

7-2000

Local demographics of the polychaete *Chaetopterus pergamentaceus* within the lower Chesapeake Bay and relationships to environmental gradients

ML Thompson

Linda C. Schaffner
College of William and Mary

Follow this and additional works at: <https://scholarworks.wm.edu/vimsarticles>



Part of the [Marine Biology Commons](#)

Recommended Citation

Thompson, ML and Schaffner, Linda C., "Local demographics of the polychaete *Chaetopterus pergamentaceus* within the lower Chesapeake Bay and relationships to environmental gradients" (2000). *VIMS Articles*. 1529.
<https://scholarworks.wm.edu/vimsarticles/1529>

This Article is brought to you for free and open access by the Virginia Institute of Marine Science at W&M ScholarWorks. It has been accepted for inclusion in VIMS Articles by an authorized administrator of W&M ScholarWorks. For more information, please contact scholarworks@wm.edu.

LOCAL DEMOGRAPHICS OF THE POLYCHAETE *CHAETOPTERUS PERGAMENTACEUS* WITHIN THE LOWER CHESAPEAKE BAY AND RELATIONSHIPS TO ENVIRONMENTAL GRADIENTS

Michelle L. Thompson and Linda C. Schaffner

ABSTRACT

Chaetopterus pergamentaceus is an abundant and functionally important species within the soft sediment, subtidal benthic community of lower Chesapeake Bay. The present study elucidates spatial relationships in density, individual ash-free dry weight, total station ash-free dry weight and growth rates for juveniles and adults from 2 yrs of sampling (1994, 1995) at 12 stations in the lower Chesapeake Bay. A strong inverse relationship ($r^2 = 0.69$) was observed between growth rates and total density for juveniles when data from a low (1994) and high (1995) recruitment year were considered. Common parameters among stations characterized by high density/low growth were: (1) depth (maximum for region); (2) proximity to the center of a major circulation eddy; (3) proximity to a channel; (4) higher food concentration (indexed by chl-*a* in surface sediment layer); and (5) higher physical energy in the benthic boundary layer region. The study provides evidence that spatial variation in population processes, concordant with major environmental gradients, strongly influences population dynamics. The effects of these environmental parameters on the population dynamics of this polychaete cannot yet be clearly resolved because the parameters are confounded.

Chaetopterus pergamentaceus (provisional specification, Mary Petersen, pers. comm.; Eckberg and Hill, 1996; formally *Chaetopterus variopedatus*, e.g., Enders, 1909) is an abundant species within the soft-sediment, subtidal benthic community of lower Chesapeake Bay, where relatively high densities of this polychaete have been observed for at least the last 15 yrs (Diaz et al., 1985; Schaffner and Diaz, 1987; Schaffner, 1990, 1993). This suspension feeding polychaete inhabits a parchment-like semicircular tube that can penetrate over 15 cm below the sediment surface. Specialized parapodia pump water through its tube. The water is filtered with a mucus net, formed into a food ball, and then transported into the mouth (Enders, 1909; MacGinitie, 1939; Brown, 1975; Flood and Fiala-Medioni, 1982; Riisgård, 1989). The tubes are well oxygenated, house commensal organisms and are likely to have significant effects on sediment biogeochemistry. Some aspects of the ecology of *C. pergamentaceus* are known from previous investigations outside of Chesapeake Bay. McNulty and Lopez (1969) reported year-round recruitment of this polychaete in Florida, while in North Carolina recruitment occurred in early summer with rapid growth to adulthood by the end of summer (Enders, 1909).

Within the Chesapeake Bay, Schaffner (1990) found that *C. pergamentaceus* positively influenced macrofaunal abundance and altered community diversity and composition. In studies of benthic boundary layer processes within the lower bay, Wright et al. (1997) concluded that tubes of *C. pergamentaceus* and associated epifauna increased the hydraulic roughness of the sediment bed thereby modifying the near-bed flow regime, as well as sediment resuspension and transport processes. The feeding activity of this polychaete also alters particle size distributions via pelletization of suspended material and enhances deposition of organic matter, which may have important implications for ecosystem processes (Wright et al., 1997; Neubauer, 2000; Thompson and Schaffner, unpubl.

data). Thus, this polychaete is a functionally important species and serves as an important link in benthic-pelagic coupling. Despite its importance in the Chesapeake Bay estuary, the ecology of *C. pergamentaceus* in the lower bay remains poorly described.

The lower Chesapeake Bay study region is part of a physically complex estuarine environment. Schaffner et al. (1987) described a general environmental gradient in the lower mainstem bay of higher physical energy, salinity, and fine sand sediments in the southeast compared to the northwest. Wright et al. (1997) reported an increase in physical energy toward the southeast associated with wave agitation in proximity of the bay mouth and relatively strong tidal currents while a moderation of physical energy in the northwest is evident in boundary layer processes and sea bed dynamics (Wright et al., 1997; Dellapenna et al., 1998). Surface sediment labile organic matter, an indicator of suspension feeder food availability, increases toward the southeastern portion of the bay (Neubauer, 2000). This food gradient may be tied to the presence of a residual circulation pattern in the bay—a strong, cyclonic eddy with related regional up-welling and down-welling (Fig. 1; Hood et al., 1998). High concentrations of pelagic organisms such as phytoplankton and various larvae are retained within this residual water circulation feature. Both physical and biological gradients may play a role in regulating local scale population trends of *C. pergamentaceus*.

