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Morphological responses of macrobenthic polychaetes to low oxygen on the Oman continental slope, NW Arabian Sea

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Abstract

Morphological adaptation to low dissolved oxygen consisting of enlarged respiratory surface area is described in polychaete species belonging to the family Spionidae from the Oman margin where the oxygen minimum zone impinges on the continental slope. Similar adaptation is suggested for species in the family Cossuridae. Such morphological adaptation apparently has not been previously recorded among polychaetes living in hypoxic conditions. The response consists of enlargement in size and branching of the branchiae relative to similar species living in normal levels of dissolved oxygen. Specimens were examined in benthic samples from different depths along a transect through the oxygen minimum zone. There was a highly significant trend shown to increasing respiratory area relative to body size in two undescribed spionid species with decreasing depth and oxygen within the OMZ. Yet the size and number of branchiae are often used as taxonomic characters. These within-species differences in size and number of branchiae may be a direct response by the phenotype to intensity of hypoxia. The alternative explanations are that they either reflect a pattern of differential post-settlement selection among a highly variable genotype, or represent early genetic differentiation among depth-isolated sub-populations. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

Behavioural, physiological and metabolic responses to temporary hypoxia have been described in several polychaete worms (e.g. Dales and Warren, 1980; Schottler

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and Grieshaber, 1988) and in various other invertebrates (reviewed by Grieshaber et al., 1994). In contrast to coastal areas experiencing episodic hypoxia (usually caused by eutrophication), the oxygen minimum zone (OMZ) in the northern Arabian Sea impinges on the continental margin creating permanently hypoxic conditions in the deep coastal to bathyal benthic environment. On the Oman margin the OMZ extends down from about 60 m to about 1000 m depth, with gradually increasing dissolved oxygen below this depth to 'normal' near-saturated oxygen levels by 2000–2500 m. The upper boundary consists of a sharp break between the OMZ and the well-oxygenated surface layer above. Although some information on organism adaptation to permanent hypoxia exists (reviewed by Childress and Seibel, 1998), little is known of metabolic, behavioural and morphological responses of benthic organisms.

In the present study, we investigate morphological adaptation of respiratory structures of two species of the polychaete family Spionidae to persistent hypoxia within the OMZ off Oman. In the undescribed spionid species, *Prionospio (Minusopio)* sp. A, we test the hypothesis that a within-species response of increasing branchial area in proportion to the body size will be greatest at depths where oxygen depletion is most intense. Similar changes in branchial area proportion with depth within species are also examined in *Paraprionospio* sp. A. Within-species variation in branchial area, to our knowledge, has not been reported previously. Our findings therefore have implications for taxonomic studies of polychaetes because these normally utilise the number and morphology of branchiae in species descriptions. Preliminary observations on enlargement of the median filament of species of the family Cossuridae, and of branchiae in the family Paraonidae, are also described.

2. Materials and methods

2.1. Sampling procedures

Macrofauna samples were taken with the 0.25 m^2 USNEL box corer fitted with a 'vegematic' sub-coring device to yield a grid of 25 sub-cores. The top 20 cm of sediment from each 10×10 cm sub-core were washed through a 300 μm mesh sieve with filtered sea water. The sievings were fixed in 4% buffered sea-water formaldehyde for 3–7 d before transfer to 90% ethanol with 2% propylene glycol. Other sampling details are described in Levin et al. (2000). Sorting of fauna in the material was aided by staining with Rose Bengal. Specimens examined in the present study were from vegematic sub-cores from the stations listed in Table 1. In one case cossurid specimens were obtained from a multicorer sample where the box corer was unable to operate owing to the very soft sediment.

2.2. Specimen measurement

In comparing morphological changes within polychaete species across the OMZ, species having (a) well-developed and measurable branchiae or other respiratory structures, (b) a distribution over a large range of depth along the transect, (c) large

Table 1
Station details from R.R.S. *Discovery* Cruise 211 for polychaete specimens used in this study, MC, Barnett–Watson multicorer; SBC, USNEL-pattern box corer

