

GEOGRAPHICAL DIFFERENCES IN BEHAVIORAL RESPONSES TO HYPOXIA: LOCAL ADAPTATION TO AN ANTHROPOGENIC STRESSOR?

MARY BETH DECKER,^{1,2,4} DENISE L. BREITBURG,² AND NANCY H. MARCUS³

¹Horn Point Laboratory, University of Maryland Center for Environmental Science, Cambridge, Maryland 21613-0775 USA

²The Academy of Natural Sciences, Estuarine Research Center 10545 Mackall Road, St. Leonard, Maryland 20685 USA

³Department of Oceanography, Florida State University, Tallahassee, Florida 32306 USA

Abstract. Stressors resulting from, or exacerbated by, human activities increasingly alter ecological systems. Behavioral responses that enhance survival of stressed individuals may be critical for local populations to persist. Although the types and intensities of stressors can vary over the geographic range of a species, little is known regarding geographical variation in adaptive behavioral responses to stressors, especially in marine and estuarine species subject to human impact. To explore varied behavior in response to low dissolved oxygen (a human perturbation), we examined two geographically distinct populations of the copepod, *Acartia tonsa*. Chesapeake Bay copepods, historically exposed to oxygen gradients, avoided hypoxic bottom waters. In contrast, Florida copepods not typically exposed to hypoxia did not avoid lethal oxygen concentrations. Our results suggest that local behavioral adaptations may result from consequences of anthropogenic perturbations and may limit the ability to apply biological data across regions. Geographical differences in behavioral responses of important prey species may also result in geographic variation in the severity of disruption of aquatic food webs.

Key words: *Acartia tonsa*; behavioral adaptation; Chesapeake Bay; copepods; eutrophication; Florida; hypoxia; oxygen, low; stressor; vertical distribution; zooplankton.

INTRODUCTION

A species can occur widely in time and space such that individuals from different portions of the species' range can encounter different intensities and arrays of stressors (i.e., factors that perturb a system from its normal functioning [Auerbach 1981]). Environmental stressors, both natural and anthropogenic, can lead to sharp declines in population sizes (Glynn 1988, Hoffman and Parsons 1991). Because of their effects on fitness, stressful conditions potentially promote local adaptation and divergence among populations of the same species. For example, rapid morphological changes within bird populations have occurred due to extreme climatic stresses (Grant and Grant 1989, Brown and Brown 1998), and life-history changes within fish populations have resulted from predation pressure (Reznick and Endler 1982, Reznick et al. 1990).

Much less is known about how populations respond to selection resulting from anthropogenic stressors, although some examples exist, such as the evolution of pesticide and heavy metal resistance (Macnair 1993, McKenzie and Batterham 1994). Although behavioral responses to stressors have been observed in aquatic animals (Akberali and Black 1980, Akberali et al. 1981,

Renaud 1986, Spoor 1990, Breitbart 1994), to our knowledge, differences among populations in the ability to avoid an anthropogenic stressor have not been documented in marine and estuarine systems. The potential for local behavioral adaptation to stressful conditions may determine whether a population persists in an area altered by human activities.

Hypoxia is an increasingly widespread consequence of anthropogenic nutrient loading in stratified coastal waters (Diaz and Rosenberg 1995). We examined the possibility that zooplankton populations historically exposed to hypoxia have a genetically based behavioral response to hypoxia that potentially reduces mortality, whereas populations that have not evolved in the presence of hypoxia lack such a response and therefore may be more vulnerable to hypoxia. Because local adaptation may result in behavioral differences among populations, it is also important to determine whether biological results obtained from only a single locality can be broadly applied to other regions.

Acartia tonsa is a calanoid copepod that occurs throughout the coastal and estuarine waters of the western Atlantic, Indopacific, and coastal European waters (Brylinski 1981, Raymond 1983). Habitat varies greatly within the range of this species. *Acartia tonsa* can tolerate temperatures ranging from -1° to 32°C (Gonzalez 1974) and is commonly found in salinities ranging from 5 to 33 on the Practical Salinity Scale (Brylinski 1981, Cervetto et al. 1999). Some estuaries in which *A. tonsa* occurs experience seasonal hypoxia (i.e., bottom water

Manuscript received 5 October 2001; revised 1 October 2002; accepted 31 October 2002; Corresponding Editor: J. E. McDowell.