Given the significant environmental gradients observed within the study region, it is of interest to determine how factors and mechanisms that affect individual organisms may interact to regulate overall population structure for this species. The goal of this paper is to identify spatial trends in *C. pergamentaceus* population dynamics and potential links with known environmental gradients. We present evidence for the existence of distinct spatial patterns with respect to juveniles, not adults, in density, individual ash-free dry weight (AFDW), and total station AFDW within a high recruitment year, but causal relationships with environmental gradients require further investigation.

MATERIALS AND METHODS

The study region, referred to as the bay stem plains (Wright et al., 1987) within lower Chesapeake Bay (Fig. 1), has bottom salinities of 20–27 ‰, bottom temperatures of 4–25°C, a mean tidal range of 60 cm, tidally induced maximum current speeds of 20–40 cm s⁻¹ at 1 m above the bed, and sediment primarily consisting of silt (40–50%) and fine sand (40–50%) (Schaffner, 1990; Wright et al., 1992). Summer hypoxia or anoxia are not observed in this region of the bay. The benthic fauna consists of a diverse assemblage of suspension and deposit feeders with *Chaetopterus pergamentaceus* often being the biomass dominant (Schaffner, 1990; Wright et al., 1997).

FIELD SAMPLING.—Each of 12 stations were sampled for a period of 2 yrs beginning January 1994 and ending December 1995. Worms were collected using a U.S. Naval Electronic Laboratory spade box core (20 × 30 × 30 cm deep). One box core per station was collected during year 1 (1994) while two box cores per station were collected during year 2 (1995), in order to increase the number of worms collected. Samples were collected monthly from each station during winter and spring and semimonthly during summer and fall, the periods of recruitment and rapid growth. Due to extreme weather and loss of a boat engine, some scheduled 1995 sampling dates were missed. Three methods were utilized to ensure complete removal of *C. pergamentaceus* from each core. First, a 5 cm diameter by 5 cm deep subcore was collected and fixed intact to retain fragile new recruits. Second, the remaining surface sediment, 0–2 cm, was removed and elutriated onto a 125 μm screen to collect the very small worms. Last, larger worms were removed directly from the remaining sedi-