Station	Depth (m)	Latitude (N)	Longitude (E)	Date (E)	Gear (E)
12700#2	368	19° 21.88′	58° 15.37′	24 Oct. 94	MC
12698#1	379	19° 21.78′	58° 15.49′	24 Oct 94	SBC
12695#7	401	19° 21.83′	58° 15.42′	23 Oct 94	SBC
12695#4	406	19° 21.92′	58° 15.49′	23 Oct 94	SBC
12692#4	417	19° 21.97′	58° 15.59′	22 Oct 94	SBC
12685#3	622	19° 18.99′	58° 15.47′	14 Oct 94	SBC
12685#6	688	19° 18.88′	58° 15.46′	15 Oct 94	SBC
12685#8	690	19° 18.66′	58° 15.64′	15 Oct 94	SBC
12711#2	840	19° 14.21′	58° 23.11′	27 Oct 94	SBC
12722#1	992	19° 16.09′	58° 29.68′	2 Oct 94	SBC
12687#1	3372	19° 59.51′	59° 00.76′	18 Oct 94	SBC
12687#9	3392	18° 59.77′	59° 00.49′	20 Oct 94	SBC

numbers of individuals available, and (d) an anterior body character correlating with body size to make use of the many head-end fragments present in the samples, are desirable. Two undescribed spionids, *Prionospio (Minuspio)* sp. A and *Paraprionospio* sp. A, best met these requirements (Fig. 1A–C).

The length of the cirriform branchiae of *Prionospio (Munispio)* sp. A (Fig. 1C) was considered to equate to branchial area and was measured by tracing the median outline of each branchia in turn on a sheet of paper using a camera lucida mounted on a binocular microscope. Twenty-two complete specimens of *Prionospio (Minuspio)* sp. A were available in order to explore whether development of branchiae could be related to body size, expressed as the number of setigers (segments). Incomplete specimens (which tend to be numerous in deep-sea samples) could then be utilised in further analysis using this relationship as a proxy for body size. In most cases individual branchiae had to be laboriously teased out into observable form before tracing. The lengths of traced branchiae were measured with a geared map-measuring device. All animals were preserved in 90% ethanol. It is likely that shrinkage caused by the preservative would be the same for the structures of interest on all specimens. It was not possible to lay branchiae flat for measurement, and some measurement error was therefore unavoidable. This probably accounts for the slight deviations from a smooth increase and decrease between length of branchiae on successive setigers. Regenerating and broken branchiae were excluded.

Paraprionospio sp.A (Fig. 1A,B) presented fewer problems in branchial size estimation as the total number of pinnule pairs was found to be an adequate representation of branchial area. It was possible to count pinnules on the three pairs of branchiae on 32 specimens.

Statistical analysis (linear regression and analysis of covariance) was undertaken using Minitab (v. 12.1) software.

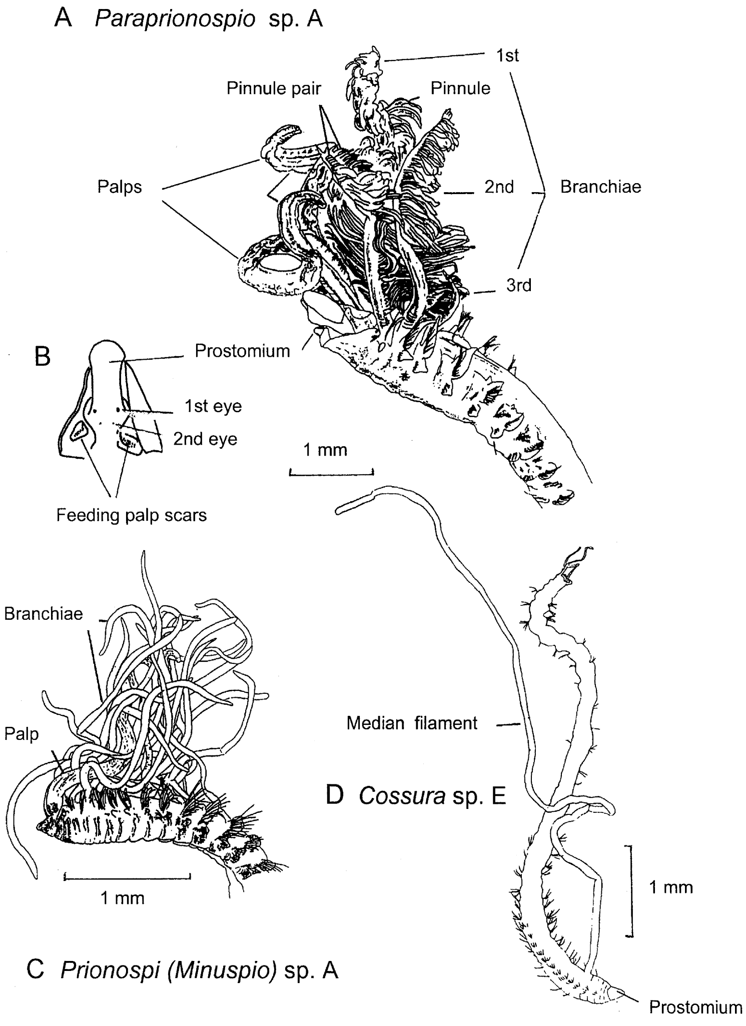

Fig. 1. A. *Paraprionospio* sp. A. Lateral anterior view showing one pair of feeding palps and 3 pairs of branchiae with the right branchiae in each pair omitted for clarity. B. dorsal view of head showing arrangement of two pairs of eye spots. The first pair of eye spots are larger and darker than the second pair in this species. *C. Prionospio (Minuspio)* sp.A, lateral anterior view showing feeding palps (one pair) and ten pairs of branchiae (scale bar = 1 mm) of specimen from 398 m. D. outline drawing of *Cossura* sp. E showing typical proportion of median filament to body (scale bar = 1 mm).

