

2000

## Ecological interactions between benthic oyster reef fishes and oysters

Juliana Maria Harding

*College of William and Mary - Virginia Institute of Marine Science*

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



Part of the [Aquaculture and Fisheries Commons](#), [Ecology and Evolutionary Biology Commons](#), [Marine Biology Commons](#), and the [Oceanography Commons](#)

---

### Recommended Citation

Harding, Juliana Maria, "Ecological interactions between benthic oyster reef fishes and oysters" (2000). *Dissertations, Theses, and Masters Projects*. Paper 1539616684.  
<https://dx.doi.org/doi:10.25773/v5-ksj7-wy23>

This Dissertation is brought to you for free and open access by the Theses, Dissertations, & Master Projects at W&M ScholarWorks. It has been accepted for inclusion in Dissertations, Theses, and Masters Projects by an authorized administrator of W&M ScholarWorks. For more information, please contact [scholarworks@wm.edu](mailto:scholarworks@wm.edu).

## **INFORMATION TO USERS**

**This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.**

**The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.**

**In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.**

**Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.**

**Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.**

**Bell & Howell Information and Learning  
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA  
800-521-0600**

**UMI<sup>®</sup>**



***ECOLOGICAL INTERACTIONS BETWEEN BENTHIC  
OYSTER REEF FISHES AND OYSTERS***

---

**A Dissertation**

**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  
Doctor of Philosophy**

---

**by**

**Juliana M. Harding**

**© 2000**

**UMI Number: 9974955**

**Copyright 2000 by  
Harding, Juliana Maria**

**All rights reserved.**

**UMI<sup>®</sup>**

---

**UMI Microform 9974955**

**Copyright 2000 by Bell & Howell Information and Learning Company.**

**All rights reserved. This microform edition is protected against  
unauthorized copying under Title 17, United States Code.**

---

**Bell & Howell Information and Learning Company  
300 North Zeeb Road  
P.O. Box 1346  
Ann Arbor, MI 48106-1346**

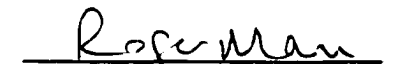
**APPROVAL SHEET**

**This dissertation is submitted in partial fulfillment of  
the requirements for the degree of**


**Doctor of Philosophy**

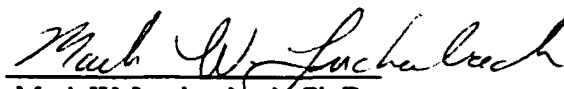
  
**Juliana M. Harding**

Approved, April 2000

  
**Roger E. Mann, Ph.D.**  
Committee Chairman/Advisor

  
**David A. Evans, Ph.D.**

  
**John J. Govoni, Ph.D.**  
NOAA/National Ocean Service  
Beaufort, NC

  
**Mark W. Luckenbach, Ph.D.**

  
**John E. Olney, Ph.D.**

  
**Mark R. Patterson, Ph.D.**

**DEDICATION**

**This dissertation is dedicated to my family, especially:**

**Helen R. Harding**

**James D. Harding**

**Teresa H. Kennedy**

**Lawrence P. Kennedy**

**and**

**Helen R. Williams**  
*(1912 - 1996)*

**Their support has been unwavering,  
their patience infinite.**

## TABLE OF CONTENTS

ACKNOWLEDGMENTS.....	vii
LIST OF TABLES .....	ix
LIST OF FIGURES .....	xi
ABSTRACT .....	xiv
INTRODUCTION .....	2
<b>CHAPTER 1: Estimates of naked goby (<i>Gobiosoma bosc</i>), striped blenny (<i>Chasmodes bosquianus</i>), and Eastern oyster (<i>Crassostrea virginica</i>) larval production around a restored Chesapeake Bay oyster reef .....</b>	<b>11</b>
<b>ABSTRACT .....</b>	<b>11</b>
<b>INTRODUCTION .....</b>	<b>12</b>
<b>METHODS .....</b>	<b>14</b>
Study site .....	14
Oyster population estimates .....	18
Fish population estimates .....	18
Data analyses .....	19
<b>RESULTS .....</b>	<b>27</b>
Water temperature and salinity data .....	27
Oyster population data .....	27
Fish population data .....	34
<b>DISCUSSION .....</b>	<b>37</b>
<b>CHAPTER 2: Temporal variation and patchiness of zooplankton around an intertidal oyster reef .....</b>	<b>40</b>
<b>ABSTRACT .....</b>	<b>40</b>
<b>INTRODUCTION .....</b>	<b>41</b>
<b>METHODS .....</b>	<b>44</b>
Study site .....	44
Sampling protocol .....	46
Data analyses .....	48
Water temperature and salinity data .....	48
Seasonal, diel, and tidal abundance patterns .....	48
Seasonal and diel horizontal distribution .....	50
Seasonal and diel zooplankton community composition .....	50



<b>RESULTS</b> .....	50
Water temperature and salinity data .....	50
Seasonal and diel abundance estimates .....	51
Seasonal and diel horizontal distribution .....	66
Seasonal and diel zooplankton community composition .....	66
<b>DISCUSSION</b> .....	82
<b>CHAPTER 3: Selective feeding behavior of larval naked gobies (<i>Gobiosoma bosc</i>) and blennies (<i>Chasmodes bosquianus</i> and <i>Hypsoblennius hentzi</i>): preferences for bivalve veligers</b> .....	86
<b>ABSTRACT</b> .....	86
<b>INTRODUCTION</b> .....	87
<b>METHODS</b> .....	88
Larval fish culture .....	88
Preliminary laboratory feeding experiments .....	89
Multi-factorial laboratory feeding experiments .....	90
Prey items .....	90
Experimental protocol .....	91
Data analyses .....	92
Effects of predator age, predator concentration, and prey type .....	92
Prey selectivity .....	92
<b>RESULTS</b> .....	98
Preliminary laboratory feeding experiments .....	98
Multi-factorial laboratory feeding experiments .....	98
Effects of predator age, predator concentration and prey type. ....	98
Prey Selectivity. ....	99
<b>DISCUSSION</b> .....	101
<b>CHAPTER 4: Distribution and diet of naked goby (<i>Gobiosoma bosc</i>) and striped blenny (<i>Chasmodes bosquianus</i>) larvae in relation to an intertidal oyster reef</b> .....	105
<b>ABSTRACT</b> .....	105
<b>INTRODUCTION</b> .....	106
<b>METHODS</b> .....	106
Study site .....	106
Data analyses .....	113
Water temperature and salinity data .....	113
Larval fish density and distribution patterns .....	113
Diets of larval naked gobies and striped blennies .....	114
<b>RESULTS</b> .....	116
Water temperature and salinity data .....	116
Larval fish density and distribution patterns .....	116
Diets of larval naked gobies and striped blennies .....	131

<b>DISCUSSION</b> .....	139
<b>SYNTHESIS</b> .....	150
<b>APPENDIX 1: Derivation of light attenuation profile for Palace Bar reef, Piankatank River, Virginia.</b> .....	164
<b>LITERATURE CITED</b> .....	167
<b>VITA</b> .....	187

## ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Roger Mann, for his guidance and support throughout this process. The contributions made by the other members of my advisory committee: Drs. David Evans, Mark Luckenbach, John Olney, Mark Patterson, and Jeff Govoni (NOAA/NOS, Beaufort, NC) are gratefully acknowledged. This document has benefited from their careful reviews and thoughtful comments. Drs. John Graves, James Perry, James Wesson, and Richard Wetzel provided valuable statistical and technical advice.

Funding for this project was provided by the U.S. E.P.A. Chesapeake Bay Program (CB 993267-02-1, CB 993267-03, and CB 993777-01), the VIMS/SMS Minor Research Grant Fund, and the VIMS Department of Fisheries Science.

The copious field assistance provided by Missy Southworth and Kenny Walker during 1996 and 1997 is gratefully acknowledged. Field, laboratory, and/or technical support was also provided by:

F. Arzayus	J. Duggan	R. Morales	J. Walker
K. Arzayus	K. Farnsworth	A. Mueller	J. Walter
B. Anderson	C. Fennessy	J. Nestlerode	L. Ward
I. Bartol	D. Fridley	M. Neubauer	G. White
G. Battisto	S. Gaichas	S. Neubauer	S. Wilson
H. Berquist	J. Goins	J. Newton	H. Yarnall
R. Boger	C. Goodbred	M. Nizinski	
D. Bonniwell	S. Goodbred	J. Oliver	
R. Bonniwell	V. Harmon	P. Richardson	
S. Brooke	A. Hayes	W. Reisner	
J. Brust	E. Hinchey	C. Robertson	
L. Calvo	M. Horvath	V. Roggero	
M. Cavalluzzi	K. Hovel	W. Rose	
V. Clark	D. Kerstetter	H. Simpkins	
G. Cicchetti	B. Kraus	C. Squyars	
C. Conrath	R. Kraus	S. Snyder	
P. Crewe	M. Lara	B. Trainum	
A. Curry	N. Lewis	M. Vogelbein	
T. Dellapenna	T. Lewis	M. Wagner	

**I would never have finished this process without the patient and loving encouragement provided by my family and friends; notably: Julie Modlin, Greg and Colleen Klimczak, Elizabeth Manning, Mary Jaworski, George and Kristen Padavick, and Dan Klco. Thanks also to my friends at VIMS for their support and encouragement.**

**Finally, I would like to thank the three men who inspired this journey and supported it throughout - teachers, role models, and friends: Drs. Albert J. Burky, James L. Heft, and P. Kelly Williams.**

## LIST OF TABLES

<b>Table 1: Summary of oyster length frequency estimates at Palace Bar reef, Piankatank River, Virginia for June 1996 from November 1996 length-frequency data. ....</b>	<b>22</b>
<b>Table 2: Average densities of oyster adult, spat, and boxes m<sup>2</sup> from diver surveys of Palace Bar reef in November 1995 and June and October 1996. ....</b>	<b>29</b>
<b>Table 3: Summary of ANOVAs used to compare oyster adult, spat, and box density data from diver surveys of Palace Bar reef during 1995 and 1996. ....</b>	<b>30</b>
<b>Table 4: Summary of fish density data from diver counts (fish m<sup>2</sup> ± standard error of the mean) of naked gobies and striped blennies from Palace Bar reef, Piankatank River, Virginia made bi-monthly from May through September, 1996. ....</b>	<b>31</b>
<b>Table 5: Summary of ANOVAs used to evaluate adult benthic fish densities from diver surveys of Palace Bar reef from May through September, 1996. ....</b>	<b>32</b>
<b>Table 6: Eastern oyster larval production and recruitment estimates for Palace Bar reef, Piankatank River, Virginia. ....</b>	<b>33</b>
<b>Table 7: Naked goby larval production and recruitment estimates for Palace Bar reef, Piankatank River, Virginia. ....</b>	<b>35</b>
<b>Table 8: Striped blenny larval production and recruitment estimates for Palace Bar reef, Pianatank River, Virginia. ....</b>	<b>36</b>
<b>Table 9: Summary of representative studies on estuarine zooplankton community composition and/or abundance in relation to spatial and/or temporal scales. ....</b>	<b>42</b>
<b>Table 10: Summary of species-specific seasonal zooplankton abundance estimates (± standard error ) from samples collected at Palace Bar reef, Piankatank River, Virginia from May through October 1996 and 1997. ....</b>	<b>53</b>
<b>Table 11: Summary of Kruskal-Wallis test results for plankton abundance during 1996 and 1997, Piankatank River, Virginia. ....</b>	<b>57</b>

<b>Table 12: Summary of species-specific diel zooplankton abundance estimates (<math>\pm</math> standard error ) from samples collected at Palace Bar reef, Piankatank River, Virginia during 36 h stations in June and August 1996. ....</b>	<b>59</b>
<b>Table 13: Summary of Kruskal-Wallis test results for plankton abundance from the June 27-28, 1996 station, Piankatank River, Virginia. ....</b>	<b>62</b>
<b>Table 14: Summary of Kruskal-Wallis test results for plankton abundance from the August 29-30, 1996 station, Piankatank River, Virginia. ....</b>	<b>65</b>
<b>Table 15: Summary of laboratory feeding experiments to evaluate feeding preferences of larval oyster reef fishes. ....</b>	<b>93</b>
<b>Table 16: Summary of ANOVAs performed on data from laboratory feeding experiments on individual species of larval fishes. ....</b>	<b>100</b>
<b>Table 17: Summary of larval fish samples collected near Palace Bar reef, Piankatank River, Virginia during 1996.....</b>	<b>117</b>
<b>Table 18: Summary of ANOVA tests for fish densities from bongo tows made during daylight hours from May through August 1996 near Palace Bar reef, Piankatank River, Virginia. ....</b>	<b>118</b>
<b>Table 19: Summary of ANOVA tests for fish densities from bongo tows made during the June 27-28 and August 29-30 stations near Palace Bar reef, Piankatank River, Virginia. ....</b>	<b>121</b>
<b>Table 20: Summary of ANOVA tests on numbers of feeding larval fishes caught in bongo tows near Palace Bar reef. ....</b>	<b>133</b>
<b>Table 21: Summary of dietary analyses for larval gobies and blennies from Palace Bar reef, Piankatank River, Virginia. ....</b>	<b>134</b>
<b>Table 22: Summary of Kruskal-Wallis tests comparing total number of prey items consumed by individual fishes between developmental stages within species. ..</b>	<b>135</b>

## LIST OF FIGURES

Figure 1: Conceptual model describing ecological interactions between oysters (keystone species) and benthic fishes (intermediate consumers). . . . .	9
Figure 2: Map of the Virginia portion of the Chesapeake Bay highlighting the Piankatank River and locating Palace Bar reef . . . . .	15
Figure 3: Schematic diagram of Palace Bar reef, Piankatank River, Virginia showing substrate composition and sampling grid layout. . . . .	17
Figure 4: Length-frequency diagrams with midpoint of the shell length class (mm) plotted against the percentage of the population within a shell length class for the Palace Bar reef oyster population. . . . .	21
Figure 5: Mean salinity (ppt, A.) and water temperature (°C, B.) patterns observed at Palace Bar reef, Piankatank River, Virginia during May through September 1996. . . . .	28
Figure 6: Map of the Piankatank River, Virginia in relation to the Chesapeake Bay showing Palace Bar reef (A.) and a schematic diagram of the reef including substrate composition (B.). . . . .	45
Figure 7: Mean salinity (ppt, A.) and water temperature (° C, B.) values (± standard error) for Palace Bar reef, Piankatank River, Virginia from May to October 1996. . . . .	52
Figure 8: Summary of seasonal zooplankton abundance patterns around Palace Bar reef, Piankatank River, Virginia. . . . .	54
Figure 9: Summary of zooplankton abundance patterns observed during June 27-28 1996 around Palace Bar reef, Piankatank River, Virginia. . . . .	60
Figure 10: Summary of zooplankton abundance patterns observed during August 29-30 1996 around Palace Bar reef, Piankatank River, Virginia. . . . .	63
Figure 11: Species-specific mean abundance (counts sample <sup>-1</sup> ) for the six most common	

zooplankton taxa plotted in relation to species-specific variance for 1996 and 1997 regular zooplankton collections around Palace Bar reef. ....	67
<b>Figure 12: Species-specific mean abundance (counts sample<sup>-1</sup>) for calanoid copepod adults and decapod zoea plotted in relation to species-specific variance for June 27-8, 1996 plankton collections around Palace Bar reef. ....</b>	<b>74</b>
<b>Figure 13: Species-specific mean abundance (counts sample<sup>-1</sup>) for the six most common zooplankton taxa plotted in relation to species-specific variance for August 29-30, 1996 plankton collections around Palace Bar reef. ....</b>	<b>76</b>
<b>Figure 14: Species-sample biplots for detrended correspondence analyses (DCA) describing seasonal changes in zooplankton community assemblage and species abundance for 1996 (A.) and 1997 (B.). ....</b>	<b>80</b>
<b>Figure 15: Species-sample biplots for detrended correspondence analyses (DCA) describing diel changes in zooplankton community assemblage and species abundance for June (A.) and August 1996 (B.). ....</b>	<b>81</b>
<b>Figure 16: Percentage consumption of prey items and prey-specific veliger abundance plotted in relation to percentage availability for laboratory feeding experiments with naked gobies, feather blennies, and striped blennies. ....</b>	<b>95</b>
<b>Figure 17: Map of the Piankatank River, Virginia in relation to the Chesapeake Bay showing Palace Bar reef (A.) and the river reach bounded by Ginney Point (1.) and Stove Point Neck (2.). ....</b>	<b>109</b>
<b>Figure 18: Summary of seasonal larval fish densities around Palace Bar reef, Piankatank River, Virginia. ....</b>	<b>119</b>
<b>Figure 19: Summary of larval fish densities observed during June 27-28 1996 around Palace Bar reef, Piankatank River, Virginia. ....</b>	<b>122</b>
<b>Figure 20: Summary of larval fish densities observed during August 29-30, 1996 around Palace Bar reef, Piankatank River, Virginia. ....</b>	<b>124</b>



**Figure 21: Length-frequency distribution for preflexion (A.) and post-flexion (B.) naked goby larvae collected around Palace Bar reef, Piankatank River, Virginia from May through August, 1996. .... 127**

**Figure 22: Length-frequency distribution for preflexion (A.) and post-flexion (B.) striped blenny larvae collected around Palace Bar reef, Piankatank River, Virginia from May through August, 1996. .... 128**

**Figure 23: Densities of larval naked gobies and striped blennies observed around Palace Bar reef, Piankatank River, Virginia between 18:00 on June 27, 1996 and 05:00 on June 28, 1996 from three collection locations: north (A.), south (B.) and in the tidal wake zone (C.) in relation to tidal flow (D.). .... 129**

**Figure 24: Percentage consumption of prey items by larval gobies and blennies plotted in relation to percentage availability in the plankton for (A.) preflexion naked gobies, (B.) post-flexion naked gobies, (C.) preflexion striped blennies, and (D.) post-flexion striped blennies. .... 136**

**Figure 25: Light attenuation profiles and vertical distribution of feeding larval naked gobies and striped blennies near Palace Bar reef, Piankatank River, Virginia at dawn (A.), noon (B.), dusk (C.) and midnight (D.).. .... 142**

**Figure 26: Frequency histogram describing temporal patterns of oyster spawning (A.) and settlement (B.) in the Piankatank River, Virginia from 1970 - 1999..... 155**

**Figure A1: Light attenuation data for the Piankatank River (Chesapeake Bay Program station LE3.7) for June 12, 1996. .... 166**

## ABSTRACT

Restoration of oyster reef structures rehabilitates habitats and the multi-level ecological communities built on eastern oysters (*Crassostrea virginica*), the keystone species. Quantitative descriptions of ecological interactions within a habitat are required to delineate essential fish habitats for management and protection. Parallel development of primary (oysters) and secondary trophic levels (benthic fishes) offer an ecological metric of restoration progress over time. The interaction between larval oysters and larval fishes (e.g., *Gobiosoma bosc*, *Chasmodes bosquianus*) is quantitatively examined. Oyster settlement estimates for Palace Bar reef, Piankatank River, Virginia are of the same order of magnitude as field densities of recently settled oysters. Benthic fish settlement estimates are within an order of magnitude of observed adult densities. Zooplankton community composition around the reef is temporally variable and plankton densities range from  $10^2$  -  $10^6$  animals per  $m^3$  across temporal scales. Nocturnal densities of naked goby and striped blenny larvae around Palace Bar reef were 3 to 4 orders of magnitude higher than densities observed during daylight hours. Diurnal changes in larval fish abundance near Palace Bar reef are related to ambient light intensities and diurnal vertical migration by prey species. Naked goby, striped blenny, and feather blenny (*Hypsoblennius hentzi*) larvae selectively consumed bivalve veligers in multi-factorial laboratory feeding experiments. Temporal co-occurrence of larval oysters and larval fishes was not observed in 1996 field collections although historic oyster settlement data strongly support the probability of co-occurrence during most years. Two different methods are used to estimate the larval oyster - larval fish interaction in the absence of field data. Given existing oyster and fish demographics on Palace Bar reef, larval fishes have the capacity to drastically reduce, perhaps eliminate, local veliger populations if they co-occur. The strength of this interaction is directly related to oyster demography-fecundity relationships. In the absence of veligers, larval fishes consume other plankton taxa that are abundant around the reef. Naked gobies and striped blennies are generalists. Oyster reefs provide optimal rather than essential habitat. Reef restoration will facilitate development of related ecological communities by providing optimal habitat conditions for these ubiquitous estuarine species.

**Key words:** oyster, *Crassostrea virginica*, oyster reef, restoration, essential fish habitat, keystone species, ecological interaction, estuarine habitat, naked goby, *Gobiosoma bosc*, striped blenny, *Chasmodes bosquianus*

***ECOLOGICAL INTERACTIONS BETWEEN BENTHIC  
OYSTER REEF FISHES AND OYSTERS***

## INTRODUCTION

Estuarine restoration efforts are gaining support as the complexity of the original systems and extent of ongoing habitat degradation are realized. As estuarine habitats evolved over geologic time, the associated ecological communities moved toward temporal persistence in numbers, species richness, species composition, and trophic composition or stability per Sale (1980). Middle Atlantic estuaries such as Chesapeake Bay are geologically quite young (Hargis, 1999) but supported multi-level ecological communities including oyster reefs until modern times. Many ecological communities contain keystone species or species that determine community structure and play a critical role in community function (Paine, 1969). In Chesapeake Bay, the eastern oyster (*Crassostrea virginica*) was a keystone species. Indeed, the Chesapeake Bay's oyster reef system and associated fauna were "its (the Bay's) most important, characteristic and productive community before its destruction." (Hargis, 1999).

Oysters and oyster reefs were a dominant feature of the shallow (<9 m depth) portions of Chesapeake Bay and its tributaries in pre-colonial times. Physical intertidal reef structures created by oysters and their shells were so abundant that they were navigational hazards for early colonists (Hargis, 1999). Locally, these large reefs structures probably affected circulation patterns and water column mixing thus enhancing the food supply for resident oysters (Newell, 1988; Hargis, 1999). Oysters are filter feeding bivalves that remove suspended organic and inorganic particles from the water column and produce mucus-bound biodeposits that may be used by benthic organisms (Newell, 1988). Oysters were a keystone species in that their filtration and deposition abilities provided an important trophic link

between pelagic and benthic food webs (Newell, 1988; Baird and Ulanowicz, 1989). Oysters produce habitat and food resources (biodeposits) that attract and sustain representatives of higher trophic levels including benthic invertebrates and fishes as well as pelagic finfishes. Benthic fishes such as naked gobies (*Gobiosoma bosc*) and striped blennies (*Chasmodes bosquianus*) forage on invertebrates and macroalgae on the reef's surface and use the habitat services provided by the reef structure i.e., shelter and nesting sites. Piscivorous finfishes including striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and summer flounder (*Paralichthyes dentatus*), which use reef habitats as nursery grounds and feeding areas, consume naked gobies and striped blennies (e.g., Markle and Grant, 1970; Mann and Harding, 1997, 1998; Harding and Mann, 1999; Breitbart, 1999). Thus, as oyster reefs developed in Chesapeake Bay, multi-level ecological communities centered on the reefs developed in parallel. Many of the reef-associated organisms have broad habitat or niche requirements. Functionally, competition for resources may limit exploitation of the habitat, thus an animal's realized niche may be narrower than its fundamental niche.

Within the last century, most of the resident oyster populations along the Atlantic and Gulf coasts have declined to a fraction of their original size reducing or eliminating natural reef fields and the ecological communities that they supported. Natural intertidal oyster reefs in the Chesapeake were essentially non-existent by the 1980's. Surviving Chesapeake Bay oyster reefs are subtidal and have been drastically reduced in terms of vertical relief and basal extent (Hargis, 1999). Coordinated oyster reef restoration efforts in the Chesapeake Bay gained prominence in the early 1990s (see Luckenbach et al., 1999 and references therein) and continue to advance not only in the Chesapeake Bay region, but throughout the southeastern United States (Coen and Luckenbach, 1999; Luckenbach, et al., 1999; Mann, 2000).

Current efforts are beginning to focus on the restoration of degraded estuarine communities for ecological purposes under the auspices of the Magnuson Fishery

Conservation and Management Act (Public Law 94-265) as amended by The Sustainable Fisheries Act (Public Law 104-297). The amended Magnuson Act provides for the protection, restoration, and enhancement of all essential fish habitats (EFH) and defines EFH as “those waters and substrate necessary to fish for spawning, breeding, feeding, and or growth to maturity”. Finfish, molluscs, crustaceans, and all other marine animals and plants except marine mammals and birds are included in the definition of “fish”. With the explicit requirement to consider EFH in management decisions, the amended Magnuson Act focuses on fish production in the context of integrated ecosystem-based management aimed at preserving habitat function and integrity (Benaka, 1999 and references therein). Identification of EFH involves describing the geographic range and habitat requirements for all life history stages of each target species across relevant temporal and spatial scales (Schmitt, 1999). Designation of a habitat as EFH per guidelines suggested by the National Marine Fisheries Service (NMFS; 1997) would attempt to incorporate the following four levels of information (as described by Minello, 1999):

- **Level 1: presence/ absence or frequency of occurrence of a fisheries species. These basic data may be used to describe the geographic range of a species and the habitat if sampling methods are adequate.**
- **Level 2: distribution and abundance information for a fisheries species. These data should be collected with comparable methods across similar scales and should be representative of the intrahabitat types available to the species within a system. Per Minello (1999) “intrahabitat” describes smaller areas within a habitat characterized by distinct features important to fisheries species.**
- **Level 3: functional relationships between species and intrahabitats: reproduction, growth, and survival.**
- **Level 4: fisheries species production in relation to intrahabitat type.**

**Currently there are some data sets for particular systems that can be used to address Level 3**

questions (See Minello, 1999 and Able, 1999) but collection of data sets amenable to Level 4 interpretation will require methodological changes and consideration of landscape level processes (Able, 1999). Under these guidelines, intrahabitats that are important to the long term productivity of a species or unusually sensitive to degradation may be designated as habitat areas of particular concern (HAPC; NMFS, 1997). Consideration of species EFH requirements will facilitate qualitative descriptions of the ecological communities associated with specific habitat types.

This dissertation contributes to the oyster reef restoration effort in that its overall goal is to describe a component of the oyster reef system, an estuarine intrahabitat (Minello, 1999), in a quantitative manner. We have an idea of how the restoration of oyster reef communities should progress based on both observation of historical components and conceptual models (e.g., Baird and Ulanowicz, 1989; Hartman and Brandt, 1995a and b). The conceptual model presented by Baird and Ulanowicz (1989) depicting the oyster as a primary source of benthic-pelagic coupling in Chesapeake Bay has been subsequently entrenched in the literature. Conceptual EFH models (see Benaka, 1999 and references therein) are just emerging. The practicality and application of EFH models to oyster reefs has yet to be tested beyond EFH Level 2 per Minello (1999). It should be possible to test and revise existing EFH models with the quantitative data presented herein.

Ongoing oyster reef restoration projects and companion monitoring studies in Virginia are beginning to provide qualitative and quantitative data that may be used to evaluate restoration methods (e.g., Luckenbach et al., 1999) as well as the function of oyster habitats within the EFH perspective. Bartol and Mann (1997, 1999a and b) have demonstrated the positive effects of protected microhabitats within three dimensional reef habitat on oyster settlement and survival. Oyster settlement and adult densities on restored reefs, shell plants, and local natural reefs are monitored annually (J. Wesson, VMRC, unpublished data; R. Mann, VIMS, unpublished data). Reef-associated benthic invertebrate communities on restored reefs are being described along a salinity gradient (J. Nestlerode, VIMS, unpublished

data). Comparisons between use of reef versus non-reef habitat by ecologically and commercially valuable finfishes and decapod crustaceans are in progress in the Piankatank River (Harding and Mann, 1999; J. Harding and R. Mann, VIMS, unpublished data) and at Fishermen's Island (J. Nestlerode, M. Luckenbach, and F. O'Beirn, VIMS, unpublished data).

Oysters are keystone species but the exact nature of this trophic relationship has yet to be quantified. Oyster reefs support complex trophic systems (Baird and Ulanowicz, 1989; Hartman and Brandt, 1995a and b) so examination of oysters alone is only the beginning. Other trophic levels need to be examined quantitatively to fully understand the scope of trophic interactions within oyster reef communities as well as longer term recruitment processes that shape these communities over time. Restored oyster reef communities should develop towards climax or equilibrium (*sensu* Whittaker, 1953). Examination of restored communities from the construction of physical habitat onwards over appropriate temporal and spatial scales provides a method to describe this progression toward climax. One of many potential ecological metrics of restoration progress over time is the development of reef fish assemblages as examples of higher trophic levels moving towards stability in numbers, species richness, species composition, or trophic composition (Sale, 1980). The development of secondary trophic levels (benthic fishes) when the first level (oysters) is stable is part of the ecological progression. This dissertation builds upon oysters *per se* to establish an oyster - benthic fish trophic relationship. This study focuses on the larval oyster - larval benthic fish pathway to examine the keystone relationship presented by Baird and Ulanowicz (1989) because benthic fishes do not eat oysters except in the larval stages.

From an ecological perspective, there may be merit in using estimates of larval production for a reef as a metric of restoration success *i.e.*, does the oyster population on a reef produce enough larvae to maintain observed adult oyster densities and be considered self-sustaining? A combination of oyster larval settlement estimates with similar estimates for benthic reef fish species is worthy of examination as a meaningful metric of reef



community development with self-sustaining populations of both oysters and benthic fishes as a restoration goal or criteria for success. Presumably, if a reef supports self-sustaining lower and intermediate trophic levels, upper level community relationships should also be developing. To that end, adult naked goby, striped blenny, and oyster density patterns on Palace Bar reef, Piankatank River, Virginia, are described and related to reef-specific larval production and recruitment estimates for all three species in Chapter 1: Estimates of naked goby (*Gobiosoma bosc*), striped blenny (*Chasmodes bosquianus*), and Eastern oyster (*Crassostrea virginica*) larval production around a restored Chesapeake Bay oyster reef.

Many species of oyster reef benthic macrofauna, including oysters and reef fishes, produce planktonic larvae that seasonally enrich the plankton community around the reef. A diverse and abundant plankton community provides food resources for local planktivores as well as the potential for interaction between oyster veligers and larval reef fishes depending upon the spatial and temporal distribution of both predators and prey. The horizontal spatial (100s of m) and temporal (seasonal, tidal, diel) patterns in zooplankton community composition and thus, the potential prey field for larval reef fishes, around Palace Bar reef are described in Chapter 2: Temporal variation and patchiness of zooplankton around an intertidal oyster reef.

Successful consumption of oyster veligers by reef fish larvae in nature depends on many factors operating on a range of spatial and temporal scales. Multi-factorial laboratory feeding experiments provide a controlled setting to test the assumption that oyster reef fish larvae will selectively consume oyster veligers if they spatially and temporally co-occur. A series of laboratory feeding experiments designed to examine interactions between larval fishes and bivalve veligers by testing the effects of predator (larval fish) age, predator concentration, and prey type on feeding selectivity using bivalve veligers, wild plankton, or veliger-wild plankton mixtures as prey for laboratory cultured naked goby, striped blenny, and feather blenny larvae are described in Chapter 3: Selective feeding behavior of larval naked gobies (*Gobiosoma bosc*) and blennies (*Chasmodes bosquianus* and *Hypsoblennius hentzi*):

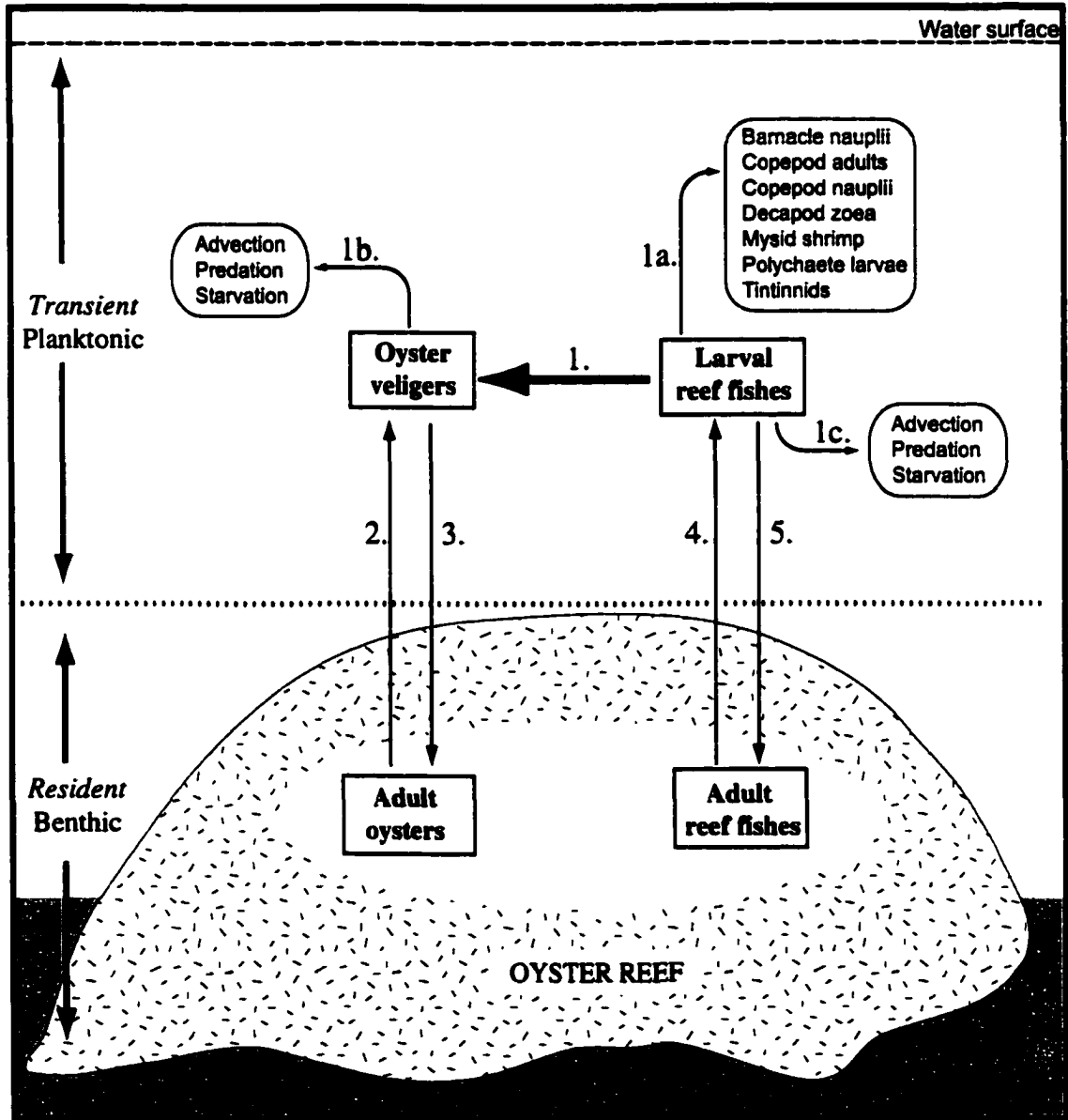
preferences for bivalve veligers.

Even if larval reef fishes selectively consume bivalve veligers in laboratory experiments, a more realistic examination of this predator-prey relationship requires field collections of larval fish predators and their prey field on similar spatial and temporal scales. Thus, the abundance, distribution, and diets of naked goby and striped blenny larvae associated with Palace Bar reef across seasonal and diurnal temporal scales are described and placed in context with the available prey field data in Chapter 4: Distribution and diet of naked goby (*Gobiosoma bosc*) and striped blenny (*Chasmodes bosquianus*) larvae in relation to an intertidal oyster reef.

These four chapters provide data that are used to quantitatively assess the role of the larval oyster-larval fish interaction on the development of oyster reef communities post-restoration. A conceptual model describing ecological interactions between oysters (keystone species) and benthic fishes (intermediate consumers) is proposed (Figure 1). The growing oyster reef data set furthers understanding of existing conceptual models of Bay trophic structure (Baird and Ulanowicz, 1989; Hartman and Brandt, 1995a and b) and EFH (Benaka, 1999). Focused examination of these models is needed to place current and future restoration projects in an appropriate ecological framework.

**Figure 1: Conceptual model describing ecological interactions between oysters (keystone species) and benthic fishes (intermediate consumers). The following questions relate to Figure 1 and the processes depicted graphically therein.**

- 1. Is there predation on larval oysters by larval fishes?**
  - 1a. What are other possible sources of food for larval fishes around the reef?**
  - 1b. What are alternate sources of mortality for larval oysters?**
  - 1c. What are potential sources of mortality for larval fishes?**
- 2. How many oyster larvae are produced by the reef's oyster population?**
- 3. How many oyster larvae settle onto the reef?**
- 4. How many naked goby and striped blenny larvae are produced by the reef's fish populations?**
- 5. How many fish larvae settle onto the reef?**



Portions of this chapter have been previously published:

Harding, J.M. and R. Mann. 2000. *Bulletin of Marine Science*. 66(1): 29-45.

## CHAPTER 1

Estimates of naked goby (*Gobiosoma bosc*), striped blenny (*Chasmodes bosquianus*), and Eastern oyster (*Crassostrea virginica*) larval production around a restored Chesapeake Bay oyster reef

### ABSTRACT

Naked gobies (*Gobiosoma bosc*) and striped blennies (*Chasmodes bosquianus*) rely on oyster reefs for nesting sites, feeding grounds, and refugia from predation by upper level piscivores. Seasonal densities of eastern oysters (*Crassostrea virginica*), naked gobies, and striped blennies on Palace Bar reef, Piankatank River, Virginia were quantified and used to develop species-specific larval production estimates. Densities of oyster adults, juveniles, and articulated shell valves (the result of recent mortality) did not significantly change from November 1995 to November 1996. Adult naked goby and striped blenny densities varied with substrate type and season; highest fish densities for both species were observed in August 1996. Areas where shell substrate dominated the bottom supported fish densities up to 14 times greater than those observed in habitat areas lacking shell. Larval production and recruitment estimates for Palace Bar reef oysters are of the same order of magnitude as observed field densities. Benthic fish larval production estimates are within an order of magnitude of adult densities and are similar to previous recruitment estimates for Chesapeake Bay naked gobies. Species-specific production estimates for both oysters and fishes are sufficient to sustain observed adult densities on Palace Bar reef, Piankatank River, Virginia.

## INTRODUCTION

Oyster reefs were physical and biological cornerstones for shallow water communities in the Chesapeake Bay until the early 20<sup>th</sup> century. The physical reef structures created by eastern oyster (*Crassostrea virginica*) shells created both navigational hazards and highly heterogeneous three-dimensional habitats for benthic estuarine fauna. The living oysters helped maintain shallow water quality by filtering (Newell, 1988) and were central in the complex trophic structure that supported nursery and feeding grounds for both recreational and commercial finfishes e.g., striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), spotted seatrout (*Cynoscion nebulosus*), Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and Atlantic menhaden (*Brevoortia tyrannus*); (Harding and Mann, 1999; Coen et al., 1999; see also Luckenbach et al., 1999 and references therein). As oyster populations have declined because of overfishing, disease, and habitat degradation, the associated shallow water communities and the fisheries that they supported have suffered. Current oyster reef restoration activities are examining the trophic networks centered on oyster reefs as an index of oyster restoration success and potential associated fishery rehabilitation (Coen et al., 1997, Mann and Harding, 1997, 1998; Coen et al., 1999; O'Beirn et al., 1999).

The life history of the eastern oyster has been described (Kennedy et al., 1996 and references therein). Adult oysters increase metabolic activity as water temperatures rise in the spring. Oysters reach sexual maturity after one year or at approximately 18 to 23 mm shell length. Spawning activity begins when water temperatures are above 12 to 15°C (e.g. in Virginia: May to June), and continues until late summer. The veliger larvae are planktonic for 14 to 21 days after which they settle onto hard substrate and metamorphose. Continued growth as sessile bivalves creates and maintains three dimensional reef habitats.

Several benthic fish species including naked gobies (*Gobiosoma bosc*) and striped

blennies (*Chasmodes bosquianus*) commonly inhabit oyster reef interstices and rely on oyster reefs for nest sites, feeding grounds, and shelter (Wells, 1961; Dahlberg and Conyers, 1973). Habitat use by these fishes is not restricted to the three-dimensional hard structure of reefs, but the reef's structural relief and heterogeneity increase shell surface area and available benthic fish habitat (Bahr, 1974) much as the heterogeneity of coral reefs is facilitated by living corals (Ebeling and Hixon, 1991). These small (< 65 mm) benthic fishes are intermediate in the oyster reef trophic structure. Adult gobies and blennies graze on infaunal and epibenthic invertebrates (Dahlberg and Conyers, 1973; Nero, 1976) and are prey items for juvenile apex predators (e.g., striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*)) associated with reef communities (Markle and Grant, 1970; Nero, 1976; Mann and Harding, 1997; Breitburg, 1999; Harding and Mann, 1999).

Seasonal abundance estimates for benthic reef fishes (i.e., naked gobies and striped blennies) must consider overwintering and spawning patterns. During the winter months when temperatures are low (<10°C), adult fishes move into deeper water and burrow into mud (Hildebrand and Cable, 1938; Dahlberg and Conyers, 1973; Fritzsche, 1978) or simply reduce activity and become more cryptic (Nero, 1976). As temperatures rise, fish activity increases and both naked goby and striped blenny adults are more visible within the reef matrix (Dahlberg and Conyers, 1973).

