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Interaction between water flow and oxygen deficiency on growth in the infaunal brittle star *Amphiura filiformis* (Echinodermata: Ophiuroidea)

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Abstract

Interactions between ‘oxygen concentration’ (normoxia: >80% oxygen saturation, and hypoxia: 18% oxygen saturation) and ‘water flow velocity’ (low: 0.1 cm s^{-1} , and moderate: 0.5 cm s^{-1}) were studied on growth rates in the brittle star *Amphiura filiformis* in a flow-through aquaria system. Effects of ‘sublethal predation’ on growth rates were investigated as ‘number of amputated arms’ (1 and 3 arms) and ‘amputation of the disk’. A significant interaction between oxygen concentration and water flow velocity was observed in mean arm regeneration rate, but in both flow velocities higher mean arm regeneration rates were observed in normoxia compared to hypoxia. In hypoxia a positive response in arm regeneration rate was observed in moderate flow compared to low flow velocity. In normoxia, however, no response to flow velocity was observed. The latter observation indicates that *Amphiura filiformis* is able to maintain the ventilation of the burrow at low flow velocities, but in low oxygen concentrations hydrodynamic forces seem to affect growth. A significant interaction between oxygen concentration and disk amputation was observed in both arm and disk regeneration rates, indicating that the disk is the major organ for gas exchange in this species. The number of arms amputated, however, did not affect mean arm regeneration rate. The results obtained in this study suggest that the secondary production in subtidal infaunal populations could be negatively affected by low oxygen concentrations and that this response is even more negative in combination with low flow velocities in the near-bottom water. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: hypoxia; eutrophication; arm regeneration; water current; benthos; energy translocation

1. Introduction

It has long been recognised that whether a stratified area becomes hypoxic or not depends primarily on the balance between the rate of renewal of bottom water and the oxygen consumption rate below the pycnocline, which largely depends on the rate at which organic matter is introduced (Richards, 1965). During

the last decades increased organic enrichment in coastal areas acts as an enhancing factor to oxygen depletion in the near-bottom water, and when coupled with adverse meteorological and hydrodynamic events, hypoxia increases in frequency and severity (Diaz and Rosenberg, 1995). During hypoxic events in Limfjorden and Kattegat, resulting in high mortality rates of benthic macrofauna, a strong vertical gradient in oxygen concentration just some cm to dm above the sediment surface has been observed (Jørgensen, 1980; Rosenberg and Loo, 1988). The

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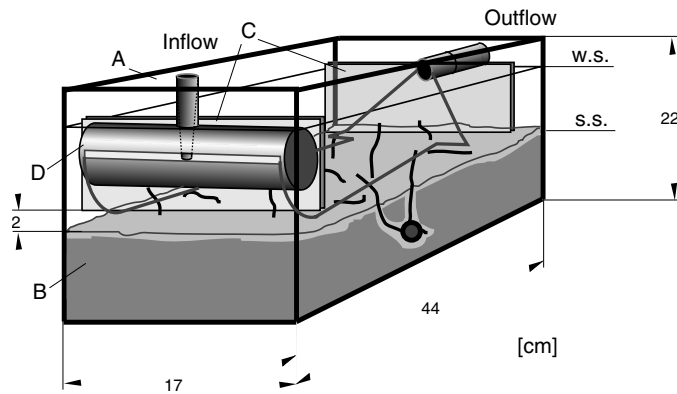


Fig. 1. The design of the flow-through aquaria and its measure: (A) aquaria, (B) sediment, (C) Plexiglas plates, (D) the diffuser with the pipette tip, (s.s.) sediment surface, and (w.s.) water surface. Arrow indicates the flow direction.

diffusive boundary layer above the sediment surface creates a steep oxygen gradient at the sediment surface and the depth of the diffusive boundary layer is dependent on flow and sediment roughness. At smooth sediment surfaces this boundary layer is thin (≤ 1 mm) (Gundersen and Jørgensen, 1990). However, the sediment topography and the topography due to the fauna — bioroughness — have been shown to significantly influence the hydrodynamic environment (Eckman, 1983; Eckman and Nowell, 1984; Vogel, 1994), and the exchange of solutes between sediment and water (Huettel and Gust, 1992).