Bottom water oxygen were was derived from data obtained on *Discovery* cruises 210 and 212 (Burkill, 1998) as described in Levin et al. (2000). Increasing oxygen concentration increased with depth. The shallowest station sampled, around 400 m, had the lowest O_2 values at 0.14 ml/l. These increased to 0.16 ml/l at about 700 m, 0.20 ml/l at about 850 m, 0.27 ml/l at about 1000 m and 0.52 ml/l at stations around 1250 m.

3. Results

3.1. *Prionospio (Minuspio) sp. A*

This species (Fig. 1C) dominates the macrofauna at 400 m and is also numerous in the 600–800 m samples, composing 66 and 69% of the polychaetes, respectively (see Levin et al., 2000). The specimens examined had several pairs of cirriform branchiae. Observations indicated a trend of greater branchial length in relation to body size at shallower depths where oxygen was lowest (Table 2, Fig. 2). Three individuals of 55 setigers are compared in Fig. 3 to illustrate this trend. When the 417 and 690 m animals are compared, juveniles of about 55 setigers have developed seven branchial

Table 2
Prionospio (*Minuspio*) sp. A; mean branchial lengths (mm) of specimens (Sp.) from three depths

Branchial pair Sp.	setigers	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th
R.R.S. *Discovery* Station 12692 # 4, depth 417 m													
A8	47	1.07	1.16	1.16	1.34	0.98	1.00	0.71					
A7	49	1.61	1.45	1.16	1.41	1.43	1.34	0.95	0.18				
A6	55	1.64	1.66	1.49	1.34	1.61	1.69	1.72	1.38	0.63			
A2	73	2.48	2.41	2.63	2.68	2.41	2.59	2.59	2.64	2.41	1.88		
A1	78	2.89	3.02	2.92	×	3.04	2.77	×	×	2.75	2.50	2.05	0.36
A3	80	2.95	2.50	2.99	2.63	2.41	2.46	2.28	2.30	1.88	1.90		
A5	81	2.23	2.63	2.68	2.77	2.95	3.21	2.81	2.95	2.95	2.72	1.96	
A4	86	2.10	1.96	1.92	×	1.96	1.88	1.96	1.68	1.96	1.61	1.61	
R.R.S. *Discovery* Station 12685 # 6, depth 688 m													
C5	55	1.23	1.10	1.31	1.16	1.30	1.16	1.16					
C6	59	1.38	1.29	1.34	1.24	1.34	1.34	1.21					
C2	75	1.88	2.46	2.23	2.41	2.54	2.34	2.37	2.19	2.10	1.79	1.34	
C4	82	1.86	1.79	1.80	1.90	1.96	2.14	1.98	2.05	2.14	2.05	1.88	
C1	83	1.47	1.92	1.96	1.92	2.14	1.96	2.14	2.01	2.14	2.05	1.61	
C3	84	2.01	1.88	1.70	1.68	2.18	2.16	1.94	1.83	1.85	1.79	1.83	
R.R.S. *Discovery* Station 12685 # 8, depth 690 m													
D6	51	0.92	0.94	0.89	0.88	0.89	0.67	0.07					
D5	54	1.03	0.91	1.03	0.96	0.98	0.89	1.01					
D4	55	0.94	0.94	0.96	1.00	1.00	1.12	0.71					
D7	56	1.14	1.23	1.18	1.33	1.23	1.14	1.04					
D1	80	1.24	1.29	1.34	1.52	1.43	1.38	1.52	1.56	1.43	1.36		
D8	85	1.74	1.81	1.96	1.90	1.88	2.01	1.80	1.85	1.68	1.72	1.43	
D2	86	1.96	1.88	1.96	1.96	1.90	1.96	1.96	1.88	1.79	1.88		
D3	92	1.70	1.54	1.74	1.74	1.96	1.92	1.92	1.83	1.88	1.70	1.96	

Where branchiae are missing or incomplete, measurement of the other branchia of pair was taken. '×' indicates where both branchiae of the pair are missing. Estimated measuring error ± 0.01 mm.

