Dissolved oxygen dynamics in salt marsh pools and its potential impacts on fish assemblages

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ABSTRACT: In order to determine the dynamics of dissolved oxygen (DO) in salt marsh pools and its effect on their respective fish assemblages, DO was measured in 5 high-salinity pools in a *Spartina alterniflora* marsh in southern New Jersey over ten 24 h periods, from 2 July to 22 October 1990, to determine daily and monthly fluctuations. Typically, DO peaked at approximately 16:00 h, and reached a minimum by about 05:00 h. The greatest variation occurred in mid-July, when DO ranged from over 20 ppm at midday, to 0 ppm in the early morning. From mid- to late August, DO remained at very low concentrations (<1.0 ppm) for long periods (11.7 ± 1.7 h). DO concentrations varied among marsh pools, but there was no interaction between pool and time of day. The young-of-the-year (YOY) of the dominant 5 species of fishes in these pools were tested for tolerance and behavioral responses to low DO in laboratory aquaria. *Fundulus heteroclitus* survived the longest at low DO, and *Menidia menidia* was least tolerant. Aquatic surface respiration (ASR) was the primary behavioral response to low DO for all species tested. All species, including *Cyprinodon variegatus*, *Lucania parva*, and *M. beryllina*, survived at DO < 0.5 ppm when they used ASR; however, when fish were denied access to the air–water interface, only *F. heteroclitus* was able to survive more than 1 h. All species initiated ASR at ca. 1 ppm, with the exception of *M. menidia*, which began ASR at 2.6 ppm and survived only at higher concentrations of DO. In summary, although the salt marsh pools showed extreme diurnal variability in DO, with rapid drops from supersaturation to anoxic conditions, all of the fish species, with the exception of *M. menidia*, were well adapted to survive these fluctuations. This lack of tolerance to low DO by *M. menidia* may seasonally limit its occurrence in marsh pools, but this is not the case for the congener *M. beryllina*, or the other resident fishes.

KEY WORDS: Dissolved oxygen · Salt marshes · Pools · Killifishes · Silversides · Young-of-the-year

INTRODUCTION

Hypoxic and anoxic conditions occur in many estuarine and marine systems (Diaz & Rosenberg 1995, Diaz 2000, Wannamaker & Rice 2000, Rabalais & Turner 2001). In deeper estuarine systems, stratification and organic decay lead to large-scale anoxic events (Officer et al. 1984, Sanford et al. 1990, Breitburg 1992, Keister et al. 2000), which can be of long duration. Many shallow water systems and shallow water portions of deeper systems have shorter, often diel cycles in dissolved oxygen (DO; Kenney et al. 1988), with lowest levels observed in the early morning and highest levels during the afternoon. This diel variation in DO is driven by autotrophic production of oxygen (Kenney et al. 1988), with relatively constant oxygen consumption. Hypoxia and anoxia are known to be significant factors in determining the distribution and habitat shifts (Pihl et al. 1991, Breitburg 1992, 1994, Howell & Simpson 1994, Thiel et al. 1995), diet (Pihl et al. 1992), growth (Bejda et al. 1992, Peterson & Pihl 1995, Phelan et al. 2000, Taylor & Miller 2001), mortality (Breitburg et al. 1997, 1999), and community structure of estuarine and marine fauna (Tunnicliffe 1981). Fishes have a variety of adaptations to survive in hypoxic habitats, through both behavioral (Magnuson

et al. 1985, Kramer 1987) and physiological changes (Greaney et al. 1980, Peterson 1990). Fish can react behaviorally to hypoxia and anoxia by increasing their ventilation rate (Kramer 1987, Pihl et al. 1991), moving out of areas of stress (Congleton 1980, Bejda et al. 1987, Breitburg 1992, Wannamaker & Rice 2000) or by reducing activity levels (Fischer et al. 1992). Many shallow water fish initiate aquatic surface respiration (ASR) when DO drops to low levels (Gee et al. 1978, Kramer & McClure 1981, Kramer 1983), and some species have morphological adaptations that increase the efficiency of ASR (Lewis 1970).