The life histories of striped blennies and naked gobies have been previously described (Nero, 1976, Fritzsche, 1978; Breitburg, 1988, 1989, 1991, 1999; Harding, 1999 [see Chapter 3 of this volume]). Naked gobies reach sexual maturity at the beginning of their second year (total length (TL) approximately 24 mm, Nero, 1976). Gobies spawned early in the spawning season (e.g., May to June) grow to approximately 16 mm TL by the end of September or October. By the beginning of the following spawning season, these same fishes are at least 22 to 26 mm TL and sexually mature (Nero, 1976). Adult gobies and blennies build nests in clean, articulated empty oyster shells in early to mid-summer after

water temperatures increase above 19 to 20°C (Dahlberg and Conyers, 1973). The adhesive eggs hatch after 1 to 2 weeks (Nero, 1976). Nests are maintained and defended by male fishes. Gobies and blennies are polygamous; multiple females may visit a male's nest during the course of a spawning season. Naked goby and striped blenny larvae begin feeding within 2 h after hatching (J. Harding, unpublished data) and are planktonic for 2 to 3 weeks (Breitburg, 1989, 1991; Harding, 1999 [see Chapter 3 of this volume]). Seasonally, goby larvae may dominate ichthyoplankton collections within the Chesapeake Bay (Shenker et al., 1983; Cowan and Birdsong, 1985; Olney, 1983, 1996). Laboratory experiments have shown that larval naked gobies and striped blennies preferentially prey on oyster veligers and may be a significant source of veliger mortality (Harding, 1999 [see Chapter 3 of this volume]). Selective consumption of bivalve veligers by larval gobies has been demonstrated in Biscayne Bay by Houde and Lovdal (Gobiidae, 1984) and the Chesapeake Bay by Olney (*Gobiosoma ginsburgi*, 1996).

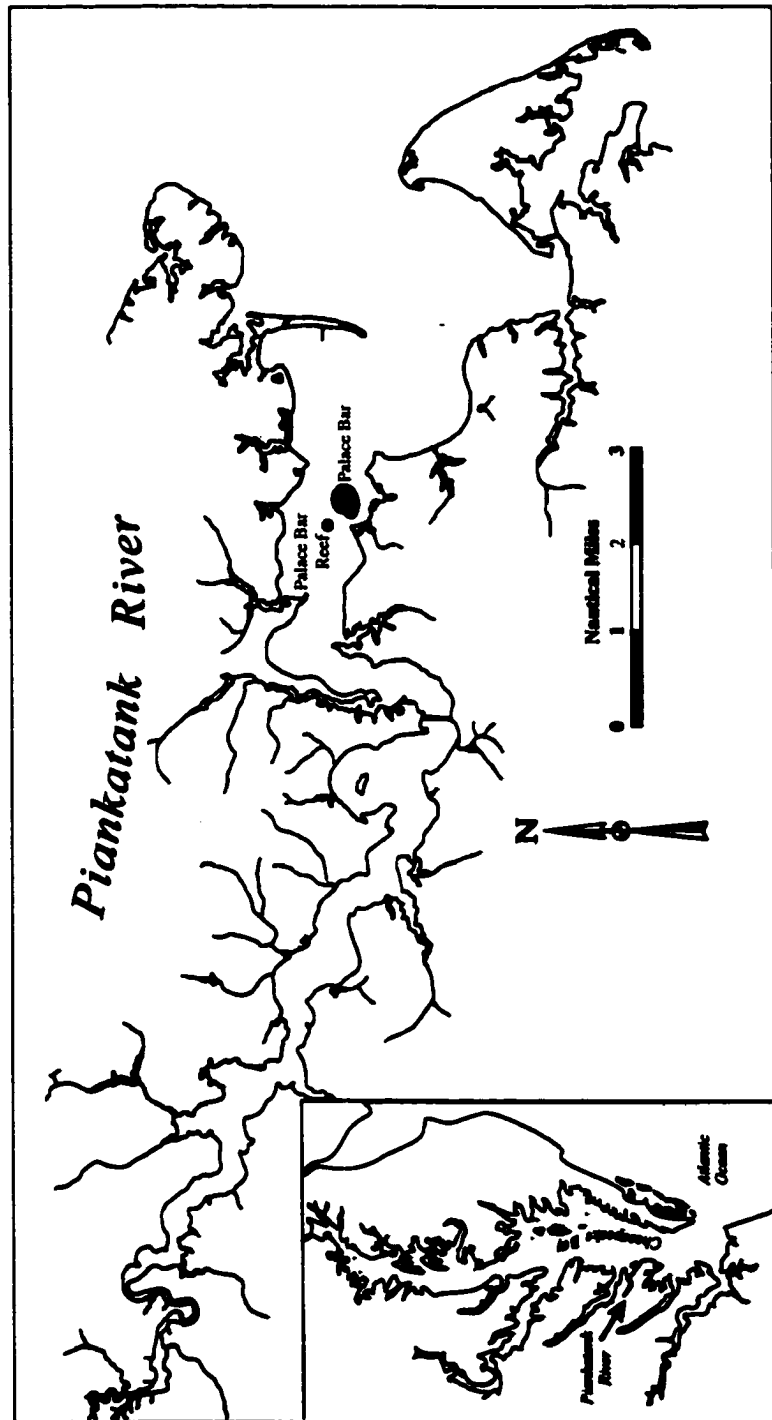
While oyster densities are fundamental to the maintenance of living oyster reef communities, larval fish densities are partially driven by the presence of appropriate habitat (feeding and nesting) for adult fishes. Densities of naked gobies and striped blennies are dependent upon the presence of oyster shells for nesting habitat. In this sense, reef communities are dependent on larval production of both veligers and benthic fishes being sufficient to sustain recruitment levels necessary to yield observed adult densities; i.e., the community is at equilibrium with respect to lower trophic levels. The objectives of this study were to describe adult naked goby, striped blenny, and oyster density patterns on Palace Bar reef, Piankatank River, Virginia, and relate observed adult densities to larval production and recruitment estimates for all three species.

## METHODS

### *Study site*

Palace Bar reef, Piankatank River, Virginia was the study site for benthic fish and oyster reef surveys. Palace Bar reef is an intertidal oyster reef (300 x 30 m, reef depth range



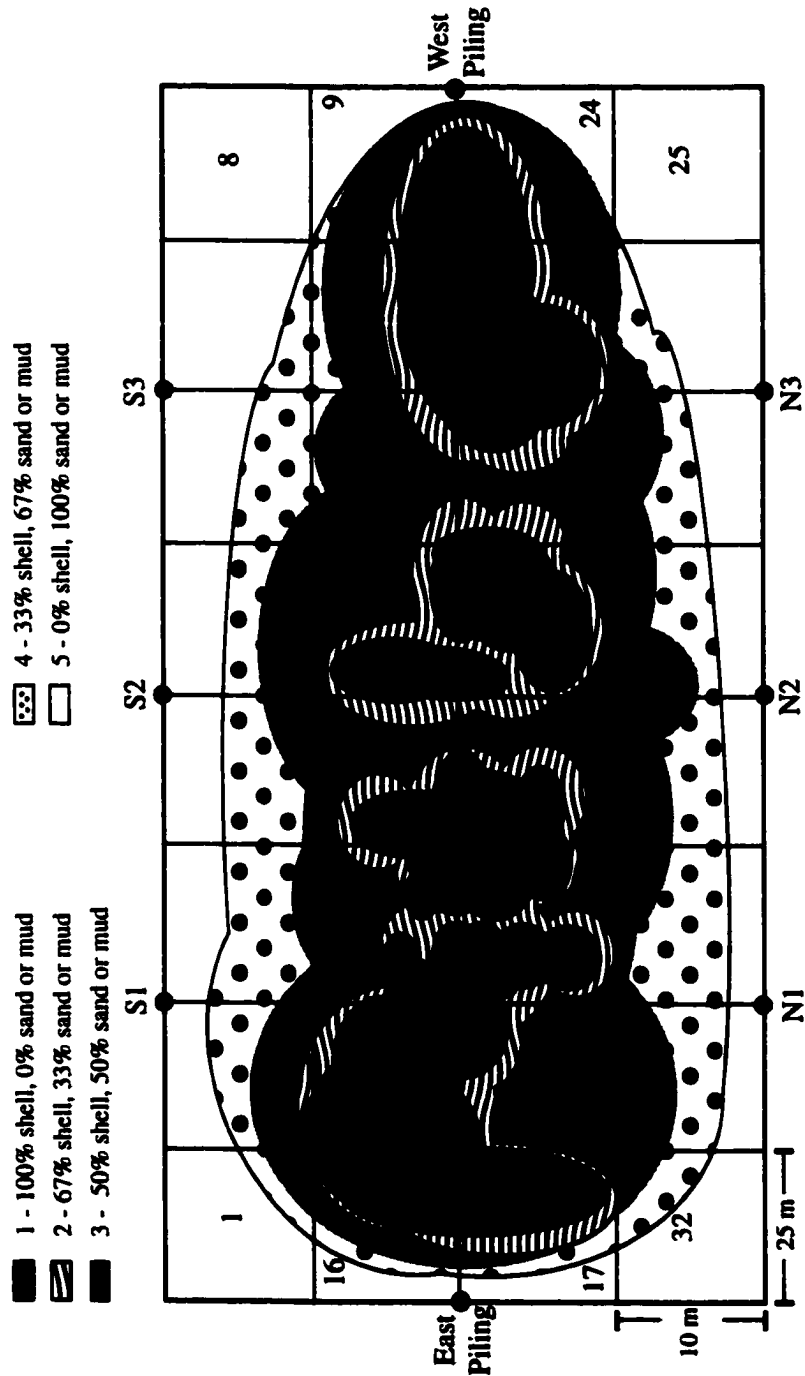


**Figure 2:** Map of the Virginia portion of the Chesapeake Bay highlighting the Piankatank River and locating Palace Bar reef (N 37° 31' 41.69", W 76° 22' 25.98") adjacent to Palace Bar oyster grounds.

of 0.5 m above MLW to 3 m below MLW) adjacent to the historic Palace Bar oyster grounds (Bartol and Mann, 1997; Figure 2). The reef was built in 1993 by the Virginia Marine Resources Commission (VMRC) Shellfish Replenishment program as a series of shell mounds centered on and around an east-west centerline 300 m long (Mann et al., 1996). The reef perimeter is marked on north and south sides by a series of yellow marker buoys (Figure 3; N1-N3 and S1-S3). Approximately 70% of the reef (0.63 ha) is composed of oyster shell, while the remaining area (0.27 ha) is crushed clam shell (Figure 3). Since its construction in 1993, Palace Bar reef has received annual oyster spat settlement (Bartol and Mann, 1997; J. Wesson, Virginia Marine Resources Commission, Newport News, Virginia, unpublished data) and all oysters on the reef are due to natural settlement and recruitment i.e., the reef was not initially seeded with oysters.

The area delineated by the reef marker buoys was divided into 32 grid squares for the benthic fish surveys described herein; substrate within these grid squares spans a range of conditions including mud (at the edge of the reef area) sand, shell, and various mixtures (Figure 3). Mean tidal range in the Piankatank River is approximately 0.4 m. Water temperature and salinity were recorded at the reef once a week in conjunction with benthic fish surveys and other monitoring studies from May to October during 1996. Water samples were taken at the surface and just above the bottom with a Niskin bottle. Temperature was measured immediately with a thermometer ( $\pm 0.5^{\circ}\text{C}$ ) and salinity was measured with a refractometer ( $\pm 1\text{‰}$ ).

Palace Bar, a natural shell bar (approximately 31 hectares), is immediately adjacent (within 200 m) to Palace Bar reef (Figure 2). The bar is surveyed annually by the Virginia Institute of Marine Science (VIMS) Molluscan Ecology stock assessment program; stock assessment data from Palace Bar were used to conservatively estimate length-frequency relationships for Palace Bar reef oysters (see Oyster length-frequency distribution below). Water depth at Palace Bar ranges from 1 to 4 m; water temperatures and salinities at Palace Bar are similar to those observed at Palace Bar reef (1993-95; R. Mann, Dept. of Fisheries



**Figure 3:** Schematic diagram of Palace Bar reef, Piankatank River, Virginia showing substrate composition and sampling grid layout. The East and West marker pilings and North (N1 - N3) and South (S1 - S3) lines of marker buoys form the boundaries for the reef perimeter. The grid within the reef perimeter forming squares (1 to 32) was used as a reference for randomly selecting sites for diver surveys of benthic fishes.

Science, VIMS, Gloucester Point, Virginia, unpublished data).

### *Oyster population estimates*

**Adult oyster, spat, and box density:** Diver surveys of Palace Bar reef were conducted in November 1995, June 1996, and October 1996 through a joint effort by the VIMS Molluscan Ecology program and the VMRC Shellfish Replenishment program (Mann and Wesson, 1996a). Divers removed all oysters and shell from within randomly selected squares 0.5 m per side by 0.15 m deep. The material was sorted and oyster adults (oysters > 30 mm (maximum dimension)), juveniles ("spat" or oysters < 30 mm (maximum dimension)), and clean, empty articulated shells without oysters ("boxes") were counted.

**Oyster length-frequency distribution:** Patent tong surveys were conducted on Palace Bar oyster grounds, immediately adjacent to Palace Bar reef (Figure 2) in November 1996 as part of the annual VIMS Molluscan Ecology stock assessment program. Standard hydraulic patent tongs were used to collect 1 m<sup>2</sup> bottom samples. Oysters were counted (adults, spat, boxes as in the diver surveys above) and measured to the nearest 1.0 mm and a length-frequency distribution was constructed for the population using 5 mm shell length intervals (Mann and Wesson, 1996b). This length frequency distribution was used for Palace Bar reef oyster population production estimates (see Oyster production estimates below).

### *Fish population estimates*

**Adult fish density:** Density estimates for adult naked gobies and striped blennies at Palace Bar reef were determined from May through September 1996 with a second, distinct set of diver surveys. The bi-monthly benthic fish survey schedule was disrupted on 25 July and 6 September 1996 by the presence of hurricane or tropical storm remnants. On each sampling date, 12 grid squares were randomly chosen out of the 32 grid squares available on the reef using a random number table prior to going in the field (Figure 3). Within each target grid square divers placed a 0.25 m<sup>2</sup> square frame (0.5 m per side) on the bottom, waited for slack-tide when visibility was approximately 1 m, and then counted all adult fishes visible

on or within the substrate. "Adult" fish were > 40 mm long and displayed breeding coloration from May through late July. Two divers began facing each other over the square frame and then slowly worked around all 4 sides of the frame in a clockwise fashion counting fishes in the interior of the frame as well as along the edges. Substrate composition and water depth were recorded within each square. Substrate was classified into 5 categories by its percentage composition of shell: 100% shell, 67% shell/ 33% sand or mud, 50% shell/50% sand or mud, 33% shell/67% sand or mud, or 100% sand or mud (Figure 6). Water depths were considered either deep (> 1.5 m) or shallow (< 1.5 m).

#### *Data analyses*

Significance levels for all analyses were established *a priori* at  $p = 0.05$ . Assumptions of homogeneity of variance were tested with Bartlett's test and assumptions of normality were tested using the Ryan-Joiner test (similar to Shapiro-Wilks test per Minitab, 1995) for normality. Unless otherwise noted, all data met both assumptions without transformation or were transformed to meet these assumptions. Fisher's least significant difference (LSD) pairwise comparison test was used for post-hoc multiple comparisons (Minitab, 1995; Zar, 1996). All statistical tests were completed using Minitab software (v. 10x; Minitab, 1995).

#### Water temperature and salinity data

Water temperature and salinity data collected weekly from May to October 1996 at Palace Bar reef were  $\log_e$  transformed prior to analyses and satisfied assumptions of both homogeneity of variance and normality after transformation. Temperature and salinity data taken at the surface and just above the substrate (within 0.25 m) adjacent to the reef (within 5 m) were each compared with an ANOVA.

#### Adult oyster, spat, and oyster box density

Density estimates (animals  $m^{-2}$ ) from diver surveys of Palace Bar reef for adult oysters and oyster spat were available for November 1995, June 1996 and October 1996; oyster box data were available only for November 1995 and June 1996. Reef oyster density data were evaluated with 2-factor ANOVAs (year x month). Adult oyster density data were

transformed prior to analyses with the reciprocal transformation (Zar, 1996) to achieve homogeneity of variance. While both spat and box density data satisfied the assumption of homogeneity of variance with the reciprocal transformation, neither data type met the assumption of normality regardless of the transformation (sqrt + 1, ln + 1, reciprocal, arcsin).

### *Oyster production estimates*

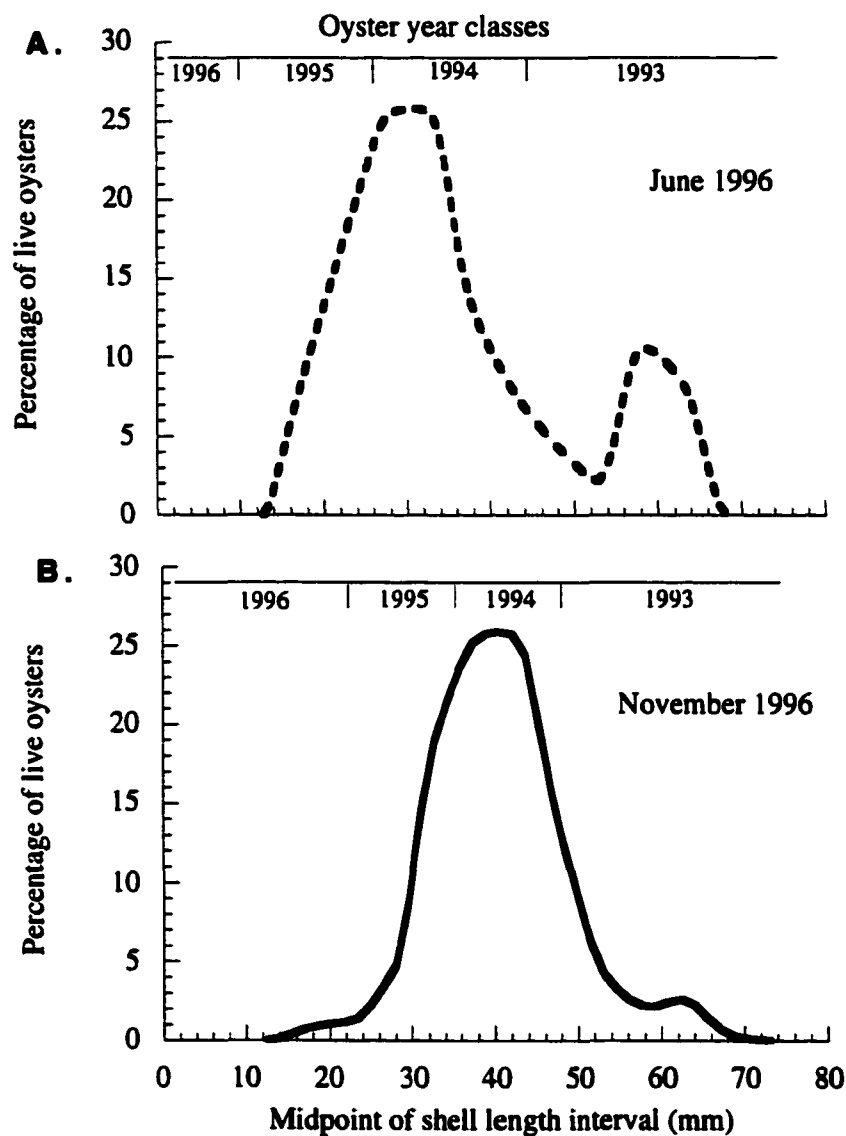
Size-specific fecundity estimates ( $F_{ind}$ ) for June 1996 were made with the oyster length frequency data from the Palace Bar patent tong survey conducted in November 1996. The Palace Bar oyster length-frequency data (Figure 4) were adjusted for year-class size distinctions (Mann and Evans, 1998; Evans and Mann, In review), growth rates (Evans and Mann, In review), growing season (Evans and Mann, In review), senescence mortality for oysters > 55 mm (Mann et al., 1995), and larval mortality (Table 1) according to Mann and Evans (1998). Evans and Mann (In review) apply a growth burst function model using the positive half cycle of a sinusoid to James River, Virginia oyster data. This model describes a temperature dependent growth pattern that follows seasonal variation and ceases when temperatures go below a critical value and is common among sessile marine invertebrates (Evans and Mann, In review). This growth model gives a residual sum of squares value equal to 19.98 when applied to James River oyster data as in Evans and Mann (In review).

Size-specific individual oyster fecundities were calculated using the relationship:

$$\text{Fecundity } (F_{ind}) = 39.06 * (0.000423 * \text{Length (mm)}^{1.75})^{2.36}; (r^2 = 0.89)$$

where  $F_{ind}$  is millions of gametes per individual oyster. This equation is modified from Cox and Mann (1992), Thompson et al. (1996), and Mann and Evans (1998) by substituting the weight to length conversion recommended by Mann and Evans (1998) for oyster weight (mg of dry tissue). Total oyster fecundity ( $F_{tot}$ ) within a size class was calculated by summing the product of  $F_{ind}$  and the number of individuals within each size class across size classes for June 1996 (Table 1).

Mann and Evans (1998) describe a modifier for salinity effects ( $F_s$ ), propose 13.5‰ as a threshold for salinity effects on oyster fecundity, and report 8.5‰ as the lowest salinity



**Figure 4:** Length-frequency diagrams with midpoint of the shell length class (mm) plotted against the percentage of the population within a shell length class for the Palace Bar reef oyster population. Patent tong data from November 1996 (b) were used to estimate a length-frequency distribution for the Palace Bar reef population in June 1996 (a) in the absence of spring patent tong data.

**Table 1:** Summary of oyster length frequency estimates at Palace Bar reef, Piankatank River, Virginia for June 1996 from November 1996 length-frequency data. June 1996 length-frequency distributions were used to estimate individual oyster fecundities ( $F_{ind}$ ) and total oyster fecundity meter<sup>-2</sup> ( $F_{tot}$ ) per Mann and Evans (1998). All calculations are described in the text. Oyster daily growth rates were estimated with the positive half of the sinusoidal oyster growth model developed by Evans and Mann (In review); a summary of the model is provided in the text. The mortality estimate used is for senescence mortality per Mann et al. (1995).



Shell length (SL) interval midpoint (mm)	% of population within SL interval 11/96	Daily growth rate (G) (mm)	Growth estimate from 6-11/96 (mm)	Estimated SL interval 6/96 (mm)	Portion of SL interval useful for 6/96 fecundity estimates	Mortality estimate for 6 - 11/96 (%)	% of population within SL interval 11/96	% of population within SL interval 6/96	Oyster density by SL interval 6/96 (animal m <sup>-2</sup> )	Individual Fecundity estimates (F <sub>ind</sub> )
18	0.87	0.09	13.97	4.03	none					
23	1.30	0.10	14.38	8.62	none					
28	4.76	0.10	14.79	13.21	none					
33	19.48	0.10	14.79	18.21	0.5	0.50	19.48	9.74	3.41	33.46
38	25.54	0.07	9.86	28.14	all		25.54	25.54	8.94	528.35
43	25.54	0.07	9.86	33.14	all		25.54	25.54	8.94	1037.25
48	12.99	0.05	7.40	40.60	all		12.98	12.99	4.55	1219.19
53	4.33	0.03	4.93	48.07	all		4.33	4.33	1.52	815.21
63	2.60	0.02	3.29	59.71	all	8.00	2.60	10.60	3.71	4881.85
68	0.43	0.02	2.54	65.46	all	8.00	0.43	8.43	2.95	5675.80

level where viable eggs have been found; i.e.,  $F_s$  equals 0 when salinities are  $\leq 8.5$  ‰ and equals 1 when salinities are  $\geq 13.5$ ‰. Since Piankatank River salinities ranged from 11 to 15 ‰ during 1996, but were usually  $< 13$ , the sex ratio for this oyster population was assumed to be 1:1 (per Cox and Mann, 1992), and the sex-related fecundity factor ( $F_q$ ) was set at 0.5. Oyster fertilization efficiency ( $F_f$ ) is dependent on the total oyster density (oysters  $m^{-2}$ ). Mann and Evans (1998) apply a correction factor based on Levitan (1991) to estimate  $F_f$ :

$$F_f = 0.0049 * \text{Oyster density}^{0.72}$$

These F factors are combined to yield a total oyster production estimate for a given area in units of oyster embryos  $m^{-2}$  in the relationship:

$$\text{Oyster Embryo Production (F)} = F_{tot} * F_q * F_s * F_f$$

This oyster embryo production estimate was combined with oyster density data from diver surveys to yield estimates of fecundity or larval production  $m^{-2}$  and then converted to larval production per reef assuming 0.63 ha of reef are available for settlement and production (Table 4). A time stepped larval mortality function ( $L_{mort}$ ) describing the daily larval mortality rate (Mann and Evans, 1998) was used to make predictions regarding production of oyster spat (settled larvae) or the proportion of larval oyster survivorship on Palace Bar reef (Table 6):

$$\text{Larval oyster survivorship} = (1 - L_{mort})^t$$

where  $L_{mort}$  or the larval mortality function may range from 0.0 (all living) to 1.0 (all dead). A value of 0.07 was used for  $L_{mort}$  (per hatchery data from the VIMS Aquaculture Breeding and Technology center as in Mann and Evans, 1998) and the time to oyster settlement ( $t$ ) was set at 21 days following Mann and Evans (1998) for James River, Virginia oysters. Effects of physical transport of eggs and larvae onto and off of Palace Bar reef were unknown.

#### *Fish population data*

**Adult fish density:** Density estimates of adults (fish  $m^{-2}$ ) for both fish species were transformed with the reciprocal transformation (Zar, 1996) to meet assumptions of

homogeneity of variance and normality and were analyzed with species-specific ANOVAs. Month, water depth, and substrate type were factors in both analyses.

**Larval fish production estimates:** Larval production estimates for naked gobies or striped blennies relying on numbers of eggs per nest must be distinguished from published fecundity estimates for these fishes using numbers of eggs per female; e.g., Nero (1976) for a Virginia population of naked gobies. Fecundity estimates for female naked gobies range from 250 to 1,977 eggs per female (Deary Cove, Virginia; Nero, 1976). A value of 1,200 eggs per nest, (per Hildebrand and Cable, 1938 (North Carolina); Massmann et al., 1963 (Virginia); Dahlberg and Conyers, 1973 (Georgia); Nero, 1976 (Virginia)) was used to estimate naked goby nest production ( $F_{i_{nest}}$ ). Striped blenny nests collected from Palace Bar reef during 1995 and 1996 contained between 1,000 and 1,600 eggs per nest ( $n = 25$ ; J. Harding, unpublished data); a value of 1,300 eggs per nest was used to estimate striped blenny nest production ( $F_{i_{nest}}$ ).

Sources of egg mortality for both species include predation by xanthid crabs (Crabtree and Middaugh, 1982), cannibalism by guarding males (particularly for naked gobies; Dahlberg and Conyers, 1973), poor egg condition, and nest fungus (J. Harding, unpublished data). Stage duration for incubation, determined from laboratory culture of both species (Harding, 1999 [see Chapter 3 of this volume]) and field observations of naked gobies (Deary Cove, Virginia; Nero, 1976), was estimated at 9 days for both species. Total mortality of eggs in the nest ( $N_{nest}$ ) was estimated at 1% day<sup>-1</sup> for 9 days of incubation (Harding, 1999 [see Chapter 3 of this volume]). The percentage nest survivorship was estimated using a general larval survivorship function for marine fishes modified from Houde (1989).

$$100 N_{nest} = e^{-0.01 \cdot 9}$$

Average adult fish densities (fish m<sup>-2</sup>) for each species from Palace Bar reef during 1996 were used to calculate species-specific larval fish production (larval fish m<sup>-2</sup>) using the equation:

$$\text{Larval fish production m}^{-2} = F_{i_{nest}} * F_{i_q} * N_{nest} * \text{Average number of adult fish m}^{-2}$$

where  $F_{i_q}$  is the sex-related fecundity factor. Nero (1976) reports a 1:1 sex ratio for adult naked gobies; striped blennies were assumed to have similar sex ratios, giving  $F_{i_q}$  a value of 0.5. The effects of salinity and temperature on naked goby and striped blenny nest production and success are unknown. Estimates of larval fish production  $m^{-2}$  for each species were combined with estimates of reef habitat suitable for nesting (0.63 ha) to yield species-specific larval fish production estimates for Palace Bar reef (Tables 7 and 8).

An average daily growth rate ( $G$ ) for striped blennies from laboratory cultured blennies was estimated by fitting a four parameter logistic regression to length-at-age data for pre-settlement and settlement stage fish using the equation:

$$L = L_0 + \frac{a}{1 + e^{-\left|\frac{t-t_0}{b}\right|}}$$

where  $L_0$  is the fish length (mm) at hatch or  $t = 0$ ,  $a$  is a coefficient describing the maximum length at settlement,  $t$  is time post-hatch or age in days,  $t_0$  is the time corresponding to the midpoint of the rise, and  $b$  is a coefficient describing larval stage duration. The resulting average growth rate ( $G$ ) of  $0.129 \text{ mm d}^{-1}$  (standard error = 0.06;  $R^2 = 0.91$ ) is based on data from 312 blennies ranging in age from 1 to 22 d. Attempts to fit the same growth model to naked goby growth data from laboratory cultures were unsuccessful because data were only available for 4 fish ages. Alternatively, a larval naked goby growth rate of  $0.146 \text{ mm d}^{-1}$  from Houde and Zastrow (1993) for gobies held at  $26^\circ\text{C}$  in laboratory experiments was used (E. Houde, University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, Solomons, Maryland; personal communication).

Larval stage duration ( $D$ ), or time from post-yolk sac to settlement, was set at 18 d given stage duration estimates of 15 to 21 d for laboratory cultured blennies (Harding, 1999 [see Chapter 3 of this volume]) and approximately 18 to 20 d for field caught naked gobies (Breitburg, 1989, 1991). Instantaneous daily mortality ( $Z$ ) was estimated from average  $G$  values using the relationship given by Houde (1989):

$$Z = 0.0303 + 1.3085 (G)$$

The percentage of larval fishes surviving to settlement was calculated using the relationship given in Houde (1989) for fishes surviving to metamorphosis ( $N_{met}$ ):

$$100 N_{met} = e^{-Z D}$$

This survivorship function was used to adjust larval fish production estimates per reef for mortality prior to settlement. Adjusted estimates of larval fish production per reef were used to calculate species-specific settlement estimates per reef and per  $m^2$  (Tables 7 and 8). Larval transport into and out of the reef system by physical forces was unknown.

## RESULTS

### *Water temperature and salinity data*

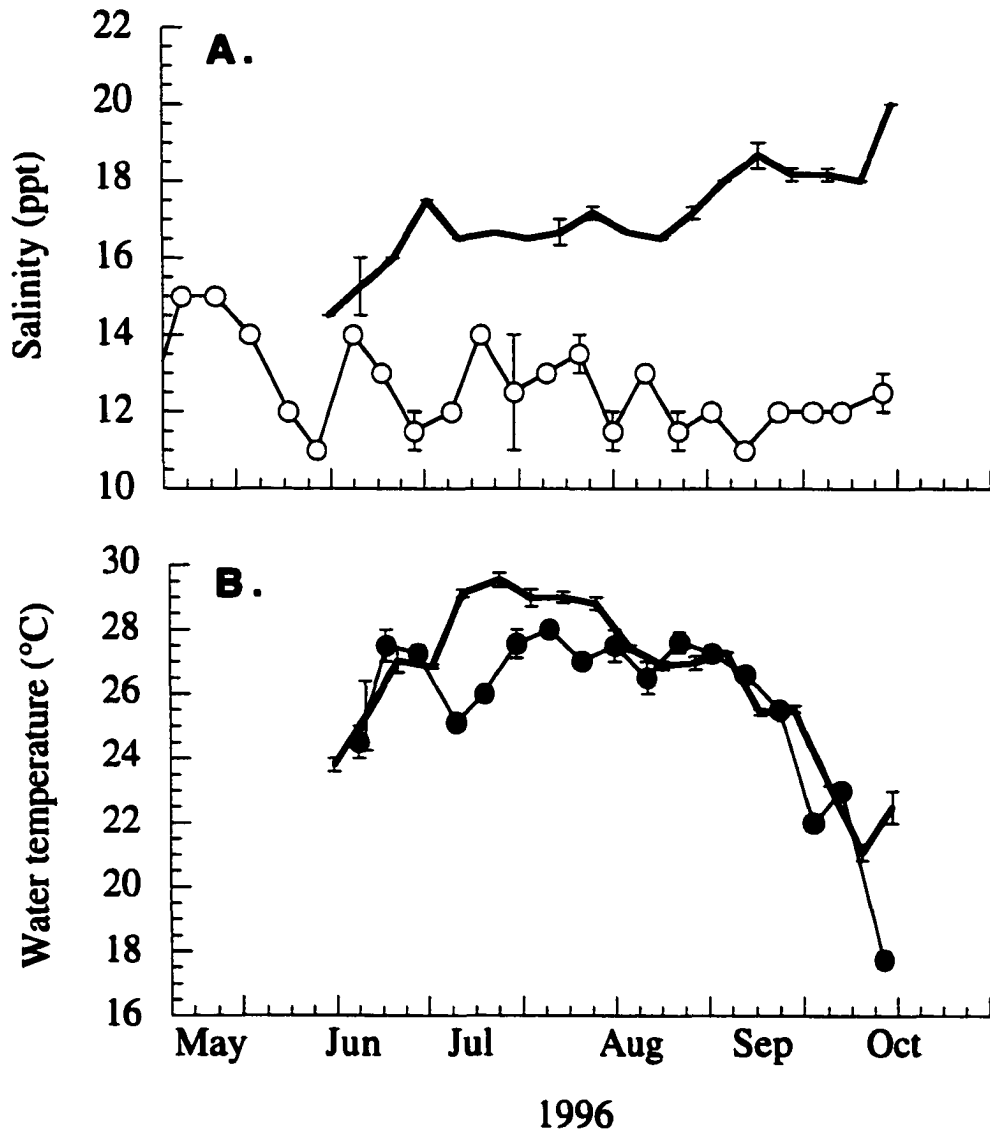
There was no significant difference between surface and bottom water temperatures (ANOVA,  $p = 0.29$ ) or salinities (ANOVA,  $p = 0.53$ ) on any date indicating that the water column at Palace Bar reef was well mixed. Therefore, surface and bottom temperature and salinity data for each day were pooled for presentation and discussion (Figure 5). Recorded water temperatures in 1996 were similar to those observed during 1993-95 (Figure 5, R. Mann, unpublished data). Salinities observed in 1996 were lower than those observed from 1993-5.

### *Oyster population data*

Adult oyster, spat, and oyster box density: There was no significant difference in adult oyster, spat, or box densities at Palace Bar reef between 1995 and 1996 or months (ANOVAs,  $p > 0.05$ , Tables 2 and 3); oyster density data from diver surveys of the reef were used for oyster production calculations and comparisons (Table 2). Winter mortality during 1995-96 was low. Increases in average adult oyster densities between June 1996 and October 1996 were most likely due to the development of June 1996 spat (juveniles) into adults.

### Oyster production estimates

Estimates of larval oyster production and subsequent survival to settlement predict annual recruitment of 68 to 83 spat  $m^{-2}$  (Table 6) to the reef and are similar to actual observed



**Figure 5:** Mean salinity (ppt, A.) and water temperature ( $^{\circ}\text{C}$ , B.) patterns observed at Palace Bar reef, Piankatank River, Virginia during May through September 1996. Data from surface and bottom measurements were averaged since there was no significant difference in temperature or salinity between depths (ANOVAs,  $p > 0.05$ ). Reference mean values for temperature and salinity data from Palace Bar reef during 1993-95 are plotted with a solid line ( $\pm$  standard error). Data from 1996 are indicated by lines with symbols ( $\pm$  standard error).

**Table 2:** Average densities of oyster adult, spat, and boxes  $m^{-2}$  from diver surveys of Palace Bar reef in November 1995 and June and October 1996. Data are presented with standard error (SE); n refers to the number of samples collected. "Adult" oysters are oysters  $> 30$  mm (maximum dimension); "spat" refers to oysters  $< 30$  mm (maximum dimension); while "boxes" are pairs of clean, articulated oyster valves. "NA" indicates data that were not available.

Date	n	Average adult oyster density (oyster $m^{-2}$ )	Average spat density (spat $m^{-2}$ )	Average box density (boxes $m^{-2}$ )
Nov 95	30	36.14 (5.84)	32.33 (5.73)	80.86 (11.84)
Jun 96	30	34.46 (4.72)	53.33 (8.34)	61.80 (0.31)
Oct 96	30	54.66 (4.27)	23.45 (2.87)	NA

**Table 3: Summary of ANOVAs used to compare oyster adult, spat, and box density data from diver surveys of Palace Bar reef during 1995 and 1996.**

<b>Oyster stage</b>	<b>Analysis</b>	<b>Factor</b>	<b>df</b>	<b>p-value</b>
<b>Adults</b>	<b>ANOVA</b>	<b>Year</b>	1	0.34
		<b>Month</b>	2	0.15
<b>Boxes</b>	<b>ANOVA</b>	<b>Year</b>	1	0.76
		<b>Month</b>	1	0.77
<b>Spat</b>	<b>ANOVA</b>	<b>Year</b>	1	0.33
		<b>Month</b>	2	0.16



**Table 4:** Summary of fish density data from diver counts (fish m<sup>-2</sup> ± standard error of the mean) of naked gobies and striped blennies from Palace Bar reef, Piankatank River, Virginia made bi-monthly from May through September, 1996. Few (<1%) fishes were observed in areas with 100% sand substrate. Twelve total counts were made on every sampling day; the n values represent the number of counts on substrate with shell.

Date	n	Average naked goby density (±SE) (fish m <sup>-2</sup> )	Average striped blenny density (±SE) (fish m <sup>-2</sup> )
17 May 96	6	18.0 (4.47)	6.0 (2.87)
31 May 96	3	18.0 (8.0)	8.0 (6.11)
14 Jun 96	8	6.5 (1.67)	4.0 (1.51)
28 Jun 96	4	7.0 (2.51)	6.0 (2.0)
11 Jul 96	7	18.3 (2.11)	10.3 (3.47)
9 Aug 96	8	33.5 (8.68)	9.0 (3.91)
23 Aug 96	5	40.8 (9.1)	20 (7.26)
20 Sep 96	5	30.4 (5.15)	11.2 (4.08)

**Table 5:** Summary of ANOVAs used to evaluate adult benthic fish densities from diver surveys of Palace Bar reef from May through September, 1996.

<b>Fish species</b>	<b>Analysis</b>	<b>Factors</b>	<b>df</b>	<b>p value</b>	<b>Multiple comparison results (Fisher's LSD pairwise comparison)</b>
<b>Naked goby</b>	<b>ANOVA</b>	<b>Month</b>	<b>4</b>	<b>0.02</b>	<b>*</b> August > May, June
		<b>Water depth</b>	<b>1</b>	<b>0.37</b>	
		<b>Substrate type</b>	<b>2</b>	<b>0.00</b>	<b>*</b> 100% shell, 67% shell/33% sand, 50% shell/50% sand > 33% shell/67% sand, 100% sand
<b>Striped blenny</b>	<b>ANOVA</b>	<b>Month</b>	<b>4</b>	<b>0.05</b>	<b>*</b> August > June
		<b>Water depth</b>	<b>1</b>	<b>0.81</b>	
		<b>Substrate type</b>	<b>2</b>	<b>0.00</b>	<b>*</b> 100% shell, 67% shell/33% sand > 50% shell/50% sand, 33% shell/67% sand, 100% sand

**Table 6:** Eastern oyster larval production and recruitment estimates for Palace Bar reef, Piankatank River, Virginia. Oyster densities are from diver surveys of Palace Bar reef in June, 1996. Symbols and calculations are detailed in the text; calculations for reef areas use 0.63 ha, the area of Palace Bar reef with shell as a portion of the substrate.

	Average density (oysters m <sup>-2</sup> ) - SE	Average density (oysters m <sup>-2</sup> )	Average density (oysters m <sup>-2</sup> ) + SE
$F_{tot}$	14,844	14,844	14,844
$F_q$	0.50	0.50	0.50
$F_s$	0.75	0.75	0.75
$F_r$	0.0564	0.0627	0.0688
Oyster embryo production (embryos m <sup>-2</sup> )	314.05	349.14	382.91
Oyster embryo production (embryos reef <sup>1</sup> )	1,978,539	2,199,624	2,412,372
Larval oyster survivorship	0.2178	0.2178	0.2178
Larval oyster settlement (spat reef <sup>1</sup> )	431,009	479,171	525,516
Larval oyster settlement (spat m <sup>-2</sup> )	68	76	83

densities (Table 2). Field estimates of spat abundance range from 53.33 m<sup>-2</sup> in June 1996 to 23.45 m<sup>-2</sup> in November 1996 (Table 2). Densities of adult oysters were greater in October than in June 1996, as would be expected given the maturation of the 1996 year class throughout the growing season.

#### *Fish population data*

**Adult fish density:** In May 1996, densities of both naked gobies and striped blennies were approximately 18 to 20 fishes m<sup>-2</sup> (Table 4). Naked goby densities were significantly higher on substrate that was composed of at least 50% shell (ANOVA,  $p < 0.05$ ; Fisher's LSD pairwise comparison,  $p < 0.05$ ; Table 5) while striped blenny densities were significantly higher in areas with greater than 67% shell substrate (ANOVA,  $p < 0.05$ ; Fisher's LSD pairwise comparison,  $p < 0.05$ ; Table 5). Areas where shell substrate dominated the bottom supported fish densities up to 14 times greater than those observed in habitat areas lacking shell. Only 1 site of the 49 sites sampled in grid squares (Figure 3) with substrate composition of less than 50% shell contained benthic fishes; naked gobies were present at a density of 4 m<sup>-2</sup>. Goby densities 10 times higher occurred in concurrently surveyed grid squares with greater than 50% shell substrate. Goby and blenny densities declined during June 1996, but increased throughout July with maximum numbers of both fishes observed in August 1996 (Table 4). Densities of naked gobies were significantly higher in August than in May or June (ANOVA,  $p < 0.05$ ; Fisher's LSD pairwise comparison,  $p < 0.05$ ; Table 5). Striped blenny densities in August were significantly higher than those observed in June (ANOVA,  $p < 0.05$ ; Fisher's LSD pairwise comparison,  $p < 0.05$ ; Table 5).