⁴ Present address: Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520 USA. E-mail: marybeth.decker@yale.edu

dissolved oxygen <2.0 mg/L) due to density stratification, high nutrient loadings, and resultant microbial respiration. The generation time of *A. tonsa* is 7–9 d at 22–25°C (Heinle 1966); thus, adaptive changes arising from natural selection are likely to occur over short periods of time.

The Chesapeake Bay, including its major tributaries (e.g., the Patuxent River), is a partially mixed estuary in which strong thermohaline stratification develops in late spring and summer. In many areas of the Chesapeake system, waters below the pycnocline are hypoxic or anoxic for periods of days to months (Taft et al. 1980, Sanford et al. 1990). Historically, the Chesapeake Bay system has experienced periods of seasonal hypoxia that were probably related to its strong density stratification and relatively long flushing time (Cooper and Brush 1993). However, anthropogenic nutrient loading and deforestation are thought to have increased the extent and severity of oxygen depletion in this area since European colonization, and especially during the period from the 1930s or 1940s to the present (Cooper and Brush 1993, Karlson et al. 2000, Zimmerman and Canuel 2000). Hypoxia has been a regularly occurring stress to the Chesapeake Bay population of *A. tonsa* during the last 50–250 yr.

In contrast, the waters along the coast of the northeastern Gulf of Mexico between Apalachicola and Apalachee Bay, Florida, are very shallow and presumably well mixed. Hypoxia events are rare and localized, primarily restricted to the upper portions of estuaries (Engle et al. 1999, Livingston 2001; R. J. Livingston, unpublished data). Thus, it is unlikely that exposure to extensive and regularly occurring hypoxia has been a major feature of the evolutionary history of the coastal Floridian *A. tonsa* population.

Seemingly contradictory results of previous studies indicated the potential for geographic variation in behavioral responses to low dissolved oxygen. The tolerance of *Acartia tonsa* to low oxygen concentrations is similar over a large geographical range with LC₅₀ estimates ranging from 0.95 to 1.4 mg/L (Roman et al. 1993, Stalder and Marcus 1997). In the Chesapeake Bay, *A. tonsa* is rare in subpycnocline waters when the bottom dissolved oxygen concentrations are below 2 mg/L (Roman et al. 1993, Keister et al. 2000). (The pycnocline is the water layer in which density changes most rapidly with depth.) This spatial pattern is suggestive of avoidance of hypoxic waters; however, many factors may covary with dissolved oxygen. These include physical forcing (Haury et al. 1983, Vermeer et al. 1987, Franks 1992), prey availability (Dagg et al. 1997, Groenkjaer and Wieland 1997), and presence of predators (Bollens and Frost 1991, Atkinson et al. 1999), all of which can affect vertical distributions of zooplankton in the field. Furthermore, Stalder and Marcus (1997) found that *A. tonsa* collected from waters off of the north Florida Gulf Coast do not avoid lethal concentrations of dissolved oxygen in the bottom wa-

ters of a stratified water column in the laboratory. Mortality during experiments resulted from animals entering and remaining in the severely hypoxic layer. Our experiments were designed to determine the potential for *A. tonsa* from a system historically exposed to low oxygen (Chesapeake Bay) to manifest different behavioral responses to a stratified and hypoxic system compared with *A. tonsa* from an area not characterized by extensive hypoxia (the northern Gulf Coast of Florida).

METHODS

We compared the ability of field-collected Chesapeake Bay and northern Gulf Coast of Florida *A. tonsa* populations to avoid hypoxic bottom water in an experimental water column. To determine whether the response of the Chesapeake Bay *A. tonsa* to low dissolved oxygen was an innate or learned behavior, we also compared the behavioral response to a hypoxic bottom layer of field-collected Chesapeake Bay copepods to that of Chesapeake Bay copepods raised in the laboratory. We conducted experiments during September and October 2000 on three different groups of *A. tonsa*: field-collected copepods from a subestuary of Chesapeake Bay (the Patuxent River), Maryland, USA (38°21.4' N, 76°30.5' W; Fig. 1), field-collected copepods from Turkey Point, Florida, USA (29°51' N, 84°31' W), and Chesapeake Bay copepods reared for one generation in the laboratory. The purpose of testing laboratory-raised copepods was to ensure that the observed behavioral responses to hypoxia were truly innate behaviors. Since one generation is not sufficient time for major genetic changes to occur, examination of lab-reared animals would eliminate the possibility that the copepods' responses to low dissolved oxygen were "learned," (i.e., that they became acclimated to hypoxic conditions in the field).