Water flow is a dominant factor limiting macrofaunal productivity via its influence on food and oxygen supply in the benthic boundary layer (Wildish, 1977). However, to my knowledge this is the first time the interaction between water flow and oxygen concentration has been examined on growth in benthic macrofauna. In this study, I address the question whether ‘water flow dynamics’ and ‘oxygen concentration’ interact on growth and behaviour in the common infaunal brittle star species *Amphiura filiformis*. The experiment was performed at oxygen concentrations which have been shown to affect arm regeneration rates in *Amphiura filiformis* (Nilsson and Sköld, 1996; Nilsson, 1999) and have frequently been observed seasonally in large areas of Kattegat inhabited by this brittle star species (Rosenberg and Loo, 1988), without affecting their behaviour or mortality (Nilsson and Rosenberg, 1994; Nilsson and Sköld, 1996). Ophiuroids are well known for their ability to lose body parts as a result of injury or predation and to subsequently regenerate the

missing body part (Hyman, 1955, p. 644; Wilkie, 1978; Emson and Wilkie, 1980). It has also been shown that regeneration rates in ophiuroids are sensitive to changing environmental conditions (Donachy and Watabe, 1986; Walsh et al., 1986; Nilsson and Sköld, 1996; Nilsson, 1999). Both arms and disk take part in oxygen transport and gas exchange (Gislén, 1924; Woodley, 1975). Therefore a second question to be addressed was how these factors interact with the amount of ‘sublethal predation’ (arms and disk amputation) on the brittle stars’ capacity to regulate the oxygenation of their burrow.

2. Material and methods

2.1. Sampling

Individuals of the infaunal brittle star *Amphiura filiformis* and sediment were collected with a box-corer (0.1 m^2) at 30 m depth from the inner part of Gullmarsfjord, Skagerrak, west Sweden. The Gullmarsfjord is a 60-km-long true fjord, 118 m deep, with a sill at about 40 m depth. After collection, animals were gently rinsed (to prevent breakage of arms) from sediment. The sediment used in aquaria was sieved (2.5 mm) to exclude adult brittle stars and larger infauna specimens.

2.2. Experimental set-up

The experimental factors, oxygen concentration (OX, normoxia: $>80\%$ oxygen saturation, and hypoxia: 18% oxygen saturation), and water flow velocity (FL, low:

$12.6 \text{ dm}^3 \text{ h}^{-1} = \text{about } 0.1 \text{ cm s}^{-1}$, and moderate: $66.0 \text{ dm}^3 \text{ h}^{-1} = \text{about } 0.5 \text{ cm s}^{-1}$) were replicated four times in totally 16 flow-through aquaria.

A unidirectional water flow in the aquaria was obtained by dividing each aquarium into three sections with two vertical Plexiglas plates, which press the flow between the Plexiglas plate and the sediment surface (Fig. 1; Nilsson, 1999). This construction minimises the gas flux between water and air in the experimental section of the aquaria, since the surface water will become more or less stagnant. The flow velocity was calculated from the size of the open cross section area between the sediment surface and the Plexiglas plates divided by water renewal. Flow velocity was also estimated by tracing suspended particles and the flow was adjusted to be as similar as possible between and within aquaria. Water flow velocity was adjusted by regulating the water level between a common header tank and the aquaria, the position of Plexiglas plates, and the aperture of the tip of the pipette, which supplied the aquaria through a horizontal diffuser with incoming water from the header tank.

The regulation and logging of oxygen concentration was performed by oxygen probes (Jenaway Ltd, UK) and a multi channel computer system (LabView 3.1) connected to magnetic valves regulating the bubbling of nitrogen to reduce the oxygen concentration in the common header tank. In the normoxic treatment aquaria the incoming water from the header tank was re-saturated to $\geq 80\%$ oxygen saturation by constantly bubbling air in the inflow section of the aquaria. Calibration between oxygen probes and aquaria was done with a Winkler (SIS, 1975) calibrated YSI 58 oxygen meter. In the hypoxic treatment oxygen saturation varied between 16 and 20% during the treatment period. Temperature was kept at 10°C in both air and water, and salinity was 33 psu.

