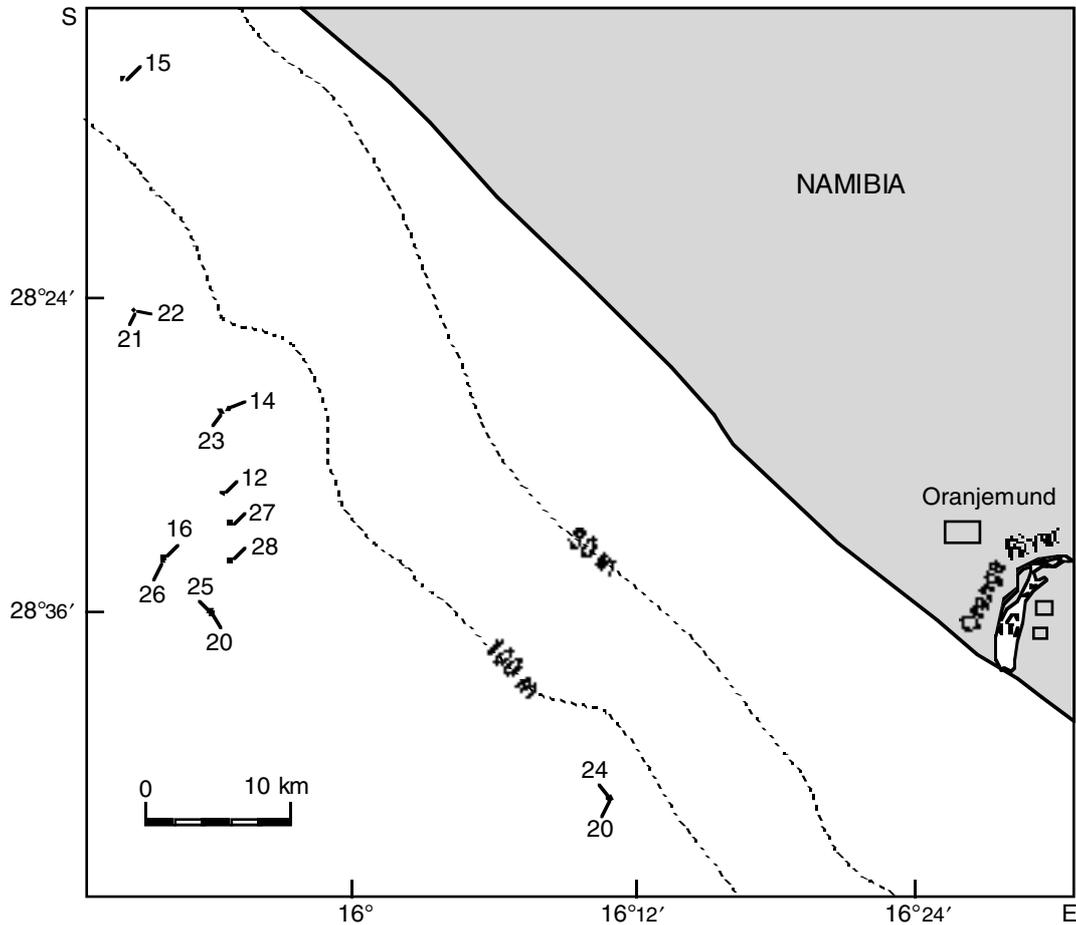


Fig. 1: Map of the study area showing location of the dive sites

panned or moved during the survey. The submersible stopped at times, either to collect samples or to zoom in on particular features, or it moved away from the bottom. Videotape recorded during these stoppages, or when visibility was impaired as a result of silt disturbance, was not examined. The video camera was equipped with a clock synchronized to that aboard the *M. V. Zealous*, making it possible to relate sections of the videotape to the actual position of the submersible on the dive-track.

#### Analysis of the videotapes

The videotapes were examined with frequent reversals and pauses. The viewer recorded the physical features of the environment (see Table I) and sedentary

biological features, and counted all nekton within videotape segments. The length (in seconds) of these segments was delimited by the major substratum features present. When the submersible moved into an area with a different substratum, new records were kept.