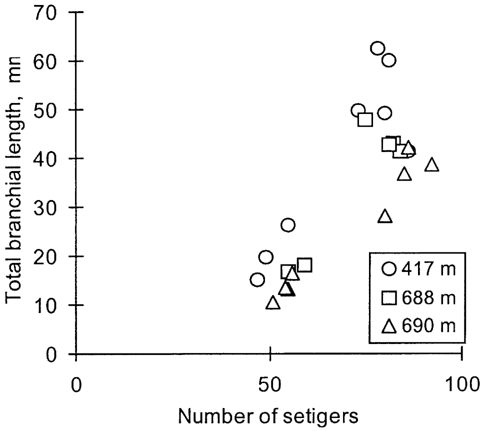

Fig. 2. *Prionospio (Minuspio)* sp. A. Total branchial length plotted in relation to body size as represented by number of setigers on individuals from two depth levels (417 and '700 m').

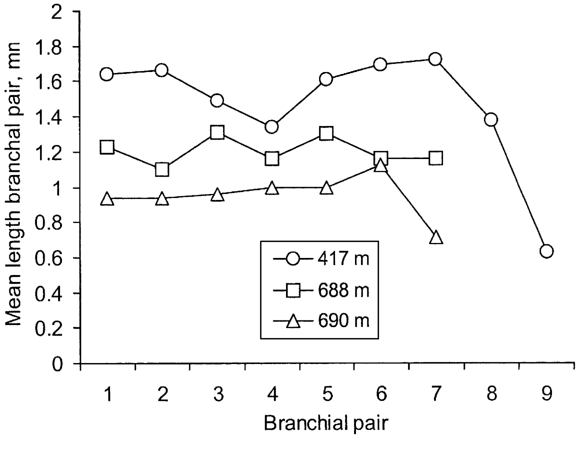

Fig. 3. Mean length of branchial pair in three individuals of *Prionospio (Minuspio)* sp. A each of 55 setigers from three different depths. Data from Table 2.

pairs in the higher oxygen levels at the 690 m site. At around the same setiger number juveniles of the 417 m site have developed eight and nine pairs of branchiae (Table 2). Adult branchial lengths in relation to body size were markedly different between specimens from 417 m and the two deeper stations (688 and 690 m), but not between the two deeper stations themselves (Table 2). All adults from 690 m had branchiae shorter than 2 mm in length and 11 pairs or less. In animals from the 417 m sample many branchiae were longer than 2 mm, with some almost reaching 3 mm. One specimen examined was developing a 12th pair. The specimens from 688 m show development of branchiae similar to the 690 m specimens. This is to be expected since the 417 m is about 5.6 km from the two deeper cores, the latter pair of stations being only about 0.47 km distant from each other, and were therefore probably subject to the same oxygen regime. We shall hereon consider the samples from these two deeper stations together as '700 m'. No other morphological differences have been observed between specimens from the 417 and '700 m' stations.

Analysis of covariance (Zar, 1984) confirmed the differences between the 417 and '700 m' stations (Table 4). The interaction term indicates no significant difference in the slope of linear regression for this relationship at the two depth levels. But an analysis of variance testing for differences in the elevations (the vertical position, or *Y*-intercepts of the assumed parallel regression lines) showed a highly significant difference in the response variable (total branchial length) in relation to body size (number of setigers) for the two depth levels.

The resulting regression model for the two stations together is

Number of branchial pairs = 0.8975 (number of setigers) $-\,b_1$, or b_2

where b_1 (417 m, $n = 8$) = 21.121, b_2('700 m', $n = 14$) = 27.816.

The proportion of total variability in the response (dependent) variable explained by the variation observed in the independent variables (body size, depth), provides the 'overall' $R^2 = 0.829$. Table 3 makes clear that although more than half of this value results from the relationship between body size and number of branchial pairs, a very substantial amount derives from depth.

There are few, easily measured, anterior morphological features on *Prionospio (Minuspio)* sp. A. However, prostomium length showed a close linear relation to number of setigers (setiger number = 185.79 prostomium length + 20.28, $r^2 = 0.910$, $P < 0.01$, $n = 22$). This relationship could be used with incomplete animals to estimate body size.