At the start of the experiment, 40 adult individuals of *Amphiura filiformis* were introduced to each aquarium, giving a density of 619 ind. m^{-2} , similar to the densities observed in hypoxia-stressed areas in Kattegat (Rosenberg and Loo, 1988). Before the brittle stars were added, a single arm or tree arms were amputated (AR) between the 7th and 8th arm segment in half of the specimens, respectively. In both groups the disk was removed (DI) in half of the specimens resulting in a total of 10 replicates of brittle stars in each of the four groups of 'sublethal predation' in each aquarium.

The experiment lasted 49 days and the oxygen concentration and water flow velocity were regulated to treatment levels for 21 days. During the rest of the time the experimental conditions were normoxia and low flow velocity treatments in all aquaria.

The brittle stars were fed once at the start of the hypoxic treatment with dried and powdered green macroalgae (*Cladophora* spp. and *Enteromorpha* spp.) corresponding to $4.7 \text{ g organic C m}^{-2}$. The great extent of this food-pulse should also minimise the effect of different water flow velocities on the amount of available food for the brittle stars, since the amount of seston introduced by the flow should only be a fraction of the added amount of algal food.

2.3. Measurements

At the end of the experiment all brittle stars were video recorded under a dissection microscope and regenerated arms and disk area were measured by image analysis (NIH Image 1.6 for Macintosh computers; Nilsson and Sköld, 1996).

Dry weight (DW) of regenerated arm tips was estimated after freeze-drying for 24 h. Total organic carbon (TOC), total carbon (C_{tot}) and nitrogen (N) content in arm tips were analysed with a NA 1500 NC analyser (Fisons, Italy). In each of the four treatment combinations (arm and disk amputation) regenerated arm tip tissue from 100 individuals was equally divided into five length groups. This was done to obtain a measurable amount of tissue and to analyse whether any size dependency in the dependent variables could be observed. The C_{tot} and N content was only analysed in specimens with three arms amputated, since the amount of tissue was too small to be divided into specimens with one arm amputated.

Total number of arms raised into the water column was estimated in each aquarium at least every third day, as a measurement of filter feeding activity.

2.4. Statistics

Possible differences in arm regeneration rates and disk area were evaluated with a balanced 5-factor nested analysis of variance (ANOVA) with number of amputated arms (AR), disk removal (DI), oxygen concentration (OX) and water flow velocity (FL) as fixed factors, and aquaria (AQ) nested in oxygen concentration and water flow velocity. Analysis of

Table 1

Statistical comparison of treatment effects, disk (DI), arms (AR), oxygen concentration (OX), water flow velocity (FL) and Aquaria (AQ) on \log^{10} (arm length) and \log^{10} (disk area). Significance levels are abbreviated with: ns = $p > 0.05$ (non significant), * = $p < 0.05$

