

Abstract—Videotapes collected by the research submersible *Jago* in the Benguela ecosystem during spring 1997 were analyzed to determine demersal nekton assemblage composition, fish behavior, and microscale habitat association, and habitat selection. Demersal fish assemblage diversity was generally low, and their composition was a function of substratum type. Individual species showed an often marked association with either rocky or soft substrata (or both), and a strong or weak selection for the associated biota. Soles and dragonets actively selected areas of bioactive soft substrata, to which they are behaviorally and morphologically adapted. False jacobever were associated with crevices in areas of high-relief rocky substrata. Kingklip are piscivorous and were largely confined to holes at the base of rocks and favored areas without a conspicuous epifauna. Juvenile hake and gobies avoided extremely rocky areas and were largely indifferent to the presence of benthic invertebrates—behavior that is consistent with their planktonic diets. These results represent the first direct observations of demersal nekton in the region and are important because they allow better interpretations of the results of trawl studies.

Habitat use by demersal nekton on the continental shelf in the Benguela ecosystem, southern Africa.

Mark J. Gibbons

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

André J. J. Goosen

Patti A. Wickens

De Beers Marine (Pty) Ltd.
PO Box 87
Cape Town 8000, Republic of South Africa

The Benguela ecosystem is characterized by dynamic coastal upwelling (Shannon, 1985). It is among the most productive ecosystems in the world (Cushing, 1971) and supports several commercially valuable pelagic and demersal fisheries. Although we have a fairly good understanding of the role that the physical and biological environment play in influencing pelagic fishes (see references in Payne et al., 1987, 1992), the same cannot be said for the demersal species.

Although phytoplankton biomass and production in the Benguela ecosystem are high (Brown et al., 1991), there is a large mismatch with zooplankton (Hutchings, 1992) that results in significant sedimentation (Hutchings, 1992), and periodic anoxia on the bottom (Bailey and Rogers, 1997). Bottom currents are generally sluggish to the south (Shannon, 1985), and the seafloor is characterized by quartz sands, diatomaceous ooze, and foraminiferal deposits (Bailey and Rogers, 1997). Trawl studies have revealed that demersal fish diversity in the region is low and that assemblages can be subdivided into those inhabiting neritic, shelf, and slope areas (Macpherson and Roel, 1987; Roel, 1987; Macpherson and Gordoa, 1992; Smale et al., 1993). Correlations between demersal assemblages and the biophysical milieu (including landscape) have not

been made owing to the general lack of environmental data, especially at the microscale.

Submersibles provide a way to sample and observe the biophysical environment of the sea floor. Although the method precludes an appreciation of the infauna, the technique allows for the simultaneous collection of information on the macroscopic benthic fauna and fishes, as well as on the physical features of the environment, across a wide variety of substrata. Elsewhere in the world, submersibles have been used to describe the physical and biological environment of benthic communities (Sibuet et al., 1988) to determine habitat use by nekton (Parker and Ross, 1986; Felley and Vecchione, 1995) and in data collection for stock assessment (Parker and Ross, 1986; Giguère and Brulotte, 1994).

During 1996, the research submersible *Jago* was used to examine some offshore areas near the mouth of the Orange River. A total of 17 dives were made and the archived videotapes were subjected to semiquantitative biological analysis (Gibbons et al., 2000). The *Jago* was commissioned again (by De Beers Marine [Pty.] Ltd.) in 1997 to collect a larger number of higher quality videotapes from the same area. In this article, we report on microscale habitat association and habitat selection by

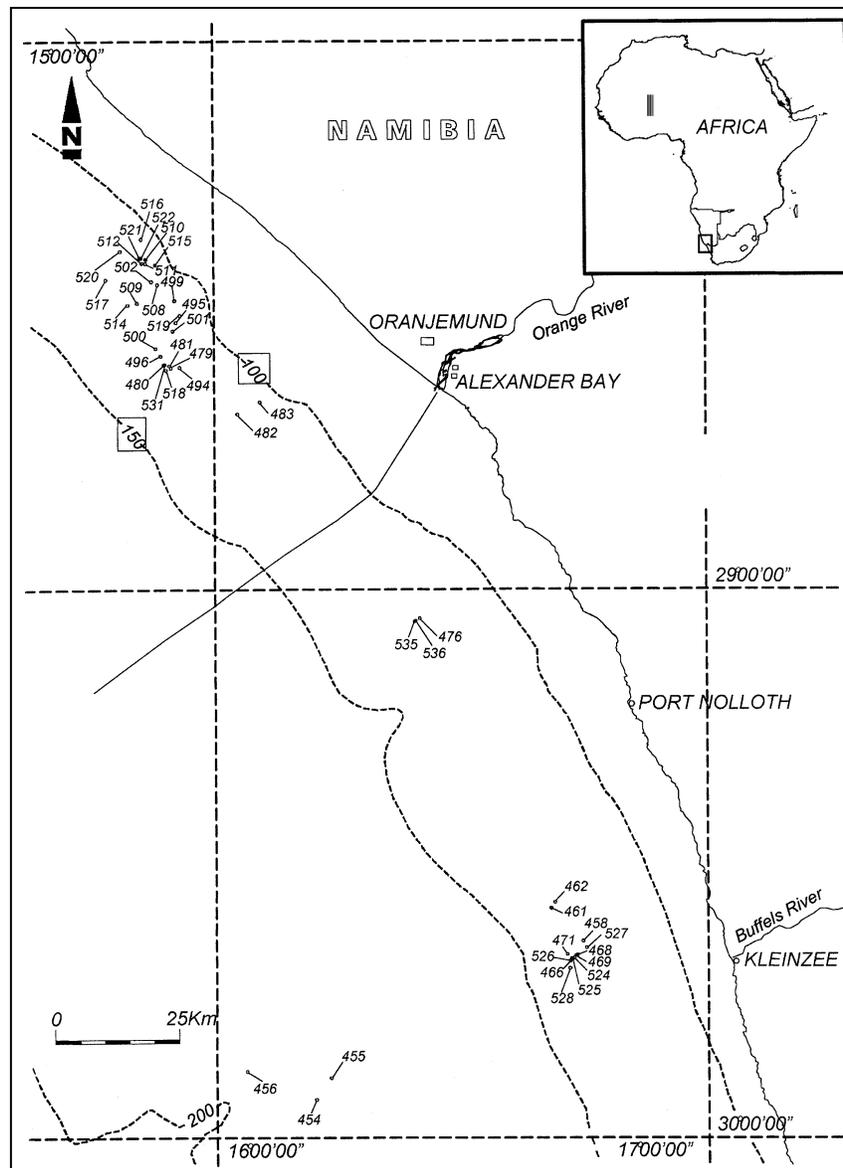


Figure 1

Map of the study area showing location of the dive sites and bathymetry. Numbers represent *Jago* dive numbers.

the common demersal nekton from these videotapes and examine fish behaviors and demersal fish assemblages.

Materials and methods

Field sampling

Videotapes of 44 diving sites in the Orange River delta area between 28°15'S and 29°40'S were analyzed. Surveys were conducted at depths between 100 and 140 m in the middle shelf (Fig. 1). Twenty-six dives were conducted north of the river mouth, and 18 were conducted to the south.

The submersible was launched from a support ship (MV *Zealous*) and towed by an inflatable dinghy to the first way-point of each dive survey. The position of the submersible was tracked every 31 seconds by using an acoustic transponder array. Accuracy of the positioning system was within approximately 5.0 m. A fairly detailed track-chart of the dive was produced and overlaid onto maps of underlying bathymetry.

Videotapes were recorded as the submersible cruised along the seabed (generally at speeds of 0.25 knots) by using a digital video camera. The camera usually faced forward and downward through the front acrylic dome-window and was only occasionally panned or moved during the survey. The submersible stopped at times, either so

Table 1

Distribution of number of samples (n) and area (m^2) in the different areas, among the major substratum types (by nature). Sand = soft sand, of variable texture and topography. With or without biogenic holes. Depth variable. Bioturbation maybe evident. Cobbles = fist-size rocks of claystone, sandstone, or quartzite. Of smooth and rounded appearance. Scattered or aggregated (sometimes densely) on sediment surface, and occasionally projecting through. With or without sediment layer or epifauna. Rock debris = smaller than boulders but larger than cobbles or gravel. Generally of irregular shape and not always smooth. Composed of sandstone or claystone. May project through, or sit on, sediment surface. Scattered or aggregated densely. With or without sediment on upper face. Epifauna maybe present. Boulders = massive, freestanding outcrops of rock, of high vertical relief, generally projecting through the sediment surface. Composed of either sandstone or claystone. Usually with some sediment on upper face. With or without encrusting fauna. Flat bedrock = slab-like sandstone or claystone rock of low vertical relief (<0.5 m), on sediment surface, usually with a thin sediment layer over upper surface. Epifauna on edges.