Salt marsh pools (also known as pannes or potholes) are a prominent feature of salt marshes along the NE Atlantic Coast of North America (Chapman 1960). Pools are permanent bodies of water that are flooded during spring and storm (Able et al. in review) high tides. Little is known about DO dynamics in these pools, although an earlier study indicated that DO can fluctuate over a wide range in the summer (Christian 1981). Marsh pools are important habitats for several species of fishes in the families Cyprinodontidae, Fundulidae and Atherinidae (Talbot et al. 1986, Smith & Able 1994, Able et al. 1996), however we know relatively little about the responses of some of these species to rapid changes in DO, although responses to static DO levels have been observed (Voyer & Hennekey 1972). Recently, the effect of abiotic and biotic factors on transient fishes was examined from some barrier island ponds (Layman et al. 2000). The goals of our study were to (1) examine changes in monthly and daily fluctuations in DO concentrations in salt marsh pools over summer and fall, when temperatures are warmest, and (2) test, in the laboratory, the tolerance and behavior of the dominant fishes found in these pools, in order to better understand the effect of low DO on the behavior and composition of fish assemblages.

MATERIALS AND METHODS

Field observations. Observations of salt marsh pools were made in the relatively unaltered Sheepshead Meadows salt marshes in the Jacques Cousteau National Estuarine Research Reserve at Mullica River, Great Bay (Psuty et al. 1993, Lathrop et al. 2000), a salt marsh peninsula near Tuckerton, New Jersey, USA (39° 30′ N, 74° 19′ W; Fig. 1). Salt marsh pools selected were among those included in a concurrent study on fish distribution (Smith 1995). For the purposes of this paper we define salt marsh pools as sunken areas in the marsh, typically with vertical or overhanging edges (Pennings & Bertness 2000). Many of the marsh pools have partially submerged clumps of algae (primarily of *Cladophora* sp. and blue greens; Moul 1958). The algae are temporally variable because they are dispersed with tidal innundation (author's pers. obs.). The dominant emergent vegetation in the study area was short-form *Spartina alterniflora*, and the dominant submerged aquatic vegetation in some of the salt marsh pools was *Ruppia maritima* (Table 1).

Five salt marsh pools were sampled biweekly from 2 July to 22 October in 1990 (Table 1, Fig. 1). Each of the 9 sampling days was initiated at 11:00 h Eastern Standard Time (EST), continued overnight and ended at 11:00 h EST on the following day, and is designated by the initiation date. Physical parameters (DO, temperature, salinity) were measured every 2 h for a total of 13 times each sampling day per pool (Fig. 1, Table 1). All pools were measured within a 30 min period to decrease the effects of time on differences in DO between pools, based on preliminary observations of its variability (Smith 1995). DO (ppm) and water temperature (°C) were measured with a YSI Model 57 meter at both the surface and bottom of the water column, air temperature (°C) with an alcohol field thermometer, and salinity (‰) with an American Optical refractometer. At the start, middle, and end of each sampling run, water samples were collected and fixed for Winkler titration analysis, to check the YSI Model 57 meter measurements. Marsh pools were compared for variability in magnitude of DO change, and length of hypoxic period (DO < 1.0 ppm) over the entire sampling season using a 2-way ANOVA with pool and time-of-day as main effects.

Laboratory observations. Fish response to changing DO was determined in laboratory aquaria between 28 July and 4 August 1992. Previous field observations indicated fishes in
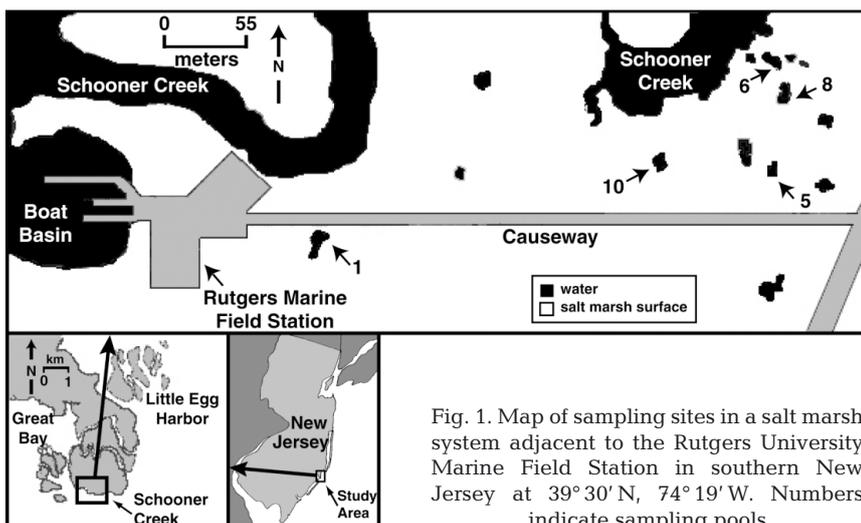

Fig. 1. Map of sampling sites in a salt marsh system adjacent to the Rutgers University Marine Field Station in southern New Jersey at 39° 30′ N, 74° 19′ W. Numbers indicate sampling pools

