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Estuarine epifauna recruit despite periodic hypoxia stress

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Abstract In some estuaries, the recruitment of epifaunal benthic invertebrates coincides with a significant environmental stress, low water-column dissolved oxygen, termed hypoxia (≥ 2 mg O₂ l⁻¹). Recruitment of epifaunal species was measured in the lower York River, a subestuary of the Chesapeake Bay, USA, which experiences predictable, periodic hypoxia associated with neap/spring tidal cycling during summer. Recruitment substrata were exposed during 48-h deployments in two areas with differing levels of hypoxia, and epifauna were allowed to recruit during periods of low oxygen (neap tides) and high oxygen (spring tides) in 1996 and 1997. Recruitment was often high during neap tides, even when severe oxygen depletion (< 0.5 mg O₂ l⁻¹, < 0.71 ml O₂ l⁻¹) occurred during deployments; indeed, peak recruitment episodes of several dominant epifaunal taxa, and of total epifauna, coincided with hypoxic events during both summers. Increased recruitment during neap tides suggests that factors besides hypoxia influenced recruitment in the York River; these factors may have included changes in larval availability and lower current speeds. This study illustrates how the relationship between recruitment and large-scale stresses, such as hypoxia, may be difficult to predict, since large-scale stresses are often correlated with numerous other factors. Short-term hypoxia appears to have little effect on recruitment in the field for many epifaunal species in this ecosystem, which may explain, in part, why substrata exposed for longer durations (1 month) in this

system showed few effects of hypoxia on community composition or diversity. High larval tolerance of hypoxic stress may allow communities to persist even though the summer hypoxia season coincides with the recruitment of many epifaunal species.

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Introduction

Environmental stress and recruitment are major regulators of community structure and community processes (Menge and Sutherland 1987). Stress can alter recruitment at numerous stages, by decreasing fecundity of adults (Sanders 1986; Weimeyer et al. 1988) and/or survival of propagules, by altering settlement patterns (Connell et al. 1997), or by changing growth of or predation rates on recent settlers (Osman et al. 1992; Minchinton and Scheibling 1993). At the community level, the effects of stress on recruitment depend on the timing of stress relative to the recruitment of dominant species (Sousa 1984; Breitburg 1992). Disturbed communities often recover through the arrival of recruits (Sousa 1984) or migration of adults (Palmer et al. 1996). Thus, if the recruitment of dominant species is impeded by stressful events, recovery may be slow, or the community composition may be permanently changed.

Depletion of water-column dissolved oxygen is among the most common of the environmental stresses affecting coastal systems (Diaz and Rosenberg 1995). While any discrete boundary between “hypoxia” and “normoxia” is necessarily arbitrary, and oxygen levels that stress animals vary from species to species, 2 mg O₂ l⁻¹ is one widely accepted level at which oxygen concentrations no longer stress many organisms (Tyson and Pearson 1991). In the present paper we define hypoxia as oxygen concentrations, in the water column, of < 2 mg O₂ l⁻¹

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(corresponding to approximately $2.86 \text{ ml O}_2 \text{ l}^{-1}$), and we define oxygen concentrations $>2 \text{ mg O}_2 \text{ l}^{-1}$ as “non-hypoxia”. Dissolved oxygen concentrations $<0.1 \text{ mg O}_2 \text{ l}^{-1}$ ($0.14 \text{ ml O}_2 \text{ l}^{-1}$) (anoxia) often have severe impacts on ecosystems (Diaz and Rosenberg 1995). Hypoxia and anoxia are becoming more widespread and persistent because of accelerating anthropogenic eutrophication (Officer et al. 1984). Hypoxia can change behavior, decrease growth, and kill macrofauna (Forbes and Lopez 1990; Llanso 1991; Diaz and Rosenberg 1995). It can also change the diversity (Llanso 1992), biomass, species composition (Jorgensen 1980; Rosenberg et al. 1983), and function (Schaffner et al. 1992) of benthic communities.

Hypoxia can change recruitment for some species. Exposure to low oxygen caused higher mortality in larvae than in adults of bivalve species (Widdows et al. 1989; Wang and Widdows 1991), although some invertebrate larvae may be highly tolerant of hypoxia. For example, larvae of the clam *Mercenaria mercenaria* showed no change in growth or survival after 24 h at $1 \text{ mg O}_2 \text{ l}^{-1}$ (McMurrer Huntington and Miller 1989), and larval survival of the polychaete *Streblospio benedicti* was unaffected by 92 h at 14.5% saturation (Llanso 1991). Often, larval tolerance increases as larvae develop (Wang and Widdows 1991; Spicer 1995), because the ability to control metabolic expenditures increases with larval stage (Widdows et al. 1989) and because the youngest larvae have reduced defenses such as blood pigments with lower oxygen affinities (Spicer 1995). Larvae of some taxa exposed to hypoxia can stop eating and/or growing (Wang and Widdows 1991; Baker and Mann 1992; Nebeker et al. 1996), leading to delayed development and prolonged larval stages (Widdows et al. 1989). Recruitment during hypoxia may be particularly difficult, because settlement and metamorphosis require abundant energy and larvae primarily have energy in the form of fats that cannot be used for anaerobic metabolism (Baker and Mann 1992). Hypoxia decreases settlement of some species; for example oysters (*Crassostrea virginica*) reduced settling rates at oxygen concentrations $<1.5 \text{ mg O}_2 \text{ l}^{-1}$, and completely stopped settling during anoxia (Baker and Mann 1992). The larvae of some species can avoid low-oxygen water, resulting in decreased settlement in hypoxic areas (Powers et al. 2001).

The implications of hypoxia's effects on recruitment in a particular community will depend, in part, on the species composition and the timing of hypoxia. If the larvae of dominant species have low hypoxia tolerance, or if some species are more tolerant than others, hypoxia may change the community composition and may indirectly influence interactions among species. Similarly, if the timing of hypoxia coincides with the recruitment of dominant species, the community composition may shift.

In this study, we examined the effects of hypoxia on recruitment in an estuarine epifaunal community. The timing of hypoxia in this system coincides with the recruitment of dominant species, yet the community persists (Sagasti et al. 2000). Complex, diverse epifaunal

communities consisting of several layers of epifauna living on top of each other thrive in this system in the summer, despite multiple periods of hypoxia (Sagasti et al. 2000). Because these species grow so quickly, one possible reason for their persistence may be that they can recruit and grow sufficiently between hypoxic episodes to complete their life cycle. Alternatively, they may be so tolerant of short-term oxygen stress that they can recruit, survive, and grow in hypoxic conditions. Our objectives in this study were to determine whether low-oxygen events decrease recruitment by the larvae of epifaunal species in the field. By examining the relationship between hypoxic stress and recruitment, we hope to better understand how epifaunal species persist in an area where hypoxia may deter recruitment.

