1996

Effects of Periodic Environmental Hypoxia on Predator Utilization of Macrobenthic Infauna

Janet A. Nestlerode
College of William and Mary - Virginia Institute of Marine Science

Recommended Citation

Nestlerode, Janet A., "Effects of Periodic Environmental Hypoxia on Predator Utilization of Macrobenthic Infauna" (1996). *Dissertations, Theses, and Masters Projects.* Paper 1539617700.
https://dx.doi.org/doi:10.25773/v5-21fp-2929

EFFECTS OF PERIODIC ENVIRONMENTAL HYPOXIA ON PREDATOR UTILIZATION OF MACROBENTHIC INFAUNA

A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

----

by
Janet A. Nestlerode
February 1996

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Arts

Janet A. Nestlerode

Approved, February 1996

Robert J Diaz

Robert J. Diaz, Ph.D.
Committee Chairman/Advisor

Albert Y. Kuo

Albert Y. Kuo, Ph.D.

Romuald N. Lipcius, Ph.D.

Mark W. Luckenbach, Ph.D.

Mark R. Patterson

Mark R. Patterson, Ph.D.

S. Laurie Sanderson, Ph.D.

TABLE OF CONTENTS

ACKNOWLEDGMENTS

I greatly appreciate the constant support, guidance, infinite patience, and statistical insight of my major professor, Dr. Robert J. Diaz, during this research project. I thank him for introducing me to the muddy and fascinating field of Benthic Ecology, for reading numerous drafts of this thesis, and for giving me the idea for this project and allowing me to get creative with it.

I would like to thank the other members of my Advisory Committee, Drs. Al Kuo, Rom Lipcius, Mark Luckenbach, Mark Patterson, and Laurie Sanderson for their expertise, interest, and constructive input.

I am indebted to the many people who helped me in my quest to obtain the seemingly impossible. I thank Shirley Crossley, Charles Machen, Lewie Lawrence, George Pongonis, and the rest of the Vessels Operations staff for their willingness to help (even in the evenings and on weekends). I thank Danny Gouge for his patience and last-minute approval of my dive plans. Thanks go to Steve Snyder and Sam Wilson for field advice and for allowing me to borrow lots of equipment. Thanks also go to Gary Anderson for providing tide data.

This project could not have been completed without the help of everyone who went out in the field with me. I thank the many fellow graduate students who served as boat operators, bubble-watchers, and human fork-lifts during my field work. Special thanks go to my fellow VIMS divers, Marty Cavalluzzi, Tom Chisholm, Danny Gouge, Monica Lara, Adele Pile, and Rochelle Seitz, for braving the often miserable (yet exciting), cold, dark, fast-moving waters of the York River and the occasional Navy ship passing overhead. I am especially thankful to my fellow Benthons: Giancarlo Cicchetti, Randy Cutter, Beth Hinchey, and Eric Wooden for their unselfish assistance throughout this entire project, the many fun days in the field, and countless hours of helpful discussions. I am proud to have had the opportunity to work with such a great group of scientists.

I would also like to thank Beth Hinchey, Mike Land, Mark and Chandell Terwilliger, Giancarlo Cicchetti, Eric Wooden, and Marty Cavalluzzi for their friendship, never-ending encouragement, and for banishing me to the library.

Finally, I would like to thank my family for their support (moral and often financial), optimism, and interest in my endeavors.

LIST OF TABLES

LIST OF FIGURES

ABSTRACT:

Hypoxia and anoxia have significant deleterious ecological effects on living resources throughout many estuarine and marine ecosystems worldwide. Brief periods of low oxygen facilitate transfer of benthic production to higher trophic levels as many benthic infaunal species have shallower sediment depth distributions during hypoxic events. A baited time-lapse camera equipped with a water quality datalogger was used to document *in situ* exploitation of oxygen-stressed benthic invertebrate prey organisms by mobile fish and crustacean predators during alternating normoxia-hypoxia cycles in the York River. Based on photographic and diver observations, this hypoxia-induced benthic-pelagic transfer of production is more likely to occur when environmental dissolved oxygen concentrations rise above an apparent threshold between 1 and 2 ml/l. When oxygen concentrations decline below 2 ml/l, the functional response of the predator to increased prey availability is interrupted. There is no energy gain by the predator until oxygen concentrations rise above this critical level when predators return to affected areas and resume feeding activity.

EFFECTS OF PERIODIC ENVIRONMENTAL HYPOXIA ON PREDATOR UTILIZATION OF MACROBENTHIC INFAUNA

INTRODUCTION

Hypoxia and anoxia (defined as environmental dissolved oxygen concentrations less than 2 ml/l and near 0 ml/l, respectively) (Tyson & Pearson 1991) have significant deleterious ecological effects on living resources in many ecosystems throughout the world (Diaz & Rosenberg 1995). Oxygen deficiency in bottom waters is a common feature in fjords (Richards 1965, Rosenberg 1980), lakes (Wetzel 1983), near-coastal areas (Stachowitsch 1984, Swanson & Parker 1988, Weigelt 1991, Rabalis *et al.* 1994), and estuaries (Tenore 1972, May 1973, Rainer & Fitzhardinge 1981, Welsh & Eller 1991), including Chesapeake Bay (Officer *et al.* 1984, Seliger *et al.* 1985), which is the most studied of these systems in terms of oxygen dynamics (Diaz & Rosenberg 1995).

There is increasing evidence supporting the relationship between eutrophication-induced organic enrichment and low dissolved oxygen development in bottom waters (Stachowitsch 1984, Rosenberg & Loo 1988, Baden *et al.* 1990). However, hypoxia can be a natural phenomenon determined primarily by physical factors, such as water mass movements and temperature and salinity stratification (Breitburg 1990, Tyson & Pearson 1991). In many shallow marine systems, oxygen depletion occurs primarily during the summer when high levels of primary production combine with density stratification of the water column which isolates bottom waters from reaeration (Kuo & Neilson 1987, Rabalis *et al.* 1991). For example, deep water in the mainstem of Chesapeake Bay may become hypoxic in the late spring and remain hypoxic/anoxic until autumn winds initiate vertical mixing and destratification of the water column (Taft *et al.* 1980, Officer *et al.* 1984, Seliger *et al.* 1985).

Taft *et al.* (1980) stated three processes which lead to low dissolved oxygen concentrations in the mainstem of Chesapeake Bay. First, the spring freshet from snow melt and heavy spring rains establishes a vertical salinity stratification. Buoyant freshwater flows over denser sea water and a pycnocline between the two layers is formed. Depending on the degree of stratification, which is influenced by the intensity of the freshet, bottom water remains isolated from replenishment by atmospheric oxygen (Kuo & Neilson 1987). Second, oxygen deficiency occurs when the oxygen demand for the metabolism of organic material exceeds the rate of oxygen supply (Jonas 1987, Tyson & Pearson 1991). Increased water temperature in the spring leads to increased water column and benthic metabolism which results in an increased oxygen demand (Graf *et al.* 1983, Graf 1987, Smith 1987, Malone 1992). This increase in temperature also decreases dissolved oxygen solubility (Colt 1984). Third, phytoplankton from the spring bloom and other organic material settle to the bottom increasing oxygen demand. Aerobic decomposition of this detritus in the water column and on the bottom contributes to depletion of bottom water dissolved oxygen concentrations. The degradation of excess primary production brought on by eutrophication also increases the demand for oxygen and makes these areas more prone to severe deoxygenation (Rosenberg & Loo 1988, Tyson & Pearson 1991).

In a stratified water column where the bottom region becomes increasingly oxygen-deficient, mobile fish and crustaceans are believed to avoid severely hypoxic areas by seasonal or daily migrations into oxygenated regions (Suthers & Gee 1986, Pihl *et al.* 1991, Breitburg 1992). Breitburg (1992) describes such behavior in the naked goby (*Gobiosoma bosc*), a benthic fish, which survive intrusions of severely hypoxic water by temporarily migrating inshore. The blue crab, *Callinectes sapidus*, responds to oxygen deficiency by moving out of hypoxic deep areas to shallower, more normoxic regions (Officer *et al.* 1984, Pihl *et al.* 1991). This may lead to crowding along the shore and emergence onto land (Loesch 1960, May 1973). Increased fish mobility in the SE Kattegat on the west coast of Sweden caused by avoidance of areas affected by hypoxia may have influenced reported increased catches of demersal fish species (Baden *et al.* 1990). In another survival strategy, many fish species swim to the surface and irrigate their gills with more highly oxygenated water in the surface film (Holeton 1979, Kramer & McClure 1982, Kramer 1987). Karr and Freemark (1985) suggest that evolutionary selection on mobile organisms leads to behaviors that enable these animals to move within the environment in such a way as to reduce or avoid premature mortality from a wide variety of disturbances, such as hypoxia.

The severity and consequences of hypoxic events on benthic systems varies with the intensity, extent, and frequency of low dissolved oxygen events and the relative ability of various species and groups to withstand exposure to physiologically stressful or lethal dissolved oxygen concentrations (Pearson & Rosenberg 1992, Llansó 1992). Many macrobenthic organisms cannot tolerate prolonged exposure to hypoxic conditions and respond to oxygen stress with increased mortality and/or reduced recruitment, diversity, and productivity (Rainer & Fitzhardinge 1981, Gaston 1985, Holland 1985, Breitburg 1992).

The majority of benthic fauna have limited mobility and migration out of hypoxic regions is not possible (Breitburg 1992). Through a combination of behavioral and physiological adaptations, fluctuating and short-term hypoxia is survivable by these organisms (Diaz & Rosenberg 1995). Many species that are unable to escape hypoxic conditions begin a series of sub-lethal responses to oxygen stress. For example, as oxygen concentrations decline, many infaunal organisms migrate to the sediment surface. Sea cucumbers swell to increase their surface area:volume ratio to promote oxygen uptake through the body surface and to store oxygen in the increased volume of coelomic fluid (Astall & Jones 1991). Bivalves increase pumping rates, extend their siphons above the bottom in search of oxygenated water, decrease burrowing rates, increase exposure of parts or all of their bodies on the sediment surface, and/or reduce activity levels (Tyson & Pearson 1991, Pihl *et al.* 1992, Jørgensen 1980). Worms emerge from their burrows and begin undulatory body movements which draw water down from above in an attempt to enhance surrounding oxygen levels (Llansó 1991). If dissolved oxygen concentrations continue to fall, the worms' activity ceases and they lie quiescent on the sediment surface until succumbing to death (Tyson & Pearson 1991). However, if hypoxic episodes are brief (on the order of hours or days) many species that become limp and motionless can recover from oxygen depletion and reburrow as oxygen conditions improve (Diaz *et al.* 1992, Jørgensen 1980).

Some macrobenthic mortality and reduced biomass in oxygen-deficient waters may be the result of increased predation resulting from these behavioral modifications induced by low oxygen stress (Pihl *et al.* 1992, Sandberg 1994). Because benthic invertebrates vary in their ability to tolerate hypoxia and in their vulnerability to predators, periods of benthic hypoxia could lead to selective predation on some taxa and be influential in structuring benthic communities (Kolar & Rahel 1993).

Behavioral avoidance of unfavorable abiotic conditions may result in migration to an area of increased predation (Kolar & Rahel 1993). For example, during the summer in prairie ponds, brook stickleback (*Culaea inconstans*) and juvenile yellow perch (*Perca flavescens*) move out of hypoxic cattail beds into higher oxygen, open-water areas of greater predation risk (Suthers & Gee 1986). Larval mayflies in ice-covered lakes experience increased mortality due to fish predation during hypoxia (Rahel & Kolar 1990). As benthic oxygen levels decline, mayflies increase their activity levels, leave their benthic refuge, and move up into the water column in search of higher oxygen concentrations where they become more susceptible to predation. Additionally, Diaz *et al.* (1992) report that many benthic infaunal species have shallower sediment depth distributions during hypoxic events than before or after the onset of hypoxia. Since burial in the sediment provides refuge (Diaz *et al.* 1992, Pihl *et al.* 1992), these stressed organisms may be more susceptible to predation. Prey species are faced with conflicting demands whereby avoidance of one factor, such as low oxygen, may increase the risk of mortality from another factor, such as predation (Rahel & Kolar 1990).

Predator species are reported to endure trade-offs between abiotic stress and optimal foraging opportunities. For instance, nektonic squid (*Lolliguncula brevis*) have been observed off Louisiana diving into hypoxic bottom waters (0.5 ml l^{-1}) (Vecchione & Roper 1991). This behavior is believed to allow the squid to prey upon oxygen-stressed benthic fauna (benthic polychaetes have been found in stomach contents of this species) or to avoid pelagic predators confined to normoxic water higher in the water column (Vecchione 1991). Pavela *et al.* (1983) speculate that many pelagic fishes (several species of sharks, jacks, and mackerels) observed swimming near the surface in the Gulf of Mexico during a hypoxic event may have avoided oxygen-depleted bottom waters while attracted to an unusual food opportunity of vulnerable bottom fauna distressed by hypoxia. Rahel and Nutzman (1994) report that mudminnows (*Umbra limi*) venture into hypoxic bottom waters of stratified Wisconsin lakes to forage on insect larvae using the hypoxic region as a refuge from predation.

Under hypoxic conditions, deep-burrowing species that migrate to the sediment surface, such as infaunal polychaetes and the burrowing anemone *Edwardsia elegans*, are consumed by epibenthic predators (Pihl *et al.* 1992). The diet of Chesapeake Bay demersal fish changed immediately following hypoxic events such that prey items normally found deep in the sediments were consumed after low oxygen events (Pihl *et al.* 1992). To maximize energy intake, these predators seem to forage optimally on weakened prey of the largest size. Brief periods of hypoxia, which are typical during the summer in the York River estuary and many other estuarine systems (Diaz & Rosenberg 1995), may facilitate the transfer of benthic production to predator (fisheries) species (Diaz & Schaffner 1990). Two possible explanations of this transfer of prey to predators during hypoxic events have been suggested (Pihl *et al.* 1991, Pihl *et al.* 1992, Pihl 1994). First, predators may migrate out of hypoxic waters, returning for temporary feeding "excursions" during hypoxia to exploit exposed infauna driven out of the sediment by the oxygen stress. Second, predators may return just after the oxygen levels rise and feed on easily-accessible infauna prey items that have not yet fully recovered from stress.

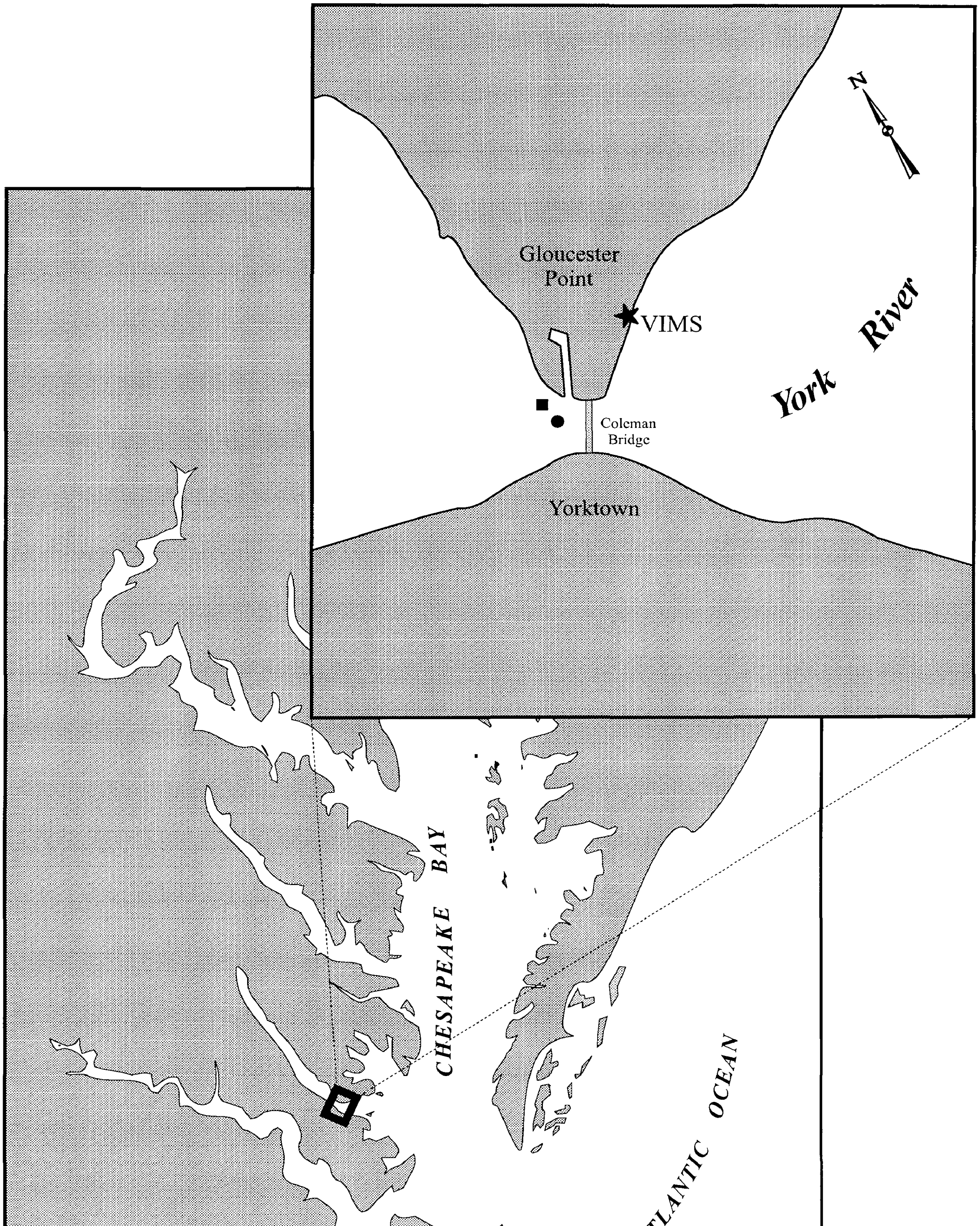
The functional relationship between macrobenthic invertebrates and demersal fishes is a significant component in estuarine ecosystems (Baird & Ulanowicz 1989). One would expect, based on the background synthesis of information, that predators would only subject themselves to abiotic stress if it would lead to energetic benefits otherwise unavailable to them. If predators endure such abiotic stress, energy rewards of locating food may outweigh the physiological expense of foraging in low oxygen environments.

The objective of this study was to examine the effect of hypoxia on food acquisition behavior of bottom-feeding predators through field observations and specifically to address whether epibenthic predators, such as demersal fishes and crustaceans, enter hypoxic water masses to feed on stressed macrobenthic infauna driven out of the sediment by low oxygen concentrations during or immediately after hypoxia.

STUDY AREA

The York River estuary, a sub-estuary of Chesapeake Bay, is located in southeastern Virginia. Study sites were located in the York off Gloucester Point (37° 15' N, 76° 30' W) near the Virginia Institute of Marine Science in approximately 17 and 21 m of water (Figure 1). This system was selected because of its predictable periodic summer hypoxic events. Deep areas of the lower reaches of the York experience periodic hypoxic events (defined as short term or intermittent hypoxia occurring at irregular times of the year) that can last from days to weeks (Haas 1977, Kuo & Neilson 1987, Diaz et al. 1992). The forcing mechanism driving the fortnightly cycle of establishment and breakdown of hypoxic conditions in the York is the lunar neap-spring tidal cycle (Haas 1977). Decreased turbulent mixing during a neap tide leads to a stratified water column and consequently, hypoxic conditions in the isolated bottom water layer. Increased mixing associated with increased tidal currents during spring tides leads to a shift from a stratified, hypoxic water column to a more homogeneous, normoxic water column (Haas 1977). Superimposed on the neap-spring hypoxia cycle is a semi-diurnal tidal cycle of the hypoxic water mass (Diaz *et al.* 1992). Low-oxygen, high-salinity bottom water from the mainstem of the Bay moves upriver on a flood tide and down river on an ebb tide. Therefore, lower bottom water dissolved oxygen concentrations are associated with a rising tide and higher dissolved oxygen concentrations are typically associated with a falling tide (Diaz *et al.* 1992, Kuo & Park 1993). The regular periodicity of these cycles allows an opportunity to anticipate normoxic and hypoxic conditions in the bottom waters of deep areas of the river.

FIGURE 1: The lower York River showing study site. Site of Deployment 1 is indicated by a filled circle (●). Site of Deployment 2 is indicated by a filled square (■).