Table 1. Characteristics of individual pools. Pool locations shown in Fig. 1. Surface area estimated from aerial photographs (Smith 1995). Physical characteristics indicated as mean ± SE (range). Submerged aquatic vegetation was *Ruppia maritima*. DO: dissolved oxygen

Pool	Surface area (m^2)	Depth (cm)	Submerged aquatic vegetation	Salinity (‰)	Water temperature (°C)	Surface DO (ppm)	Bottom DO (ppm)
1	116	30.2 ± 5.9 (24−45)	Absent	29.9 ± 0.3 (20−35)	23.7 ± 0.4 (15.5−32.8)	5.5 ± 0.5 (0−20)	4.1 ± 0.4 (0−18.4)
5	37	29.3 ± 5.1 (23−34)	Absent	29.4 ± 0.3 (19−36)	23.7 ± 0.4 (14.9−33.1)	5.4 ± 0.4 (0−15.2)	3.1 ± 0.3 (0−12.8)
6	23	38.6 ± 3.7 (36−45)	Absent	29.3 ± 0.2 (24−32)	23.6 ± 0.4 (14.5−32.6)	4.6 ± 0.4 (0−20)	3.3 ± 0.3 (0−14.8)
8	128	40.6 ± 10 (25−50)	Present	29.3 ± 0.2 (22−33)	23.7 ± 0.4 (15−32.2)	6.3 ± 0.4 (0.1−14.9)	4.6 ± 0.4 (0−17.3)
10	70	36.9 ± 6 (25−47)	Absent	29.9 ± 0.1 (26−33)	23.8 ± 0.4 (14.9−32.9)	5.8 ± 0.4 (0−16.6)	5.1 ± 0.4 (0−16.1)

salt marsh pools would experience extreme fluctuations of DO during this period. The 5 dominant species of fishes (*Cyprinodon variegatus*, *Fundulus heteroclitus*, *Lucania parva*, *Menidia beryllina*, and *M. menidia*) collected on salt marsh surface habitats (Smith 1995, Able et al. 1996) were tested for behavioral responses and tolerance to naturally observed and rapid decreases in DO. Individuals were collected from salt marsh pools in the study area (Smith 1995) with quatrefoil plexi-glass traps (Secor et al. 1992). These traps served as passive collectors that prevented larger individuals from entering.

Fishes were maintained in the laboratory in large flow-through aquaria for 2 to 6 d prior to each experiment and fed *Artemia* and flake food. The water for the aquaria was drawn from Schooner Creek, a subtidal creek adjacent to the marsh pool sites (Fig. 1). Mean size and number of fish tested varied among species (Table 2) but all were young-of-the-year (YOY) based on length (Able 1990, Able & Fahay 1998). Six 11.4 l aquaria, with opaque partitions separating them, were placed on a table under fluorescent lights with a 14:10 h light:dark cycle. All aquaria were initially on flow-through ambient water, but at the start of the experiment, flow-through was turned off and each aquarium was randomly assigned as either a control (n = 2) or a treatment (n = 4) condition. As a result, all aquaria started an experiment with the same water at the same water temperature and DO concentration. All fishes were acclimated to the experimental aquaria overnight, and each experiment was initiated at 06:00 h EST the following day. Fishes were not fed during the acclimation period or the experiment.

To provide low DO water for each experimental run, ambient water (30‰ salinity) was run through a nitrogen stripping column to a level of 0.5 ppm oxygen, and stored overnight. During the experiment, DO was decreased in treated aquaria through water changes of $\frac{1}{3}$ of the volume every 30 min. Water was added and removed using stationary submerged hoses to minimize disturbance to the fish. Control aquaria received normoxic ambient water during similar water changes. Once DO decreased to 1 ppm, water changes were replaced by gentle bubbling of N$_2$ through an air stone in treatment aquaria, and ambient air in control tanks. In the treated aquaria this continued to reduce DO to about 0.5 ppm. To decrease DO below this level, a plastic film was laid across the surface of the water of all aquaria to prevent diffusion across the air−water interface. Each run consisted of replicates of experimental and control aquaria for a single species. Experiments continued until at least 50% mortality occurred in each treatment aquarium. DO decreased at about the same rate for all experimental runs (Fig. 2). Counts of individuals exhibiting specific responses (e.g. swimming through the water column, surface skimming

Table 2. Experimental arrangement for dissolved oxygen tolerance studies of salt marsh pool fishes in 11.4 l aquaria. Mean (range) of total lengths (TL) based on combined data from all tanks