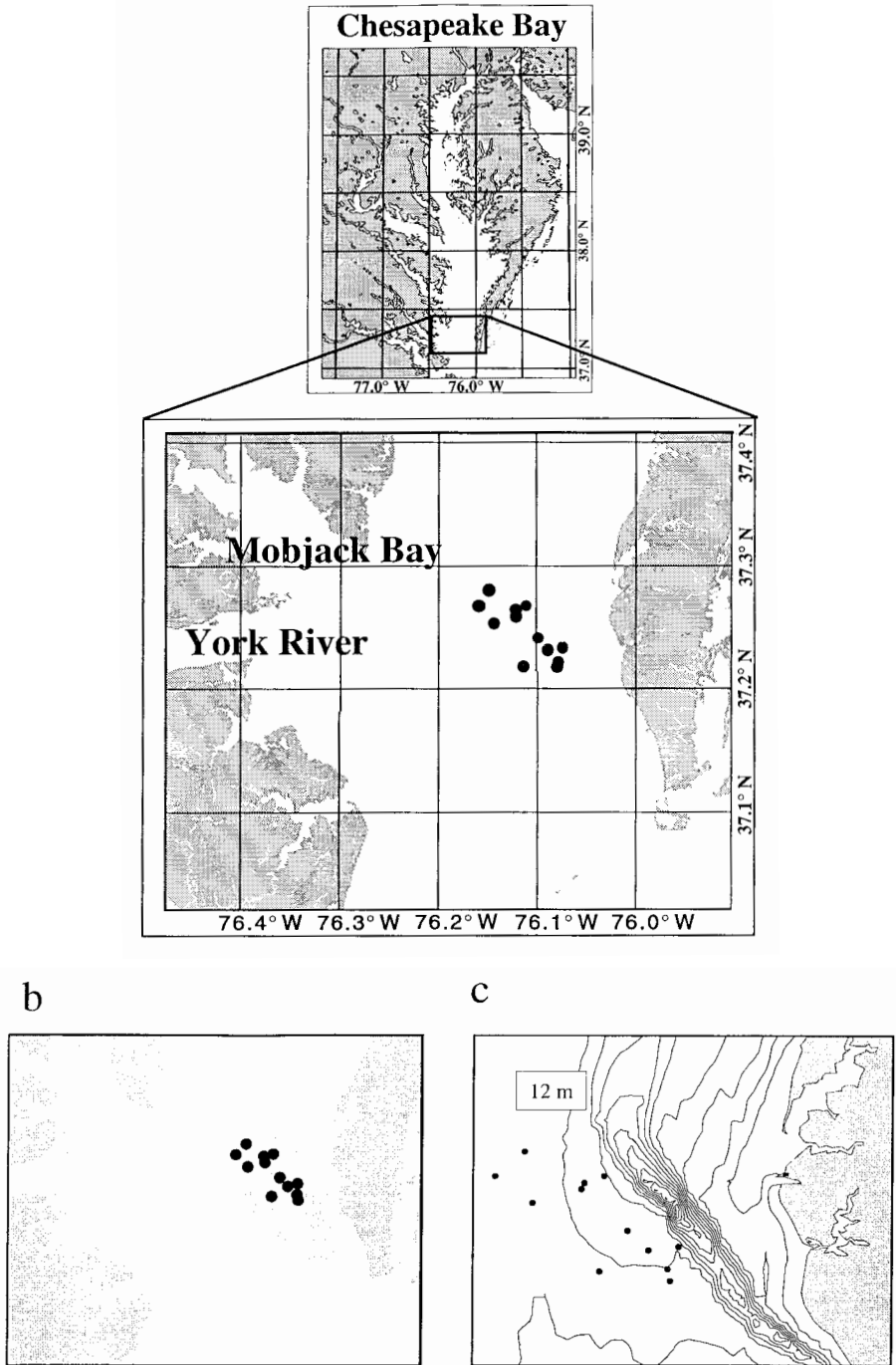


Figure 1. a) Study region in the lower Chesapeake Bay with solid circles (●) indicating station locations. b) stations relative to the overlying residual water circulation eddy, as indicated by shaded area in which the lighter portion represents the eddy center (adapted from Hood et al., 1998). c) stations relative to depth contours of 3 m increments.

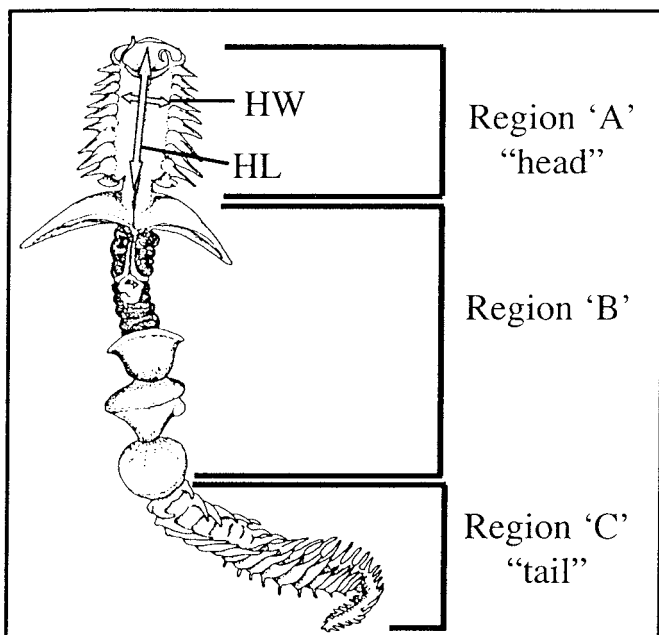


Figure 2. Drawing of *Chaetopterus pergamentaceus* indicating body regions (adapted from Gilbert 1984). HW is width of Region 'A' at setiger 4; HL is length of Region 'A'.

ment. All *C. pergamentaceus* removed from the cores were fixed in 10% formalin and stored in 2% formalin until laboratory analysis.

LABORATORY METHODS.—Density, individual AFDW, and total station AFDW were determined for each sample. Briefly, length of body region A and width (at setiger 4), collectively termed head area, were measured to the nearest 0.1 mm (Fig. 2) using a dissecting scope equipped with ocular micrometer for smaller specimens and Vernier calipers for larger specimens. Head area was found to be a reliable indicator of worm size described by the equation $AFDW = [(0.0224 \text{ length}) + (0.0303 \text{ width})]^3$ ($n = 40$; $r^2 = 0.93$; $P < 0.001$; due to heteroscedasticity, observations were weighted by $1/\text{variance}$; Neter et al., 1990). Size measurements were then used to calculate AFDW using this regression.

Using distinct modes in the size distribution, the population was separated into juveniles and adults. The adult category is likely represented by more than one cohort of mature individuals since tagging of individual worms in a population in South Carolina has shown that these polychaetes can live over 3 yrs (Michael Grove, pers. comm.), yet once adult size is reached the cohorts cannot be distinguished. After the data were separated into juveniles and adults, they were then grouped by season. General trends in density, individual AFDW and total station AFDW were graphed as area bubble plots with stations spatially arranged by latitude and longitude. Juvenile growth rate, found by regressing head area (mm^2) against time (julian date), was plotted versus density to detect general trends.