Materials and methods

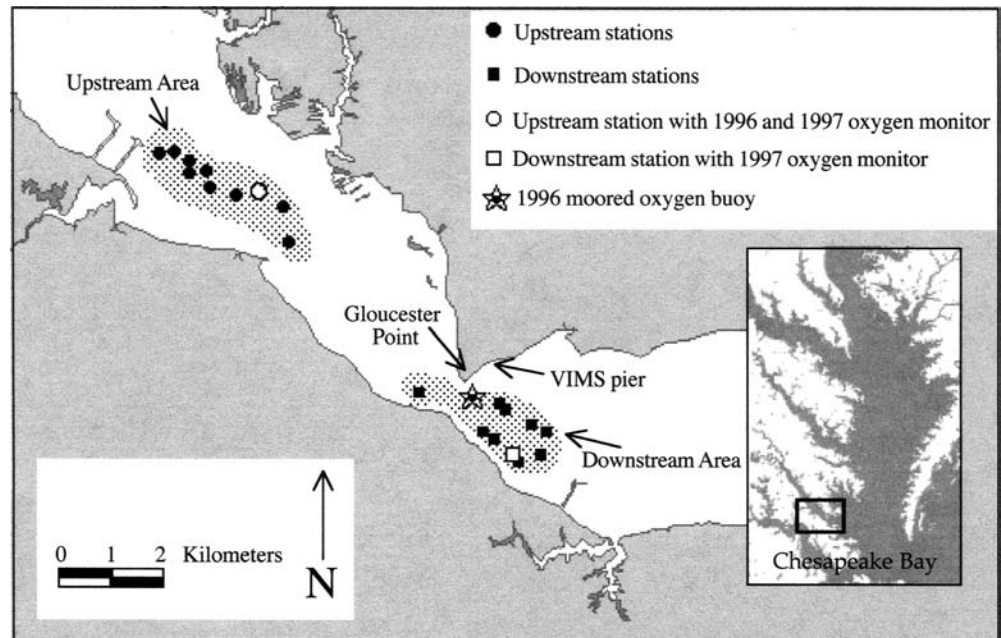
Recruitment by epifaunal invertebrates was characterized in the York River, Virginia, a subestuary of the Chesapeake Bay, USA, where the timing and spatial extent of hypoxia are relatively predictable (Haas 1977; Kuo and Nielson 1987). The York River experiences well-described cycles of hypoxia ($\geq 2 \text{ mg O}_2 \text{ l}^{-1}$) and non-hypoxia ($>2 \text{ mg O}_2 \text{ l}^{-1}$) in the summer (Haas 1977). During spring tides, tidal currents are sufficient to destratify the water column, re-oxygenating deep layers and preventing hypoxia. During neap tides, currents are too weak to prevent stratification and hypoxia typically occurs below 9 m (Pihl et al. 1992). During these hypoxic episodes, oxygen concentrations are often lowest near the mouth of the York River and increase upstream (Sisson et al. 1991; Kuo et al. 1993). Therefore, hypoxia usually occurs during neap tides in the summer and is often most severe downstream of Gloucester Point (Fig. 1) (Haas 1977; Kuo et al. 1993). An additional factor often associated with hypoxia is hypercapnia, an increase in water-column CO_2 concentrations that can lead to decreased pH (Cochran and Burnett 1996). In the York River, pH remains above 7.2, except in the deepest areas ($=20 \text{ m}$) following prolonged ($>24 \text{ h}$) anoxia (J.A. Nesterode, personal communication).

To compare epifaunal recruitment in high versus low oxygen conditions, we collected recruits of dominant species on artificial substrata during both spring and neap tides (corresponding with high- and low-oxygen periods) and in two areas (upstream and downstream) (Fig. 1). During hypoxic episodes, dissolved oxygen concentrations in the downstream area are generally lower than concentrations in the upstream area by $0.5\text{--}1 \text{ mg O}_2 \text{ l}^{-1}$ ($0.7\text{--}1.4 \text{ ml O}_2 \text{ l}^{-1}$), but the two areas are similar in nutrient concentrations, sediment composition, temperature, salinity, and epifaunal communities (Sagasti et al. 2000). Within each area, oxygen concentration is similar among stations (Sagasti et al. 2000).

In each area (downstream and upstream) we randomly chose eight station locations (1996) or ten station locations (1997) along the 15 m depth contour, where hypoxia generally occurs each summer, but where hypercapnia is unlikely. At each station we deployed a PVC pipe frame, to which we attached settlement substrates (Sagasti et al. 2000). By the end of the summer in 1996, we had lost the sampling units at half of the stations in each area due to collisions with boats or other accidents. In 1997, sampling units at each station were replaced as soon as they were lost and we ended the summer with all stations intact.

Epifauna were allowed to settle on $10 \times 10 \text{ cm}$ PVC panels (Sagasti et al. 2000). Panels were lightly sanded and allowed to develop natural microbial films, which enhance settlement (Coe and Allen 1937; Keough and Raimondi 1996). To develop microbial films, panels were immersed for 48 h in $10\text{-}\mu\text{m}$ -filtered York River water. Panels were attached to the frames oriented perpendicular to the substratum and placed in randomly chosen locations on each frame.

Fig. 1 Sampling stations in the York River, Virginia in 1996 and 1997. Locations were chosen randomly along the 15 m depth contour (modified from Sagasti et al. 2000) (VIMS Virginia Institute of Marine Science)



Panels were deployed at each station and retrieved after 2 days, a duration designed to measure short-term recruitment. We placed one panel at each station during deployments in 1996 and four panels at each station in 1997. We had a total of ten deployments in 1996, five during neap and five during spring tides, and eight deployments in 1997, four during neap and four during spring tides. All deployments occurred between June and September, coinciding with the season of peak epifaunal recruitment in the Chesapeake Bay (Abbe 1987) and with the maximum occurrence of hypoxia (Officer et al. 1984).

To retrieve panels, the entire PVC frame was brought to the surface by hand (1996) or with a mechanical winch (1997). Panels were then removed and placed into 1-l containers filled with 10- μ m-filtered York River water, kept in coolers, and held upright without dislodging or damaging recruits. Panels were systematically searched using a dissecting microscope, and all recruits were identified to the lowest possible taxonomic level. Colonial protists were not enumerated, because it was impossible to distinguish among colonies. For some groups, such as campanularid hydroids, the recruits were too small to identify to species. We counted all recruits within 1 day of retrieval.