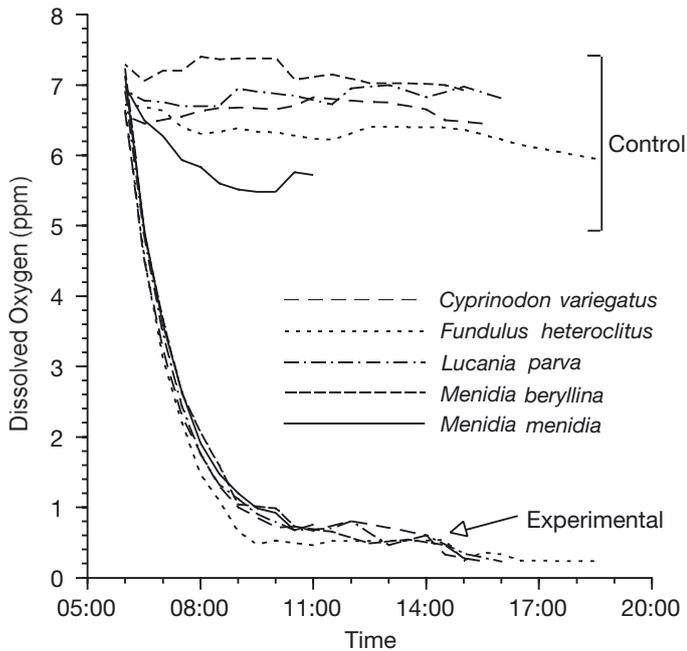| Species	No. per aquaria	No. tested	Mean TL mm ± SD	Time period (h)
Cyprinodon variegatus	8	48	24.8 ± 5.1 (13−31)	06:00−15:30
Fundulus heteroclitus	10	58	29.7 ± 4.5 (19−37)	06:00−18:30
Lucania parva	10	58	19.1 ± 2.9 (13−24)	06:00−16:00
Menidia menidia	10	60	31.2 ± 3.2 (25−37)	06:00−11:00
Menidia beryllina	10	57	23.3 ± 3.1 (18−30)	06:00−15:30

Fig. 2. Mean dissolved oxygen (DO) values relative to time during all experimental runs of the low tolerance experiment. Mean values were based on 4 replicates for experimental treatments, and 2 replicates for control treatments

[ASR], resting on the bottom, and presence of dead fish [no opercular activity]) were recorded separately for each aquarium ca. every 30 min. Fish were observed through a blind during each experimental run to reduce disturbance by the observer. After each behavioral observation, DO and water temperature were recorded, and the water was adjusted as needed. A YSI Model 57 meter was used to measure DO, and at the start and end of each trial. In each instance the YSI probe was submerged, with care taken not to disturb the air–water interface. Water samples for Winkler titration analysis (100 ml) were collected with a hose that was fixed inside each aquarium to check the YSI Model 57 meter measurements. Subsequent observations of fish behaviour were made 20 min after the water was tested in order to reduce the likelihood that the activity disturbed the fish.

Log linear analysis was used to test the effect of time on measured response variables (mortality, ASR, midwater swimming, resting on bottom). This analysis created a predicted response curve from the observed distribution of fishes among the 4 possible responses. A maximum likelihood ANOVA tested for significant effects of time on distribution patterns. Statistical analyses were conducted using the SAS 6.03 statistical package for personal computers (SAS Institute 1988).

RESULTS

DO dynamics

DO concentrations changed dramatically on a daily and monthly basis. Time of day significantly affected DO ($F_{12, 520}$ = 56.9, p < 0.0001), and DO was consistently cyclical for all the pools, peaking at ca. 16:00 h, and reaching a minimum by ca. 05:00 h (Fig. 3). After sunrise, DO increased rapidly during the summer months; however, during late October, when temperatures were lower, the rate of increase was greatly reduced. The mean maximum value for all pools and all dates was 10.3 ± 0.7 ppm at 17:00 h, and the mean minimum value was 1.02 ± 0.3 ppm at 05:00 h. The greatest range in DO occurred on 15–16 July, with values over 20 ppm at midday to 0 ppm in the early morning (Fig. 3). Individual pools varied in the magnitude of their diel DO cycles, and differences between pools did not remain constant over all dates. DO varied significantly among pools ($F_{4, 520}$ = 5.31, p < 0.001), and there was no interaction between pool and time of day ($F_{4, 520}$ = 0.53, p < 0.99). There were no significant differences between pools in length of period of DO below 1.0 ppm ($F_{4, 40}$ = 1.35, p < 0.27) or overall magnitude of DO values ($F_{4, 40}$ = 1.67, p < 0.18). Pool 1 tended to drop to lower oxygen levels at night, and remain low for long periods of time. Pool 8 was similar to other sites in peak oxygen values, but did not drop as low as the other sites at night.