Source	Df	Error term	Arm length		Disk area	
			F-value	Sign	F-value	Sign
DI	1	DI × AQ(OX×FL)	695.30	*	2140.94	*
AR	1	AR × AQ(OX × FL)	0.17	ns	12.40	*
OX	1	AQ(OX × FL)	42.14	*	5.63	*
FL	1	AQ(OX × FL)	13.12	*	0.04	ns
AQ(OX × FL)	12	RES	2.67	*	1.11	ns
DI × AR	1	DI × AR × AQ(OX × FL)	0.35	ns	1.23	ns
DI × OX	1	DI × AQ(OX × FL)	12.89	*	5.00	*
DI × FL	1	DI × AQ(OX × FL)	0.00	ns	1.87	ns
DI × AQ(OX × FL)	12	RES	2.14	*	1.37	ns
AR × OX	1	AR × AQ(OX × FL)	1.03	ns	0.87	ns
AR × FL	1	AR × AQ(OX × FL)	0.06	ns	0.12	ns
AR × AQ(OX × FL)	12	RES	1.03	ns	1.27	ns
OX × FL	1	AQ(OX × FL)	4.98	*	0.00	ns
DI × AR × OX	1	DI × AR × AQ(OX × FL)	0.07	ns	0.33	ns
DI × AR × FL	1	DI × AR × AQ(OX×FL)	0.35	ns	0.42	ns
DI × AR × AQ(OX × FL)	12	RES	0.93	ns	1.29	ns
DI × OX × FL	1	DI × AQ(OX × FL)	1.56	ns	2.43	ns
AR × OX × FL	1	AR × AQ(OX × FL)	1.38	ns	1.42	ns
DI × AR × OX × FL	1	DI × AR × AQ(OX × FL)	2.10	ns	1.79	ns
RES	448					
TOT	511					

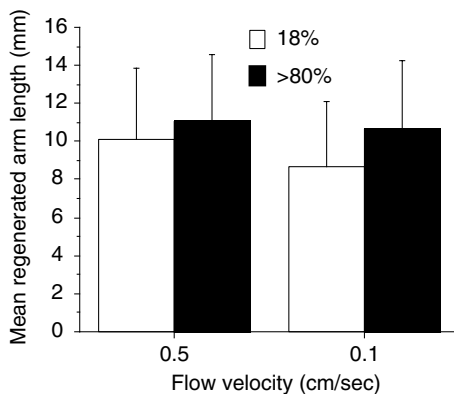


Fig. 2. Interaction plot between ‘oxygen concentration’ and ‘water flow velocity’ on mean regenerated arm length \pm SD ($n = 128$) at the termination of the experiment. [(hypoxia, low flow) < (hypoxia, moderate flow), (normoxia, low flow) = (normoxia, moderate flow), (hypoxia, low flow) < (normoxia, low flow), and (hypoxia, moderate flow) < (normoxia, moderate flow); SNK, $p < 0.05$].

differences in TOC was tested by a 2-way ANOVA with AR and DI as fixed factors. All measurements were $\log^{10}(X)$ transformed before statistical analysis to assess relative differences between treatments, since the removal of disk introduced significant variances in both regenerated arm length and disk area. The homogeneity of variances was examined using Cochran’s *C* test (Snedecor and Cochran, 1967). Multiple comparison of means was done by Student–Newman–Keuls test (SNK). The significance level was set to $p < 0.05$ and at significant interactions, main factors were not interpreted (Underwood, 1981). The biometric relationship between arm length and DW was analysed with a simple linear regression.

3. Results

3.1. Arm regeneration and disk growth

A significant interaction between ‘water flow velocity’ and ‘oxygen concentration’ was observed on arm