Patuxent River zooplankton were collected with a 202- μ m net and were held overnight in 11-L aquaria prior to behavioral observations. Animals from Turkey Point, Florida, were collected with a 243- μ m net and shipped overnight delivery to Maryland on the day after they were collected and then held in 11-L aquaria. Observations were conducted on the morning following their arrival. The lab-reared group was collected from the Patuxent River and held for 4 d in 3-L containers of filtered seawater. Eggs were separated from naupliar and copepodite stages, placed in 3-L containers, and allowed to develop to maturity. First generation adult females were used in the lab-reared Chesapeake Bay trials. All Chesapeake Bay copepods were fed an equiproportional mixture of *Thalassiosira weissflogii* and *Isochrysis galbana* (*T. iso*) at 600 cells/mL. Animals from Florida were fed an equiproportional mixture of *Gymnodinium nelsoni*, *Scrippsiella trochoideum*, and *Prorocentrum micans* at 300 cells/mL. The animals were held at ambient temperature and salinity (Patuxent River 21°C, salinity ~12 on the Practical Salinity Scale; Turkey Point 21°C, salinity ~33). Dissolved ox-

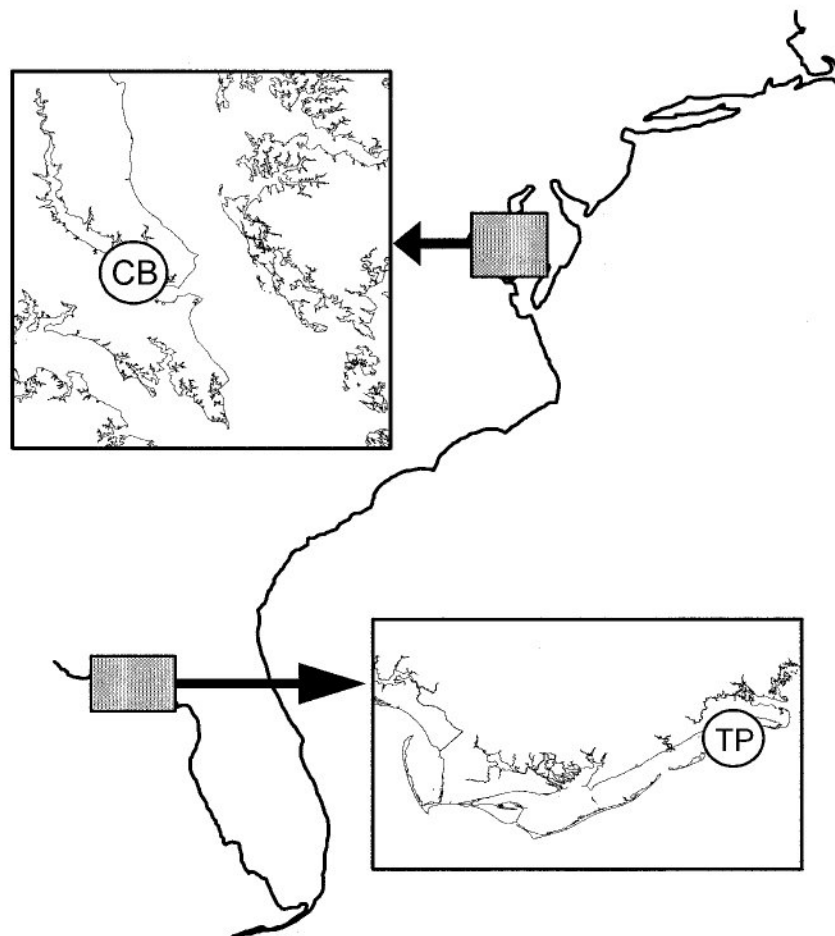


FIG. 1. Collection locations: Patuxent River, Chesapeake Bay (CB), and Turkey Point (TP), Florida, USA.

xygen levels in the holding containers were maintained at saturation by gentle bubbling and/or stirring. After the overnight acclimation period, adult females were gently transferred to 5-mL glass vials with a wide-bore pipette (1–15 per vial) and then placed in the test aquarium.