Monthly variation in DO varied largely because values remained low for long periods of time during mid- and late August sampling dates (Fig. 3), from midnight until 07:00 h (<1 ppm). During 12–13 August, DO ranged from 0 to 16 ppm and remained below 1 ppm for the longest period of time (11.7 ± 1.7 h, Fig. 3). Pools over the same dates also showed the most rapid rate of decrease in DO (1.3 ppm h^{-1}). Extended low DO periods were also observed on 25 August for several pools. In September and October, daily DO variation leveled off, and although pools remained below 1 ppm for several hours, they did not drop to 0 ppm for longer than 4 h.

Fish behavior and mortality

All species in the treatment aquaria responded to decreasing DO by moving from midwater to the water surface and using ASR (Fig. 4, Table 3), with the exception of *Cyprinodon variegatus*, which responded to decreasing DO by resting on the bottom of the aquaria (Fig. 4). Most species initiated ASR at approximately 1 ppm DO, but *Menidia menidia* started at 2.6 ppm (Table 3). Attempts at ASR were continued by
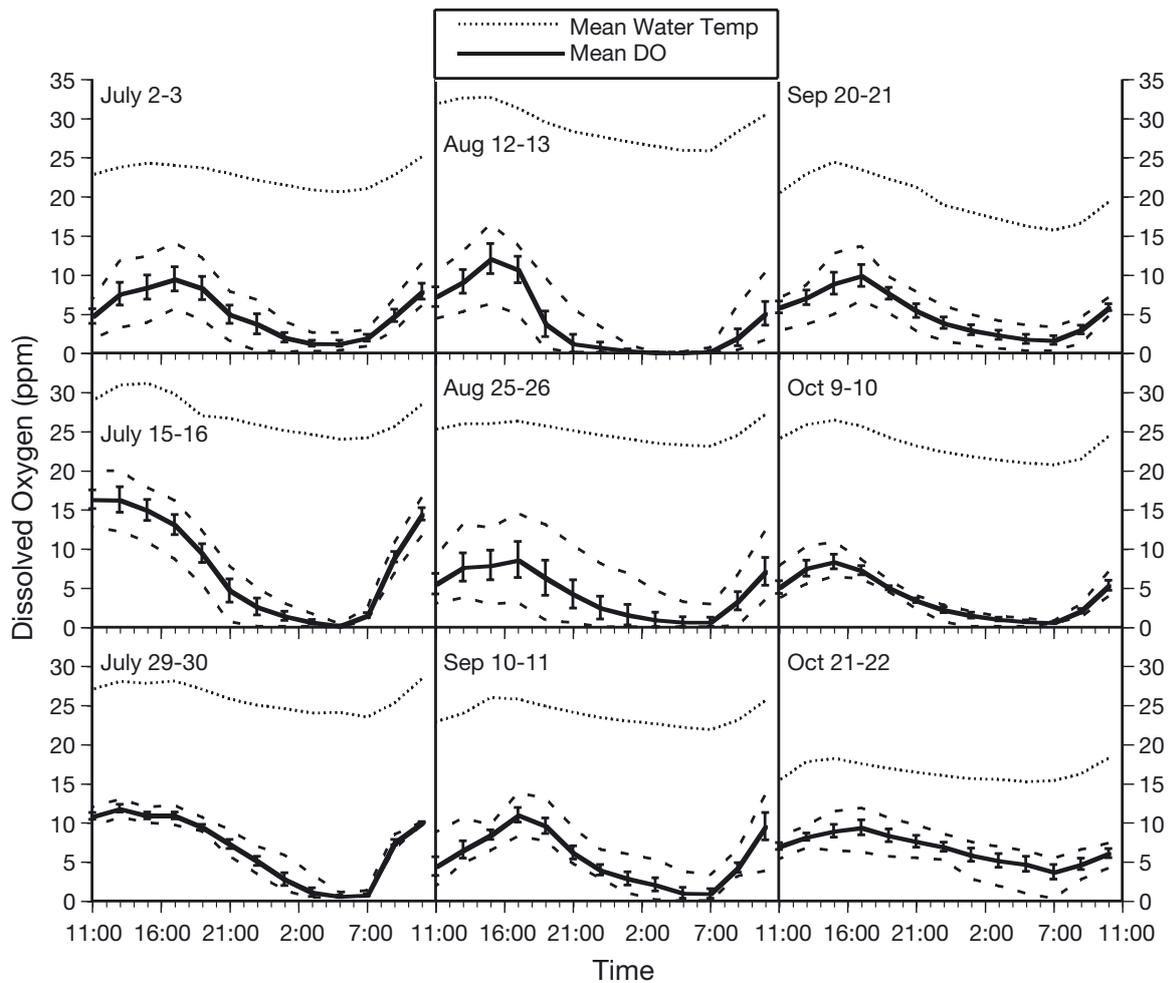
Fig. 3. Dissolved oxygen profiles for 5 salt marsh pools over 9 sample runs during 1990. Values are averaged (±1 SE), with minimum and maximum values. Mean surface water temperature is plotted for each date. Measurements were taken every 2 h, beginning at 11:00 h EST and concluding at 11:00 h EST on the following day