Major substratum	Substratum nature	North		South	
		n	Area	n	Area
Boulders	hard	3	61.53	1	12.41
Cobbles	hard	12	250.62	0	0
Cobbles	mixed	10	333.71	0	0
Rock debris	hard	40	1008.02	13	239.00
Flat bedrock	hard	9	199.86	0	0
Sand	mixed	97	3158.03	11	316.04
Sand	soft	80	2279.27	105	2123.85

that samples could be collected or to zoom in on particular features, and at other times it moved away from the bottom. Videotape recorded during these times, and when visibility was impaired due to silt disturbance, was not examined. The camera was rarely operated for the full duration of any one dive, and its use depended largely upon the interest of the geological observer. The video camera was equipped with a clock that was synchronized to that aboard the support vessel, so that it was possible to relate sections of the videotape to the actual position of the submersible on the dive-track. Illumination of the sea floor was provided by five 150-W halogen projectors arranged along a bar above the dome-window. A pair of red lasers (positioned 50 cm apart) were projected onto the sea floor to provide a moving scale.

Although the entire videotape from each dive was inspected, only samples of videotape were examined in detail and analyzed. The samples from each tape met the following criteria:

- 1 they were recorded along linear sections of the dive-track, as determined from the track-chart (to avoid looping and re-examination of previously sampled areas);
- 2 the submersible was moving at a slow (0.25 knots) but constant speed; and
- 3 there was no suspended sediment to impair visibility.

Samples were in multiples of selections that were 31 seconds in length. The bottom cover in each sample was first categorized by major (>50%) and subsidiary (>20%) substratum type (see descriptions in legend to Table 1), and then all sedentary biological features were recorded (as present or absent). A total of 381 samples was analyzed, most of which

were in the northern area (Table 1). All nekton were identified and counted. Counts were subsequently converted to densities (m^2) with a knowledge of both the horizontal distance traversed by the *Jago* (calculated from the dive track with Autocad [Autodesk Inc., 1988]), and the width of the video-frame (calculated by using the distance between the two lasers, approx. 1–1.5 m).

Statistical analysis

Associations with environmental features The association between nekton and features of the physical and biological environment was examined by following Felley et al. (1989) and Felley and Vecchione (1995). In each sample, the primary substratum was given a score of 0.75, and the subsidiary substratum was allocated a score of 0.25: sedentary biological features were scored as either 1 (present) or 0 (absent). The mean environment was then calculated for each species, after weighting values of each of the environmental variables in each sample by density of individuals in that sample. Samples where no individuals were seen, made no contribution (since they had a weight of 0), whereas samples where the species was abundant made a marked contribution to the species mean. The mean for a variable reflected the relative state of that variable in samples where the species was most likely to be found, and can be thought of as its preference for that variable. A correlation matrix was then generated from all means for the measured environmental variables. Patterns of habitat use by species were reflected in patterns of interrelations among variables. Principal components analysis (PCA) was then performed on the correlation matrix. PCA resolves patterns of interrelationships among variables into a smaller set of composite variables (PCs) to which

observed variables (species abundances) were correlated. Each PC represents a particular trend in habitat use, and the axis differentiates among sets of species that are likely to be found in contrasting conditions for variables that define the PC. Because the PCs define axes, it is possible to plot species on these axes (using the PC scores) and thus identify those with contrasting or similar patterns of habitat use. Species with intermediate scores might be characteristic of intermediate environments, or they might be found over the entire range of environments reflected by a PC (because a species' score is the weighted mean of scores of samples where it was found). Habitat associations by demersal nekton were investigated separately from sites in the north and south because previous observations have suggested that areas to the north and south of the Orange River are distinct (Field et al., 1996).

Habitat selection by individual species can be determined by comparing species' variances on each PC with variance of the environment. Environmental variance on a PC was determined by calculating PC scores for each sample, following standardization with the appropriate mean of means, and standard deviation of means (see Felley and Vecchione, 1995). Then the scoring function was applied to each sample and the variance determined as the variance of sample scores. The score of each sample was assigned to each individual of all species seen in that sample. A species' variance was then calculated for each species as the variance of these scores. Levene's test was used to compare the species' variance with environmental variance. The null hypothesis invoked for these tests was "species" variance is not significantly different from environmental variance with respect to each factor." Active habitat selection by a species was inferred when a species variance was significantly smaller than the observed environmental variance (1-tailed test). This implies that the species was actively selecting a subset of the available environment with respect to that PC, i.e. species distribution in the study area was not random (see Felley et al., 1989). Comparisons of species variances with sample variances on each axis were performed only on the most common species, in each area because the sample sizes for most species were too small to allow statistically meaningful tests.

Assemblages Principal component analysis of the data revealed how species were distributed along composite environmental axes. Although species that are distributed in a similar way on a PC axis can be interpreted to share common responses to that axis, they do not necessarily occur together in the same assemblage. Alternative methods of analysis for examining species associations directly can be used to determine assemblage composition; as an alternative method, the software package PRIMER (Clarke and Warwick, 1994) was used in our study. With this software, descriptive, multivariate statistics allowed an examination of the relationships among the samples (based on similarities in specific composition of nekton) to determine how they were distributed with respect to the physical environment. Abundance of only those species that occurred in greater than 5% of the samples

were root-root transformed, and a similarity matrix was constructed between the samples containing two or more species by using the Bray-Curtis index (Field et al., 1982). These matrices were used to plot classification diagrams of percentage similarity between samples by means of group-average sorting (fuller details of this method are provided by Field et al., 1996). Owing to the small area filmed in individual videotape samples (mean 26.20 m², SD 11.24 m²), and the generally low density of most fish species, the samples were pooled (as in Dennis and Bright, 1988) by the nature of the substratum within a dive (hard, soft, mixed), so that replicates were of dives and not of individual videotape samples.

Activities In an effort to understand the behavior of demersal fishes in their natural environment, the activity of each demersal fish (on first sighting) was assigned to one of the following behavior patterns:

- 1 hovering off the substratum;
- 2 positioned on the substratum;
- 3 swimming in the water column;
- 4 positioned in a crevice or under an overhang;
- 5 occupying a shelter hole;
- 6 buried (fully or partially) in the substratum.

Observations of the substratum over which the fish was seen were also recorded, in the hope that it would be possible to correlate behaviors with the environment. The activity of each of the dominant species of demersal fishes was analyzed by using percent occurrence. This value was calculated by dividing the sum of all individuals observed in each activity (per major substratum type) by the total number of individuals of the species for which activities were recorded.

Results

Associations with environmental features

A total of 22 different taxa of demersal nekton were identified from the samples (Table 2). Eight of these were seen only once or twice, and only hakes occurred in more than 50% of the samples. The hakes were assumed to be *Merluccius capensis* on the basis of their inshore distribution (Roel, 1987). It was not always possible to clearly separate gobies, *Sufflogobius bibarbatus*, from dragonets, *Paracallionymus costatus*, and all cases of ambiguity were eliminated (i.e. only those fish that could be identified to species were included in the analyses).

Each species tended to be associated with slightly different features of the physical or biotic environment (or both).

North Eleven species were seen among these samples, and their mean environments are given in Table 3. PCA of the correlation matrix, generated from the mean environments of the six dominant species of nekton, produced three PCs with eigenvalues greater than one (Table 4). PC1 alone explained more than 60% of the variance in the

Table 2
Full list of all demersal nekton observed on the vidoetapes; * = observed once only.

Common name	Scientific name	Common name	Scientific name
Octopus	<i>Octopus vulgaris</i>	Kingklip	<i>Genypterus capensis</i>
Cuttlefish	<i>Sepia</i> spp.	Pelagic goby	<i>Sufflogobius bibarbatus</i>
Chokka squid	<i>Loligo vulgaris reynaudii</i>	Cape gurnard	<i>Chelidonichthys capensis</i>
Sixgill shark	<i>Hexanchus griseus</i> *	West coast sole	<i>Austroglossus microlepis</i>
Smooth hound	<i>Mustelus mustelus</i> *	Rough scale grenadier	<i>Caelorinchus simorhynchus</i>
Izak catshark	<i>Holohalaelurus regani</i>	Ladder dragonet	<i>Paracallionymus costatus</i>
St Joseph's shark	<i>Callorhinchus capensis</i> *	Cape dory	<i>Zeus capensis</i> *
Spearnose skate	<i>Raja alba</i> *	Monk	<i>Lophius vomerinus</i> *
Shallow-water Cape hake	<i>Merluccius capensis</i>	Cape conger eel	<i>Conger wilsoni</i> *
False jacoever	<i>Sebastes capensis</i>	Snoek	<i>Thyrstites atun</i> *
Jacoever	<i>Helicolenus dactylopterus</i>	Maasbanker	<i>Trachurus trachurus capensis</i>

data and contrasted species found over soft bio-active substrata (sole, *Austroglossus microlepis*, and to a lesser extent hakes) with those over more mixed and hard substrata (false jacoever, *Sebastes capensis*). The other species were located midway along this axis (Fig. 2).