Behavioral responses of copepods in a stratified water column were monitored as in Stalder and Marcus (1997). We established the water columns in rectangular Plexiglas aquaria ($5 \times 5 \times 30$ cm, with wall thickness of 2 mm). The walls of the aquaria were finely etched in 2-cm increments from the base to the top on all sides. Density stratification was established in both the control and the experimental aquaria by manipulating the salinity and temperature of the water column. We established three-layer water columns by using a peristaltic pump to gently add higher salinity water below less saline upper layers. Use of a peristaltic pump to fill the experimental aquaria prevented aeration of hypoxic water. Mean salinity in all Chesapeake Bay trials was 11 (± 0.0 SE) in the upper layer, 12 (± 0.0 SE) in the pycnocline, and 14 (± 0.0 SE) in the bottom layer. Mean salinity in the Florida trials was 31.9 (± 0.4

SE) in the upper layer, 32.9 (± 0.4 SE) in the pycnocline, and 34.9 (± 0.4 SE) in the bottom layer. Pycnocline salinities were chosen to match ambient salinities at which copepods were collected. Salinity differences between experimental conditions for the two populations reflect true differences in field conditions. Control aquaria had dissolved oxygen concentrations near air saturation throughout the water column. In experimental aquaria, oxygen concentrations were near air saturation in the upper and intermediate layers and hypoxic in the bottom layer. Mean dissolved oxygen concentration in the control aquaria was 6.6 mg/L (± 0.03 SE). In experimental columns, oxygen concentration was 6.8 mg/L (± 0.03 SE) in the upper and intermediate layers and 0.5 mg/L (± 0.01 SE) in the hypoxic bottom layer. To create a thermocline, we placed the aquaria in a 16°C circulating water bath that extended 14 cm up the water column. Mean temperature in all thermocline trials was 22.5°C (± 0.04 SE) in the upper layer, 19.6°C (± 0.13 SE) in the intermediate layer, and 17.1°C (± 0.03 SE) in the bottom layer.

We conducted observations on individual copepods and on groups of 8–15 copepods introduced into the

top layer of the Plexiglas aquaria. We used two measures of response to the presence or absence of hypoxia in the bottom layer: (1) the proportion of time individuals spent in the bottom layer, and (2) the proportion of individuals in the bottom layer at 60 min after copepods were introduced to aquaria. Individual Chesapeake Bay field-collected copepods were observed continually and their positions recorded for 60 min to determine their behavioral response to hypoxia. We determined the proportion of time individuals spent in the bottom layer after their initial crossing of the pycnocline; individuals that did not cross the pycnocline were excluded from this analysis. We used a Student's *t* test to compare dissolved oxygen treatments. In addition, the vertical locations of groups of copepods were recorded after the copepods acclimated to and explored the experimental water column for 1 h. Individual animals were used only once. All observations were conducted in a dark temperature-controlled room illuminated with two 8-W red darkroom lights positioned 0.5 m behind the test aquaria. We used a two-way analysis of variance (ANOVA) to compare the proportion of copepods in the bottom layer between dissolved oxygen treatments and among populations. This ANOVA model was simplified to eliminate statistical interactions that we did not wish to examine in this study. Contrast statements (SAS Institute, Cary, North Carolina, USA) were used to test preplanned comparisons between Chesapeake Bay and Florida field-collected animal responses to bottom dissolved oxygen (field population \times bottom oxygen interaction) and field-collected and lab-reared Chesapeake Bay animal responses to bottom dissolved oxygen (Chesapeake source \times bottom oxygen interaction). Because these two contrasts address the anticipated alternative hypotheses exactly, we interpret them directly without presenting the general interaction first (E. Perry, *personal communication*.)