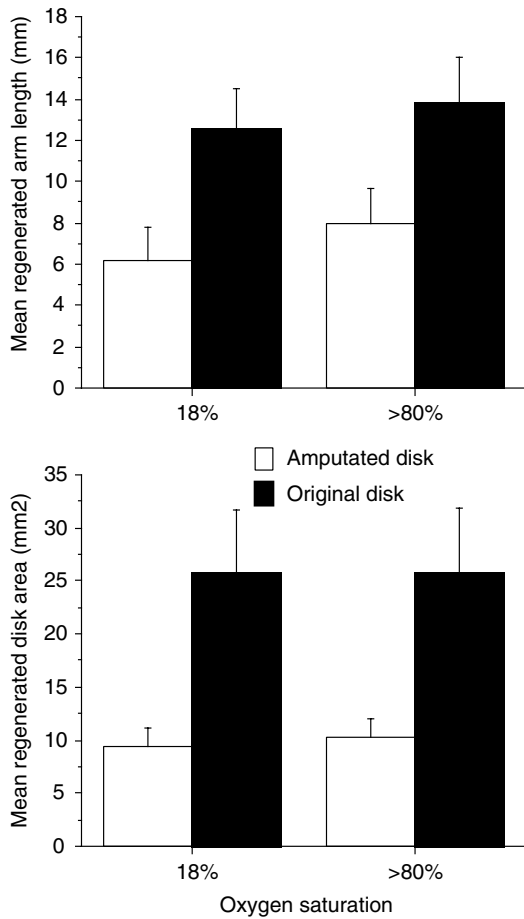


Fig. 3. (a) The interaction plot between ‘oxygen concentration’ and ‘amputation of disk’ on mean regenerated arm length \pm SD ($n = 128$) at the termination of the experiment. [(amputated disk, hypoxia) < (amputated disk, normoxia), (original disk, hypoxia) < (original disk, normoxia), (amputated disk, hypoxia) < (original disk, hypoxia), and (amputated disk, normoxia) < (original disk, normoxia); SNK, $p < 0.05$]. (b) The interaction plot between ‘oxygen concentration’ and ‘amputation of disk’ on mean arm regenerated disk area \pm SD ($n = 128$) at the termination of the experiment. [(amputated disk, hypoxia) < (amputated disk, normoxia), (original disk, hypoxia) = (original disk, normoxia), (amputated disk, hypoxia) < (original disk, hypoxia), and (amputated disk, normoxia) < (original disk, normoxia); SNK, $p < 0.05$].

regeneration rate (Table 1), but in both low and moderate water flow velocity significantly higher mean arm regeneration rates were observed in normoxia compared to hypoxia (Fig. 2). In hypoxia a significantly increased arm regeneration rate was

observed in moderate water flow velocity compared with low water flow velocity. However, no difference in arm regeneration rates was observed in normoxia between low and moderate water flow velocity.

Significant interactions between ‘oxygen concentration’ and ‘amputation of disk’ were observed in both arm regeneration rate (Fig. 3a) and disk growth (Fig. 3b). Significantly larger differences between normoxia and hypoxia were observed in specimens with amputated disk than in specimens with the original disk left. On average, lower arm regeneration rates and smaller disk area were observed at the end of the experiment in hypoxia compared to normoxia if the disk was amputated at the start of the experiment. However, only mean arm regeneration rates were lower in hypoxia compared to normoxia in specimens with their original disk left. The disk area was significantly larger in specimens with one arm amputated (18.5 mm^2) compared with specimens with three arms amputated (17.1 mm^2) at the termination of the experiment.

A significant ‘aquaria effect’ was observed in arm regeneration rates; however, no separation between ‘bad and good’ aquaria was to be expected since the ‘aquaria effect’ interacts with the treatment ‘amputation of disk’. In only one of the 16 treatment combinations at this level multiple comparisons (SNK-test) found significant differences between aquaria because of overlap between groups. In the treatment combination normoxia and low flow velocity, in specimens with their original disk left, the aquaria were divided into ‘two bad and two good’ aquaria; however, this could not be realised in the other treatment combinations.

3.2. Biometrical relationship and organic content

The relationship between regenerated arm length (L , mm, in the span between 4.2 and 18.1 mm) and DW of arm tip (mg) was calculated with a simple linear regression, which resulted in the following relationship: $DW = 0.0295L - 0.0670$, $r^2 = 0.77$.

A significantly (ANOVA, $F_{1,16} = 42.4$, $p < 0.05$) higher percent TOC was observed in arm tips belonging to specimens with their original disk left compared to specimens with a regenerated disk (Table 2). No effects of number of arms amputated or interactions between amputation of disk and arms were observed

Table 2

Mean TOC \pm SD, C_{tot} \pm SD and nitrogen content \pm SD in the four treatment combination of disk (No: amputated disk, Yes: original disk) and arm (-1: 1 arm amputated, -3: 3 arms amputated) amputation at the end of the experiment

Disk	Arm	Arm length (range, mm)	TOC (%)	SD	C_{tot} (%)	SD	N (%)	SD
No	-1	4.2–10.9	11.0	1.0				
No	-3	4.3–11.8	11.4	0.4	18.2	0.9	2.6	0.2
Yes	-1	9.5–17.8	13.0	0.4				
Yes	-3	9.2–18.1	13.6	0.7	20.6	0.7	3.0	0.1

in TOC content. The differences observed in TOC between specimens with their original disk left and specimens with a regenerated disk were also observed in total carbon and nitrogen content.