PC2 accounted for almost 25% of the variance in the data set (Table 4). The significant loadings on the environmental variables essentially contrasted broken expanses of hard substrata (cobbles, and the biota associated with more open areas) with unbroken expanses of "lifeless" bedrock (Table 4). Those species that were previously contrasted along the PC1 axis were grouped together (false jacoever and sole) and set against those that were positioned midway between them (kingklip, *Genypterus capensis*, and goby) (Fig. 2).

PC3 was responsible for almost 10% of the variance in the data set (Table 4). It can be interpreted in terms of biological richness and contrasted gobies and soles with kingklip and hake (Table 4).

South A total of 10 species were seen in these samples, and their mean environments are given in Table 5. PCA of the correlation matrix generated from the dominant species' means produced four PCs with eigenvalues greater than one (Table 6). The first two PCs explained almost 75% of the variance in the data, although PC1 extracted only ~60%. A clear trend that differentiated the species was determined by PC1, which contrasted dragonets and soles with kingklip and false jacoever (Fig. 2). The loadings on the variables of PC1 (Table 6) opposed hard substrata and their associated epifauna at one extreme with sand and its associated organisms and structures at the other. PC2 contrasted gobies, kingklip, and hake with false jacoever and, to a lesser extent, jacoever, *Helicolenus dactylopterus* (Fig. 2). Interpretation of this PC is difficult because few

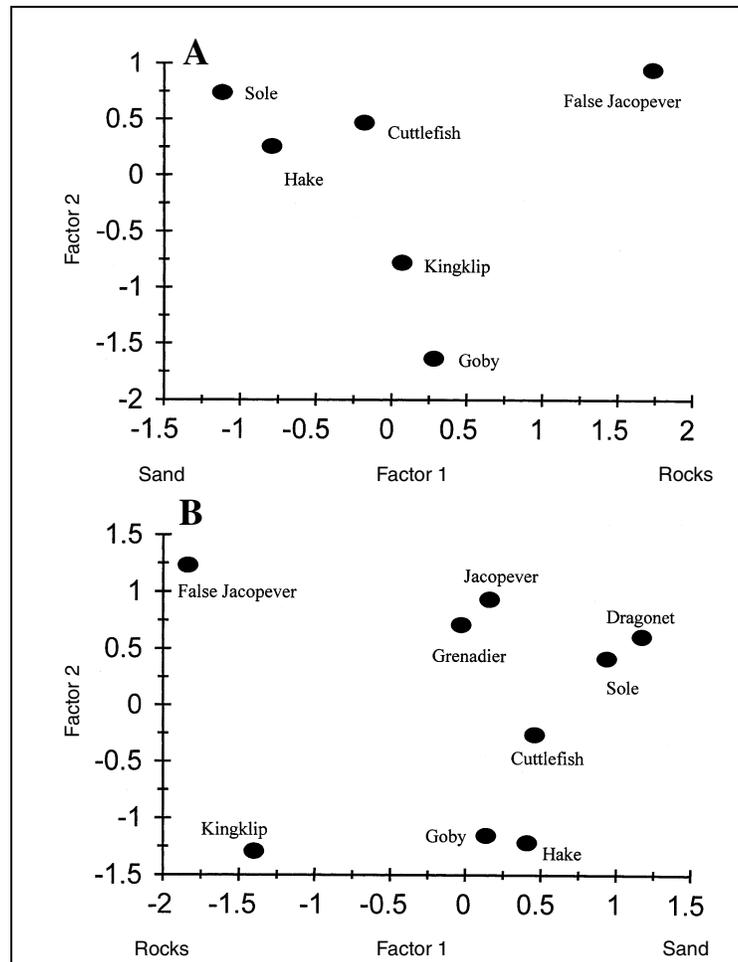


Figure 2

Distribution of species scores along the first and second axes representing habitat use by nekton species in the sites to the north (A) and south (B) of the Orange River mouth. PC1 (north and south) represented habitat use according to hard and soft substrata. PC2 (north) corresponded to the broken or continuous nature of the substratum, and PC2 (south) represented biological richness (see text).

Table 3

Species means for environmental variables in the undisturbed sites in the northern sampling area. Also given are the sample means total number of individuals of each species seen in samples (*n*). Data in bold typeface indicate those species used in the principal components

Species	Samples	Area	<i>n</i>	Sand	Cobbles	Debris	Boulders	Bedrock	Mounds
Hake	177	5569.47	561	0.8266	0.0602	0.0971	0.0058	0.0102	0.9430
False jacobever	34	931.3	40	0.3750	0.1188	0.3750	0.0750	0.0563	0.7000
Jacobever	1	18.93	1	0.2500	0	0	0	0.7500	1
Kingklip	21	601.555	23	0.6087	0.0326	0.3261	0	0.0326	0.9565
Goby	21	604.98	25	0.5000	0.0300	0.3500	0	0.1200	0.8000
Gurnard	4	88.2	4	0.8125	0	0.1875	0	0	1
Sole	11	484.99	11	0.7727	0.1591	0.0682	0	0	1
Grenadier	1	18.41	1	0	1	0	0	0	0
Dory	1	20.04	1	0.7500	0	0.2500	0	0	1
Octopus	4	94.86	4	0.6250	0.0625	0.3125	0	0	0.7500
Cuttlefish	114	3721.355	183	0.7281	0.1011	0.1380	0.0041	0.0287	0.8852
Environment	251	7291.03	251	0.6434	0.1116	0.1922	0.0149	0.0378	0.8207

Table 4

Eigenvalues generated from the principal components analysis (PCA) of the species means in the northern study site, using the dominant species only (Table 3). PC loadings of environmental means, and PC scores of the dominant species are also shown. The representations below are of the unrotated principle components. PC loadings greater than 0.50 are in bold typeface. F1, F2, F3 refer to factors 1–3, respectively, generated by the PCA.

	F1	F2	F3
Eigenvalue	9.14	3.481	1.40
% Total variance	60.95	23.21	9.33
Cumulative eigenvalue	9.14	12.62	14.02
Cumulative % variance	60.95	84.15	93.48
Sand	-0.98	0.18	0.11
Cobbles	0.34	0.89	-0.18
Rock Debris	0.92	-0.37	0.02
Boulders	0.83	0.49	-0.05
Bedrock	0.53	-0.77	-0.32
Mounds	-0.92	-0.10	0.21
Holes	-0.83	-0.47	0.07
Tracks	-0.55	-0.33	-0.71
Bryozoans	0.93	-0.25	0.20
Ascidians	0.81	-0.21	-0.51
Sponges	0.94	-0.10	-0.14
Cerianthids	0.54	0.62	0.15
Corals	0.82	0.55	-0.03
Asteroids	-0.80	0.54	-0.25
Hake	-0.79	0.26	0.92
False Jacobever	1.73	0.94	-0.20
Kingklip	0.07	-0.78	1.26
Goby	0.28	-1.63	-1.04
Sole	-1.12	0.74	-1.18
Cuttlefish	-0.18	0.47	0.23

of the environmental variables had significant loadings (Table 6); however, it would appear to reflect some level of biological richness.

PC3 accounted for 13% of the variance in the data set (Table 6), whereas PC4 was responsible for only 7%. The significant loadings on the environmental variables of the former contrasted the biota on hard substrata of high relief (boulder and reefs) with the biota of low relief areas (Table 6). PC4 contrasted (much of) the biota with the substrata, although few of the environmental variables had significant loadings (Table 6).

Selection of environmental features

The observed associations between nekton and the bio-physical environment were often due to active selection. In the north only hake selected subsets of the available environment based on major substratum type (and its associated biota) (Table 7). This species avoided the rocky extremes, but otherwise showed a pattern of distribution that resembled that of the samples (Fig. 3A). Although false jacobever and hake selected opposite environments based on the broken or unbroken nature of the rock debris (PC2), it would appear that hakes again tended to avoid the extremes (Fig. 3, B and C). The other environmental PCs were not significantly selected for by any species.

Although interpretation of the results generated from the northern data set is confounded by the (mixed) nature of the samples (see Table 1), the same problems did not hamper the data from the south. In the south, six species of demersal nekton selected subsets of the available environment based on the identified axes (Table 7). Hake, goby, sole, and dragonet all appeared to select their environments on the basis of general physical features (PC1). As in the northern area, hake did not show a strong selection for axis extremes (e.g. Fig. 4A), which in itself could mean that hake did not favor very rocky or sandy areas. Dragonets and sole

for each variable, the total number of samples in which each species was seen, and the total area that these represented, as well as the analysis (PCA) (Table 4).