RESULTS

Our experiments on field-collected Chesapeake Bay *A. tonsa* indicate that animals in this population respond to and have the ability to avoid lethal levels of dissolved oxygen in a stratified experimental water column. We present representative observations from individuals in experimental (Fig. 2a) and control (Fig. 2b) water columns. After each encounter with the hypoxic bottom layer, copepods in the experimental aquaria immediately hopped up and out of this layer (Fig. 2a). In contrast, copepods in the control containers (Fig. 2b) explored the entire water column and crossed the pycnocline (at 16 cm) multiple times. In addition, these individuals remained in the bottom layer for longer periods than the copepods in the experimental containers. Similar behavioral responses were observed for 9 different individuals (4 controls, 5 experimental). The proportion of time that the copepods spent in the bottom layer was significantly less in the experimental

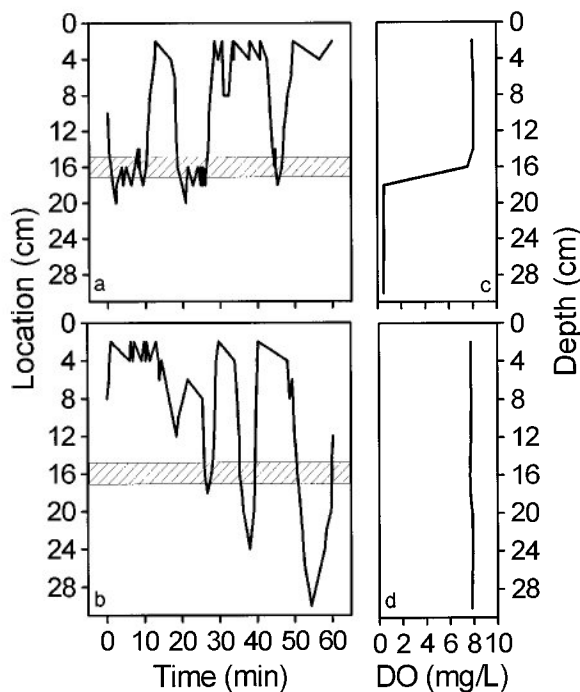


FIG. 2. Continuous observations of the vertical location of individual Chesapeake Bay field-collected *Acartia tonsa* in a column containing (a) hypoxic bottom water, and (b) normoxic bottom water. The right-hand panels show vertical profiles of dissolved oxygen concentrations (mg/L) in (c) experimental and (d) control water columns.

group tested in columns with a hypoxic bottom layer (0.08 ± 0.03 SE) than in the high bottom oxygen control (0.5 ± 0.17 SE; $t = -2.732$, $df = 7$, $P = 0.029$).

Chesapeake Bay copepods exhibited a very different response to hypoxia than their conspecifics from Turkey Point; that is, the Chesapeake Bay animals clearly avoided low dissolved oxygen in the bottom layer while the Florida population of *A. tonsa* did not (Fig. 3). A two-way ANOVA on rank-transformed data indicated that the proportion of copepods in the hypoxic bottom layer differed between the Chesapeake Bay and Florida field-collected animals (contrast: $F = 8.25$, $df = 1$, $P < 0.005$). Our results for Florida *A. tonsa* were quite similar to those originally obtained by Stalder and Marcus (1997). In contrast, laboratory-raised *A. tonsa* exhibited the same response to hypoxia as did *A. tonsa* that were collected directly from Chesapeake Bay (Fig. 3; contrast: $F = 0.01$, $df = 1$, $P = 0.94$), strongly suggesting that the behavioral response of Chesapeake Bay *A. tonsa* to low oxygen is not a learned behavior.