all species even after the air–water interface was removed. Fish in control aquaria showed little or no change in response over the experimental period.

Decreasing DO significantly altered fish survival (Tables 3 & 4, Fig. 4). *Fundulus heteroclitus* survived the longest under low oxygen conditions, up to 4 h, with DO < 1.0 ppm and no air–water interface. A mortality of 50% occurred in *F. heteroclitus* at a DO of 0.23 ± 0.02 ppm, 240 min after the air–water interface was removed. At the other extreme, *Menidia menidia* did not survive longer than 30 min once DO dropped below 1.0 ppm. This species was not tested with removal of the air–water interface. *M. beryllina*, *Cyprinodon variegatus*, and *Lucania parva* were all intermediate in survival time between *F. heteroclitus* (most tolerant), and *M. menidia* (least tolerant). No mortality of control fish occurred for *C. variegatus*, *F. heteroclitus*, or *M. beryllina*; however, 1 *M. menidia* and 1 *L. parva* died in control aquaria.

DISCUSSION

Salt marsh pools in southern New Jersey undergo rapid and severe fluctuations in DO, comparable in magnitude to barrier island ponds in Virginia (Layman et al. 2000) and brackish ponds used in commercial fish culture (Szyper & Ebeling 1993). The greatest range in DO and the longest hypoxic periods in New Jersey occur in midsummer (mid-July to late August), when oxygen production and consumption peak (Christian 1981). DO increases rapidly during the day from photosynthesis of benthic algae, phytoplankton and submerged aquatic vegetation, and decreases after nightfall when oxygen production ceases but oxygen consumption continues (Christian 1981). We observed supersaturated conditions (Ross et al. 2001), which can result from intense photosynthesis, during the mid-afternoon. Reductions in DO over time observed in this study are similar to those observed by Layman et al.
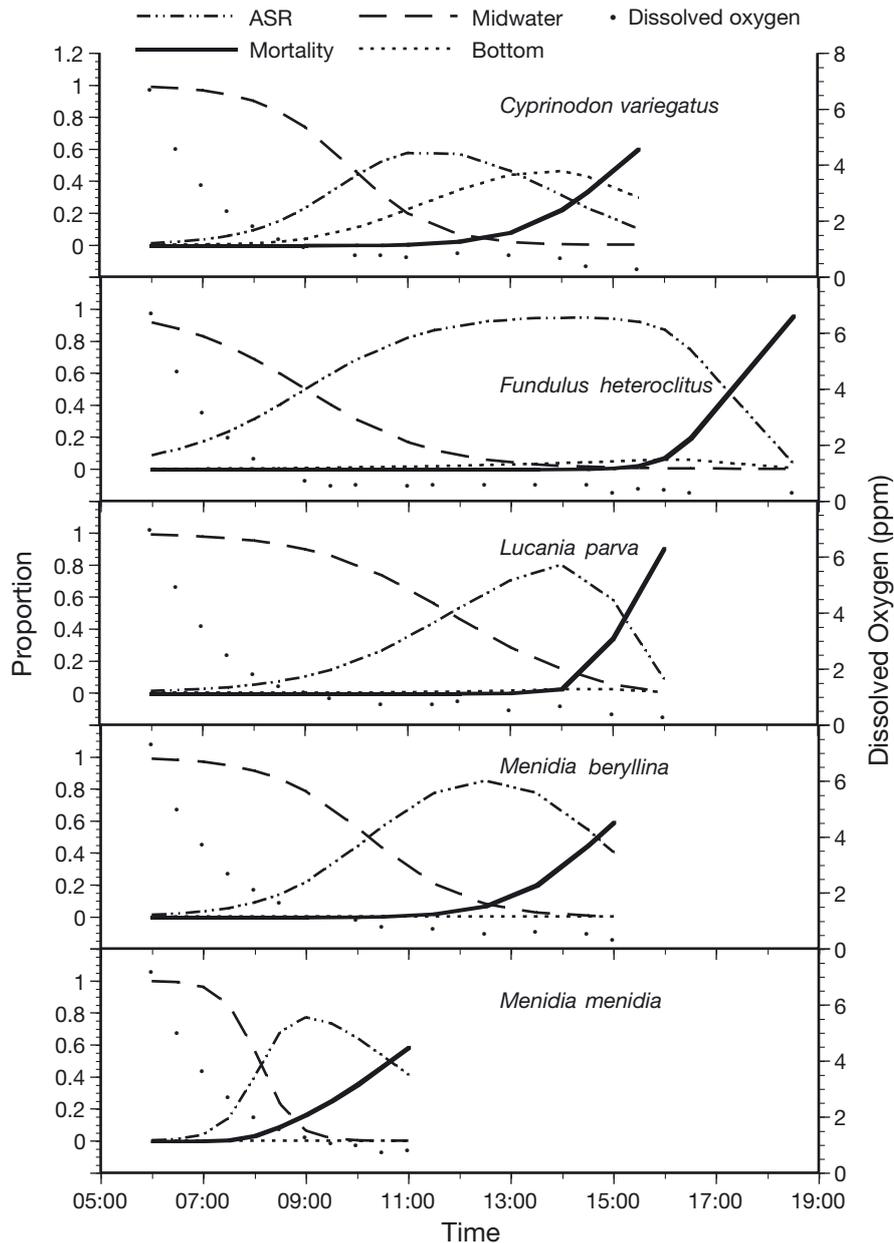
Fig. 4. Log-linear analysis predicted response patterns by marsh pool fish species in experimental treatments. See Table 2 for experimental arrangement. Responses over time, for all aquaria, presented as proportion of fish found either at the water surface (aquatic surface respiration; ASR), in midwater, resting on the bottom, or dead. Mean change in dissolved oxygen for all experimental replicates also shown. Experiments were concluded when at least 50 % mortality occurred in each experimental tank