Gloucester Point
VIMS
York River
Coleman Bridge
Yorktown
N
CHESAPEAKE BAY
ATLANTIC OCEAN

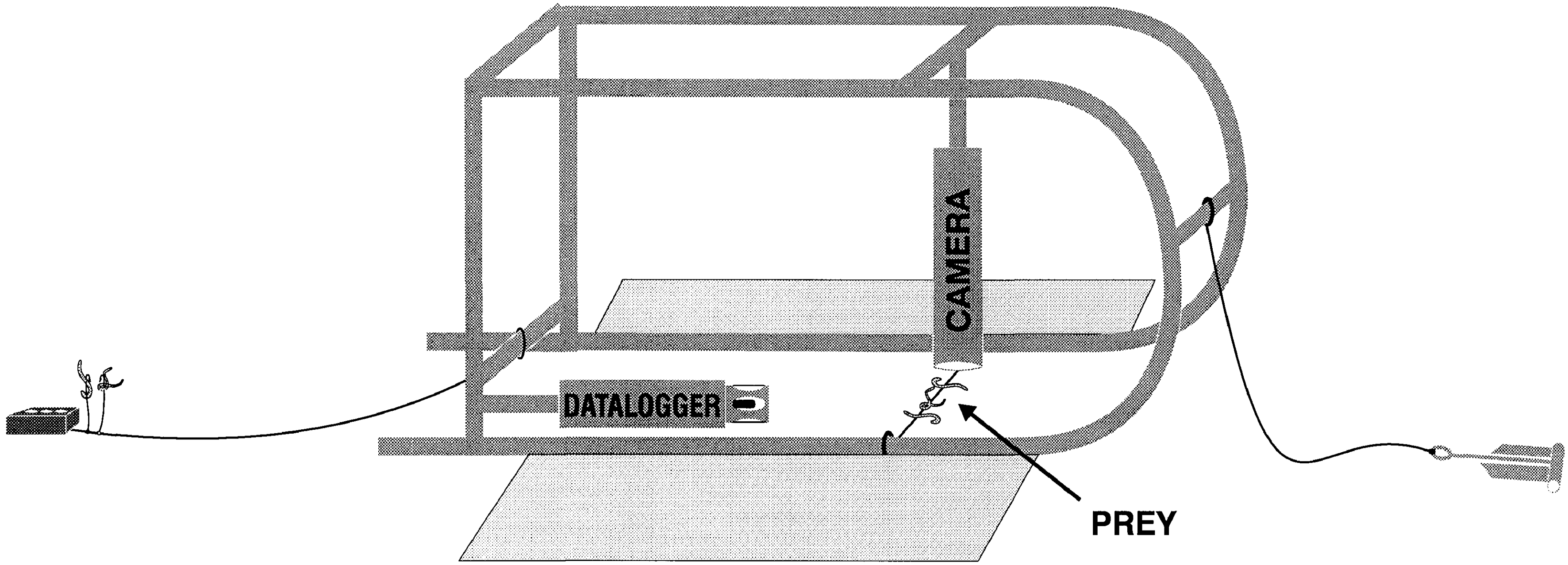
METHODS

Observational field experiments were conducted over two hypoxic events. Prey organisms (Polychaeta:*Glycera americana*) were attached to an aluminum camera frame (Figure 2) and placed in an area of the York River known to undergo hypoxia during the summer (>15 m depth) (Diaz *et al.* 1992, Kuo & Neilson 1987). *G. americana* was chosen as the prey organism because it is large enough to be easily seen in the photographs, is commercially available as fish bait (bloodworms), and was found in the gut contents of demersal fishes from the York River (Pihl *et al.* 1992). Predator activity was monitored using a time lapse underwater still camera (Benthos model 372A) mounted directly above the prey.

A self-contained water quality datalogger (Hydrolabs Datasonde 3) was mounted on the camera frame 20 cm above the sediment surface and used to record near-bottom water column conditions (i.e. dissolved oxygen, salinity, temperature, pH). The Datasonde was calibrated prior to each deployment. Winkler oxygen titrations of bottom water samples from the study site were performed each occasion the prey were replaced to verify the calibration of the Datasonde oxygen sensor. Results of the Winkler titration were compared with the sensor data for the time the water sample was collected. It was determined that the sensor performed well throughout the study period.

During the first deployment (26 August - 9 September 1994), a water quality reading was taken every 5 minutes and one photograph was taken every 15 minutes. Unfortunately, the power system for the camera strobes was unreliable which resulted in gaps in the photographic record. In an effort to prolong battery life during the second deployment (16 - 22 September 1994)

FIGURE 2: Diagram of camera frame apparatus deployed in the lower York River.


CAMERA
DATALOGGER
PREY

exposure frequency was changed to once per hour. Each photograph frame was inscribed with the date and time the image was taken. This labeling facilitates matching photographs with Datasonde readings during data analysis.

Using monofilament, ten *G. americana* were tethered across the short axis of the frame under the camera within the 15 cm x 30 cm field of view. Small lead sinkers were placed on the monofilament to keep the worms on the sediment surface and within the camera's focus range. Bait was replaced daily (weather permitting) by divers at slack tide. Any remaining worms were removed before fresh bait was attached to the frame. Tethered worms placed on the sediment surface were intended to mimic the natural infaunal emergence response to hypoxic conditions (Tyson & Pearson 1991). Although the presence of infaunal organisms exposed on the sediment surface is not normal under normoxic conditions, predation pressures can be compared by exposing tethered prey during both hypoxia and normoxia.

As a control for structure effects (i.e. attraction of predators to the frame), a baited line was extended 2 m away from the frame and anchored in place with a cement brick. Prey were attached to this line 0.25 m from the brick with monofilament and fishing hooks. Presence or disappearance of bait attached to this line was monitored daily by divers.

RESULTS

I. Environmental Conditions:

Two hypoxic events (encompassing approximately 28 August - 4 September 1994 and 16 - 19 September 1994) were observed during my study (Figures 3 and 4). Temporal patterns of near-bottom dissolved oxygen concentrations coincided with the neap/spring tidal cycle as predicted by Haas (1977). Oxygen concentrations also displayed a semi-diurnal signal that coincided with the flood and ebb tidal currents (Figures 5 and 6) (National Ocean Survey 1993). During normoxic periods (typically associated with the spring tide portion of the deployments) oxygen concentrations typically varied 2 to 3 ml/l during a tidal cycle 20 cm above the sediment surface. Conversely, during hypoxic periods, dissolved oxygen concentrations remained in a narrower range of ± 1 ml/l per tidal cycle.

The camera frame apparatus was deployed on 25 August 1994 in 21 m water depth (37°14'39" N 76°30'33" W) at the onset of a neap tide cycle. Approximately 2 days following deployment, divers discovered that the frame was sinking into the soft mud sediment. The entire apparatus was immediately retrieved, thus creating a gap in the water quality time series data, and modified (rectangular fiberglass extensions were added along the long axis of the frame to help dissipate the weight) so as to keep the frame on the sediment surface. The frame was re-deployed to the same site on 30 August 1994. By the time of re-deployment, the near-bottom dissolved oxygen concentration was nearly anoxic and remained well below 2 ml/l for the following four days. Minimum dissolved oxygen values below 2 ml/l

FIGURE 3: Tidal height, dissolved oxygen, temperature, and salinity measurements for Deployment 1 (28 August 1994 - 8 September 1994). Labels along the horizontal axis represent midnight of the day indicated. No water quality measurements were recorded for the periods of 28 - 30 August and 2 - 3 September due to equipment recovery for modification and service.

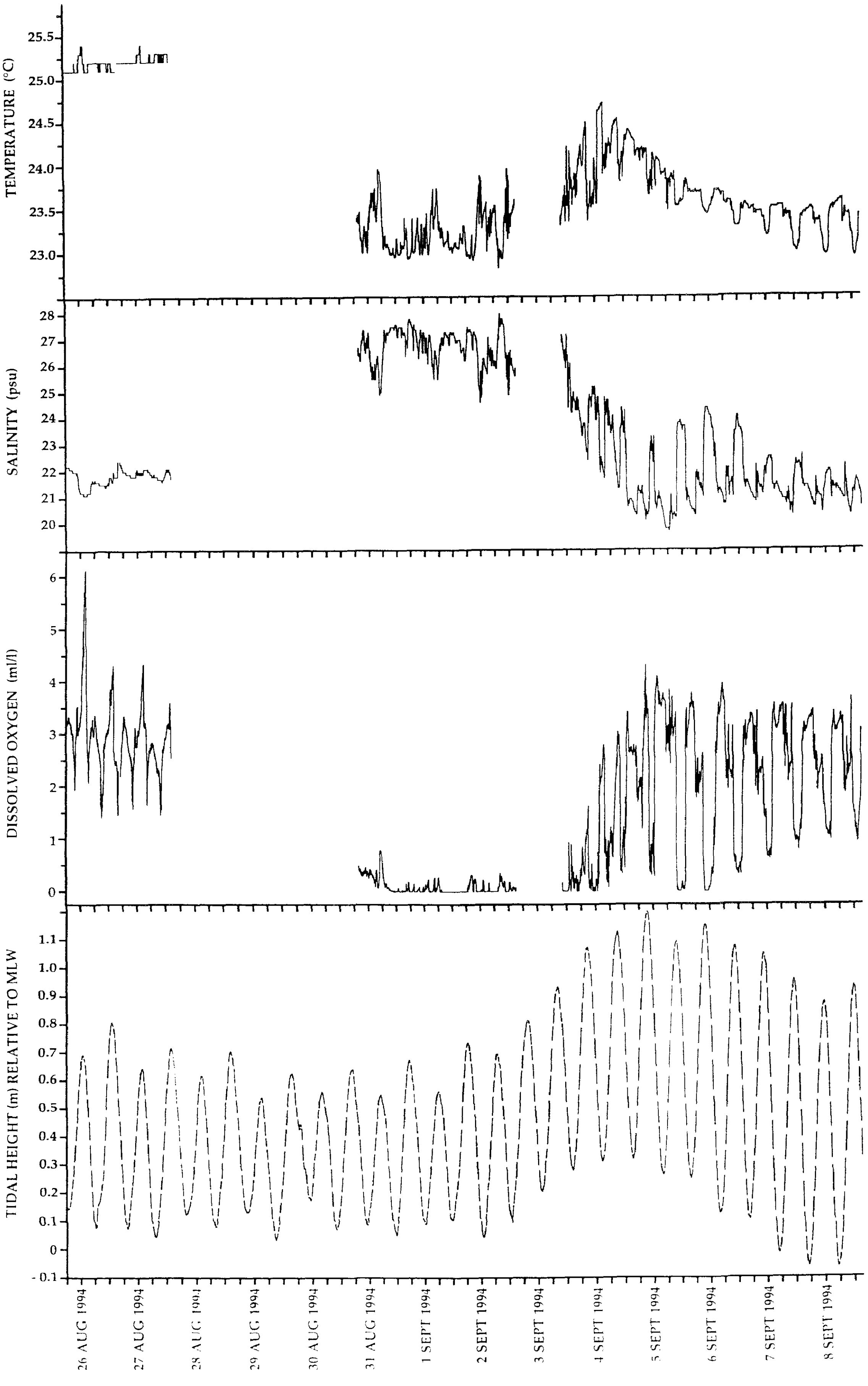
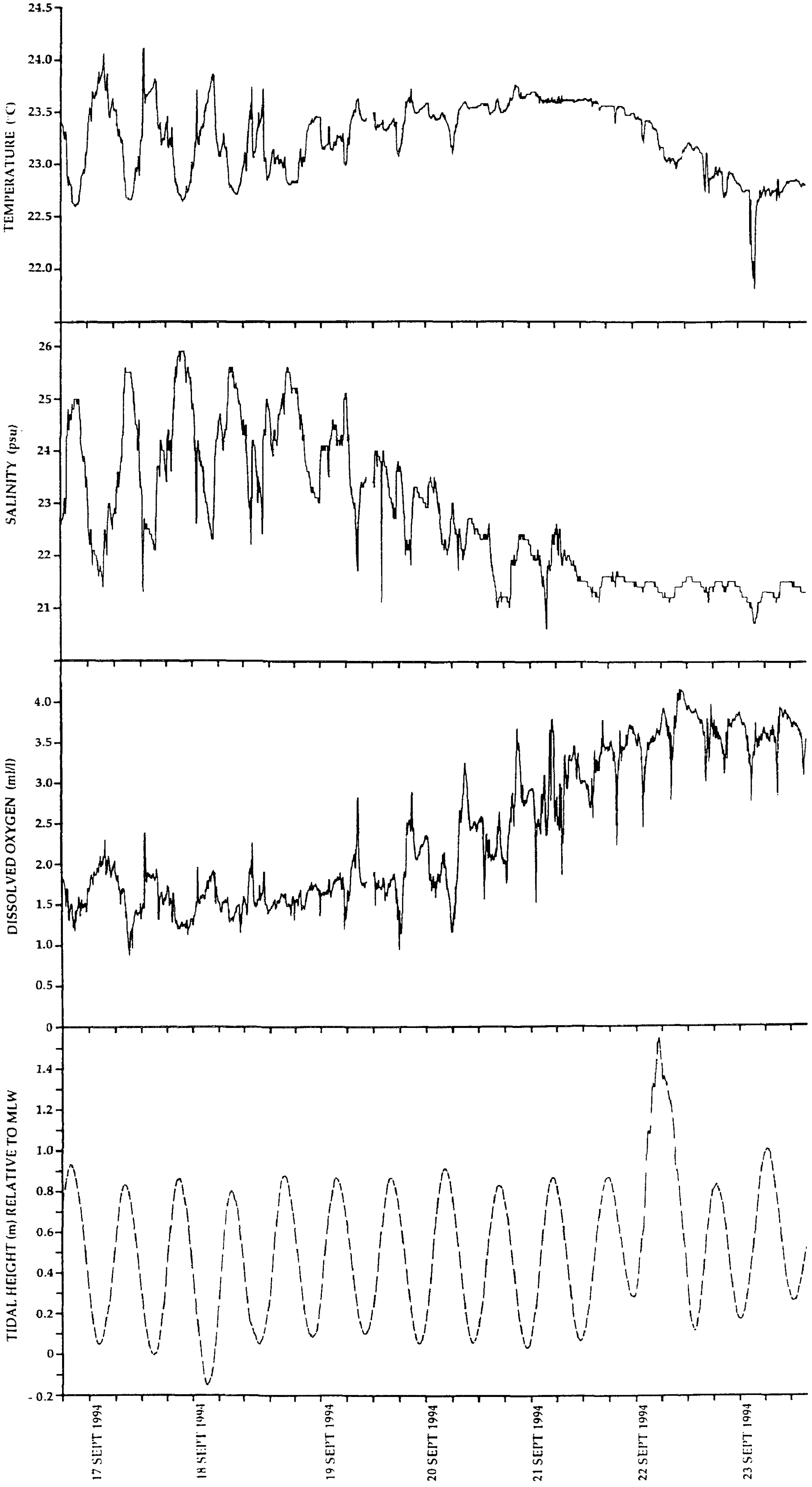

TEMPERATURE (°C)
25.5
25.0
24.5
24.0
23.5
23.0
SALINITY (psu)
28
27
26
25
24
23
22
21
20
DISSOLVED OXYGEN (ml/l)
6
5
4
3
2
1
0
TIDAL HEIGHT (m) RELATIVE TO MLW
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
- 0.1
26 AUG 1994
27 AUG 1994
28 AUG 1994
29 AUG 1994
30 AUG 1994
31 AUG 1994
1 SEPT 1994
2 SEPT 1994
3 SEPT 1994
4 SEPT 1994
5 SEPT 1994
6 SEPT 1994
7 SEPT 1994
8 SEPT 1994

FIGURE 4: Tidal height, dissolved oxygen, temperature, and salinity measurements for Deployment 2 (16 - 22 September 1994). Labels along the horizontal axis represent midnight of the day indicated.



TEMPERATURE (°C)
24.5
24.0
23.5
23.0
22.5
22.0
SALINITY (psu)
26
25
24
23
22
21
DISSOLVED OXYGEN (ml/l)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
TIDAL HEIGHT (m) RELATIVE TO MLW
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
- 0.2
17 SEPT 1994
18 SEPT 1994
19 SEPT 1994
20 SEPT 1994
21 SEPT 1994
22 SEPT 1994
23 SEPT 1994

FIGURE 5: Temporal and tidal current variability in near-bottom dissolved oxygen concentrations. Means and maximum/minimum ranges for near-bottom dissolved oxygen (at 21 m depth) in York River are plotted for each flood and ebb current during 28 August - 4 September 1994. Means are based on 5 minute interval data collected 20 cm above the sediment surface. Dates and times along the horizontal axis represent time of maximum flood or ebb current. Filled squares (■) indicate flood means. Open circles (○) indicate ebb means. Maximum/minimum ranges and means were calculated from the time of slack water to the time of the next slack water to include the tidal current extreme.