DISCUSSION

The implications of our results are twofold: (1) there is the potential for local adaptation in the behavioral responses of populations to arise resulting from exposure to an environmental factor that is strongly influenced by human activities, and (2) differences exist

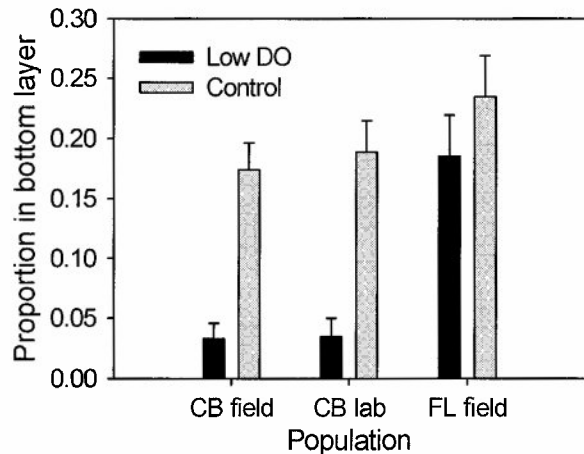


FIG. 3. Proportion of *Acartia tonsa* occupying the bottom layer after a 1-h period. Key to population abbreviations: CB field = Chesapeake Bay, field-collected; CB lab = Chesapeake Bay, lab-reared; FL field = Turkey Point, Florida, field-collected.

among populations in behavioral responses that could influence susceptibility of a system to anthropogenic stressors.

The *A. tonsa* population inhabiting a stratified and seasonally hypoxic estuarine system clearly shows evidence of behavioral avoidance of low oxygen. In contrast, populations without pre-exposure to strong oxygen gradients apparently do not have the ability to avoid lethal dissolved oxygen concentrations. While the mechanism that allows *A. tonsa* to respond to low oxygen remains unknown, organisms inhabiting the Chesapeake Bay system have been exposed to seasonal hypoxia throughout their recent evolution (i.e., during the past 50–250 yr). Because the generation time of *A. tonsa* is ~7–9 d at 22–25°C (Heinle 1966), there has likely been sufficient time for adaptive changes to have occurred in the Chesapeake Bay *A. tonsa* population. Copepods that vertically migrated but did not avoid lethal hypoxic conditions would experience substantial mortality in the Chesapeake Bay system, indicating that there may be strong selection for avoidance of hypoxic bottom waters. It is unknown if the common ancestor of the Chesapeake and Florida populations lived in an oxygen-stressed environment. Whether or not the ancestor evolved in hypoxic conditions, our results indicate that present day *A. tonsa* populations are highly variable in their ability to deal with anthropogenic stressors. One other study documented the diurnal migration of *A. tonsa* into the anoxic layer of a meromictic lake (De Meester and Vyverman 1997). Because *A. tonsa* is geographically widespread, these two studies taken together strongly indicate that the species is labile in its ability to become locally adapted to oxygen-stressed environments.

Whether or not behavioral differences reflect evolved responses to anthropogenic changes to coastal envi-

ronments, our study suggests that populations may vary widely in their response to environmental changes brought about by human activities. In the case of *A. tonsa*, we have found differential susceptibility of a key organism in the food web. As a result of this variation, some systems may be more susceptible than others to anthropogenic stressors. If local adaptation occurs and is rapid, this disruption may be transient. However, if local adaptation is slow or does not occur, the disruption may be persistent. The expanse of hypoxia is increasing in coastal waters worldwide (Diaz and Rosenberg 1995). Thus, populations not currently adapted to low dissolved oxygen concentrations in their local habitat may be most vulnerable during future hypoxic events. The severity of the effects of anthropogenic alterations on a population not currently expressing appropriate behavioral responses will depend on both the genetic variability within the population and the rate of environmental change. Recently, humans have accelerated the rate of environmental changes in many systems (e.g., climatic shifts, pollution, habitat destruction). Expression of appropriate behavioral responses potentially determines whether or not populations are affected in areas recently altered by human activities. Our study indicates that populations vary greatly in their susceptibility to anthropogenic perturbations to the environment. In addition, our results warn that differences in behavioral responses among local populations may limit the ability to apply biological data from one locale to another. Similarly, it may be inappropriate to directly apply results from laboratory bioassays to real world situations without careful consideration of variability in the behavioral responses of the individuals under consideration. In the face of increasing hypoxia in estuarine and coastal waters, coastal resource managers need to consider the potential for populations to vary in their responses to this human-induced stress. Our study suggests that it is inadvisable for managers to apply results from studies conducted in areas historically affected by an anthropogenic stress to areas only recently affected by the same human perturbation.