(2000) during the summer in Virginia barrier island ponds. Results from their field enclosure studies on fishes found in the barrier island ponds indicated that abiotic stresses such as low DO could contribute to higher mortalities in less tolerant surf-zone fish species.

Of the fish species we tested in the laboratory, *Fundulus heteroclitus* was the most tolerant of low DO, and is also the dominant species in salt marsh pools at the study site (Able et al. 1996), and in New Jersey (Talbot

et al. 1986) and elsewhere in the NE USA (Collette & Klein-MacPhee 2002). Layman et al. (2000) found similar dominance in abundance for this species in coastal Virginia ponds, and a similar tolerance to extremely low DO under laboratory conditions. Other laboratory studies have only tested relatively high levels of DO (2.4 to 7.5 mg DO l^{-1}; Voyer & Hennekey 1972). Some of the other species tested (*Cyprinodon variegatus*, *Lucania parva*, *Menidia beryllina*) have somewhat lower tolerance to hypoxia. *C. variegatus* and *L. parva*

Table 3. Summary of experimental conditions and fish responses for laboratory study on tolerance of low dissolved oxygen (DO). DO decrease values were natural log-transformed; all other DO values in ppm. Survival times are maximum estimates since observations were collected at ca. 30 min intervals. ASR = aquatic surface respiration. Time since air removal was the number of minutes when 50% of the fish survived after fish were denied access to the water surface by covering it with plastic sheeting

Species	DO decrease	Mean water temp. (°C)	DO at start of ASR	DO at initial mortality	DO at 50% mortality	Time (min) DO < 1.0	Time (min) DO < 0.5	Time (min) since air removal
Cyprinodon variegatus	−0.277	24.0	1.00 ± 0.01	0.67 ± 0.07	0.33 ± 0.03	330	60	40
Fundulus heteroclitus	−0.229	24.5	1.09 ± 0.02	0.36 ± 0.03	0.23 ± 0.02	570	540	240
Lucania parva	−0.293	23.0	0.91 ± 0.02	0.34 ± 0.09	0.23 ± 0.04	390	180	60
Menidia beryllina	−0.317	23.0	1.04 ± 0.02	0.49 ± 0.03	0.27 ± 0.04	300	150	30
Menidia menidia	−0.467	22.5	2.64 ± 0.10	1.91 ± 0.06	0.76 ± 0.02	30	N/A	N/A

are usually found in salt marsh pools, while *M. beryllina* is collected in both salt marsh pools (Able et al. 1996) and intertidal creeks (Bengston 1984, Rountree et al. 1992, Smith 1995, Able et al. 1996). *M. beryllina* may use the marsh pools as a nursery, since primarily juveniles have been collected in these habitats (Coorey et al. 1985, authors' unpubl. data). These 3 species are not as abundant in many of the shallow, muddy habitats that *F. heteroclitus* dominates.