RESULTS AND DISCUSSION

For juveniles, spatial patterns in density, individual and total station AFDW, and growth rate were observed when recruitment was highly successful (1995), but not during a low recruitment year (1994) (Figs. 3–5). In 1995, stations with higher worm densities had lower individual AFDWs but overall higher total station AFDW. Common parameters

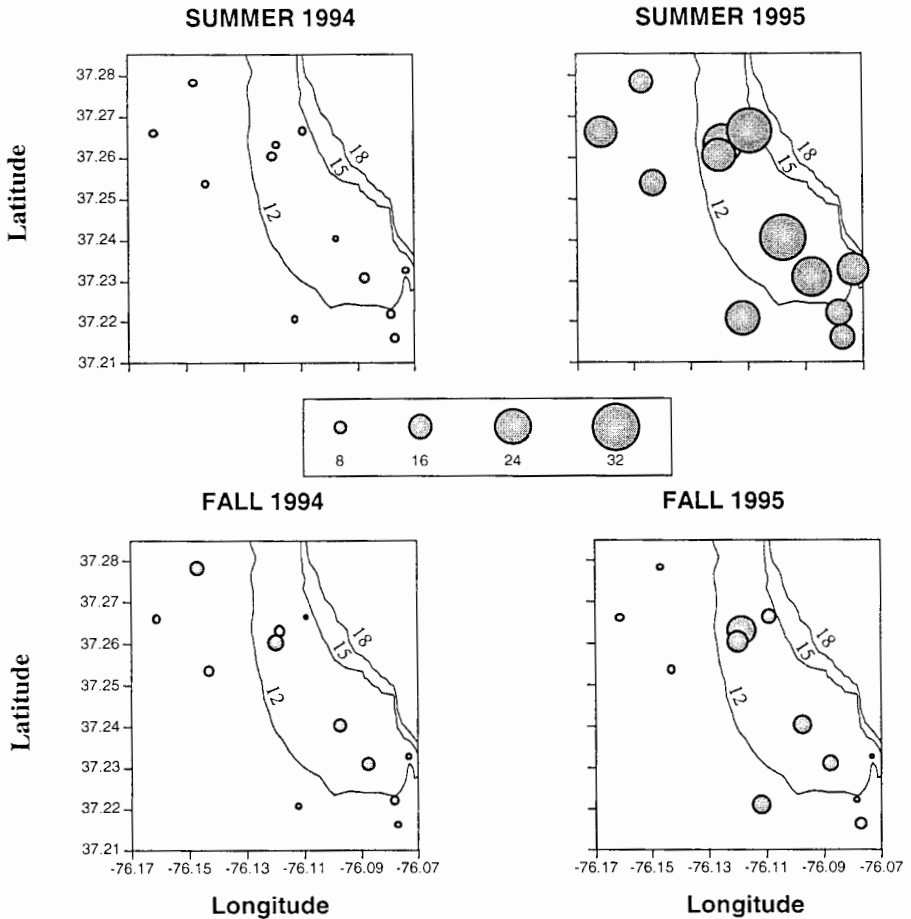


Figure 3. Juvenile average density (ind 0.06 m^{-2}). Data are graphed as area bubble plots by station arranged by latitude and longitude, separated by year, and grouped by season. Solid lines are depth contours in meters.

among these stations were depth (maximum in the study region), proximity to central portion of the residual water circulation eddy, proximity to a channel edge, in an area of greater food concentration, and in an area of higher physical energy within the benthic boundary layer. No obvious spatial patterns were observed for adults (data not shown).

The spatial pattern in the juvenile population of *C. pergamentaceus* in the lower Chesapeake Bay may be influenced by environmental gradients driven by physical processes. Physical processes affect populations directly via alterations in processes such as recruitment and feeding success, and indirectly via effects on biotic interactions (Menge and Olson, 1990; Hall, 1994; Cosson et al., 1997). Effects may be positive or negative, depending on the intensity, scale and nature of physical factors in the system (Hall, 1994). Environmental gradients driven by physical processes are important features of estuarine environments (Boesch et al., 1976; Wright et al., 1987; Day et al., 1989; Schaffner et al., in press). Unfortunately, effects of major physical gradients and the cyclonic eddy feature of the lower bay on the population dynamics of this polychaete can not be clearly resolved