3.3. Behaviour

The brittle stars burrowed into the sediment a few minutes after they had been put on the sediment surface. After this, no disks were seen on the sediment during the experiment. In all treatments the filter-feeding activity increased from about 0.5 arm per individual to 1 arm per individual after two weeks with a significant increase the day after the food pulse of macroalgae (Fig. 4). No significant differences in number of arms raised into the water column

were observed between either the oxygen concentration or the water flow velocity treatments.

4. Discussion

It has earlier been established that moderate hypoxic oxygen saturations (18–30%) do not affect the behaviour or mortality of *Amphiura filiformis*, but may have a negative influence on their growth (Nilsson and Sköld, 1996; Nilsson, 1999). *Amphiura filiformis* living under moderate hypoxic (18% oxygen saturation) conditions, in conjunction with accumulated organic matter on the sediment surface may, however, respond with increased ventilation to exclude harmful sulphide concentrations and to maintain the oxygenation of their burrow (Nilsson, 1999).

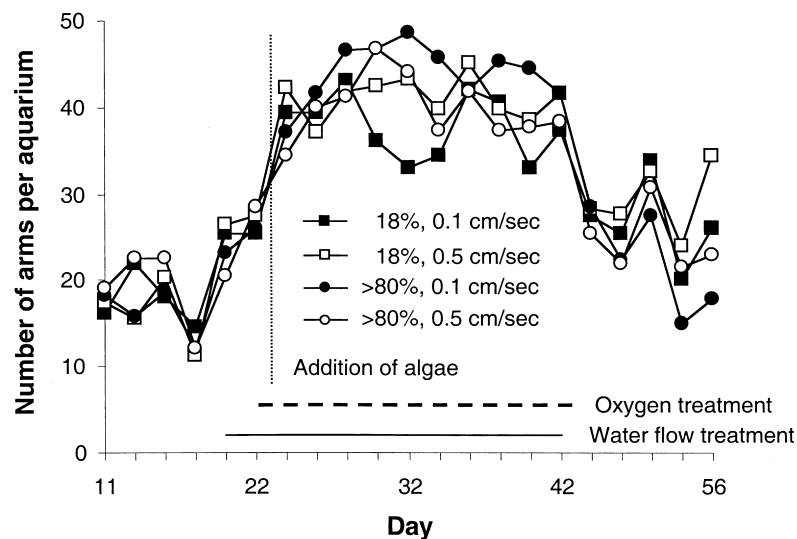


Fig. 4. Mean number of filter feeding arms (defined as arms raised into the water column) in the four treatment combinations, (hypoxia, low flow), (hypoxia, moderate flow), (normoxia, low flow), and (normoxia, moderate flow) during the experiment. The horizontal lines show the duration of the treatments of water flow velocity and oxygen concentration. The vertical line indicates the addition of algae.

Flow velocity has been shown to influence several benthic processes such as sedimentation, resuspension, exchange of solutes between water and sediment, benthic microbial development, faunal recruitment and particle feeding, which affect both benthic community structures and productivity (Wildish, 1977; Eckman and Nowell, 1984; Jumars and Nowell, 1984; Huettel and Gust, 1992; Graf and Rosenberg, 1997). In the present paper, a significant interaction between oxygen concentration and water flow velocity is demonstrated for arm regeneration rates when oxygen is limiting for growth.