#### **Larval fish production estimates:**

Species - specific estimates of benthic larval fish production and survival to recruitment for Palace Bar reef ranged from 192 to 246 juvenile naked gobies m<sup>-2</sup> (Table 7) and 125 to 173 juvenile striped blennies m<sup>-2</sup> (Table 8). These estimates of larval fish production are within an order of magnitude of field observations for adult fishes on Palace Bar reef during 1996 i.e., 18 to 24 naked gobies m<sup>-2</sup> and 7 to 10 striped blennies m<sup>-2</sup> (Table 4) and are well within

**Table 7: Naked goby larval production and recruitment estimates for Palace Bar reef, Piankatank River, Virginia. Fish densities are from benthic fish surveys of Palace Bar reef from May through September, 1996. Symbols and calculations are detailed in the text; calculations for reef areas use 0.63 ha, the area of Palace Bar reef with shell as a portion of the substrate.**

	Average density (fish m <sup>-2</sup> ) - SE	Average density (fish m <sup>-2</sup> )	Average density (fish m <sup>-2</sup> ) + SE
$F_{i_q}$ (Nero, 1976)	0.5	0.5	0.5
$F_{i_{nest}}^1$	1200	1200	1200
$N_{nest}^2$	0.9139	0.9139	0.9139
Average fish density (fish m <sup>-2</sup> )	18.86	21.47	24.08
Larval fish production (larvae m <sup>-2</sup> )	10,342	11,773	13,204
Larval fish production (larvae reef <sup>1</sup> )	65,154,885	74,171,547	83,188,209
G (mm day <sup>-1</sup> ; Houde and Zastrow, 1993)	0.146	0.146	0.146
D (days) <sup>3</sup>	18	18	18
Z (from G, per Houde, 1989)	0.2213	0.2213	0.2213
$N_{met}$ (per Houde, 1989)	0.0186	0.0186	0.0186
Larval fish settlement (larvae reef <sup>1</sup> )	1,212,433	1,380,220	1,548,006
Larval fish settlement (larvae m <sup>-2</sup> )	192	219	246

<sup>1</sup>Hildebrand and Cable, 1938 (North Carolina); Massmann et al., 1963 (Virginia); Dahlberg and Conyers, 1973 (Georgia); Nero, 1976 (Virginia).

<sup>2</sup> Per Houde (1989) based on laboratory culture of naked goby larvae from Harding (1999 [see Chapter 3 of this volume]).

<sup>3</sup> Per Breitburg (1989,1991) and Harding (1999 [see Chapter 3 of this volume]).

**Table 8:** Striped blenny larval production and recruitment estimates for Palace Bar reef, Pianatank River, Virginia. Fish densities are from benthic fish surveys of Palace Bar reef from May through September, 1996. Symbols and calculations are detailed in the text; calculations for reef areas use 0.63 ha, the area of Palace Bar reef with shell as a portion of the substrate.

	Average density (fish m <sup>-2</sup> ) - SE	Average density (fish m <sup>-2</sup> )	Average density (fish m <sup>-2</sup> ) + SE
$Fi_q$ (per Nero, 1976)	0.5	0.5	0.5
$Fi_{nest}^1$	1300	1300	1300
$N_{nest}^2$	0.9139	0.9139	0.9139
Average fish density (fish m <sup>-2</sup> )	7.58	9.03	10.48
Larval fish production (larvae m <sup>-2</sup> )	4,503	5,364	6,226
Larval fish production (larvae reef <sup>1</sup> )	28,368,515	33,795,210	39,221,905
$G$ (mm day <sup>-1</sup> ) <sup>3</sup>	0.129	0.129	0.129
$D$ (days) <sup>4</sup>	18	18	18
$Z$ (from $G$ , per Houde, 1989)	0.1990	0.1990	0.1990
$N_{nest}$ (per Houde, 1989)	0.0278	0.0278	0.0278
Larval fish settlement (larvae reef <sup>1</sup> )	787,842	938,551	1,089,260
Larval fish settlement (larvae m <sup>-2</sup> )	125	149	173

<sup>1</sup> J. Harding, unpublished data.

<sup>2</sup> Per Houde (1989) based on laboratory culture of striped blenny larvae from Harding (1999 [see Chapter 3 of this volume]).

<sup>3</sup> Calculated from laboratory culture data (Harding, (1999 [see Chapter 3 of this volume]); J. Harding, unpublished data)

<sup>4</sup> Per Harding (1999 [see Chapter 3 of this volume]).

Breitburg's (1999) estimate of an average recruitment rate of 272 individual naked goby larvae  $m^{-2} month^{-1}$  for Flag Pond oyster bar near Cape Conoy, Maryland. Similar goby abundance estimates ( $207 \pm 29$  goby larvae  $m^{-3}$ ) have been reported by Allen and Barker (1990) from tidal creeks in North Inlet Estuary, South Carolina.

## DISCUSSION

Larval production and recruitment estimates for Palace Bar reef oysters are of the same order of magnitude as observed field densities. Benthic fish larval production estimates are within an order of magnitude of adult densities and are similar to previous recruitment estimates for Chesapeake Bay naked gobies (Breitburg, 1999). Interactions between life history stages of oysters and benthic fishes are pivotal to reef community structure and form foundations for upper and apex trophic levels. Larval gobies (Houde and Lovdal, 1984; Olney, 1996; Harding, 1999 [see Chapter 3 of this volume]) and blennies (Harding, 1999 [see Chapter 3 of this volume]) selectively feed on bivalve veligers. Larval fish survival is enhanced by high growth rates (due to preferred prey availability) and subsequent reduction of the time period to settlement (Shepherd and Cushing, 1980; Houde, 1987). Post-settlement naked gobies and striped blennies are prey items for upper level predators (e.g. juvenile striped bass (Markle and Grant, 1970; Harding and Mann, unpublished data), bluefish (Mann and Harding, 1997, 1998)). Densities of adult reef fishes are driven by availability of suitable nesting habitat and predation shelters, as well as by the success of larval fish recruitment from the plankton.

The three - dimensional habitat created by the living oyster reef is highly heterogenous and offers many habitat refugia. Complex reef habitats offer more shelter for benthic fishes than two dimensional shell or sand habitats where suitable cover and substrate are limiting factors (Bahr, 1974). Nero (1976) reports densities of 8 naked goby adults  $m^{-2}$  in Deary Cove, Virginia where the dominant habitat type was sand bottom with sparse shell substrate and the primary nesting and habitat substrates available to gobies were discarded aluminum cans (Nero, 1976). Naked goby densities on Palace Bar reef during 1996 ranged from 7 to

40 fish m<sup>-2</sup>. Reef substrate heterogeneity and relief have been previously correlated with increased fish densities and species richness for coral reefs (Roberts and Ormond, 1987; Ebeling and Hixon, 1991; Friedlander and Parrish, 1998) and oyster reefs (e.g., Coen et al., 1999; Harding and Mann, 1999).

Naked gobies were more numerous than striped blennies on Palace Bar reef. Fish size and morphology may influence selection of oyster shell nesting sites and habitat refugia by both species (Crabtree and Middaugh, 1982). Adult striped blennies are longer and of greater body depth than adult naked gobies and adult males of both species may occupy shells with the smallest gaps that would accommodate the fish's total length (Crabtree and Middaugh, 1982). Naked gobies occupied shells that had significantly smaller total shell lengths than shells occupied by striped blennies (Crabtree and Middaugh, 1982) and may avoid competition for suitable shell refugia and nesting sites by using the smallest shells available. Smaller shells would give gobies refuge from predation by piscivorous apex predators and egg predation by xanthid crabs (Crabtree and Middaugh, 1982). Given the low densities of large (> 50 mm shell length) oysters on Palace Bar reef and, consequently, potentially low availabilities of large intact articulated oyster shell valves, suitable shell refugia may be a limiting factor for the Palace Bar reef adult striped blenny population.

Shell size and morphology may not be the only determining factors in benthic fish selection of articulated oyster shell valves for nesting sites and refugia. Fouling may place an important role in nest site selection by these fishes. Dahlberg and Conyers (1973) describe "clean" oyster shell as suitable for attachment of adhesive goby and blenny eggs. Biofouling in relation to nest site selection and egg attachment has not been quantitatively investigated. Rheinhardt and Mann (1990) and Mann and Evans (1998) report a one third reduction of appropriate settlement surfaces for oyster spat at biofouling levels ranging from 14 to 37% biofouling of available oyster shell in the James River, Virginia. Adult benthic fishes are probably capable of reducing or eliminating oyster shell coverage by sediment or detritus (abiotic fouling); they may remove also remove biofouling and subsequently increase the



availability of clean substrate necessary for oyster settlement by their foraging and nesting behavior. Similar selective grazing or “gardening” behavior by tropical damselfishes maintains coral reef algal communities at early successional stages precluding the development of encrusting algal mats (Lassuy, 1980; Montgomery, 1980).

Goby larvae seasonally dominate Chesapeake Bay ichthyoplankton (Dovel, 1971; Shenker et al., 1983; Cowan and Birdsong, 1985; Olney, 1996); 55% of all fish larvae collected by Dovel (1971) were naked gobies. Densities of up to 19,980 naked goby larvae per 30 min tow were reported by Massmann et al. (1963) for the Pamunkey River, Virginia. Shenker et al. (1983) reports 22 to 6,063 larval naked gobies per 100 m<sup>-3</sup> in the Patuxent River, Maryland. Larval recruitment estimates for Palace Bar reef, Virginia and Flag Pond, Maryland (Breitburg, 1999) predict greater than 200 juvenile naked gobies m<sup>-2</sup>; similar larval goby recruitment estimates have been made for South Carolina estuaries (Allen and Barker, 1990).

The impacts of numerically dominant taxa on related trophic levels are potentially high. Sympatric larval fishes with similar prey and settlement requirements (e.g., naked gobies and striped blennies) may be at a competitive disadvantage for resources, but may benefit from potential numeric “swamping” of predators (e.g., striped bass). Predation by larval gobies (Olney, 1996; Harding, 1999 [see Chapter 3 of this volume]) and blennies (Harding, 1999 [see Chapter 3 of this volume]) on bivalve veligers, may affect subsequent recruitment patterns of oysters. Historically, goby and oyster populations were well established throughout the intertidal areas of the Chesapeake Bay. Previous population levels of gobies and blennies are unknown, but it is likely that benthic fish densities have declined as suitable habitats, in the form of living oyster reefs, have disappeared (Luckenbach et al., 1999; Coen et al., 1999). In areas that currently support modest densities of adult benthic fishes and adult oysters, species-specific production by both oysters and fishes may be appropriate to sustain observed adult densities as observed on Palace Bar reef, Piankatank River, Virginia.

## CHAPTER 2

### Temporal variation and patchiness of zooplankton around an intertidal oyster reef

#### ABSTRACT

Zooplankton is an important component of many estuarine food webs. Zooplankton distribution and abundance have the potential to affect recruitment success of several trophic levels. Estuarine plankton communities are seasonally dominated by larval forms of benthic and pelagic invertebrates. Abundance and distribution were determined for six seasonally important invertebrate taxa (bivalve veligers, gastropod veligers, polychaete larvae, barnacle nauplii, calanoid copepod adults, and calanoid copepod nauplii) and a diurnally important taxon (decapod zoea) around an oyster reef in the Piankatank River, Virginia, on spatial scales of 100s of m and seasonal (May through October), diel (day-night), and tidal (6 h) temporal scales. Significant seasonal and diel patterns in abundance were observed for all species. Tidal influences alone appear to be less important than seasonal and diel patterns for most taxa, but the interaction of tidal and diel cues may cause the observed diel zooplankton distribution patterns in both June and August 1996. Zooplankton taxa around the reef were distributed non-randomly (patchily) regardless of their horizontal location with regard to the reef. Seasonal pulses in zooplankton abundance relate directly to life history patterns and reproductive cycles for individual taxa; as a result, reef benthic fauna have the capacity to influence the community composition and absolute abundance of the overlying zooplankton community.

## INTRODUCTION

The high productivity of temperate estuaries makes them important feeding and nursery areas for upper level consumers. Zooplankton occupy intermediate trophic levels in estuarine food webs. Many of the seasonally abundant estuarine zooplankton are larval forms of resident benthic or pelagic fauna. Thus, zooplankton community composition and distribution within an estuary may influence recruitment and abundance patterns of benthic and pelagic parent species (e.g., Dovel, 1971; Mann, 1988; Laprise and Dodson, 1990; Hill, 1998) as well as planktonic predators (e.g., Fortier and Leggett, 1983; Houde and Lovdal, 1984, 1985; Breitburg et al., 1995; McGovern and Olney, 1996; Robichaud-LeBlanc et al., 1997).

Estuarine zooplankton communities have been described across a range of spatial and temporal scales (Table 9). Observed spatial and temporal variations in estuarine zooplankton community composition and abundance may reflect the influence of biological factors (e.g., life history, migratory behavior), physical oceanographic features (e.g., tidal fronts, thermal stratification), or both. The spatial heterogeneity or patchiness of zooplankton distributions is widely acknowledged (e.g., Owen, 1989) and has been demonstrated for oceanic (e.g., Wiebe, 1970; Fasham et al., 1974; Genin et al., 1994), coastal (e.g., Smith et al., 1976), and estuarine (e.g., Houde and Lovdal, 1985; Currie et al., 1998) plankton communities on a variety of scales ranging from tens to thousands of meters. Temporal changes in zooplankton distribution and abundance have been documented for a variety of estuarine taxa across seasonal, tidal, and diel (day-night) scales (Table 9). Even in very shallow estuaries, most zooplankton taxa follow a pattern of diel vertical migration with highest surface abundances occurring nocturnally (Minello and Matthews, 1981).

Many small estuaries and tributaries of larger systems such as Chesapeake Bay are dominated by shallow (< 3 m), well-mixed regions with low tidal current influence and no vertical stratification. These areas often support complex communities centered on biogenic structure, e.g., oyster reefs and seagrass beds. In Chesapeake Bay, the reef-forming oysters,

Table 9:

Summary of representative studies on estuarine zooplankton community composition and/or abundance in relation to spatial and/or temporal scales. "NA" designates categories that are not applicable for particular papers.

Author	Year	Estuary	Maximum depth sampled (m)	Spatial scale	Temporal scale	Target organisms	Sampling gear	Mesh size ( $\mu\text{m}$ )
Buskey	1993	Nueces Estuary, TX, USA	2.4	Horizontal: 100s of m	Seasonal: biweekly for 13 months	microzooplankton	whole -water subsurface samples	NA
						mesozooplankton	0.2 m diameter nets	153
Conley and Turner	1991	Westport River, MA, USA	4.0	NA	Seasonal: 1-5 times per month from April - November 1980	zooplankton	Nets	73 and 363
Cronin et al.	1962	Delaware River, USA	12.2	Horizontal: 100s of m	Seasonal: quarterly over 2 years	zooplankton	Clark-Bumpus samplers	370
Currie et al.	1998	St. Lawrence Estuary, Canada	8.0	Horizontal: 100s of m	NA	zooplankton	Optical plankton counter	NA
Durbin and Durbin	1981	Narragansett Bay, RI, USA	7.5	Horizontal: 100s of m	Seasonal: weekly from March-October 1976	crustacean zooplankton	Pump	60
Herman et al.	1968	Patuxent River, MD, USA	20.0	Horizontal: 100s of m	Seasonal: biweekly for 20 months	zooplankton	0.5 m diameter net	370
Houde and Lovdal	1984, 85	Biscayne Bay, FL, USA	3.2	NA	Seasonal: 24 days over 13 months	microzooplankton	0.6 m diameter nets	35 and 333
Houser and Allen	1996	Oyster Landing Creek - North Inlet, SC, USA	1.7	NA	Seasonal (diurnal or day to day): May-October	macro and mesozooplankton	pump and 0.5 m diameter net	153 and 365
					Tidal: throughout 4 consecutive tidal cycles	macro and mesozooplankton	pump and 0.5 m diameter net	153 and 365
					Diel (day-night): hourly for 48 h	macro and mesozooplankton	pump and 0.5 m diameter net	153 and 365

Jenkins	1988	Port Phillip Bay, Australia	9.0	Horizontal: 10s of m; Vertical: meters	Seasonal: July-August 1984	microzooplankton	Pump	35
Laprise and Dodson	1994	St. Lawrence Estuary, Canada	21.0	Horizontal: 100s of m	Seasonal: June-July 1987	macrozooplankton	Tucker trawl	510
				Vertical: 10s of m	Seasonal: June-July 1987	mesozooplankton	0.5 m diameter net	63
Lee and McAlice	1979	Damariscotta River, ME, USA	11.0	Horizontal: 100s of m	Tidal: every 2 h for two tidal cycles	zooplankton	0.5 m diameter net	150
Lonsdale and Coull	1977	North Inlet, SC, USA	3.0	Horizontal: 100s of m	Seasonal: biweekly for 20 months	zooplankton	0.3 m diameter net	153
Mallin	1991	Neuse River, NC, USA	4.0	Horizontal: 100s of m	Seasonal: monthly for 20 months	crustacean zooplankton	Pump	76
Minello and Matthews	1981	West Bay, TX, USA	1.8	NA	Diel: every 4 h for 44 h	zooplankton	0.5 m diameter net	241
Olney	1996	mouth of Chesapeake Bay, VA, USA	12.0	Horizontal: 10s of m; Vertical: 10s of m	Seasonal: day to day	microzooplankton	Tucker trawl	35
Stubblefield et al.	1984	Calcasieu Estuary, LA, USA	1.5	Horizontal: 100s of m; Vertical: meters	Seasonal: monthly for 1 year	zooplankton	0.5 m diameter net	153
Thayer et al.	1974	Newport River, NC, USA	1.0	Horizontal: 100s of m	Seasonal: bimonthly for 2 years	zooplankton	0.3 m diameter net	160
Turner	1982	Peconic Bay, NY, USA	9.0	NA	Seasonal: weekly for approximately one year	zooplankton	0.3 m diameter nets	73
					Seasonal: weekly for approximately one year	zooplankton	0.7 m diameter nets	202
					Seasonal: weekly from September-May	ichthyoplankton	0.5 m diameter	505
Woolridge and Erasmus	1980	Sundays River, South Africa	5.0	Horizontal: 100s of m	Tidal: one 12 h cycle (ebb to ebb)	zooplankton	0.5 m diameter nets	190

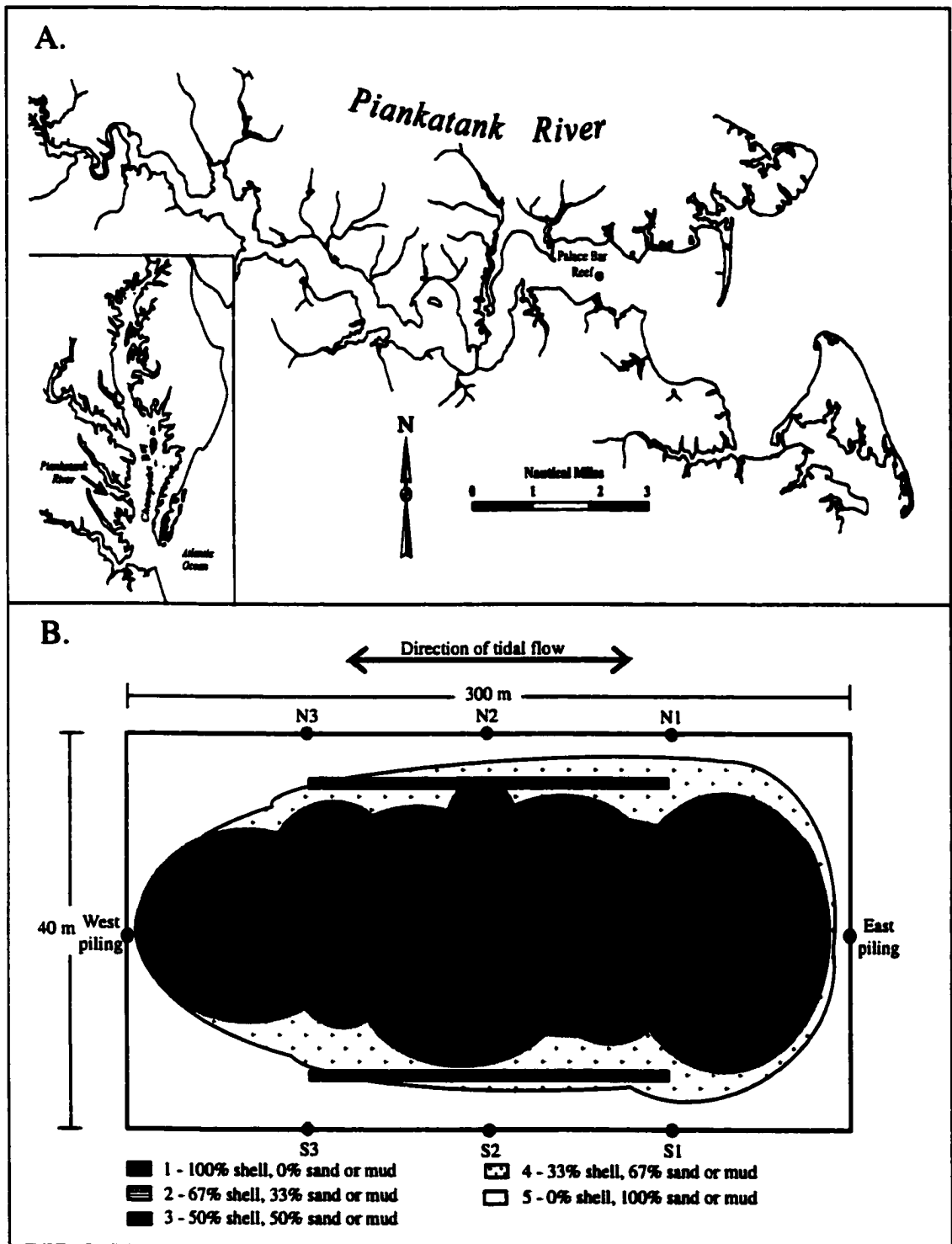
Table 9 (continued)

*Crassostrea virginica*, historically were the dominant primary consumers (see Newell, 1988; Kennedy et al., 1996 and references therein) that simultaneously increased local habitat relief, heterogeneity, and substrate availability for associated invertebrates including polychaetes, gastropods, and a range of crustaceans e.g., barnacles, shrimp, and crabs. Recent declines in Chesapeake Bay oyster reef communities have reduced shallow water habitat complexity in terms of both larval production and shell habitat for subsequent recruitment of benthic fauna including oysters (Hargis and Haven, 1988, 1999; Hargis, 1999). Restoration of three-dimensional oyster reef structures directly increases habitat availability for benthic invertebrates and may indirectly increase local zooplankton abundance and diversity. Many benthic invertebrates produce planktonic larvae that are prey items for planktivorous fishes as well as gelatinous predators. Increased zooplankton abundance or prey availability for larval fish predators would increase growth rates and potentially shorten the larval development period and increase larval fish recruitment rates. In the context of oyster reef communities, increased recruitment of benthic fishes such as naked gobies (*Gobiosoma bosc*) and striped blennies (*Chasmodes bosquianus*) would translate into increased prey availability for juvenile piscivorous predators (e.g., striped bass [*Morone saxatilis*], bluefish [*Pomatomus saltatrix*]) that consume gobies and blennies (Markle and Grant, 1970; Mann and Harding, 1997, 1998). Zooplankton community composition and abundance on and around estuarine oyster reef communities are unknown. The objective of this study was to describe horizontal spatial (100s of m) and temporal (seasonal, tidal, diel) variation in zooplankton community composition around an intertidal oyster reef in a Chesapeake Bay subestuary.

## METHODS

### *Study site*

Zooplankton samples were collected immediately adjacent to Palace Bar oyster reef, Piankatank River, Virginia (N 37° 31' 41.69", W 76° 22' 25.98"; Figure 6). The Piankatank River is a small estuary that flows directly into the Chesapeake Bay. Palace Bar reef is an



**Figure 6:** Map of the Piankatank River, Virginia in relation to the Chesapeake Bay showing Palace Bar reef (A.) and a schematic diagram of the reef including substrate composition (B.). Tow paths for all zooplankton tows are indicated by the dark black lines just inside the reef buoys (N1, N2, N3, S1, etc.) on north and south sides of the reef. Tidal flow generally runs east-west (parallel to the main reef axis) and is indicated by the double-headed arrow.

intertidal oyster reef (300 m x 30 m, reef depth range of 0.5 m above MLW to 3 m below MLW per Bartol and Mann, 1997) that was constructed in July, 1993 adjacent to the historic Palace Bar oyster grounds (Figure 6). Approximately 70% of the reef (0.63 ha) is composed of oyster shell, while the remaining area (0.27 ha) is crushed clam shell (see Bartol and Mann, 1997 for a detailed site description). Palace Bar reef receives annual oyster spat settlement (Bartol and Mann, 1997; J. Wesson, Virginia Marine Resources Commission, Newport News, Virginia, unpublished data) and currently supports an oyster population similar to that observed at an adjacent natural oyster bar (Harding and Mann, 1999; R. Mann, Dept. of Fisheries Science, Virginia Institute of Marine Science, Gloucester Point, Virginia, unpublished data). Mean tidal range at Palace Bar reef is approximately 0.4 m, while maximum tidal current at the reef is approximately  $0.12 \text{ m s}^{-1}$  (Chen et al., 1977).

The longitudinal axis of Palace Bar reef runs east to west, parallel the Piankatank River channel (Figure 6). The northern reef perimeter is on the channel side and the southern reef perimeter is inshore of the channel; both perimeters grade from oyster shell into hard sand bottom (Figure 6). Depth on the northern (channel) side is approximately 3 m from the reef to the channel. A sand flat extends inshore at a depth of 2.5 to 3 m from the southern reef perimeter for 200 m and then grades into a shallow sand bar (depth < 2 m) that continues inshore.

#### *Sampling protocol*

Three sequential replicate zooplankton samples were collected on north (channel) and south (inshore) sides of the reef (6 samples total) to describe spatial variation in zooplankton abundance and community structure that results from water movement in relation to the intertidal reef structure.

Seasonal zooplankton samples were collected weekly from May through September 1996 and 1997, between 0800 and 1600 EDT. During 1996, seasonal samples were collected at two different tidal stages (usually ebb and flood) on each sampling day (6 samples on each tidal stage, 12 total samples per day). In 1997, seasonal samples were collected on



only one tidal stage (6 total samples per day). On June 27-28 and August 29-30, 1996, diel plankton samples were collected over 36 h periods spanning three tidal cycles. Six samples (3 north, 3 south) were collected every 3 h corresponding to differing tidal stages: flood, slack onto ebb, ebb, and slack onto flood.

Microplankton nets (80  $\mu\text{m}$  Nytex mesh, 0.3 m diameter, 3:1 aspect ratio) were towed in the direction of tidal current parallel to the reef axis on the north (channel) and south (in-shore) sides of the reef (Figure 6). Total elapsed time for the sets of 6 sequential samples (tows) was approximately 30 min (15 to 18 min on each side of the reef). A General Oceanics mechanical flow meter (Model 2030) was suspended in the net mouth and average volume of water filtered per tow ( $14.43 \text{ m}^{-3}$  [std. deviation =  $0.10 \text{ m}^{-3}$ ]) was calculated. Nets were towed horizontally 0.05 to 0.10 m below the water surface in the direction of the prevailing tidal current for 2 min (approximately 180 m) at approximately  $1.5 \text{ m s}^{-1}$  through the water (tow speed combined with tidal speed). All samples were preserved in 10% buffered seawater formalin immediately after collection.

Water samples for salinity and temperature measurements were taken immediately adjacent to the reef (within 5 m) at the surface and 0.25 m above the substrate with a Niskin bottle each day. Temperature was measured immediately with a thermometer ( $\pm 0.5 \text{ }^\circ\text{C}$ ) and salinity was measured with a hand-held refractometer ( $\pm 1\text{‰}$ ).

In the laboratory, all zooplankton samples were subsampled with a standard 0.5 L Folsom plankton splitter but both replicate splits were completely enumerated to test statistical performance. To verify that the splitter was dispensing equal volumes, multiple "splits" were made using tap water. Volume of the original sample and each of five splits using tap water were measured to the nearest 0.1 ml and recorded; the difference in volumes dispensed between subsamples was less than 1%. To verify adequate mixing, i.e., a homogeneous distribution of animals within the sample, coefficients of variation were calculated for both replicate sub-samples for all plankton samples following Van Guelpen et al. (1982). Subsampling error was minimized by keeping within-sample coefficients of variation below

0.2 (per Van Guelpen et al., 1982; Mohlenberg, 1987) for at least one numerically dominant taxa per sample. Counting error was estimated by re-examining previously counted aliquots under higher magnification; 20% of all aliquots were re-examined. Counting error was low (less than 2%). Counting error of the total abundance of animals within a sample was kept to 10% or less by ensuring that a minimum of 100 animals from at least one numerically dominant taxa were counted in each sub-sample. Abundance estimates (animals  $m^{-3}$ ) for each taxa within a sample were computed from subsample counts. Individual organisms were identified to the nearest practical taxon, e.g., bivalve veligers, polychaete larvae, calanoid copepod adults.

#### *Data analyses*

*A priori* significance for all hypothesis tests was  $p = 0.05$ . Assumptions of homogeneity of variance were tested using Bartlett's test, while assumptions of normality were tested with the Ryan-Joiner test (similar to Shapiro-Wilks test per Minitab, 1995). Unless otherwise noted, data satisfied both of these assumptions. Fisher's least significant difference pairwise comparison test was used for parametric multiple comparisons (Minitab, 1995; Zar, 1996). When data did not meet the assumptions of homogeneity of variance or normality, non-parametric Kruskal-Wallis tests were followed by Dunn tests for multiple comparisons (Zar, 1996). Unless otherwise noted, statistical analyses used Minitab software (version 10.5; 1995).

#### Temperature and salinity data

Water temperature and salinity data collected weekly from May to October 1996 and 1997 at Palace Bar reef were  $\log_e$  transformed prior to analyses and satisfied assumptions of both homogeneity of variance and normality. Temperature and salinity data taken at the surface and just above the substrate (within 0.25 m) adjacent to the reef were each compared with a single factor ANOVA (water depth).

#### Seasonal, diel, and tidal abundance patterns

Total zooplankton abundance (density) estimates (total number of animals  $m^{-3}$ ) were

calculated for each plankton tow by summing the total number of animals counted within the tow and then dividing the total number of animals by the total volume of water ( $m^{-3}$ ) filtered by each tow. Abundance (density) estimates were also made for each taxonomic category.

Seasonal abundance estimates are presented for the total number of animals (the sum of animals from all taxa) and the six taxa that occurred in greater than 50% of all samples collected from May through October. The percentage that each taxa contributed to the total number of animals sampled on each day throughout the season was calculated by dividing the taxon-specific abundance estimates (animals  $m^{-3}$ ) by the total number of animals sampled (animals  $m^{-3}$ ).

Diel and tidal zooplankton abundance estimates from the two 36 h stations (July 27-28, 1996 and August 29-30, 1996) were made using the total number of animals  $m^{-3}$ , the 6 most seasonally common taxa, and decapod zoea, an additional taxon that was numerically important on the sampling dates. The percentage that each taxa contributed to the total number of animals sampled on each tidal stage throughout each 36 h station was calculated for June and August stations by dividing the taxon-specific abundance estimates (animals  $m^{-3}$ ) by the total number of animals sampled (animals  $m^{-3}$ ) for each tidal stage.

Transformation (reciprocal, square root, logarithm,  $\log_e$ , arcsine), of seasonal, diel, and tidal zooplankton abundance estimates (animals  $m^{-3}$ ) did not satisfy the assumptions of homogeneity of variance or normality. Multiple Kruskal-Wallis tests were used to evaluate the effects of year, day of the year, horizontal location, tidal stage, and time of day on seasonal plankton abundance estimates for the 6 common taxa as well as total plankton abundance estimates. Diel plankton abundance estimates from the two 36 h stations were also compared with multiple Kruskal-Wallis tests to evaluate the effects of time of day, tidal stage, and location. Dunn's tests were used for post-hoc non-parametric multiple comparisons.

### Seasonal and diel horizontal distribution

The local spatial variability (100s of m) of zooplankton in relation to the reef was described for seasonally and diurnally abundant taxa using a qualitative graphic method combined with a quantitative determination of confidence intervals based on the Poisson distribution. For each taxa, mean abundance from a series of replicate samples ( $n = 3$ ) on a given sampling day was plotted in relation to the corresponding sample variance. A diagonal line was plotted to show the 1:1 relationship of mean abundance to variance that is indicative of a random occurrence using the Poisson distribution. Points above the diagonal line are indicative of aggregation; points below it show uniformity. Monte Carlo simulations were used to determine the 95% confidence intervals above which the distribution of plankton taxa are significantly aggregated (non-random).

### Seasonal and diel zooplankton community composition

Seasonal and diel species abundance associations within the zooplankton community were compared using detrended correspondence analysis (DCA) (Hill and Gauch, 1980). DCA was used as a descriptive tool to compare zooplankton assemblages associated with Palace Bar reef on seasonal and diel temporal scales by spatially aggregating similar samples (tows) and separating dissimilar ones on the basis of taxa abundances within a sample. All DCA analyses (CANOCO for Windows version 4.0, 1998) were detrended with second order polynomials per ter Braak (1995) to avoid potential loss of gradient information during the detrending procedure (Minchin, 1987). Taxa-samples biplots for seasonal and diel data were made using CANODRAW software (version 3.1; Similauer, 1998).

## RESULTS

### Temperature and salinity data

There was no significant difference between surface and bottom water temperatures (ANOVA,  $p = 0.34$ ) or salinities (ANOVA,  $p = 0.55$ ) on any date indicating that the water column was well mixed. Therefore, surface and bottom temperature and salinity data for each day were pooled for presentation and discussion (Figure 7). Recorded water

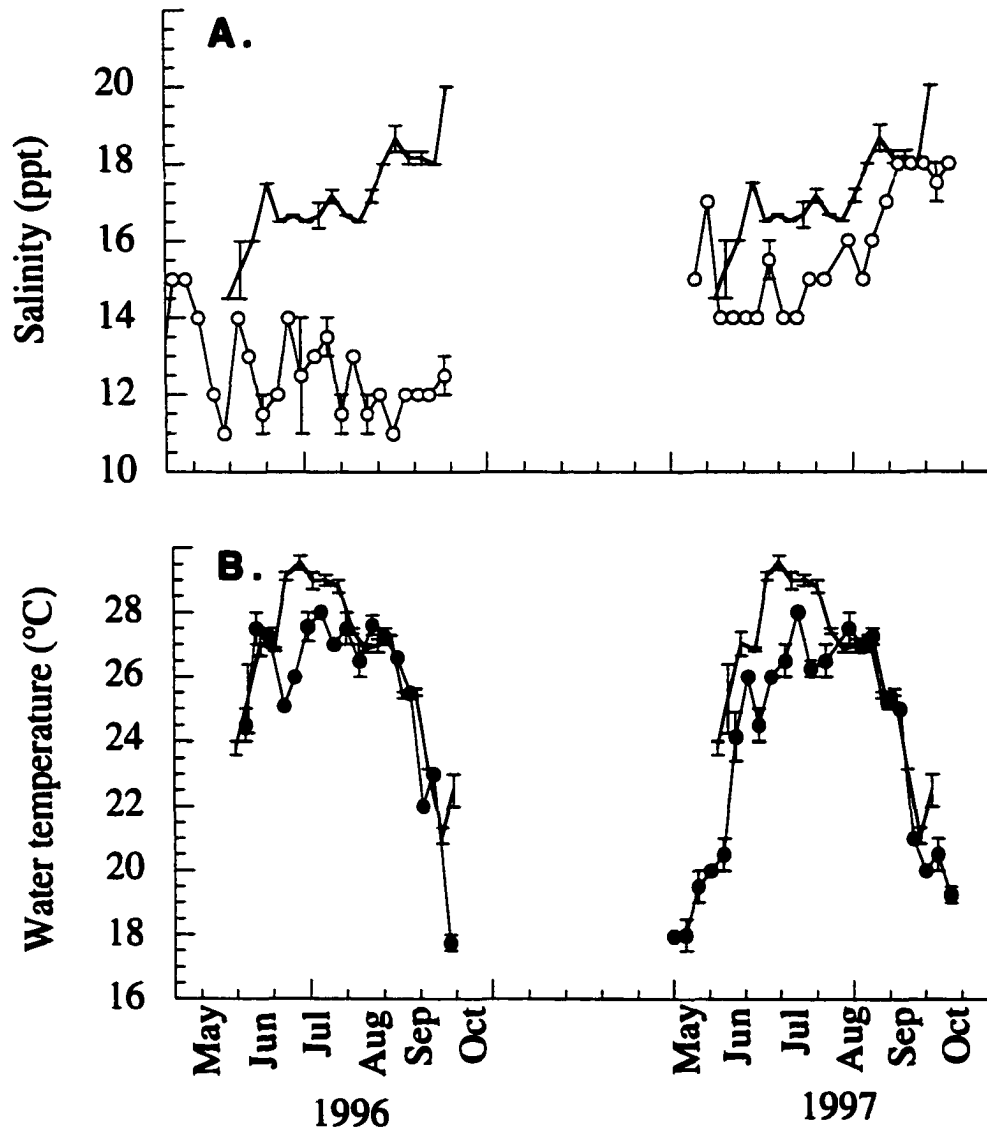
temperatures in 1996-7 were similar to those observed during 1993-95 (Figure 7, R. Mann, Dept. of Fisheries Science, VIMS, Gloucester Point, VA, unpublished data). Salinities observed in 1996 were the lowest observed from 1993-7.

#### Seasonal and diel abundance estimates

Bivalve veligers, gastropod veligers, polychaete larvae, adult calanoid copepods, calanoid copepod nauplii, and barnacle nauplii occurred in greater than 50% of all samples collected from May through October (Table 10). Less abundant taxa observed in the plankton included ostracods, tintinnids, non-calanoid copepod adults, dipteran larvae, chironomids, and decapod megalopa during both 1996 and 1997.

Zooplankton abundance was strongly influenced by season (as indicated by day of the year). A seasonal succession of taxa, in terms of percent composition of the total number of animals present, corresponding to seasonal reproductive events, was observed for polychaete larvae, barnacle nauplii, gastropod veligers, and bivalve veligers (Table 10, Figure 8). Total plankton abundance peaked in mid to late summer during both 1996 and 1997 (Figure 8). Maximum total zooplankton abundances were observed during September 1996 (56,888 animals  $m^{-3}$ ) and July 1997 (65,802 animals  $m^{-3}$ ). In both years, total plankton abundances increased as water temperatures rose to 26 to 28°C from May through June at the same time that gastropod veligers, polychaete larvae, and barnacle nauplii abundances were highest (Figure 8). Calanoid copepod adults and nauplii dominated the plankton community from late June through September. Recruitment of calanoid copepod nauplii to the "adult" category is probable throughout the seasonal progression and is visible in the succession of abundance peaks for both calanoid copepod adults and nauplii (Figure 8). Gastropod veligers, polychaete larvae, and barnacle nauplii occurred predominantly in May 1996 and May through June 1997. In both years, bivalve veliger abundance increased from July through September with highest abundances occurring in August (Figure 8).