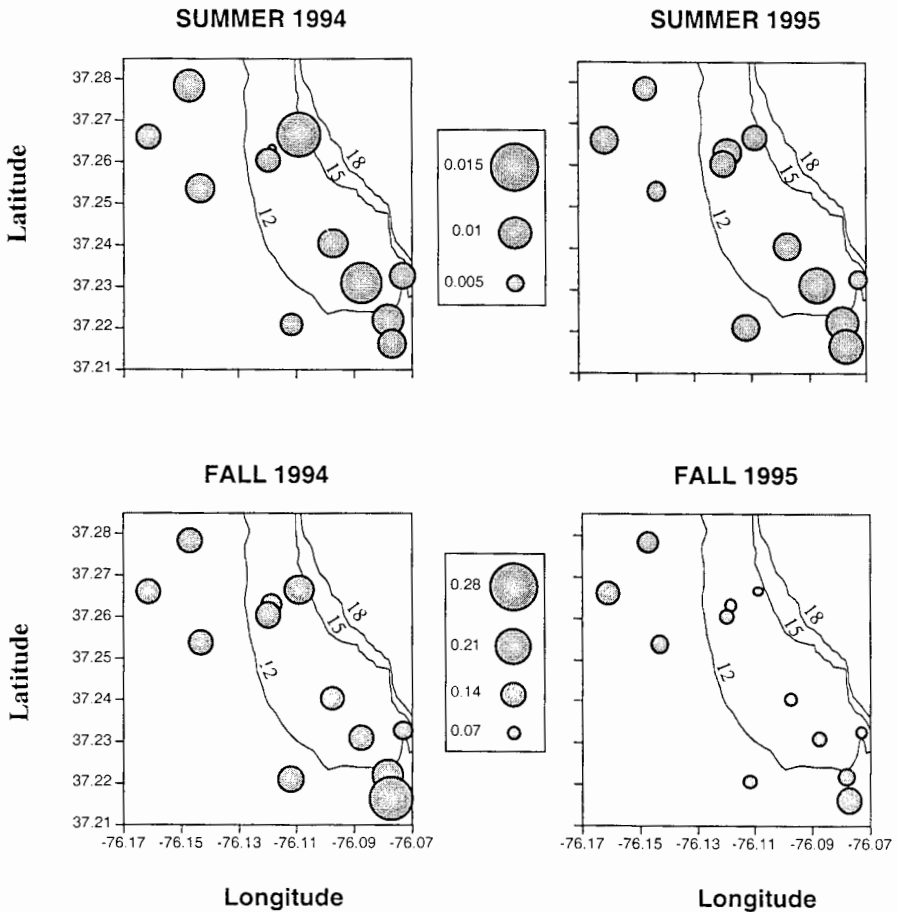


Figure 4. Juvenile average individual ash free dry weight (g AFDW ind^{-1}) with data graphed as area bubble plots with stations arranged by latitude and longitude, separated by year, and grouped by season. Note scale changes. Solid lines are depth contours in meters.

in this study because many of the gradients are confounded. Nonetheless, this study provides evidence that spatial variation in population processes, concordant with major environmental gradients, strongly influences population dynamics of *C. pergamentaceus* in this estuary. We suggest that future investigators should focus on relationships between juvenile recruitment and growth processes relative to the environmental gradients that influence benthic-pelagic coupling, larval retention processes, food availability and seabed dynamics. All of these factors are expected to play a role in the success of this polychaete in lower Chesapeake Bay.

A derived relationship for juveniles shows a strong inverse relationship between growth rates and total densities (Fig. 6). When recruitment is successful, intraspecific competition must be considered. Both food and space are potentially important density dependent factors that limit benthic suspension feeders (Frechette and Lefaivre, 1990; Kamermans et al., 1992; Beukema and Cadée, 1997; Josefsen and Conley, 1997). Crowding reduces growth rates, decreases average organism size, and skews size frequency distributions to

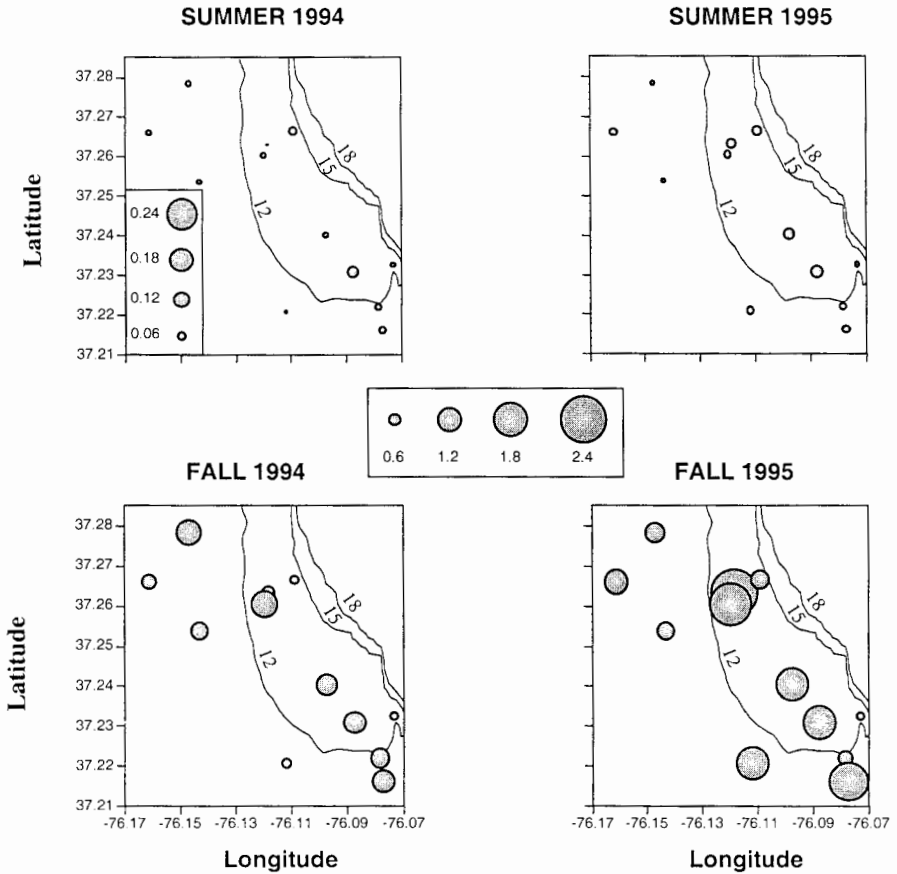


Figure 5. Total station ash free dry weight (g AFDW 0.06 m⁻²). Data are graphed as area bubble plots with stations arranged by latitude and longitude, separated by year, and grouped by season. Note scale changes; Summer 1994 is an order of magnitude less. Solid lines are depth contours in meters.

smaller size individuals (Branch, 1975; Woodin, 1976; Begon et al., 1986). This is consistent with the patterns observed for 1995. The 1995 cohort of juveniles yielded a higher total AFDW than the 1994 cohort, despite lower growth rates (Fig. 5). Individual AFDW was lower at higher density stations, particularly in the fall due to the integrated effects of time on juvenile growth and density (Fig. 4). Yet, total AFDW was highest at high density stations regardless of the lower growth rate. Although density dependent factors may affect the population, the carrying capacity of the environment with respect to *C. pergamentaceus* does not appear to have been reached.