Menidia menidia is very abundant in the surrounding intertidal and subtidal of the study area creeks, where it is the dominant species throughout the summer (Rountree & Able 1992). During the same period, it makes movements on to the marsh surface (K. W. Able unpubl. data), based on video camera images near the marsh edge, and as a result is occasionally retained in marsh pools at low tide. This is the least tolerant species to low DO of the species tested, and was collected in marsh pools only in early July as YOY (total length = 29 ± 0.8 mm, K. J. Smith unpubl. data), when DO did not remain low for long periods of time (Fig. 3). This species becomes stressed when DO decreases to 2.6 ppm (Table 3), a concentration twice as high as its congener, *M. beryllina*. *M. menidia* also has rapid metabolic and growth rates (Bengston 1984, Conover 1990), which may make it more prone to energetic constraints under low DO than is *M. beryllina*. The combination of low DO and high water temperature during mid- to late summer may explain the low abundance of *M. menidia* in these salt marsh pools, even though they are present as juveniles in the early summer. This pattern is similar to the response of the cofamilial *Membras martinica* (Layman et al. 2000).

The extremely low DO observed in the early morning in the salt marsh pools (Fig. 3) was well below lethal levels for many species of fish (Davis 1975), and has been shown to cause behavioral changes in several fishes (Kramer 1987, Beitinger 1990). Low DO conditions could influence fishes in a variety of ways. Low DO is likely to be stressful for spawning fish and their eggs; however, most of the dominant species in the marsh pools spawn prior to the season of lowest DO. Peak spawning occurs in May and June for most of the fundulids and cyprinodontids (Able 1990, Able & Fahay 1998) and atherinids (Conover & Ross 1982, Coorey et al. 1985), and during these dates low DO is less frequent and of shorter duration (authors' pers. obs.).

Low DO can increase mortality and affect species assemblages by changing predator–prey relationships (Kramer 1987), and these responses may occur in

Table 4. Summary of maximum likelihood ANOVA designed to test for effect of time on the observed distribution and survival of fishes. Degrees of freedom (df) calculated from number of behavioral responses. Chi-squared value computed for runs that showed more than 1 response (control runs for *Cyprinodon variegatus*, *Fundulus heteroclitus*, and *Menidia beryllina* only show midwater response). DO: dissolved oxygen

Species	Treatment	Source	df	χ^2	p
Cyprinodon variegatus	Low DO	Intercept	3	171.59	0.001
		Time		159.10	0.001
Fundulus heteroclitus	Low DO	Intercept	3	210.78	0.001
		Time		202.33	0.001
Lucania parva	Low DO	Intercept	3	185.16	0.001
		Time		170.48	0.001
	Control	Intercept	1	2.73	0.10
		Time		1.96	0.16
Menidia beryllina	Low DO	Intercept	2	187.32	0.001
		Time		178.18	0.001
Menidia menidia	Low DO	Intercept	2	114.54	0.001
		Time		109.42	0.001
	Control	Intercept	1	1.08	0.30
		Time		1.82	0.18

marsh pools. If predatory fishes are not tolerant of low DO, small fishes may be less susceptible to such predators in low DO areas (Poulin et al. 1987, Breitburg et al. 1994), and habitats like marsh pools may therefore serve as refuges, at least from aquatic predators. In fact, these pools appear to serve as nurseries for YOY of all of the species in this assemblage with the exception of *Menidia menidia* (authors' unpubl. data). However, avian predation success also increases as DO decreases in some habitats (Kramer et al. 1983), and some birds concentrate their foraging activities in the early morning, when DO is low (Kersten et al. 1991). Increased bird foraging clearly occurs in the study area in late summer for a variety of species including herons, egrets, terns, and gulls (authors' pers. obs.). Since predation by herons, egrets, etc. is selective toward larger fish (Britton & Moser 1982, Kneib 1982), low DO may cause a greater mortality for adults but marsh pools could still provide a refuge for smaller juveniles. This use of low DO habitats by prey species has also been observed in freshwater fish (Rosenberger & Chapman 1999).

In summary, the extreme diurnal and seasonal variability in DO in natural salt marsh pools make these habitats environmentally harsh environments for most species of fish, and ASR is a common behavioral response. Alternatively, the reduction in aquatic predators afforded by these extreme conditions may be one factor influencing the use of marsh pools as a habitat by tolerant species. Direct mortality due to low DO and indirect mortality from increased susceptibility to predation may be important factors in determining the abundance and assemblage structure of fishes in natural salt marsh pools.

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