To characterize the physical conditions during each deployment, we used a combination of data from ongoing Virginia Institute of Marine Science (VIMS) studies and data collected from our stations to parameterize the oxygen concentration, salinity, and temperature hourly in each area (see Sagasti et al. 2000 for details). In 1996, temperature, salinity, and dissolved oxygen were measured in the downstream area from a moored buoy east of Gloucester Point (Fig. 1). This buoy used an array of Hydrolab Datasonde Multiprobes to record conditions at multiple depths, including 13 and 16 m. To estimate conditions at the depth of our panels (14.5 m), we averaged the data from 13 and 16 m. In addition, we measured temperature, salinity, and dissolved oxygen at the upstream area in 1996 and in both areas in 1997 using a Hydrolab Datasonde Multiprobe at one station in each area (Fig. 1). The Hydrolab was suspended approximately 15 cm above the PVC frame, with the sensors oriented toward the frame. After retrieving a Hydrolab, we tested it against standards to make sure it was still calibrated. Readings never differed by >0.5 ppt for salinity, $>0.71^\circ\text{C}$ for temperature, or >0.32 mg O_2 l^{-1} (0.46 ml O_2 l^{-1}) for oxygen concentration. However, we lost data periodically due to battery or sensor failure.

For each year, we analyzed the number of recruits (all species combined) using a model I (fixed factor) general linear model

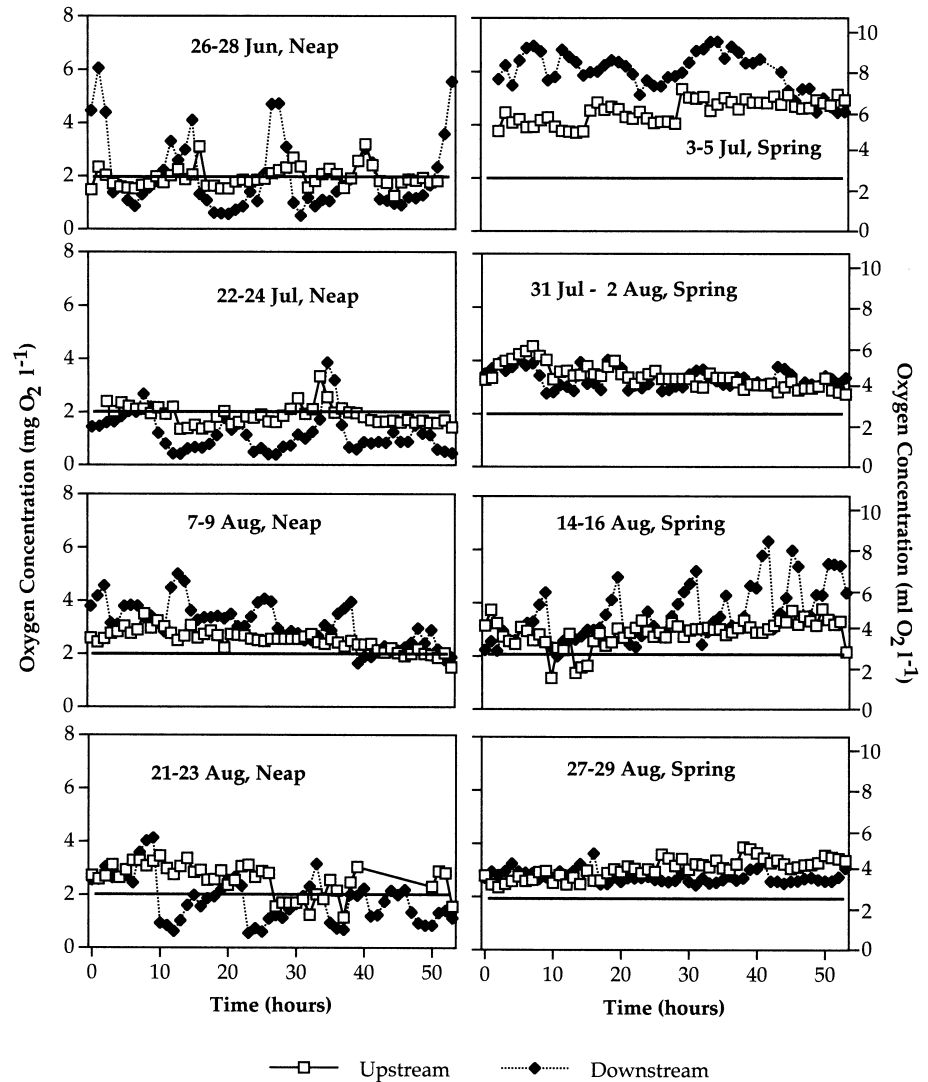
ANOVA with the factors "date", "location" (upstream or downstream), and "tidal stage" (neap or spring). Because we consider date to be a blocking factor, we did not include date in interaction terms. Assumptions of ANOVA were assessed using Cochran's test for homogeneity of variance (Underwood 1997) and the Shapiro-Wilkes test for normality (Zar 1996). In 1996, data were transformed by $\log(x+1)$ in order to meet the assumption of homogeneity of variances (Zar 1996). In 1997, the data did not meet the assumptions of homogeneity of variance even after transformation. However, because the results of ANOVA were highly significant ($P < 0.0001$) and because ANOVA is generally robust to violations of the homogeneity of variance assumption (Zar 1996), we believe the results are still useful. Because we found a significant tide \times location interaction in 1997, we performed model I general linear model ANOVAs between spring and neap tides for each location separately, and between upstream and downstream locations for each tidal stage separately.

We also analyzed the number of recruits of individual taxa as described above, but only considered taxa that either recruited during at least three deployments or comprised a large fraction ($>10\%$) of recruits during a single deployment. Because recruitment was highly seasonal for individual taxa, we included in each analysis only those time periods in which average recruitment in at least one location during neap or spring tide was equal to 10% of maximum recruitment for that taxon. For a few taxa (in 1996 *Sabellaria vulgaris* and *Hydroides dianthus*, and in 1997 *H. dianthus*) the data did not meet the assumptions of ANOVA using the tests described above, and so we did not analyze the results statistically.

Results

Hypoxia occurred during neap tides, and was usually more severe downstream. In 1996, hypoxia occurred during at least three neap tide deployments, 26–28 June, 22–24 July, and 21–23 August (Fig. 2). During each of these deployments, oxygen downstream was <0.5 mg O_2 l^{-1} (0.7 ml O_2 l^{-1}), while oxygen upstream remained >1 mg O_2 l^{-1} (1.4 ml O_2 l^{-1}) (Fig. 2). Oxygen concentrations remained high during spring tides. Oxygen

Fig. 2 Hourly dissolved oxygen concentrations at upstream and downstream monitors (14.5 m deep) during 1996 deployments. All oxygen concentrations below the *reference line* ($2 \text{ mg O}_2 \text{ l}^{-1}$, $2.86 \text{ ml O}_2 \text{ l}^{-1}$) were considered hypoxic