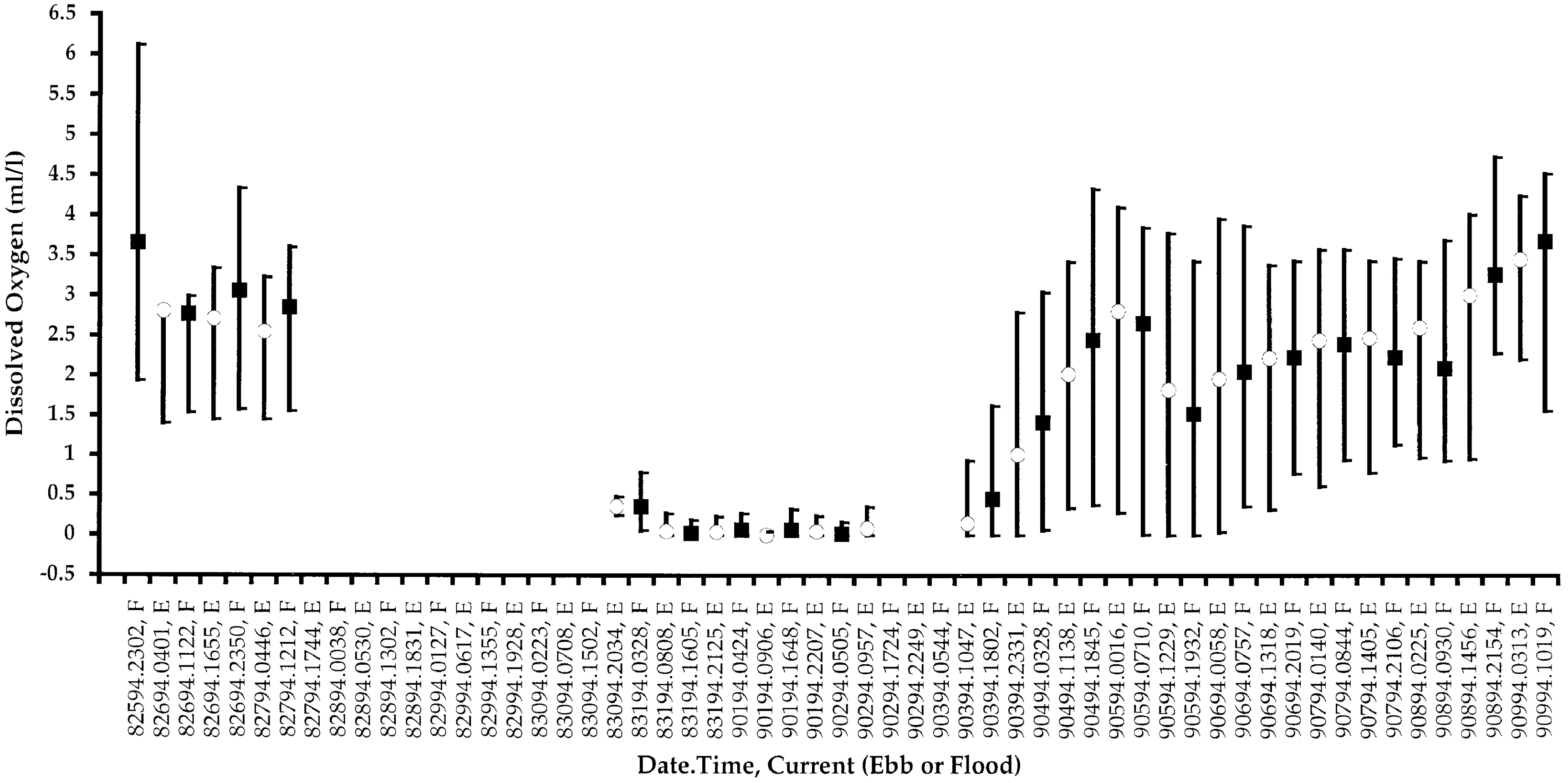
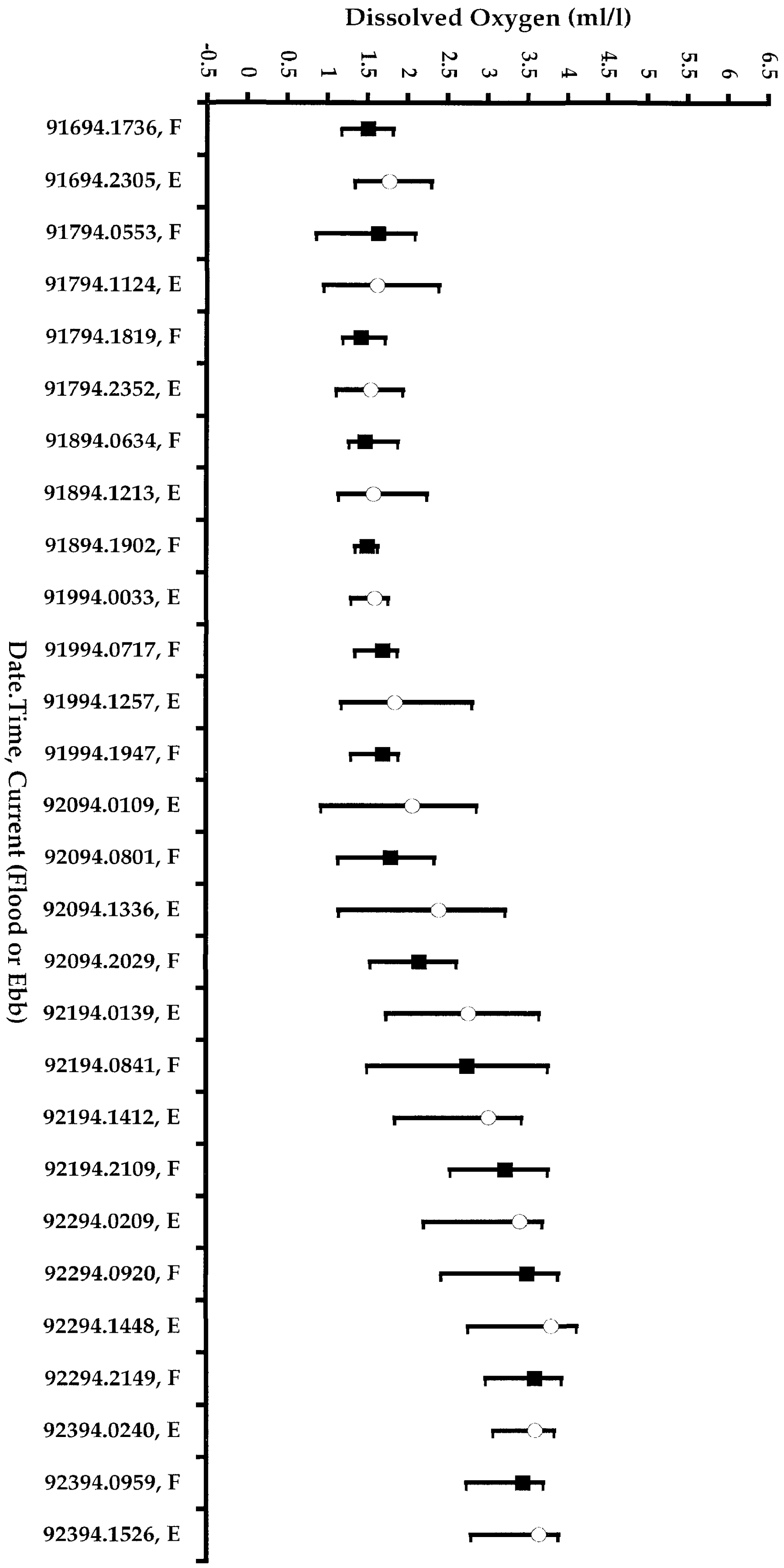

Dissolved Oxygen (ml/l)
6.5
6
5.5
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
-0.5
82594.2302, F
82694.0401, E
82694.1122, F
82694.1655, E
82694.2350, F
82794.0446, E
82794.1212, F
82794.1744, E
82894.0038, F
82894.0530, E
82894.1302, F
82894.1831, E
82994.0127, F
82994.0617, E
82994.1355, F
82994.1928, E
83094.0223, F
83094.0708, E
83094.1502, F
83094.2034, E
83194.0328, F
83194.0808, E
83194.1605, F
83194.2125, E
90194.0424, F
90194.0906, E
90194.1648, F
90194.2207, E
90294.0505, F
90294.0957, E
90294.1724, F
90294.2249, E
90394.0544, F
90394.1047, E
90394.1802, F
90394.2331, E
90494.0328, F
90494.1138, E
90494.1845, F
90594.0016, E
90594.0710, F
90594.1229, E
90594.1932, F
90694.0058, E
90694.0757, F
90694.1318, E
90694.2019, F
90794.0140, E
90794.0844, F
90794.1405, E
90794.2106, F
90894.0225, E
90894.0930, F
90894.1456, E
90894.2154, F
90994.0313, E
90994.1019, F
Date.Time, Current (Ebb or Flood)

FIGURE 6: Temporal and tidal current variability in near-bottom dissolved oxygen concentrations. Means and maximum/minimum ranges for near-bottom dissolved oxygen (at 17 m depth) in York River are plotted for each flood and ebb current during 16 - 22 September 1994. Means are based on 5 minute interval data collected by a self-contained water quality data logger positioned 20 cm above the sediment surface. Dates and times along the horizontal axis represent time of maximum flood or ebb current. Filled squares (■) indicate flood means. Open circles (○) indicate ebb means. Maximum/minimum ranges and means were calculated from the time of slack water to the time of the next slack water to include the tidal current extreme.


Dissolved Oxygen (ml/l)
-0.5
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
6.5
Date.Time, Current (Flood or Ebb)
91694.1736, F
91694.2305, E
91794.0553, F
91794.1124, E
91794.1819, F
91794.2352, E
91894.0634, F
91894.1213, E
91894.1902, F
91994.0033, E
91994.0717, F
91994.1257, E
91994.1947, F
92094.0109, E
92094.0801, F
92094.1336, E
92094.2029, F
92194.0139, E
92194.0841, F
92194.1412, E
92194.2109, F
92294.0209, E
92294.0920, F
92294.1448, E
92294.2149, F
92394.0240, E
92394.0959, F
92394.1526, E

were recorded until 8 September. Tidally-averaged dissolved oxygen measurements from the Datasonde mounted on the camera frame are shown in Figure 5. The salinity ranged from 19.7 to 28.0 psu over the course of the first deployment and the bottom water temperature ranged from 22.8 to 25.4 °C (Figure 3).

The camera frame was re-deployed on 16 September 1994 in 17 m water depth (37°14'43" N 76°30'30" W) during the peak of a neap tide cycle (Figure 4). Near-bottom dissolved oxygen concentrations remained below 2 ml/l until 19 September, the onset of a spring tide cycle. Minimum dissolved oxygen values below 2 ml/l were recorded until 21 September. Dissolved oxygen measurements averaged over each semi-tidal cycle are shown in Figure 6. Near-bottom water salinities ranged from 20.6 to 25.9 psu and temperatures ranged from 21.8 to 24.1 °C during this deployment (Figure 4).

II. Predation

Prey were made available on ten occasions during the first camera deployment and five during the second. During the first camera deployment, the first prey deployment was made prior to the onset of a periodic hypoxic cycle. The first measurement of hypoxia occurred during the third prey deployment and the environment remained hypoxic through the seventh prey deployment five days later. During the second camera deployment, prey were set after the onset of a hypoxic cycle.

Although the photographic record is often incomplete due to camera malfunction and severe turbidity that made many photographs dark or unclear, I have been able to narrow down the time predation events occurred into "predation windows" based on clear photographs and diver observations. Predation occurred on seven occasions during camera deployment 1 and on four occasions during camera deployment 2.

Predation of worms on the remote baited line occurred only when predation occurred on the camera frame. Predation of the remote prey did not occur without concurrent predation of the worms positioned under the camera.

III. Detailed descriptions of prey deployments:

(1) Prey were set at 1710 on 25 August 1994 when hypoxia was not present in the York (Figure 7). The first clear photograph at 1935 indicated no prey were present on the monofilament. Predation occurred within 2 hours, 25 minutes of prey introduction. During this time period, the near-bottom dissolved oxygen concentration ranged from 3.0 ml/l to 3.3 ml/l.

(2) Prey were set at 1555 on 26 August 1994 when the dissolved oxygen concentration was declining toward hypoxia but not yet hypoxic. At 1630, a blue crab (*Callinectes sapidus*) was photographed apparently preying on the *Glycera*. In the next photograph taken 15 minutes later, all prey items had been removed from the monofilament. Near-bottom dissolved oxygen concentrations ranged from 2.2 to 2.8 ml/l during this 50 minute time period (Figure 8).

(3) Prey were set at 1840 on 30 August 1994 after the onset of the hypoxic event and removed by divers at 1700 on 31 August 1994. Predation did not occur during this prey deployment. Near-bottom dissolved oxygen concentrations ranged from 0.0 to 0.8 ml/l during this 22 hour, 20 minute time period (Figure 9).

FIGURE 7: Near bottom dissolved oxygen levels for prey deployment 1 (beginning 25 August 1994) based on 5 minute interval data.

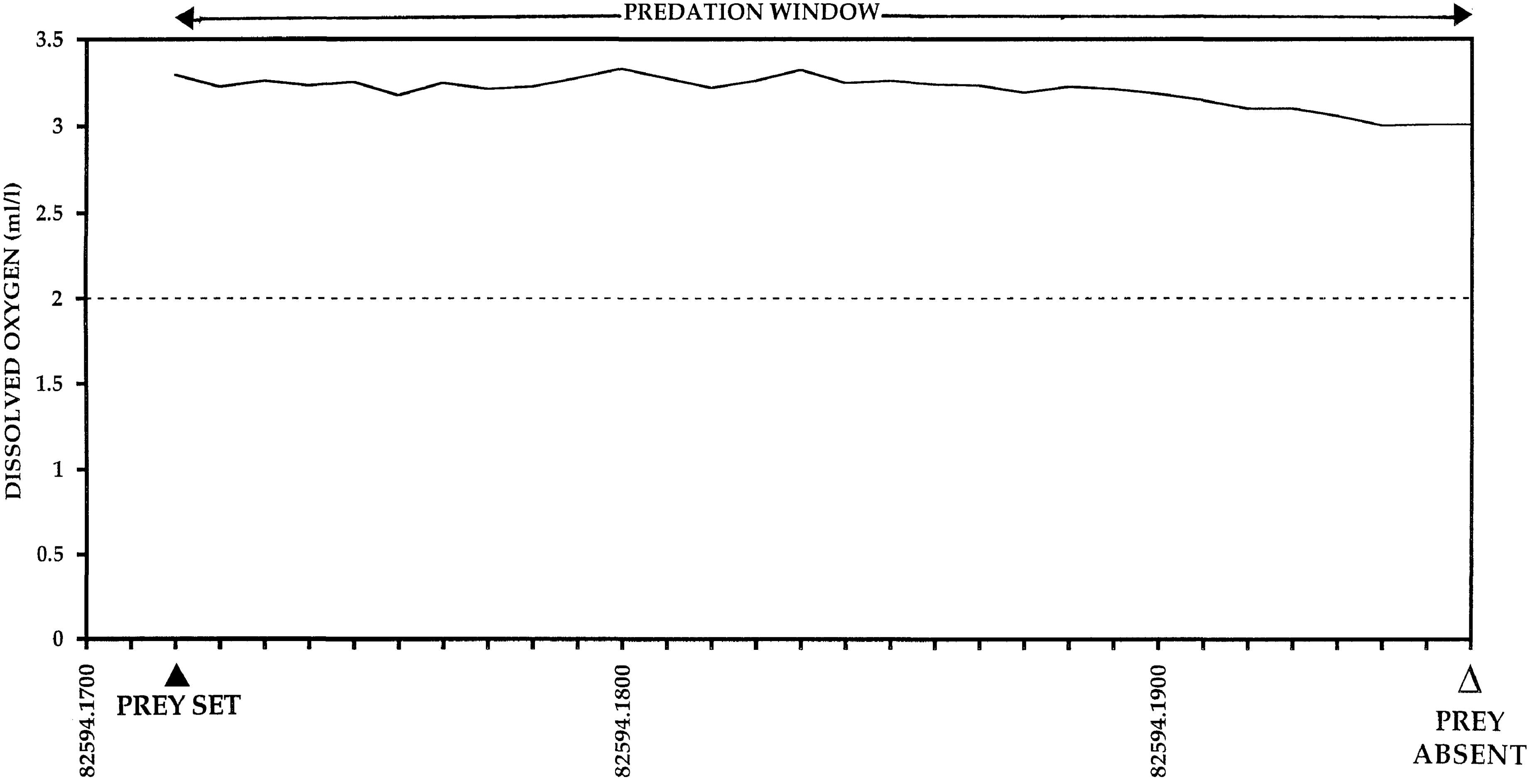

PREDATION WINDOW
DISSOLVED OXYGEN (ml/l)
3.5
3
2.5
2
1.5
1
0.5
0
82594.1700
82594.1800
82594.1900
▲ PREY SET
Δ PREY ABSENT

FIGURE 8: Near bottom dissolved oxygen levels for prey deployment 2 (beginning 26 August 1994) based on 5 minute interval data.

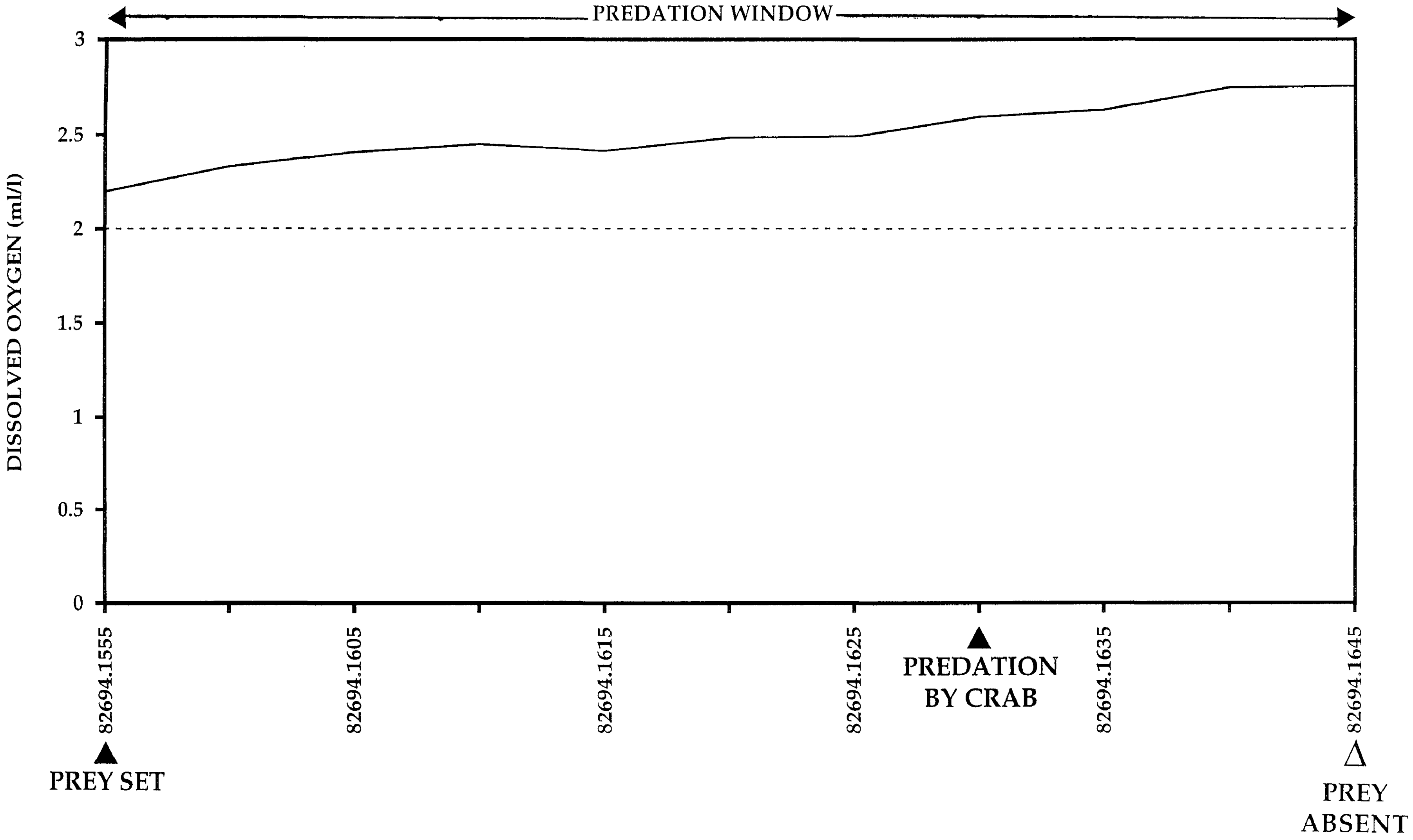
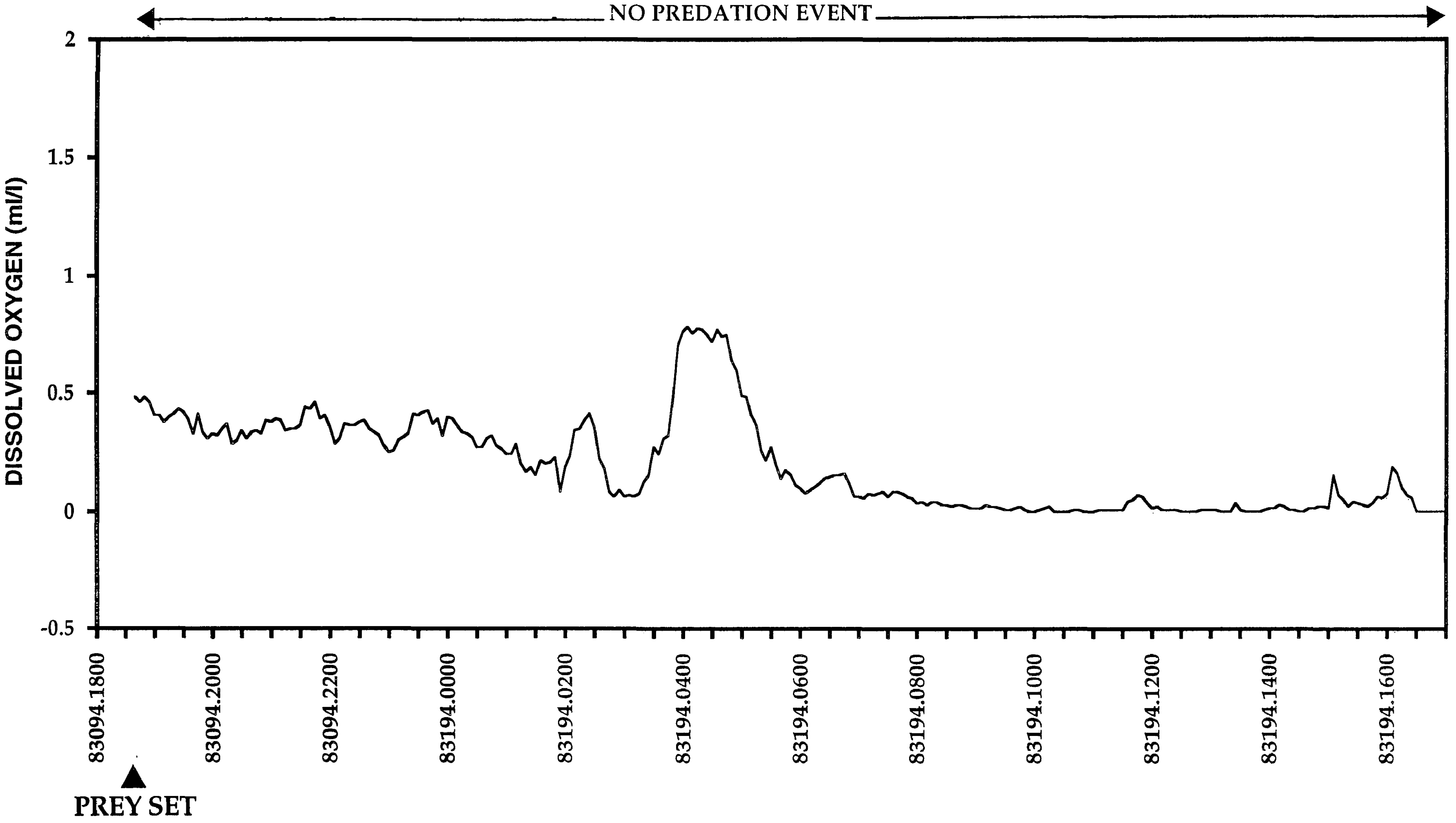

PREDATION WINDOW
DISSOLVED OXYGEN (ml/l)
3
2.5
2
1.5
1
0.5
0
82694.1555
82694.1605
82694.1615
82694.1625
82694.1635
82694.1645
PREY SET
PREDATION BY CRAB
PREY ABSENT

FIGURE 9: Near bottom dissolved oxygen levels for prey deployment 3 (beginning 30 August 1994) based on 5 minute interval data.