4.1. Behaviour

The infaunal brittle star *Amphiura filiformis* is a passive suspension feeder that is able to regulate the position of its arms and the number of arms raised depending on flow and particle concentration (Buchanan, 1964; Ockelmann and Muus, 1978; Loo et al., 1996). In the present study, I did not observe any differences in filter feeding behaviour (number of arms raised into the water column) between oxygen and flow treatments. The number of arms raised into the water column increased significantly, however, after the addition of organic matter and remained so for about three weeks, which indicates that the response was not due to momentary resuspension of sedimentary particles during the addition. This long-term behaviour response may instead indicate that the arms were raised in order to facilitate increased respiration rate triggered by the consumption of added and settled macroalgae. It has been shown that *Amphiura filiformis* can regulate the ventilation of their burrows by forcing water along the spaces between the arms and the walls of the burrow (Woodley, 1975). Either the number of amputated arms or the interaction between oxygen concentration or water flow velocity and number of amputated arms affected the mean arm regeneration rate. These results suggest that the number of arms used to regulate the ventilation of a burrow is ≤ 2 . It seems likely that only one intact arm at the time is used to pump water into the burrow, because at the same time an outflow passage must be open to keep the resistance of pumping low. Thus, the loss of three arms does not affect the ventilation capacity in *Amphiura filiformis*.

The interaction between removal of the disk and

oxygen concentration in both arm regeneration rate and disk growth indicates a reduced capability to regulate gas exchange with surrounding water during hypoxia compared with normoxia. This may support Gislén (1924, p. 255) finding that the bursa, the thin ciliated invaginated body wall, on the oral side of the disk, is the main organ for gas exchanges in *Amphiura filiformis*.

4.2. Allocation of energy

The disk area measured at the termination of the experiment decreased with increasing number of arms amputated. Similar observations have earlier been shown by Nilsson (1999) for disk area, AFDW of disk and gonad indices, and have been suggested to depend on increased allocation of energy to arm instead of disk regeneration. Furthermore, no differences were observed in DW or TOC in arm tips between specimens with one or three arms amputated, which indicates that the total energy allocated to arm regeneration is about three times higher in specimens with three arms amputated compared to one arm. The fact that the number of arms lost did not affect the arm regeneration rate even if the disk was removed indicates that arm regeneration rate at an early stage is not dependent on energy allocation from the disk.

4.3. Water flow velocity

An interaction between oxygen concentration and water flow velocity was observed in arm regeneration rates, with a positive response to higher flow in hypoxia. In normoxia, however, no significant differences between flows were observed. The latter observation indicates that *Amphiura filiformis* is able to adjust ventilation of its burrow to different flow velocities without any significant effects on growth. In normoxia this species has earlier been shown to regulate the oxygenation of the burrow, also in stagnant water conditions by increasing the arm undulation frequency (Woodley, 1975). The lack of response in arm regeneration rate due to different flow velocities in normoxia also indicates that the amount of particles they could assimilate from the incoming flow was insignificant as a food source compared to the amount of macroalgae added. However, during moderate hypoxic conditions increased flow velocity did affect the arm regeneration rate positively. One explanation

for this response may be that *Amphiura filiformis* utilised the water flow to maintain the ventilation of the burrow by the pressure gradients created by the arms protruding into the water flow. These gradients will induce a flow from the sediment surface along the arm and upward into the water column (Eckman and Nowell, 1984; Vogel, 1994; Loo et al., 1996). Such a passive flow may enhance the transport of water from the out-flow passage of the burrow, decreasing the resistance of pumping. If the capacity to maintain the oxygenation of the burrow during oxygen deficiency at low flows is insufficient, the brittle stars may be forced to decrease their aerobic metabolism, which in turn decreases the energy yield. Another explanation for the differences in arm regeneration rates in hypoxia may be that an increased ventilation activity is costly, and if sustained may decrease the amount of energy available for growth. The increased diffusive boundary layer at low flows could as well interact with declining oxygen saturation and decrease the brittle stars' ability to ventilate their burrow. In the present paper, no direct recordings of the ventilation response of the brittle star was made and it is not possible to separate the significance of the above explanations. The water flow in the experimental flow-through aquaria system was not designed for creating a true boundary layer, which could affect the extent of the observed response. However, the main conclusion is that flow dynamics influence the growth in *Amphiura filiformis* during low oxygen concentrations.

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