Table 3
Prionospio (Minusopio) sp. A. Analysis of covariance testing for homogeneity of regression coefficients for total branchial length on body size (number of setigers) of individuals collected at two depth levels

	d.f.	MS	*F*-ratio	*P*
ANOVA testing for homogeneity of slopes				
Body size	1	3683.8	67.45	< 0.001
Depth level	2	0.1	0.00	0.966
Depth * body size	2	36.2	0.66	0.426
Error	16	54.6		
Total	21			
ANOVA testing for differences in elevation of regressions (*Y*-intercepts)				
Body size	1	3744.3	69.80	< 0.001
Depth level	3	906.8	16.90	0.001
Error	18	53.6		
Total	21			

Table 4
Paraprionospio sp. A. Measurements of body size and branchiae

Station	Specimen	Depth (m)	Complete/ incomplete	Number of setigers	Length prostomium to 1st eye pair (mm)	Number of pinnule pairs
12685#3	467Eone	622	C	82	0.52	439
12685#3	467Etwo	622	C	56	0.19	178
12685#3	467Ethree	622	C	79	0.4	372
12685#3	467Efour	622	C	73	0.4	387
12685#3	467Efive	622	C	90	0.5	391
12685#3	467Esix	622	C	99	0.7	673
12685#3	467Eseven	622	I		0.65	577
12685#3	467Eeight	622	I		0.54	562
12685#6	468D9	688	C	60	0.26	—
12685#6	468D10	688	C	54	0.21	—
12685#6	468D5	688	C	58	0.23	—
12685#6	468D6	688	C	55	—	184
12685#6	468C6	688	I		—	137
12685#6	468A5	688	C	79	—	302
12685#6	468C4	688	I		—	95
12685#6	468A3	688	C	61	—	177
12685#6	468A1	688	C	73	0.41	317
12685#6	468A2	688	C	61	0.26	158
12685#6	468A4	688	C	59	0.22	104
12685#6	468C5	688	C	67	0.35	251
12685#6	468D1	688	C	64	0.29	214
12685#6	468D2	688	C	68	0.32	288
12685#6	468D3	688	C	62	0.23	192
12685#6	468D4	688	C	61	0.26	158
12685#6	468D7	688	C	58	0.25	179
12685#6	468D8	688	C	60	0.28	234
12685#6	468D11	688	C	59	0.24	175
12685#6	468D12	688	C	59	0.26	196
12711#2	503B1	840	I		0.4	164
12711#2	503B2	840	I		0.31	146
12722#1	514s7A	992	I		0.34	178
12722#1	514s7B	992	I		0.31	168

Where a branchia is missing or damaged the count for the intact branchia of the pair was doubled and added to the total count of pinnule pairs. Specimen 467Efive possessed only the second and third branchial pairs. Complete specimens are indicated by ‘C’, incomplete by ‘I’.

3.2. *Paraprionospio sp. A*

This species (Fig. 1A), which has only three pairs of branchiae, each bearing numerous plate-like pinnules, was found at 600 and 900 m and comprised 48% of the polychaetes at 700 m. Two pairs of eyespots are present on the prostomium (Fig. 1B). All measurements of body size and counts of pinnule pairs on the branchiae are listed in Table 4. A close linear relationship (setiger number = 92.023 prostomium length + 37.113, $r^2 = 0.954$, $P > 0.001$, $n = 21$) was found between setiger number (range 54

Table 5
Paraprionospio sp. A. Analysis of covariance testing for homogeneity of regression coefficients for number of pinnule pairs on body size (tip of prostomium to first eye spot pair in mm) at four different depths (622, 688, 840 and 992 m)

	d.f.	MS	F-ratio	P
ANOVA testing for homogeneity of slopes				
Body size	1	0.003630	3.48	0.082
Depth level	3	0.001813	1.74	0.202
Depth * body size	3	0.001473	1.41	0.278
Error	15	0.001042		
Total	22			
ANOVA testing for differences in elevation (Y-intercepts)				
Body size	1	0.197169	177.03	< 0.001
Depth level	3	0.012424	11.16	< 0.001
Error	18	0.0011114		
Total	22			

– 82) of intact specimens and prostomium length, measured as the distance in mm from the front of the prostomium to an imaginary line linking the first pair of eye spots, in individuals from 622 m ($n = 6$) and 688 m depth ($n = 15$). The relationship was used as a proxy for body size in an analysis of covariance that utilised the18 complete and six incomplete specimens having both data on prostomium lengths and pinnule counts. This analysis (Table 5) explores the response of number of pinnule pairs present on the three pairs of branchiae in relation to body size (as tip of the prostomium to first eye spot pair) at different depth levels. The data utilised are plotted in Fig. 4 for four depth levels. It should be noted that the body size range for the shallowest level (622 m) was considerably greater than for the other depths, and that only two individuals were available at each of the two deeper depths (840 and 992 m). As for *Prionospio (Minuspio)* sp. A, no significant difference was found between the slope of linear regression for number of pinnule pairs on body size, but there was a very highly significant difference in the elevations (Y-intercepts) of the regressions of number of pinnule pairs in relation to body size among specimens at the four depth levels shown in Fig. 4. The resulting regression model for the four depths is:

Number of pinnule pairs = $-$ 84.73 + 0.0155 (tip of prostomium to first eye spot pair in *mm*) + b_1, or b_2, or b_3, or b_4

$$\text{where } b_1 \text{ (622 m, } n = 8) = 95.90,\ b_2 \text{ (688 m, } n = 12) = 32.43,$$

$$b_3 \text{ (840 m, } n = 2) = -87.16,\ b_4 \text{ (992 m, } n = 2) = 0;\ \text{‘overall’ } R^2 = 0.965.$$

However, Table 5 makes clear that a large part of the high R^2 results from the relationship between pinnule count and body size.

One individual from 622 m (not included in the above analysis) possessed only the second and third pairs of branchiae, representing a considerable loss of respiratory

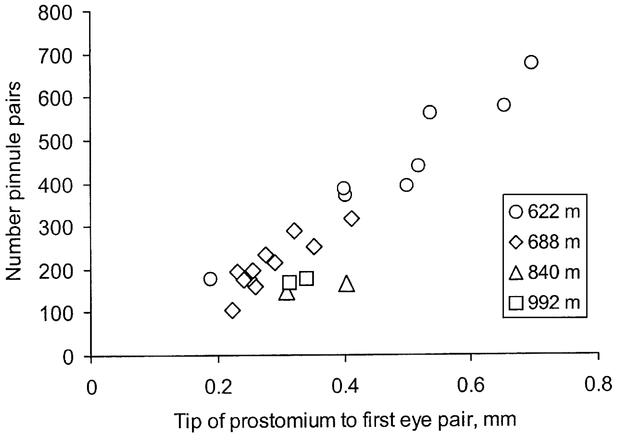

Fig. 4. *Paraprionospio* sp. A. Total branchial area as number of pinnules plotted against body size (as represented by the distance in mm from the tip of the prostomium to a point equidistant from, and the shortest distance between) the first pair of eye spots, from four depths.

surface. However, the third branchial pair in this specimen had a higher than usual number of pinnule pairs per branchia (55 compared to 17), almost restoring its total pinnule count to the normal level for its depth.

Observations of regenerating branchiae in this species suggest that predation of branchiae is common. This worm normally lives in a vertical burrow in the sediment and probably exposes its anterior branchiae into the water at the sediment surface in a manner similar to that figured by Yokoyama (1988) for his *Paraprionospio* sp. Form A (a larger sized species, or subspecies, that is distinct from the *Paraprionospio* sp. A considered here). It is reasonable to conclude that the branchiae are therefore vulnerable to cropping predators.

4. Discussion, including observations on Cossuridae and Paraonidae

Diaz and Rosenberg (1995), in their comprehensive review of marine benthic hypoxia, discuss many examples of physiological adaptations to, mainly temporary, hypoxia. Observations on morphological responses are rare. Childress and Seibel (1998) provide examples of increased gill area of pelagic crustaceans from the oxygen minima in the Pacific. Tunnicliffe (1981) reported a size-dependant respiratory tolerance in the crab *Munida quadrispina*, with only the largest animals being found at the lowest oxygen levels. Astall et al. (1997) found that among six species of thalassinidean decapods, the two regularly exposed to prolonged periods of hypoxia have proportionately larger gill areas than the others.

Our observations on polychaetes indicate that greatly enlarged respiratory structures occur compared to those of congeners from slope environments not subject to hypoxic conditions. Yokoyama and Tamai (1981), however, noted that of the pinnate branchiae present in four previously undescribed forms of *Paraprionospio*, those of his 'Form A', which is found in oxygen-depleted, organic-rich inshore areas off Japan, are elongate, with the branchial pinnae present as numerous, well-separated lamellar plates.