Holes	Tracks	Bryozoans	Ascidians	Sponges	Anemones	Cerianthids	Corals	Asteroids
0.9964	0.0392	0.7023	0.3636	0.6720	0.4920	0.0089	0.0053	0.0784
0.9000	0	1	0.8000	0.9000	0.5000	0.0250	0.0500	0
1	0	1	0	1	1	0	0	0
1	0	0.9130	0.5652	0.7826	0.5652	0	0	0
1	0.0800	0.8800	0.7600	0.8000	0.5600	0	0	0
1	0	0.7500	0	0.7500	0.7500	0	0	0
1	0.0909	0.7273	0.6364	0.8182	0.2727	0	0	0.0909
1	0	1	1	1	1	0	0	0
1	0	1	1	1	0	0	0	0
1	0	0.7500	0.5000	0.7500	0.2500	0	0	0
1	0.0219	0.8033	0.5574	0.7596	0.4262	0.0219	0.0109	0.0601
0.9482	0.0398	0.8048	0.5458	0.7610	0.5219	0.0120	0.0080	0.0478

showed distinct preferences for environments with sandy substrata (Fig. 4, B and C) and were absent from rockier areas. Dragonets and cuttlefish (*Sepia* sp.) appeared to select opposite environments along the PC2 axis, with the former favoring areas with echinoderms and sponges and the latter avoiding them. Hake again appeared to avoid extremes of environment along the PC3 axis, whereas false jacobever selected areas of high relief substrata (Fig. 4, D and E). The results suggest that hake selected areas without cerianthids (and other biota, PC4), whereas dragonet preferred areas with cerianthids (Table 7).

Assemblages

Assemblage composition was a function of substratum type. Cluster analysis of the similarity matrices generated between samples among all the data indicated a similarity in assemblage composition that was generally based on major substratum type (data not shown). These patterns were mirrored in separate analyses of the samples (Fig. 5, A and B). The communities were not always distinct, however, and samples from hard substrata were sometimes grouped with those from mixed, and even soft, substrata. A noteworthy feature of these data was the generally low level of similarity between samples, and this undoubtedly reflected their small individual size (area) and the low density of nekton.

The dendrogram produced by analysis of the species (and not sample) matrix revealed common patterns of association in both the northern and southern areas (Fig. 6, A and B). In the northern area, there were two clusters at the 30% level of similarity (with sole as an out-group) (Fig. 6A). This result is difficult to interpret clearly because the one group comprised species of both soft (hake and cuttlefish) and hard (false jacobever) substrata. These species were also the most abundant and thus the likelihood of their co-occurrence in samples was high. In the south,

two groups of associated species were also observed at the 30% level of similarity. The association between hake and cuttlefish was again tight, and both were more distantly linked to false jacobever (Fig. 6B). The other group comprised two clusters at the 40% level of similarity: one of gobies and grenadiers, *Caelorinchus simorhynchus*, and the other of species from soft (dragonets and sole) and mixed substrata.

Activities

None of the dominant species appeared to be either attracted to, or repelled by, the presence of the submersible and its lights, and avoidance behavior was seen only at the moment when the submersible was directly over the fishes.

Few of the fishes seen were actually swimming (behavior pattern 3), and most were resting on the substratum itself (Fig. 7). Indeed, all gobies and soles were seen lying on the substratum. Grenadiers seemed to hover above the substratum, and false jacobever and kingklip appeared to be situated in some sort of shelter. Although a few individual hake, kingklip, and dragonets buried themselves in sand, this behavior was otherwise uncommon. Most of the fish seemed to behave in a similar way over hard and soft substrata. The exceptions to this were kingklip and grenadiers, which tended to hide and rest, respectively, more often over hard substrata rather than soft (Fig. 7).

Discussion

The demersal nekton assemblages over the continental shelf along the west coast of southern Africa are clearly structured in a way that reflects the substratum type. This assemblage composition is in part due to the responses of individual species to the environment. These are novel observations for the region, and they provide a baseline

Table 5

Species means for environmental variables in the undisturbed sites in the southern sampling area. Also given are the sample means total number of individuals of each species seen. Data in bold typeface indicate those used in the PCA (Table 6). T-worms = tube worms.

Species	Fish no.	Samples	Area	Sand	Debris	Boulders	Reefs	Mounds	Holes	Tracks
Hake	580	110	2285.12	0.987	0.013	0	0	0.794	1	0.331
False jacoever	16	15	347.61	0.581	0.312	0.080	0.027	0.446	0.893	0.142
Jacoever	7	6	115.09	0.827	0.173	0	0	0.821	1	0.526
Kingklip	4	4	82.73	0.564	0.436	0	0	0.111	1	0
Goby	14	13	312.42	0.930	0.070	0	0	1	1	0.412
Gurnard	4	3	67.00	0.901	0.099	0	0	0.250	1	0.250
Sole	24	22	414.27	1	0	0	0	0.967	1	0.599
Grenadier	15	14	243.65	0.668	0.332	0	0	0.750	1	0.661
Dragonet	110	50	853.44	1	0	0	0	0.988	1	0.613
Cuttlefish	172	84	1814.90	0.935	0.061	0.004	0	0.828	1	0.355
Environment	130	130	2691.29	0.868	0.118	0.012	0.003	0.717	0.981	0.400

Table 6

Eigenvalues generated from the PCA of the species means in the southern study site, using the dominant species only (Table 5). PC loadings of environmental means, and PC scores of the dominant species are also shown. The representations below are of the unrotated principle components. PC loadings greater than 0.50 are in bold typeface.

	F1	F2	F3	F4		F1	F2	F3	F4
Eigenvalue	10.11	2.56	2.27	1.11	Cerianthids	0.52	0.05	0.45	0.65
% Total variance	59.45	15.06	13.38	6.54	Corals	-0.94	0.24	-0.05	0.03
Cumulative eigenvalue	10.11	12.67	14.94	16.05	Asteroids	0.72	0.15	0.43	0.36
Cumulative % variance	59.45	74.50	87.88	94.42	Ophiuroids	0.29	0.50	-0.65	-0.30
Sand	0.91	-0.17	0.30	-0.19	Echinoids	0.60	0.52	-0.43	0.28
Rock Debris	-0.85	0.08	-0.44	0.24	Tube worms	-0.90	-0.36	-0.02	0.02
Boulders	-0.68	0.46	0.54	-0.16	Hake	0.41	-1.21	0.47	-0.63
Reefs	-0.69	0.46	0.52	-0.17	False jacoever	-1.84	1.23	1.40	-0.46
Mounds	0.87	0.17	0.16	-0.34	Jacoever	0.16	0.94	-1.41	-0.77
Holes	0.69	-0.46	-0.52	0.17	Kingklip	-1.40	-1.29	-0.83	1.24
Tracks	0.80	0.45	-0.24	-0.13	Goby	0.14	-1.15	0.27	-1.33
Bryozoans	-0.99	0.07	0.01	0.02	Sole	0.94	0.42	0.11	-0.70
Ascidians	-0.94	0.08	-0.24	0.21	Grenadier	-0.03	0.72	-1.42	0.30
Sponges	0.07	0.96	-0.10	0.20	Dragonet	1.17	0.61	0.84	1.48
Anemones	-0.98	-0.06	-0.14	0.00	Cuttlefish	0.46	-0.26	0.58	0.85

set of information that should allow a more meaningful interpretation of the results of the (more typical) trawl surveys for fishes.

Species accounts

False jacoever have been positively correlated with rocky areas from a previous study of the region (Gibbons et al., 2000). Members of the genus *Sebastes* are also known as rockfish and have been reported as common over deep

rocky reefs from video-surveys (Richards, 1986; Murie et al., 1994). They seem to prefer structured and high-relief reefs, and a partitioning of the habitat has been observed among congeners (Richards, 1986). Rockfish have been reported as scarce over soft sediments (Stein et al., 1992). Our results are consistent with those from previous studies.

Jacoever was the other scorpionid fish observed in our study. It was far less common than false jacoever and appeared to have a markedly different association with environmental features. Admittedly the sample size for

for each variable, the total number of samples in which each species was seen and the total area that these represented, as well as the

Bryozoans	Ascidians	Sponges	Anemones	Cerianthids	Corals	Asteroids	Ophiuroids	Echinoids	T-worms
0.120	0.022	0.701	0.189	0.011	0.028	0.085	0.018	0.062	0.345
1	0.668	1	0.784	0	0.641	0	0	0	0.511
0.333	0.333	1	0.333	0	0.333	0	0.209	0.138	0.155
0.794	0.794	0.794	0.794	0	0.474	0	0	0	0.570
0.358	0.094	0.745	0.390	0	0.094	0	0	0	0.306
0.645	0.395	0.645	0.250	0	0.395	0	0	0	0.605
0	0	0.979	0.030	0	0	0.220	0.095	0.094	0.084
0.372	0.333	1	0.413	0	0.162	0	0.080	0.203	0.331
0.024	0	1	0.024	0.053	0	0.277	0.021	0.161	0.012
0.203	0.115	0.900	0.158	0.041	0.130	0.125	0.022	0.093	0.271
0.279	0.175	0.825	0.300	0.020	0.141	0.115	0.028	0.065	0.290

Table 7

Distribution tests of individuals of different species on principal components describing environmental use by dominant demersal fishes in the northern and southern study sites. Levene's test of variance equality was used to compare species' variances with variance of samples on each principal component. X and XX indicate a species' variance significantly smaller than location variance at the $P < 0.10$ and $P < 0.05$ level, respectively (implying that the species uses a subset of available conditions relative to that principal component).