NO PREDATION EVENT
DISSOLVED OXYGEN (ml/l)
2
1.5
1
0.5
0
-0.5
83094.1800
83094.2000
83094.2200
83194.0000
83194.0200
83194.0400
83194.0600
83194.0800
83194.1000
83194.1200
83194.1400
83194.1600
PREY SET

(4) Fresh prey items were set at 1715 on 31 August 1994 during the hypoxic event. There was no evidence of predation when the prey were removed by divers at 1830 on 1 September 1994. Near-bottom dissolved oxygen concentrations remained near 0 for most of this prey deployment and ranged from 0.0 to 0.3 ml/l (Figure 10). At the time of prey removal, divers observed hundreds of burrowing anemones (*Edwardsia elegans*) and swollen infaunal sea cucumbers (*Sclerodactyla briareus*) rolling across the sediment surface with the current.

(5) Fresh prey items were set at 1830 on 1 September 1994 during the hypoxic event. There was no evidence of predation when prey items were removed by divers at 0800 on 2 September 1994. The near-bottom dissolved oxygen concentrations never rose above 0.3 ml/l during this period, remaining at or near 0.0 ml/l (Figure 11).

(6) Fresh prey items were set at 0800 on 2 September 1994 by divers during the hypoxic event. No predation occurred between the time prey was made available and 1400 on the same day. Oxygen concentrations hovered at or near 0 ml/l for the duration of this 6 hour prey deployment and ranged from 0 to 0.3 ml/l (Figure 12). The equipment was recovered at 1400 for camera maintenance and redeployed the following day at 0920.

FIGURE 10: Near bottom dissolved oxygen levels for prey deployment 4 (beginning 31 August 1994) based on 5 minute interval data.

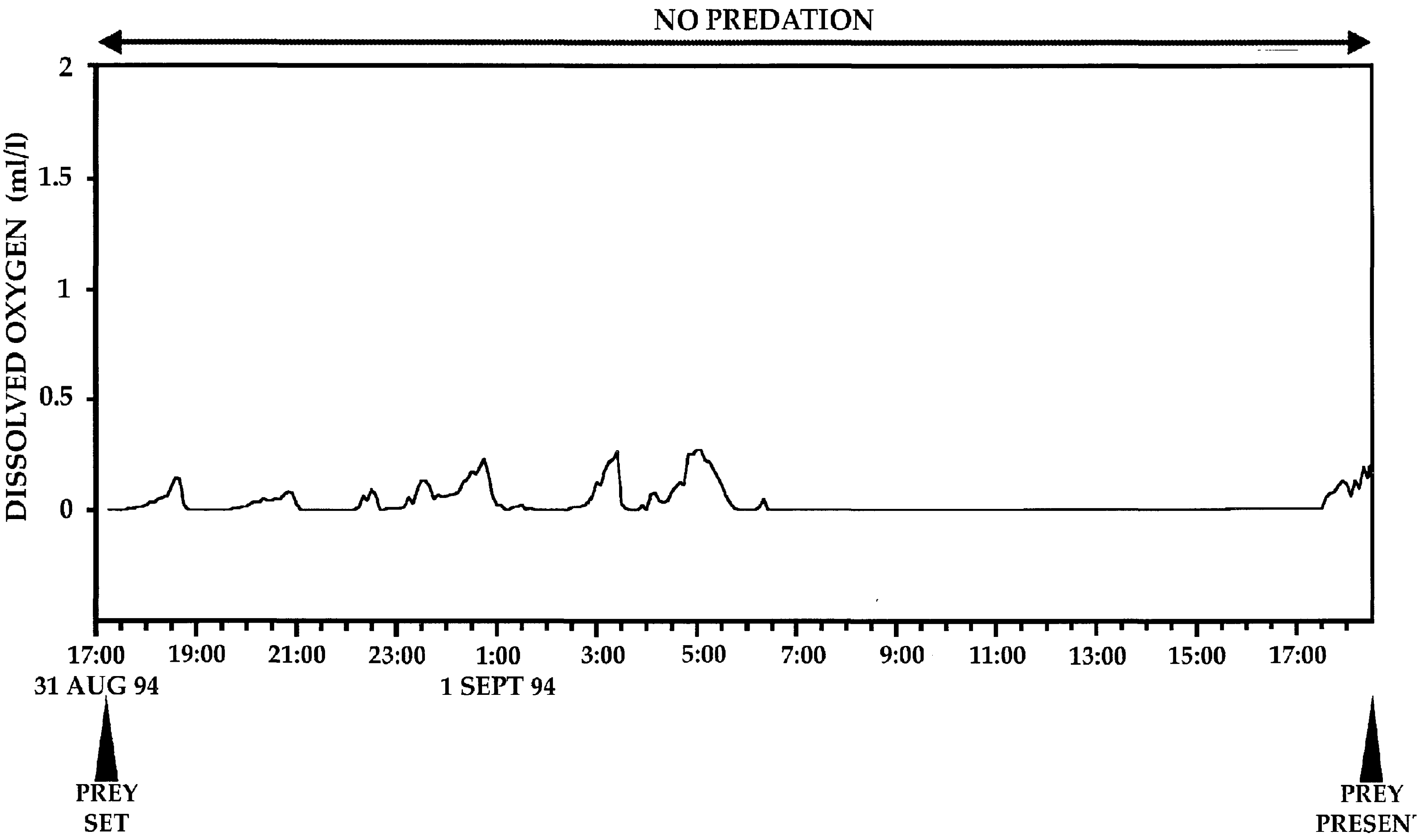

NO PREDATION
DISSOLVED OXYGEN (ml/l)
2
1.5
1
0.5
0
17:00
19:00
21:00
23:00
1:00
3:00
5:00
7:00
9:00
11:00
13:00
15:00
17:00
31 AUG 94
1 SEPT 94
PREY SET
PREY PRESEN

FIGURE 11: Near bottom dissolved oxygen levels for prey deployment 5 (beginning 1 September 1994) based on 5 minute interval data.

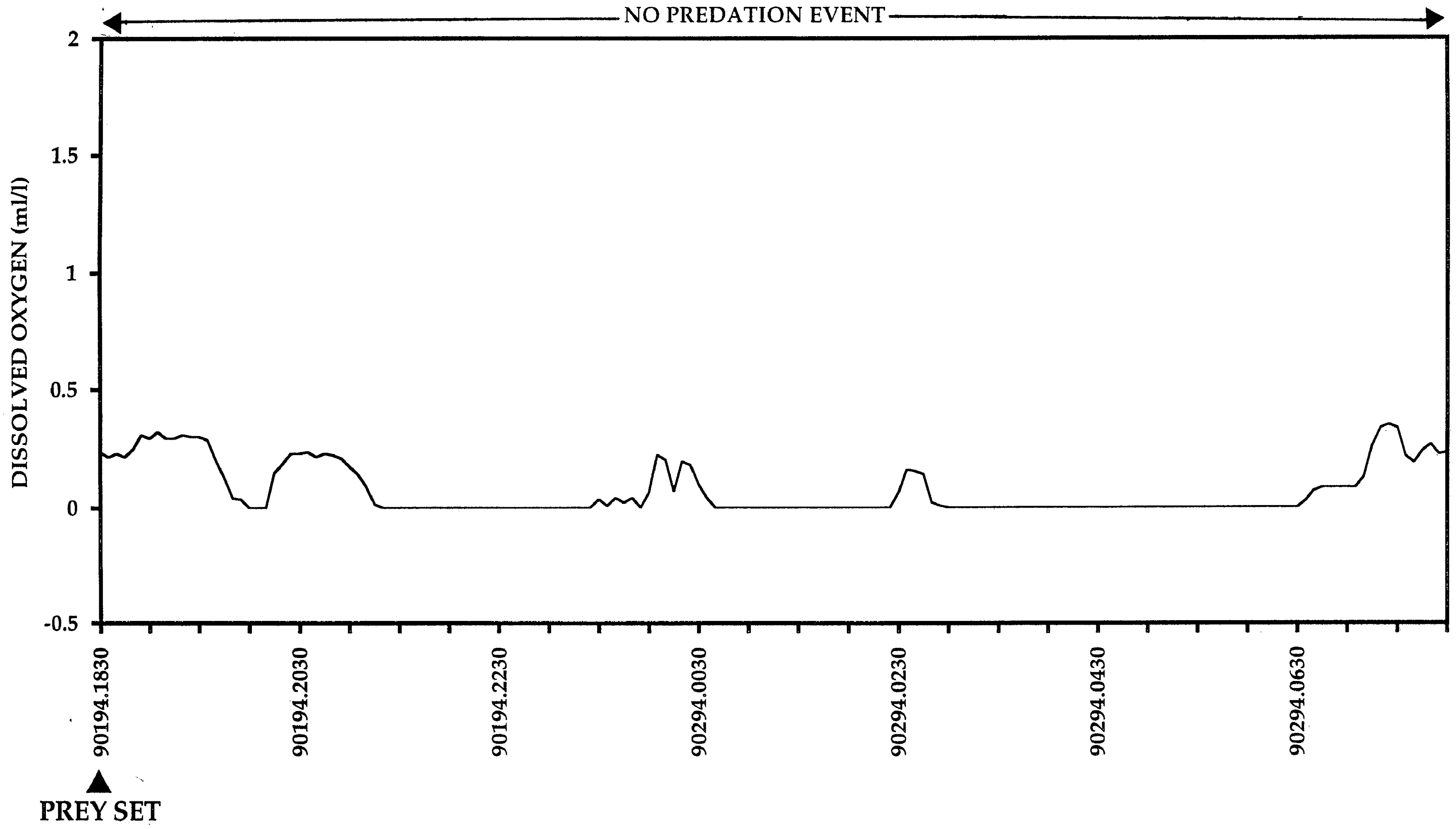
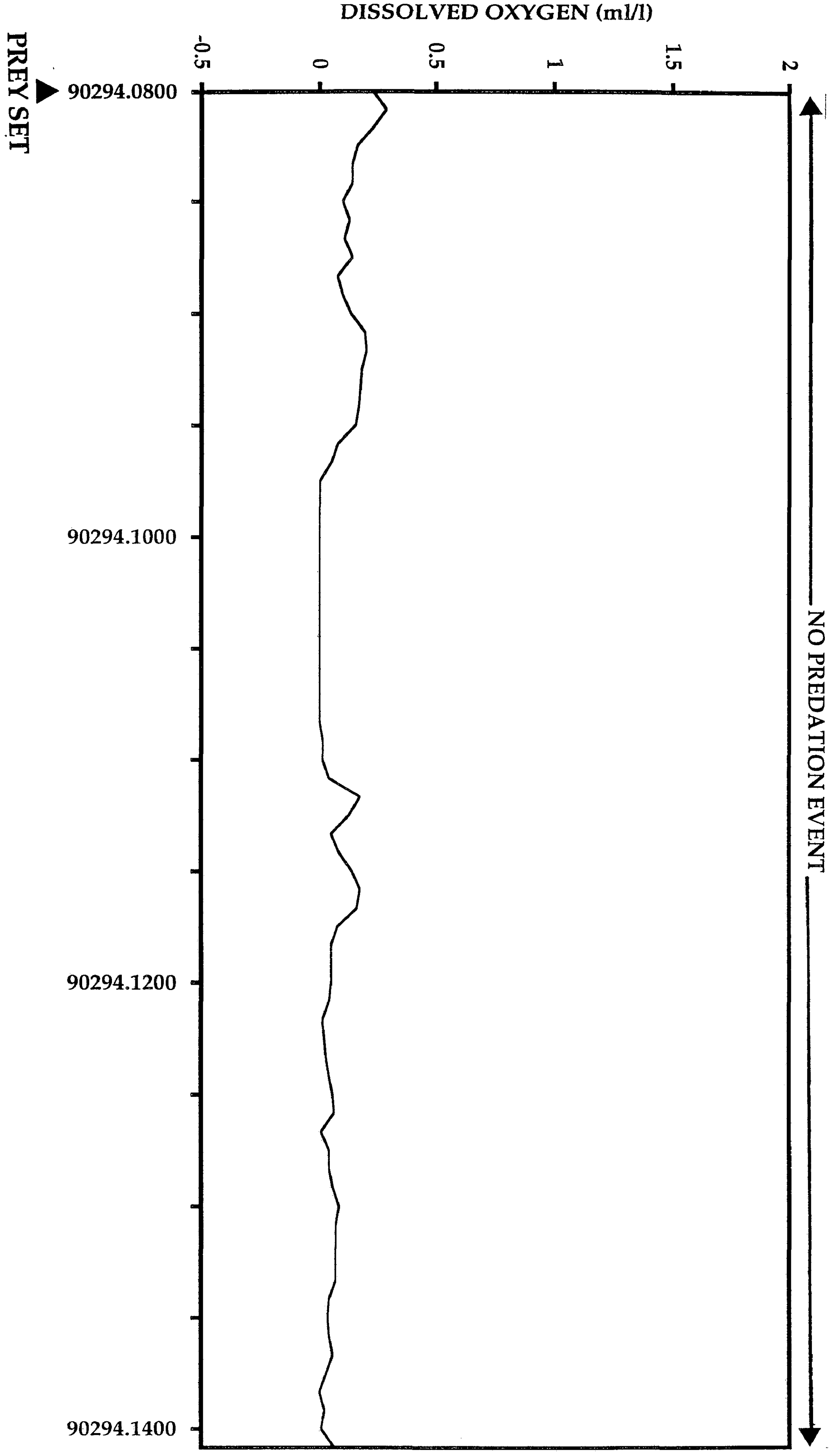

NO PREDATION EVENT
DISSOLVED OXYGEN (ml/l)
2
1.5
1
0.5
0
-0.5
90194.1830
90194.2030
90194.2230
90294.0030
90294.0230
90294.0430
90294.0630
PREY SET

FIGURE 12: Near bottom dissolved oxygen levels for prey deployment 6 (beginning 2 September 1994) based on 5 minute interval data.


DISSOLVED OXYGEN (ml/l)
-0.5
0
0.5
1
1.5
2
90294.0800
90294.1000
90294.1200
90294.1400
PREY SET
NO PREDATION EVENT

(7) Prey were set at 0920 on 3 September 1994 near the end of the hypoxic event. At 2150 (DO = 0.1 ml/l) an infaunal, burrowing anemone (*Edwardsia elegans*) was photographed as it rolled through the camera's field of view on the surface of the sediment. Near-bottom dissolved oxygen concentrations remained hypoxic until 0045 on 4 September 1994 when oxygen remained above 2 ml/l for a 2 hour window. Predation did not occur during this short normoxic period. Near-bottom dissolved oxygen concentrations then hovered around 1 ml/l until 0720. Prey remained undisturbed until the last clear photograph at 0650 (DO = 1.4 ml/l). In the next clear photograph, about 3 hours later, the prey were gone. Predation occurred sometime between 0650 and 0945. In the 0945 photograph, a sediment disturbance (resembling a feeding pit characteristic of those made by demersal fishes) was clearly evident. Within this time period, near-bottom dissolved oxygen concentrations ranged from 0.4 to 3.0 ml/l but continuously remained above 2 ml/l for 1 hour 55 minutes (Figure 13).

(8) Fresh prey items were set by divers during near-hypoxic conditions at 1830 (DO = 2.3 ml/l) on 5 September 1994. Oxygen concentrations ranged from 1.9 to 2.6 until 2015 when a rapid decline in oxygen occurred over a 30 minute period. Due to camera malfunction, a photograph was not taken until 2240. At this time, it became apparent that four worms had been removed from the monofilament sometime since deployment at 1830. Based on photographic evidence, the six remaining worms were preyed upon sometime between 0040 and 0505 on 6 September 1994. During this 4 hour, 25 minute time window, near-bottom dissolved oxygen concentrations remained hypoxic until 0140 and then rose to 4.0 ml/l at 0430 (Figure 14).

FIGURE 13: Near bottom dissolved oxygen levels for prey deployment 7 (beginning 3 September 1994) based on 5 minute interval data.