Enlargement of respiratory structures in polychaetes as a morphological response to permanently hypoxic conditions in the OMZ on the Oman margin is also seen in specimens from the families Cossuridae and Paraonidae. Cossuridae were less numerous in our samples than spionids, but the six cossurid species separated in the collections, from 368 to 3392 m, spanned the entire depth range of the transect (Levin et al., 2000). Specimens were immersed in fresh water prior to measurement resulting in swelling of the body and filament to what appeared to be maximum proportions. Body form in these species was very uniform, and a relationship between filament length and body size might be expected to apply equally to different species. One of these species is illustrated in Fig. 1D to show the very long median filament. In order to utilise both complete and incomplete material, a relationship was fitted to measurements of prostomium length and setiger number of complete specimens. Linear regression provided the best fitting model using the six complete specimens available (setiger number = 880.75* prostomium length + 1.331, $R^2 = 0.69, P = 0.04$). Filament lengths measured in complete and incomplete specimens in relation to body size as estimated by prostomium length (Table 6) suggest a similar trend of decreasing filament length relative to body size with increasing depth in this family. A respiratory function of the median filament is in agreement with Tzetlin (1994) who observed that the median filament was not used in feeding. He suggested it had a respiratory function while stretched along the body inside the mucous tube. Bachelet and Laubier (1994) claimed that the filament of the shallow water species *Cossura pygodactylata* is highly contractile and that there is no relationship between body length and filament length, but they did not state the condition of the specimens on which their measurements are based. In this study, samples were transferred after a few days in formalin to 90% ethanol with 5% propylene glycol in order to preserve the flexibility of the specimens. We believe this allowed the filament in fresh water to recover to a size close to that when living, but comparison with measurements on relaxed living specimens that would be needed to confirm this, are not available. In view of this uncertainty, and the possibility that different species may vary in the degree of contraction after fixation, our data can be regarded as indicative only of a depth-related trend in relative size of the median filament.

A paraonid identified as *Allia* sp. A, was also found to have elongated, pinnule-bearing branchiae almost twice as long as congeners described by Strelzov (1979) from normally oxygenated conditions. This species ranged from 400 to 1000 m and was most numerous in the 850 m samples where it comprised about 20% of the polychaete fauna. The presence of pinnules on the branchiae is atypical for Paraonidae.

We do not know if the polychaetes on the Oman margin OMZ possess physiological/biochemical adaptations to hypoxia. However, we note here that the branchiae of specimens examined alive soon after collection appeared well vascularised with a red, haemoglobin-like pigment. Species of the spionid *Marenzelleria,* immigrants to the Baltic and estuarine areas in the North Sea, have an ability to switch metabolism to anaerobic pathways during temporary hypoxia (Schiedek, 1997; Schiedek et al.,

Table 6
Measurements from cossurid specimens allowed to equilibrate in freshwater. Complete specimens are indicated by 'C', incomplete by 'I'

Station	Specimen	Depth (m)	Complete/ incomplete	Number of setigers	Length branchial filament (mm)	Prostomium length (mm)
12700#2	B6	368	C	35	5.09	0.12
12692#4	A10	398	I	46	9.20	0.14
12692#4	A11	398	I	77	5.84	0.16
12692#4	A9	398	I	29	6.84	0.14
12692#4	B12	398	I	55	11.43	0.16
12692#4	B13	398	I	42	7.25	0.14
12692#4	B14	398	I	39	5.77	0.16
12692#4	B15	398	C	52	4.82	0.13
12692#4	C1	398	I	50	9.46	0.17
12692#4	C2	398	C	34	3.30	0.12
12695#7	B7	401	I	27	2.68	0.14
12695#7	B8	401	C	78	1.79	0.16
12695#4	B9	406	C	29	1.96	0.08
12685#6	A2	688	I	23	2.14	0.11
12685#6	A3	688	I	24	1.88	0.11
12685#6	A4	688	I	21	1.07	0.11
12685#6	A5	688	I	19	2.59	0.11
12685#6	A6	688	I	20	1.43	0.12
12685#6	A7	688	I	13	1.52	0.09
12685#6	A8	688	I	19	1.25	0.07
12685#8	B1	690	C	36	4.59	0.13
12685#8	B2	690	C	23	3.66	0.04
12685#8	B3	690	I	29	5.45	0.11
12685#8	B4	690	I	20	1.55	0.09
12685#8	B5	690	C	48	3.39	0.12
12687#1	A1	3372	I	29	2.23	0.18
12687#9	A12	3392	I	26	2.89	0.14

1997). Such adaptation, which might be turned 'on' and 'off' in response to changing conditions, is well suited to temporary hypoxia where morphological adaptations, such as enlarged branchiae, carry added predation risk (see below). Other spionids, in particular species of *Prionospio* and *Paraprionospio*, are known to tolerate conditions of organic enrichment and hypoxia in coastal waters (e.g. Britayev et al., 1994; Carrasco, 1997; Gallardo et al., 1995; Kube and Powilleit, 1997; Lu and Wu, 1998; Tamai, 1981,1985; Yokoyama, 1994) and may be indicators of such conditions (Maurer et al., 1998). The existence of populations of these genera in permanently hypoxic conditions, combined with high levels of organic carbon in the sediment (see Levin et al., 2000), is therefore not surprising. However, within-species variability in number and development of branchiae in relation to degree of hypoxia has not previously been recorded.