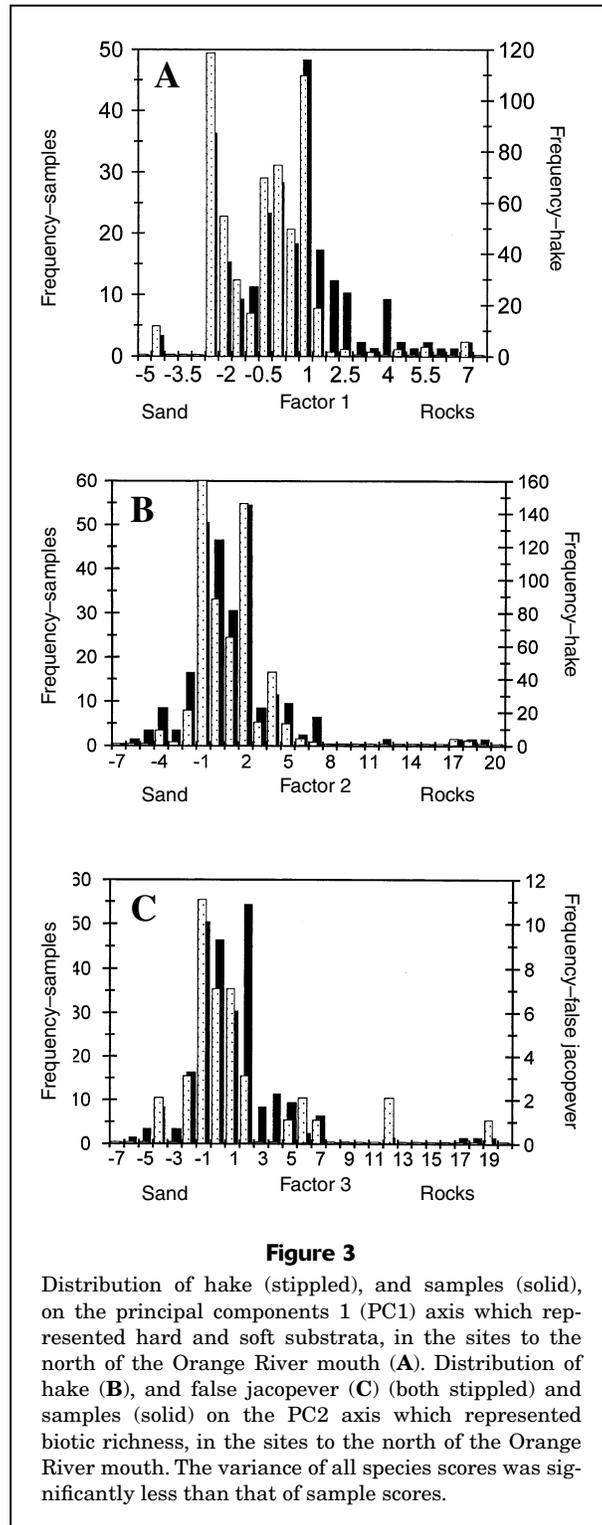
Species	PC1	PC2	PC3	Species	PC1	PC2	PC3	PC4
Hake	XX	XX		Hake	XX		XX	XX
False jacoever		XX		False jacoever			X	
Kingklip				Goby	X			
Goby				Sole	XX			
Sole				Grenadier				
Cuttlefish				Dragonet	XX	XX		X
				Cuttlefish		XX		

jacoever was very small, but it showed a weaker association with high-relief hard substrata and a greater association with more open areas. *Helicolenus dactylopterus* is a conspicuous species in trawl catches in the region (Roel, 1987), unlike *S. capensis*, and the difference in habitat use would explain this. Both species are likely to be largely piscivorous as adults (Macpherson and Roel, 1987; Meyer and Smale, 1991), and therefore the association of *S. capensis* with a rich epifauna is more likely an artifact of autocorrelation with hard substrata (per se) than real.

Kingklip have also been correlated with rock cover (Gibbons et al., 2000). Although it is a bycatch species of the commercial trawl fishery over (presumably) mixed grounds (Payne, 1985), a high CPUE is achieved by using long-lines over hard grounds (Badenhorst, 1988). This high CPUE could imply that it is found at greater densities over hard grounds and that the species shows some sort of preference

for rocky areas (as suggested by Japp, 1990). In his study of feeding patterns of kingklip, Macpherson (1983) suggested that it probably inhabited holes in the mud (or caves) during the daytime. Our observations indicated that this species hides in holes by day (Fig. 7C), but that these holes are generally at the base of rocks. Such a shelter provides them with ready access to their favored prey (demersal fishes) on the sandy areas surrounding (Macpherson, 1983; Macpherson and Roel, 1987) and would account for a lack of association with conspicuous mobile epifauna.

By contrast, sole have been observed by Stein et al. (1992) to favor areas of soft substrata and tend to be caught in greatest numbers there (Payne, 1985). Both sole and dragonets (Tables 4 and 6) certainly show morphological adaptations to this substratum type and are dorsoventrally flattened to a greater (sole) or lesser (dragonet) extent. These species were also associated with areas having



a rich infauna (Table 4), which probably reflects the strictly benthic nature of their diets (Macpherson and Roel, 1987).

An apparent lack of strong habitat preference has been observed by longfin hakes (*Urophycis chesteri*) off North Carolina (Felley and Vecchione, 1995). Although similar re-

sults were noted here for *Merluccius capensis* (e.g. Tables 4 and 6), this species tended to avoid the rocky extremes (as in Gibbons et al., 2000). Interestingly, the species was not associated with substrata that were conspicuously rich in either epifauna or infauna. However, because small hake

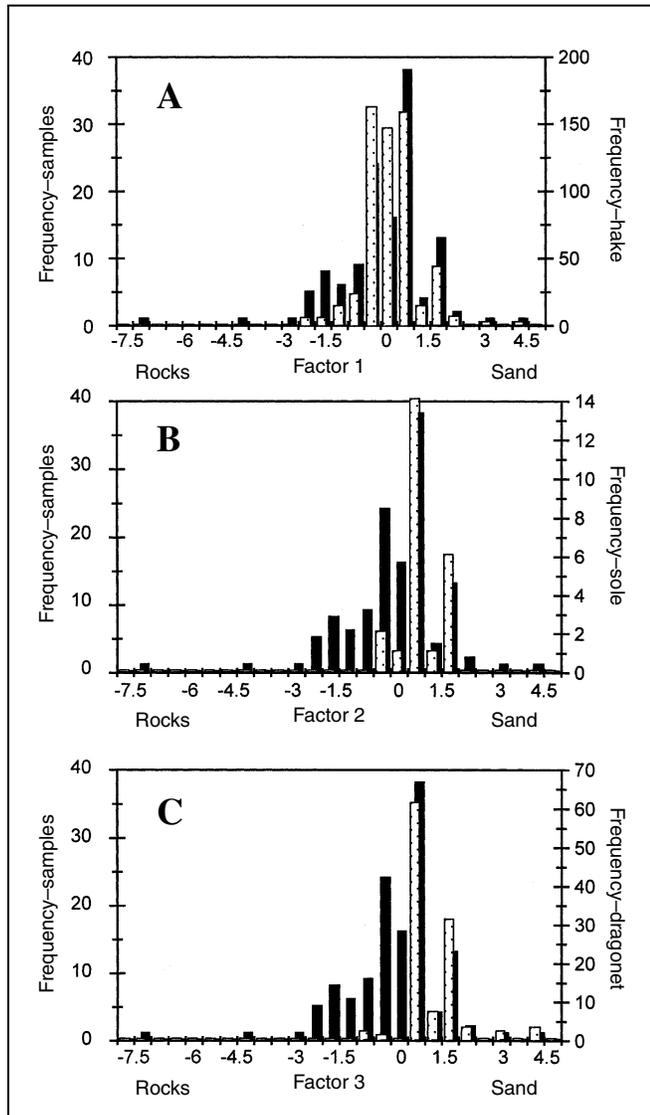


Figure 4

Distribution of hake (A), sole (B) and dragonet (C) (all stippled), and samples (solid) on the PC1 axis which represented hard and soft substrata, in the sites to the south of the Orange River mouth. Distribution of hake (D) and false jacoever (E)(both stippled), and samples (solid) on the PC3 axis which represented vertical structure, in the sites to the south of the Orange River mouth. The variance of all species scores was significantly less than that of sample scores.