Associations between nekton and environmental features were assessed by examining the relationship between the abundance of nekton in each of the 502 videotape segments and the length of time (in seconds) that each physical feature was observed in those segments. Analyses were conducted on untransformed data using multiple regression analyses (MRAs) performed using Statistica software. For purposes of presentation, the time that the different environmental features were recorded was summed for each dive to provide frequency of occurrence data (Table II). Although these are crude, they do provide some insight

Table I: Descriptions of the physical features of the benthic environment off the Orange River Mouth. The biogenic holes were identified as burrow entrances and associated mounds; size, form and density variable. The epifauna consisted of encrusting or erect, sedentary animals; the quality of the videotape material did not permit the identification of epifauna beyond the level of phylum and all have been combined here. Cerianthid sea anemones and whelks have been listed separately because they were conspicuous, could be consistently identified and were associated with a different set of physical features from the other epifauna

Feature	Size and shape	Associated biota	Other comments
Soft sand	Texture, topography and depth variable; surface often green in colour	Biogenic holes, cerianthids and whelks sometimes pre-sent	Bioturbation may be marked
Shelly sand	Soft sand, with fine shell fragments on surface	Few biogenic holes	Bioturbation not marked
Shell debris	Intact/broken mollusc shells, forming dense surface layer	None	Localized and often associated with clay
Pebbles	Small stones; angular or smooth in shape	None	Generally densely scattered at the surface; associated with gravels and cobbles
Gravel	Fist-size rocks of sandstone or clay; irregular in shape	May have some epifauna	Scattered or densely aggregated; projecting through, or forming, surface layer
Cobbles	Fist-size rocks of sandstone or clay; rounded in shape	May have some epifauna	Scattered or densely aggregated; projecting through, or forming, surface layer
Rock debris	Intermediate in size between gravel and boulders; of sandstone or clay; irregular but smooth	May have some epifauna	Scattered or densely aggregated; projecting through, or forming, surface layer; often with sediments on upper face
Boulders	Massive and free-standing; erect or horizontal; sandstone or clay	Epifauna usually present	Often with sediment on upper face
Clay	Obvious by colour and texture	None	Usually present through erosion of surface layer; may be broken

into the benthic environment.

Given that the dive surveys were not designed for biological purposes, the analysis of the videotapes could only be semi-quantitative. Although the submersible undertook approximately linear transects, the dive track occasionally crossed itself. However, the presence of duplicate observations did not compromise the data, because they were uncommon and of short duration. Although it can be argued that each videotape segment within a dive represents a pseudo-replicate, each segment represented a "habitat" that was different from that of others in that dive. In any case, data from all videotape segments from all dives were pooled in the analyses.

## RESULTS

Nine demersal fish and cephalopod species were observed on the videotapes analysed. These were cuttlefish *Sepia* spp., kingklip *Genypterus capensis*, false jacoever *Sebastes capensis*, gurnard *Chelidonichthys* spp., goby *Sufflogobius bibarbus*, juvenile hake *Merluccius* spp., several unidentified squid species, horse mackerel *Trachurus trachurus capensis* and

smooth-nosed horsefish *Congiopodus torvus*. Only the first six taxa are dealt with further. The remainder were either too rare (horsefish) or are mesopelagic (squid and horse mackerel) and therefore unlikely to show consistent habitat associations.

The frequency with which each species was found in association with the different physical features of the environment is shown in Table III. It appears that goby, juvenile hake, cuttlefish and gurnards generally preferred areas of more open substrata, whereas false jacoever and kingklip were more commonly associated with boulders and rock debris.

The results of the MRA illustrate more clearly the association between nekton and the physical environment (Table IV). However, it should be noted that, although all the MRAs were highly significant, no more than 53% (in the case of goby and less for the other taxa) of the variation in the nekton data could be explained by the analysis. Although this finding may be attributable to the crude nature of the data, it implies that some other factor/s may have been responsible for the pattern observed. Nevertheless, from Table IV it can be seen that goby, juvenile hake and cuttlefish were positively associated with soft substrata and negatively associated with elements of hard substrata (there were insufficient data for

Table II: Frequency (%) of substrata in the video images analysed from each dive (totals may exceed 100%). The mean number of demersal nekton per 1 000 seconds of videotape is also shown (calculated from total numbers per dive)