With *Prionospio* (*Minuspio*) sp. A, our results suggest more branchial pairs develop in lower oxygen conditions and at an earlier stage of development and grow longer, and in proportion faster, throughout life than those of their conspecifics living in higher oxygen conditions. This may be caused by post-settlement selection from a highly variable genotype covering a range of number and length of branchiae. Alternatively, the response may reflect early genetic differentiation of sub-populations at depths corresponding to different levels of hypoxia. However, it seems to us unlikely that the relatively small distance between the stations is enough to maintain sufficient isolation of morphotypes to promote differentiation in a species if larvae are dispersed in the water column. We have no data on how the larvae of these species are likely to be dispersed. However, we note here that the species *Paraprionospio* sp. Form A described by Yokoyama and Tamai (1981) spawns dense populations of larvae that aggregate at the lowest-oxygen levels within a coastal bay suffering oxygen depletion in Japan (Yokoyama, 1995). Yokoyama and Tamai conclude that post-settlement mortality is high in this opportunist species, with early stages having the ability to tolerate anoxic or hypoxic conditions throughout early development. If the spionid species in the present investigation have a similar early life history, and spend as long as pelagic larvae (about 2 months), then larvae may be dispersed over a wide area and depth range so that post-settlement selection may be possible if the genotype is sufficiently variable. The final alternative is a direct response of the phenotype to produce more and longer branchiae at increasing levels of hypoxia.

Enlargement of branchiae must represent an energy investment by the worm. Therefore, if selection from a variable genotype occurs, those worms with just sufficient branchial development to cope at less hypoxic conditions will have a competitive advantage over those with greater branchial enlargement. They will also have less risk of predator cropping of branchiae exposed at the sediment surface.

Enlarged branchiae, although probably effective in increasing respiratory area, may increase considerably the risk of predation of these highly vasularised structures. Predation in *Paraprionospio* sp. A was evident from the high incidence of cropped branchiae. Branchiae were observed in various stages of regeneration. Most were in process of regeneration, and only a few had a cleanly cut end. This implies that re-growth is rapid. However, we are unable to interpret from the appearance of the terminal pinnules on some specimens whether branchia had completely regenerated, or if cropping had never occurred. No likely predator has been identified from smaller macrofauna sampled by the USNEL box corer. However, motile megafauna not readily sampled by box coring may be responsible for branchial cropping. The small spider crab *Encephaloides armstrongi* occurred at extremely high densities (up to 137 m^{-2} counted from sea bed photographs) around 1000 m depth, and occurred at lower, but still relatively high, abundance (mean density of about 10 m^{-2}) between 570 and 815 m depth (Bett, 1995). The crab occurred in Agassiz trawlings as shallow as 150 m, and the high densities may be mating aggregations (Creasey et al., 1997). *E. armstrongi* is thought to be predatory and also to feed on detritus (Smallwood et al., 2000). Fish are known as active benthic croppers in other setting. No fish were observed in the bottom photographs taken on the Oman transect, and oxygen levels in this area (0.1–1.5 ml/l) may be too low for teleost fish. However, in the eastern Pacific the macrourid *Nezumia liolepis* has been recorded at oxygen levels down to 0.1–0.2 ml/l (Wishner et al., 1990). Childress and Seibel (1998) include other examples of tolerance to hypoxic conditions among midwater and benthic fishes.

Within-species variability is mostly known in terms of physiological responses or biocemical variation (e.g. Rice and Simon, 1980). In the spionid genus *Prionospio*, intergeneric variation in number of branchial pairs can be considerable. Within species the number of branchial pairs have been related to setigers (e.g. Mackie, 1983). Nateewathana and Hylleberg (1991) found the relative lengths of branchial pairs between species, of diagnostic value for describing species in a collection of undescribed *Prionospio* from the Andaman Sea off Thailand. Clearly, such within-species variability in branchial morphology as described here should be taken into account in studies of polychaete taxonomy.

In summary, it is not known at present if the branchial differences within the spionid species studied here reflect differences in the genotype or whether they are a response of the phenotype to the varying oxygen environment along the transect. If the former, it is possible they may represent the presence of otherwise morphologically indistinguishable species or subspecies. However, we feel that such genetic differentiation may be less likely than a differential selection from a highly variable genotype. If this is true, then there are implications concerning the fidelity of morphological characteristics, such as number and relative size of branchial pairs, in the taxonomic characterisation of species. In any case, the results show that considerable within-species variability may occur in spionid populations from the same general area.

Overall the results indicate that for benthic invertebrates able to tolerate permanent hypoxia, there are powerful constraints for morphological adaptation aimed towards enhancing O_2 diffusion by increasing body area/mass ratio.

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