Abundances of individual plankton taxa as well as total zooplankton abundance varied seasonally (Kruskal-Wallis,  $p < 0.05$ ; Table 12). Gastropod veligers, polychaete



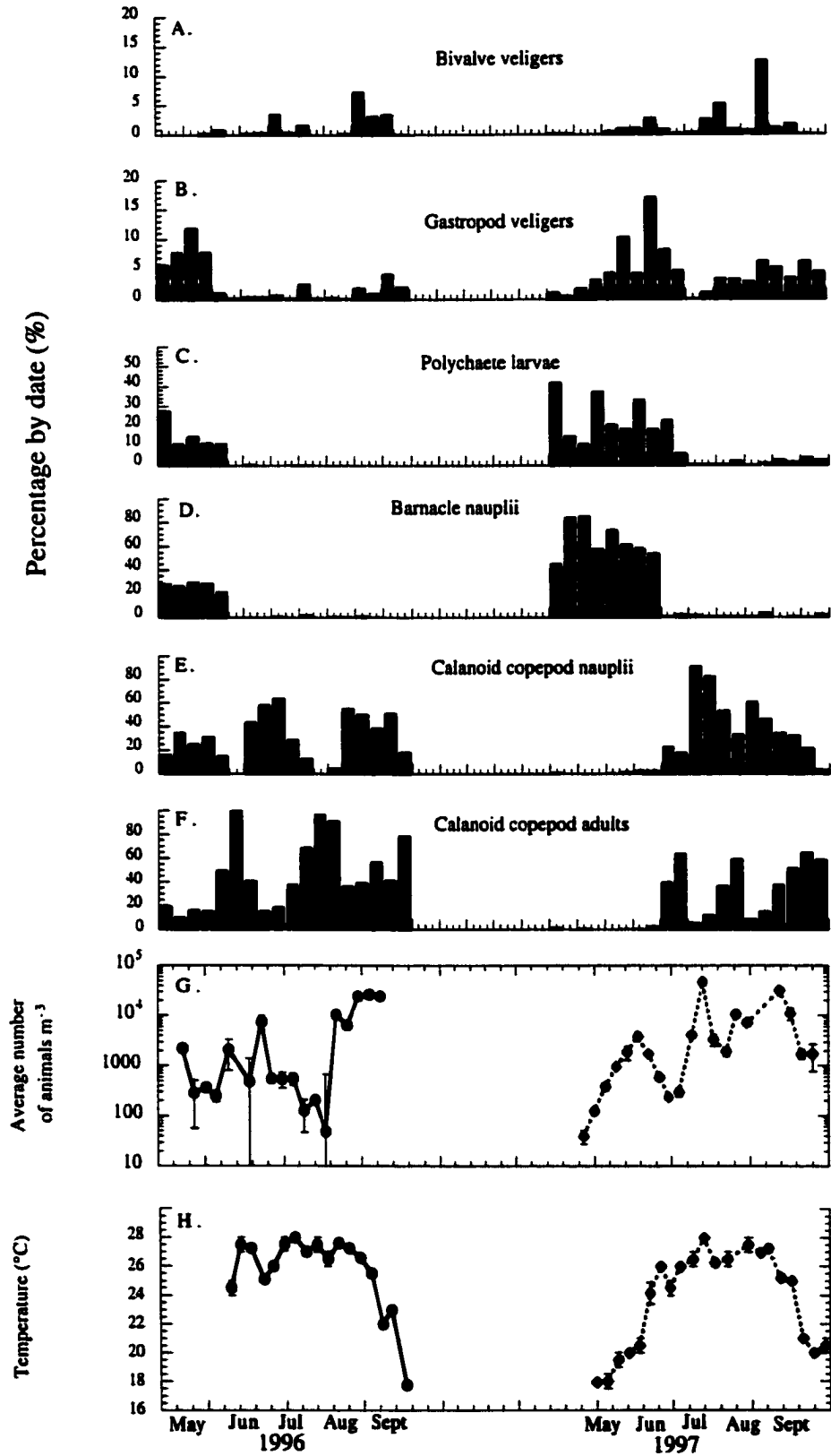
**Figure 7:** Mean salinity (ppt, A.) and water temperature ( $^{\circ}$  C, B.) values ( $\pm$  standard error) for Palace Bar reef, Piankatank River, Virginia from May to October 1996-7. Data from surface and bottom measurements were pooled since there was no significant difference in temperature or salinity measurements between depths (ANOVA,  $p < 0.05$ ). Reference mean values for temperature and salinity data from 1993-95 are plotted with a solid line ( $\pm$  standard error). Data from 1996 and 1997 are indicated by lines with symbols ( $\pm$  standard error).

**Table 10:** Summary of taxa-specific seasonal zooplankton abundance estimates ( $\pm$  standard error ) from samples collected at Palace Bar reef, Piankatank River, Virginia from May through October 1996 and 1997. n = 156 for 1996 and 115 for 1997. All abundance values given are in number of animals meter<sup>-3</sup> of water.

Taxa	Mean abundance	Standard error	Minimum abundance	Maximum abundance	% of samples occurring
<b>1996</b>					
Total zooplankton	8021	852.08	1	56889	—
Bivalve veligers	165	31.62	0	2355	65
Gastropod veligers	159	34.15	0	3080	72
Polychaete larvae	38	10.43	0	981	50
Calanoid copepod adults	4215	539.54	0	36452	99
Calanoid copepod nauplii	3156	366.39	0	21560	85
Barnacle nauplii	74	13.01	0	1037	70
<b>1997</b>					
Total zooplankton	6652	1164.75	11	65803	—
Bivalve veligers	158	33.22	0	1884	65
Gastropod veligers	218	37.85	0	2464	90
Polychaete larvae	193	25.02	0	1160	97
Calanoid copepod adults	1457	294.26	0	18480	80
Calanoid copepod nauplii	3616	878.19	0	55222	81
Barnacle nauplii	387	67.79	0	4167	89

**Figure 8:** Summary of seasonal zooplankton abundance patterns around Palace Bar reef, Piankatank River, Virginia. Seasonal plankton abundance estimates were pooled across time of day, tidal stage, and location for graphic presentation. Percentage composition of the zooplankton community by date is presented for the six taxa occurring in 50% of seasonal samples including A.) bivalve veligers, B.) gastropod veligers, C.) polychaete larvae, D.) barnacle nauplii, E.) calanoid copepod nauplii, and F.) calanoid copepod adults in relation to the average abundance of all species (G.; animals  $m^{-3} \pm$  standard error) and seasonal water temperatures (H.,  $^{\circ}C \pm$  standard error).





larvae, and barnacle nauplii abundance was significantly higher during 1997 than in 1996 (Kruskal-Wallis,  $p < 0.05$ ; Table 11). Adult calanoid copepods were significantly more abundant during 1996 than 1997 (Kruskal-Wallis,  $p < 0.05$ ; Table 11). Time of day and tidal stage significantly affected abundance for 5 of the 6 common species (Kruskal-Wallis,  $p < 0.05$ ; Table 11); barnacle nauplii were not affected by time of day and gastropod veligers were not affected by tidal stage in seasonal samples.

On June 27-28, 1996 average zooplankton abundance was greatest during the afternoon of July 27 (1200-1900; 8,091 animals  $m^{-3}$ , Table 12) as the tide was flooding (Figure 9). Bivalve veligers, barnacle nauplii, gastropod veligers, and calanoid copepod nauplii were most abundant during daylight hours (Figure 9). Calanoid copepod adults dominated the plankton from dusk on 27 June (ebbing tide) through the next afternoon (Figure 9). Decapod zoea were almost exclusively nocturnal and probably underrepresented in the seasonal samples (all of which were collected during daylight); zoea abundance was greatest on the ebb tide at approximately 0200 on 28 June. Time of day significantly affected total zooplankton abundance as well as abundance of gastropod veligers, polychaete larvae, calanoid copepod adults, and decapod zoea (Kruskal-Wallis,  $p < 0.05$ ; Table 13).

During the August 1996 36 h station, maximum average zooplankton abundance was observed at 0030 (7,561 animals  $m^{-3}$ ) on 30 August when the tide was nearing maximum ebb. Barnacle nauplii, gastropod veligers, calanoid copepod nauplii, and bivalve veligers were most abundant during the day (Figure 10). As indicated by the seasonal zooplankton collections, bivalve veligers composed a greater percentage of the total plankton in August (1 to 8%; Figure 10) than in June (0 to 0.5%; Figure 9). Calanoid copepod adults were nocturnally most abundant, as during the June 36 h station. In August, decapod zoea were primarily nocturnal, but composed a lower percentage of the total plankton (0 to 0.4% in August vs. 0.2 to 4% in June). Time of day significantly affected abundance of all taxa except barnacle nauplii (Kruskal-Wallis; Table 14). Total zooplankton abundance as well as abundance of decapod zoea were significantly affected by tidal stage (Kruskal-Wallis,  $p$

**Table 11:** Summary of Kruskal Wallis test results for plankton abundance during 1996 and 1997, Piankatank River, VA. All abundances are in number of animals meter<sup>-3</sup> of water. “\*” designates results that were significant at the  $p \leq 0.05$  level. The designation “Early” is used for days 1-10 of a month, “Mid” means days 10-20, “Late” is for days 20-30.

Response: Abundance	Factor	d.f.	p value	Multiple comparison results (Dunn's test)
Total animals	Year	1	0.45	
	Day of the year	36	< 0.01	* June 15-July 15 > May 1 - June 15, July 15 - 1 Oct
	Time of day	3	< 0.01	* 0400-0800 > 0800-1200 > 1200-1600 > 1600-2000
	Tidal stage	3	0.01	* Flood > Slack onto Flood > Ebb > Slack onto Ebb
	Location	1	0.76	
Bivalve veligers	Year	1	0.30	
	Day of the year	36	< 0.01	* Late July > Late August > Early September > May - Late July, Late September
	Time of day	3	< 0.01	* 0400-0800 > 0800-1200 > 1200-1600 > 1600-2000
	Tidal stage	3	0.04	* Flood > Ebb > Slack onto Ebb > Slack onto Flood
	Location	1	0.75	
Gastropod veligers	Year	1	< 0.01	* 1997 > 1996
	Day of the year	36	< 0.01	* Early September > May - September, Late September
	Time of day	3	< 0.01	* 0400-0800 > 0800-1200 > 1200-1600 > 1600-2000
	Tidal stage	3	0.20	
	Location	1	0.68	
Polychaete larvae	Year	1	< 0.01	* 1997 > 1996
	Day of the year	36	< 0.01	* Early May, Early June, Early September > Late May, Late June, July - August, Late September
	Time of day	3	0.01	* 0800-1200 > 1200-1600 > 0400-0800, 1600-2000
	Tidal stage	3	0.03	* Slack onto Flood > Ebb > Flood > Slack onto Ebb
	Location	1	0.96	

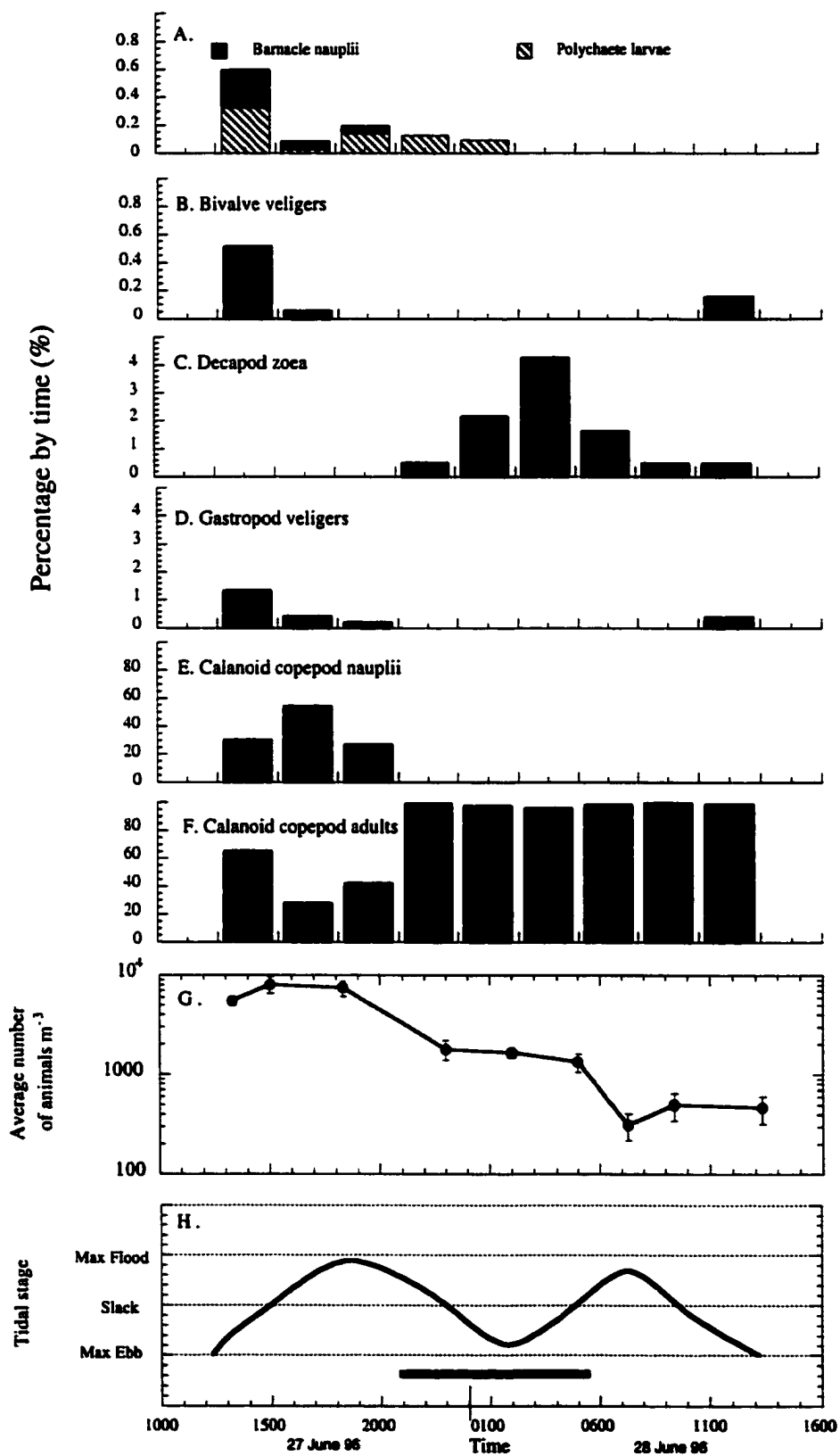
Table 11 (continued)

Calanoid copepod adult	Year	1	< 0.01	*	1996 > 1997
	Day of the year	36	< 0.01	*	Late August - Early September > May-Late August, Late September
	Time of day	3	< 0.01	*	0400-0800 > 0800-2000
	Tidal stage	3	0.01	*	Flood > Ebb, Slack onto Flood > Slack onto Ebb
	Location	1	0.94		
Calanoid copepod nauplii	Year	1	0.34		
	Day of the year	36	< 0.01	*	Mid July > May - Mid July, August - September
	Time of day	3	< 0.01	*	0400-0800 > 0800-2000; 0800-1200 > 1200-1600
	Tidal stage	3	< 0.01	*	Flood > Slack onto Ebb, Ebb, Slack onto Flood; Slack onto Flood > Slack onto Ebb
	Location	1	0.78		
Barnacle nauplii	Year	1	< 0.01	*	1997 > 1996
	Day of the year	36	< 0.01	*	Late May - Early June > Early May, Late June - September
	Time of day	3	0.14		
	Tidal stage	3	< 0.01	*	Ebb, Slack onto Flood > Flood > Slack onto Ebb
	Location	1	0.47		

**Table 12:** Summary of taxa-specific diel zooplankton abundance estimates ( $\pm$  standard error) from samples collected at Palace Bar reef, Piankatank River, VA during 36 h stations in June and August 1996.  $n = 49$  for June and 41 for August. All abundance values given are in number of animals meter<sup>-3</sup> of water. "\*" indicate total values.

Taxa	Mean abundance	Standard error	Minimum abundance	Maximum abundance
<b>June 1996</b>				
Total zooplankton	8021	852.08	67	56889
Bivalve veligers	3	1.99	0	95
Gastropod veligers	11	4.77	0	190
Polychaete larvae	3	1.32	0	54
Calanoid copepod adults	1527	173.04	67	4837
Calanoid copepod nauplii	701	208.68	0	7501
Barnacle nauplii	2	0.99	0	41
Decapod zoea	14	3.11	0	95
<b>August 1996</b>				
Total zooplankton	6097	335.59	1911	11061
Bivalve veligers	241	30.89	0	770
Gastropod veligers	76	11.50	0	308
Polychaete larvae	15	3.75	0	100
Calanoid copepod adults	3407	298.91	457	8162
Calanoid copepod nauplii	2281	217.05	353	7827
Barnacle nauplii	52	8.61	0	190
Decapod zoea	7	2.30	0	72

**Figure 9:** Summary of zooplankton abundance patterns observed during June 27-28 1996 around Palace Bar reef, Piankatank River, Virginia. Diel plankton abundance estimates were pooled across location for graphic presentation. Percentage composition of the diel zooplankton community by time is presented for the six taxa occurring in 50% of seasonal samples and decapod zoea including A.) barnacle nauplii and polychaete larvae, B.) bivalve veligers, C.) decapod zoea, D.) gastropod veligers, E.) calanoid copepod nauplii, and F.) calanoid copepod adults in relation to the average abundance of all species (G.; animals  $m^{-3} \pm$  standard error) and diel tidal patterns (H.). The black horizontal line in panel H. indicates the time interval from sunset to sunrise.

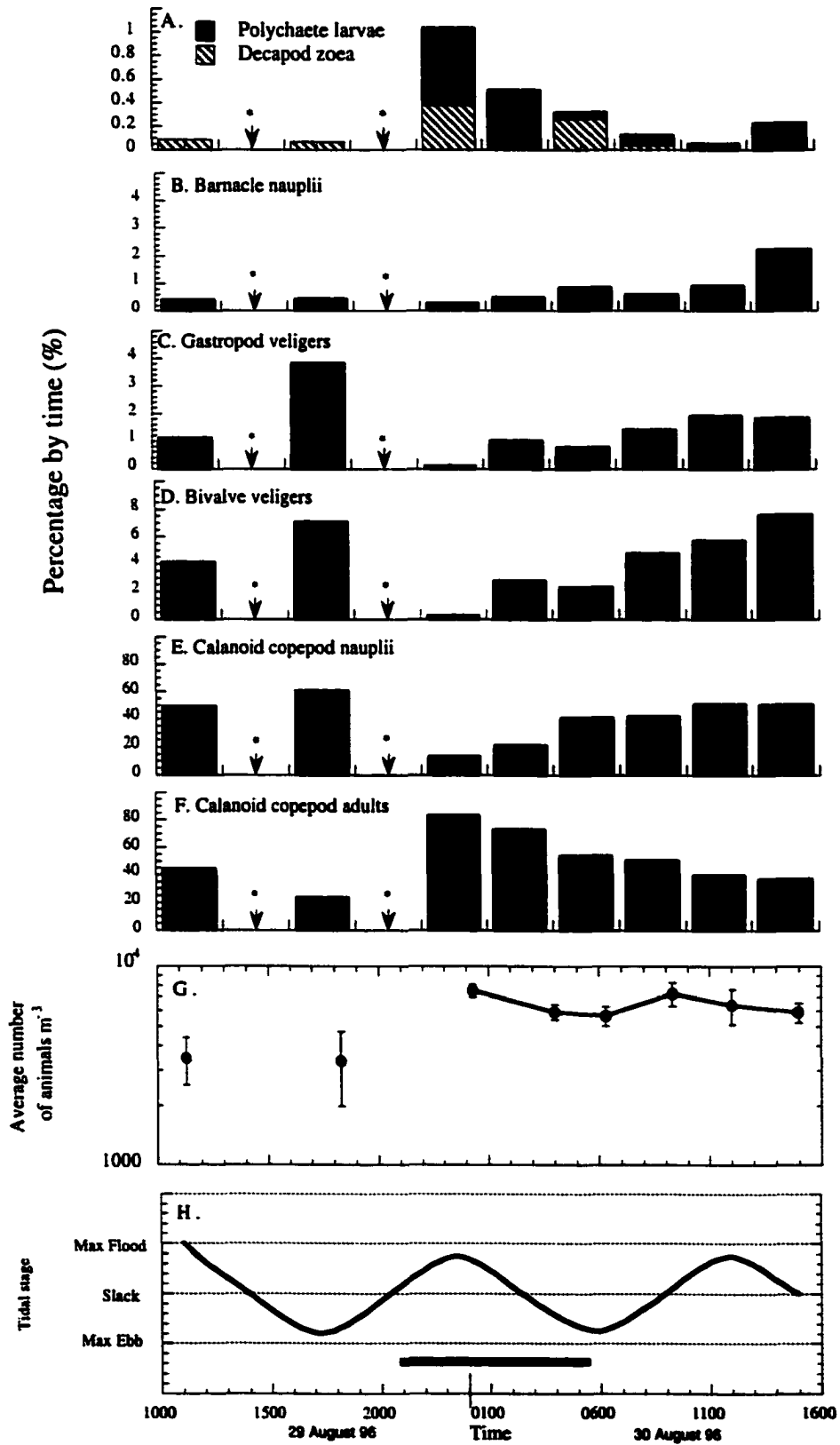


**Table 13: Summary of Kruskal-Wallis test results for plankton abundance from the June 27-28, 1996 station, Piankatank River, Virginia. All abundances are in number of animals meter<sup>-3</sup> of water. "\*" designates results that were significant at the  $p \leq 0.05$  level.**

Response: Abundance	Factor	d.f.	p value	Multiple comparison results (Dunn's test)
Total animals	Time of day	5	< 0.01	* 1600-2000 > 0000-0400, 1200-1600 > 2000-2400 > 0400-0800 > 0800-1200
	Tidal stage	3	0.21	
	Location	1	0.92	
Bivalve veligers	Time of day	5	0.06	
	Tidal stage	3	0.22	
	Location	1	0.35	
Gastropod veligers	Time of day	5	< 0.01	* 1200-1600 > 1600-2000 > 0000-0400, 0400-0800, 0800-1200, 2000-2400
	Tidal stage	3	0.17	
	Location	1	0.54	
Polychaete larvae	Time of day	5	0.03	* 1600-2000 > 2000-2400 > 0000-0400 > 1200-1600 > 0400-0800, 0800-1200
	Tidal stage	3	0.74	
	Location	1	0.70	
Calanoid copepod adults	Time of day	5	< 0.01	* 1600-2000 > 1200-1600, 2000-2400, 0000-0400 > 0400-0800 > 0800-1200
	Tidal stage	3	0.44	
	Location	1	0.78	
Calanoid copepod nauplii	Time of day	5	< 0.01	* 1600-2000 > 1200-1600 > 0000-0400, 2000-2400 > 0400-0800, 0800-1200
	Tidal stage	3	0.12	
	Location	1	1.00	
Barnacle nauplii	Time of day	5	0.12	
	Tidal stage	3	0.47	
	Location	1	0.13	
Decapod zoea	Time of day	5	< 0.01	* 0000-0400 > 0400-0800 > 2000-2400 > 0800-1200 > 1200-1600 > 1600-2000
	Tidal stage	3	0.18	
	Location	1	0.97	



**Figure 10:** Summary of zooplankton abundance patterns observed during August 29-30 1996 around Palace Bar reef, Piankatank River, Virginia. Diel plankton abundance estimates were pooled across location for graphic presentation. Percentage composition of the diel zooplankton community is presented for the six taxa occurring in 50% of seasonal samples and decapod zoea including A.) polychaete larvae and decapod zoea, B.) barnacle nauplii, C.) gastropod veligers, D.) bivalve veligers, E.) calanoid copepod nauplii, and F.) calanoid copepod adults in relation to the average abundance of all species (G.; animals  $m^{-3} \pm$  standard error) and diel tidal patterns (H.). The black horizontal line in panel H. indicates the time interval from sunset to sunrise. Sampling times marked with an asterick indicate instances where collected samples were lost due to preservation errors.



**Table 14:** Summary of Kruskal-Wallis test results for plankton abundance from the August 29-30, 1996 station, Piankatank River, Virginia. All abundances are in number of animals meter<sup>-3</sup> of water. "\*" designates results that were significant at the  $p \leq 0.05$  level. Samples from time block 6 (2000-2400) were not available for analyses.

Response: Abundance	Factor	d.f.	p value	Multiple comparison results (Dunn's test)	
Total animals	Time of day	4	0.13		
	Tidal stage	3	0.03	*	Slack onto Flood > Flood > Slack onto Ebb > Ebb
	Location	1	0.10		
Bivalve veligers	Time of day	4	< 0.01	*	1200-1600 > 0800-1200, 1600-2000 > 0400-0800 > 0000-0400
	Tidal stage	3	0.23		
	Location	1	0.86		
Gastropod veligers	Time of day	4	< 0.01	*	1600-2000 > 1200-1600 > 0800-1200 > 0400-0800 > 0000-0400
	Tidal stage	3	0.85		
	Location	1	0.15		
Polychaete larvae	Time of day	4	0.01	*	0000-0400 > 0400-0800 > 1200-1600 > 0800-1200 > 1600-2000
	Tidal stage	3	0.06		
	Location	1	0.93		
Calanoid copepod adults	Time of day	4	< 0.01	*	0000-0400 > 0400-0800 > 0800-1200 > 1200-1600 > 1600-2000
	Tidal stage	3	0.11		
	Location	1	0.45		
Calanoid copepod nauplii	Time of day	4	< 0.01	*	1200-1600 > 0800-1200 > 1600-2000 > 0400-0800 > 0000-0400
	Tidal stage	3	0.69		
	Location	1	0.39		
Barnacle nauplii	Time of day	4	0.26		
	Tidal stage	3	0.05	*	Slack onto Ebb > Slack onto Flood > Ebb > Flood
	Location	1	0.99		

< 0.05; Table 14).

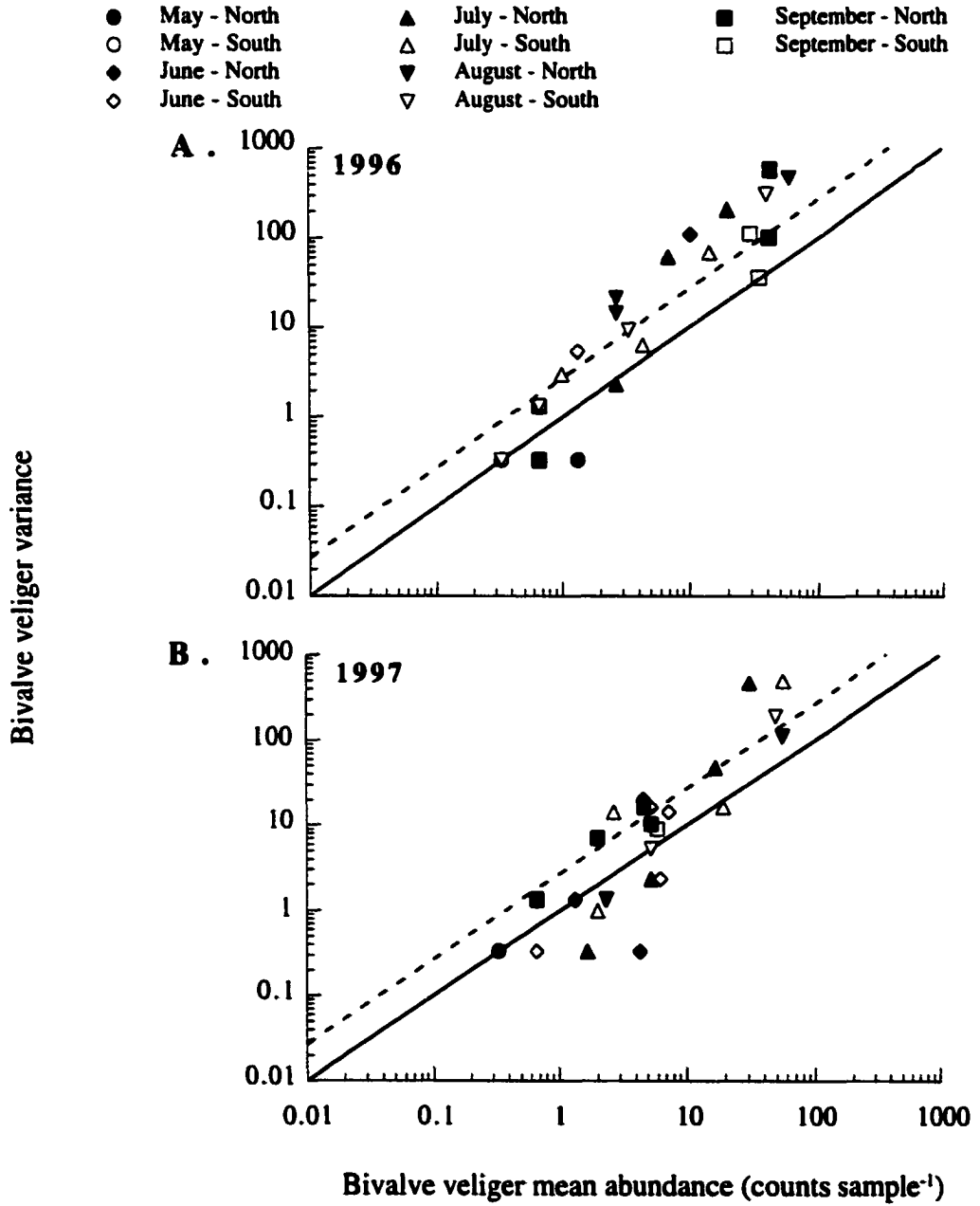
#### Seasonal and diel horizontal distribution:

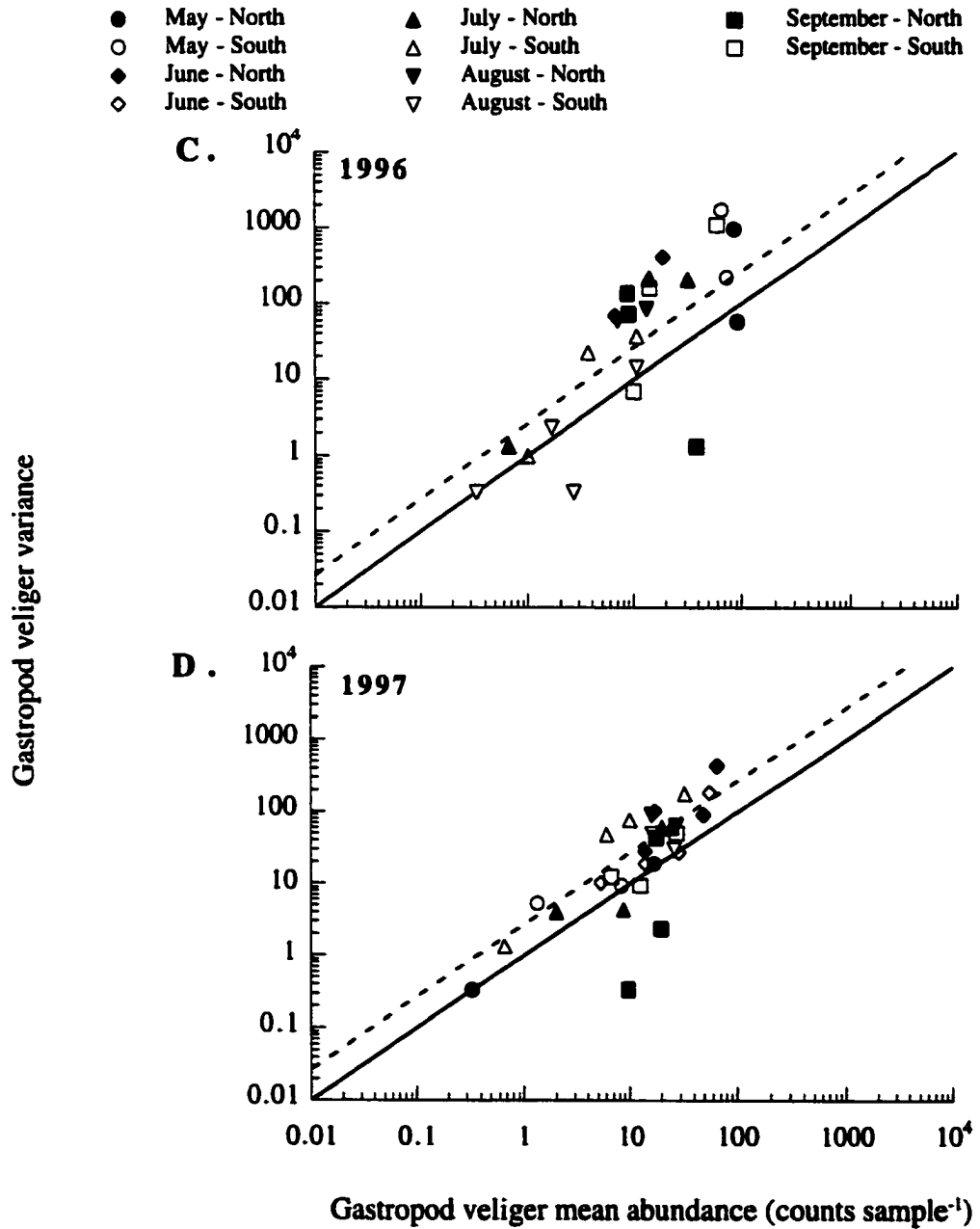
Seasonally and diurnally abundant zooplankton taxa were usually aggregated or non-randomly distributed on local spatial scales around Palace Bar reef (Figures 11, 12, and 13). In both 1996 and 1997, significant aggregation was observed in a majority of seasonal collections of calanoid copepod adults and nauplii (Figures 11G-J). Calanoid copepod adults collected during the June 27-8 and August 29-30 36 h stations were significantly aggregated in all but one collection from each station (Figure 12A and Figure 13D). Calanoid copepod nauplii collected during the August 29-30 station were significantly aggregated in all but one collection (Figure 13E).

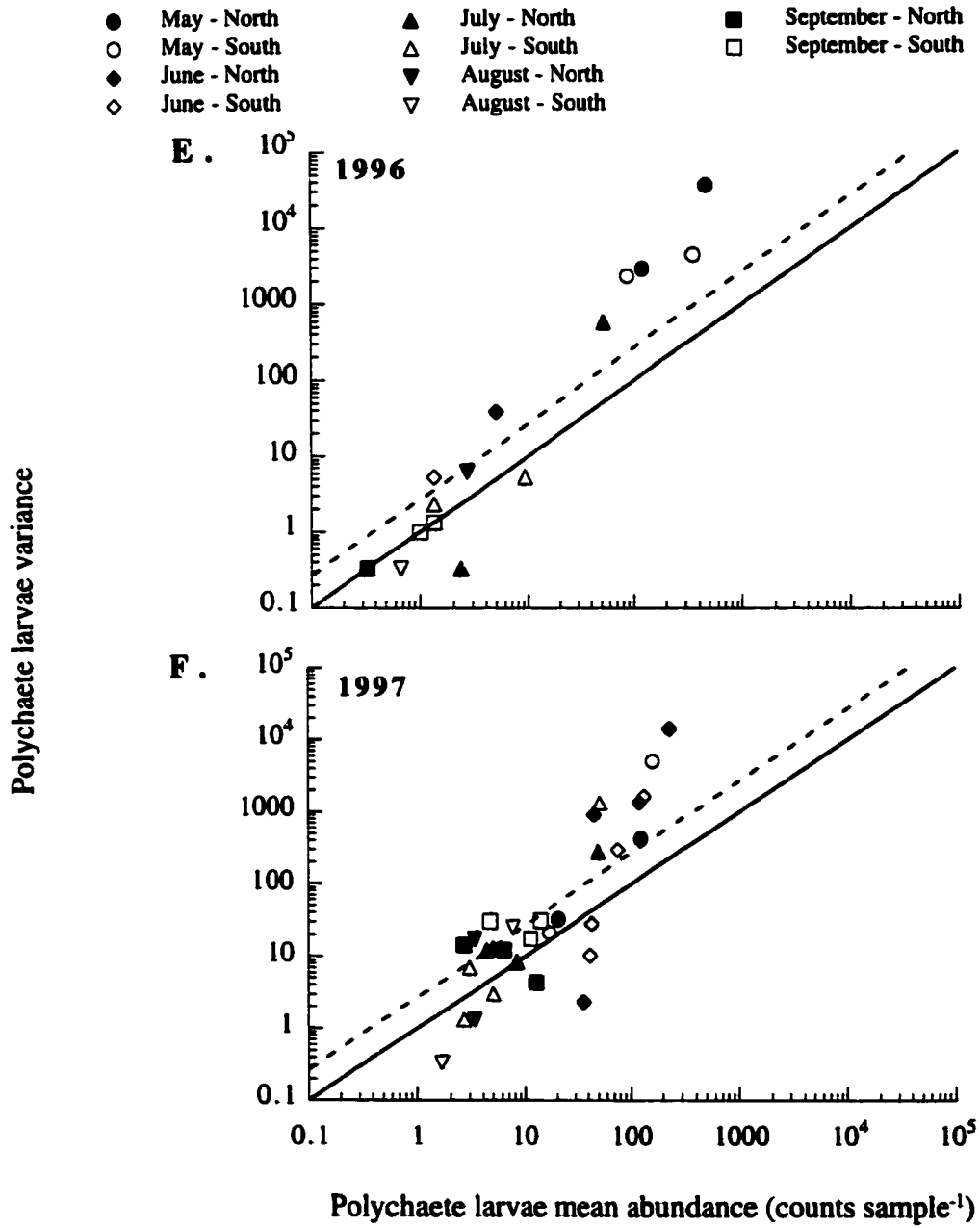
#### Seasonal and diel zooplankton community composition

The DCA of the seasonal abundance data from 1996 and 1997 grouped samples from early in the year, i.e., May and June on one end of the first ordination axis and the samples from the middle (July and August) and end (September and October) of the sampling season towards the opposite end (Figure 14). Axis I describes a seasonal gradient moving from right to left. Axis II describes a developmental or life cycle gradient for numerically dominant taxa present from July through October. Polychaete larvae, barnacle nauplii, and gastropod veligers were grouped toward the early (right) end of the first axis which reflects their high spring abundances (Figure 8). Taxa that were numerically dominant later in the year e.g., bivalve veligers, calanoid copepod nauplii, and calanoid copepod adults (Figure 3) were grouped together on the opposite end of the axis (Figure 14). The variance, as indicated by the eigenvalues, explained by the axes was 0.37 (axis I) and 0.14 (axis II) for 1996 and 0.69 (axis I) and 0.19 (axis II) during 1997. Points on the ordination diagrams were grouped on the basis of proximity related to sampling date. Groups of samples collected in May and June of both 1996 and 1997 were clearly separated from those collected later in the season (Figure 14).

**Figure 11:** Taxon-specific mean abundance (counts sample<sup>-1</sup>) for the six most common zooplankton taxa plotted in relation to species-specific variance for 1996 and 1997 regular zooplankton collections around Palace Bar reef: (A./B.) bivalve veligers, (C./D.) gastropod veligers, (E./F.) polychaete larvae, (G./H.) calanoid copepod adults, (I./J.) calanoid copepod nauplii, and (K./L.) barnacle nauplii. Samples collected on the north (channel) side of the reef are distinguished from those collected on the south (inshore) side. Only days where  $n = 3$  for both sides of the reef are presented. Points above the solid diagonal line in each panel indicate plankton collections where plankton are aggregated. The upper 95% confidence interval is indicated in each panel by a dashed diagonal line. Points above this dashed diagonal are significantly aggregated ( $p < 0.05$ ). Points below the solid diagonal line in each panel indicate plankton collections where taxa are uniformly distributed.