display strong vertical migration at night and feed primarily on macrozooplankton (Pillar and Barange, 1995), a pronounced association with a benthic fauna need not be expected. Should the use of the demersal environment by hake during the day, therefore, simply be one of a place to rest, then the preference for sandy areas needs to be interpreted in terms of favored shelter. Our observations of hake behavior (Fig. 7A) indicated that most individuals were positioned immediately on the sand, although some were buried in the upper layers of the substratum. Under

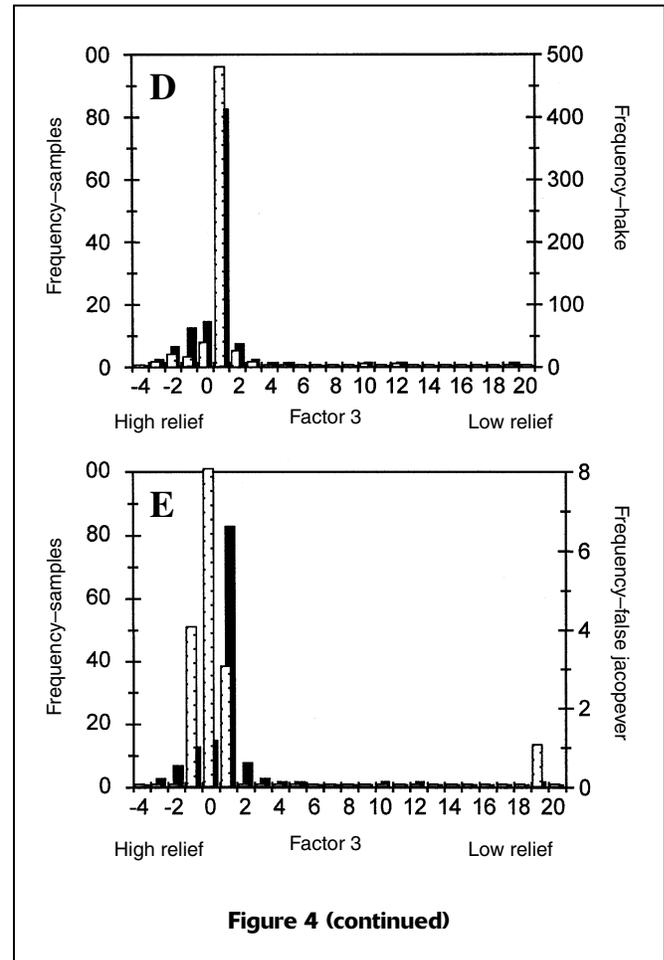


Figure 4 (continued)

the white lights of the *Jago*, these juvenile hake were pink and blotchy in color and appearance and were not strongly different from kingklip, and it is possible that such an appearance may serve to camouflage individuals.

Cuttlefish are well known to use camouflage, and this may account for the fact that they were not strongly associated with soft or hard substrata (Tables 4 and 6). Cuttlefish are the commonest cephalopod caught in demersal trawls (Japp, 1997), implying that they are known to occur over sandy and mixed substrata. Cuttlefish feed predominantly on fishes and crustaceans (Lipinski, 1992) and therefore the lack of any strong association with ophiuroids is to be expected.

Grenadiers, on the other hand, tended to be associated with brittlestars (Table 6). Unlike cuttlefish, however, grenadiers are known to feed quite extensively on ophiuroids¹ and small epifauna (Meyer and Smale, 1991) and did not seem to show any strong association with extremes of substrata and were observed in both soft and hard habitats (Table 5). The smaller species of macrourids (such as *C. simorhynchus*) form a small but conspicuous part of the

¹ Adriaans, W. 2000. Unpubl. data. Zoology Department, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa.

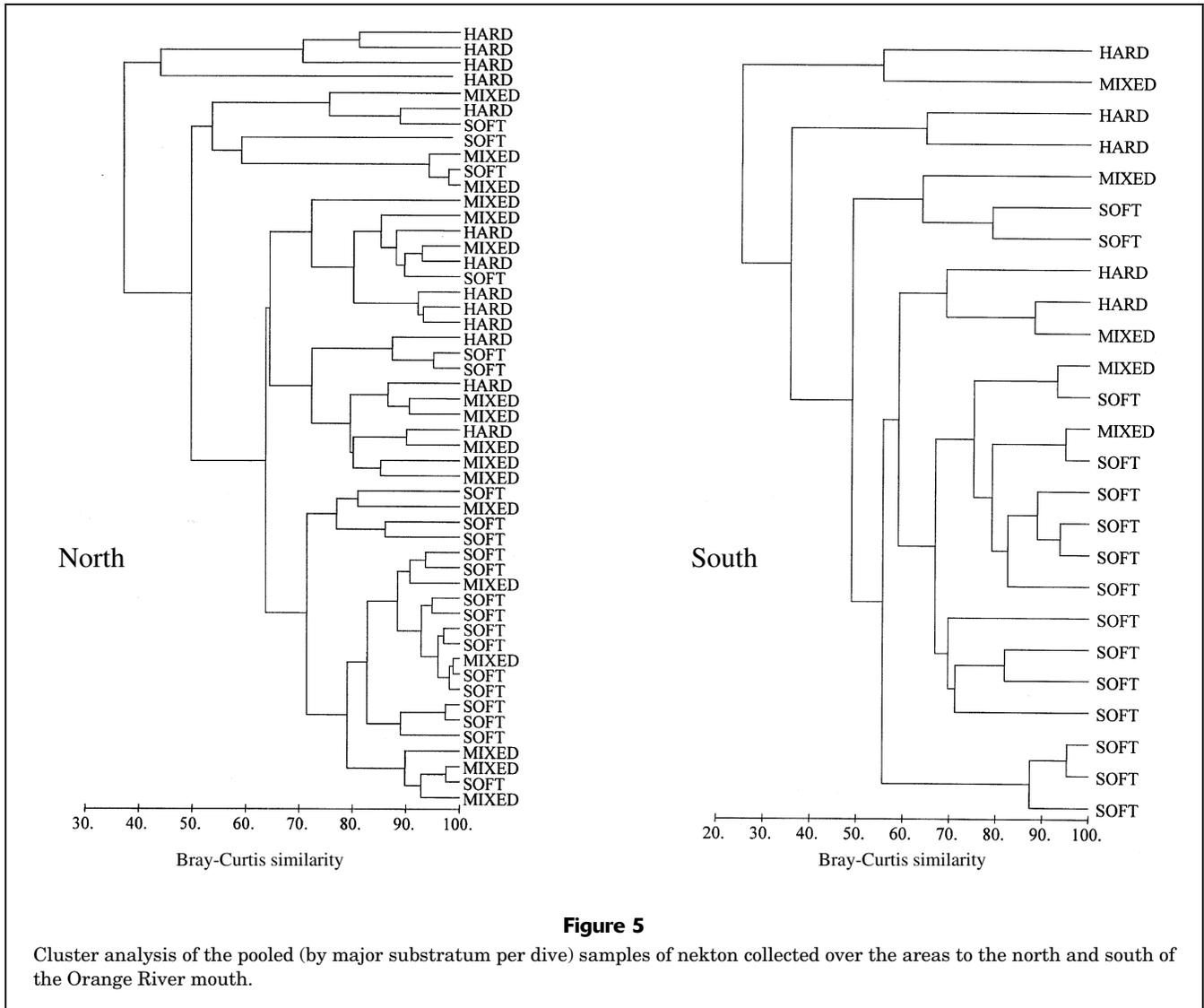


Figure 5
Cluster analysis of the pooled (by major substratum per dive) samples of nekton collected over the areas to the north and south of the Orange River mouth.

bycatch from the hake-directed trawl fishery and are thus assumed to occupy a wide range of habitats.

The gobies seen in our study tended to show neither a strong association with any substratum type (and their associated biota), nor were they linked to areas with a rich ophiuroid fauna (Tables 4 and 6). *Sufflogobius bibarbatus* is also known as the pelagic goby because it spends much of its time at night in the water column,² where it forms a conspicuous part of the fish community³ and where it feeds largely on zooplankton.² If the gobies observed in our study were *S. bibarbatus* (as postulated), then the data suggest that their use of the demersal habitat by day was primarily linked to shelter. Otherwise, it might be expected that they would be associated with areas rich in

benthic food, such as ophiuroids, which are known to form part of the diet of other gobies (Gibson, 1982).