Parameter	Frequency (%) per dive number												Total			
	12	14	15	16	19	20	21	22	23	24	25	26		27	28	29
<i>Substratum features</i>																
Soft sand	81.7	100	77.45	56.75	71.91	90.07	93.27	83.7	61.97	87.06	89.4	87.28	50.89	76.02	57.23	76.14
Shelly sand	0	64.70	0	18.84	0	32.5	0	0	41.6	1.17	0	42.19	0	25.87	0	13.76
Shell debris	51.49	0	0	0	0	0	0	0	8.5	0.95	38.54	0	0	11.56	46.87	4.87
Pebbles	69.79	38.77	0	13.91	35.37	6.69	0	21.56	74.23	63.59	57.45	45.21	33.78	62.41	81.66	34.58
Cobbles	100	69.02	0	0	0	12.19	34.76	0	41.28	12.42	0	0	0	23	0	13.12
Gravel	0	0	0	0	0	15.99	23.35	0	0	8.04	40.1	15.7	3.68	7.17	81.07	12.06
Rock debris	100	77.26	22.92	0.55	45.1	73.93	51.38	15.12	48.21	42.27	0	32.66	1.09	87.52	1.94	36.45
Boulders	81.7	57.22	22.55	88.01	68.92	51.35	42.57	65.15	83.72	44.05	54.79	83.21	68.58	34.51	49.28	57.25
Clay	100	0	0	0	18.61	0.64	17.66	0	23.35	15.09	0	11.04	3.77	70.85	1.27	11.34
<i>Biological features</i>																
Biogenic holes	51.49	48.91	77.45	46.86	63.83	85.54	100	83.7	64.9	87.06	89.4	52.77	50.89	43.52	55.28	70.45
Epifauna	0	32.64	24.74	72.41	77.06	19.29	52.23	65.15	47.65	34.86	4.11	37.49	65.32	12.77	41.55	43.17
Cerianthids	0	0	3.12	0	0	0	0	0	0	na	0	0	0	0	0	0.35
Whelks	0	0	25.16	0	0	0.35	0.18	0	0.25	na	0	0	0	0	0	2.91
<i>Nekton abundance</i>																
Goby	4.25	13.5	53.32	14.74	5.61	9.21	7.54	4.37	0	na	8.96	19.73	10.51	0.27	1.27	12.66
Hake	0	1.39	13	1.23	0.56	1.04	1.44	0.23	0.62	na	0.53	3.36	0.64	0	0	2.12
False jacobever	0	1.04	0.22	1.53	1.12	0.69	0.72	0.23	0.74	na	0	1.68	1.41	0.54	2.11	0.75
Kingklip	0	0	0.32	0.76	0.98	0.69	0.36	0.93	0.37	na	0.53	1.26	0.13	0.54	0	0.46
Cuttlefish	0	0.35	1.4	4.45	0.7	0.35	0.72	0.46	0	na	0.26	1.26	0.26	0.27	0.85	0.80
Gurnards	0	1.39	0	0.61	0.56	0.12	0.72	0.23	0	na	0.53	0	0.64	0	0	0.30
Depth (m)	129	121	96.5	126.5	123.5	129	120.5	119.5	138	115	126.5	126.5	124	124.5	114	
Total dive time (seconds)	470	2 889	9 301	6 513	7 131	8 689	5 572	4 313	8 057	9 445	3 793	1 009	7 801	3 695	2 366	82 417

na = Images too obscured to enable identification of fish

Table III: Frequency of nekton observations among substratum features. Insufficient data for shell debris

Species	Frequency (%)							
	Soft sand	Shelly sand	Pebbles	Cobbles	Gravel	Rock debris	Boulders	Clay
Goby	55.77	3.21	6.23	2.47	2.28	11.66	15.42	2.96
Hake	67.97	3.46	1.73	1.73	0.87	14.29	8.66	1.3
False jacobever	27.35	0.85	13.68	3.42	5.13	15.38	33.33	0.85
Kingklip	22.41	3.45	12.07	21.55	2.59	12.93	21.55	3.45
Cuttlefish	40.52	6.03	10.34	2.59	3.45	7.76	26.72	2.59
Gurnards	40.91	0	18.18	2.27	9.09	6.82	20.45	2.27

gurnards). In the case of kingklip and false jacobever, both were positively associated with boulders, but not with soft substrata.

## DISCUSSION

It is clear from Table II that the seabed environment off the Orange River is heterogeneous. From a physical point of view, this heterogeneity reflects local erosion of the latest Pleistocene veneer during the later Weichselian maximum low sea level, and the subsequent Holocene transgression. This has resulted in a distortion and disturbance of the bedding of the deposits and is reflected by the presence of boulders, slabs, debris, gravel, cobbles, pebbles and shell debris at the surface (Table II).