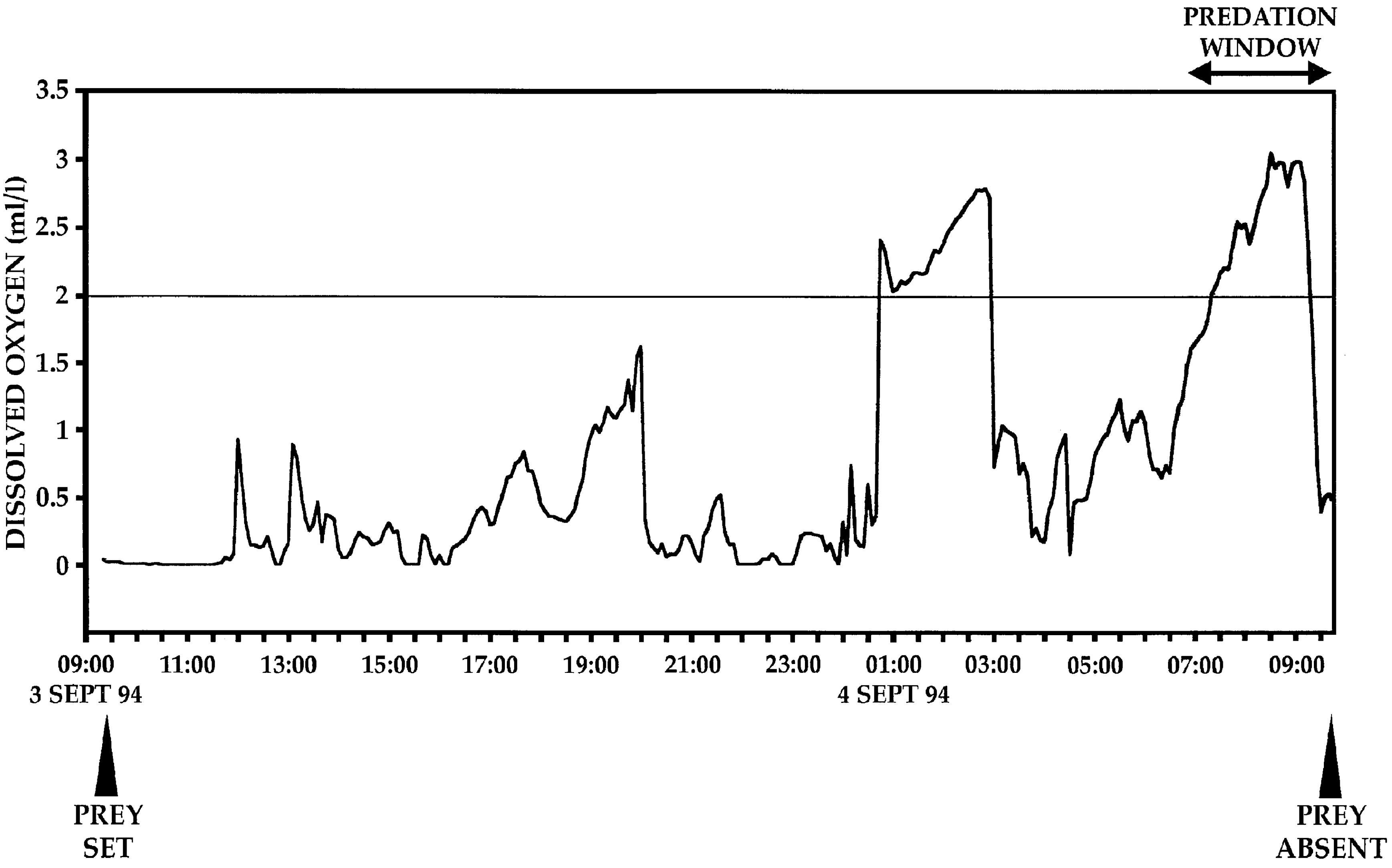
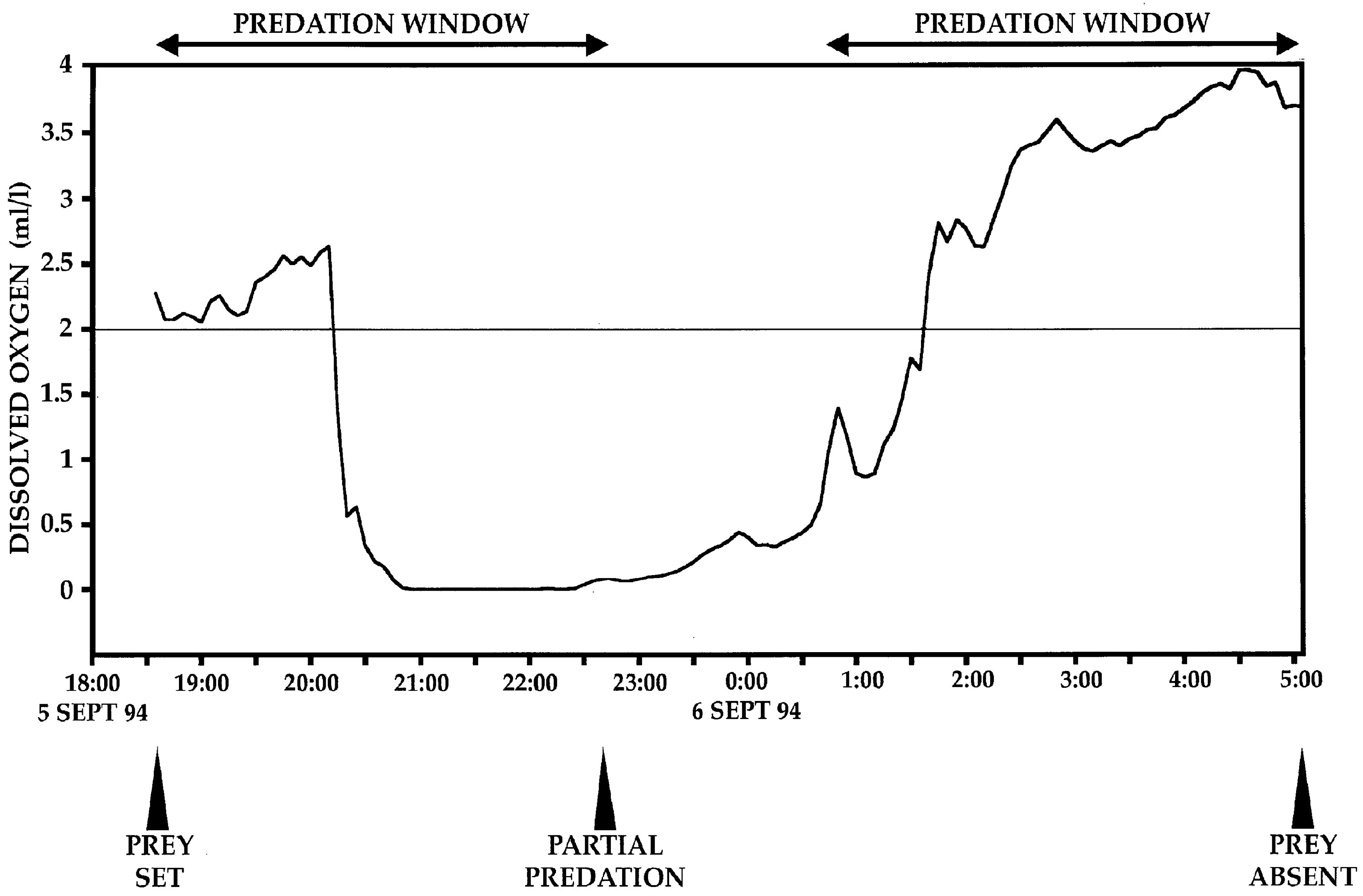

PREDATION
WINDOW
3.5
3
2.5
2
1.5
1
0.5
0
DISSOLVED OXYGEN (ml/l)
09:00
11:00
13:00
15:00
17:00
19:00
21:00
23:00
01:00
03:00
05:00
07:00
09:00
3 SEPT 94
4 SEPT 94
PREY
SET
PREY
ABSENT

FIGURE 14: Near bottom dissolved oxygen levels for prey deployment 8 (beginning 5 September 1994) based on 5 minute interval data.


PREDATION WINDOW
PREDATION WINDOW
DISSOLVED OXYGEN (ml/l)
4
3.5
3
2.5
2
1.5
1
0.5
0
18:00
5 SEPT 94
19:00
20:00
21:00
22:00
23:00
0:00
6 SEPT 94
1:00
2:00
3:00
4:00
5:00
PREY
SET
PARTIAL
PREDATION
PREY
ABSENT

(9) Prey were set at 1730 on 7 September 1994 when hypoxia was not present in the York and the dissolved oxygen level had remained normoxic since 1350. The first clear photograph taken at 1915 indicated no prey were present on the monofilament. Predation occurred within 1 hour 15 minutes of prey introduction. During this period, near-bottom dissolved oxygen concentrations ranged from 2.5 to 3.5 ml/l (Figure 15).

(10) Due to camera malfunction, there is no photographic record for this prey deployment. Predation evidence is based on diver observations. The near-bottom dissolved oxygen concentration had been above 2 ml/l for 1.5 hours when new prey were set at 1530 on 8 September 1994 (DO = 4.0 ml/l). Predation occurred sometime between this moment and 1450 on 9 September 1994 (recovery of the camera apparatus). Near-bottom dissolved oxygen concentrations during this prey deployment remained normoxic until 1255 on 9 September when dissolved oxygen concentrations fell below 2 ml/l for 1 hour 40 minutes (Figure 16).

(11) Prey were set at 1645 on 16 September 1994 after the onset of hypoxia (DO = 1.8 ml/l). Prey were removed by divers at 1000 on 17 September 1994. The near-bottom dissolved oxygen concentration ranged from 0.9 to 2.3 ml/l during this prey deployment and predation did not occur. Oxygen remained below 2 ml/l for the majority of this prey deployment except for a 3 hour window following a low tide in which dissolved oxygen concentration fluctuated between 1.9 and 2.2 ml/l (Figure 17).

FIGURE 15: Near bottom dissolved oxygen levels for prey deployment 9 (beginning 7 September 1994) based on 5 minute interval data.

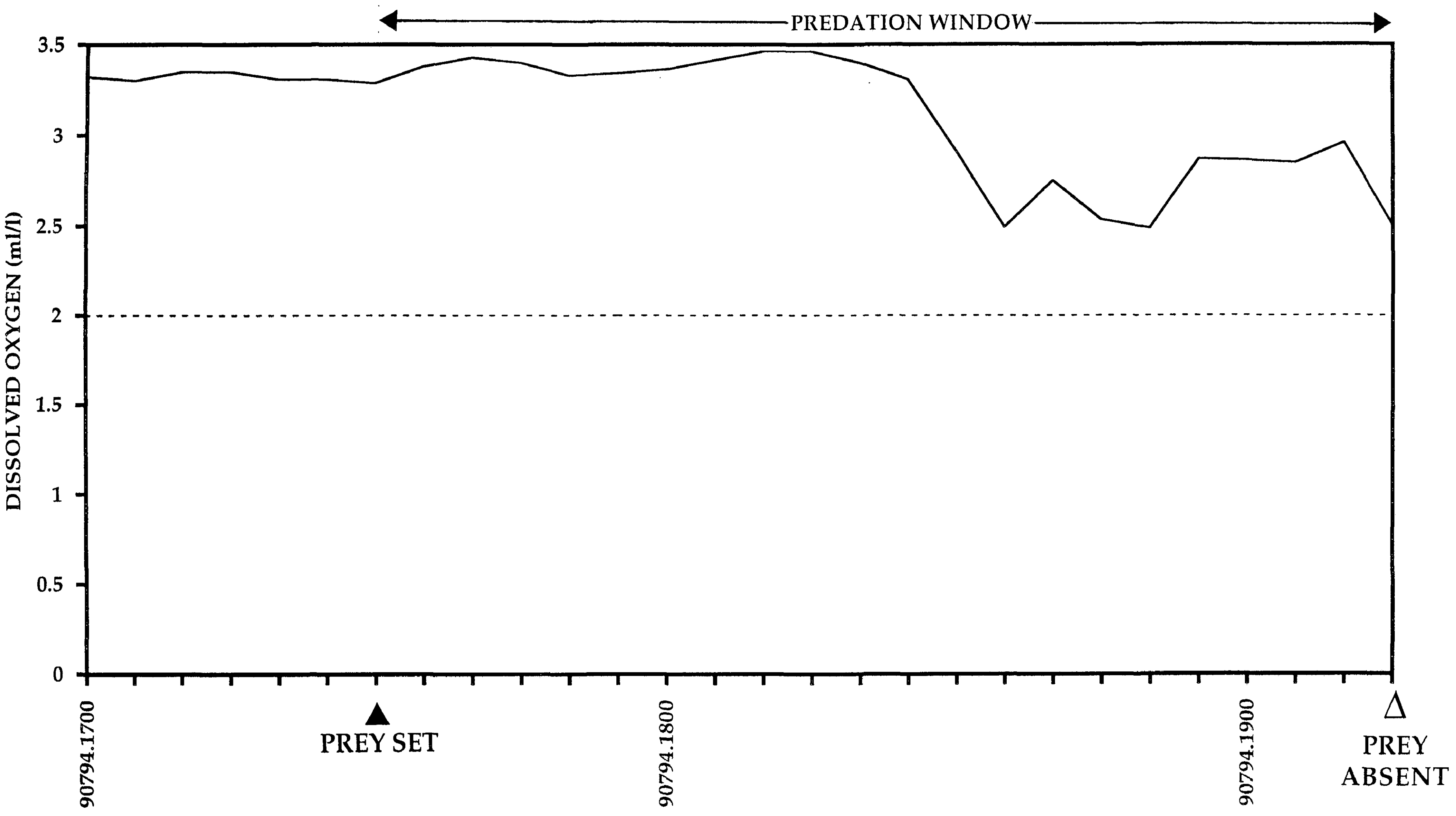

PREDATION WINDOW
DISSOLVED OXYGEN (ml/l)
3.5
3
2.5
2
1.5
1
0.5
0
90794.1700
PREY SET
90794.1800
90794.1900
PREY
ABSENT

FIGURE 16: Near bottom dissolved oxygen levels for prey deployment 10 (beginning 8 September 1994) based on 5 minute interval data.

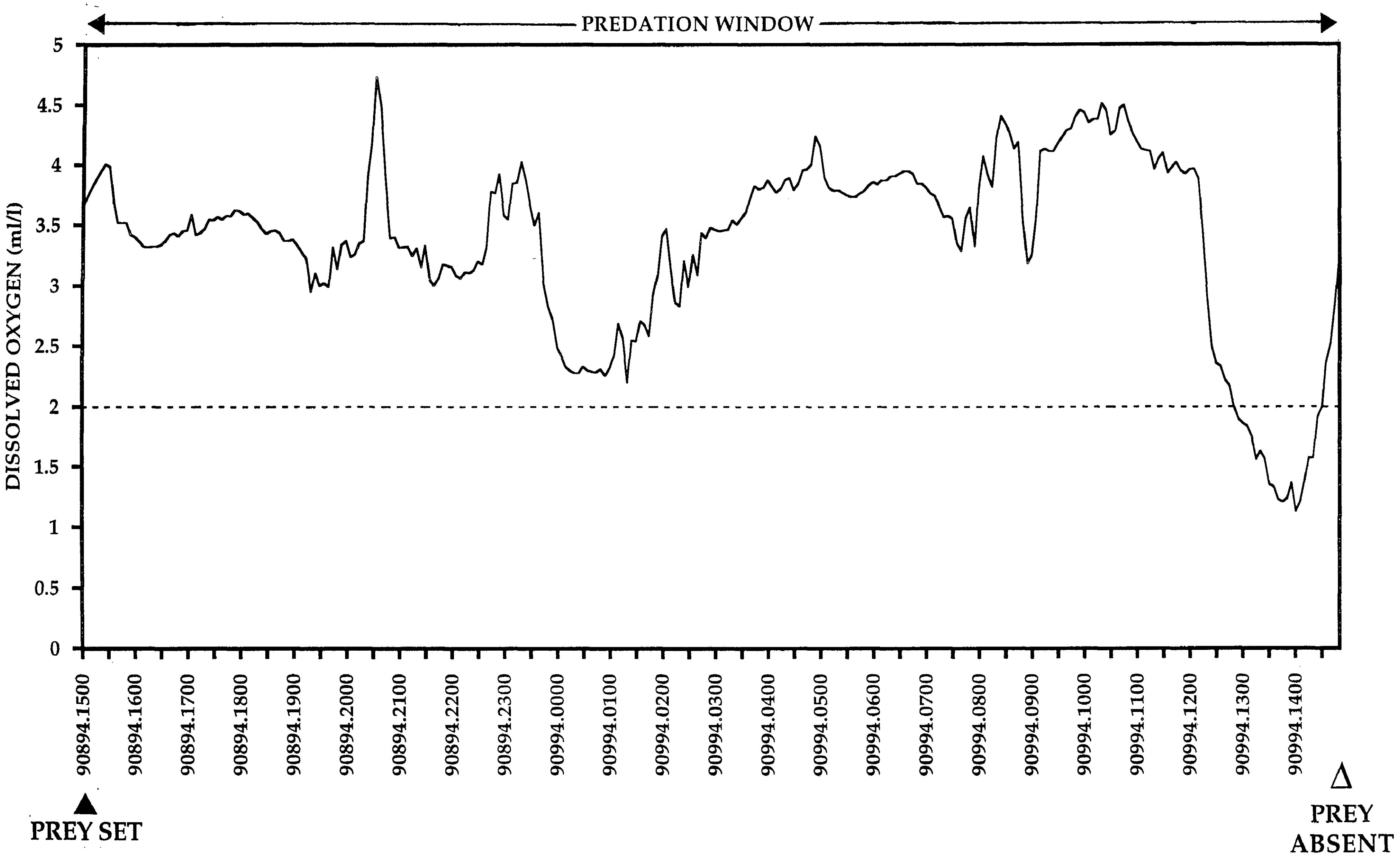
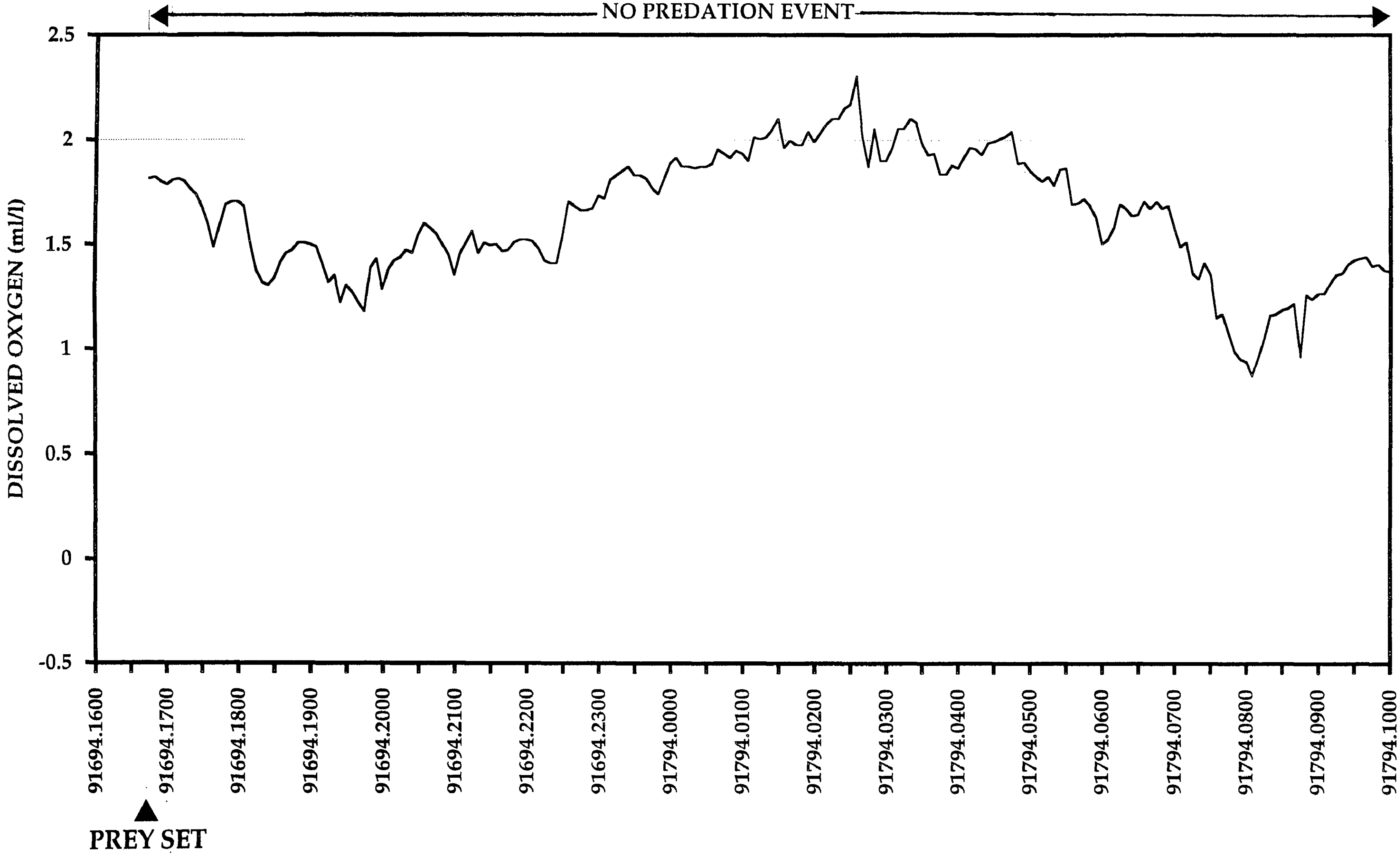
PREDATION WINDOW
DISSOLVED OXYGEN (ml/l)
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
90894.1500
90894.1600
90894.1700
90894.1800
90894.1900
90894.2000
90894.2100
90894.2200
90894.2300
90994.0000
90994.0100
90994.0200
90994.0300
90994.0400
90994.0500
90994.0600
90994.0700
90994.0800
90994.0900
90994.1000
90994.1100
90994.1200
90994.1300
90994.1400
▲ PREY SET
Δ PREY ABSENT

FIGURE 17: Near bottom dissolved oxygen levels for prey deployment 11 (beginning 16 September 1994) based on 5 minute interval data.


NO PREDATION EVENT
DISSOLVED OXYGEN (ml/l)
2.5
2
1.5
1
0.5
0
-0.5
91694.1600
91694.1700
91694.1800
91694.1900
91694.2000
91694.2100
91694.2200
91694.2300
91794.0000
91794.0100
91794.0200
91794.0300
91794.0400
91794.0500
91794.0600
91794.0700
91794.0800
91794.0900
91794.1000
PREY SET

(12) Prey were set at 1000 on 17 September 1994 during the hypoxic event (DO = 1.4 ml/l). Prey were removed by divers at 1130 on 18 September 1994. The near-bottom dissolved oxygen concentration ranged from 1.1 to 2.4 ml/l during this prey deployment and predation did not occur. Oxygen remained below 2 ml/l for the majority of this prey deployment except for a 20 minute period in which dissolved oxygen concentration briefly peaked to 2.4 ml/l (Figure 18).