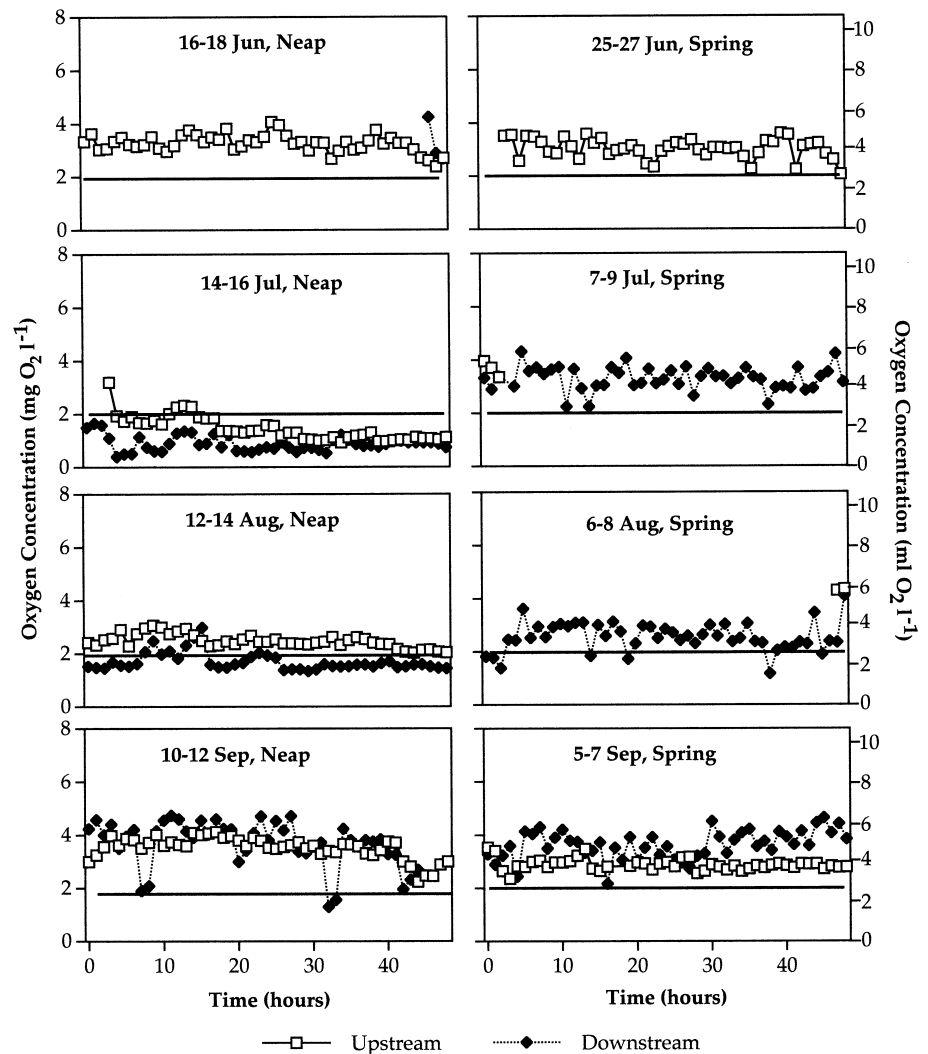
concentrations during each deployment also varied with the daily tidal cycles, falling during flood tides and briefly rising during ebb tides (Fig. 2). Low oxygen concentrations persisted for periods of ~ 10 h during the 26–28 June and 21–23 August deployments, but lasted up to 15 h during the 22–24 July deployment (Fig. 2). Oxygen data are missing for the first two deployments, 12–14 June (spring tide) and 20–22 June (neap tide).

In 1997, hypoxia occurred during neap tide deployments on 14–16 July and 12–14 August (Fig. 3). For 14–16 July, oxygen concentrations remained hypoxic throughout the entire deployment, with lower oxygen levels in the downstream area (Fig. 3). From 12–14 August, we measured hypoxic oxygen concentrations of $1\text{--}2 \text{ mg O}_2 \text{ l}^{-1}$ ($1.4\text{--}2.9 \text{ ml O}_2 \text{ l}^{-1}$) downstream during 80% of the deployment, but oxygen remained non-hypoxic upstream (Fig. 3). During some deployments, we only have data from one area of the river (Fig. 3). However, because hypoxia is so well described in the York River (Haas 1977), it may be possible to reconstruct the missing data. For example, during spring tide deployments (25–27 June, 7–9 July, and 6–8 August),

oxygen conditions remained largely non-hypoxic, except for a few hours during 6–8 August when oxygen downstream became slightly hypoxic. Because our other deployments (Figs. 2, 3) show a close relationship during spring tides between oxygen upstream and downstream and because oxygen is usually lower downstream than upstream (Sisson et al. 1991), it is likely that oxygen in both areas remained largely non-hypoxic during these (25–27 June, 7–9 July, and 6–8 August) spring tide deployments. During the neap tide deployment on 16–18 June, oxygen concentrations upstream were mostly $> 3 \text{ mg O}_2 \text{ l}^{-1}$ ($4.3 \text{ ml O}_2 \text{ l}^{-1}$) (Fig. 3). Although we have no data downstream during this deployment, data from other deployments suggest that during neap tides oxygen downstream is generally $0.5\text{--}1 \text{ mg O}_2 \text{ l}^{-1}$ ($0.7\text{--}1.4 \text{ ml O}_2 \text{ l}^{-1}$) below oxygen concentrations upstream, and therefore it is likely that oxygen concentrations downstream remained non-hypoxic during this deployment (16–18 June).

We observed recruitment by all of the sessile epifaunal taxa recently reported as dominant in the York River during a concurrent study (Sagasti et al. 2000)

Fig. 3 Hourly dissolved oxygen concentrations at upstream and downstream monitors (14 m deep) during 1997 deployments. All oxygen concentrations below the *reference line* ($2 \text{ mg O}_2 \text{ l}^{-1}$, $2.86 \text{ ml O}_2 \text{ l}^{-1}$) were considered hypoxic