From a biological standpoint, this heterogeneity is reflected in, for example, the presence of cerianthid

anemones in the area of Dive 15, whereas whelks were only observed on four of the 15 transects. High variability in the composition of infaunal communities in the same region was also noted by Field *et al.* (1995, 1996). Those authors attributed this to variations in sediment structure and composition, because infauna are known to be sensitive to the grain size and organic content of their habitat (Newell 1977). However, as Field *et al.* (1995, 1996) pointed out, some of their results could have indicated localized natural disturbance. This would account for the observations made here during dives such as 20 and 24 (Table II), where extensive areas of hard substrata were without any notable epifauna. The present study area has been closed to demersal fishing activities since 1990, and so this argument cannot be used to account for the observed heterogeneity.

A high degree of spatial variability in the composition and structure of benthic communities in deep-sea environments has frequently been reported (see Gage

Table IV: Significance ( $p$ ) of slope parameters ( $B$ ) between abundance of demersal nekton and the various substratum features of the environment, calculated using multiple regression analysis. Emboldened data are significant at the 95% level. Also shown are the correlation coefficients for the multiple regression model ( $r^2$ )

Parameter	Species									
	Goby		False jacobever		Kingklip		Cuttlefish		Hake	
	$B$	$p$	$B$	$p$	$B$	$p$	$B$	$p$	$B$	$p$
Intercept		0.06		0		<b>0.02</b>		0.12		<b>0</b>
Soft sand	<b>0.81</b>	<b>0</b>	0	0.97	0.01	0.83	<b>0.4</b>	<b>0</b>	<b>0.79</b>	<b>0</b>
Shelly sand	-0.03	0.43	-0.12	0.09	0.01	0.9	0.02	0.73	-0.02	0.62
Shell debris	<b>-0.14</b>	<b>0.03</b>	<b>-0.23</b>	<b>0</b>	0.08	0.3	<b>-0.16</b>	<b>0.04</b>	-0.04	0.37
Pebbles	-0.06	0.2	0.12	0.14	0.08	0.32	-0.11	0.15	<b>-0.17</b>	<b>0</b>
Cobbles	-0.06	0.2	0.05	0.54	-0.27	0	0.05	0.48	0.06	0.23
Gravel	-0.05	0.42	0.05	0.45	-0.05	0.48	0.02	0.74	-0.06	0.15
Rock debris	-0.02	0.68	0	0.98	<b>0.14</b>	<b>0.02</b>	<b>-0.22</b>	<b>0</b>	<b>-0.15</b>	<b>0</b>
Boulders	<b>-0.11</b>	<b>0.01</b>	<b>0.3</b>	<b>0</b>	<b>0.2</b>	<b>0</b>	<b>0.2</b>	<b>0</b>	<b>-0.13</b>	<b>0</b>
Clay	0.02	0.58	<b>-0.17</b>	<b>0.02</b>	0.09	0.21	-0.06	0.39	<b>0.1</b>	<b>0.04</b>
$n$	359		392		392		392		502	
$r^2$	0.56		0.09		0.11		0.18		0.51	

$n$  = Number of observations

and Tyler 1991 and references therein). This variability has been attributed to habitat heterogeneity, as well as to patch dynamics associated with biological and physical disturbance. Although the data presented here do not permit any comment on structuring forces, similar disequilibrium explanations are likely to hold good, especially for the infaunal communities.

In comparison with bottom trawl survey data elsewhere along the west coast of southern Africa (e.g. Roel 1987), the densities of demersal fish and squid observed on the videotapes were low. The present sampling area is not generally considered to be good fishing grounds (Bruton 1996), and the abundance and diversity of the assemblage might therefore not adequately describe the fauna. On the other hand, the low numbers observed might reflect sample avoidance. However, few species of nekton appeared to flee the submersible, until the vessel was very close to them. Indeed, squid and horse mackerel were attracted to the lights at the front of the submersible (and so have been ignored in the analyses), whereas kingklip were observed to partially move out of their retreats in order to feed on organisms disturbed by it. These results contrast with comparative estimates of abundance derived by trawl and remotely operated vehicle (ROV) surveys conducted along the Pacific coast of North America (Adams *et al.*, 1995), where estimates of abundance generated from the ROV (which was of a similar width to the *Jago*) were higher (with lower CVs) than those obtained from trawls.