(13) Prey were set at 1130 on 18 September 1994 during the hypoxic event. Near-bottom dissolved oxygen concentrations remained hypoxic until 1210 on 19 September 1994. At this time, oxygen concentrations rose above 2 ml/l for 1 hour, 35 minutes and then dropped below 2 ml/l until termination of this prey deployment. Prey remained undisturbed until the last clear photograph was taken at 0555 on 19 September. Predation of 6 worms occurred sometime between 0555 and the recovery of the camera apparatus at 1515 on the same day. At this time, four undisturbed *Glycera* remained on the monofilament line. During this predation window, near-bottom dissolved oxygen ranged from 1.2 to 2.8 ml/l and remained above 2 ml/l for 1.5 hours (Figure 19).

FIGURE 18: Near bottom dissolved oxygen levels for prey deployment 12 (beginning 17 September 1994) based on 5 minute interval data.

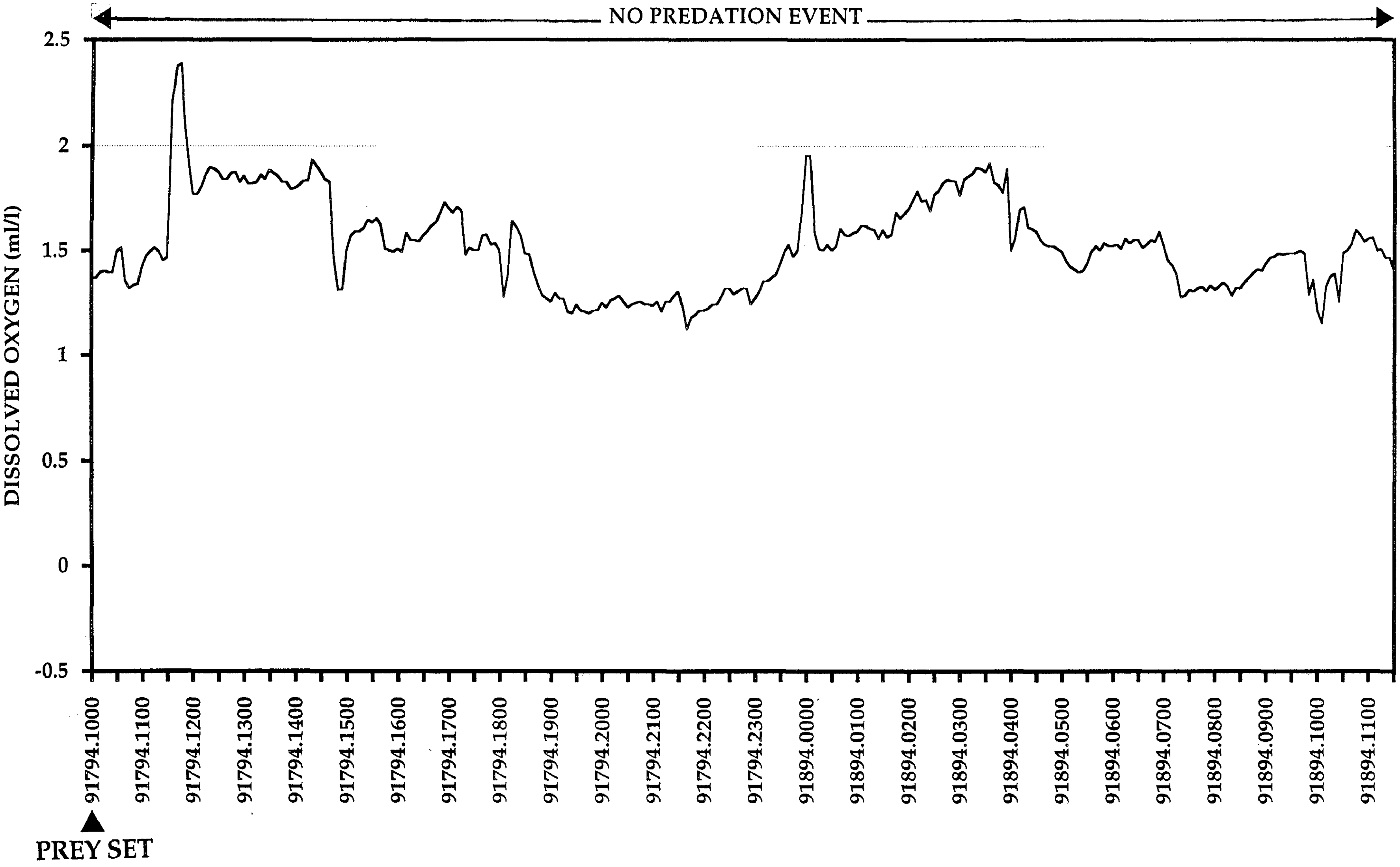
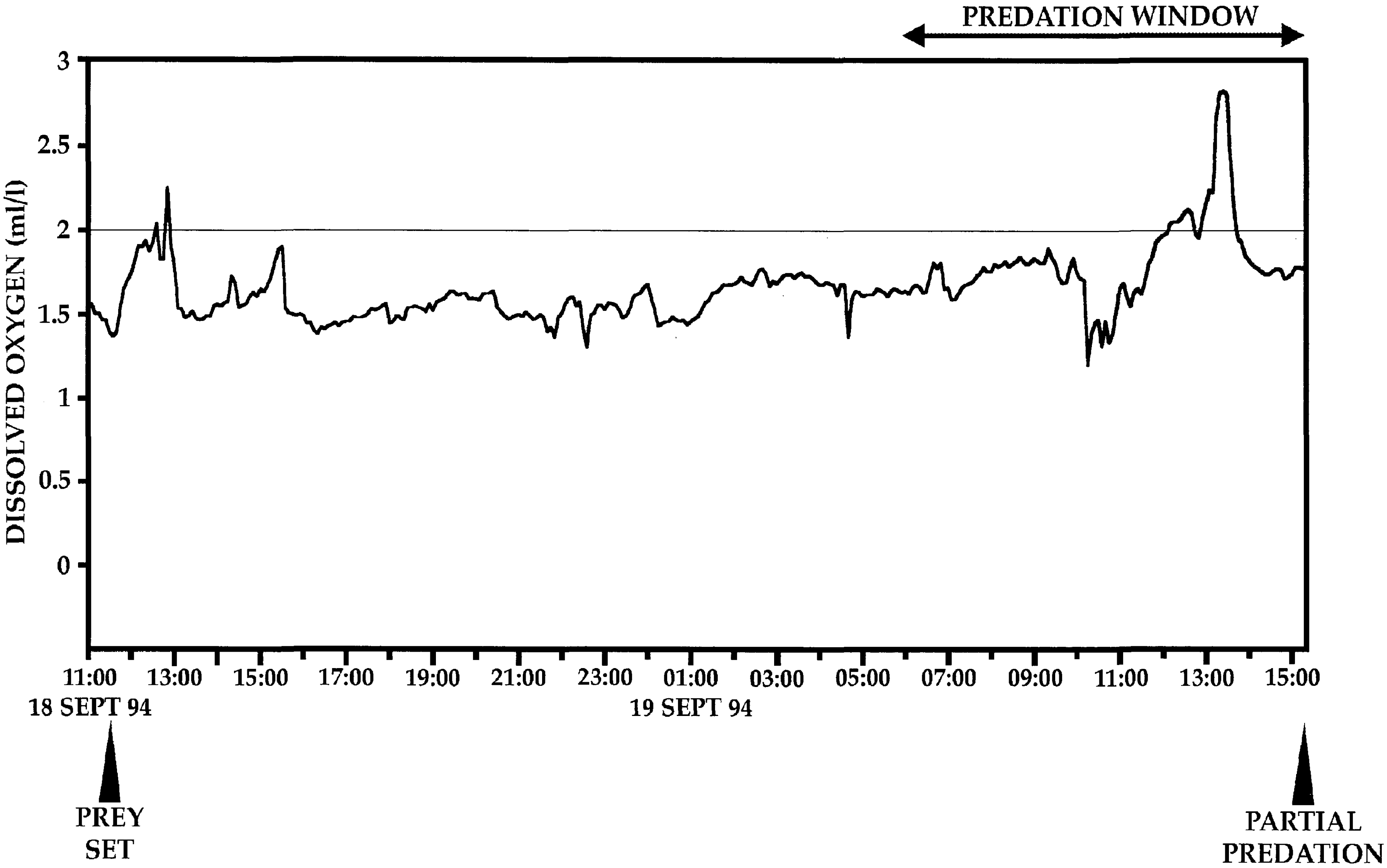

NO PREDATION EVENT
DISSOLVED OXYGEN (ml/l)
2.5
2
1.5
1
0.5
0
-0.5
91794.1000
91794.1100
91794.1200
91794.1300
91794.1400
91794.1500
91794.1600
91794.1700
91794.1800
91794.1900
91794.2000
91794.2100
91794.2200
91794.2300
91894.0000
91894.0100
91894.0200
91894.0300
91894.0400
91894.0500
91894.0600
91894.0700
91894.0800
91894.0900
91894.1000
91894.1100
PREY SET

FIGURE 19: Near bottom dissolved oxygen levels for prey deployment 3 (beginning 18 September 1994) based on 5 minute interval data.


PREDATION WINDOW
DISSOLVED OXYGEN (ml/l)
3
2.5
2
1.5
1
0.5
0
11:00
13:00
15:00
17:00
19:00
21:00
23:00
01:00
03:00
05:00
07:00
09:00
11:00
13:00
15:00
18 SEPT 94
19 SEPT 94
PREY
SET
PARTIAL
PREDATION

(14) Due to camera malfunction, there is no photographic record for this prey deployment. Predation evidence is based on diver observations. Fresh prey were set at 1655 (DO = 1.9 ml/l) on 19 September 1994 near the end of the hypoxic event. Predation occurred sometime between this moment and 1245 on 21 September 1994. Near-bottom dissolved oxygen concentrations during this prey deployment ranged from 0.9 to 3.8 ml/l and followed a semi-diurnal tidal cycle with high (normoxic) oxygen concentrations coinciding with the falling tide and low (hypoxic) oxygen concentrations coinciding with the rising tide (Figure 20).

(15) Prey were set at 1245 on 21 September 1994. Near-bottom dissolved oxygen concentrations ranged from 2.2 to 3.7 ml/l and remained normoxic for the duration of this prey deployment. The first clear photograph, taken at 2050 (DO = 3.4 ml/l), depicts undisturbed prey items on the monofilament line. At 2120, a blue crab was photographed preying upon tethered *Glycera*. In the next photograph, taken 30 minutes later at 2150, the crab was gone and five worms were removed from the monofilament line. The oxygen concentration during this "predation window" ranged from 3.3 to 3.8 ml/l. The remaining five worms remained undisturbed until sometime between 2250 (last clear photograph before gap in photographic record) and 0815 on 22 September 1994 (first photograph of empty monofilament line). During this predation window, oxygen ranged from 2.4 to 3.7 ml/l (Figure 21).

FIGURE 20: Near bottom dissolved oxygen levels for prey deployment 14 (beginning 19 September 1994) based on 5 minute interval data.

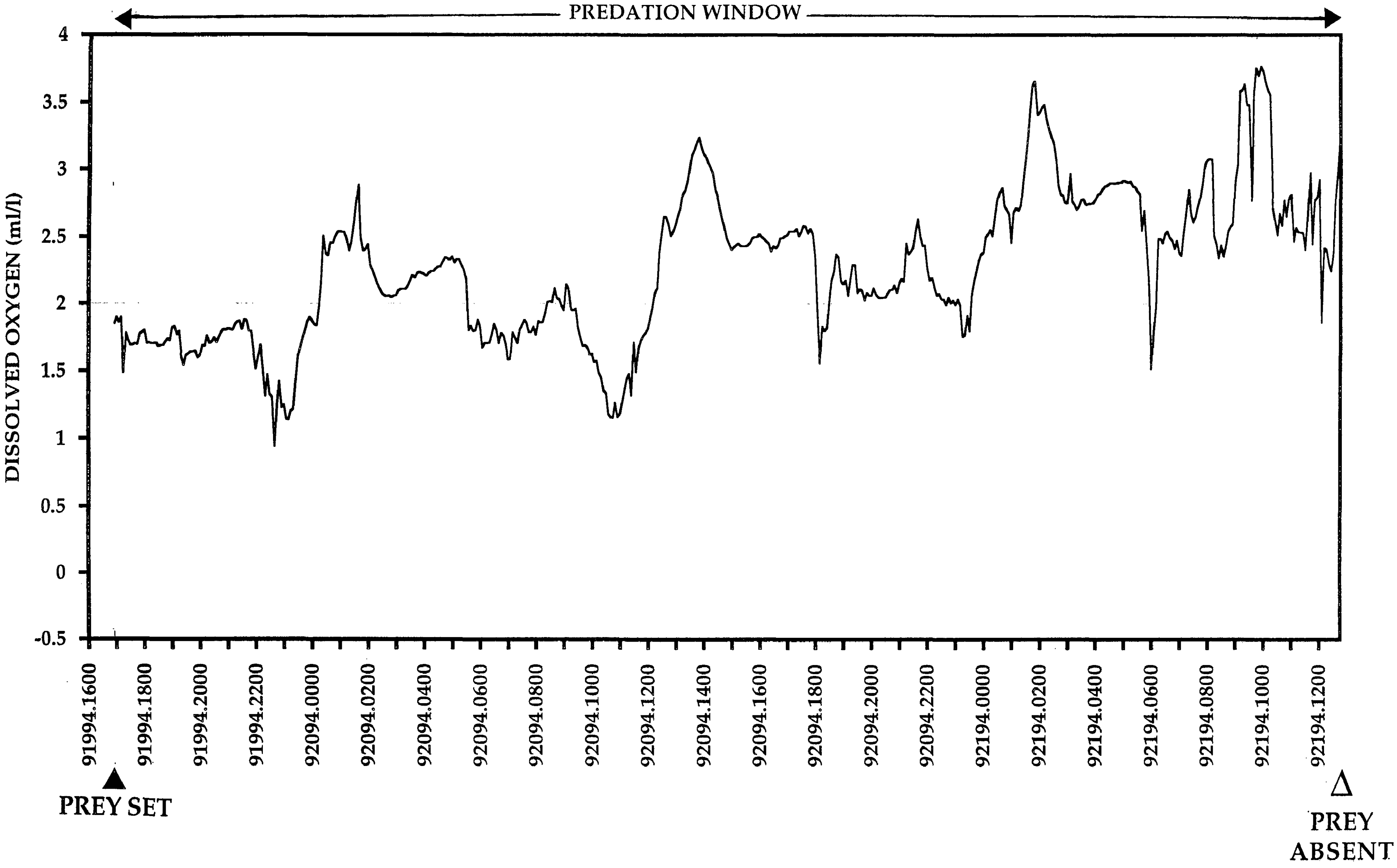
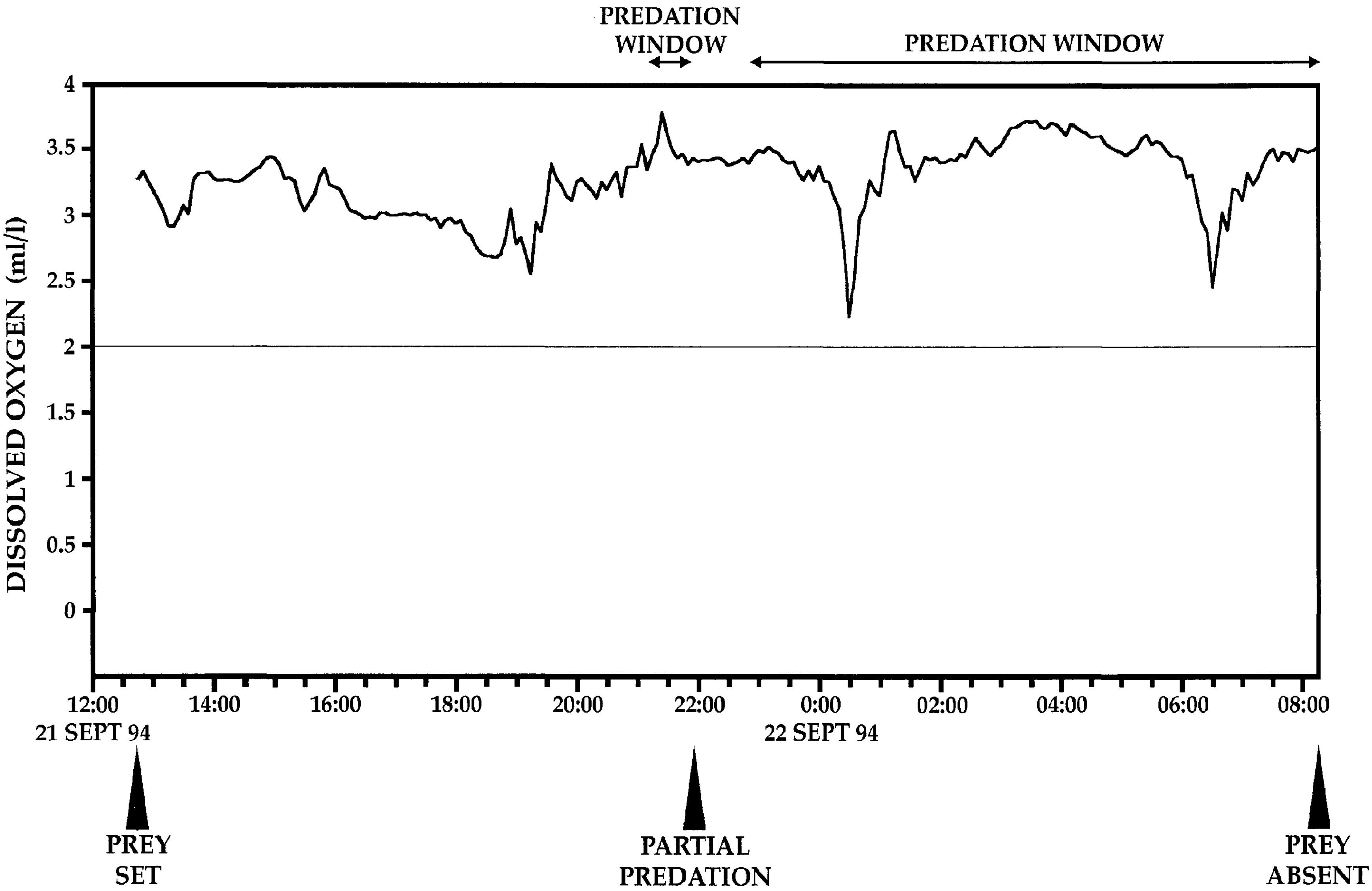

PREDATION WINDOW
DISSOLVED OXYGEN (ml/l)
4
3.5
3
2.5
2
1.5
1
0.5
0
-0.5
91994.1600
91994.1800
91994.2000
91994.2200
92094.0000
92094.0200
92094.0400
92094.0600
92094.0800
92094.1000
92094.1200
92094.1400
92094.1600
92094.1800
92094.2000
92094.2200
92194.0000
92194.0200
92194.0400
92194.0600
92194.0800
92194.1000
92194.1200
▲
PREY SET
Δ
PREY
ABSENT

FIGURE 21: Near bottom dissolved oxygen levels for prey deployment 15 (beginning 21 September 1994) based on 5 minute interval data.


PREDATION WINDOW
PREDATION WINDOW
DISSOLVED OXYGEN (ml/l)
4
3.5
3
2.5
2
1.5
1
0.5
0
12:00
21 SEPT 94
14:00
16:00
18:00
20:00
22:00
0:00
22 SEPT 94
02:00
04:00
06:00
08:00
PREY SET
PARTIAL PREDATION
PREY ABSENT

STATISTICAL ANALYSIS

The null hypothesis tested was that there is no difference in predation pressure regardless of the surrounding near-bottom dissolved oxygen concentration and that tethered prey items are just as likely to be preyed upon during hypoxia as they are during normoxia.

Diver observations were included to incorporate prey deployments for which there is no photographic record. The presence or absence of previously-set prey was noted by divers prior to each new prey deployment (for deployments with and without photographic records). Time of day of this observation was noted to obtain the corresponding environmental dissolved oxygen concentration from the water quality data. For instances of partial predation (i.e. 6 out of 10 worms were gone) the initial observation is considered "prey absent" and subsequent observations are considered "prey present" until the next indication of predation. Photographic and diver observations are categorized in the following cross-classification tables (Tables 1 and 2).