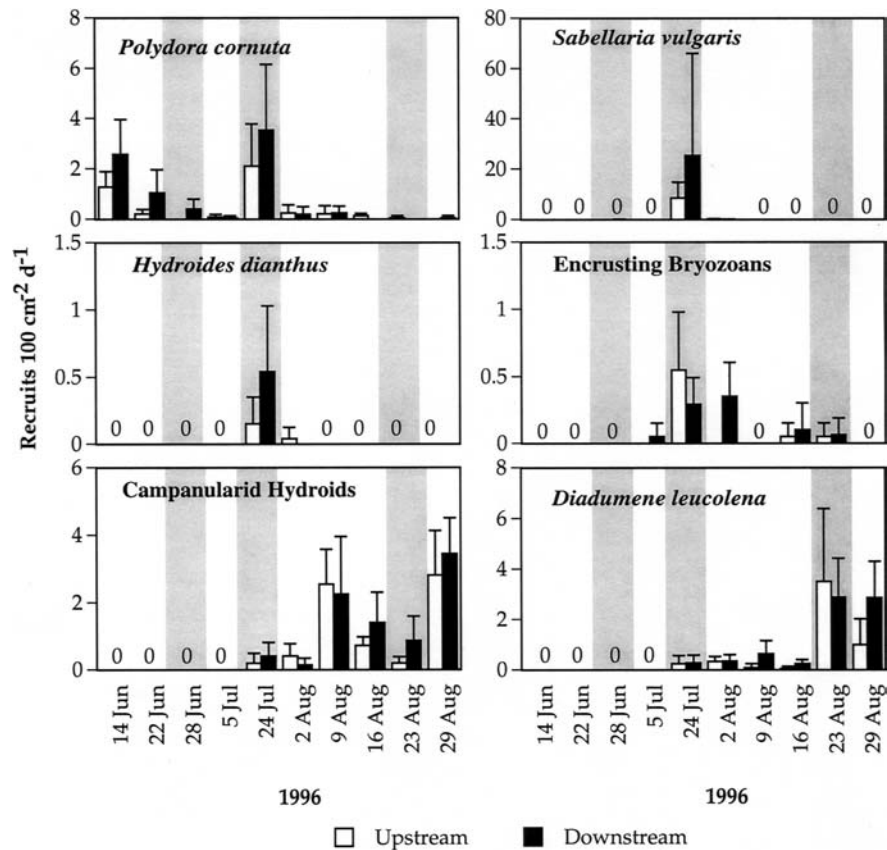


(Figs. 4, 5). These taxa represent six phyla and have a variety of larval types and life-history patterns. Each taxon showed a distinct seasonal settling pattern, as has been found elsewhere in Chesapeake Bay (Abbe 1987). The barnacle *Balanus improvisus* had high recruitment early in 1997, but we recorded only sparse recruitment in 1996, possibly because we missed the late-spring barnacle recruitment. The polychaete *Polydora cornuta* settled throughout the summer during both years, but was most abundant in June and July. Encrusting bryozoans, which we did not identify to species, but which probably included two common species, *Conopeum tenuissimum* and *Membranipora tenuis*, recruited in July and August each year. Campanularid hydroids settled from mid-July through September of both years. In 1996, the polychaetes *Sabellaria vulgaris* and *Hydroides dianthus* each recruited on only one settlement date at the end of July, but, in 1997, *S. vulgaris* recruited throughout July, August, and September. In 1997, *H. dianthus* again recruited on only one date, but in September. The anemone *Diadumene leucolela* recruited in mid- to late summer of both years. *Molgula*

manhattensis, a solitary ascidian, recruited throughout the summer of 1997. Although we did not observe *M. manhattensis* recruits in 1996, we did observe adults on panels exposed for 1 month (Sagasti et al. 2000), and it is possible that these small, transparent recruits were overlooked in 1996. For each taxon, the timing of recruitment closely matched the appearance of older individuals in a concurrent study (Sagasti et al. 2000).

During both years, recruitment for all taxa combined was highest during neap tides in the downstream area, coinciding with hypoxic conditions (Fig. 6). In 1996, date, tide, and location each had significant effects on recruitment (Table 1), with higher recruitment downstream and higher recruitment during neap tides. During the hypoxic episode on 22–24 June 1996, recruitment for all taxa combined was three to six times higher than during other deployments (Fig. 6). In 1997, recruitment varied significantly over time again, and there was a significant tide \times location interaction (Table 2). One-factor ANOVAs suggest that the difference between upstream and downstream was most significant during neap tides and the difference between spring and neap

Fig. 4 Recruitment (mean \pm SE) of common taxa during 1996 deployments. Shaded regions denote periods of hypoxia. Note variation scales of vertical axes



tides was most significant in the downstream location (Table 2). The highest recruitment for all taxa combined in 1997 occurred from 14–16 August (Fig. 6), coinciding with a mild hypoxic episode in the downstream area (Fig. 3).

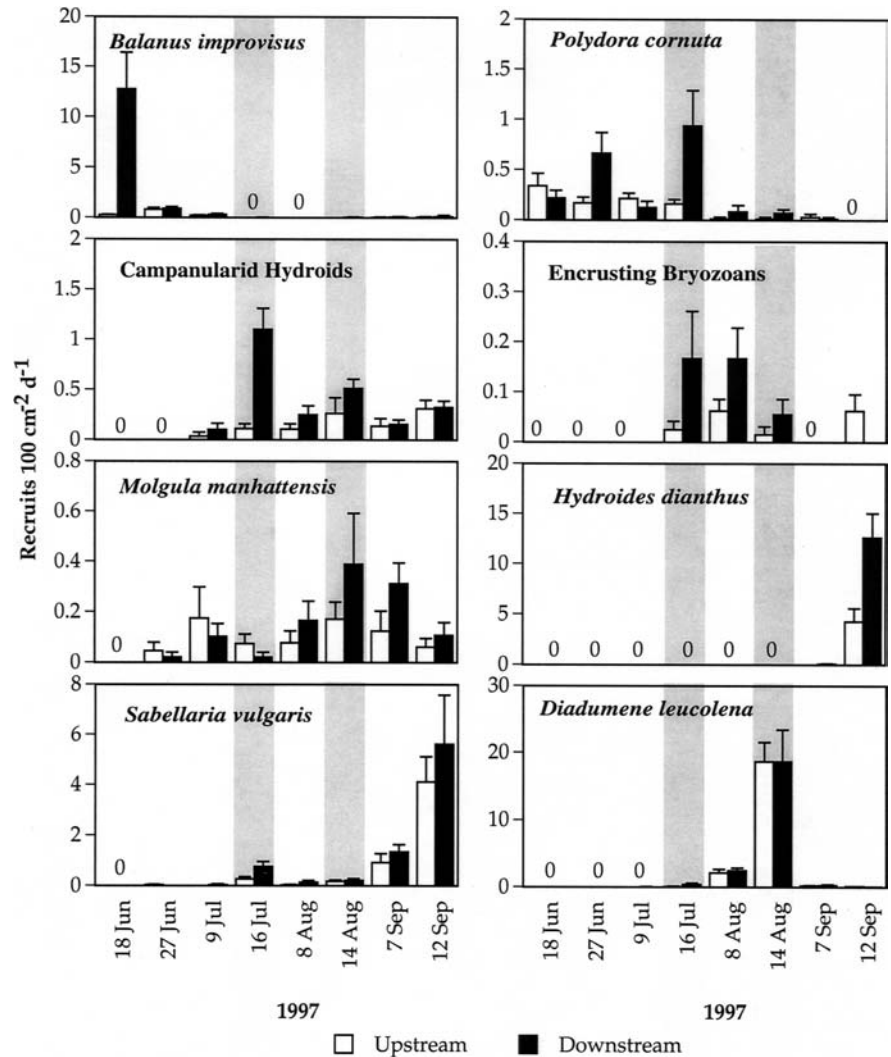
In both years, many individual taxa (five of six in 1996 and four of eight in 1997) had maximal recruitment during hypoxia (Figs. 4, 5). For example, in 1996, *Diadumene leucolena*, *Polydora cornuta*, *Sabellaria vulgaris*, encrusting bryozoans, and *Hydroides dianthus* had maximum recruitment rates during hypoxia (Fig. 4). *S. vulgaris* accounted for approximately half of all recruits during the 22–24 June deployment, which had maximum numbers of recruits and coincided with a hypoxic episode. *P. cornuta*, encrusting bryozoans, and *H. dianthus* also had high recruitment during this deployment (Fig. 4). All taxa except barnacles recruited successfully during hypoxia.