High interannual variability, resulting from variable recruitment success, was apparent for this population. Variable recruitment success led to interannual differences in factors affecting the population dynamics, e.g., an intuitive conclusion for our study is that in some years (i.e., 1994) low recruitment will limit the population while in other years (i.e., 1995) high recruitment allows for the potential of density dependent factors to limit the

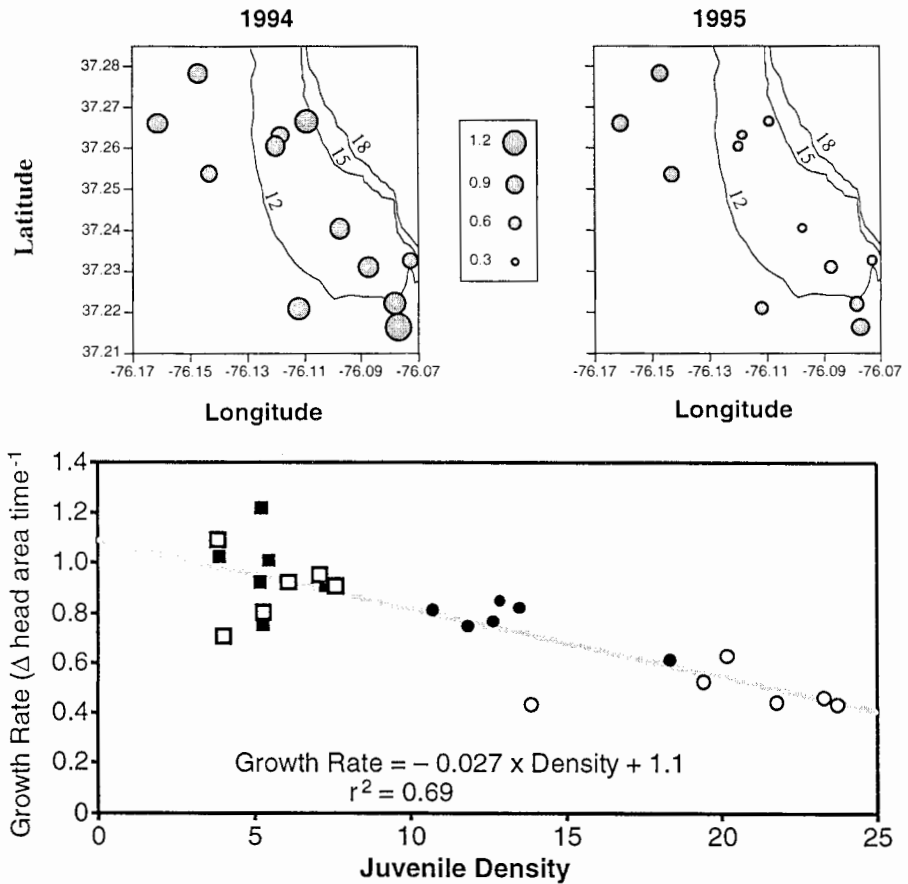


Figure 6. a) Growth rate of juveniles. Data are graphed as area bubble plots with stations arranged by latitude and longitude, separated by year, and grouped by season. Solid lines are depth contours in meters. b) Derived inverse relationship between juvenile density ($\text{ind } 0.06 \text{ m}^{-2}$) and growth rate (change in head area (mm^2) with time (julian day)). Solid squares (■) are 1994 shallow water stations (<12 m). Empty squares (□) are 1994 deep water stations (>12 m). Solid circles (●) are 1995 shallow water stations (<12 m). Empty circles (○) are 1995 deep water stations (>12 m).

population. Variable recruitment in time and space due to irregularities in physical transport of larvae, spawning, and larval survivorship within the water column is a generally recognized concept. Based on better studied species such as crabs and fish (Johnson and Hester, 1989; Norcross and Wyanski, 1994; Ault et al., 1995; and many others) we expect that physical processes affecting recruitment will be important in lower Chesapeake Bay. Although Ólafsson et al. (1994) concluded that recruitment limitation is not the dominant factor describing population patterns in marine soft-sediment communities, population patterns are still likely to correspond to recruitment peaks even if the peaks are dampened by post-recruitment density dependent factors (Caley et al., 1996). For example, Zajac and Whitlatch (1988) found that density fluctuations in the polychaete *Nephtys incisa* were primarily related to recruitment variations. Thus, the relative importance of recruitment limitation vs post-recruitment density dependent factors in affecting population structure may change temporally.