It is more likely that the low number of species and individuals observed here reflects the relatively small size of the sample. Research trawls on the West Coast are typically conducted for 30 minutes, at a towing speed of 5 knots, using German trawl gear with a horizontal mouth opening of 45–55 m. This provides a sampling area of approximately 230 000 m<sup>2</sup> per trawl. By comparison, the total area sampled by the *Jago* in this study was about 5 800 m<sup>2</sup>.

The diversity of communities along the west coast of southern Africa tends to be low (Emanuel *et al.* 1992, Gibbons and Hutchings 1996) owing to the dynamic and variable nature of the system. In the case of seabed assemblages, there may be additional stress of low-oxygen bottom water that sometimes occurs over the continental shelf (Stander 1964, De Decker 1970).

Despite the discrepancy in effective sample size, the dominant species observed here were the same as those commonly found in trawl catches throughout the Benguela (Macpherson and Roel 1987, Roel 1987, Smale *et al.* 1993). Interestingly though, while hake and kingklip are indicative of shelf-edge and slope assemblages on the South Coast (Smale *et al.* 1993), they become conspicuous components of the

shelf fauna along the West Coast (Roel 1987). The presence of large numbers of goby is not unusual for the shelf region of the northern Benguela in this region (Macpherson and Roel 1987, Roel 1987), although they are scarce farther south (Roel 1987).

Although Smale *et al.* (1993) could not determine the role that substratum type has in structuring local fish assemblages, the association between the physical features of the seabed environment and the demersal species observed directly here is similar to that deduced indirectly from commercial trawling. Juvenile hake are found closer inshore than adults (Botha 1985, Badenhorst and Smale 1991), and trawl records suggest that they are associated with soft substrata (Smale 1992), as too are gurnards. Whereas kingklip are frequently caught as a bycatch of the hake-directed trawl fishery, they are known to prefer rocky areas (Badenhorst 1988), where they are particularly susceptible to the longline fishery (Punt and Japp 1994). False jacobever is a poorly known species in local waters; other members of this genus are known as rockfish, owing to their association with rocky areas (Krieger 1993). The significance of each substratum feature to the different fish species is largely unknown, although it is likely a combination of shelter and food.

#### ACKNOWLEDGEMENTS

We thank Messrs Z. Fakier, G. Isaacs and N. Gasant (University of the Western Cape) for their help in the preliminary work for this study and for entering data onto the computer. Dr R. L. Tilney and Mr M. J. Roberts (both Marine & Coastal Management) are thanked for their comments on an earlier draft of the manuscript. The staff of the Drawing Office of the Mineral Resources Unit of De Beers Marine (Pty) Ltd are thanked for their patient delivery of maps and images. We are also grateful to the personnel of the M.V. *Zealous* for their hospitality at sea. De Beers Marine (Pty) Ltd and the University of the Western Cape are gratefully acknowledged for their financial support of the project. This manuscript has benefited greatly from the inputs provided by three anonymous referees.

#### LITERATURE CITED

- ADAMS, P. B., BUTLER, J. L., BAXTER, C. H., LAIDIG, T. E., DAHLIN, K. A. and W. W. WAKEFIELD 1995 — Population estimates of Pacific coast groundfishes from video transects and swept-area trawls. *Fishery Bull., Wash.*