Analysis for individual taxa showed that different factors affected their recruitment (Tables 3, 4). In 1996, recruitment of all taxa analyzed varied significantly over time, and both the polychaete *P. cornuta* and the anemone *D. leucolena* were significantly more likely to recruit in the downstream, lower-oxygen area (Table 3; Fig. 4). Tide had no significant effect on recruitment for the individual taxa analyzed in 1996 (Table 3). The significant increase in total recruitment during neap tide in 1996 appears driven by a single species, the polychaete *S. vulgaris*, because there was no effect of tide on total

recruitment when *S. vulgaris* was eliminated from the analysis (Appendix 1, Electronic Supplementary Material). However, these results for 1996 could be due to low sample sizes and high variability.

In 1997, when we had more stations and more settling panels per station, patterns for individual taxa were more consistent. Recruitment varied significantly over time for encrusting bryozoans, the tunicate *Molgula manhattensis*, the polychaete *S. vulgaris* and *P. cornuta*, but not campanularid hydroids (Table 4). *S. vulgaris* and *D. leucolena* were each more likely to recruit during neap tides than during spring tides. *S. vulgaris* and *P. cornuta* had significantly higher recruitment in the downstream location (Table 4; Fig. 5). There was a significant interaction between tide and location for barnacles *Balanus improvisus* and campanularid hydroids in 1997 (Table 4). Graphs for these two taxa suggest that recruitment was generally higher during neap tides and was generally higher in the downstream location and that the difference between upstream and downstream increased during neap tides (Fig. 5). Overall, for 1997, it appears that four of seven taxa analyzed had significantly higher recruitment during neap tides (*B. improvisus*, campanularid hydroids, *S. vulgaris*, and *D. leucolena*), and four of seven taxa analyzed had significantly higher recruitment in the downstream location (*B. improvisus*, *P. cornuta*, campanularid hydroids, *S. vulgaris*); none of the taxa analyzed had higher recruitment during spring tides or in the upstream location

Fig. 5 Recruitment (mean \pm SE) of common taxa during 1997 deployments. Shaded regions denote periods of hypoxia. Note variation in scales of vertical axes



(Table 4; Fig. 5). In 1997, eliminating *S. vulgaris* from the analysis had no effect on results (Appendix 1, Electronic Supplementary Material). Thus, it appears that in 1997 significant effects of tide and location on total recruitment were not driven by any single species, but by several.

Discussion and conclusions

The largest recruitment pulses in our study occurred during hypoxia. These results suggest that larvae of York River epifauna have high tolerance for low oxygen. High larval tolerance of low oxygen may allow epifaunal communities in this system to persist even though the summer hypoxia season coincides with the recruitment of many epifaunal species.

Many factors may have allowed larvae to recruit during hypoxia, including high larval tolerance of low oxygen concentrations, relatively mild hypoxic episodes, and fluctuating oxygen concentrations with windows of high oxygen conditions within hypoxic periods. Even

during neap tide conditions, currents in the York River can reach relatively fast speeds ($> 40 \text{ cm s}^{-1}$), facilitating oxygen flux to larvae. However, such factors do not explain why recruitment increased during hypoxia. Changes in predation risk, larval availability, and tidal stage may help account for increased recruitment during hypoxia.

It is possible that epifaunal larvae in this system are so tolerant of hypoxia that low oxygen conditions have no negative effect on their recruitment. However, in laboratory studies exposing larval epifauna from this system to low oxygen conditions, there was a consistent trend of decreased recruitment in low oxygen versus high oxygen conditions for all taxa analyzed, and this trend was significant for five of nine taxa analyzed (*Polydora cornuta*, campanularid hydroids, *Hydroides dianthus*, encrusting bryozoans, and the hydroid *Ectopleura dumortieri*) (Sagasti 2000). In these laboratory experiments, we never observed increased recruitment in low oxygen, but we also did not see a complete cessation of recruitment. Therefore, it seems likely that high tolerance of low oxygen conditions allowed larvae to recruit

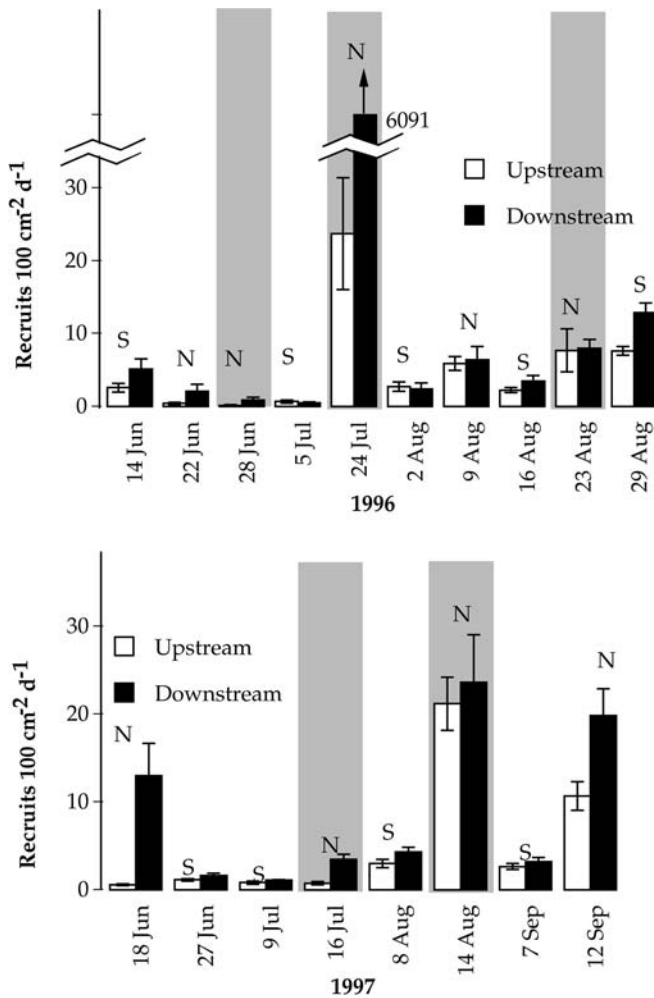


Fig. 6 Combined recruitment (mean \pm SE) of all taxa in 1996 (upper panel) and 1997 (lower panel) during spring tides (S) or neap tides (N). Shaded regions denote periods of hypoxia. Note the break in the y-axis above 30 recruits $\text{cm}^{-2} \text{day}^{-1}$ in 1996

in the field during hypoxia, and that any negative effect of hypoxia on recruitment was offset by other factors.