ACKNOWLEDGMENTS

This research was funded by Environmental Protection Agency STAR award No. 827097-01-0 to D.L.B., J. E. Purcell, M.B.D., and K. A. Rose, and NOAA-COP funding to the COASTES program. We thank M. Bundy, R. Condon, M. Grove, S. Kolesar, B. Morris, L. Chasar, C. Richmond, S. Schaefer, C. Sedlacek, and W. Yates for their assistance. E. Perry provided help with statistical analyses. We also thank R. Osman, P. Turner, and two anonymous reviewers for commenting on earlier versions of this manuscript.

LITERATURE CITED

- Akberali, H. B., and J. E. Black. 1980. Behavioral-responses of the bivalve *Scrobicularia plana* (Dacosta) subjected to short-term copper (Cu-II) concentrations. *Marine Environmental Research* 4:97–107.
- Akberali, H. B., T. M. Wong, and E. R. Trueman. 1981. Behavioral and siphonal tissue responses of *Scrobicularia pla-*

- na* (Bivalvia) to zinc. *Marine Environmental Research* **5**: 251–264.
- Atkinson, A., P. Ward, A. Hill, A. S. Brierley, and G. C. Cripps. 1999. Krill-copepod interactions at South Georgia, Antarctica. II. *Euphausia superba* as a major control on copepod abundance. *Marine Ecology Progress Series* **176**: 63–79.
- Auerbach, S. I. 1981. Ecosystem response to stress: a review of concepts and approaches. Pages 29–42 in G. W. Barrett and R. Rosenberg, editors. *Stress effects on natural systems*. John Wiley and Sons, Chichester, UK.
- Bollens, S. M., and B. W. Frost. 1991. Diel vertical migration in zooplankton: rapid individual response to predators. *Journal of Plankton Research* **13**:1359–1365.
- Breitburg, D. L. 1994. Behavioral responses of fish larvae to low dissolved oxygen concentrations in a stratified water column. *Marine Biology* **120**:615–625.
- Brown, C. R., and M. B. Brown. 1998. Intense natural selection on body size and wing and tail symmetry in cliff swallows during severe weather. *Evolution* **52**:1461–1475.
- Brylinski, J. M. 1981. Report on the presence of *Acartia tonsa* Dana (Copepoda) in the harbour of Dunkirk (France) and its geographical distribution in Europe. *Journal of Plankton Research* **3**:255–260.
- Cervetto, G., R. Gaudy, and M. Pagano. 1999. Influence of salinity on the distribution of *Acartia tonsa* (Copepoda, Calanoida). *Journal of Experimental Marine Biology and Ecology* **239**:33–45.
- Cooper, S. R., and G. S. Brush. 1993. A 2500-year history of anoxia and eutrophication in Chesapeake Bay. *Estuaries* **6**:617–626.
- Dagg, M. J., B. W. Frost, and J. A. Newton. 1997. Vertical migration and feeding behavior of *Calanus pacificus* females during a phytoplankton bloom in Dabob Bay, USA. *Limnology and Oceanography* **42**:974–980.
- De Meester, L., and W. Vyverman. 1997. Diurnal residence of the larger stages of the calanoid copepod *Acartia tonsa* in the anoxic monimolimnion of a tropical meromictic lake in New Guinea. *Journal of Plankton Research* **19**:425–434.
- Diaz, R. J., and R. Rosenberg. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioral responses of benthic macrofauna. *Oceanography and Marine Biology: An Annual Review* **33**:245–303.
- Engle, V. D., J. K. Summers, and J. M. Macauley. 1999. Dissolved oxygen conditions in northern Gulf of Mexico estuaries. *Environmental Monitoring and Assessment* **57**: 1–20.
- Franks, P. J. S. 1992. Sink or swim: accumulation of biomass at fronts. *Marine Ecology Progress Series* **82**:1–12.
- Glynn, P. W. 1988. ENSO 1982–1983. Nearshore population, community and ecosystem responses. *Annual Review of Ecology and Systematics* **19**:309–345.