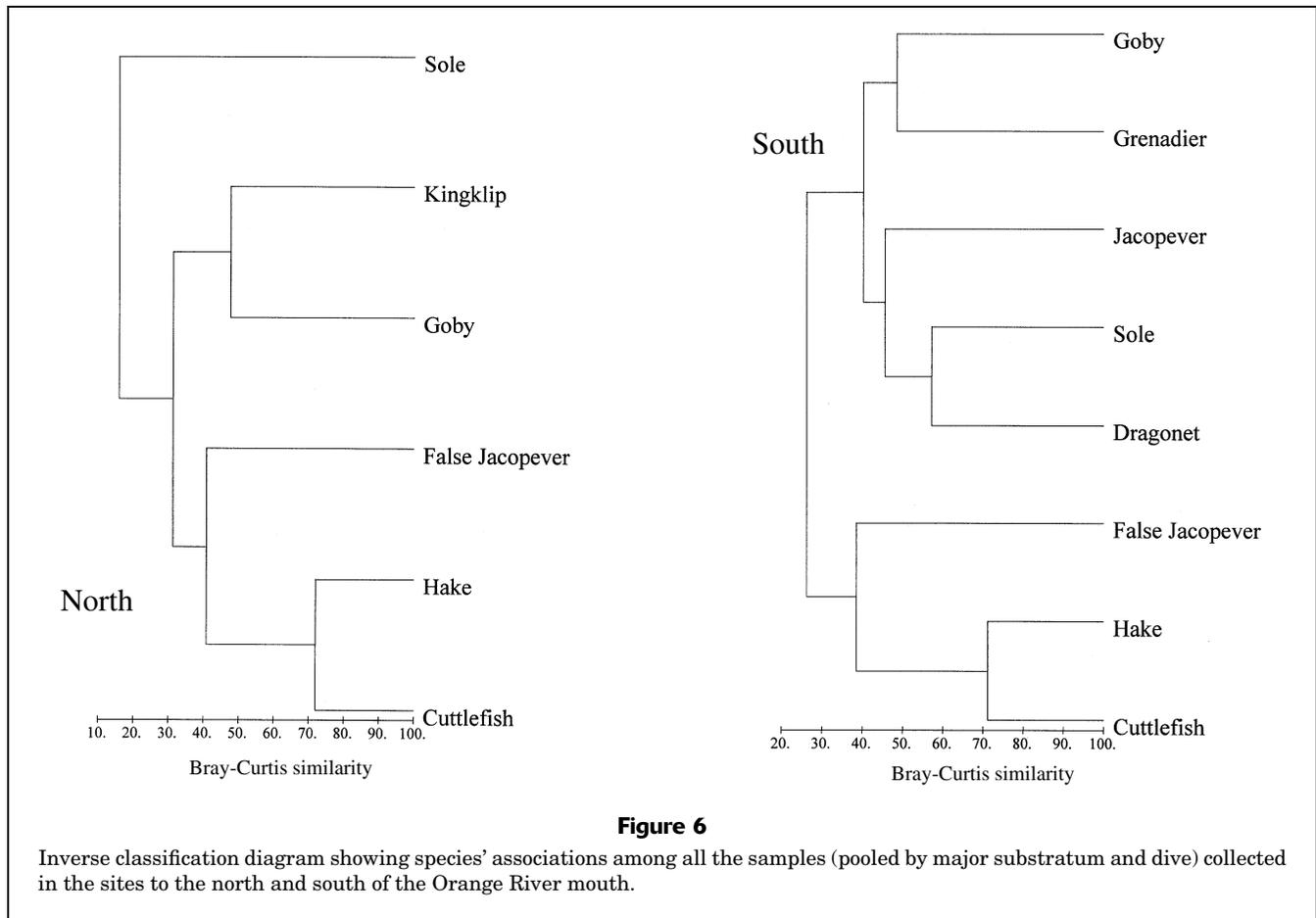
Communities

The overall diversity of the fish community observed by the *Jago* is less than that determined from the same region with trawl nets (Roel, 1987), principally because the area sampled was significantly smaller. The diversity of the fish and cephalopod fauna may also seem low by comparison with submersible surveys elsewhere (e.g. Felley et al., 1989). But, this region is not known to support a high diversity of demersal species (Mas-Riera et al., 1990) because of the perceived harshness of the prevailing environment (such as frequent intrusions of low-oxygen bottom water (Bailey and Rogers, 1997)).

The demersal nekton fauna, both as individual species and as a whole, was strongly influenced by substratum type (as in Parker et al., 1994). Despite the large research effort

² Pillar, S. C. 2000. Personal commun. Marine and Coastal Management, Cape Town, South Africa.

³ O'Toole, M. 2000. Personal commun. Ministry of Fisheries and Marine Resources, Windhoek, Namibia.



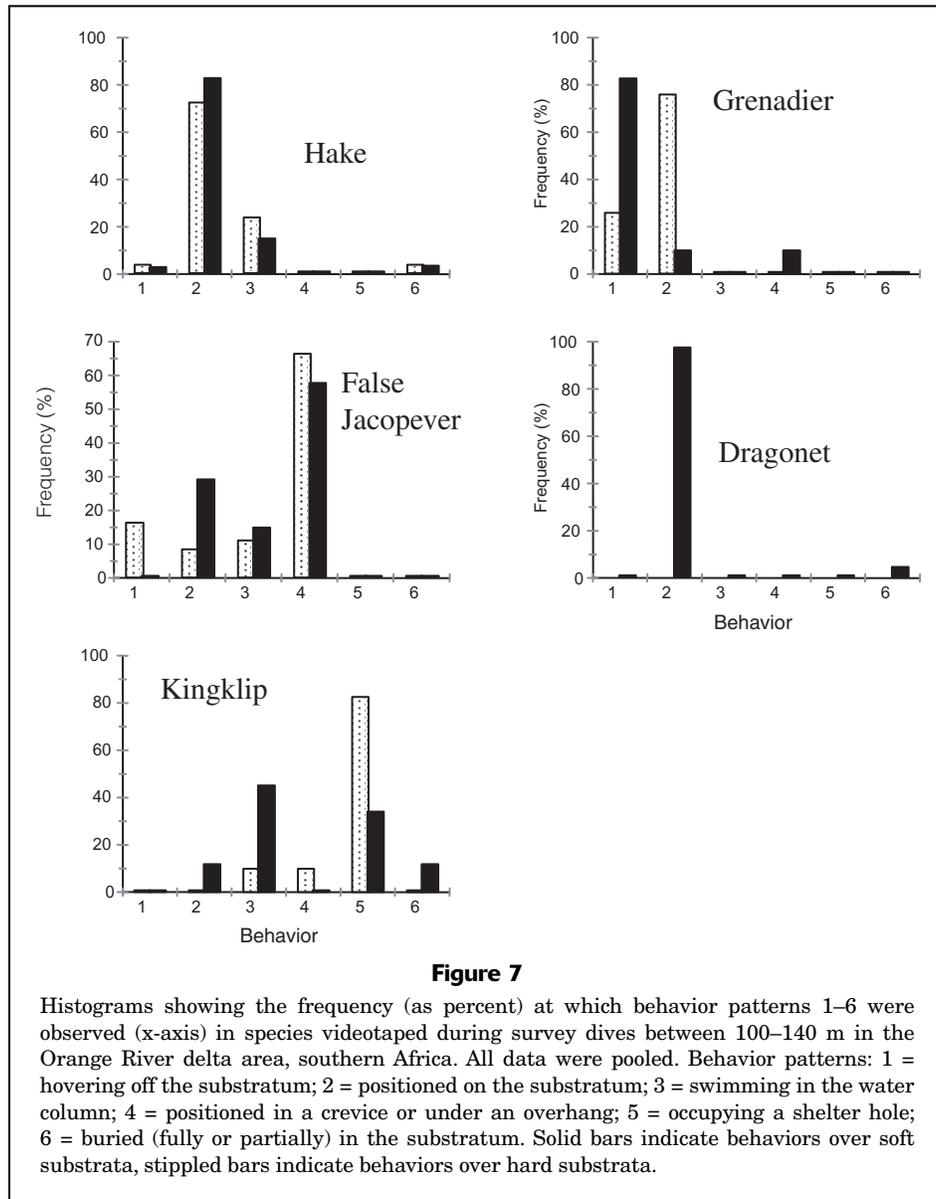
that has focussed on the commercially important demersal fisheries along the west coast of southern Africa, there is a dearth of published material that can be usefully compared to the current observations. Roel (1987) recognized that the species composition of the demersal fauna in the southern Benguela ecosystem was mainly influenced by depth, and she identified two distinct communities of demersal nekton. One of these was dominated by *Merluccius paradoxus* and occurred at depths greater than 380 m, and the other was dominated by *M. capensis* and was confined to the continental shelf. In the northern Benguela ecosystem, Macpherson and Roel (1987) recognized five distinct demersal fish communities. Two of these were distributed over the shelf (and were subdivided by latitude), and the balance was essentially depth related and ran parallel to the coastline, offshore. Similar observations on the structure of the demersal fish assemblages were made by Macpherson and Gordoa (1992) and Mas-Riera et al. (1990), who noted that latitudinal variations in community composition were generally associated with the state of upwelling. The latter authors postulated that the especially low level of diversity of the demersal fish community in the northern Benguela ecosystem (the region of our study) was due to the presence of low-oxygen bottom water. The "indicator" species for the assemblage in their analysis included *Merluccius capensis*

and *Sufflogobius bibarbatus*, which were also among the common species observed in our study.