- 93: 446–455.
- BADENHORST, A. 1988 — Aspects of the South African long-line fishery for kingklip *Genypterus capensis* and the Cape hakes *Merluccius capensis* and *M. paradoxus*. *S. Afr. J. mar. Sci.* **6**: 33–42.
- BADENHORST, A. and M. J. SMALE 1991 — The distribution and abundance of seven commercial trawlfish from the Cape south coast of South Africa, 1986–1990. *S. Afr. J. mar. Sci.* **11**: 377–393.
- BOTHA, L. 1985 — Occurrence and distribution of Cape hakes *Merluccius capensis* Cast. and *M. paradoxus* Franca in the Cape of Good Hope area. *S. Afr. J. mar. Sci.* **3**: 179–190.
- BRUTON, M. 1996 — Assessment of impact on fishes. In *Impacts of Deep Sea Diamond Mining, in the Atlantic 1 Mining Licence Area in Namibia, on the Natural Systems of the Marine Environment*. University of Cape Town; *EEU Rep.* **11/96/158**: 154–164.
- CUSHING, D. H. 1971 — Upwelling and the production of fish. *Adv. mar. Biol.* **9**: 255–334.
- DE DECKER, A. H. B. 1970 — Notes on an oxygendepleted subsurface current off the west coast of South Africa. *Investl Rep. Div. Sea Fish. S. Afr.* **84**: 24 pp.
- EMANUEL, B. P., BUSTAMANTE, R. H., BRANCH, G. M., EEKHOUT, S. and F. J. ODENDAAL 1992 — A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 341–354.
- FELLEY, J. D. and M. VECCHIONE 1995 — Assessing habitat use by nekton on the continental slope using archived videotapes from submersibles. *Fish. Bull., Wash.* **93**: 262–273.
- FIELD, J. G., WICKENS, P. A., SAVAGE, C. and H. WINCKLER 1995 — Diamond mining by De Beers Marine, impact on benthic organisms. Phase 2 Final Report. In *De Beers Marine Deep Sea Diamond Mining Initial Monitoring Report*. University of Cape Town. *EEU Rep.* **11/95/143**: 16 pp.
- FIELD, J. G., PARKINS, C. A., WINCKLER, H., SAVAGE, C. and K. VAN DER MERWE 1996 — Impact on benthic communities. In *Impacts of Deep Sea Diamond Mining, in the Atlantic 1 Mining Licence Area in Namibia, on the Natural Systems of the Marine Environment*. University of Cape Town; *EEU Rep.* **11/96/158**: 241–281.
- GAGE, J. D. and P. A. TYLER 1991 — *Deep-Sea Biology: a Natural History of Organisms at the Deep-Sea Floor*. Cambridge; University Press: 504 pp.
- GIBBONS, M. J. and L. HUTCHINGS 1996 — Zooplankton diversity and community structure around southern Africa, with special attention to the Benguela upwelling system. *S. Afr. J. Sci.* **92**: 63–76.
- GIGUÈRE, M. and S. BRULOTTE 1994 — Comparison of sampling techniques, video and dredge, in estimating sea scallop (*Placopecten magellanicus*, Gmelin) populations. *J. Shellfish Res.* **13**: 25–30.
- KRIEGER, K. J. 1993 — Distribution and abundance of rockfish determined from a submersible and by bottom trawling. *Fishery Bull., Wash.* **91**: 87–96.
- MACPHERSON, E. and A. GORDOA 1992 — Trends in the demersal fish community off Namibia from 1983 to 1990. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 635–649.
- MACPHERSON, E. and B. A. ROEL 1987 — Trophic relationships in the demersal fish community off Namibia. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 585–596.
- NEWELL, R. C. 1977 — *The Biology of Intertidal Animals*. Faversham, Kent; Marine Ecological Surveys: 781 pp.
- PAYNE, A. I. L., BRINK, K. H., MANN, K. H. and R. HILBORN (Eds) 1992 — *Benguela Trophic Functioning*. *S. Afr. J. mar. Sci.* **12**: 1–1108.
- PAYNE, A. I. L., GULLAND, J. A. and K. H. BRINK (Eds) 1987 — *The Benguela and Comparable Ecosystems*. *S. Afr. J. mar. Sci.* **5**: 957 pp.
- PUNT, A. E. and D. W. JAPP 1994 — Stock assessment of the kingklip *Genypterus capensis* off South Africa. *S. Afr. J. mar. Sci.* **14**: 133–149.
- ROEL, B. A. 1987 — Demersal communities off the west coast of South Africa. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 575–584.
- SIBUET, M., JUNIPER, S. K. and G. PAUTOT 1988 — Cold-seep benthic communities in the Japan subduction zones, geological control of community development. *J. mar. Res.* **46**: 333–348.
- SMALE, M. J. 1992 — Predatory fish and their prey – an overview of trophic interactions in the fish communities of the west and south coasts of South Africa. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 803–821.
- SMALE, M. J., ROEL, B. A., BADENHORST, A. and J. G. FIELD 1993 — Analysis of the demersal community of fish and cephalopods on the Agulhas Bank, South Africa. *J. Fish Biol.* **43**(Suppl. A): 169–191.
- STANDER, G. H. 1964 — The Benguela Current off South West Africa. *Investl Rep. mar. Res. Lab. S.W. Afr.* **12**: 43 pp. + Plates 5–81.
- STUTTAFORD, M. (Ed.) 1998 — *Fishing Industry Handbook. South Africa, Namibia and Moçambique*, 26th ed. Cape Town; Edina Griffiths: 438 pp.