SUMMARY

There are interannual differences in factors structuring the population of *C. pergamentaceus*. For juveniles, a strong inverse relationship was observed between growth rates and total density when data from a low and high recruitment year were considered. Concordant with environmental gradients, spatial patterns were evident among juveniles within a successful recruitment year. The role of gradients in physical energy, organic matter, and depth; a residual circulation pattern; and larval supply that may influence recruitment require further investigation. Experiments are needed that will help us to better understand the ecological role of *C. pergamentaceus* in this estuarine environment. Our results provide evidence that spatial variation in population processes, concordant with major environmental gradients, strongly influences population dynamics of *C. pergamentaceus* in this estuary. Due to the implications for ecosystem processes, understanding population dynamics of resident species within marine and estuarine soft-sediments warrants additional study.

ACKNOWLEDGMENTS

This is contribution number 2320 of the Virginia Institute of Marine Science. This study received major support from the Office of Naval Research - Harbor Processes Program (grant N00014-93-1-0986 to L. C. Schaffner). Special thanks to J. Kravitz at the Office of Naval Research. Additional funding to M. L. Thompson was obtained from the Lerner Grey Fund for Marine Research, the International Women's Fishing Association, VIMS Minigrant Fund, and the College of William and Mary Minigrant Fund. We are indebted to Captain D. Ward and the crew of the RV BAY EAGLE, the VIMS ITNS and library staff. We thank B. Berry for use of equipment and others, especially A. Curry, S. Horvath, B. Hinchey, P. Lay, P. Crewe, C. Brower-Reil, A. Edwards, C. Pongonis, and K. Farnsworth.

LITERATURE CITED

- Ault, J. S., E. V. Patrick and B. J. Rothschild. 1995. Physical factors affecting recruitment and abundance of the Chesapeake Bay blue crab stock. *Bull. Mar. Sci.* 57: 917.
- Begon, M., J. L. Harper and C. R. Townsend. 1986. *Ecology*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Beukema J. J. and G. C. Cadee. 1997. Local differences in macrozoobenthic response to enhanced food supply caused by mild eutrophication in a Wadden Sea area: Food is only locally a limiting factor. *Limnol. Oceanogr.* 42: 1424-1435.
- Boesch, D. F., M. L. Wass and R. W. Virnstein. 1976. The dynamics of estuarine benthic communities. Pages 177-196 *In* Estuarine processes, vol. I Uses, stresses, and adaptation to the estuary. Academic Press, New York.
- Brown, S. C. 1975. Biomechanics of water-pumping by *Chaetopterus variopedatus* Renier: skeletomusculature and kinematics. *Biol. Bull.* 149: 136-150.
- Branch, G. M. 1975. Intraspecific competition in *Patella colear* Born. *J. Animal Ecol.* 44: 263-281.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. Syst.* 27: 477-500.
- Cosson, N., M. Sibuet and J. Galeron. 1997. Community structure and spatial heterogeneity of the deep-sea macrofauna at three contrasting stations in the tropical northeast Atlantic. *Deep Sea Res.* 44: 247-269.