Oxygen concentrations in this system may not be low enough or sustained enough to deter recruitment. Oxygen at our stations fluctuated with flood and ebb tides and rarely remained $< 0.5 \text{ mg O}_2 \text{ l}^{-1}$ ($0.71 \text{ ml O}_2 \text{ l}^{-1}$) longer than a few hours (Figs. 2, 3). Lower oxygen concentrations or more sustained low oxygen conditions would likely have had more negative effects on recruitment. This

seems especially likely, because, in related laboratory studies with the tunicate *Molgula manhattensis*, larvae settled primarily at the beginning of experiments when oxygen was relatively high ($> 1 \text{ mg O}_2 \text{ l}^{-1}$) and larvae had not experienced many continuous hours of low oxygen, but then decreased recruitment rates as oxygen levels decreased (Sagasti 2000). As Baker and Mann (1992) found for larval oysters, some species may settle during mild oxygen depletion, but stop settling as oxygen decreases further.

Fluctuating oxygen concentrations in this system may also have allowed recruitment to continue during hypoxic deployments. During all three 1996 deployments when hypoxia occurred and during one of two 1997 deployments when hypoxia occurred, oxygen rose above hypoxic levels at least once. This suggests that, in the field, larvae could have settled preferentially during short periods of high oxygen. Some larvae in our system can delay settlement during hypoxia, settling after oxygen rises (Sagasti 2000). The ability to delay settlement has also been shown for an infaunal polychaete, *Paraprionospio pinnata* (Powers et al. 2001), and for certain species of bivalves, fish, and insects (Widdows et al. 1989; Keckies et al. 1996; Nebeker et al. 1996). Thus, delaying development or settlement may be a general strategy used by animals in areas with fluctuating oxygen conditions.

The ability of larvae in the York River to settle during hypoxia may also be enhanced by the fact that currents are relatively fast in this system. Current speeds during hypoxic episodes in the York River can reach 40 cm s^{-1} (Sisson et al. 1991). In this turbulent environment, the thickness of diffusive sublayers around the larvae might not have inhibited oxygen uptake.

Even if high larval tolerance and relatively favorable conditions allowed epifauna to continue to recruit during hypoxia, this does not explain why recruitment was enhanced during hypoxic episodes. In this system, many factors are correlated with low oxygen conditions, such as neap tides and decreased current speeds, and some of these factors may have had positive effects on recruitment.

Spawning or recruitment is often correlated with tidal stages (Seitz and Schaffner 1992; Robertson et al. 1999), and it is possible that epifaunal species in the York River are more likely to settle during neap tides for reasons unrelated to hypoxia. For most epifaunal species in the

Table 1 ANOVA results for recruitment in 1996. Factors were date, tide (neap or spring), and location (upstream or downstream). The response variable was the log-transformed number of recruits

Source	df	SS	MS	F	P	Variance (%)
Date	4	15.001	3.750	28.44	< 0.001	50.5
Tide	1	0.554	0.554	4.20	0.043	1.8
Location	1	0.633	0.633	4.80	0.031	2.1
Tide \times Location	1	0.054	0.054	0.41	0.524	0.1
Error	103	13.582	0.132			45.3
Total	110					

($\text{m}^{-2} \text{day}^{-1}$) for all species combined. Because time is considered a blocking factor for these 2-day experiments, interaction terms involving time were not estimated

Table 2 ANOVA results for recruitment in 1997. Factors were date, tide (neap or spring), and location (upstream or downstream). The response variable was the log-transformed number of recruits ($\text{m}^{-2} \text{day}^{-1}$) for all species combined. Because time is considered a blocking factor for these 2-day experiments, interaction terms involving time were not estimated. One-factor ANOVAs were conducted to investigate a significant tide \times location interaction

Source	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>	Variance (%)
Three-factor ANOVA						
Date	3	16.698	5.566	44.33	< 0.001	42.1
Tide	1	5.552	5.552	44.22	< 0.001	12.2
Location	1	3.340	3.340	26.60	< 0.001	8.3
Tide \times Loca tion	1	1.344	1.344	10.71	0.001	3.1
Error	120	15.065	0.126			34.3
Total	126					
One-factor ANOVA – only spring tide						
Location	1	0.322	0.322	3.39	0.071	
Error	58	5.502	0.095			
One-factor ANOVA – only neap tide						
Location	1	6.354	6.354	15.73	< 0.001	
Error	65	26.261	0.404			
Total	66	32.615				
One-factor ANOVA – only upstream						
Tide	1	0.647	0.647	1.92	0.170	
Error	69	23.209	0.336			
Total	70	23.856				
One-factor ANOVA – only downstream						
Tide	1	6.029	6.029	38.06	< 0.001	
Error	54	8.553	0.158			
Total	55	14.582				

York River, little is known about the timing of reproduction. For the few epifaunal species in this system for which information is available about the timing of reproduction, there is no suggestion that neap/spring cycles influence settlement. For example, larval availability of the polychaete *P. cornuta* does not fluctuate with spring/neap tides (Orth 1971), yet *P. cornuta* showed high settlement during neap tides in the field (Figs. 4, 5). This suggests that for some species, increased recruitment during hypoxia was not caused by neap/spring cycles in larval availability.

Lower current speeds during hypoxic episodes may facilitate recruitment in the York River by decreasing the number of larvae swept away in high currents and by allowing larvae to approach settlement surfaces more easily. The lower York River is dominated by tidal currents with maximum speeds of 40–50 cm s^{-1} during spring tides and 20–40 cm s^{-1} during neap tides (Sisson et al. 1991). Fast currents can directly interfere with settlement or can sweep invertebrate larvae away from potential settling surfaces (Eckman 1983), decreasing settlement. This effect has been noted for a wide variety of invertebrates (Eckman 1983; Pawlik and Butman 1993; Leonard et al. 1998). Conversely, low current speeds can allow larvae to reach and explore settlement surfaces, leading to increased settlement during slack tide conditions (Whitlatch and Osman 1998).

Hypoxic conditions may also be correlated with decreased predation risk for planktonic larvae or recent settlers. Hypoxia has been associated with decreased predation by fish and invertebrates (Breitburg et al. 1994; Nestlerode and Diaz 1998). Feeding and predation by a variety of different epifaunal taxa in this system decreases during hypoxia (Sagasti et al. 2001). Some of these taxa (the hydroid *Obelia bicuspidata*, the flatworm

Styllochus ellipticus, and the nudibranch *Doridella obscura*) are predators on planktonic larvae or on recent settlers, and hypoxia may provide a predation refuge for their prey species (Sagasti et al. 2001). It seems likely that hypoxia spares some planktonic larvae and recently settled juveniles from predation, allowing more to survive and recruit.