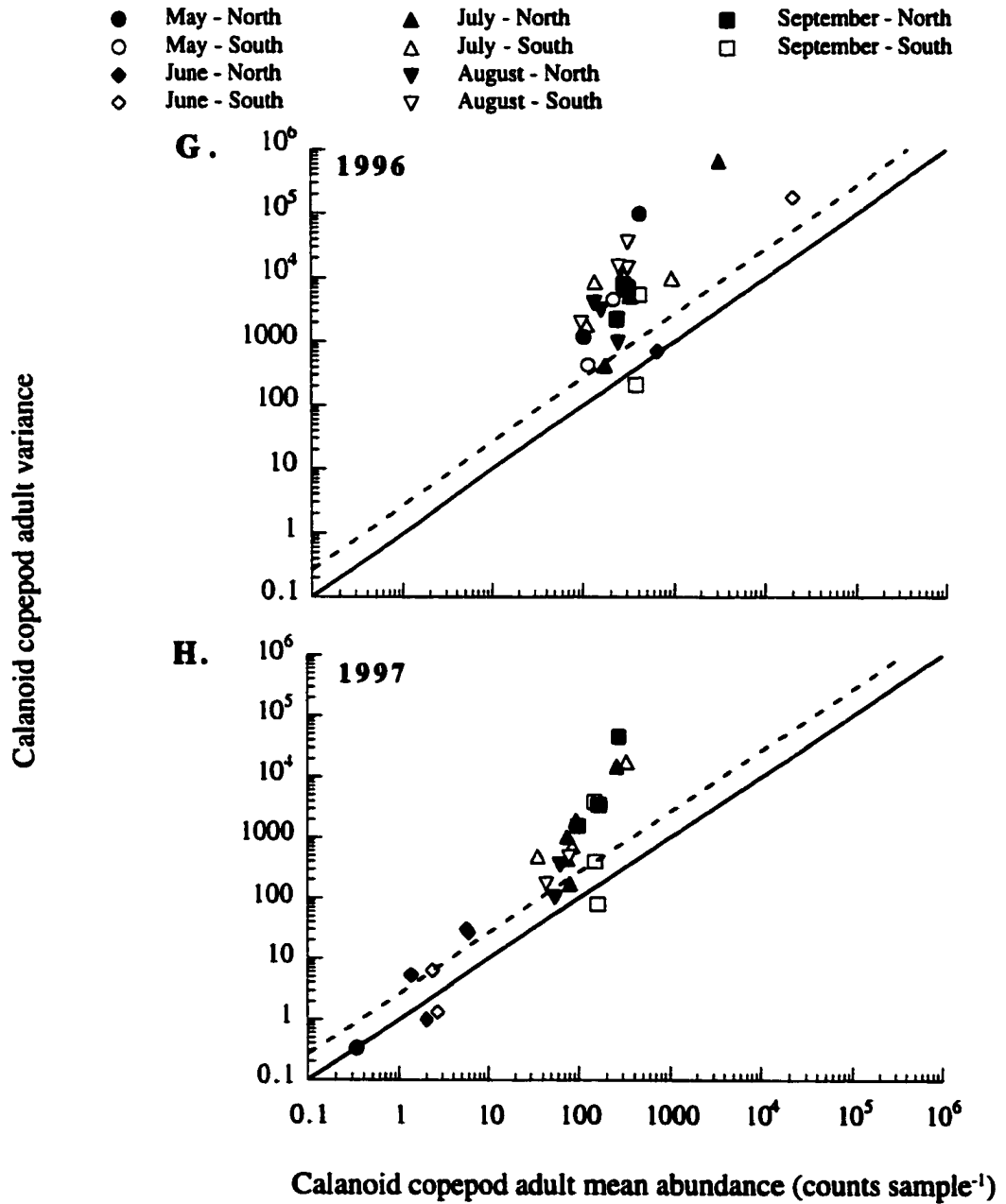


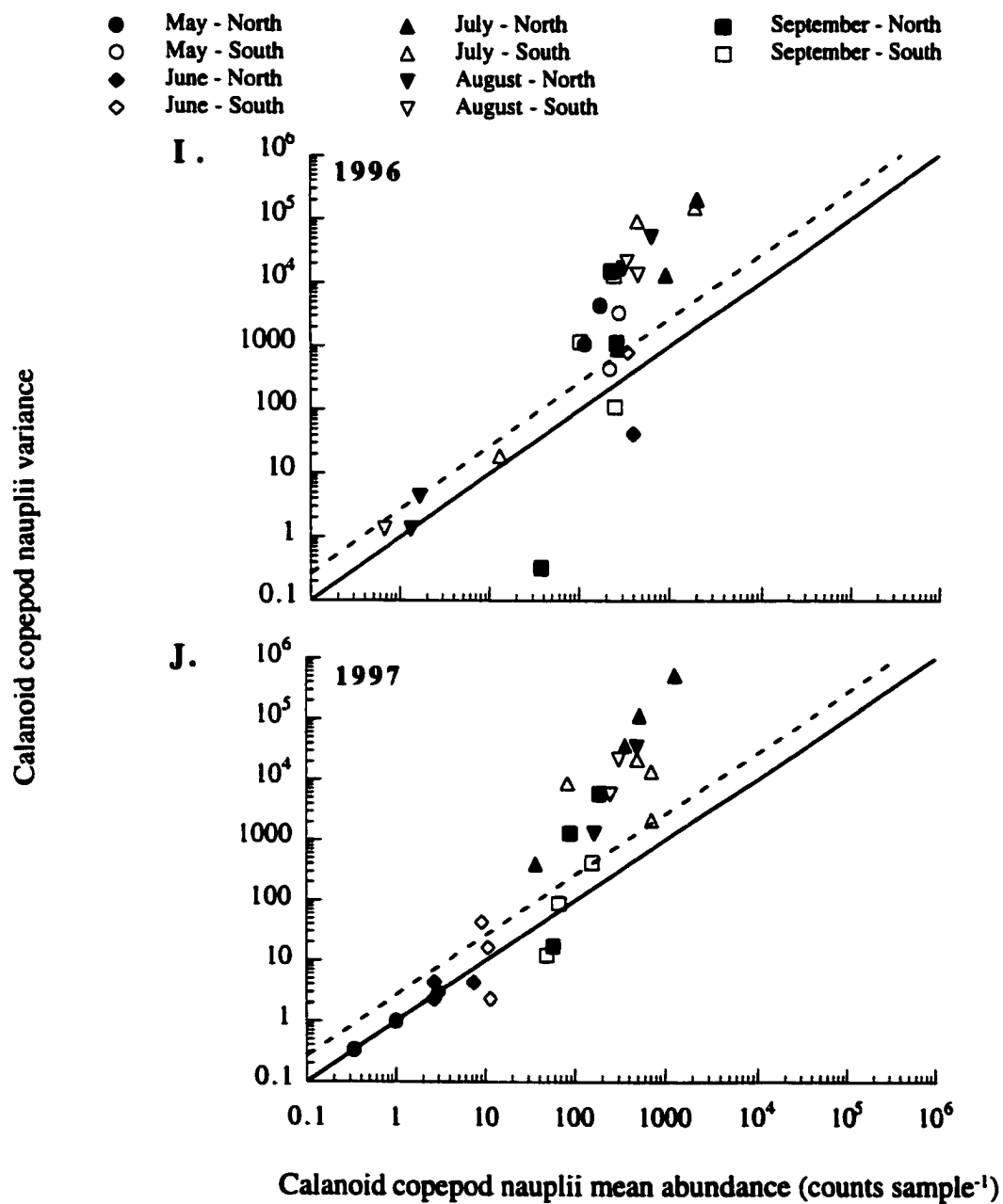


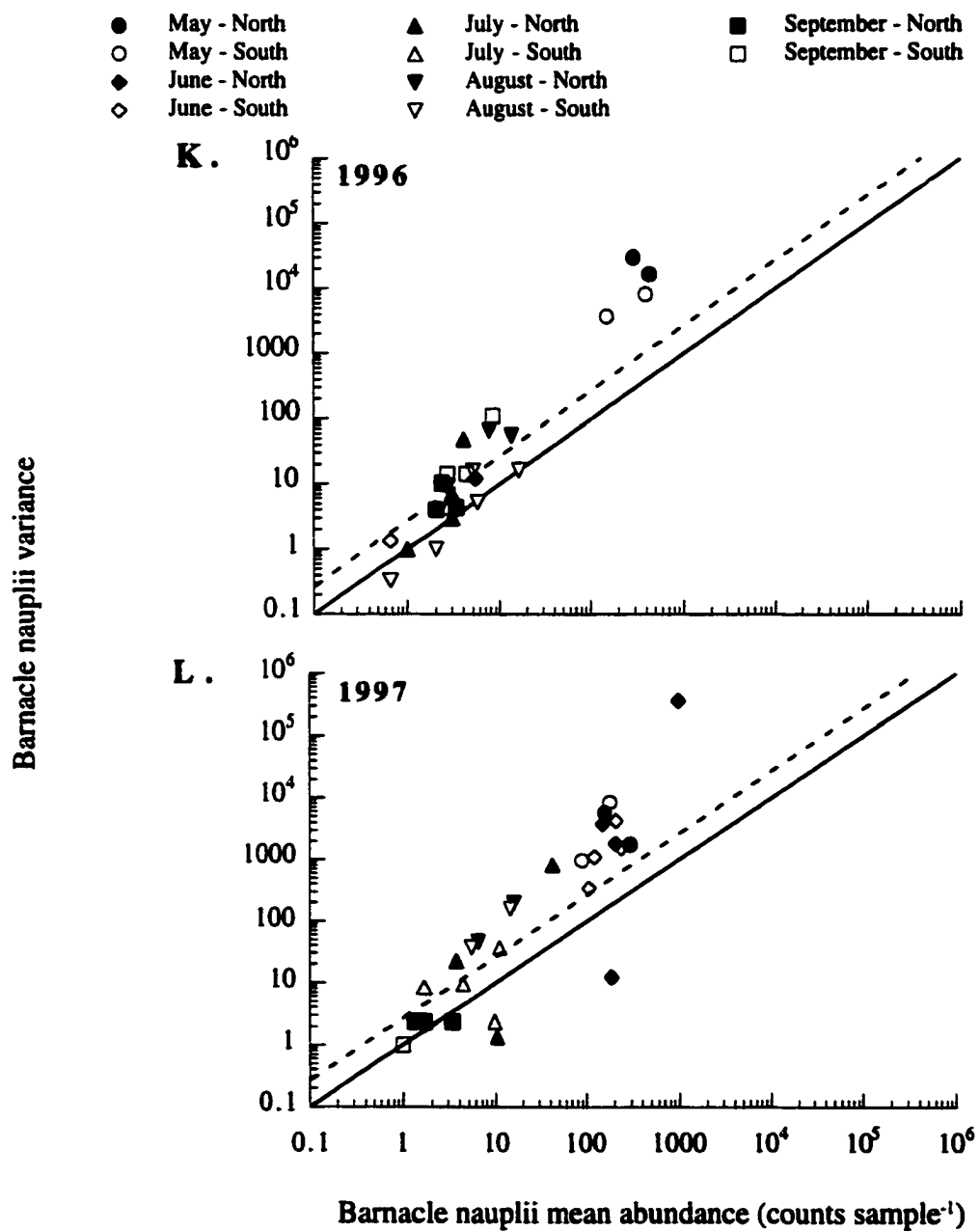


Polychaete larvae variance

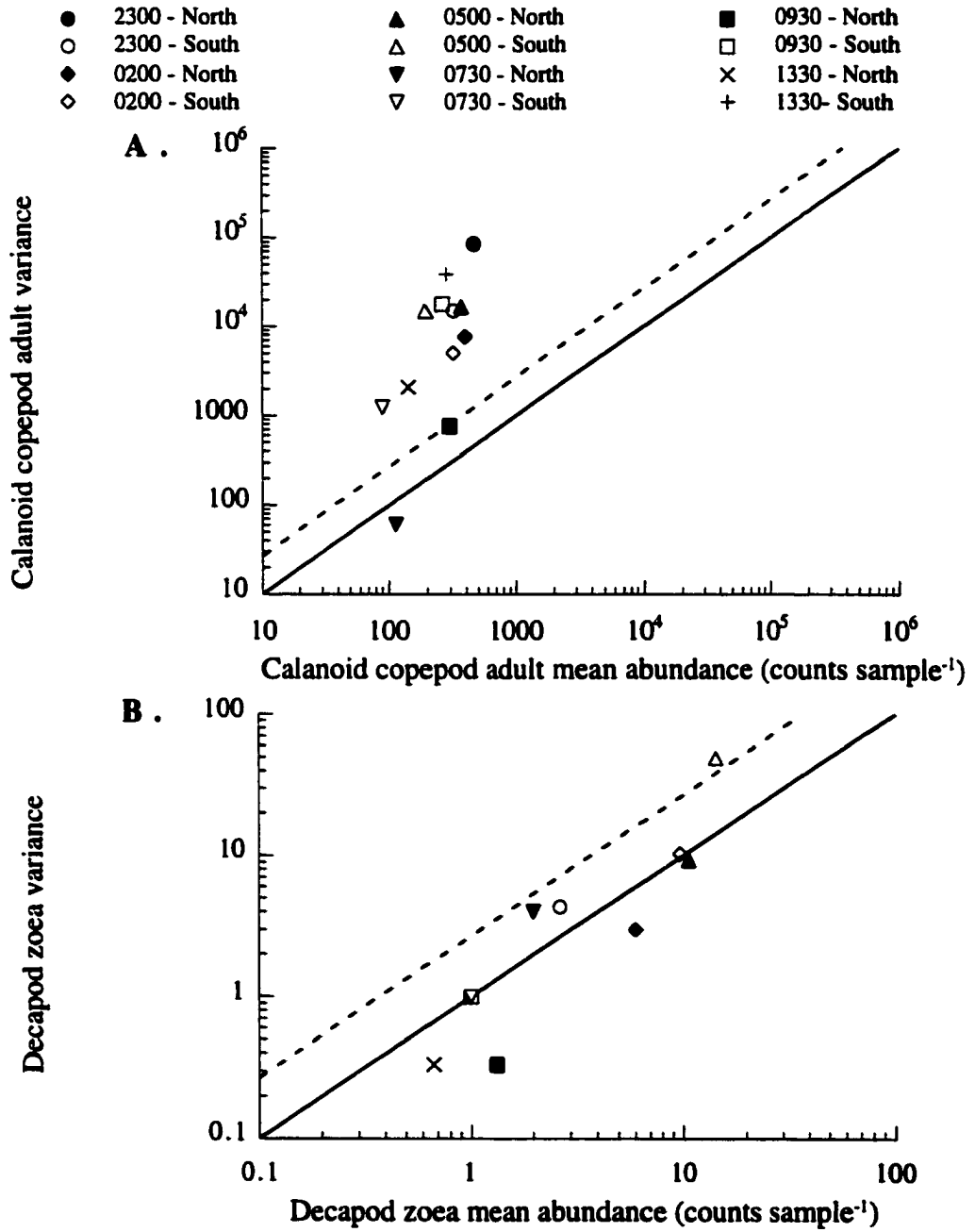




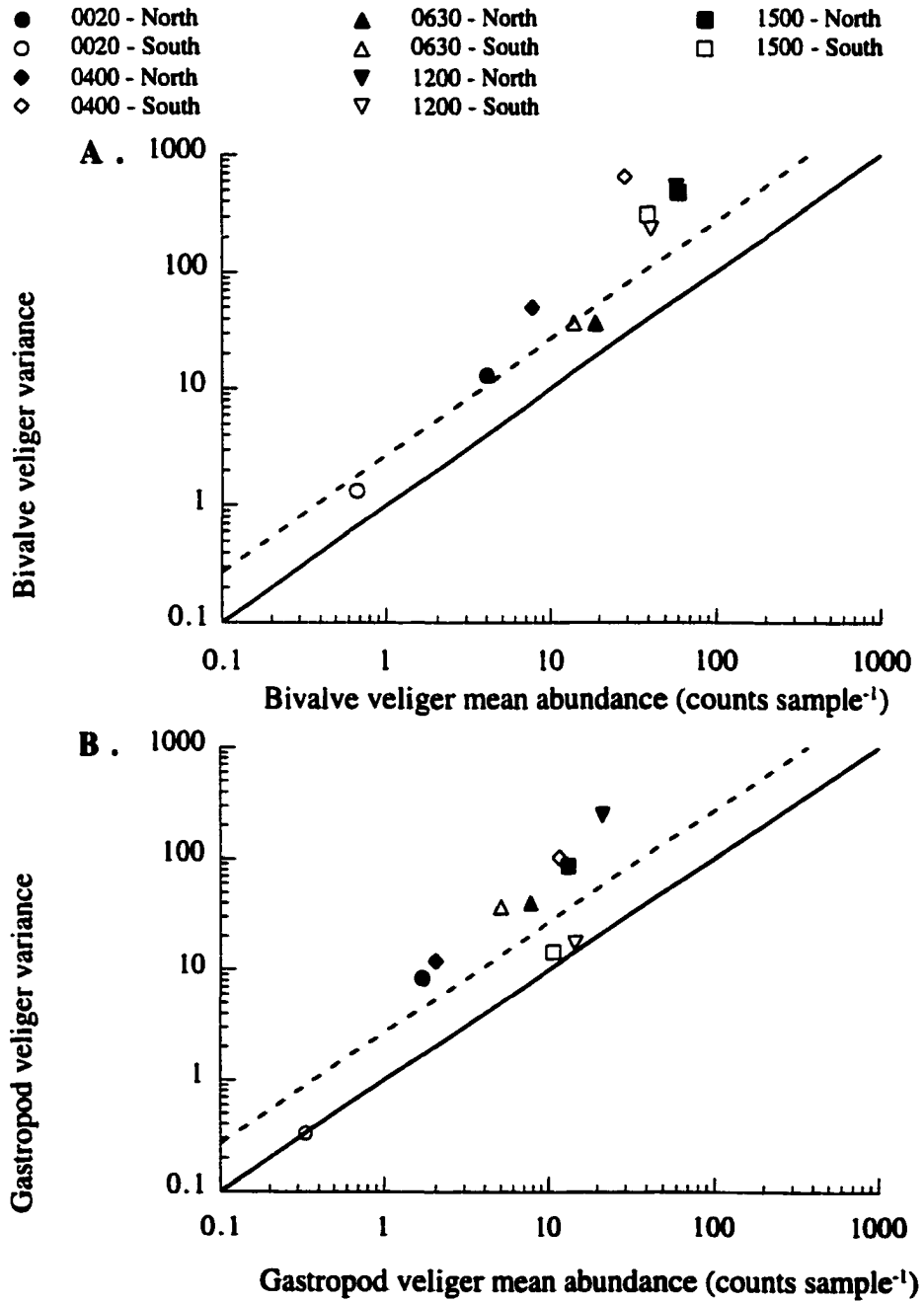


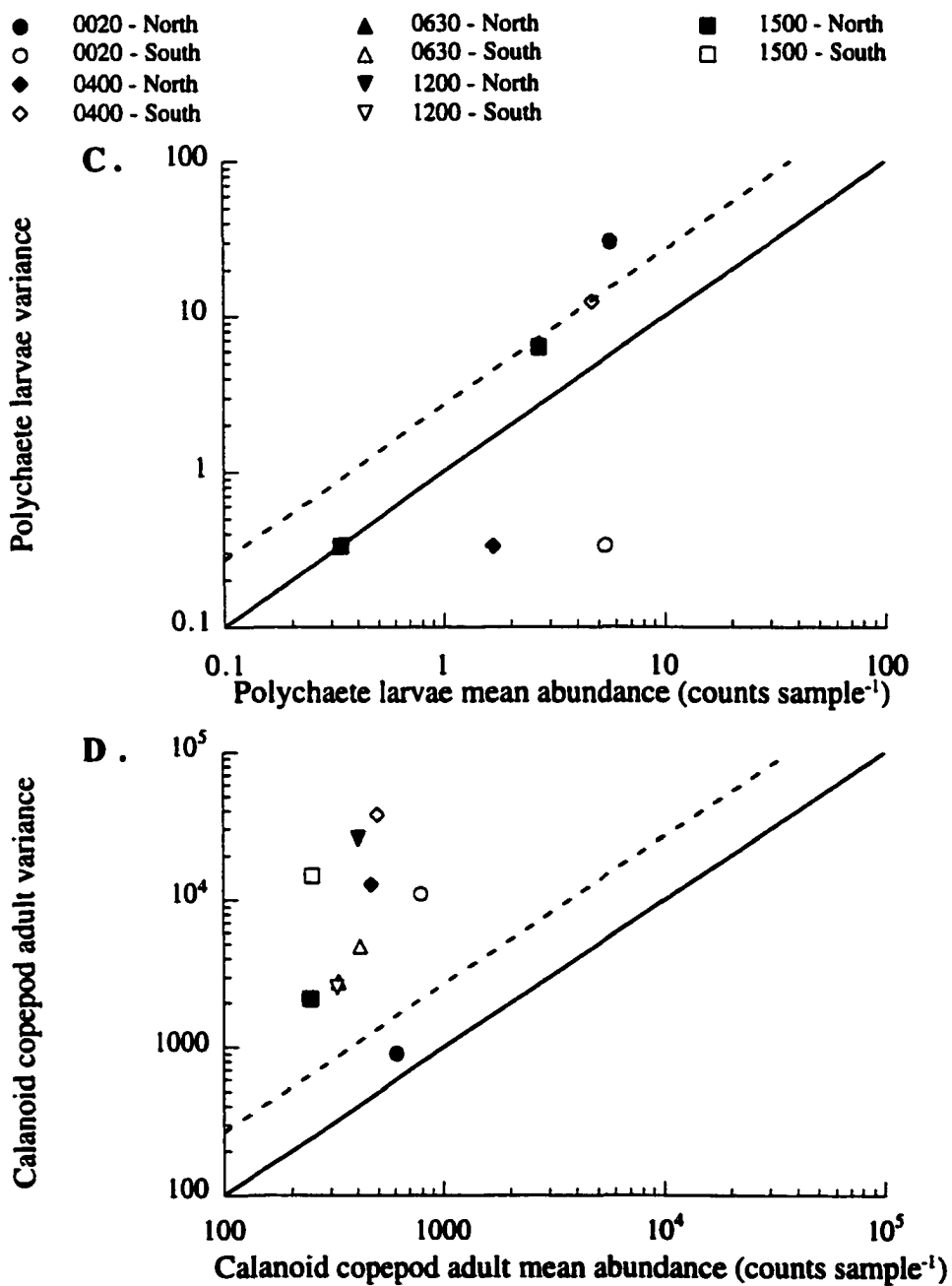


**Figure 12:** Taxon-specific mean abundance (counts sample<sup>-1</sup>) for calanoid copepod adults and decapod zoea plotted in relation to species-specific variance for June 27-8, 1996 plankton collections around Palace Bar reef: (A.) calanoid copepod adults and (B.) decapod zoea. Samples collected on the north (channel) side of the reef are distinguished from those collected on the south (inshore) side. Only times where  $n = 3$  for both sides of the reef are presented. Points above the solid diagonal line in each panel indicate plankton collections where plankton are aggregated. The upper 95% confidence interval is indicated in each panel by a dashed diagonal line. Points above this dashed diagonal are significantly aggregated ( $p < 0.05$ ). Points below the solid diagonal line in each panel indicate plankton collections where taxa are uniformly distributed.

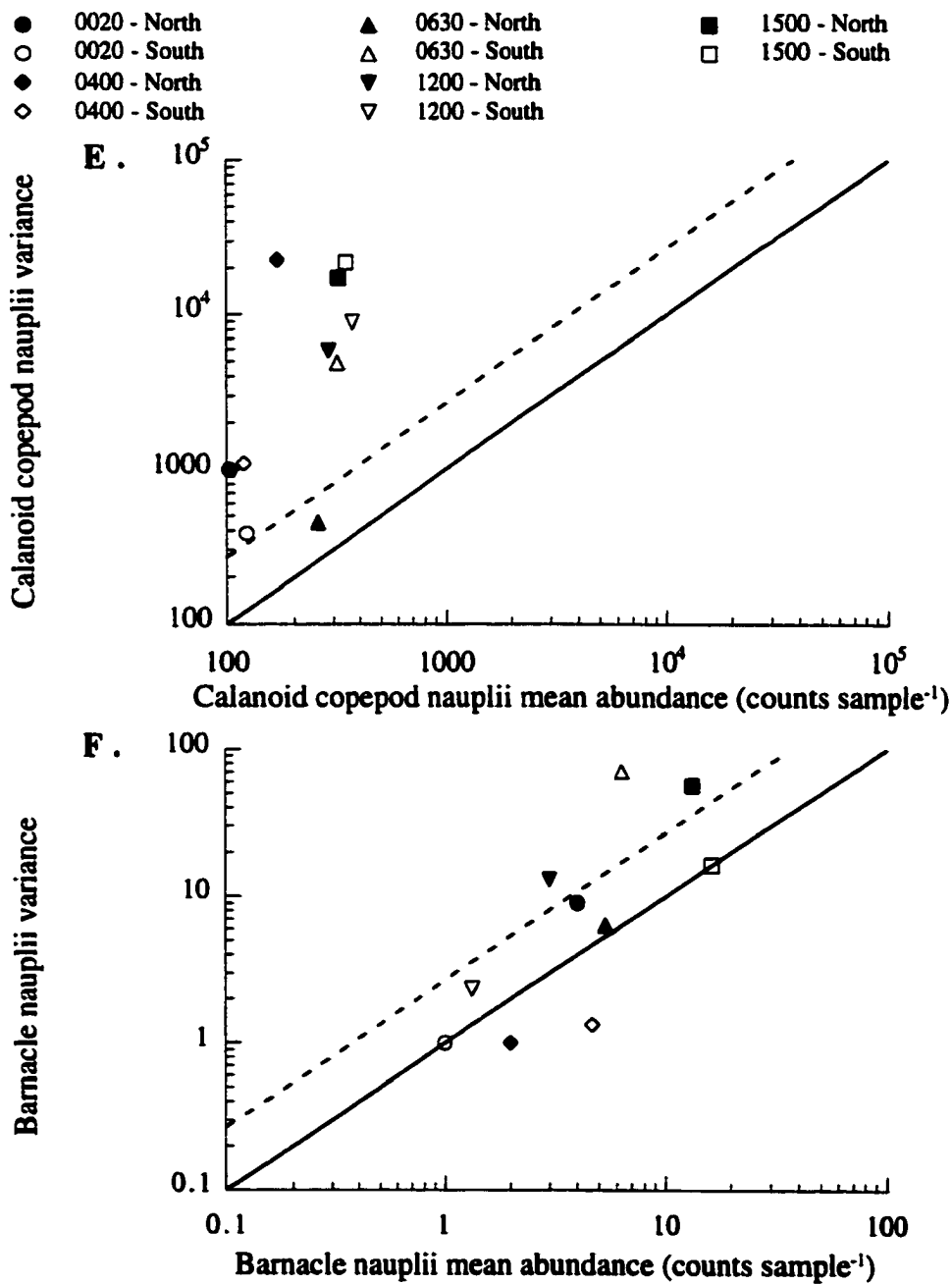


**Figure 13:** Taxon-specific mean abundance (counts sample<sup>-1</sup>) for the six most common zooplankton taxa plotted in relation to species-specific variance for August 29-30, 1996 plankton collections around Palace Bar reef: (A.) bivalve veligers, (B.) gastropod veligers, (C.) polychaete larvae, (D.) calanoid copepod adults, (E.) calanoid copepod nauplii, and (F.) barnacle nauplii. Samples collected on the north (channel) side of the reef are distinguished from those collected on the south (inshore) side. Only times where  $n = 3$  for both sides of the reef are presented. Points above the solid diagonal line in each panel indicate plankton collections where plankton are aggregated. The upper 95% confidence interval is indicated in each panel by a dashed diagonal line. Points above this dashed diagonal are significantly aggregated ( $p < 0.05$ ). Points below the solid diagonal line in each panel indicate plankton collections where taxa are uniformly distributed.









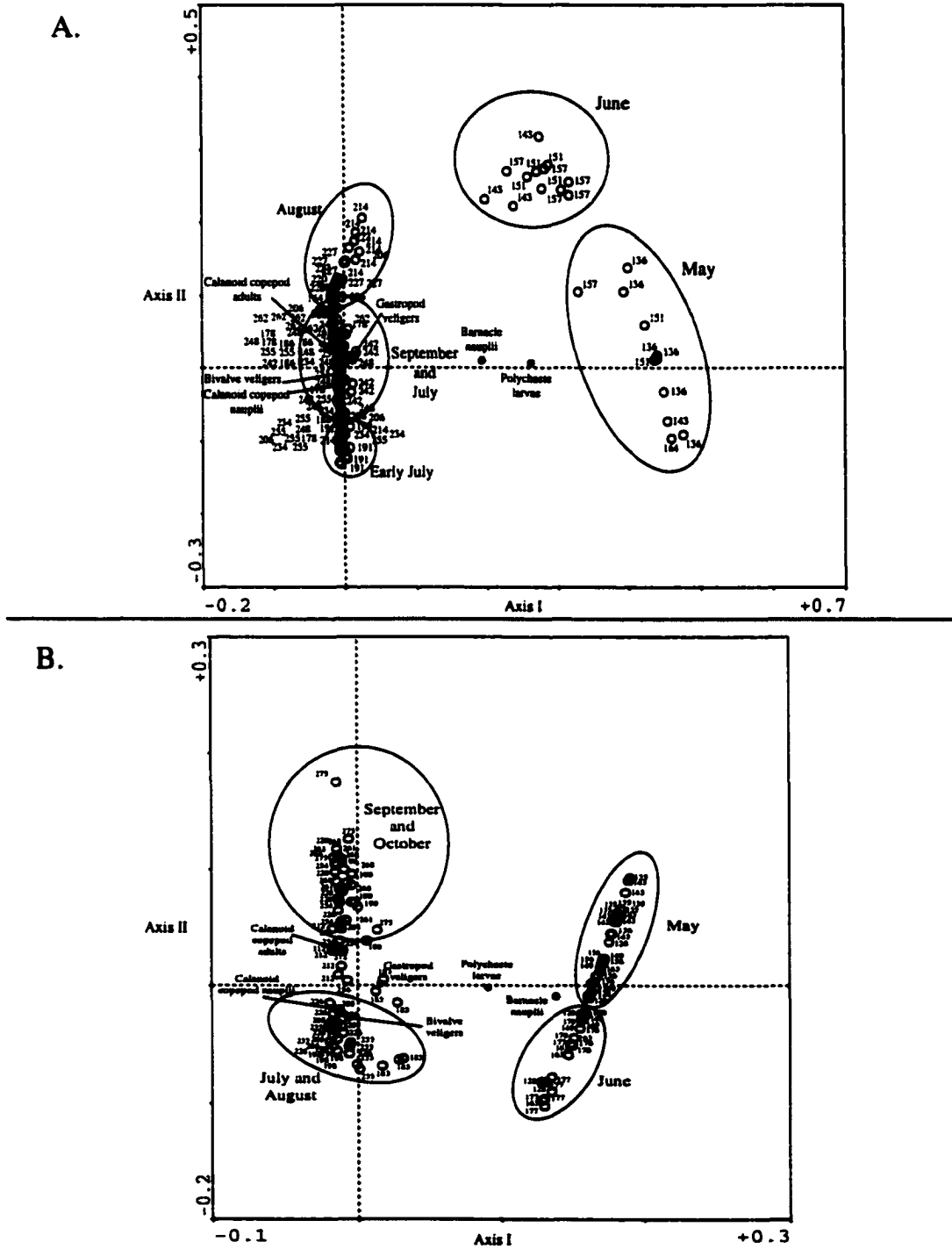


Figure 14: Taxa -sample biplots for detrended correspondence analyses (DCA) describing seasonal changes in zooplankton community assemblage and species abundance for 1996 (A.) and 1997 (B.). Individual samples are represented by open circles. Closed circles represent individual species. Numbers indicate the dates (day of the year) that samples were collected. Lines are used to distinguish groups of samples from similar seasons. The seasonal passage of time is indicated by axis I in a progression from right to left. Axis II describes a developmental or life cycle gradient for numerically dominant taxa present from July through October.

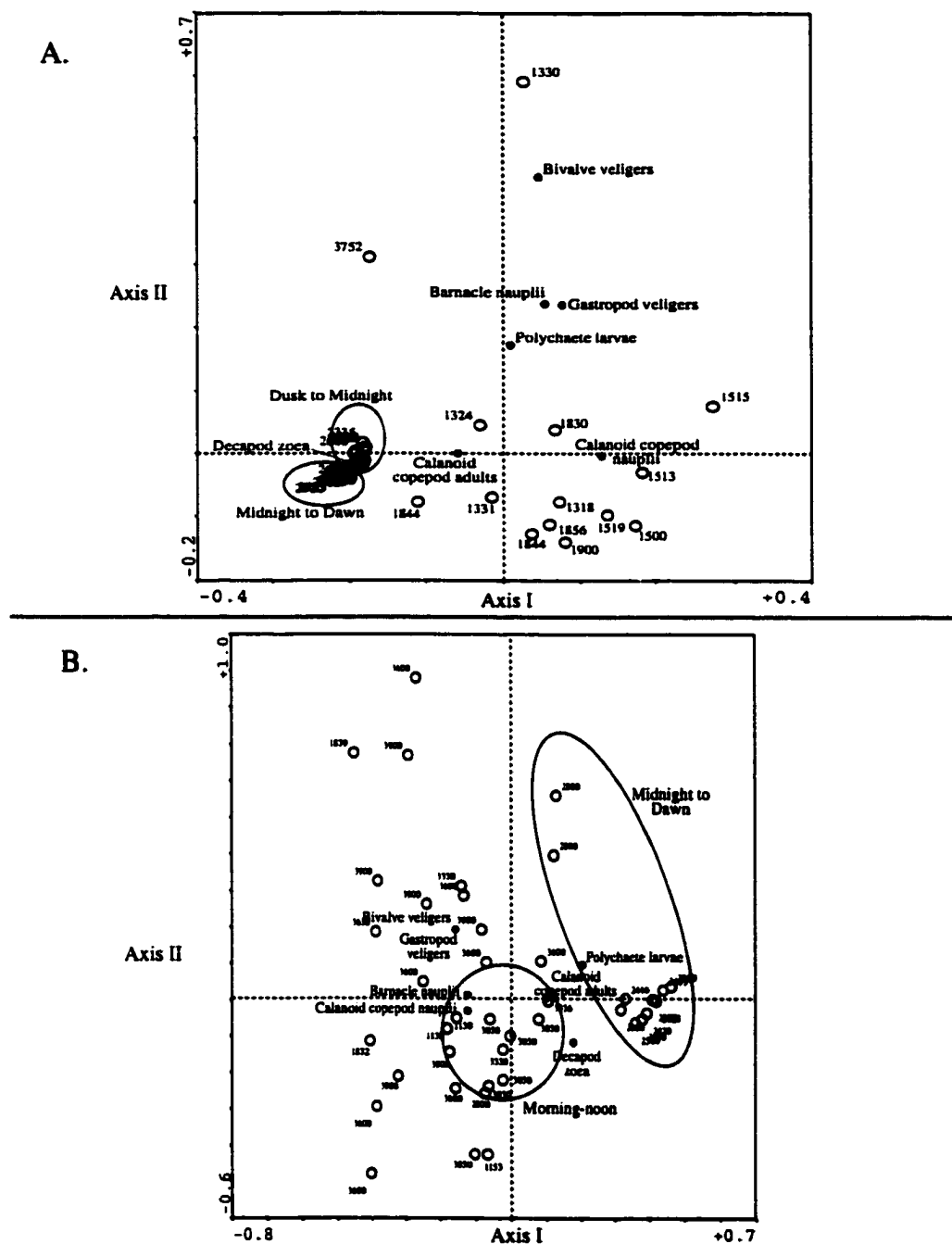


Figure 15: Taxa-sample biplots for detrended correspondence analyses (DCA) describing diel changes in zooplankton community assemblage and species abundance for June (A.) and August 1996 (B.). Individual samples are represented by open circles. Closed circles represent individual species. Numbers indicate the time during the 36 h station that samples were collected; 0000 refers to midnight on the first day of sampling. Lines are used to distinguish groups of samples from similar times. The diel passage of time in relation to tidal cycle is indicated by axis I in a progression from right to left (A.) and left to right (B.). Axis II represents a gradient in ambient light levels corresponding to diurnal variations in incident light.

DCA ordinations with the diel data from June and August 1996 grouped samples collected during flood tide on the right side of the diagram and samples collected when the tide was ebbing on the left; thus axis I represents a gradient in tidal conditions (Figure 15, Figures 9 and 10). For both 36 h stations, samples collected at night were clustered on one end of the second ordination axis and samples collected during mid to late afternoon were on the opposite side of the second axis; axis II represents a gradient in ambient light levels (Figure 15). The ordinations for both dates placed taxa that were most abundant near mid-day (bivalve veligers, barnacle nauplii, polychaete larvae, gastropod veligers, and calanoid copepod nauplii; Figures 9 and 10) towards the center of the ordination diagram. Taxa that were most abundant at night and also on the ebb tide (decapod zoea and calanoid copepod adults, Figure 9 and 10) were off-set toward the night and ebbing quadrants (Figure 15). Groups of samples collected during ebbing tide and night conditions were spatially separated from other samples and are encircled (Figure 15). Eigenvalues were 0.32 (axis I) and 0.03 (axis II) for the June ordinations and 0.17 (axis I) and 0.03 (axis II) for the August ordination analyses.

## DISCUSSION

Zooplankton around Palace Bar reef, Piankatank River, Virginia are characterized by distinct temporal patterns. Significant seasonal and diel differences in abundance were observed for six taxa that dominated seasonal and diel zooplankton collections (bivalve veligers, gastropod veligers, polychaete larvae, barnacle larvae, calanoid copepod nauplii, calanoid copepod adults), as well as a seventh diurnally important taxon (decapod zoea). Tidal influences alone were less important than seasonal and diel patterns for most taxa but may interact with diel cues to create observed diel zooplankton distribution patterns in both June and August 1996. Zooplankton taxa around the reef were distributed non-randomly (patchily) regardless of their horizontal location with regard to the reef.

In the absence of vertical stratification and strong tidal currents, observed variations in diel abundance patterns probably owe more to taxa-specific behavior than physical forces

alone. The importance of vertical stratification and tidal currents to zooplankton transport and subsequent distribution in tidally dominated estuaries is well established (Woolridge and Erasmus, 1980; Mann, 1988; Laprise and Dodson, 1996; Hill, 1998). Species-specific diel vertical migration and resulting lower daylight abundances in surface waters are also well documented for estuarine plankton. Nocturnal increases in calanoid copepod abundance in near-surface waters of well-mixed estuaries have been reported previously by Minello and Matthews (1981), Stubblefield et al. (1984), and Houser and Allen (1996). Elevated zoea abundance at night and on the ebb tide have been reported by Epifanio et al. (1984) for *Callinectes sapidus* stage I zoea and by Brookins and Epifanio (1985) for *Uca* spp. and *Pinnixa* spp. zoea and are probably related to the seasonal reproductive cycle and subsequent zoea migration to coastal waters for development. Net or gear avoidance by plankton during daylight hours may also contribute to relatively lower daylight abundances.

The seasonal abundance patterns and community composition observed in this subestuary are similar to those described for other Mid and South Atlantic estuaries (e.g., Lonsdale and Coull, 1977; Turner, 1982; Mallin, 1991; Houser and Allen, 1996). Mean seasonal zooplankton abundances in the Piankatank River during 1996 (8,021 animals m<sup>-3</sup>) and 1997 (6,652 animals m<sup>3</sup>) are similar to mean abundance values from other estuaries (e.g., Herman et al., 1968; Thayer et al., 1974; Lonsdale and Coull, 1977; Buskey, 1993). Numerical dominance of the plankton by calanoid copepods from June through September has been reported for other Chesapeake Bay tributaries including the Patuxent River, Maryland (Heinle, 1966) and the Rhode River, Maryland (Allan et al., 1976).

Seasonal pulses in zooplankton abundance relate directly to life history patterns and reproductive cycles of individual taxa e.g., the observed peaks in bivalve veliger abundances during July-August of both years occurred 2 to 3 weeks prior to pulses in local oyster settlement and recruitment described by Morales-Alamo and Mann (1997, 1998). Differences in the reef zooplankton assemblage over time were most obvious for benthic invertebrate larvae. Barnacle nauplii and polychaete larvae were the most abundant benthic

invertebrate larvae observed in the plankton during May and June of both years. Similar abundances have been observed for barnacle nauplii by Lonsdale and Coull (1977), Mallin (1991), and Houser and Allen (1996) and for polychaetes by Lonsdale and Coull (1977) and Turner (1982). Gastropod veliger abundances began to increase in June and July as barnacle nauplii and polychaete larval abundances decreased. Bivalve veliger abundances were at a maximum beginning in mid to late July and continuing through August. All of these larval forms are filter feeders and might compete for similar food resources if they occurred in the plankton simultaneously in large numbers.

The temporal separation in the presence of specific taxa potentially limits planktonic competition for food while providing a seasonally constant resource for planktonic predators including larval fishes and coelenterates. Stage duration and recruitment success of larval fishes has been related to food availability (Shepard and Cushing, 1980). The recruitment success and survival of small forage fishes (e.g., bay anchovies (*Anchoa mitchilli*), Atlantic silversides (*Menidia menidia*)) directly affects upper level predators. Palace Bar reef supports a range of planktivorous larval and juvenile fishes including naked gobies (*Gobiosoma bosc*), striped blennies (*Chasmodes bosquianus*), bay anchovies, Atlantic menhaden (*Brevoortia tyrannus*), and spot (*Leiostomus xanthurus*) (Harding and Mann, 1999) that are potential prey items for larger pelagic predators including bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and striped bass (*Morone saxatilis*) commonly found on the reef (Harding and Mann, 1999). Large numbers of coelenterates (e.g., *Aurelia* sp., *Mnemiopsis leidyi*, *Chrysaora quinquecirrha*) have been observed on and around the reef, particularly during July and August 1996 (J. Harding, unpublished data).

Zooplankton are an important component at intermediate trophic levels in estuarine food webs and the spatio-temporal abundance of zooplankton has obvious consequences for the rest of the food chain. Prior to mid-July, diets of Chesapeake Bay bluefish, striped bass, and weakfish rely heavily on benthic production (Hartman and Brandt, 1995a). In late summer and into the fall, bay anchovies and then Atlantic menhaden, both representatives

of pelagic pathways, lead to Bay apex predator production (Hartman and Brandt, 1995b). Baird and Ulanowicz (1989) placed emphasis on benthic production for predator success. Recent shifts in the relative importance of benthic and pelagic production to the Bay food web (Hartman and Brandt, 1995a, 1995b; Baird and Ulanowicz, 1989) may relate to the decline of Chesapeake Bay oyster reefs and, consequently, the complex communities they supported. Beyond the actual filtering capacity of the oysters (see Newell, 1988), living oyster reefs provide habitat complexity and physical structure that may support higher levels of species diversity and production than surrounding sand flats as do tropical coral reefs (e.g., Roberts and Ormond, 1987). Reef benthic fauna influence the overlying zooplankton community in terms of both temporal changes in community composition and absolute abundance. Future research is needed to compare estuarine plankton assemblages around oyster reefs with those observed at non-reef sites and related observed plankton community dynamics to trophic dynamics.

Portions of this chapter have been previously published:

Harding, J.M. 1999. Marine Ecology Progress Series. 179:145-153.

### CHAPTER 3

Selective feeding behavior of larval naked gobies (*Gobiosoma bosc*) and blennies  
(*Chasmodes bosquianus* and *Hypsoblennius hentzi*):  
preferences for bivalve veligers

#### ABSTRACT

Naked gobies (*Gobiosoma bosc*), striped blennies (*Chasmodes bosquianus*) and feather blennies (*Hypsoblennius hentzi*) provide important intermediate links within the trophic structure of estuarine oyster reef communities. Predator-prey interactions between planktonic larvae of these fishes and larval eastern oysters (*Crassostrea virginica*) may influence recruitment success of both groups within oyster reef communities. These three species of oyster reef fish larvae were cultured from wild nests. Multifactorial laboratory feeding experiments using larval oysters or hard clams (*Mercenaria mercenaria*) as well as wild plankton were used to determine the effects of predator age, predator concentration, and prey type on feeding selectivity of these fishes. Predator age significantly influenced feeding behavior of naked gobies and feather blennies. Predator concentration did not significantly affect feeding behavior for any of the three fish species. Prey type significantly affected feeding behavior of feather blennies and naked gobies. Naked gobies consumed bivalve veligers preferentially at all veliger concentrations. Feather blennies consumed veligers preferentially at concentrations as low as 12% of the available prey field. Striped blennies were less specialized in their feeding patterns but still consumed bivalve veligers preferentially at prey field concentrations as low as 11% veligers.



## INTRODUCTION

On the basis of numbers alone, oyster reef fish larvae are an important component of estuarine plankton: for example, naked goby (*Gobiosoma bosc*) larvae seasonally dominate Chesapeake Bay ichthyoplankton collections (Massmann et al., 1963; Shenker et al., 1983; Cowan and Birdsong, 1985). The local trophic impacts of these planktonic predators are poorly understood. The connections between adult gobies, conspecific blennies (feather, *Hypsoblennius hentzi*; striped, *Chasmodes bosquianus*), and living reefs created by eastern oysters (*Crassostrea virginica*) have long been acknowledged (e.g., Wells, 1961; Dahlberg and Conyers, 1973). Adult fishes use the heterogeneous habitat created by the matrix of adult oyster shells for shelter as well as nesting and feeding grounds.