- Day, J. W. Jr., C. A. S. Hall, W. M. Kemp and A. Yáñez-Arancibia. 1989. *Estuarine Ecology*. John Wiley & Sons, New York.
- Dellapenna, T. M., S. A. Kuehl and L. C. Schaffner. 1998. Sea-bed mixing and particle residence times in biologically and physically dominated estuarine systems: a comparison of lower Chesapeake Bay and the York River subestuary. *Estuar. Coast. Shelf Sci.* 46: 777–795.
- Diaz, R. J., L. C. Schaffner, R. J. Byrne and R. A. Gammisch. 1985. Baltimore Harbor and Channels aquatic benthos investigations. Final Rpt. U.S. Army Corps of Engineers, Baltimore District. 255 p.
- Eckberg, W. R. and S. D. Hill. 1996. *Chaetopterus* - oocyte maturation, early development, and regeneration. *Mar. Mod. Elec. Rec.* [serial online; cited {4 November 1997}]. Available from <http://www.mbl.edu/html/BB/MMER/ECK/EckTit.html>
- Enders, H. E. 1909. A study of the life history and habits of *Chaetopterus variopedatus*, Renier et Claparede. *J. Morph.* 20(3): 479–531.
- Flood, P. R. and A. Fiala-Medioni. 1982. Structure of the mucous feeding filter of *Chaetopterus variopedatus* (Polychaeta). *Mar. Biol.* 72: 27–33.
- Frechette, M. and D. Lefaivre. 1990. Discriminating between food and space limitation in benthic suspension feeders using self-thinning relationships. *Mar. Ecol. Prog. Ser.* 65: 15–23.
- Gilbert, K. M. 1984. Family Chaetopteridae, vol. II. Pages 1–13 in J. M. Uebelacker and P. G. Johnson, eds. Taxonomic guide to the polychaetes of the northern Gulf of Mexico. Final Rpt. Minerals Management Service, contract 14-12-001-29091. Barry A. Vittor & Associates, Inc, Mobile Alabama. 7 vols.
- Hall, S. J. 1994. Physical disturbance and marine benthic communities: Life in unconsolidated sediments. *Oceanogr. Mar. Biol. Ann. Rev.* 32: 179–239.
- Hood, R. R., H. V. Wang, J. E. Purcell, E. D. Houde and L. W. Harding. 1998. Modeling particles and pelagic organisms in Chesapeake Bay: convergent features control plankton distributions. *J. Geophys. Res.* 104: 1223–1243.
- Johnson, D. R. and B. S. Hester. 1989. Larval transport and its association with recruitment of blue crabs to Chesapeake Bay. *Estuar. Coast. Shelf Sci.* 28: 459–472.
- Josefson, A. B. and J. Conley. 1997. Benthic response to a pelagic front. *Mar. Ecol. Prog. Ser.* 147: 49–62.
- Kamermans, P., H. W. van der Veer, L. Karczmarski and G. W. Doeglas. 1992. Competition in deposit- and suspension feeding bivalves: experiments in controlled outdoor environments. *J. Exp. Mar. Biol. Ecol.* 162: 113–135.
- MacGinitie, G. E. 1939. The method of feeding of *Chaetopterus*. *Biol. Bull.* 77: 117–118.
- Menge, B. A. and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community. *Trends. Ecol. Evol.* 5: 52–67.
- McNulty, J. K. and N. N. Lopez. 1969. Year-round production of ripe gametes by benthic polychaetes in Biscayne Bay, Florida. *Bull. Mar. Sci.* 19: 945–954.
- Neter J., W. Wasserman and M. Kutner. 1990. *Applied linear statistical models*, IRWIN.
- Neubauer, M. T. 2000. Demographics, production, and benthic-pelagic coupling by the suspension feeding polychaete *Chaetopterus pergamentaceus* in the lower Chesapeake Bay. Ph.D. Dissertation, The College of William and Mary, Williamsburg, VA.
- Norcross, B. L. and D. M. Wyanski. 1994. Interannual variation in the recruitment pattern and abundance of age-0 summer flounder, *Paralichthys dentatus*, in Virginia estuaries. *Fish. Bull.*, U.S. 92: 591–598.
- Ólafsson, E. B., C. H. Peterson and W. G. Jr. Ambrose. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanogr. Mar. Biol. Ann. Rev.* 32: 65–109.
- Riisgård, H. U. 1989. Properties and energy cost of the muscular piston pump in the suspension feeding polychaete *Chaetopterus variopedatus*. *Mar. Ecol. Prog. Ser.* 56: 157–168.
- Schaffner, L. C. 1990. Small-scale organism distribution and patterns of species diversity: Evidence for positive interaction in an estuarine benthic community. *Mar. Ecol. Prog. Ser.* 61: 107–117.

- _____. 1993. Baltimore Harbor and Channels Aquatic Benthos Investigations at the Wolf Trap Alternate Disposal Site in Lower Chesapeake Bay. Final Rpt. U.S. Army Corps of Engineers, Baltimore District. 120 p.
- _____ and R. J. Diaz. 1987. Overwintering blue crab populations in the lower Chesapeake Bay during winter 1985–86. Final Rpt. U.S. Army Corps of Engineers, Baltimore District. 24 p.
- _____, _____ and R. J. Byrne. 1987. Processes affecting recent estuarine stratigraphy. Pages 584–599 in N. C. Kraus, ed. Proc. ASCE Coastal Sediments'87 New Orleans, Louisiana, May 12–14. Amer. Soc. Civil Engineers.
- _____, T. M. Dellapenna, E. K. Hinchey, C. T. Friedrichs, M. L. Thompson, M. E. Smith and S. A. Kuehl. In press. Physical energy regimes, sea-bed dynamics and organism-sediment interactions along an estuarine gradient. In J. Y. Aller, S. A. Woodin and R. C. Aller, eds. Organism-Sediment Interactions. Univ. South Carolina Press, Columbia, South Carolina.
- Woodin, S. A. 1976. Adult-larval interaction in dense infaunal assemblages: patterns of abundance. J. Mar. Res. 34: 25–41.
- Wright, L. D., D. B. Prior, C. H. Hobbs, R. J. Byrne, J. D. Boon, L. C. Schaffner and M. O. Green. 1987. Spatial variability of bottom types in the lower Chesapeake Bay and adjoining estuaries and inner shelf. Estuar. Coast. Shelf Sci. 24: 765–784.
- _____, J. D. Boon, J. P. Xu and K. C. Kim. 1992. The bottom boundary layer of the bay stem plains environment of lower Chesapeake Bay. Estuar. Coast. Shelf Sci. 35: 17–36.
- _____, L. C. Schaffner and J. P.-Y. Maa. 1997. Biological mediation of bottom boundary layer processes and sediment suspension in the lower Chesapeake Bay. Mar. Geo. 141: 27–50.
- Zajac, R. N. and R. B. Whitlatch. 1988. Population ecology of the polychaete *Nephtys incisa* in Long Island Sound and the effects of disturbance. Estuaries 11: 117–133.

ADDRESS: College of William and Mary, School of Marine Science, Virginia Institute of Marine Science, P.O. Box 1346, Gloucester Point, Virginia 23062. CORRESPONDING AUTHOR: M. L. Thompson, P.O. Box 1346, Gloucester Point, Virginia 23062. E-mail: <michel@vims.edu>.