TABLE 1: Cross-classification of prey presence by dissolved oxygen concentration (2.0 ml/l categories).

n_{ij} = observed frequency
p_{ij} = joint probability expressed as a percent
$\Omega = n_{ij} / n$ = odds = relative risk
$\Theta = \Omega_1 / \Omega_2$ = odds ratio

	Prey Present (1+)	Prey Absent (2+)		Odds
< 2 ml/l (+1)	$n_{11} = 285$ $p_{11} = 58.28$	$n_{21} = 46$ $p_{21} = 9.41$		$\Omega_1 = p_{11}/p_{21}$ $\Omega_1 = 3.011$
> 2 ml/l (+2)	$n_{12} = 11$ $p_{12} = 2.25$	$n_{22} = 147$ $p_{22} = 30.06$		$\Omega_2 = p_{12}/p_{22}$ $\Omega_2 = 0.073$
			$n_{total} = 489$ $p_{total} = 100$	

$$\text{Standard Error}_{\Theta} = \Theta\ (\ 1/n_{11} + 1/n_{21} + 1/n_{12} + 1/n_{22}\ )^{0.5} = 14.857$$

$$\Theta = \Omega_1\ /\ \Omega_2 = 41.246 \pm 14.857$$

TABLE 2: Cross-classification of prey presence by dissolved oxygen concentration (1.5 ml/l categories).

n_{ij} = observed frequency
p_{ij} = joint probability expressed as a percent
$\Omega = n_{ij} / n$ = odds = relative risk
$\Theta = \Omega_1 / \Omega_2$ = odds ratio

	Prey Present (1+)	Prey Absent (2+)		Odds
<1.5 ml/l (+1)	$n_{11} = 253$ $p_{11} = 51.74$	$n_{21} = 24$ $p_{21} = 4.91$		$\Omega_1 = p_{11}/p_{21}$ $\Omega_1 = 10.551$
>1.5 ml/l (+2)	$n_{12} = 38$ $p_{12} = 7.77$	$n_{22} = 174$ $p_{22} = 35.58$		$\Omega_2 = p_{12}/p_{22}$ $\Omega_2 = 0.219$
			$n_{total} = 489$ $p_{total} = 100$	

$$\text{Standard Error}_{\Theta} = \Theta\ (\ 1/n_{11} + 1/n_{21} + 1/n_{12} + 1/n_{22}\ )^{0.5} = 13.427$$

$$\Theta = \Omega_1\ /\ \Omega_2 = 48.174 \pm 13.427$$

Based on the above figures, odds ratios were calculated to test the null hypothesis. Using the Fisher's Exact Test (SAS Institute 1992) the null hypothesis of independence can be rejected. Prey are 41.2 (± 14.9) times more likely to be present in when near-bottom dissolved oxygen concentration is <2 ml/l than when near bottom dissolved oxygen is >2 ml/l. Prey are 48.2 (±13.4) times more likely to be present when near-bottom dissolved oxygen concentration is < 1.5 ml/l than when near bottom dissolved oxygen is > 1.5 ml/l.

Near-bottom dissolved oxygen variability during each "predation window" and non-predation prey set are plotted in Figure 22. Based on mean dissolved oxygen levels for each predation and non-predation event, prey deployments were categorized into one of four dissolved oxygen concentration ranges. These ranges and corresponding proportional predation values and predicted probabilities are listed in Table 3.

FIGURE 22: Near-bottom dissolved oxygen variability during each "predation window" and non-predation prey set. Means (◆) and maximum/minimum ranges for near-bottom dissolved oxygen in York River for each occasion in which predation took place. Means are based on 5 minute interval data recorded from the last observation (photographic or diver) of undisturbed prey to the first observation (photographic or diver) of absent or partially predated prey. Means (◇) and maximum/minimum ranges for near-bottom dissolved oxygen are plotted for non-predation prey sets. Means are based on 5 minute interval data recorded from the moment of prey introduction to the moment of prey removal by divers. Horizontal axis represents dates on which the predation window or non-predation prey set began. Figure numbers in parentheses refer to the corresponding figure that details the prey set.

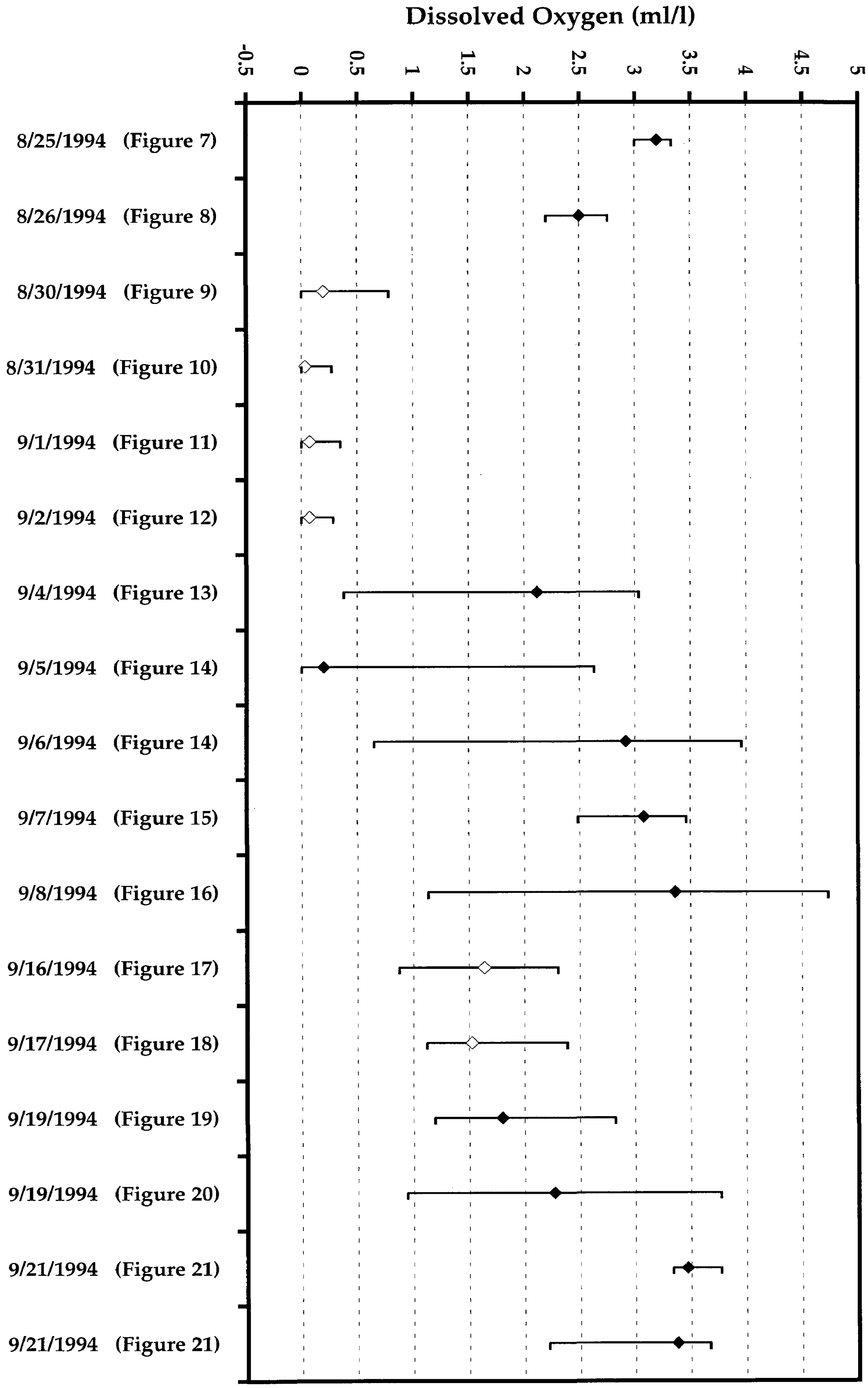

Dissolved Oxygen (ml/l)
-0.5
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
8/25/1994 (Figure 7)
8/26/1994 (Figure 8)
8/30/1994 (Figure 9)
8/31/1994 (Figure 10)
9/1/1994 (Figure 11)
9/2/1994 (Figure 12)
9/4/1994 (Figure 13)
9/5/1994 (Figure 14)
9/6/1994 (Figure 14)
9/7/1994 (Figure 15)
9/8/1994 (Figure 16)
9/16/1994 (Figure 17)
9/17/1994 (Figure 18)
9/19/1994 (Figure 19)
9/19/1994 (Figure 20)
9/21/1994 (Figure 21)
9/21/1994 (Figure 21)

Table 3: Categorized near-bottom dissolved oxygen ranges during each "predation window" and non-predation prey set and corresponding proportional predation values and predicted probabilities.

Dissolved Oxygen (ml/l)	Predation Events	Non-Predation Events	Proportional Predation	Proportional Non-Predation	Predicted Probability (Predation)	Predicted Probability (Non-Predation)
0 - 1	1	4	0.20	0.80	0.015	0.985
1 - 2	1	2	0.33	0.67	0.124	0.876
2 - 3	4	0	1.00	0.00	0.572	0.428
3 - 4	5	0	1.00	0.00	0.926	0.074

These data indicate a predation threshold somewhere between the 0-1 and 1-2 ml/l categories. Logistic regression (SAS Institute 1992) was used to describe the relationship between dissolved oxygen concentration and predation (Figure 23).

The logistic function (-2 Log Likelihood = 11.6) was:

$$p = \frac{e^{(-4.1945 + 2.2419\ (DO))}}{1 + e^{(-4.1945 + 2.2419\ (DO))}}$$

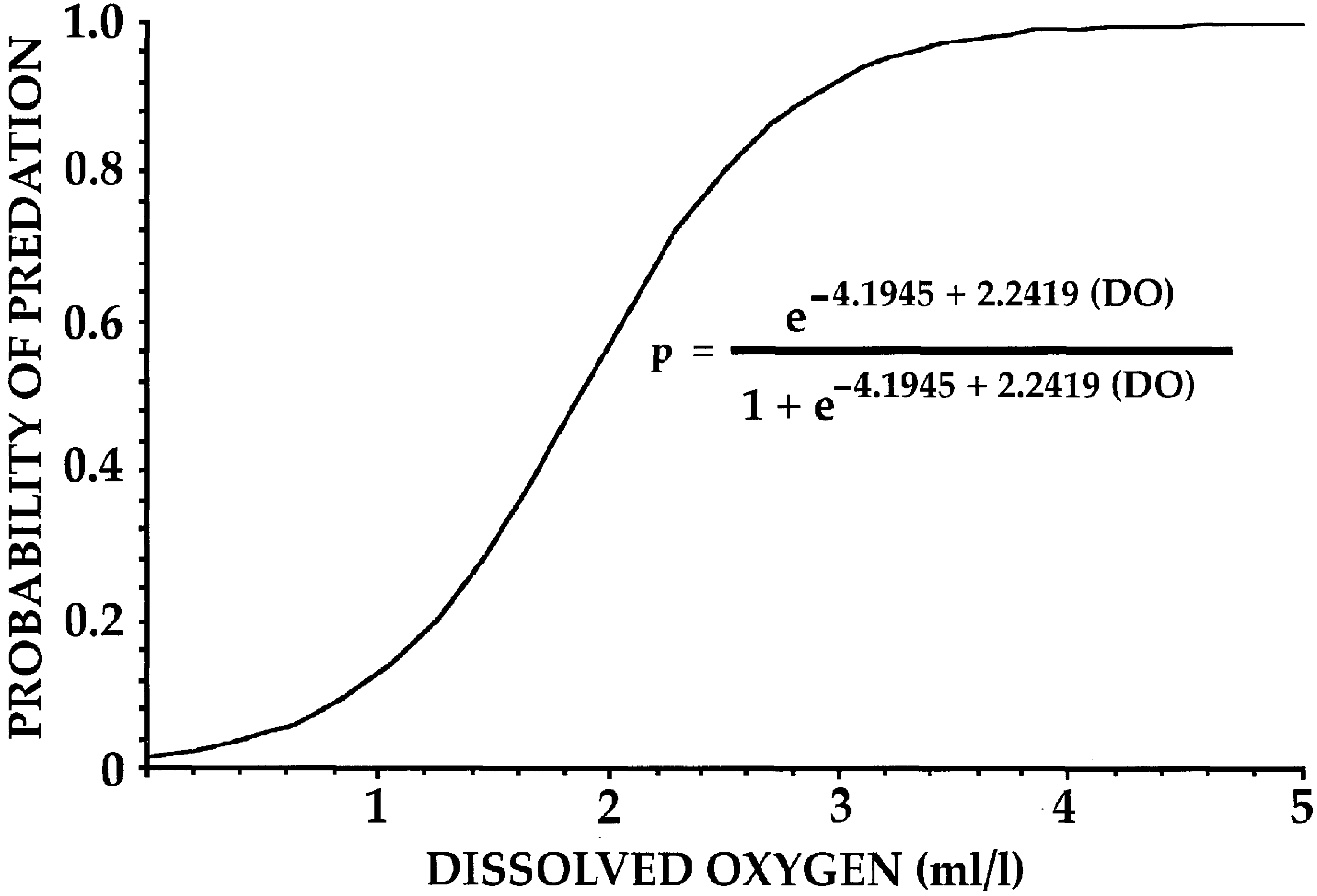
where: p is the probability of predation,

(DO) is the dissolved oxygen concentration,

$\mathbf{e^{-4.1945 + 2.2419\ (DO)}}$ is the logistic regression equation.

Following a hypoxic event, but before infaunal recovery, the chances of predation of hypoxic-stressed infauna by nektonic predators increases asymptotically with increasing dissolved oxygen concentration. The dissolved oxygen concentration at $p_{0.5}$ is 1.87 ml/l. At this dissolved oxygen concentration, the is a 50% chance that emerged benthic infauna will be preyed upon by nektonic predators.

FIGURE 23: Logistic regression curve used to describe relationship between dissolved oxygen and predation.



$$p = \frac{e^{-4.1945 + 2.2419\,(DO)}}{1 + e^{-4.1945 + 2.2419\,(DO)}}$$

DISCUSSION

Many estuarine systems around the world experience seasonally mild to severe hypoxia or anoxia (Whitledge 1985, Diaz & Rosenberg 1995). These low dissolved oxygen conditions in bottom waters are a contributing factor in the major reduction of living resources of many estuarine and coastal systems (Harper *et al.* 1981, Baden *et al.* 1990, Desprez *et al.* 1992). Despite the disparate nature of physical conditions and faunal composition, the responses of benthic community structure to seasonal hypoxia were found to be consistent between ecosystems and depend on the frequency and duration of the hypoxia (Diaz & Rosenberg 1995). The basic behavioral modifications benthic infauna use to survive oxygen deficiency potentially enhance their vulnerability to predators (Diaz *et al.* 1992). Nektonic predator species are not immune to low dissolved oxygen concentrations and respond mainly through avoidance of affected areas (Breitburg 1992, Pihl *et al.* 1991). The dissipation of hypoxia, however, may lead to an opportunistic response by predators to increased availability of hypoxia-stressed prey.

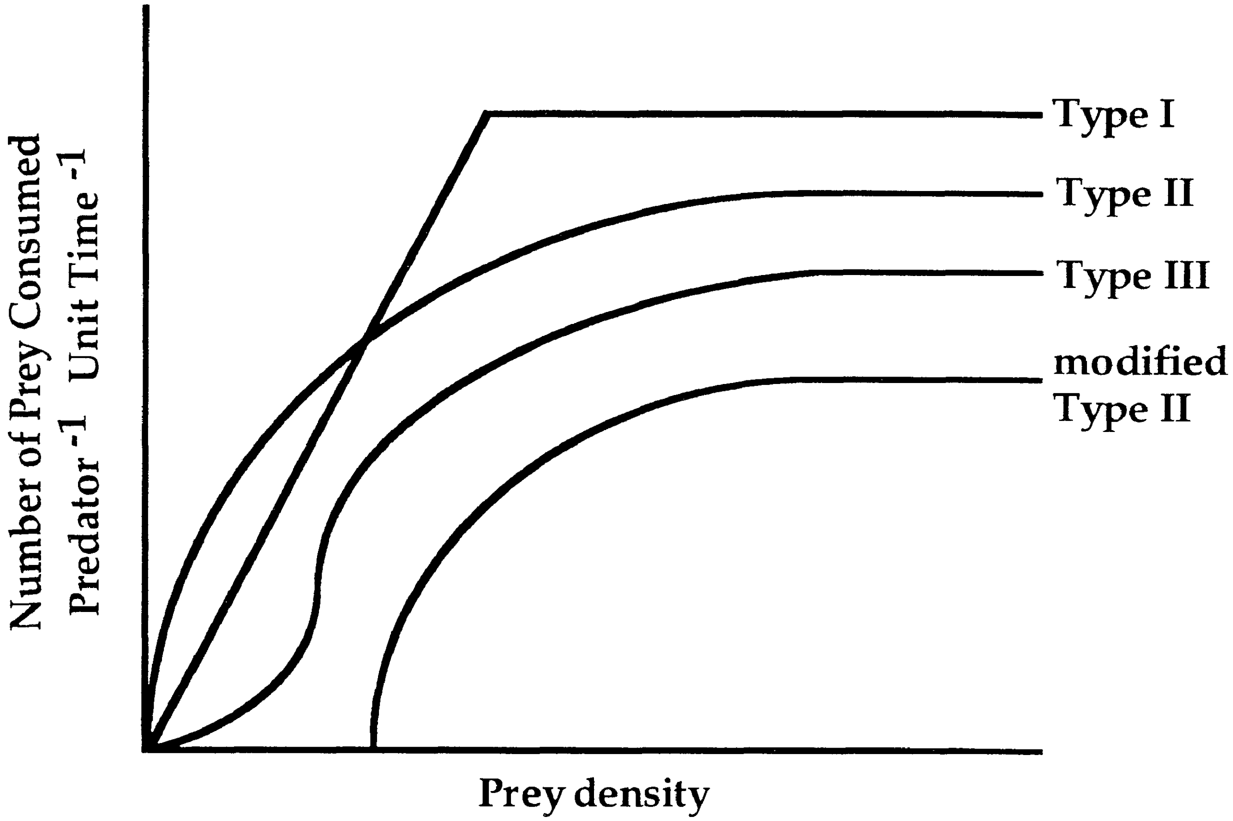
Fluctuating hypoxia and normoxia facilitate the transfer of benthic secondary production to mobile predator species. This study suggests that predators are likely to take advantage of hypoxia-stressed infaunal organisms once environmental dissolved oxygen concentrations rise above 1.5 ml/l (Figure 22). If all prey deployments are included in this analysis, there is no clear separation between the dissolved oxygen concentrations in which predation occurs and does not occur. By removing those prey deployments that have large oxygen variations within the "predation window" and those with few observations over a long time frame, there is an apparent separation around 1.5 ml/l such that predation does not occur below, but does occur above, this level (Figure 23). Since predation does not occur when dissolved oxygen concentrations are consistently below 1.5 ml/l, the functional response of the predator to increased prey availability is interrupted.

The functional response is a relationship between prey consumption per predator and prey density (Holling 1959, Hassell 1978). There are three general types of functional response curves used to describe predator-prey dynamics (Figure 24) (Hassell 1978, Valiela 1984). The type I response curve rises linearly to a plateau (representing predator gut capacity and handling time) and is typical of aquatic filter-feeding invertebrates (Hassell 1978). Predators consume a linearly-increasing number of prey as density increases until a satiation point is reached (Valiela 1984). In the type II response, which is most common and typical of many invertebrates, prey consumption increases at a decelerating rate as prey density increases (Hassell 1978, Lipcius & Hines 1986). This curve rises at a continually decreasing rate to an upper asymptote which represents the predator's maximum attack rate (Hassell 1978). In the density-dependent 'modified' type II functional response, consumption ceases below some low prey density threshold because of behavioral or environmental characteristics that prevent predators from finding prey (Valiela 1984). The type III response curve, typical of vertebrate and arthropod predators and parasitoids and functionally the same as the 'modified' type ii response, is sigmoid (Holling 1959, Hassell *et al.* 1977). This functional response shows an initial lag in the response of the predator at low prey densities (Ricklefs 1973, Eggleston 1990a). As the prey density increases, encounter rate increases, and the functional response increases more rapidly. At high prey densities, predator satiation and the reduction of required searching time cause the functional response to level off (Ricklefs 1973).