Growth and mortality patterns for larval fishes are strongly influenced by food availability and determine observed community recruitment relationships (Shepherd and Cushing, 1980; Houde, 1989). Within oyster reef communities, planktonic fish larvae may be major predators on planktonic oyster larvae or “veligers”. Benthic reef fishes and oysters spawn within the same approximate temporal or seasonal window, producing larvae that occur concurrently and undergo planktonic development followed by subsequent settlement and recruitment to the benthos. For larval fishes, abundant food supplies, as potentially available around and on oyster reefs, increase growth rates and shorten the planktonic larval development period, reducing predation risks from pelagic invertebrate and vertebrate predators (Houde and Schekter, 1980; Hunter, 1981). Reduction of time to settlement potentially increases recruitment of these intermediate reef fishes (Shepherd and Cushing, 1980). Increased densities of benthic reef fishes provide more potential prey items for apex pelagic predators that use oyster reefs as feeding grounds and nursery areas.

Larval fish preference for bivalve veligers from the ambient prey field has been previously documented. Houde and Lovdal (1984) and Govoni et al. (1986) reported strong preferences for veligers by several species of larval fishes in Biscayne Bay and the Gulf of Mexico. Olney (1996) described feeding behavior and preference for veligers by larval

seaboard gobies (*G. ginsburgi*) collected from the Chesapeake Bay plume. Checkley's (1982) laboratory experiments with herring larvae (*Clupea harengus*) using wild zooplankton as prey showed significant preferences for mollusc veligers.

Breitburg (1989, 1991) conducted field and laboratory studies with pre-settlement and settlement stage naked goby larvae to determine feeding incidence in relation to demersal schooling behavior and settlement. Gut contents from field caught demersal naked goby larvae were dominated by crustaceans (n fishes = 22, Breitburg, 1989; n fishes = 72, Breitburg, 1991). Laboratory experiments testing prey selectivity of planktonic goby or blenny larvae have not previously been described.

The objectives of this study were to test the effects of predator age, predator concentration, and prey type on feeding selectivity using bivalve veligers as the principal prey of cultured naked goby, striped blenny, and feather blenny larvae. A selected prey item is one whose proportional occurrence in gut contents is greater than its proportion in the available prey field.

## METHODS

### *Larval fish culture*

Larval gobies and blennies used in laboratory feeding experiments were cultured using nests that were collected from naturally occurring or artificially deployed oyster shell substrate. Fish nests were identified by egg morphology (size, color) and the identity of the guarding parents. Nests were transported to the laboratory in individual plastic bags filled with river water. In the laboratory, nests were carefully placed in 0.5 L beakers filled with a mixture of water from the field site and sand-filtered seawater. All beakers were maintained at 24°C and 12 to 17 ‰ under a 14 h light/10 h dark regime; i.e., summer field conditions.

As larvae hatched, they were moved to finger bowls filled with 1 L of sand-filtered seawater; larval densities were kept at approximately 150 per finger bowl. Larvae were fed rotifers (*Branchionus plicatilis*) several times daily from day 0 post-hatching until approximately day 8. During days 8 to 18, larval fishes were fed a mixture of rotifers and

fresh (< 1 d old) *Artemia* sp. nauplii (Carolina Biological Supply, Inc.). The feeding mixture was gradually changed from 100% to 0% rotifers by day 14 to 18 or when fishes began settlement. After 18 d, or the initiation of settlement, fishes were transferred to aquaria filled with 30 L of aerated, filtered seawater; fishes were maintained at densities less than 100 tank<sup>-1</sup> and were fed three times daily with fresh *Artemia* sp. nauplii. After 21 d, clean oyster shell was placed in each tank to provide shelter and feedings were reduced to two larger portions of 2 to 3 d-old *Artemia* sp. nauplii.

#### *Preliminary laboratory feeding experiments*

**Gut residence time:** The results of preliminary feeding experiments to determine gut residence time were used to establish the appropriate duration for subsequent larval feeding experiments. Experiments had to be long enough to allow prey items to pass into the gut but short enough to avoid defecation. Individual striped and feather blennies of various ages were allowed to feed in chambers containing high densities (> 8000 prey L<sup>-1</sup>) of prey items (either rotifers dyed with acridine orange or *Artemia* sp. nauplii) until guts were visibly full (approximately 2 h). Individual fishes were then placed in chambers containing 0.15 L of filtered seawater. Every 30 min for 5 h, fishes were examined under a dissecting microscope to determine levels of gut fullness. Guts were considered empty when all of the brightly colored prey items were defecated.

**Habituation effects:** To avoid experimental biases resulting from previous larval fish feeding experience (Mills et al., 1987; Connaughton and Epifanio, 1993) and to verify that larval fishes would feed in the experimental chambers, several feeding trials were completed under identical conditions using either rotifers at concentrations > 5000 L<sup>-1</sup> or 16 d-old *Crassostrea* veligers at concentrations > 16,000 L<sup>-1</sup>. Five d-old feather blennies, cultured exclusively on rotifers, were starved for 4 h and then placed in individual chambers containing 0.15 L filtered seawater and either rotifers or veligers. Fish larvae were allowed to feed for 90 min at 24°C under light conditions and were then preserved in 10% neutral buffered formalin for subsequent dissection and gut content analyses. An image analyses system was used

to measure notochord length and veliger length to the nearest 0.01 mm after preservation.

### *Multi-factorial laboratory feeding experiments*

Multifactorial feeding experiments were designed to test the effects of predator age and concentration on larval fish feeding and to evaluate prey selectivity with regard to bivalve veligers. To avoid potential habituation effects, culture food organisms (rotifers or *Artemia* sp. nauplii) were never used as experimental prey items (Checkley, 1982; Lindberg and Doroshov, 1986; Mills et al., 1987; Connaughton and Epifanio, 1993). Fishes used in any given experiment were usually from the same brood or nest. Experimental conditions were the same as fish culture conditions. Six to 8 h before an experiment (5 to 7 h before being placed in experimental chambers), larval fishes were removed from culture chambers, placed in aerated, filtered seawater at 24°C, and starved until the experiment began.

### Prey items

**Zooplankton prey field:** Eight to 12 h prior to an experiment, two microplankton nets (80µm Nytex mesh, 0.3 m diameter, 3:1 aspect ratio) were deployed in the lower York River, Virginia. The lower York River supports neither oyster reefs nor a large oyster population (Morales-Alamo and Mann, 1998), thus these plankton samples are representative of conditions at sites away from oyster reefs. Nets were oriented to face into the current such that the top of the mouth support ring was within 0.1 m of the surface. The microplankton collected from each net were sieved through a 202 µm Nytex mesh to remove coelenterates, ctenophores, and any larval fishes, taken to the laboratory, and held in 2 L of filtered, well-aerated seawater in light conditions. Debris and sediment were allowed to settle out before experimental aliquots of plankton were removed. Before plankton aliquots were added to the experimental chambers, representative aliquots were examined under a dissecting microscope to verify that the plankton were alive and swimming.

**Veliger prey field:** Bivalve veligers were obtained from either the Virginia Institute of Marine Science (VIMS) or VIMS Eastern Shore Laboratory (ESL) hatchery facilities at least 18 h before an experiment. Veligers from the VIMS Hatchery required no salinity

acclimatization, whereas ESL veligers (rearing salinities of 33 to 35‰) were acclimated to lower York River salinities at a rate of 1 to 2 ‰ per 2 h to reach an endpoint equal to ambient York River salinities (12 to 17‰). Either *Crassostrea virginica* or *Mercenaria mercenaria* veligers were used in experiments; bivalve species were never mixed. Samples of veligers were sacrificed and measured to the nearest 0.01 mm with a computer image analysis system prior to experiments. Veligers were maintained in aerated, filtered seawater post-acclimation and before addition to the experimental chambers. Veligers were fed algae (*Isochrysis galbana* or *Pseudoisochrysis paradoxa*) 4 to 6 h before experiments began.

**Mixture of wild plankton and veligers:** Wild plankton were supplemented with bivalve veligers to approximate field concentrations of veligers (38 oyster pediveligers L<sup>-1</sup>, Southworth, 1998) observed in proximity to restored oyster reefs in Virginia (e.g., Shell Bar Reef, Great Wicomico River, Virginia) during the seasonal window when larval fishes and oyster veligers cooccur in the plankton i.e., June through July.

#### Experimental protocol

Feeding experiments were conducted using 150 ml beakers as feeding chambers. Beakers were filled with 50 ml of filtered seawater at 24 to 26°C and were maintained in artificial light conditions throughout experiments. Larval fishes were added to each chamber 1 h before prey items were added. Different concentrations of fishes and different mixtures of prey items were tested for each fish species. Larval fish (predator) concentrations were 1, 3, or 5 fishes per beaker. Fishes from each predator concentration were offered bivalve veligers, wild plankton, or a mixture of wild plankton supplemented with bivalve veligers.

Experiments were initiated by the addition of a 5 ml aliquot of concentrated prey to each chamber. Wild plankton collections were combined to give total prey densities in each chamber of > 1000 prey L<sup>-1</sup> to ensure that food was not limiting (Connaughton, 1994). These concentrations are similar to prey concentrations reported in other studies of larval fish feeding behavior (Mathias and Li, 1982; Stoecker and Govoni, 1984; Munk and Kiorboe, 1985; Mills et al., 1987; Chesney 1989).

Prey density or availability was determined by enumerating individual organisms in 5 ml aliquots taken from experimental chambers and fixed in 70% ethanol. Fishes were allowed to feed undisturbed for 3 h. Experiments were ended by the removal of fishes from the chambers 3 h after prey addition. All fish were immediately placed in 10% neutral buffered formalin and saved for subsequent dissection and gut content analyses. Notochord length was determined to the nearest 0.01 mm post-preservation using an image analysis system.

#### *Data analyses*

Only fishes that had consumed at least one prey item were used in these analyses. The percentage of fishes feeding (Table 15) was calculated for each experimental block or predator concentration/prey type combination (e.g., 1 fish per beaker fed only veligers) by dividing the number of fish with food items in their guts by the total number of fish used in the experiment. *A priori* significance levels for statistical tests were  $p = 0.05$ . Assumptions of homogeneity of variance were tested using Bartlett's test (Zar, 1996) while assumptions of normality were tested with the Ryan-Joiner test (similar to Shapiro-Wilks per Minitab, 1995). Unless otherwise noted, data satisfied both of these assumptions. Fisher's Least significant difference pairwise comparison test (Minitab, 1995; Zar, 1996) was used as a posthoc multiple comparison test.

**Effects of predator age, predator concentration, and prey type:** Total numbers of prey items consumed by each species satisfied the assumptions of homogeneity of variance and normality after transformation with the reciprocal transformation (Zar, 1996). The influence of predator age, predator concentration, and prey type on feeding behavior for individual species of larval fishes were evaluated with 3 factor ANOVAs (one per species).

**Prey selectivity:** Two different graphical methods were used to qualitatively describe feeding selectivity by these reef fishes. First, percentages of prey items consumed or used by each fish species were plotted against percentages of prey available in the habitat (Figure 16) using a modification of the technique proposed by Costello (1990). Each point on the graph

**Table 15: Summary of laboratory feeding experiments to evaluate feeding preferences of larval oyster reef fishes. Bivalve veligers, wild plankton (WP), and mixtures of both were used as prey items. NA: prey items not available for consumption in a particular experimental block. n: number of individual fish per treatment. Vel: bivalve veligers; Cop: copepods; Pol: larval polychaetes; Dia: diatoms.**

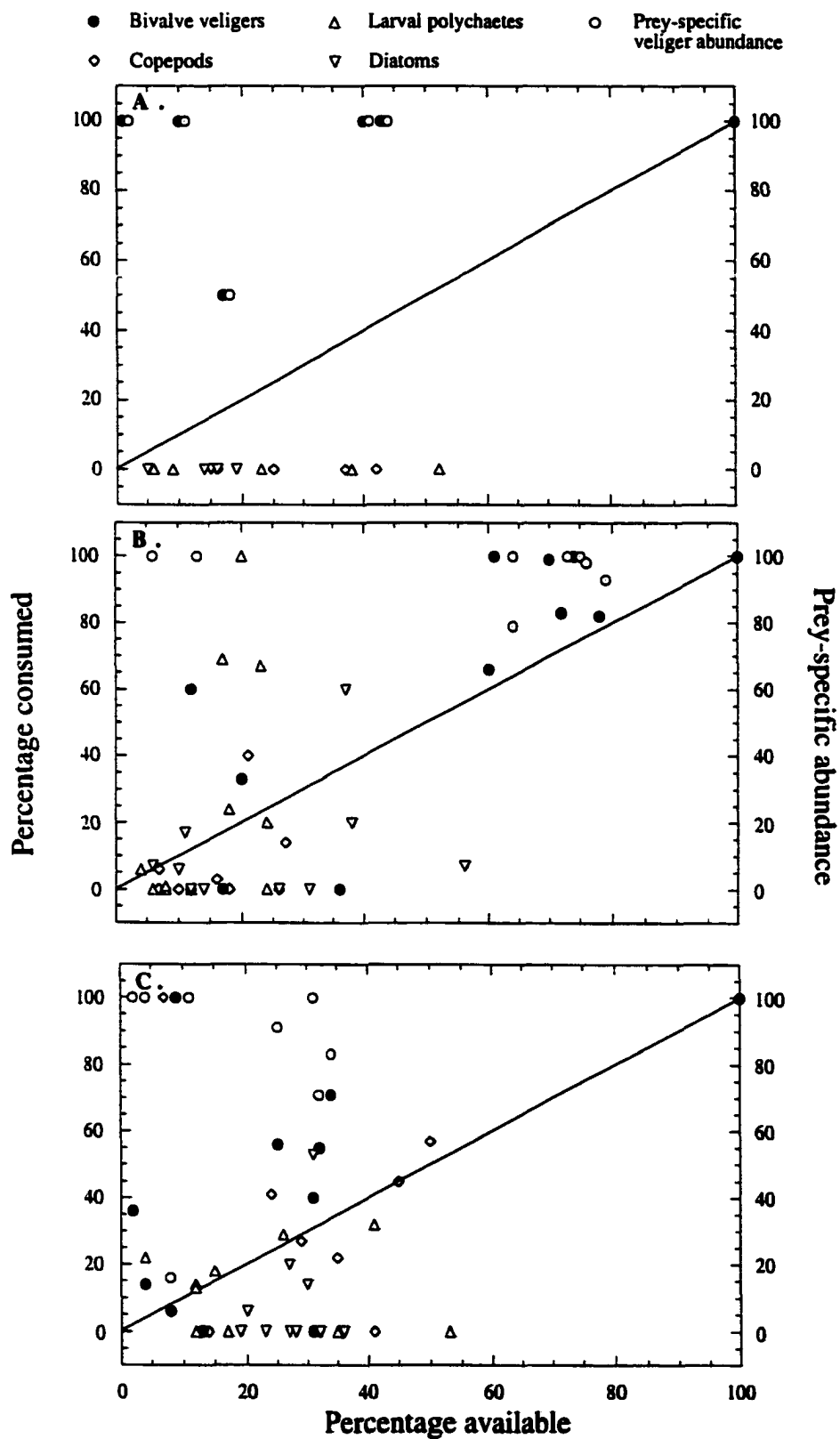
Predator Age Treatment	n	Mean notochord length (mm) ± SE	% fish feeding	Mean prey concentration (1000 L <sup>-1</sup> )	Prey field composition (% of total)				Chesson's Alpha				
					Vel	Cop	Pol	Dia	Vel	Cop	Pol	Dia	
<b>Naked goby</b>													
<b>5 d</b>													
Veliger - 1 fish	6	3.97 ± 0.11	33	1	100					1	NA	NA	NA
WP - 1 fish	4	3.78 ± 0.09	0	10	15	18	39	28		-	-	-	-
Veliger + WP - 1 fish	6	3.60 ± 0.06	17	6	18	28	35	18		0.6	0.4	0	0
Veliger - 3 fish	7	3.70 ± 0.07	14	1	100					1	NA	NA	NA
Veliger + WP - 3 fish	8	3.69 ± 0.06	25	4	20	22	35	22		1	0	0	0
<b>15 d</b>													
Veliger - 1 fish	6	4.19 ± 0.17	67	3	100					1	NA	NA	NA
WP - 1 fish	5	4.30 ± 0.14	0	11	10	43	21	26		-	-	-	-
Veliger + WP - 1 fish	6	4.16 ± 0.06	100	9	40	22	16	21		1	0	0	0
Veliger - 3 fish	17	4.14 ± 0.05	53	3	100					1	NA	NA	NA
WP - 3 fish	15	4.07 ± 0.05	13	11	10	47	26	16		1	0	0	0
Veliger + WP - 3 fish	14	4.30 ± 0.06	50	6	31	30	11	27		1	0	0	0
<b>Feather blenny</b>													
<b>3 d</b>													
Veliger - 1 fish	6	3.86 ± 0.04	83	36	100					1	NA	NA	NA
WP - 1 fish	6	3.87 ± 0.05	0	3	17	27	16	39		-	-	-	-
Veliger + WP - 1 fish	6	4.02 ± 0.08	16	18	72	7	8	12		1	0	0	0
Veliger - 3 fish	18	3.90 ± 0.03	30	29	100					1	NA	NA	NA
WP - 3 fish	18	3.87 ± 0.04	28	7	12	26	24	38		0.6	0	0.2	0.2
Veliger + WP - 3 fish	18	3.95 ± 0.08	56	22	72	10	6	11		0.9	0	0	0.1
Veliger + 5 fish	25	3.83 ± 0.04	36	25	100					1	NA	NA	NA
WP - 5 fish	30	3.89 ± 0.04	10	6	20	26	23	31		0.33	0	0.67	0
Veliger + WP - 5 fish	23	3.97 ± 0.05	39	40	78	7	4	10		0.70	0.08	0.11	0.11

Table 15 (continued)

Predator Age Treatment	n	Mean notochord length (mm) ± SE	% fish feeding	Mean prey concentration (1000 L <sup>-1</sup> )	Prey field composition (% of total)				Chesson's Alpha				
					Vel	Cop	Pol	Dia	Vel	Cop	Pol	Dia	
<b>Feather blenny (con't)</b>													
<b>5 d</b>													
Veliger - 1 fish	6	4.01 ± 0.11	67	10	100					1	NA	NA	NA
WP - 1 fish	6	4.12 ± 0.06	33	5	36	18	20	26		0	0	1	0
Veliger + WP - 1 fish	7	3.88 ± 0.04	71	17	61	12	12	14		1	0	0	0
Veliger - 3 fish	17	3.96 ± 0.05	88	11	100					1	NA	NA	NA
WP - 3 fish	18	3.87 ± 0.03	39	7	17	21	24	37		0	0.38	0	0.62
Veliger + WP - 3 fish	17	3.82 ± 0.06	76	9	60	16	0	24		0.47	0.05	0.42	0.06
Veliger + 5 fish	20	3.89 ± 0.03	70	13	100					1	NA	NA	NA
WP - 5 fish	20	4.18 ± 0.06	35	7	0	27	17	56		0	0.14	0.71	0.14
Veliger + WP - 5 fish	20	3.95 ± 0.06	70	20	70	8	8	14		0.94	0	0.06	0
<b>Striped blenny</b>													
<b>2 d</b>													
Veliger - 1 fish	6	3.92 ± 0.08	33	3	100					1	NA	NA	NA
WP - 1 fish	5	4.34 ± 0.11	20	13	11	39	19	31		1	0	0	0
Veliger + WP - 1 fish	6	4.21 ± 0.09	33	12	33	30	16	21		0	1	0	0
Veliger - 3 fish	16	4.23 ± 0.05	25	2	100					1	NA	NA	NA
WP - 3 fish	17	4.13 ± 0.05	29	11	9	49	13	29		0.20	0.44	0.16	0.20
Veliger + WP - 3 fish	17	4.12 ± 0.06	35	16	32	34	7	27		0.53	0.19	0.28	0
Veliger + 5 fish	30	4.12 ± 0.03	23	8	100					1	NA	NA	NA
WP - 5	30	4.15 ± 0.04	33	12	7	37	16	40		0.40	0.43	0.17	0
Veliger + WP - 5 fish	30	4.09 ± 0.04	43	16	30	28	15	26		0.31	0.31	0.15	0.23
<b>5 d</b>													
Veliger - 1 fish	6	4.46 ± 0.11	33	1	100					1	NA	NA	NA
WP - 1 fish	5	4.91 ± 0.11	20	6	24	18	37	20		0	1	0	0
Veliger + WP - 1 fish	6	4.76 ± 0.05	50	10	41	14	24	21		0.51	0	0.49	0
Veliger - 3 fish	9	4.66 ± 0.12	56	1	100					1	NA	NA	NA
WP - 3 fish	17	4.77 ± 0.07	59	6	16	25	29	29		0.03	0.65	0	0.32
Veliger + WP - 3 fish	18	4.64 ± 0.06	56	10	27	11	39	21		0.46	0.10	0.38	0.06



**Figure 16:** Percentage consumption of prey items and prey-specific veliger abundance plotted in relation to percentage availability for laboratory feeding experiments with naked gobies (A., n = 32), feather blennies (B., n = 157), and striped blennies (C., n = 82). Points above the diagonal line indicate prey items that are consumed at a higher proportion than their availability in the plankton. In cases where points representing percent bivalve veligers consumed overlapped completely with points for prey-specific veliger abundances, percent bivalve veliger abundance points were offset one x-axis unit (a percentage point) to the left and prey-specific veliger abundance points were offset one x-axis unit to the right.



represents the percentage availability in the habitat and percentage consumption by fish for a specific prey taxon. Amundsen et al. (1996) recommend another graphic method that relies on the variable prey-specific abundance which they suggest provides a more detailed diet description when plotted against the frequency of occurrence of a prey item. Prey-specific abundance is calculated as follows (Amundsen et al. 1996):

$$P_i = (S_i / S_{\Sigma}) \times 100$$

where  $P_i$  = Prey-specific abundance of prey taxon  $i$ ;  $S_i$  = the number of prey taxon  $i$  in the stomach; and  $S_{\Sigma}$  = the total stomach contents in only those predators with prey taxon  $i$  in their stomachs. Prey-specific abundances for the three predator species used in this study were calculated for bivalve veligers and plotted against the percent availability of veligers in the habitat for experimental trials with wild plankton or wild plankton supplemented with veligers (Figure 16).

Chesson's Alpha was used to quantitatively describe feeding selectivity by fishes where multiple prey types were offered. Chesson's Alpha (Chesson, 1978) ranges from 1 (exclusive ingestion) to 0 (complete avoidance). Relative preference for a prey type in relation to other available prey types is inherent in the calculated alpha values. Chesson's Alpha is calculated using:

$$\text{Alpha} = \frac{(r_i)}{(n_i)} \left[ \sum_{i=1}^m \frac{r_i}{n_i} \right]^{-1}$$

where  $r_i$  = portion of prey taxon  $i$  in the ingested food;  $n_i$  = portion of prey taxon  $i$  available in the habitat; and  $m$  = number of prey taxa considered. The limitations of Chesson's Alpha have been previously described by Lechowicz (1982): it is nonlinear, asymmetrical for more than two prey taxa, and sensitive to sampling error for rare prey taxa. However, Chesson's Alpha is also insensitive to the relative abundance of food taxa and does not change unless the behavior of the predator changes (Chesson, 1983) allowing "meaningful between sample comparisons" per Lechowicz (1982). Chesson's Alpha was used herein

because of its relationship to predator behavior and stability at different prey densities (Pearre, 1982).

## RESULTS

### *Preliminary laboratory feeding experiments*

**Gut residence time:** Gut residence time was greater than 3 h for all ages of blennies and types of prey items; naked gobies were assumed to have similar residence times. Gobies were not tested explicitly because they were much harder to culture and all live fishes were needed to ensure adequate replication in feeding experiments. Fish age ranged from 2 d through 31 d and length ranged from 2.8 to 15 mm notochord length. Although the 31 d old fishes were post-settlement and, by definition, no longer larvae, they were included in these experiments to ensure an adequate size range of animals for accurate determinations of gut residence time; it is possible for goby larvae to be planktonic for longer than 4 weeks under natural field conditions (Breitburg, 1989). All fishes were fed the prey items on which they had been cultured and greater than 90% of the fishes tested were feeding during the window when prey were offered.

**Habituation effects:** Two-thirds of 5 d old feather blennies cultured exclusively on rotifers did not feed on veligers when offered this novel prey. In experiments where 3 d and 5 d feather blenny larvae cultured on rotifers were fed rotifers, percentage of blennies feeding varied from 38% to 60% during habituation trials. Prey widths for both veligers and rotifers were within the range 60 to 120  $\mu\text{m}$  and were suitably sized for consumption by this size range of fishes (Hunter, 1981; J. Harding, unpublished data). Fishes consumed an average of one prey item each; however, information describing percentage of successful strikes, handling time, or ease of handling is unavailable for these fishes with regard to either rotifers or veligers. It is possible that larger numbers of fishes would have fed on the novel prey item if the experiments had lasted for longer than 90 min.

### *Multi-factorial laboratory feeding experiments*

**Effects of predator age, predator and prey type:** Predator age significantly affected feeding

behavior of naked gobies and feather blennies (ANOVAs,  $p < 0.05$ ; Table 16). Older fishes consumed more prey items than younger fishes in the case of both naked gobies (15 d old vs. 5 d old) and feather blennies (5 d old vs. 3 d old).

Predator concentration did not significantly affect the total number of prey consumed by any larval fish species. Total prey consumption by naked gobies and feather blennies was significantly affected by the type of prey offered (ANOVAs,  $p < 0.05$ ; Table 16). Bivalve veligers and veliger-supplemented wild plankton were consumed by naked gobies and feather blennies at significantly higher rates than were wild plankton. The interactions between prey type and predator concentration and prey type, predator concentration, and predator age were significant for naked gobies (ANOVA,  $p < 0.05$ ; Table 16).

**Prey Selectivity:** Larval reef fishes selectively consumed bivalve veligers from mixed prey fields. This preference is demonstrated both qualitatively (Figure 16) and quantitatively (selectivity index values; Table 15). Specialization on a diet item is indicated graphically by points with low availability and high consumption (Costello, 1990). Naked gobies showed strong preferences for bivalve veligers, regardless of their availability (Table 15, Figure 16).

The average percentage of feeding naked goby larvae increased with age. At 5 d, 18% of the larvae fed; at 15 d, 47% of naked goby larvae fed (Table 15). The range of prey items consumed by gobies during these experiments was 1 to 7 individual prey. Feeding naked gobies preferred veligers when offered a mix of veligers and wild plankton at both predator concentrations (Table 15).

The average percentage of feeding 3-d-old and 5-d-old feather blenny larvae was 36% and 59%, respectively (Table 15). Feather blennies preferentially consumed bivalve veligers at veliger concentrations as low as 12% of the available prey field (3-d-old, Wild plankton (WP)-3). The maximum number of prey items consumed by an individual feather blenny, or an individual fish of any species, during the 3-h experimental window was 24 *Crassostrea virginica* veligers by a 5-d old blenny. Within the same cohort of fish larvae

Species	Test	Factors	df	p value		Multiple comparison results (Fisher's LSD pairwise comparison)
Naked goby	ANOVA	Predator age	1	0.02	*	15 d > 5 d
		Predator concentration	2	0.08		
		Prey type	2	< 0.001	*	Veligers, Veligers + WP > WP
		Predator age x Predator concentration	1	0.08		
		Predator age x Prey type	2	0.15		
		Predator concentration x Prey type	2	0.04	*	
		Predator age x Predator concentration x Prey type	2	0.01	*	
Feather blenny	ANOVA	Predator age	1	0.04	*	5 d > 3 d
		Predator concentration	2	0.82		
		Prey type	2	0.01	*	Veligers, Veligers + WP > WP
		Predator age x Predator concentration	2	0.35		
		Predator age x Prey type	2	0.49		
		Predator concentration x Prey type	4	0.45		
		Predator age x Predator concentration x Prey type	3	0.91		
Striped blenny	ANOVA	Predator age	1	0.06		
		Predator concentration	2	0.66		
		Prey type	2	0.11		
		Predator age x Predator concentration	1	0.03	*	
		Predator age x Prey type	2	0.30		
		Predator concentration x Prey type	4	0.73		
		Predator age x Predator concentration x Prey type	2	0.35		

**Table 16:** Summary of ANOVAs performed on data from laboratory feeding experiments on individual species of larval fishes. Asterisks (\*) indicate significance at the  $p = 0.05$  level.

during the 3 h experiment, 2 other blennies consumed 9 prey items each and a third ate 14 different prey items. Three-day-old feather blennies preferred veligers in all but one trial; larval polychaetes were preferred when wild plankton was offered at densities of 5 fish chamber<sup>-1</sup> (Table 15). When veligers supplemented wild plankton, veligers were strongly preferred prey for feather blennies of both ages (Table 15). Five-day-old feather blenny larvae did not consume veligers in wild plankton experiments perhaps due to relatively low veliger availability (Table 15).

For striped blennies, the average percentage of feeding fish was 30% for the 2-d-old larvae and 46% for the 5-d-old larvae (Table 15). The number of prey consumed by an individual striped blenny during the experiments ranged from 1 to 6 prey. When veligers were offered as the exclusive prey item, they were consumed at all predator densities by both 2- and 5-d-old larvae. Striped blennies consumed bivalve veligers preferentially at concentrations as low as 11% of the available prey field (2-d-old, WP -1). When offered wild plankton, copepods or larval polychaetes were preferred over veligers at most predator concentrations, possibly reflecting relatively low availability of veligers in wild plankton (Table 15). When wild plankton supplemented with veligers was offered to striped blennies, veligers were selected for in all cases but one (2-d-old; Veliger + WP - 1 fish) where copepods were consumed exclusively (Table 15).

## DISCUSSION

Larval stages of benthic oyster reef fishes fed selectively on bivalve veligers in multifactorial laboratory experiments. Diet preferences for veligers were demonstrated using qualitative (Figure 16) and quantitative methods (e.g., selectivity indices, Table 13). These feeding patterns indicate selection for and specialization on bivalve veligers by all three species of larval fishes (Costello, 1990; Amundsen et al., 1996). Low preference for veligers indicated by the Chesson's Alpha values may be an artifact of relatively low veliger availability (Table 13) rather than active "rejection".

Feeding behavior of these fishes was significantly affected by age; older fishes

consumed more prey items than younger fishes. Olney (1996) reports similar feeding patterns for seaboard gobies (*G. ginsburgi*). Predator concentration did not have a significant effect on larval goby and blenny feeding behavior in these experiments. Experimental chamber dimensions and volume (0.15 L) were small enough that any potential benefits offered by schooling behavior for prey location were probably negligible. Conversely, feeding behavior may have been inhibited by lack of schooling opportunities. Demersal naked gobies have been observed schooling directly above shell substrate or other structure immediately prior to settlement (Breitburg, 1989). Behavior of planktonic goby and blenny larvae in relation to conspecifics is unknown. Predator concentrations in the chambers may not have been high enough (1, 2, 3, and 5 fishes) to cause competitive responses among individuals, especially in light of the high availability of food items.

Total prey concentrations were greater than 1000 prey L<sup>-1</sup> for all experiments to ensure that food was not limiting. Connaughton (1994) established 1000 prey L<sup>-1</sup> as a threshold value at which the maximum number of weakfish (*Cynoscion regalis*) larvae had food occurring in their guts and above which consumption did not significantly increase even with an order of magnitude increase in prey availability. Natural plankton distributions are patchy (e.g., Wiebe, 1970; Houde and Lovdal, 1985; Owen, 1989; Genin et al., 1994; see Chapter 2 of this volume). Wild plankton abundance estimates may vary across several orders of magnitude depending upon the species of interest and the measurement scales used (e.g., Wiebe, 1970; Gallagher et al., 1996). Local concentrations of 1,500 to 2,000 *Pleuromamma gracilis* L<sup>-1</sup> (Sixtymile Bank, California, Genin et al., 1994), > 181,000 *Calanus* sp. L<sup>-1</sup> (St. Margaret's Bay, Nova Scotia, Sameoto, 1975), and 600,000 *Limacina retroversa* L<sup>-1</sup> (Great South Channel, Georges Bank, Gallagher et al., 1996) have been recorded. Houde and Lovdal (1985) report concentration ranges of 31.9 to 184.4 copepod nauplii L<sup>-1</sup>, 6.7 to 916.2 tintinnids L<sup>-1</sup>, and 0.6 to 9.7 mollusc veligers L<sup>-1</sup> for Biscayne Bay, Florida. Olney (1996) provides similar mean density estimates for copepod nauplii (4.6 to 69.2 L<sup>-1</sup>) and bivalve larvae (0.1 to 8.3 L<sup>-1</sup>) from the Chesapeake Bay plume. Southworth (1998)



reports oyster pediveliger concentrations of up to 38 L<sup>-1</sup> near Shell Bar Reef, Great Wicomico River, Virginia and estimates that pediveligers composed approximately 10% of the total prey field (M. Southworth, Virginia Institute of Marine Science, Gloucester Point, Virginia; personal communication). Although the small-scale prey abundances experienced by goby and blenny larvae in the field are unknown, it is reasonable to suggest that they may encounter differences in total prey abundance encompassing several orders of magnitude during development. In light of the natural variability observed in plankton abundances, 1000 total prey L<sup>-1</sup> is a concentration threshold for optimal feeding (Connaughton, 1994) as well as a reasonable representation of "patch" abundances.

The prey items used in these experiments were small enough to be vulnerable to predation from larval reef fishes. Prey size in relation to larval fish mouth width or gape strongly influences consumption of any prey items (Hunter, 1981). If a prey item is larger in all dimensions than the mouth width or height (gape) of a potential predator, its chances of being successfully captured by that predator are small. The veligers and a large portion of wild plankton used herein were within the range of prey widths vulnerable to predation from these fishes (i.e., 0.08 - 0.3 mm, depending on the fish size).

Previous experience with a prey item, or habituation (Checkley, 1982; Mills et al., 1987; Connaughton and Epifanio, 1993), may also affect larval fish feeding success. None of the fishes used in these experiments had been previously exposed to either veligers or a mixture of prey types. Both Connaughton and Epifanio (1993) and Mills et al. (1987) found that habituation to a familiar prey type affects laboratory feeding results depending on predator age and prey size. Gobies and blennies used in these experiments were cultured exclusively on rotifers and, subsequently, for the 15 d naked gobies, *Artemia* sp. nauplii, effectively removing habituation to a particular experimental prey type as a potential source of experimental bias.

Larval fishes are visual predators. Variations in incident light have been correlated with reduced growth rates and/or feeding efficiency for bream (*Abramis brama*, Townsend

and Risebrow, 1982), striped bass (*Morone saxatilis*, Chesney, 1989), and herring (*Clupea harengus*, Batty, 1987; Batty et al., 1990). Experimental chamber shape may have an impact on fish perception of prey. Bending of light through chamber corners may change perception and, subsequently, searching behavior for those fishes that rely on the dark background outside Snell's window to highlight prey (Janssen, 1981). Since these experiments were conducted in light conditions using round chambers, visual conditions were appropriate for successful predation by larval fishes.

Morphologically and behaviorally, bivalve veligers are vulnerable to predation by larval fishes. Capture success with regard to a particular prey type is a function of both predator perception and ease of handling (Hunter, 1981). Bivalve veligers move slowly in the vertical plane, either actively swimming or passively sinking (Mann and Wolf, 1983; Mann et al., 1991). The smooth rounded veliger morphology may make capture relatively simple for a larval fish as compared to ingestion of a prey item with multiple protruding appendages or more active swimming patterns e.g., copepod nauplii (Van Duren and Videler, 1995) or polychaete larvae (Mileikovskiy, 1973). As larval fishes grow and develop, they may become better suited to capture more active prey items.

High degrees of feeding specialization in fishes have been correlated with narrow niche width (Amundsen et al., 1996). While ontogeny of feeding behavior in naked gobies, feather blennies, and striped blennies may eventually reduce these high levels of specialization, in the earliest "critical" period of larval development high abundances of preferred prey items (veligers) would facilitate growth. Larval fishes that have higher growth rates will settle more quickly thus escaping or avoiding potential larval stage mortality sources, e.g., starvation and predation (Shepherd and Cushing, 1980). Selective feeding by larval reef fishes on bivalve veligers may be an important mechanism by which larval reef fishes reduce the length of their larval planktonic phase and, consequently, increase recruitment success.

## CHAPTER 4

### Distribution and diet of naked goby (*Gobiosoma bosc*) and striped blenny (*Chasmodes bosquianus*) larvae in relation to an intertidal oyster reef

#### ABSTRACT

Adult and larval benthic oyster reef fishes including naked gobies (*Gobiosoma bosc*) and striped blennies (*Chasmodes bosquianus*) are important intermediates in estuarine food webs. Patterns of adult reef fish abundance and distribution are influenced by larval fish survival and settlement success. Oyster reefs and reef-associated macrobenthos may positively affect larval fish survival by enhancing local food supplies and providing appropriate settlement habitat. Larval naked goby and striped blenny abundance, distribution, and diet were examined across seasonal and diurnal temporal scales in relation to Palace Bar reef, an intertidal oyster reef in the Piankatank River, Virginia. Seasonally, larval fishes were most abundant from mid-May through June. Nocturnal densities of naked goby and striped blenny larvae were 3 to 4 orders of magnitude higher than densities of these fish observed during daylight hours. Larval naked gobies of all developmental stages were more abundant than striped blenny larvae at night, particularly in the reef's tidal wake zone. Diurnal changes in larval fish abundance are related to ambient light intensities and diurnal vertical migration by prey species. Post-flexion fishes of both species consumed significantly more prey items than preflexion fishes. Calanoid copepod adults, calanoid copepod nauplii, and larval polychaetes were consumed most frequently by preflexion and postflexion fishes of both species. Calanoid copepod nauplii and larval polychaetes were consumed preferentially by preflexion gobies and blennies.

## INTRODUCTION

Temperate estuaries are important nursery areas for many species of larval fishes. Seasonally high estuarine productivity and a range of suitable habitat types facilitate larval fish growth and potentially shorten the time to successful recruitment (Shepherd and Cushing, 1980; Houde, 1989). Although some estuarine-dependent larval fishes originate from off-shore spawning grounds and actively or passively migrate into estuarine habitats (e.g., McHugh, 1967; Musick, 1972; Weinstein, 1979; Olney, 1983; Able and Fahay, 1998), many are spawned within the estuary (e.g., McHugh, 1967; Musick, 1972; Olney, 1983; Olney and Boehlert, 1988; Able and Fahay, 1998). Estuarine fish larvae benefit from abundant estuarine zooplankton food resources (e.g., Houde and Lovdal, 1984, 1985; Laprise and Dodson, 1989) in that growth and mortality patterns for larval fishes are strongly influenced by food availability and determine observed community recruitment relationships (Shepherd and Cushing, 1980; Houde, 1989). Estuarine larval fishes are potential prey items for larger pelagic predators although turbidity conditions within the estuary may reduce predation pressure on larvae by reducing visibility (Blaber and Blaber, 1980; Boehlert and Morgan, 1985).

Naked goby (*Gobiosoma bosc*) larvae dominate Chesapeake Bay ichthyoplankton in early summer (Dovel, 1971; Massmann et al., 1963; Shenker et al., 1983); 55% of the fish larvae collected by Dovel (1971) were naked gobies. Adult naked gobies and several other species of benthic oyster reef fishes including striped blennies (*Chasmodes bosquianus*) use the oyster reef shell matrix for nesting sites, feeding grounds, and refugia (Wells, 1961; Dahlberg and Conyers, 1973; Harding and Mann, 2000 [see Chapter 1 of this volume]). Adults of both fish species lay demersal eggs that release planktonic larvae that eventually recruit back to the benthos. These benthic reef fishes are important intermediates in oyster reef trophic webs; gobies and blennies are prey items for transient pelagic predators such as juvenile striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), and weakfish

(*Cynoscion regalis*) that use oyster reefs as feeding grounds (Markle and Grant, 1970; Breitburg, 1999; Harding and Mann, 1999).

The reef structure plays an important role in larval settlement and subsequent recruitment patterns of naked gobies (Breitburg 1989, 1991; Breitburg et al., 1995) and striped blennies. Reef substrates and/or structural heterogeneity may provide important cues for transition from planktonic to benthic life history forms in temperate reef fishes (Marliave, 1977, 1986; Kingsford and Choat, 1989; Breitburg 1989, 1991). Similar habitat-larval interactions have been documented for many species of coral reef fishes (e.g., Sale, 1970; Kobayashi, 1989; Leis, 1991). Planktonic reef fish larvae may resist transport from the reef environment using a combination of behavioral and hydrodynamic factors (e.g., Sale, 1970; Johannes, 1978; Leis, 1986; Marliave, 1986; Kobayashi, 1989). Larval proximity to reefs, habitat for larval settlement and adult residency, during the period when larvae are morphologically competent to settle to the benthos from the plankton may increase settlement success of benthic reef fishes such as naked gobies (Breitburg, 1989, 1991).

In the Chesapeake Bay, the reef-forming oysters, *Crassostrea virginica*, historically were the dominant primary consumers (see Newell, 1988; Kennedy et al., 1996 and references therein) which simultaneously increased local habitat relief, heterogeneity, and substrate availability for associated benthic reef fishes such as naked gobies and striped blennies. Recent declines in Chesapeake Bay oyster reef communities have reduced shallow water habitat complexity in terms of both larval production and habitat for subsequent recruitment (Hargis and Haven, 1988). Current oyster reef restoration efforts are focused on restoring local reef structures and resident oyster populations (Southworth and Mann, 1998; Luckenbach et al., 1999 and references therein). Successful restoration of intertidal reef structures and oyster populations will have a cascade effect on benthic species such as naked gobies and striped blennies that use the reef habitat.