Smale et al. (1993) observed three demersal communities over the Agulhas Bank (south coast of South Africa) which were related to depth; inshore (<100 m), shelf (90–190 m), and slope (>200 m). Although the species observed in the our surveys were all conspicuous components of the shelf communities identified by these authors, they were relatively rare (or absent) from the samples collected by Smale et al. (1993). Unfortunately, the nature of these authors' data (30–60 minute trawls) is such that they do not provide any fine-scale information on species associations, and this effectively limits further comparison.

There appears to be a difference in the community of fishes from the northern and southern study sites (e.g. the presence of dragonets in the south but not in the north). Differences in the infaunal communities from undisturbed sites to the north and south of the Orange River were noted by Field et al. (1996). Gibbons and Sulaiman⁴

⁴ Gibbons, M. J., and A. Sulaiman. 1998. A video-description of the mid-shelf benthic environment off the west coast of southern Africa, with a comment on the habitat association of demersal nekton. A report to De Beers Marine (Pty) Ltd., Cape Town 8000, Republic of South Africa, 62 p.



also commented on some discrepancies in the structure of the physical and biological environment in regions to the north and south of the Orange River, which can be partly explained by the latitudinal influence of the River and by biogeography (Emanuel et al., 1992; Gibbons and Hutchings, 1996).

Acknowledgments

We are very grateful to James Felley (Office of Information Technology, Smithsonian Institution, Washington DC) for his assistance with some of the statistical analyses of the data, and for his comments on an earlier draft of the manuscript. We would like to thank the three anonymous

referees for their valuable comments, which served to focus the text. The staff at the drawing office of De Beers Marine (Pty.) Ltd. are thanked for their patient delivery of maps, images, and yet more maps, and for putting up with the persistent glare of the television screen. We would like to thank Hans Fricke, Jurgen Schauer, and Karen Hissman for their safe delivery of personnel (and videotapes) from the bottom of the sea: rarely have we felt in such capable hands. We are also grateful to the personnel of the MV *Zealous* for their hospitality at sea, and to the helicopter pilots for ensuring speedy transport from ship to shore. De Beers Marine (Pty.) Ltd. are gratefully acknowledged for their financial support of the project and for being prepared to allow us to publish the data contained in our article.

Literature cited

- Autodesk Inc.
1988. Auto CAD LT 98. Autodesk Inc., Cupertino, CA.
- Badenhorst, A.
1988. Aspects of the South African longline fishery for kingklip *Genypterus capensis* and the cape hakes *Merluccius capensis* and *M. paradoxus*. S. Afr. J. Mar. Sci. 6:33–42
- Bailey, G. C., and J. Rogers.
1997. Chemical oceanography and marine geoscience off southern Africa: past discoveries in the post-Gilchrist era, and future prospects. Trans. Roy. Soc. S. Afr. 52:51–79.
- Brown P. C., K. L. Cochrane, and S. J. Paiting.
1991. Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. S. Afr. J. Mar. Sci., 11:537–564.
- Clarke, K. R., and R. M. Warwick.
1994. Change in marine communities: an approach to statistical analysis and interpretation, 144 p. Plymouth Marine Laboratory, UK.
- Cushing, D. H.
1971. Upwelling and the production of fish. Adv. Mar. Biol. 9:255–334.
- Dennis, G. D., and T. J. Bright.
1988. Reef fish assemblages on hard banks in the North-eastern Gulf of Mexico. Bull. Mar. Sci. 43: 280–307.
- Emanuel, B. P., R. H. Bustamente, G. M. Branch, S. Eekhout, and F. J. Odendaal.
1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. 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. 93:262–273.
- Felley, J. D., M. Vecchione, G. R. Gaston, and S. M. Felley.
1989. Habitat selection by demersal nekton: analysis of videotape data. NE Gulf Sci. 10:69–84
- Field, J. G., K. R. Clarke, and R. M. Warwick.
1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8: 37–52.
- Field, J. G., C. A. Parkins, H. Winckler, C. Savage, 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. EEU (Environmental Evaluation Unit) Report 11/96/158, 370 p. University of Cape Town, Cape Town, South Africa.
- 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.
- Gibbons, M. J., A. Sulaiman, K. Hissmann, J. Schauer, and P. A. Wickens.
2000. Video observations on the habitat association of demersal nekton in the mid-shelf benthic environment off the Orange River mouth. S. Afr. J. Mar. Sci., 22:1–7.
- Gibson, R. N.
1982. Recent studies on the biology of intertidal fishes. Oceanogr. Mar. Biol. Ann. Rev. 20:363–414.
- 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.
- Hutchings, L.
1992. Fish harvesting in a variable productive environment—searching for rules or searching for exceptions? S. Afr. J. Mar. Sci. 12: 297–318.
- Japp, D. W.
1990. A new study on age and growth of kingklip *Genypterus capensis* off the South and West coasts of South Africa, with comments on its use for stock identification. S. Afr. J. Mar. Sci. 9:223–237.
1997. Discarding practices and bycatches for fisheries in the Southeast Atlantic region (area 47). FAO Fish. Rep. 547 (suppl.):235–256.
- Lipinski, M. R.
1992. Cephalopods and the Benguela ecosystem: trophic relationships and impact. S. Afr. J. Mar. Sci., 12:791–802.
- Macpherson, E.
1983. Feeding of the kingklip (*Genypterus capensis*) and its effect on the hake (*Merluccius capensis*) resource off the coast of Namibia. Mar. Biol., 78:105–112
- Macpherson, E., and A. Gordo.
1992. Trends in the demersal fish community off Namibia from 1983–1990. S. Afr. J. Mar. Sci., 12: 635–649.
- Macpherson, E., and B. A. Roel.
1987. Trophic relationships in the demersal fish community off Namibia. S. Afr. J. Mar. Sci. 5: 585–596.
- Mas-Riera, J., A. Lombarte, A. Gordo, and E. Macpherson.
1990. Influence of Benguela upwelling on the structure of demersal fish populations off Namibia. Mar. Biol. 104: 175–182.
- Meyer, M., and M. J. Smale.
1991. Predation patterns of demersal teleosts from the Cape South and West coasts of South Africa. 2. Benthic and epibenthic predators. S. Afr. J. Mar. Sci., 11:409–442.
- Murie, D. J., D. C. Parkyn, B. G. Clapp, and G. C. Krause.
1994. Observations on the distribution and activities of rockfish, *Sebastes* spp., in Saanich Inlet, British Columbia, from the Pisces IV submersible. Fish. Bull. 92:313–323.
- Parker, R. O., and S. W. Ross.
1986. Observing reef fishes from submersibles off North Carolina. NE Gulf Sci. 8:31–49.
- Parker, R. O., A. J. Chester, and R. S. Nelson.
1994. A video transect method for estimating reef fish abundance, composition, and habitat utilization at Gray's Reef National Marine Sanctuary, Georgia. Fish. Bull. 92: 787–799.
- Payne, A. I. L.
1985. The sole fishery off the Orange River, southern Africa. In International symposium on the most important upwelling areas off western Africa (Cape Blanco and Benguela) (C. Bas, R. Margaleff, and P. Rubiés, eds.), p. 1063–1079. Instituto de Investigaciones Pesqueras, Barcelona.
- Payne, A. I. L., K. H. Brink, K. H. Mann, and R. Hilborn.
1992. Benguela trophic functioning. S. Afr. J. Mar. Sci., 12: 1–1108.
- Payne, A. I. L., J. A. Gulland, and K. H. Brink.
1987. The Benguela and comparable ecosystems. S. Afr. J. Mar. Sci. 5:1–957.
- Pillar, S. C., and M. Barange
1995. Diel feeding periodicity, daily ration and vertical migration of juvenile Cape hake off the west coast of South Africa. J. Fish Biol. 47:753–768.
- Richards, L. J.
1986. Depth and habitat distribution of three species of rockfish (*Sebastes*) in British Columbia: observations from the submersible PISCES IV. Env. Biol. Fish. 17:13–21.
- Roel, B. A.
1987. Demersal communities off the west coast of South Africa. S. Afr. J. Mar. Sci. 5:575–584.

Shannon, L. V.

1985. The Benguela ecosystem. I. Evolution of the Benguela, physical features and processes. *Oceanogr. Mar. Biol. Ann. Rev.* 23:105–182.

Sibuet, M., S. K. Juniper, 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., B. A. Roel, A. Badenhorst, 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.

Stein, D. L., B. N. Tissot, M. A. Hixon, and W. Barss.

1992. Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. *Fish. Bull.* 90:540–551.