FIGURE 24: Hypothetical functional response curves. The height of the asymptote is not an important consideration.

The point at which the modified Type II curve crosses the horizontal axis is the threshold density below which no feeding takes place.

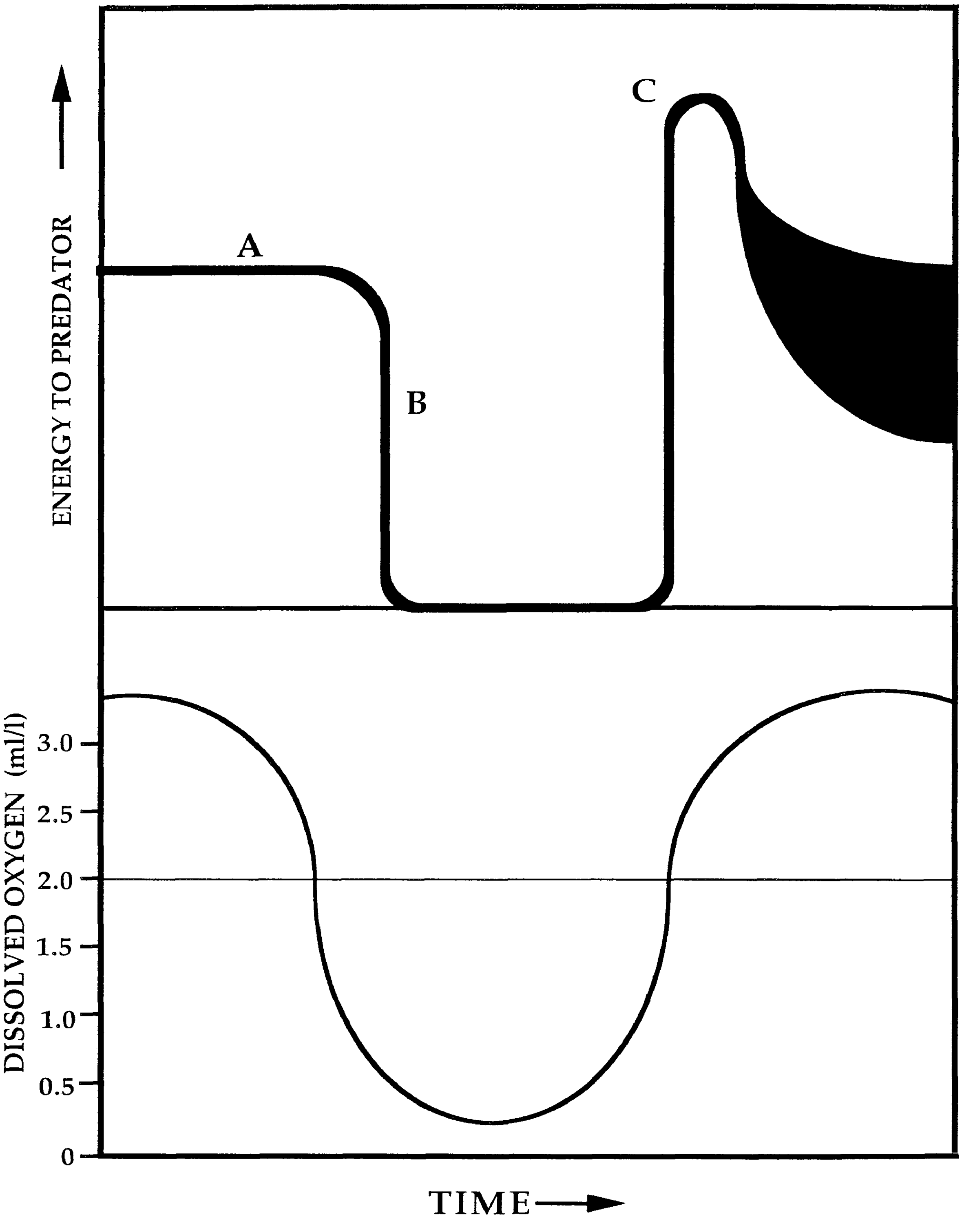
Adapted from Valiela (1984).


Type I
Type II
Type III
modified
Type II
Number of Prey Consumed
Predator $^{-1}$ Unit Time $^{-1}$
Prey density

The form of the functional response varies with different predator-prey combinations and physical environmental conditions (Lipcius & Hines 1986, Eggleston 1990a). For example, Lipcius and Hines (1986) found that sediment type modified the functional response of blue crabs preying on the clam *Mya arenaria*. Blue crabs exhibited a density-dependent type III functional response in sand and a density-independent type II response in mud. Eggleston (1990 b) found that the functional response of blue crabs preying on juvenile oysters *Crassostrea virginica* varied significantly in type and intensity as a function of temperature. Crabs displayed a 'modified' type II density-dependent functional response at low temperatures (13-14 °C), a type III density-dependent response at intermediate temperatures (19-20 °C), and a type II inversely density-dependent response at high temperatures (26-27 °C). The possibility exists that a predator's functional response may be modified by hypoxia. At low dissolved oxygen concentrations, if the encounter rate with prey is enhanced, then predator feeding thresholds may be lowered substantially such that there is a loss of the low-density refuge for the prey (Lipcius, personal communication). Conversely, if there is a loss of feeding efficiency for the predators due to low dissolved oxygen concentrations, then the threshold may be increased for the prey.

Based on these functional response models, one would expect that an increase in available prey density would lead to a general increase in prey consumption (Valiela 1984, Eggleston 1990a). However, the results of this study suggest that, although densities of available prey are enhanced, the entire functional response is interrupted during hypoxia (Figure 25). Under normoxic conditions the transfer of energy to predators can be characterized by one of the functional response models, with the time interval prior to hypoxia representing a steady net energy transfer level (Figure 25A). When

FIGURE 25: Hypothetical variations in energy transfer to predators in response to declining and increasing environmental dissolved oxygen concentrations. See text for further explanation.


ENERGY TO PREDATOR
A
B
C
D
E
DISSOLVED OXYGEN (ml/l)
3.0
2.5
2.0
1.5
1.0
0.5
0
TIME

dissolved oxygen concentrations drop below approximately 2.0 ml/l, predators escape low oxygen areas (Diaz & Rosenberg 1995). Predation begins to decline when dissolved oxygen concentrations drop below 2 ml/l and ceases somewhere between 1.0 and 2.0 ml/l (Figure 25B). When oxygen concentrations become tolerable to predator species, predators quickly move back into the affected areas and there may be an initial increase in the amount of energy gain from predation on oxygen-stressed macrobenthos. Hypoxia induced behavioral and physiological stress on these prey species potentially makes them more vulnerable to predation and available at higher densities (Figure 25C). The predators ability to avoid hypoxic areas eliminates any recovery time from oxygen stress before they can commence feeding. The predators are able to move into affected areas as soon as oxygen levels are tolerable and take advantage of the increased prey availability before the prey organisms recover and reburrow in the sediment.

With recovery and reburrowing of prey organisms over time, the elevated level of energy transfer to predators declines to the pre-hypoxic condition and the functional response may return to its pre-hypoxic state (Figure 25D). If significant numbers of prey are removed, either by predators or hypoxia-induced mortality, the functional response may be altered and the energy transfer to the predators will be further reduced below pre-hypoxic levels (Figure 25E). The level of reduction will be a function of the production capacity of the prey and needs further study.

LITERATURE CITED

Astall, C.M. and M.B. Jones. 1991. Respiration and biometry in the sea cucumber *Holothuria forskali* . Journal of the Marine Biological Association of the United Kingdom 71:73-81.

Baden, S.P., L. Loo, L. Pihl, and R. Rosenberg. 1990. Effects of eutrophication on benthic communities including fish: Swedish west coast. Ambio 19:113-122.

Baird, D. and R.E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay Ecosystem. Ecological Monographs 59:329-364.

Breitburg, D.L. 1990. Near-shore hypoxia in the Chesapeake Bay: patterns and relationships among physical factors. Estuarine and Coastal Shelf Science 30:593-609.

Breitburg, D.L. 1992. Episodic hypoxia in Chesapeake Bay: interacting effects of recruitment, behavior, and physical disturbance. Ecological Monographs 62:525-546.

Colt, J. 1984. Computation of dissolved gas concentrations in water as functions of temperature, salinity, and pressure. American Fisheries Society Special Publication 14.

Desprez, M., H. Rybarczyk, J.G. Wilson, J.P. Ducrotoy, F. Sueur, R. Olivesi, B. Elkaim. 1992. Biological impact of eutrophication in the Bay of Somme and the induction and impact of anoxia. Netherlands Journal of Sea Research. 30:149-159.

Diaz, R.J., R.J. Neubauer, L.C. Schaffner, L. Pihl, and S.P. Baden. 1992. Continuous monitoring of dissolved oxygen in an estuary experiencing periodic hypoxia and the effect of hypoxia on macrobenthos and fish. Pages 1055-1068 *In:* Science of the Total Environment. Elsevier Science Publishers B.V., Amsterdam.

Diaz, R.J. and R. Rosenberg. 1995. Marine benthic hypoxia: review of ecological effects and behavioural responses on benthic macrofauna. Oceanography and Marine Biology Annual Review 33:245-303.

Diaz, R.J. and L.C. Schaffner. 1990. The functional role of estuarine benthos. Pages 25-56 *In:* M. Haire and E. Krome (eds.). Perspectives on the Chesapeake Bay, 1990. Chesapeake Bay Program Publ. No. CBP/TRS41/90.

Eggleston, D.B. 1990a. Foraging behavior of the blue crab, *Callinectes sapidus,* on juvenile oysters, *Crassostrea virginica*: effects of prey density and size. Bulletin of Marine Science 46:62-82.

Eggleston, D.B. 1990b. Behaviuoral mechanisms underlying variable functional responses of blue crabs, *Callinectes sapidus* feeding on juvenile oysters, *Crassostrea virginica.* Journal of animal Ecology 59:615-630.

Gaston, G.R. 1985. Effects of hypoxia on macrobenthos of the inner shelf off Cameron, Louisiana. Estuarine and Coastal Shelf Science 20:603-613.

Graf, G. 1987. Benthic energy flow during a simulated autumn bloom sedimentation. Marine Ecology Progress Series 39:23-29.

Graf, G., R. Schulz, R. Peinert, L.-A. Meyer-Reil. 1983. Benthic response to sedimentation events during autumn to spring at a shallow-water system in the Western Kiel Bight. Marine Biology 77:235-246.

Haas, L.W. 1977. The effect of the spring-neap tidal cycle on the vertical salinity structure of the James, York, and Rappahannock Rivers, Virginia, USA. Estuarine and Coastal Shelf Science 5:485-496.

Harper, D.E., L.D. McKinney, R.B. Salzer, and R.J. Case. 1981. The occurence of hypoxic bottom water off the upper Texas coast and its effects on the benthic biota. Contributions in Marine Science of the University of Texas 24:53-79.

Hassell, M.P. 1978. The dynamics of arthropod predator-prey systems. Monographs in Population Biology 13.

Hassell, M.P., J.H. Lawton, and J.R. Beddington. 1977. Sigmoid functional responses by invertebrate predators and parasitoids. Journal of Animal Ecology 46:249-262.

Holeton, G.F. 1979. Oxygen as an environmental factor of fishes. Pages 7-32 *In:* M.A. Ali (ed). Environmental Physiology of Fishes. Plenum Press, New York, USA.

Holland, A.F. 1985. Long-term variation of macrobenthos in a mesohaline region of Chesapeake Bay. Estuaries 8:93-113.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91:385-398.

Jonas, R.B. 1987. Chesapeake Bay dissolved oxygen dynamics: roles of phytoplankton and microheterotrophs. Pages 75-80 *In:* G.B. Mackiernan (ed). Dissolved Oxygen in the Chesapeake Bay: Processes and effects. Proceedings of a seminar on hypoxic and related processes in Chesapeake Bay. UM-SG-TS-87-03. Maryland Sea Grant College Publication. College Park, Maryland, USA.

Jørgensen, B.B. 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. OIKOS 34:68-76.

Karr, J.R. and K.E. Freemark. 1985. Disturbance and vertebrates: an integrative perspective. Pages 153-168 *In:* S.T.A. Pickett and P.S. White (eds). The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, Florida, USA.

Kolar, C.S. and F.J. Rahel. 1993. Interaction of a biotic factor (predator presence) and an abiotic factor (low oxygen) as an influence on benthic invertebrate communities. Oecologia 95:210-219.

Kramer, D.L. 1987. Dissolved oxygen and fish behavior. Environmental Biology of Fishes 18:81-92.

Kramer, D.L. and M. McClure. 1982. Aquatic surface respiration, a widespread adaptation to hypoxia in tropical freshwater fishes. Environmental Biology of Fishes 7:47-55.

Kuo, A.Y. and B.J. Neilson. 1987. Hypoxia and salinity in Virginia estuaries. Estuaries 10:277-283.

Kuo, A.Y. and K. Park. 1993. Transport of hypoxic waters: an estuary-subestuary exchange. Pages 599-615 *In*: D. Prandle (ed.) Dynamics and Exchanges in Estuaries and the Coastal Zone. American Geological Union, Washington, D.C.

Lipcius, R.N. and A.H. Hines. 1986. Variable functional response of a marine predator in dissimilar homogeneous microhabitats. Ecology 67:1361-1371.

Llansó, R.J. 1991. Tolerance of low dissolved oxygen and hydrogen sulfide by the polychaete *Streblospio benedicti* (Webster). Journal of Experimental Marine Biology and Ecology 153:165-178.

Llansó, R.J. 1992. Effects of hypoxia on estuarine benthos of the lower Rappahannock River (Chesapeake Bay), a case study. Estuarine and Coastal Shelf Science 35:491-515.

Loesch, H. 1960. Sporadic mass shoreward migrations of demersal fish and crustaceans in Mobile Bay, Alabama. Ecology 41:292-298.

Malone, T.C. 1992. Effects of water column processes on dissolved oxygen: nutrients, phytoplankton and zooplankton. Pages 61-112 *In:* D. Smith, M. Leffler, and G. Mackiernan (eds). Oxygen dynamics in the Chesapeake Bay: a synthesis of recent research. Maryland Sea Grant College Publication, College Park, Maryland, USA.

May, E.B. 1973. Extensive oxygen depletion in Mobile Bay, Alabama. Limnology and Oceanography 18:353-366.

National Ocean Survey. 1993. Tidal Current Tables 1994, Atlantic Coast of North America. National Oceanic and Atmospheric Administration (NOAA), U.S. Department of Commerce. 201 pp.

Officer, C.B., R.B. Biggs, J.L. Taft, L.E. Cronin, M.A. Tyler, W.R. Boynton. 1984. Chesapeake Bay anoxia: Origin, development, and significance. Science 223:22-27.

Pavela, J.S., J.L. Ross, M.E. Chittenden. 1983. Sharp reductions in abundance of fishes and benthic macroinvertebrates in the Gulf of Mexico off Texas associated with hypoxia. Northeast Gulf Science 6:167-173.

Pearson, T.H. and R. Rosenberg. 1992. Energy flow through the SE Kattegat: a comparative examination of the eutrophication of a coastal marine ecosystem. Netherlands Journal of Sea Research 28:317-34.

Pihl, L. 1994. Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden. Canadian Journal of Fisheries and Aquatic Science 51:321-336.

Pihl, L., S.P. Baden, and R.J. Diaz. 1991. Effects of periodic hypoxia on the distribution of demersal fish and crustaceans. Marine Biology 108:349-360.

Pihl, L., S. Baden, R. Diaz, and L. Schaffner. 1992. Hypoxia-induced structural changes in the diet of bottom feeding fish and Crustacea. Marine Biology 112:349-361.

Rabalis, N.N., R.E. Turner, W.J. Wiseman Jr., and D.B. Bosch. 1991. A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985-1988. Pages 35-47 *In*: R.V. Tyson and T.H. Pearson (eds.). Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. 58, The Geological Society, London.

Rabalis, N.N., W. J. Wiseman, Jr., and R.E. Turner. 1994. Comparison of continuous records of near-bottom dissolved oxygen from the hypoxia zone along the Louisiana coast. Estuaries. 17:850-861.

Rahel, F.J. and C.S. Kolar. 1990. Trade-offs in the response of mayflies to low oxygen and fish predation. Oecologia 84:39-44.

Rahel, F.J. and J.W. Nutzman. 1994. Foraging in a lethal environment: fish predation in hypoxic waters of a stratified lake. Ecology 75:1246-1253.

Rainer, S.F. and R.C. Fitzhardinge. 1981. Benthic communities in an estuary with periodic deoxygenation. Australian Journal of Marine and Freshwater Research 32:227-243.

Richards, F.A. 1965. Anoxic basins and fjords. pages 611-645 *In*: J.P. Riley and G. Skirrow (eds.) Chemical Oceanography, Academic Press, New York.

Ricklefs, R.E. 1973. Ecology. Chiron Press, Newton, Massachusetts.

Rosenberg, R. 1980. Effect of oxygen deficiency on benthic macrofauna in fjords. Pages 499-514 *In*: H.J. Freeland, D.M. Farmer, and C.D. Levings (eds.). Fjord Oceanography. Plenum Publishing Corp., New York, USA.

Rosenberg, R. and L. Loo. 1988. Marine eutrophication induced oxygen deficiency: Effects on soft bottom fauna, Western Sweden. Ophilia 29:213-225.

Sandberg, E. 1994. Does short-term oxygen depletion affect predator-prey relationships in zoobenthos? Experiments with the isopod *Saduria entomon*. Marine Ecology Progress Series 103:73-80.

SAS Institute, Inc. 1992. Cary, NC.

Seliger, H.H., J.A. Boggs, W.H. Biggley. 1985. Catastrophic anoxia in the Chesapeake Bay in 1984. Science 228:70-73.

Smith, K.L. 1987. Food energy supply and demand: a discrepancy between particulate organic carbon flux and sediment community oxygen consumption in the deep ocean. Limnology and Oceanography 32:201-220.

Stachowitsch, M. 1984. Mass mortality in the Gulf of Treiste: the course of community destruction. P.S.Z.N.I: Marine Ecology 5:243-264.

Suthers, I.M. and J.H. Gee. 1986. Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. Canadian Journal of Aquatic Science 43:1562-1570.

Swanson, R.L. and C.A. Parker. 1988. Physical environmental factors contributing to recurring hypoxia in the New York Bight. Transactions of the American Fisheries Society 117:37-47.

Taft, J.L., E.O. Hartwig, and R. Loftus. 1980. Seasonal oxygen depletion in Chesapeake Bay. Estuaries 3:242-247.

Tenore, K.R. 1972. Macrobenthos of Pamlico River Estuary, North Carolina. Ecological Monographs 42:51-69.

Tyson, R.V. and T.H. Pearson. 1991. Modern and ancient continental shelf anoxia: an overview. Pages 1-24 *In:* R.V. Tyson & T.H. Pearson (eds). Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. 58, The Geological Society, London.

Valiela, I. 1984. Marine Ecological Processes. Springer-Verlag, New York.

Vecchione, M. 1991. Dissolved oxygen and the distribution of the euryhaline squid *Lolliguncula brevis*. Bulletin of Marine Science 49:668-669.

Vecchione, M. and C.F.E. Roper. 1991. Cephalopods observed from submersibles in the western North Atlantic. Bulletin of Marine Science 49:433-445.

Weigelt, M. 1991. Short- and long-term changes in the benthic community of the deeper parts of Kiel Bay (western Baltic) due to oxygen depletion and eutrophication. Meeresforschung 33:197-224.

Welsh, B.L. and F.C. Eller. 1991. mechanisms controlling summertime oxygen depletion in western Long Island Sound. Estuaries 14:265-278.

Wetzel, R.G. 1983. Limnology. Saunders, Philadelphia, Pennsylvania, USA.

Whitledge, T.E. 1985. Nationwide review of oxygen depletion and eutrophication in estuarine and coastal waters. National Oceanic and Atmospheric Administration Informal Report, BNL 37144. Rockville, Maryland, USA.

VITA

Janet Andrea Nestlerode

Born at Fort Belvior, Virginia on October 4, 1969. Graduated from T. A. Edison High School, Alexandria, Virginia in 1987. Earned a B.S. degree in Biology from Mary Washington College, Fredericksburg, Virginia in 1991. Entered the Masters program at the College of William and Mary, School of Marine Science in August 1992.