Monitoring of intermediate fauna e.g., gobies and blennies, may provide a more robust indicator of reef community restoration success than monitoring of oyster population

levels alone. Evaluation of secondary ecological effects of oyster reef restoration requires a baseline understanding of the interactions between reef species (all life history stages) and the reef itself. Wells (1961), Dahlberg and Conyers (1973), Breitburg (1988, 1989, 1991, 1999) and Harding and Mann (2000 [see Chapter 1 of this volume]) have described use of temperate reef habitats by settled naked gobies and striped blennies. However, the dynamics of planktonic naked goby and striped blenny larvae with regard to reef structures, their source and eventual settlement habitat, are largely unknown. The objectives of this study were to describe the abundance, distribution, and diet of naked goby and striped blenny larvae associated with an intertidal oyster reef across seasonal (months) and diurnal (hours) temporal scales.

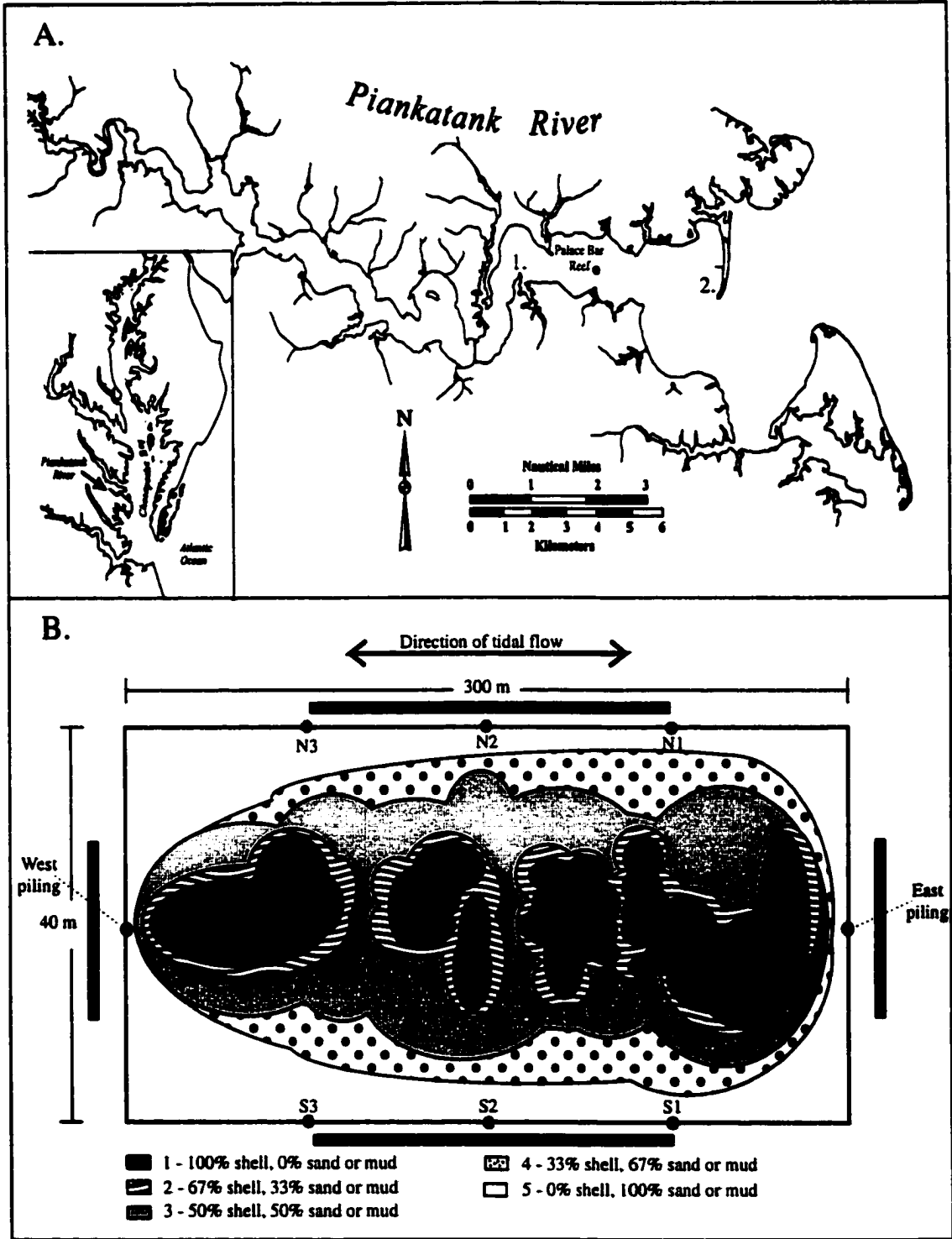
## METHODS

### *Study site*

Larval fish samples were collected immediately adjacent to Palace Bar oyster reef, Piankatank River, Virginia (N 37° 31' 41.69", W 76° 22' 25.98"; Figure 17). The Piankatank River is a small estuary that flows directly into the Chesapeake Bay. Palace Bar reef is an intertidal oyster reef (300 m x 30 m, reef depth range of 0.5 m above MLW to 3 m below MLW) that was constructed in July, 1993 adjacent to the historic Palace Bar oyster grounds (Figure 17). Approximately 70% of the reef (0.63 ha) is composed of oyster shell, while the remaining area (0.27 ha) is crushed clam shell (see Bartol and Mann, 1997 for a detailed site description). Palace Bar reef receives annual oyster spat settlement (Bartol and Mann, 1997; J. Wesson, Virginia Marine Resources Commission, Newport News, Virginia, unpublished data) and currently supports an oyster population similar to that observed at an adjacent natural oyster bar (Harding and Mann, 1999; R. Mann, Dept. of Fisheries Science, Virginia Institute of Marine Science, Gloucester Point, Virginia, unpublished data). Mean tidal range at Palace Bar reef is approximately 0.4 m, while maximum tidal current at the reef is approximately 0.12 m s<sup>-1</sup> (Chen et al., 1977).

The longitudinal axis of Palace Bar reef runs east to west, parallel to the Piankatank

**Figure 17:** Map of the Piankatank River, Virginia in relation to the Chesapeake Bay showing Palace Bar reef (A.) and a schematic diagram of the reef including substrate composition (B.). Larvae are retained in the river reach bounded by Ginney Point (1.) and Stove Point Neck (2.). Tow paths for all bongo tows are indicated by the dark black lines just outside the reef buoys (N1, N2, N3, S1, etc.) on north and south sides of the reef and the end pilings on east and west sides of the reef (downstream locations during the ebb and flood tides, respectively). Tidal flow generally runs east -west (parallel to the main reef axis) and is indicated by the double-headed arrow.





River channel (Figure 17). The northern reef perimeter is on the channel side and the southern reef perimeter is inshore of the channel; both perimeters grade from oyster shell into hard sand bottom (Figure 17). Depth on the northern (channel) side is approximately 3 m from the reef to the channel (15 m). A sand flat extends inshore at a depth of 2.5 to 3 m from the southern reef perimeter for 200 m and then grades into a shallow sand bar (depth < 2 m) that continues inshore. The bottom type on both eastern (downriver) and western (upriver) reef perimeters is sand (depth approximately 3 m for both).

#### *Sampling protocol*

On each sampling day, larval fish samples were collected sequentially on north (channel), south (inshore), and downstream of the reef in the tidal wake zone (either east or west depending upon the direction of tidal current) sides of the reef (3 samples total) to describe spatial variation in larval fish abundance in relation to the intertidal reef structure.

Seasonal larval fish samples were collected weekly during daylight hours from May through August 1996, between 0800 and 1600 EDT. On June 27-28 and August 29-30, 1996, diel plankton samples were collected over 36 h periods spanning two complete tidal cycles. During these 36 h sampling events (both on the full moon), three larval fish samples (1 north, 1 south, and 1 in the tidal wake zone) were collected every 3 h corresponding to differing tidal stages: flood, slack onto ebb, ebb, and slack onto flood.

Paired bongo nets (202  $\mu\text{m}$  Nytex mesh, 0.6 m diameter, 3:1 aspect ratio) were towed with the tidal current parallel to the reef axis on the north (channel) and south (inshore) sides of the reef as well as within reef's tidal wake zone on either the east (downriver) or west (upriver) side of the reef (Figure 17). Total elapsed time for the sets of 3 sequential tows was approximately 60 min (20 minutes at each location). A General Oceanics mechanical flow meter (Model 2030) was suspended in the net mouth and average volume of water filtered per tow (overall average = 27.14  $\text{m}^3$  [std. error of the mean = 1.17  $\text{m}^3$ ]) was calculated. Nets were towed horizontally 0.5 to 1.5 m below the water surface in the direction of the prevailing tidal current for 2 min (approximately 180 m) at approximately

1.5 m s<sup>-1</sup> (the sum of tow speed and tidal velocity). All bongo samples were preserved in buffered seawater - formalin immediately after collection.

Water samples for salinity and temperature measurements were taken immediately adjacent to the reef (within 5 m) at the surface and 0.25 m above the substrate with a Niskin bottle each day. Temperature was measured immediately with a thermometer ( $\pm 0.5$  °C) and salinity was measured with a hand-held refractometer ( $\pm 1$ ‰).

Bongo samples were sorted in the laboratory using a stereo-dissecting microscope. All larval fishes were removed from each sample, larval naked gobies and striped blennies were identified, separated from other larval fishes, and stored in 95% EtOH. Naked goby and striped blenny larvae were classified in terms of developmental or notochord flexion stage i.e., preflexion or post-flexion to examine potential ontogenetic differences in diet and temporal abundance or habitat use. Preflexion fishes have a notochord that is straight at the caudal tip and post-flexion fishes have a fully formed hypural plate and a notochord that is flexed dorsally at the caudal peduncle. Prior to dissection, larval fish lengths were also measured using an image analysis system (Image Pro Plus software, version 2.0); notochord length (tip of the snout to the end of the notochord, mm) was measured on preflexion fishes and standard length (tip of the snout to the hypural plate, mm) was measured on post-flexion fishes.

In bongo samples with less than 100 fish of each developmental stage and species, every goby and blenny was dissected. Samples with more than 100 larval fishes of each species and developmental stage were subsampled by randomly selecting 100 fish of each species and developmental stage (i.e., 100 preflexion gobies, 100 preflexion blennies, 100 post-flexion gobies, and 100 post-flexion blennies) for dissection and dietary analyses. Each fish was randomly selected by removing an individual fish larvae that had been stored in a species and developmental stage-specific jar. (e.g., preflexion naked gobies) after shaking the jar for at least a minute. Fish were removed, measured, dissected, and then archived in a different jar. The entire gastrointestinal tract of each larval fish was carefully removed

with dissecting needles examined under a compound microscope for the presence of food items. All food items were counted and identified to taxonomic categories (e.g., larval polychaetes, bivalve veligers, calanoid copepod adults).

#### *Data analyses*

*A priori* significance levels for all hypothesis tests were  $p < 0.05$ . Assumptions of homogeneity of variance were tested using Bartlett's test, while assumptions of normality were tested with the Shapiro-Wilks test (Zar, 1996). Unless otherwise noted, data satisfied both of these assumptions. Fisher's least significant difference (LSD) pairwise comparison test was used for parametric multiple comparisons (Minitab, 1995; Zar, 1996). All statistical analyses used Minitab software (version 10.5; 1995).

#### Water temperature and salinity data

Water temperature and salinity data collected weekly from May through August 1996 at Palace Bar reef were  $\log_e$  transformed prior to analyses and satisfied assumptions of both homogeneity of variance and normality. Temperature and salinity data taken at the surface and just above the substrate (within 0.25 m) adjacent to the reef were each compared with an ANOVA.

#### Larval fish density and distribution patterns

Larval fish abundances (numbers of fishes per tow) were standardized to densities (number of fishes  $m^{-3}$ ) using the tow volumes recorded by the General Oceanics flowmeters on each tow. Total ichthyoplankton densities (number of fishes  $m^{-3}$ ) were transformed using the reciprocal transformation (Zar, 1996) to satisfy assumptions of homogeneity of variance and normality. The transformed fish density data for bongo tows conducted during daylight hours were compared with an ANOVA using month, tidal stage, and collection location (north, south, or tidal wake zone) as factors. Densities of both naked gobies and striped blennies from seasonal daylight samples were transformed (reciprocal transformation; Zar, 1996) and evaluated using similar ANOVAs for each species (month x time of day x tidal stage x collection location).

Total larval fish densities as well as densities of naked gobies and striped blennies observed during both June and August 36 h sampling events were transformed (reciprocal transformation; Zar, 1996) to meet the assumptions of homogeneity of variance and normality and then compared with ANOVAs for (1) all larval fishes and (2) species-specific for naked gobies and striped blennies within each sampling event using time of day, tidal stage and collection location as factors.

#### Diets of larval naked gobies and striped blennies

Naked goby and striped blenny larvae were separated into preflexion and postflexion categories for dietary analyses to examine potential ontogenetic diet differences. Fish within the same developmental stage and species were compared with each other but not the other species or developmental stage within the species. The percentage of feeding larval fishes was calculated by dividing the number of naked gobies or striped blennies per sample with identifiable food items in their guts by the total number of fish from that particular species and developmental stage.

Densities of feeding fish larvae were transformed with the reciprocal transformation (Zar, 1996) to meet the assumptions of homogeneity of variance and normality and were compared within species and developmental stage using ANOVAs. Preflexion naked gobies, post-flexion naked gobies, and post-flexion striped blennies occurred in sufficient numbers for statistics only during the June 36 h sampling event; thus these groups were compared with ANOVAs incorporating time of day and collection location (3 total ANOVAs). Densities of feeding preflexion striped blenny larvae were compared with an ANOVA incorporating month, time of day, and collection location.

Transformation ( $\log_e$ ,  $\log_e + 1$ ,  $\log + 1$ ,  $\sqrt{+ 1}$ , reciprocal) of the total number of prey items consumed by individual fishes failed to satisfy the assumptions of homogeneity of variance or normality. Kruskal-Wallis tests were used to compare the total number of prey items consumed by fishes of different developmental stages within the same species. Dunn's tests were used for post-hoc non-parametric multiple comparisons.

Gut contents of each developmental stage and species were compared to ambient concentrations of major prey items or prey items composing > 20% of the diet. Ambient concentrations of major prey taxa (e.g., larval polychaetes, calanoid copepod adults, calanoid copepod nauplii; mean density  $m^{-3}$ ) were obtained from concurrently collected zooplankton samples (see Chapter 2 of this volume). Larval fish diets herein are discussed only in relation to prey items known to contribute to the fishes' diets not in terms of absolute prey preference (Govoni, 1983; Jenkins, 1987).

Larval fish diets were compared qualitatively by plotting the percentages of prey items consumed or used by each fish species in relation to the percentages of prey available in the habitat using a modification of the technique proposed by Costello (1990) (Harding, 1999; see Chapter 3 of this volume). Each point on a graph represents the percentage availability in the habitat and percentage consumption by a fish for a specific prey taxon.

Chesson's alpha was used to quantitatively describe feeding selectivity by larval fishes when multiple prey types were consumed. Chesson's Alpha (Chesson, 1978) ranges from 1 (exclusive ingestion) to 0 (complete avoidance). Relative preference for a prey type in relation to other available prey types is inherent in the calculated alpha values. Chesson's Alpha is calculated using:

$$\text{Alpha} = \frac{(r_i)}{(n_i)} \left[ \sum_{i=1}^m \frac{r_i}{n_i} \right]^{-1}$$

where  $r_i$  = portion of prey taxon  $i$  in the ingested food;  $n_i$  = portion of prey taxon  $i$  available in the habitat; and  $m$  = number of prey taxa considered. The limitations of Chesson's Alpha have been previously described by Lechowicz (1982): it is nonlinear, asymmetrical for more than two prey taxa, and sensitive to sampling error for rare prey taxa. However, Chesson's Alpha is also insensitive to the relative abundance of food taxa and does not change unless the behavior of the predator changes (Chesson, 1983) allowing "meaningful between sample comparisons" per Lechowicz (1982). Chesson's Alpha was used herein

because of its relationship to predator behavior and stability at different prey densities (Pearre, 1982).

## RESULTS

### Water temperature and salinity data

There was no significant difference between surface and bottom water temperatures (ANOVA,  $p = 0.29$ ) or salinities (ANOVA,  $p = 0.53$ ) on any date indicating that the water column was well mixed. Therefore, surface and bottom temperature and salinity data for each day were pooled for presentation and discussion (Figure 5). Recorded water temperatures in 1996 were similar to those observed during 1993-95 (Figure 5, R. Mann, Dept. of Fisheries Science, Virginia Institute of Marine Science, Gloucester Point, Virginia, unpublished data). Salinities observed in 1996 were the lowest observed from 1993-7.

### Larval fish density and distribution patterns

Larval fishes collected near Palace Bar reef included larval bay anchovies (*Anchoa mitchilli*), Atlantic silversides (*Menidia menidia*), and skilletfish (*Gobiesox strumosus*) as well as naked gobies and striped blennies. Densities of total larval fishes, naked gobies and striped blennies (Table 17) observed from May through August during daylight hours (8:00 to 16:00 EDT) were significantly affected by month (ANOVA,  $p < 0.05$ ; Table 18); significantly higher densities of fishes were observed in June (Fisher's LSD pairwise comparison test,  $p < 0.05$ ; Table 18, Figure 18). Total larval fish densities observed in daylight samples ranged from 0 to 1.27 fish  $m^{-3}$ . Densities of larval naked gobies observed during daylight hours ranged from 0 to 0.04 fish  $m^{-3}$ . Striped blenny larvae were more abundant with daylight densities ranging from 0 to 0.22 fish  $m^{-3}$ . Larval naked gobies and striped blennies were most abundant from mid-May through early July (Figure 18).

During the June and August 36 h sampling events, significantly more larval fishes were collected at night and in the early morning (20:00 to 8:00) than during daylight hours (8:00 to 20:00; ANOVA,  $p < 0.05$ ; Fisher's LSD pairwise comparison test,  $p < 0.05$ ; Table 19, Figures 19 and 20). Naked goby densities increased from 0.02 fish  $m^{-3}$  at 1130 to 11.75

**Table 17:** Summary of larval fish samples collected near Palace Bar reef, Piankatank River, Virginia during 1996. All fish densities are fish m<sup>-3</sup> of water. Asterisks (\*) indicate total values. The single vertical black line indicates samples that were collected during the June 27-8, 1996 sampling event. The vertical double line indicates samples that were collected during the August 29-30, 1996 sampling event. Tidal stages are abbreviated as follows: SF: slack onto flood; F: flood; SE: slack onto ebb; E: ebb.

Date	Time	Tidal stage	Average larval fish density $\pm$ standard error		
			All fishes	Naked goby	Striped blenny
5/23/96	1030	SF	0	0	0
5/30/96	1400	E	0	0	0
6/6/96	1527	SE	0.12*	0	0.12*
6/20/96	1458	SE	0.72*	0.02	0.16*
6/27/96	1130	E	0.56 $\pm$ 0.37	0.02 $\pm$ 0.01	0.04 $\pm$ 0.02
	1430	SF	0.24 $\pm$ 0.16	0.01 $\pm$ 0.01	0.09 $\pm$ 0.07
	1800	F	1.03 $\pm$ 0.15	0	0.14 $\pm$ 0.05
	2210	SE	16.76 $\pm$ 12.98	11.75 $\pm$ 10.79	2.39 $\pm$ 2.35
6/28/96	0115	E	2.78 $\pm$ 1.09	0.70 $\pm$ 0.32	0.07 $\pm$ 0.02
	0415	SF	1.90 $\pm$ 0.40	0.63 $\pm$ 0.29	0.02 $\pm$ 0.01
	0645	F	0.36 $\pm$ 0.30	0.05 $\pm$ 0.03	0.04 $\pm$ 0.02
	0920	SE	0.17 $\pm$ 0.09	0.01 $\pm$ 0.01	0.09 $\pm$ 0.02
	1245	E	0.10 $\pm$ 0.09	0	0.06 $\pm$ 0.05
7/5/96	1500	F	0.38 $\pm$ 0.26	0.01 $\pm$ 0.01	0.07 $\pm$ 0.05
7/10/96	1400	E	0.03 $\pm$ 0.02	0	0
7/18/96	1240	E	0.08 $\pm$ 0.05	0	0.04 $\pm$ 0.03
7/25/96	1500	E	0.08 $\pm$ 0.05	0	0
8/2/96	1400	SE	0.04 $\pm$ 0.02	0	0
8/8/96	1430	F	0	0	0
8/15/96	1325	E	0	0	0
8/22/96	1335	F	0	0	0
8/29/96	1300	SE	0.03 $\pm$ 0.02	0	0
	1526	E	0	0	0
	1910	SF	0	0	0
	2220	F	0.27 $\pm$ 0.04	0	0
8/30/96	0139	SE	0.26 $\pm$ 0.09	0.03 $\pm$ 0.02	0
	0500	E	0 $\pm$ 0.03	0	0
	0745	SF	0.04 $\pm$ 0.04	0	0.02 $\pm$ 0.02
	1030	F	0	0	0
	1337	SE	0	0	0
	1610	E	0.01 $\pm$ 0.01	0	0.01 $\pm$ 0.01

**Table 18:** Summary of ANOVA tests for fish densities from bongo tows made during daylight hours from May through August 1996 near Palace Bar reef, Piankatank River, Virginia. All densities are in number of fish meter<sup>-3</sup> of water. “\*” designates results that were significant at the  $p \leq 0.05$  level.

Group	Test	Factors	df	p-value		Multiple comparison results (Fisher's LSD pairwise comparison test)
All larval fishes	ANOVA	Month	3	0.01	*	June > August
		Time of day	1	0.59		
		Tidal stage	3	0.24		
		Location	2	0.43		
Naked gobies	ANOVA	Month	3	0.06		
		Time of day	1	0.27		
		Tidal stage	3	0.06		
		Location	2	0.11		
Striped blennies	ANOVA	Month	3	0.05	*	June > August
		Time of day	1	0.25		
		Tidal stage	3	0.63		
		Location	2	0.33		



**Figure 18:** Summary of seasonal larval fish densities around Palace Bar reef, Piankatank River, Virginia. Seasonal larval fish density estimates were pooled across time of day, tidal stage, and location for graphic presentation. Average percentage composition of the larval fish community is presented for naked gobies (A.), and striped blennies (B.) in relation to the average densities (fishes  $m^{-3} \pm$  standard error) of naked gobies (C.), striped blennies (D.), and all species collected (E.).

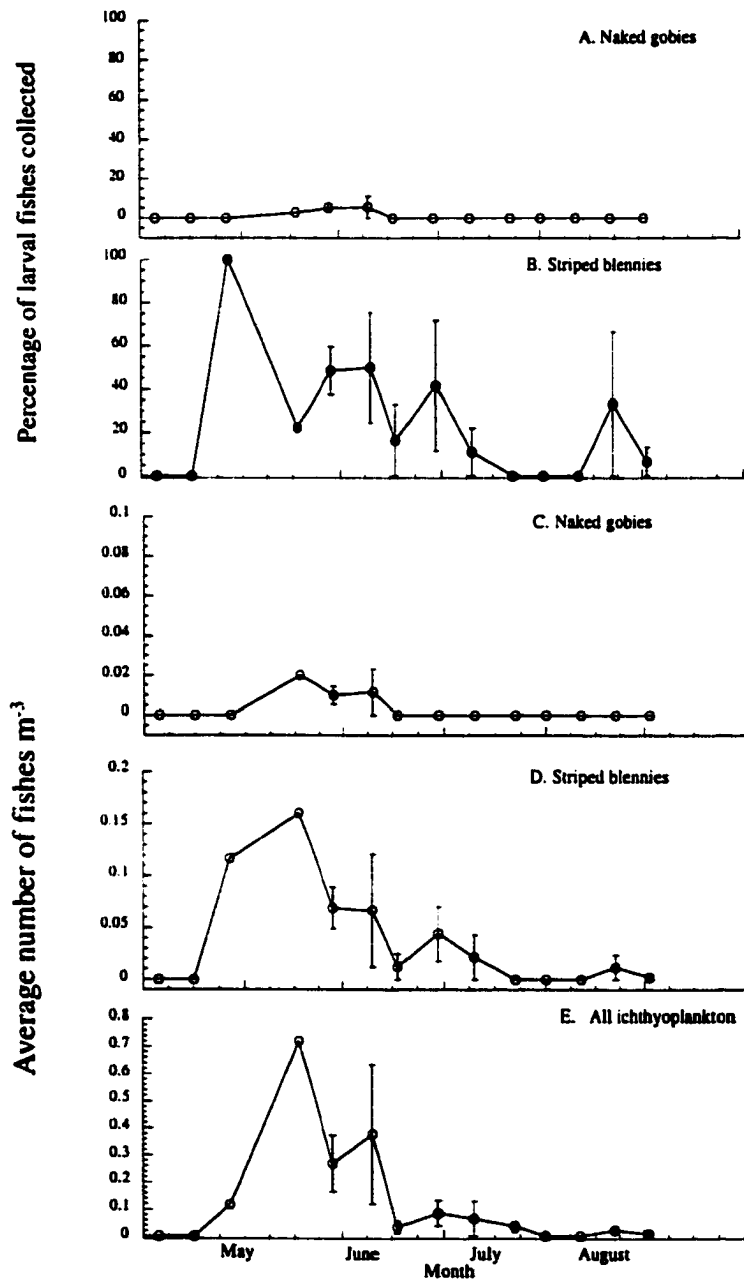
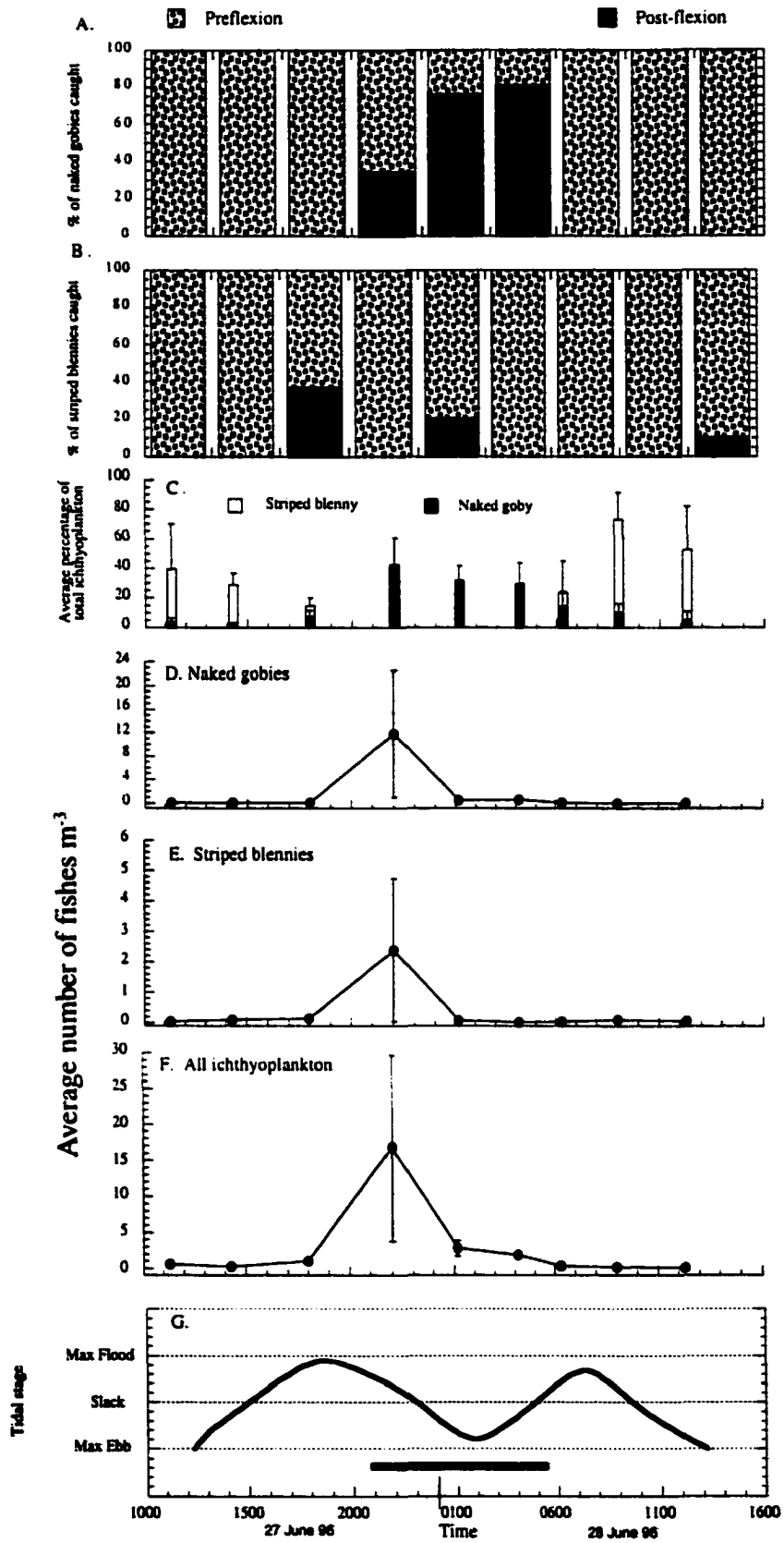


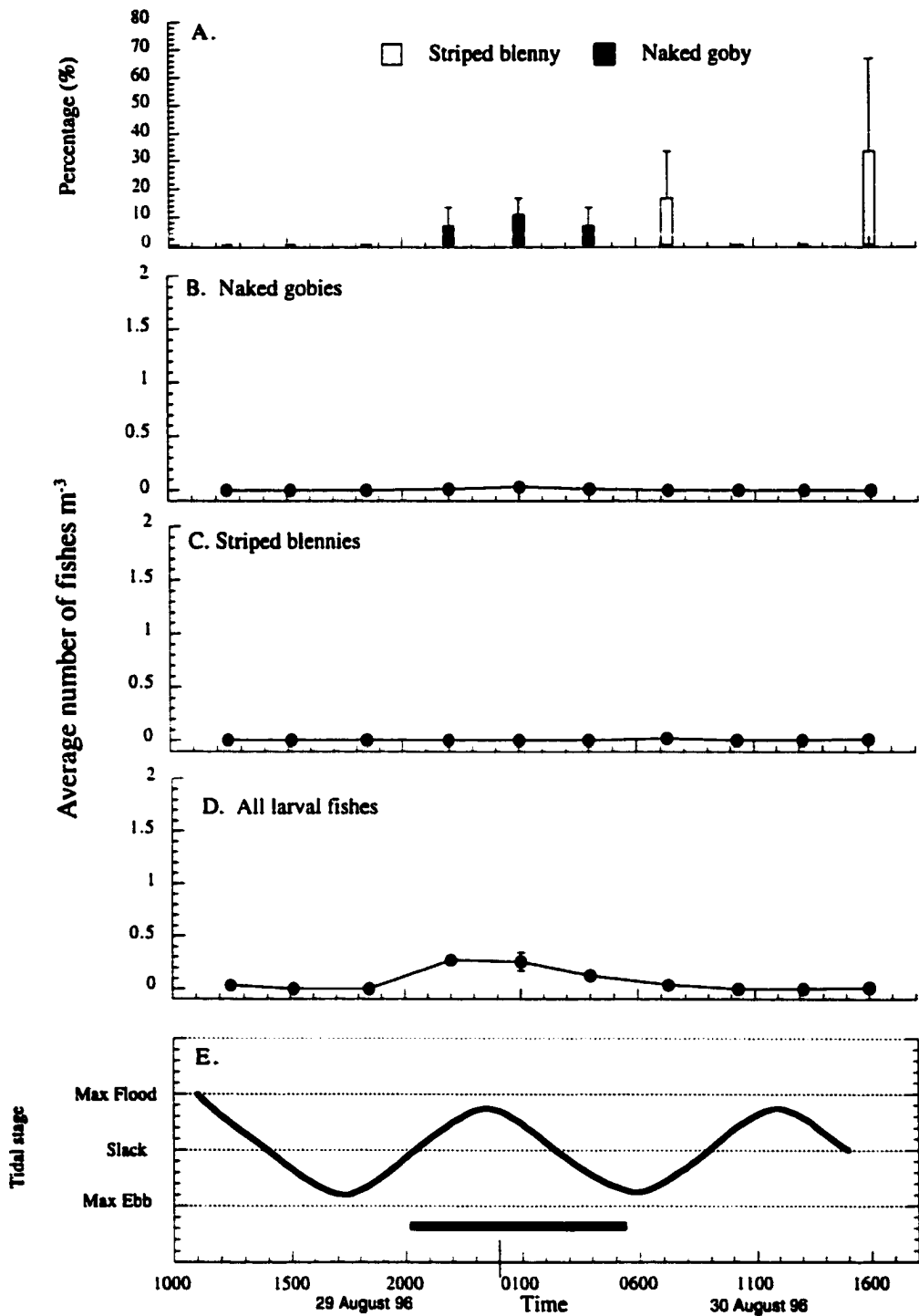
Table 19: Summary of ANOVA tests for fish densities from bongo tows made during the June 27-28 and August 29-30 stations near Palace Bar reef, Piankatank River, Virginia. All densities are in number of fish meter<sup>-3</sup> of water. "\*" designates results that were significant at the  $p \leq 0.05$  level.

Sampling date	Group	Test	Factors	df	p-value	Multiple comparison results (Fisher's LSD pairwise comparison test)
June 27-8, 1996	All larval fishes	ANOVA	Time of day	5	0.00 *	2000-2400 > 0400-1600
			Tidal stage	3	0.01 *	Slack onto Ebb > Ebb, Flood, Slack onto Flood
	Naked gobies	ANOVA	Location	2	0.10	
			Time of day	5	0.00 *	2000-2400 > 0400-2000
			Tidal stage	3	0.23	
			Location	2	0.76	
August 29-30, 1996	All larval fishes	ANOVA	Time of day	5	0.00 *	2000-0400 > 0400-0800 > 0800-2000
			Tidal stage	3	0.77	
			Location	2	0.11	
			Time of day	5	0.03 *	0000-0400 > 1200-2000
	Naked gobies	ANOVA	Tidal stage	3	0.99	
			Location	2	0.70	
Striped blennies	ANOVA	Time of day	5	0.69		
		Tidal stage	3	0.61		
		Location	2	0.65		
		Time of day	5	0.69		

**Figure 19:** Summary of larval fish densities observed during June 27-28 1996 around Palace Bar reef, Piankatank River, Virginia. Diel larval fish density estimates were pooled across location for graphic presentation. The percentage of preflexion and post-flexion fishes collected is presented for naked gobies (A.) and striped blennies (B.) in relation to the percentage composition of the larval fish community contributed by gobies and blennies (C.), average densities (fishes  $m^{-3} \pm$  standard error) of naked gobies (D.), striped blennies (E.), and all larval fishes (F.) and diel tidal patterns (G.). The black horizontal line in panel G. indicates the time interval from sunset to sunrise.



**Figure 20:** Summary of larval fish densities observed during August 29-30, 1996 around Palace Bar reef, Piankatank River, Virginia. Diel larval fish density estimates were pooled across location for graphic presentation. The percentage composition of the larval fish community contributed by gobies and blennies (A.), average densities (fishes  $m^{-3} \pm$  standard error) of naked gobies (B.), striped blennies (C.), and all larval fishes (D.) and diel tidal patterns (E.). The black horizontal line in panel E. indicates the time interval from sunset to sunrise.



fish  $m^{-3}$  at 22:00 (Table 17, Figure 19); an increase of 4 orders of magnitude. Striped blenny densities were also several orders of magnitude higher at night (2.39 fish  $m^{-3}$ ) than during the day (0.04 fish  $m^{-3}$ ; Table 17, Figure 19). Net avoidance (Olney, 1996) and/or diurnal vertical migration patterns related to changes in light intensity (Boehlert and Morgan, 1985; Munk et al., 1989; see below) by larval fishes may have played a role in relatively low fish abundances in daylight collections, particularly for post-flexion fishes with more advanced vision and swimming abilities. Post-flexion fish larvae may have been on the bottom (Stubblefield et al., 1984) or in the reef structure during daylight hours and thus unavailable for sampling by the bongo nets (see below). In June, naked goby densities were significantly higher between 20:00 and midnight than at any other time (ANOVA,  $p < 0.05$ ; Fisher's LSD pairwise comparison test,  $p < 0.05$ ; Table 19, Figure 19) and post-flexion naked gobies were collected exclusively between 22:00 and 05:00 (Figure 19). In June, total larval fish densities were significantly higher when the tide was changing from flood to ebb i.e., slack onto ebb (ANOVA,  $p < 0.05$ ; Fisher's LSD pairwise comparison test,  $p < 0.05$ ; Table 19, Figure 19) than at any other tidal stage.

A total of 1,002 preflexion (2.0 - 5.0 mm NL, Figure 21) naked gobies were collected; more than 99% of these were collected during the June 36 h sampling series (Figure 19). Of the 345 preflexion (2.0 to 4.6 mm NL, Figure 22) striped blenny larvae collected, 80% were collected during the June 36 h sampling event. Nine post-flexion (5.3 to 10.4 mm SL, Figure 22) striped blennies were collected; 89% of these were collected during the June 36 hr sampling series. All of the 611 post-flexion (4.2 to 14.4 mm SL; Figure 21) gobies were collected between 22:00 and 05:00 on June 27-28, 1996.

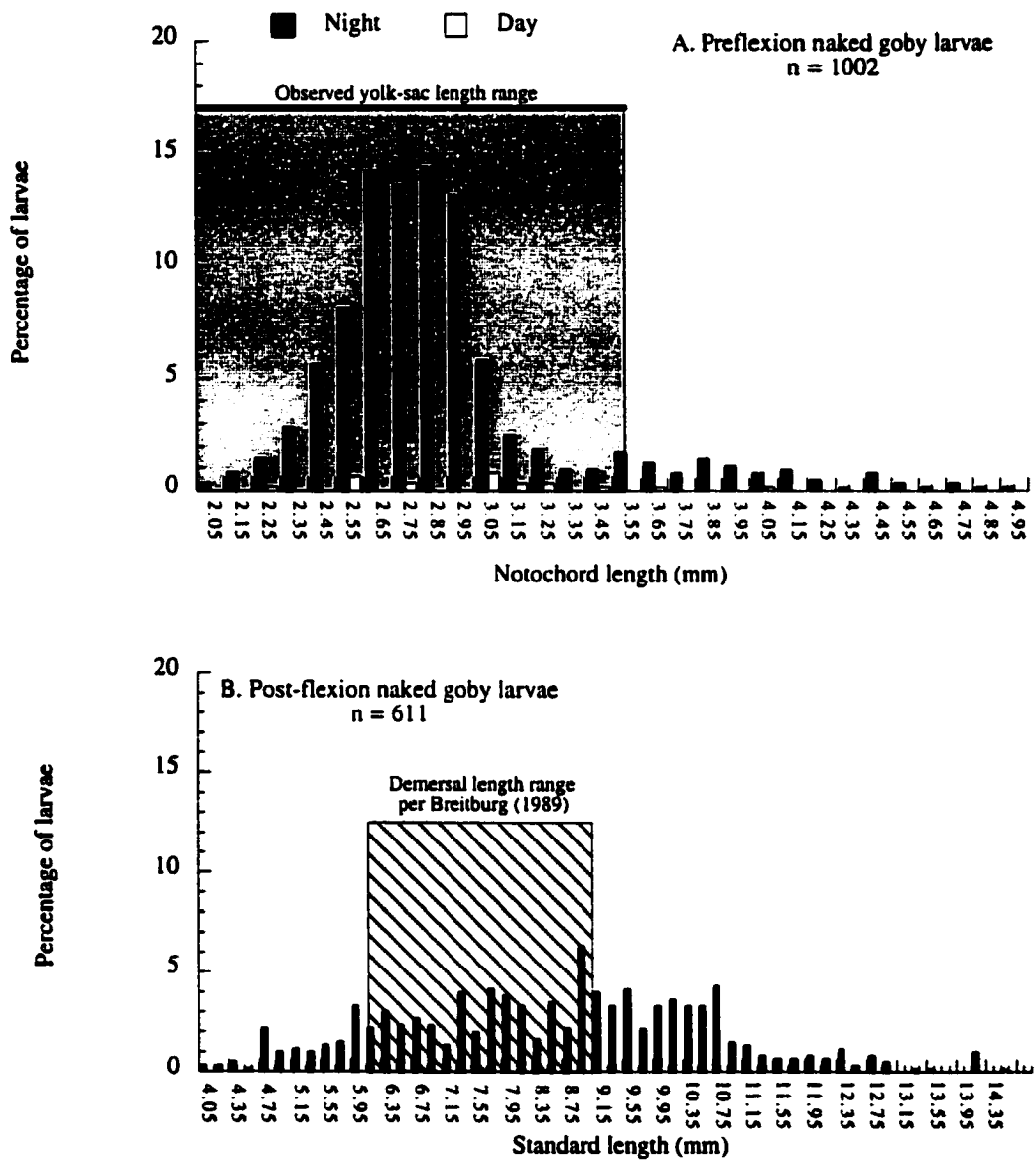
While the tide was ebbing on the evening of June 27, there was an increase in the density of fish larvae, particularly naked gobies, found in the tidal wake zone (East side of the reef on the ebb tide) compared to fish densities on either the channel (north) or inshore (south) sides of the reef (Figure 17, Figure 23). Naked goby densities in the tidal wake zone at 22:00 were almost an order of magnitude higher than those observed in the tidal wake



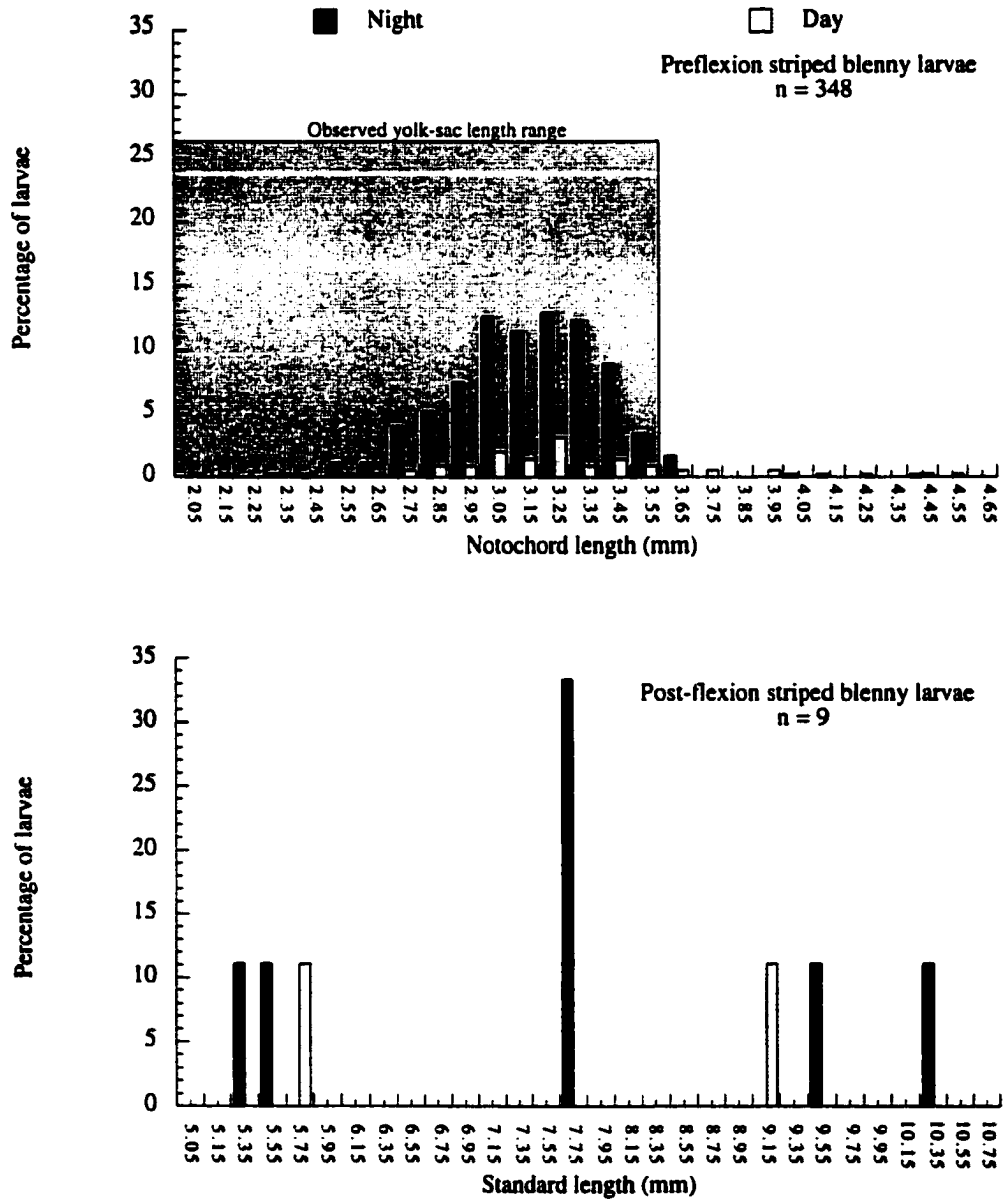
fish  $m^{-3}$  at 22:00 (Table 17, Figure 19); an increase of 4 orders of magnitude. Striped blenny densities were also several orders of magnitude higher at night (2.39 fish  $m^{-3}$ ) than during the day (0.04 fish  $m^{-3}$ ; Table 17, Figure 19). Net avoidance (Olney, 1996) and/or diurnal vertical migration patterns related to changes in light intensity (Boehlert and Morgan, 1985; Munk et al., 1989; see below) by larval fishes may have played a role in relatively low fish abundances in daylight collections, particularly for post-flexion fishes with more advanced vision and swimming abilities. Post-flexion fish larvae may have been on the bottom (Stubblefield et al., 1984) or in the reef structure during daylight hours and thus unavailable for sampling by the bongo nets (see below). In June, naked goby densities were significantly higher between 20:00 and midnight than at any other time (ANOVA,  $p < 0.05$ ; Fisher's LSD pairwise comparison test,  $p < 0.05$ ; Table 19, Figure 19) and post-flexion naked gobies were collected exclusively between 22:00 and 05:00 (Figure 19). In June, total larval fish densities were significantly higher when the tide was changing from flood to ebb i.e., slack onto ebb (ANOVA,  $p < 0.05$ ; Fisher's LSD pairwise comparison test,  $p < 0.05$ ; Table 19, Figure 19) than at any other tidal stage.