- Gonzalez, J. G. 1974. Critical thermal maxima and upper lethal temperatures for the calanoid copepods *Acartia tonsa* and *A. clausi*. *Marine Biology* **27**:219–223.
- Grant, B. R., and P. R. Grant. 1989. Natural selection in a population of Darwin's finches. *American Naturalist* **133**: 377–393.
- Groenkjaer, P., and K. Wieland. 1997. Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. *Marine Ecology Progress Series* **154**:91–105.
- Haurly, L. R., P. H. Wiebe, M. H. Orr, and M. G. Briscoe. 1983. Tidally generated high-frequency internal wave packets and their effects on plankton in Massachusetts Bay. *Journal of Marine Research* **41**:65–112.
- Heinle, D. 1966. Production of a calanoid copepod, *Acartia tonsa*, in the Patuxent River Estuary. *Chesapeake Science* **7**:59–74.
- Hoffman, A. A., and P. A. Parsons. 1991. *Evolutionary genetics of environmental stress*. Oxford University Press, Oxford, UK.
- Karlsen, A. W., T. M. Cronin, S. E. Ishman, D. A. Willard, R. Kerhin, C. W. Holmes, and M. Marot. 2000. Historical trends in Chesapeake Bay dissolved oxygen based on benthic foraminifera from sediment cores. *Estuaries* **23**:488–508.
- Keister, J. E., E. D. Houde, and D. L. Breitburg. 2000. Effects of bottom layer hypoxia in abundance and depth distribution of organisms in Patuxent River. *Marine Ecology Progress Series* **205**:43–59.
- Livingston, R. J. 2001. Eutrophication processes in coastal systems. Origin and succession of plankton blooms and effects on secondary production in Gulf Coast estuaries. CRC Press, Boca Raton, Florida, USA.
- Macnair, M. R. 1993. The genetics of metal tolerance in vascular plants. *New Phytologist* **124**:541–559.
- McKenzie, J. A., and P. Batterham. 1994. The genetic, molecular, and phenotypic consequences of selection for insecticide resistance. *Trends in Ecology and Evolution* **9**: 166–169.
- Raymont, J. E. G. 1983. *Plankton and productivity in the oceans*. Volume 2. Zooplankton. Pergamon Press, Oxford, UK.
- Renaud, M. L. 1986. Detecting and avoiding oxygen deficient sea water by brown shrimp, *Penaeus aztecus* (Ives), and white shrimp, *Penaeus setiferus* (Linnaeus). *Journal of Experimental Marine Biology* **98**:283–292.
- Reznick, D. N., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. *Nature* **346**:357–359.
- Reznick, D. N., and J. A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* **36**:160–177.
- Roman, M. R., A. L. Gauzens, W. K. Rhinehart, and J. R. White. 1993. Effects of low oxygen waters on Chesapeake Bay zooplankton. *Limnology and Oceanography* **38**:1603–1614.
- Sanford, L. P., K. G. Sellner, and D. L. Breitburg. 1990. Covariability of dissolved oxygen with physical processes in the summertime Chesapeake Bay. *Journal of Marine Research* **48**:567–590.
- Spoor, W. A. 1990. Distribution of fingerling brook trout, *Salvelinus fontinalis* (Mitchill), in dissolved oxygen concentration gradients. *Journal of Fish Biology* **36**:363–373.
- Stalder, L. C., and N. M. Marcus. 1997. Zooplankton responses to hypoxia: behavioral patterns and survival of three species of calanoid copepods. *Marine Biology* **127**: 599–607.
- Taft, J. L., W. R. Taylor, E. O. Hartwig, and R. Loftus. 1980. Seasonal oxygen depletion in Chesapeake Bay. *Estuaries* **4**:242–247.
- Vermeer, K., I. Szabo, and P. Greisman. 1987. The relationship between plankton-feeding Bonaparte's and Mew Gulls and tidal upwelling at Active Pass, British Columbia. *Journal of Plankton Research* **9**:483–501.
- Zimmerman, A. R., and E. A. Canuel. 2000. A geochemical record of eutrophication and anoxia in Chesapeake Bay sediments: anthropogenic influence on organic matter composition. *Marine Chemistry* **69**:117–137.