Our results appear to contrast greatly with those of a similar study (Powers et al. 2001) in the Gulf of Mexico. In that study, barnacle cyprids and other meroplankton seemed to avoid hypoxic locations, leading to decreased recruitment in hypoxic areas. Major differences between physical conditions in the York River estuary and those of the Gulf of Mexico include differences in currents and differences in the timing and severity of oxygen depletion. In the York River, tidal currents maintain relatively fast water movement, except during slack tide, but in the Gulf of Mexico currents are relatively weak (Powers et al. 2001). Oxygen concentrations in the Gulf of Mexico can continuously remain $< 0.1 \text{ mg O}_2 \text{ l}^{-1}$ for 2–3 weeks at a time (Powers et al. 2001), but hypoxia in the York River is milder and rarely lasts more than a week. Indeed, in this study hypoxia generally lasted about 10–15 h. It seems likely that persistently slow currents, continuous hypoxia, and near-anoxic conditions account for the lack of recruitment in the Gulf of Mexico and that the lack of these conditions allowed recruitment in the York River.

Differences in the duration of hypoxia between the York River and the Gulf of Mexico could also result in different strategies by larvae. In the York River, where hypoxic episodes last a week or less, high recruitment during hypoxia could be explained by the ability of larvae to delay settlement and metamorphosis. If larvae can delay settlement during hypoxia, this could increase the

Table 3 Results of ANOVAs for recruitment of individual taxa in 1996. Factors were date, tide (neap or spring), and location (upstream or downstream). The response variable was the number of recruits ($m^{-2} day^{-1}$) or the log-transformed number of recruits ($m^{-2} day^{-1}$). Because time is considered a blocking factor for these 2-day experiments, interaction terms involving time were not estimated. For each taxon, only dates where average recruitment in at least one location during neap or spring tide was at least equal to 10% of maximum recruitment were considered. For some taxa, the assumptions of ANOVA were not met even after transformation, and no analyses were performed

Source	df	SS	MS	F	P
<i>Polydora cornuta</i> 14 June–2 August					
Date	2	3.895	1.948	14.97	0.000
Tide	1	0.231	0.231	1.78	0.187
Location	1	1.019	1.019	7.83	0.007
Tide×Location	1	0.345	0.345	2.65	0.108
Error	66	8.588	0.130		
Total	71				
Encrusting bryozoans 24 July–29 August					
Date	2	0.711	0.355	11.85	0.000
Tide	1	0.064	0.064	2.14	0.149
Location	1	0.039	0.039	1.30	0.259
Tide×Location	1	0.118	0.118	3.95	0.052
Error	55	1.650	0.030		
Total	60				
Campanularid hydroids 24 July–29 August					
Date	2	3.712	1.856	15.16	0.000
Tide	1	0.251	0.251	2.05	0.158
Location	1	0.085	0.085	0.69	0.408
Tide×Location	1	0.015	0.015	0.13	0.725
Error	55	6.736	0.123		
Total	60				
<i>Diadumene leucolena</i> 24 July–29 August					
Date	2	6.030	3.015	39.14	0.000
Tide	1	0.076	0.076	0.99	0.324
Location	1	0.454	0.454	5.89	0.018
Tide×Location	1	0.028	0.028	0.36	0.552
Error	55	4.237	0.077		
Total	60				

abundance of competent larvae that are ready to set, triggering high recruitment when oxygen increases. High recruitment could occur in an oxic window during a hypoxic event. In contrast, larvae in the Gulf of Mexico, where low-oxygen episodes last several weeks, might have a higher likelihood of death while delaying settlement (but at least one species in the Gulf of Mexico, the polychaete *Paraprionospio pinnata*, does delay settlement for over a week) (Powers et al. 2001). A more successful strategy in the Gulf of Mexico may be to avoid hypoxic water masses by swimming toward the surface (Powers et al. 2001).

In this study, the larvae of a variety of epifaunal taxa showed similar responses to hypoxia, suggesting that the observed levels of oxygen stress do not impact the relative recruitment success of different species. We studied a variety of taxa during five hypoxic episodes spanning 2 years, and found a consistent result of no negative effect of hypoxia on recruitment despite the wide taxonomic and environmental variation. Recruitment continued despite clearly stressful oxygen levels, perhaps because there are many additional factors that influence recruitment in the field.

Table 4 Results of ANOVAs for recruitment of individual taxa in 1997. Factors were date, tide (neap or spring), and location (upstream or downstream). The response variable was the number of recruits ($m^{-2} day^{-1}$) or the log-transformed number of recruits ($m^{-2} day^{-1}$). Because time is considered a blocking factor for these 2-day experiments, interaction terms involving time were not estimated. For each taxon, only dates where average recruitment in at least one location during neap or spring tide was at least equal to 10% of maximum recruitment were considered. For some taxa, the assumptions of ANOVA were not met even after transformation, and no analyses were performed

Source	df	SS	MS	F	P
<i>Balanus improvisus</i> 18 June–27 June					
Tide	1	0.477	0.477	3.29	0.080
Location	1	3.988	3.988	27.54	0.000
Tide×Location	1	3.315	3.315	22.89	0.000
Error	28	4.055	0.145		
Total	31				
<i>Polydora cornuta</i> 18 June–14 August					
Date	2	2.304	1.152	12.74	0.000
Tide	1	0.024	0.024	0.27	0.608
Location	1	0.417	0.417	4.61	0.035
Tide×Location	1	0.010	0.010	0.11	0.738
Error	89	8.050	0.090		
Total	94				
Encrusting bryozoans 9 July–12 September					
Date	2	0.185	0.093	3.53	0.033
Tide	1	0.012	0.012	0.47	0.493
Location	1	0.050	0.050	1.92	0.170
Tide×Location	1	0.001	0.001	0.04	0.842
Error	89	2.335	0.026		
Total	94				
Campanularid hydroids 9 July–12 September					
Date	2	4.480	2.240	0.41	0.663
Tide	1	116.684	116.684	21.50	0.000
Location	1	81.011	81.011	14.93	0.000
Tide×Location	1	34.775	34.775	6.41	0.013
Error	89	483.046	5.427		
Total	94				
<i>Molgula manhattensis</i> 18 June–12 September					
Date	3	1.157	0.386	5.93	0.001
Tide	1	0.124	0.124	1.91	0.169
Location	1	0.084	0.084	1.29	0.258
Tide×Location	1	0.029	0.029	0.44	0.507
Error	120	7.801	0.065		
Total	126				
<i>Sabellaria vulgaris</i> 9 July–9 September					
Date	2	18.077	9.038	108.93	0.000
Tide	1	4.131	4.131	49.79	0.000
Location	1	0.503	0.503	6.06	0.016
Tide×Location	1	0.002	0.002	0.02	0.877
Error	89	7.384	0.083		
Total	94				
<i>Diadumene leucolena</i> 8 August–14 August					
Tide	1	5.181	5.181	41.28	0.000
Location	1	0.019	0.019	0.15	0.702
Tide×Location	1	0.101	0.101	0.81	0.377
Error	27	3.389	0.126		
Total	30				

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