A total of 1,002 preflexion (2.0 - 5.0 mm NL, Figure 21) naked gobies were collected; more than 99% of these were collected during the June 36 h sampling series (Figure 19). Of the 345 preflexion (2.0 to 4.6 mm NL, Figure 22) striped blenny larvae collected, 80% were collected during the June 36 h sampling event. Nine post-flexion (5.3 to 10.4 mm SL, Figure 22) striped blennies were collected; 89% of these were collected during the June 36 hr sampling series. All of the 611 post-flexion (4.2 to 14.4 mm SL; Figure 21) gobies were collected between 22:00 and 05:00 on June 27-28, 1996.

While the tide was ebbing on the evening of June 27, there was an increase in the density of fish larvae, particularly naked gobies, found in the tidal wake zone (East side of the reef on the ebb tide) compared to fish densities on either the channel (north) or inshore (south) sides of the reef (Figure 17, Figure 23). Naked goby densities in the tidal wake zone at 22:00 were almost an order of magnitude higher than those observed in the tidal wake

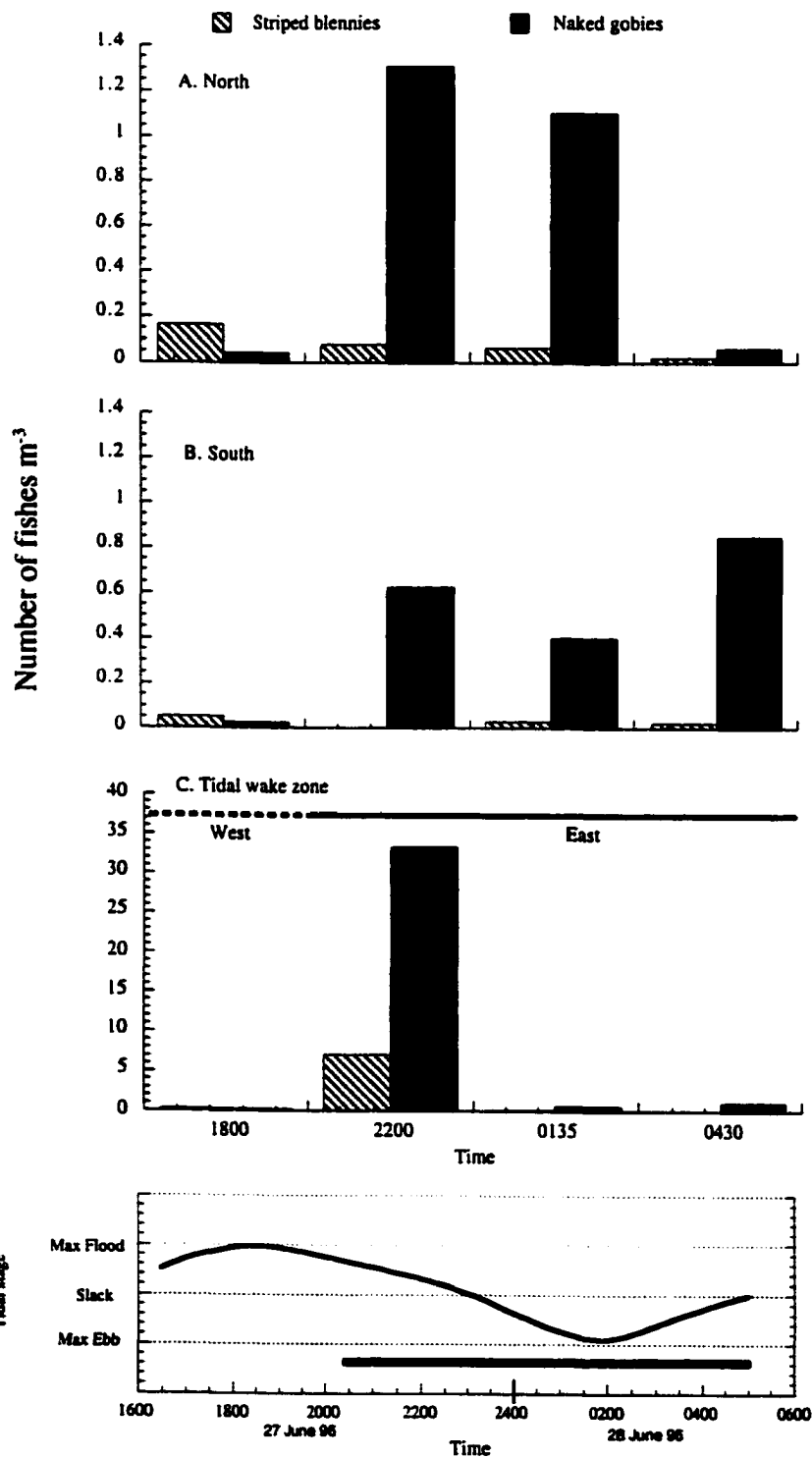


**Figure 21:** Length-frequency distribution for preflexion (A.) and post-flexion (B.) naked goby larvae collected around Palace Bar reef, Piankatank River, Virginia from May through August, 1996.



**Figure 22:** Length-frequency distribution for preflexion (A.) and post-flexion (B.) striped blenny larvae collected around Palace Bar reef, Piankatank River, Virginia from May through August, 1996.

**Figure 23:** Densities of larval naked gobies and striped blennies observed around Palace Bar reef, Piankatank River, Virginia between 18:00 on June 27, 1996 and 05:00 on June 28, 1996 from three collection locations: north (A.), south (B.) and in the tidal wake zone (C.) in relation to tidal flow (D.). The black horizontal line in panel D. indicates the time interval from sunset to sunrise. Note the difference in vertical scale between panels A./B. and panel C.



zone at 18:00, 01:35, or 04:30. Preflexion fish larvae of both species and post-flexion naked gobies were observed in the tidal wake zone. Many of the preflexion fishes were yolk-sac fishes (2.14 to 3.57 mm NL naked gobies, 1.69 to 3.64 mm NL striped blennies; Figures 21 and 22) that may have hatched after sunset (see Dietary analyses below) and been carried off the reef into the flow shadow by the ebbing tide (Figure 23). In the absence of multiple bongo tows from each side of the reef (north, south, downstream or tidal wake zone) at the same time, these data lack the replication necessary for statistical analyses.

#### Diets of larval naked gobies and striped blennies

Larval fishes examined for diet descriptions were separated by species and developmental stage. Within a species and developmental stage, fish were classified into 4 groups on the basis of their gut contents: larval fishes with empty guts, larval fishes with empty guts and a yolk sac, larval fishes that consumed prey but still had a yolk sac (first-feeding larvae), and larval fishes that consumed prey (feeding larvae). All larvae used for diet descriptions and analyses were feeding or first-feeding larvae; 3% ( $n = 2/68$ ) of feeding naked goby larvae and 19% ( $n = 14/74$ ) of feeding striped blenny larvae were first-feeding. Most striped blenny (88%;  $n = 68/77$ ) and naked goby (90%;  $n = 59/66$ ) yolk sac larvae were observed during the June 36 h sampling event. Yolk sac larvae of both species were most frequently observed in larval fish collections made between 18:00 and 6:00 (91% for both species) and 18:00 and midnight (88% of striped blennies ( $n = 60/68$ ), 61% ( $n = 40/59$ ) of naked gobies). Length ranges of yolk sac naked gobies (2.14 to 3.57 mm NL; Figure 21) and striped blennies (1.69 to 3.64 mm NL; Figure 22) observed near Palace Bar reef were similar to the upper limits of the size-at-hatch ranges reported by Fritzsche (1978) for naked gobies (2.0 to 2.6 mm NL) and for striped blennies (3.56 to 3.78 mm NL).

Feeding fishes from regular ichthyoplankton samples and the August 36 h samples were pooled with those from the June 36 h sampling event ( $n = 283$  from both species and developmental stages) for dietary analyses because the number of feeding fishes of both species collected during regular daylight samples ( $n = 7$ ; 6 preflexion and 1 post-flexion

striped blennies) and the August 36 h sampling ( $n = 2$  preflexion blennies) were relatively small. Feeding naked gobies (both preflexion and post-flexion) were observed exclusively between 22:00 on June 27, 1996 and 05:00 on June 28, 1996. The density of feeding preflexion naked gobies was significantly higher between 20:00 and midnight than from midnight to 08:00 (ANOVA,  $p < 0.05$ ; Fisher's LSD pairwise comparison test,  $p < 0.05$ ; Table 20). A majority of feeding post-flexion striped blennies (67%) were collected at 18:00 on June 27. Most feeding preflexion striped blennies (63%) were collected between 20:00 and midnight on June 27. Regardless of species, a higher percentage of post-flexion fishes were feeding than preflexion (Table 21).

A majority (77%) of all feeding fishes, regardless of developmental stage or species, consumed only one prey taxa (Table 21). The total number of prey items consumed per fish ranged from 1 to 4 in preflexion fishes and 1 to 9 in post-flexion fishes. Post-flexion fishes consumed significantly more total prey items than preflexion fishes regardless of species (Kruskal-Wallis,  $p < 0.05$ ; Dunn's test,  $p < 0.05$ ; Table 22). Larval polychaetes, calanoid copepod adults, and calanoid copepod nauplii were major prey taxa (prey items composing  $> 20\%$  of the diet) for both species. Fishes also consumed low numbers of adult polychaetes, barnacle nauplii, mysid shrimp, invertebrate eggs, and decapod zoea. Preflexion fishes consumed neither barnacle nauplii nor adult polychaetes. Similar prey suites have been described for field-caught naked gobies (Breitburg, 1989, 1991) and striped blennies offered wild plankton in laboratory feeding experiments (Harding, 1999; see Chapter 3 of this volume).

Preflexion fishes of both species consumed larval polychaetes and calanoid copepod nauplii at higher proportions than their availability in the plankton (Table 21, Figure 24). Specialization on a diet item is indicated graphically by points with low availability and high consumption (Costello, 1990). Preflexion naked gobies that consumed multiple prey taxa consumed larval polychaetes and calanoid copepod nauplii preferentially over calanoid copepod adults (Chesson's alpha values approximately 1, Table 21; Figure 24). Postflexion

Table 20: Summary of ANOVA tests on numbers of feeding larval fishes caught in bongo tows near Palace Bar reef. "\*" designates results that were significant at the  $p \leq 0.05$  level.

Sampling date	Fish	Test	Factors	df	p-value	Multiple comparison results (Fisher's LSD pairwise comparison test)
May-Aug 1996	Preflexion striped blennies	ANOVA	Day of the year	5	0.99	
			Time of day	4	0.10	
			Location	2	0.16	
June 27-8, 1996	Preflexion naked gobies	ANOVA	Time of day	2	0.00	* 2000-2400 > 0000-0800
			Location	2	0.08	
			Time of day	2	0.52	
	Post-flexion naked gobies	ANOVA	Location	2	0.34	
	Post-flexion striped blennies	ANOVA	Time of day	2	0.06	
			Location	2	0.13	



**Table 21:** Summary of dietary analyses for larval gobies and blennies from Palace Bar reef, Piankatank River, Virginia. Observed notochord length (NL, mm) and standard length (SL, mm) ranges are given for developmental stages of both fishes. Prey items that were not consumed frequently enough to be considered major prey taxa (--) are distinguished from prey items that were not consumed at all (NC).

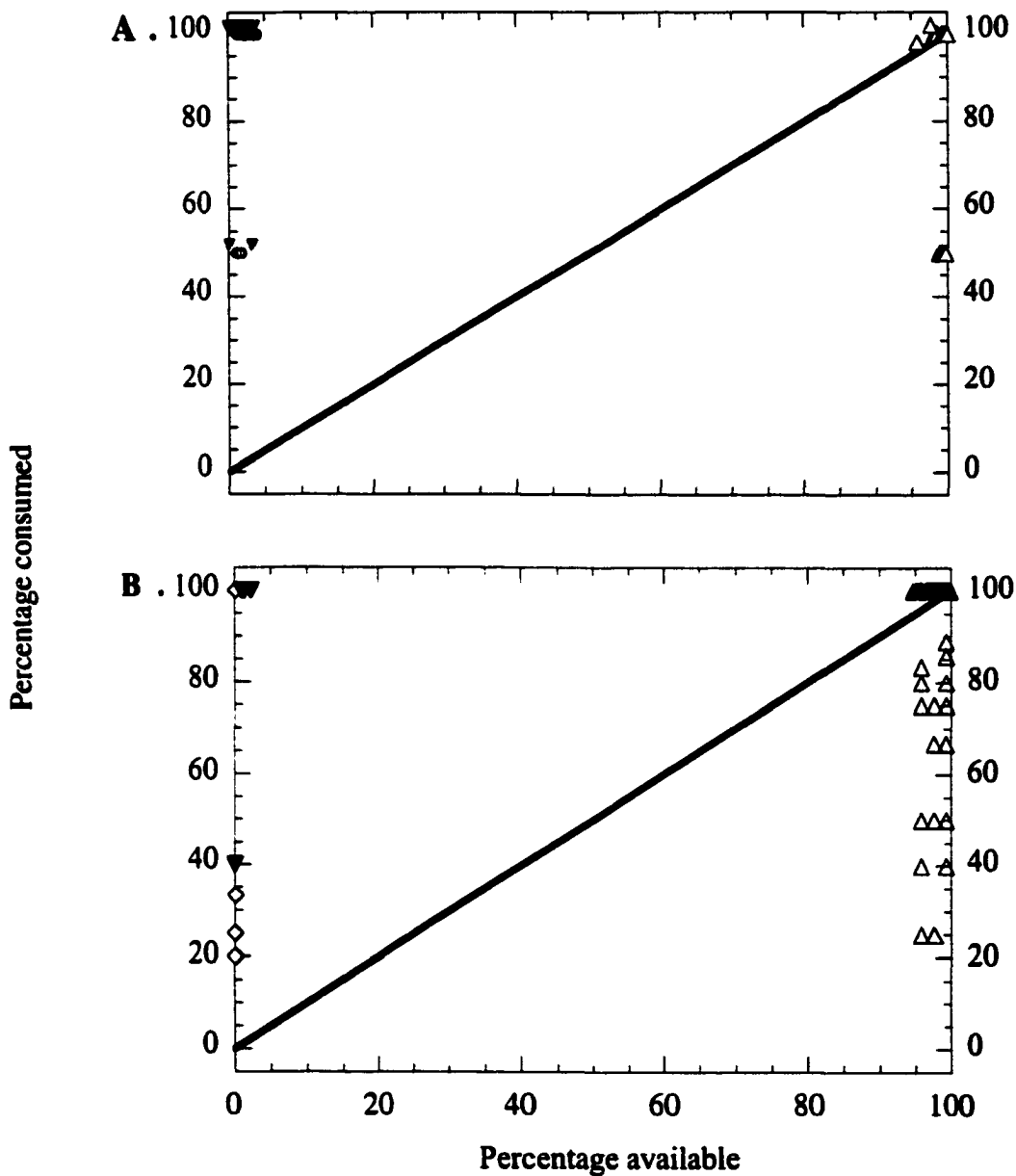
Developmental stage	Naked gobies		Striped blennies	
	Preflexion	Post flexion	Preflexion	Post flexion
Length range	2.0 - 4.8 mm NL	4.9 - 14.8 mm SL	1.6 - 4.9 mm NL	5.0 - 10.5 mm SL
n dissected	221	212	172	9
Percent feeding (%)	31	67	43	100
<b>Proportion of fishes consuming only one major prey type</b>				
Larval polychaetes	16/63	7/141	—	NC
Calanoid copepod adults	8/63	97/141	17/74	5/9
Calanoid copepod nauplii	24/63	3/141	45/74	1/9
Total percentage of fishes consuming only one major prey type (%)	76%	76%	84%	67%
<b>Proportion of fish where the proportion of prey items in the gut exceeded the relative proportion in the ambient plankton</b>				
Larval polychaetes	20/63	8/141	—	NC
Calanoid copepod adults	5/63	97/141	3/74	7/9
Calanoid copepod nauplii	28/63	4/141	54/74	1/9
Overall percentage of fishes where the proportion of a prey item in the gut exceeded the relative proportion in the plankton (%)	84%	77%	77%	89%
<b>Chesson's Alpha values for major prey taxa</b>				
n fish consuming multiple prey taxa	6	8	6	3
Larval polychaetes	0.24	1.00	—	0.00
Calanoid copepod adults	0.00	0.00	0.00	0.20
Calanoid copepod nauplii	0.75	—	1.00	0.72

**Table 22:** Summary of Kruskal-Wallis tests comparing total number of prey items consumed by individual fishes between developmental stages within species. “\*” designates results that were significant at the  $p \leq 0.05$  level.

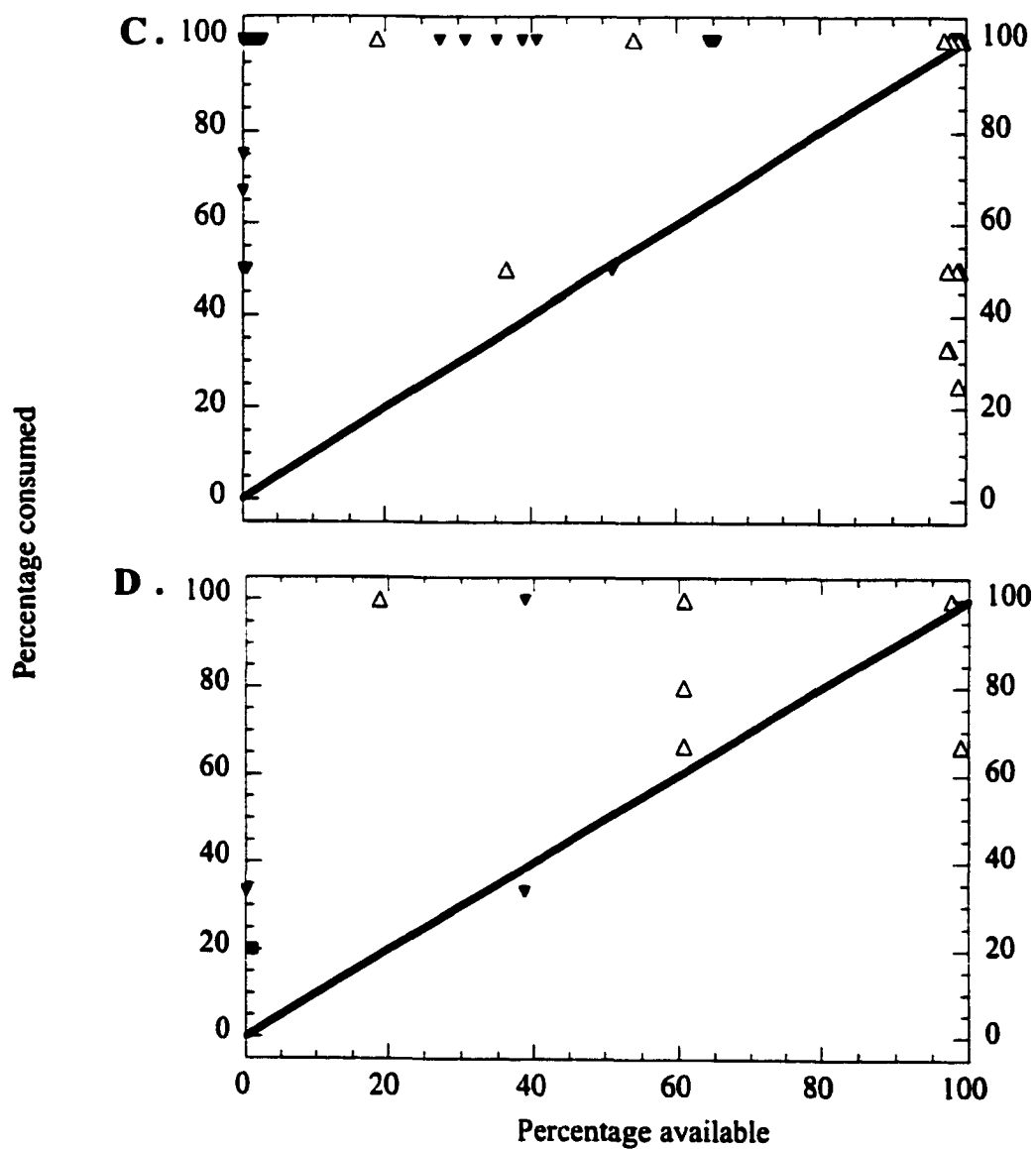
<b>Fish species</b>	<b>Factor</b>	<b>df</b>	<b>p-value</b>		<b>Multiple comparison results (Dunn's Test)</b>
Naked goby	Developmental stage	1	0.00	*	Postflexion > preflexion
Striped blenny	Developmental stage	1	0.01	*	Postflexion > preflexion

**Figure 24:** Percentage consumption of prey items by larval gobies and blennies plotted in relation to percentage availability in the plankton for (A.) preflexion naked gobies (n = 63), (B.) post-flexion naked gobies (n = 141), (C.) preflexion striped blennies (n = 74), and (D.) post-flexion striped blennies (n=9). Points above the diagonal line indicate prey items that were consumed at a higher proportion than their availability in the plankton. In cases where points representing percent prey items consumed overlapped completely with each other, data points were offset horizontally by less than one percentage point.

- Polychaete larvae      △ Calanoid copepod adults      ■ Barnacle nauplii
- ◇ Polychaetes          ▼ Calanoid copepod nauplii



- Polychaete larvae      △ Calanoid copepod adults      ■ Barnacle nauplii  
 ◇ Polychaetes      ▼ Calanoid copepod nauplii



naked gobies showed relative preferences for larval polychaetes over calanoid copepod adults (Chesson's alpha value = 1, Table 21; Figure 24). Both striped blenny developmental stages showed higher relative preferences for calanoid copepod nauplii than calanoid copepod adults (Table 21; Figure 24). However, preflexion striped blennies showed stronger preferences for calanoid copepod nauplii than post-flexion blennies (Chesson's alpha value = 1, Table 21; Figure 24).

## DISCUSSION

Larval naked gobies and striped blennies were most abundant around Palace Bar reef, Piankatank River, Virginia from mid-May through early July. This seasonal increase in larval goby and blenny abundance corresponds to the spawning season for both fishes (Dahlberg and Conyers, 1973; Nero, 1976; Breitburg, 1989, 1991; Harding, 1999). Seasonal increases in larval naked goby abundance have been observed in other estuarine habitats e.g., Patuxent River, Maryland (Shenker et al., 1983), York River, Virginia (Massmann et al., 1963), Beaufort Inlet, North Carolina (Hettler and Chester, 1990) and North Inlet Estuary, South Carolina (Allen and Barker, 1990). Similar early summer increases in larval striped blenny abundances have been observed by Olney and Boehlert (1988) in lower Chesapeake Bay and Hettler and Chester (1990) in Beaufort Inlet, North Carolina.

Nocturnal densities of larval naked gobies and striped blennies around Palace Bar reef were 3 to 4 orders of magnitude higher than densities of these larval reef fishes observed during daylight hours. Larval naked gobies of all developmental stages were more abundant than striped blenny larvae at night, particularly in the reef's tidal wake zone. Similar patterns of diurnal goby abundance have been reported by Massmann et al. (1963), Raynie and Shaw (1994), Olney and Boehlert (1988), and Olney (1996) for other estuarine habitats. Massmann et al. (1963) report average abundances of naked goby larvae per 5 min Clark-Bumpus tow of 8.2, 147.2, and 123.2 larvae per daylight tow from depths of 0 m (surface), 3 m, and 6 m, respectively, in the York and Pamunkey Rivers, Virginia. During nocturnal tows, naked goby abundances of 41.4 and 106.8 larvae per tow were observed at 0 m and 6

m, respectively (Massmann et al., 1963). Raynie and Shaw (1994) report a significant increase in both the overall density of larval naked gobies and the density of post-flexion gobies at night in Oyster Bayou, Louisiana. Olney and Boehlert (1988) observed almost an order of magnitude increase in nocturnal *Gobiosoma* sp. larval densities near seagrass beds in lower Chesapeake Bay when compared to daylight samples. Olney (1996) observed that seaboard goby (*G. ginsburgi*) larvae were rarely caught during daylight hours and were completely absent at noon in samples collected at depths less than 5.7 m near the mouth of Chesapeake Bay. Stubblefield et al. (1984) collected significantly more Gobiids within 12 cm of the bottom than just below the water surface during daylight in Calcasieu Lake, LA. In the absence of distinct water column stratification and related physical barriers (thermocline, pycnocline), larval fish distributions in shallow turbid habitats, such as the Pianktank River, may be strongly influenced by ambient light levels and the distribution of prey species per Fortier and Leggett (1983) and Munk et al. (1989).

Fortier and Leggett (1983) describe nocturnal migrations of capelin (*Mallotus villosus*) larvae in the St. Lawrence estuary and suggest that the vertical migrations by larger larvae are related to optimum light intensities; similar patterns of day-night vertical migration have been described for larval yellowtail flounder (*Limanda ferruginea*; Smith et al., 1978), spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*; Weinstein et al., 1980) and seaboard gobies (Olney, 1996). Illumination levels affect fishes' orientation to reef structures (see below; Marliave, 1986; Kobayashi, 1989; Lara, 1999) as well as feeding behavior (Confer et al., 1976; Robinson and Tash, 1979; Blaxter, 1986).

Most newly hatched larval fishes lack the rod photoreceptors (Blaxter, 1986; Fuiman and Delbos, 1998; Lara, 1999) that are responsible for visual discrimination at very low light intensities. The ontogeny of vision in fishes includes the development of scotopic (dim-light) vision that is facilitated by increasing numbers of cone photoreceptors and developing rod photoreceptors with age (Blaxter, 1969; Fuiman and Delbos, 1998; Higgs and Fuiman, 1998; Pankhurst and Hilder, 1998). Blaxter (1986) describes 0.1 to 0.01 lux

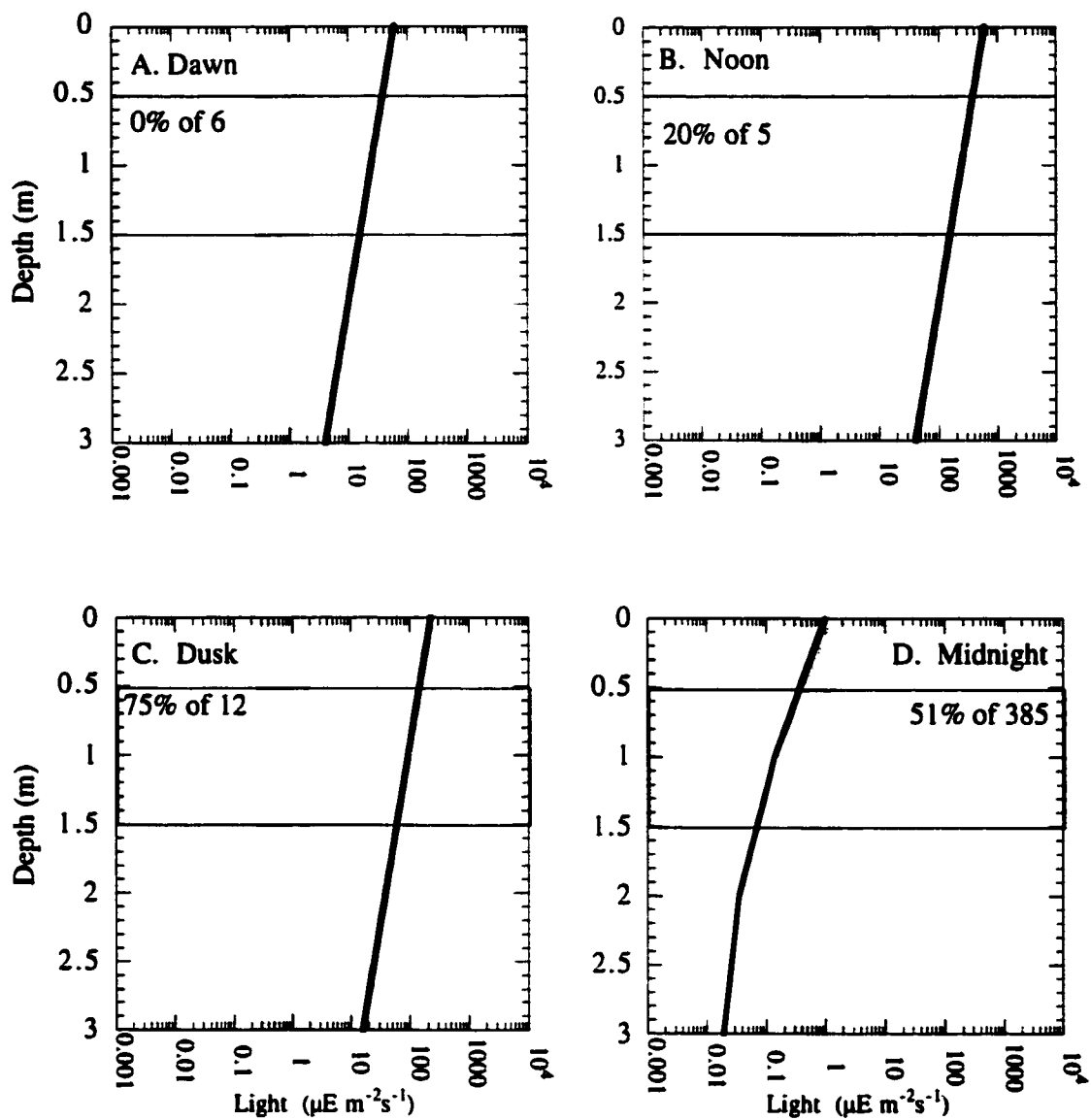
(approximately 1.8 to 0.18  $\mu\text{E m}^2 \text{s}^{-1}$ ; per Li-Cor, 1979) as the lower threshold light intensity range for vision in most larval fishes. Threshold levels for scotopic vision (lowest light intensity that caused an optomotor response) in red drum (*Sciaenops ocellatus*) larvae decreased with increasing age and ranged from  $7.38 \times 10^{-1} \mu\text{E m}^2 \text{s}^{-1}$  for smaller fishes (approximately 2 mm total length) to  $1.47 \times 10^{-4} \mu\text{E m}^2 \text{s}^{-1}$  for larger, older fishes (22 mm total length; Fuiman and Delbos, 1998). As larvae develop scotopic vision, they may become more sensitive to bright light (photopic sensitivity) as cone cells develop and multiply (Poling and Fuiman, 1997). These changes in visual sensitivity have been observed concurrently with habitat shifts in red drum (Fuiman and Delbos, 1998) and Atlantic croaker (Poling and Fuiman, 1997) and several species of coral reef fishes (Shand, 1997; Lara, 1999).

From dawn to dusk, estimated light levels at the bottom near Palace Bar reef are above the minimum threshold range for low-light vision by larval fishes (Blaxter, 1986; Figure 25; see Appendix I for derivation of light attenuation curves). At midnight, ambient moon-light would be sufficient to maintain light levels near the minimum visual threshold at the sampling depth (0.5 to 1.5 m; Figure 25), especially for post-flexion larvae with presumably higher visual acuity that were caught almost exclusively at night. Naked goby and striped blenny larvae near Palace Bar reef would be able to find similar light conditions in near-bottom habitat from dawn through dusk (Figure 25). Light intensities in the 0.5 to 1.5 m range near Palace Bar reef are greater than  $30 \mu\text{E m}^2 \text{s}^{-1}$  at all times but midnight (Figure 25); similar patterns of seaboard goby abundance and feeding incidence in relation to surface light levels were observed by Olney (1996). Light intensities in the upper part of the water column near Palace Bar reef during daylight hours (Figure 25) may be too bright for naked goby and striped blenny larvae to feed effectively, particularly older larvae with better developed visual acuity. During periods of high surface illumination, larval fishes near Palace Bar reef may use the reef structure as a shelter.

Diurnal patterns of vertical migration by larval fishes may be related to the spatial distribution of potential prey species as well as optimum illumination. Vertical migration



**Figure 25:** Light attenuation profiles and vertical distribution of feeding larval naked gobies and striped blennies near Palace Bar reef, Piankatank River, Virginia at dawn (A.), noon (B.), dusk (C.) and midnight (D.). Details of light attenuation profile derivation are provided in Appendix 1. Light attenuation at each time is represented by the thick black line. The threshold range of light intensity for larval fish feeding described by Blaxter (1986) is indicated by the vertical grey bar ( $1.8 - 0.18 \mu\text{E m}^{-2} \text{s}^{-1}$ ). Bongo tows were made at depths between 0.5 to 1.5 m. The pair of numbers given for each sampling depth presents the percentage of fish feeding at each depth at each time (%) of the total number of fish examined for that depth and time.



may increase encounter rates with potential prey species around Palace Bar reef during evening hours. Many estuarine plankton taxa also migrate diurnally with peak surface densities occurring nocturnally (e.g., Minello and Matthews, 1981; Fortier and Leggett, 1983; Hill, 1998; and Chapter 2 of this volume). During the same temporal window that preflexion gobies and blennies were most abundant around Palace Bar reef during June 27-28, 1996, the average zooplankton concentration around Palace Bar reef was 1,780 animals  $m^{-3}$  (standard error of the mean = 395.6) (see Chapter 2 of this volume). Average densities of larval polychaetes, calanoid copepod adults, and calanoid copepod nauplii, the dominant diet items for preflexion fishes herein were 2.26 (S.E. = 1.01), 1,767.2 (S.E. = 396.7), and 0.75 (S.E. = 0.75) animals  $m^{-3}$ , respectively (see Chapter 2 of this volume). Increased encounter rates with prey may shorten the time to successful first-feeding and reduce the possibility of yolk-sac depletion before first feeding and possible starvation (Hunter, 1976).

Although such high prey concentrations probably increase the likelihood of successful feeding encounters by young fish larvae, the prey field composition and concentration is not guaranteed. The three zooplankton taxa that were consumed most frequently by these larval fishes are distributed non-randomly (patchily) around Palace Bar reef (see Chapter 2 of this volume). Successful feeding by these fish larvae requires both spatial and temporal (seasonal and diurnal) overlap with prey species. Bivalve veligers were not observed in the diets of these larval fishes. Preferential feeding on bivalve veligers by larval fishes has been observed in laboratory feeding experiments (Checkley, 1989 [herring *Clupea harengus*], Harding, 1999 [naked gobies, striped blennies, feather blennies *Hypsoblennius hentzi*]; see Chapter 3 of this volume). Field collections of fish larvae by Houde and Lovdal (1984, 1985), Govoni et al. (1986), and Olney (1996) in Biscayne Bay, the Gulf of Mexico, and the Chesapeake Bay entrance, respectively, have also described preferential consumption of bivalve veligers by larval fishes. However, bivalve veligers were completely absent from the prey field around Palace Bar reef during the temporal window that a majority of the feeding larval gobies and blennies were collected (see Chapter 2 of this volume) making

it impossible for larval fish predators and bivalve prey to co-occur spatially or diurnally in June, 1996. In the absence of bivalve veligers, preflexion fishes preferentially consumed polychaete larvae and calanoid copepod nauplii. Although both of these prey types have multiple protruding appendages or more active swimming patterns (copepod nauplii :Van Duren and Videler, 1995; polychaete larvae: Mileikovsky, 1973:) than bivalve veligers (Mann and Wolf, 1983; Mann et al., 1991), copepod nauplii or polychaete larvae may be easier for small larval fishes to successfully capture than calanoid copepod adults. Preflexion blennies showed stronger preferences for calanoid copepod nauplii than post-flexion blennies. This difference in relative prey preference between preflexion and post-flexion blennies may relate to ontogenetic diet shifts. Olney (1996) observed a shift in the importance of nonnaupliar copepods in the diets of larval seaboard gobies at 5 to 6 mm SL. Harding (1999, see Chapter 3 this volume) observed an increase in the number of prey consumed with predator age in laboratory experiments with cultured naked gobies and feather blennies (*Hypsoblennius hentzi*).

The Piankatank River is a trap type estuary and historically was a noted area of seed-oyster production because retention of oyster veligers in the system was sufficient to achieve good settlement and recruitment (Andrews, 1979). Larval retention in the Piankatank system is facilitated by a series of gyres that trap and recirculate larvae between Stove Point Neck and Ginney Point (Chen et al., 1977; Harding and Mann, unpublished data; Figure 17). Just as these gyres contribute to annual settlement of Palace Bar reef's oyster population, they probably recirculate larval reef fishes locally until they are ready to settle or begin their demersal phase. Leis (1986) suggested that demersally hatched coral reef larval fishes may be able to take advantage of windward reef circulation patterns to avoid export from their natal habitats. Sale (1970) described the entrapment of acanthurid larvae in surface current gyres off the coast of Oahu, Hawaii and suggested that gyres passively keep the larvae near appropriate settlement habitat (reefs) during development. Johannes (1978) describes similar gyral circulation of presettlement larval reef fishes near the tip of Peleliu Island, Palau. The

nocturnal increase in yolk-sac and yolk-sac sized gobies and blennies observed in the length-frequency distributions of both gobies and blennies from Palace Bar reef (Figures 21A and 22A) is probably the result of hatching events on the reef during the evening of June 27, positively phototactic behavior of the newly hatched fishes (Johannes, 1978), and subsequent larval transport downriver on the ebbing tide. Similar dusk-evening increases in yolk sac larvae of fish with demersal eggs have also been observed in coral reef fishes (e.g., Gladstone and Westoby, 1988). Demersal eggs of coral reef fishes are thought to hatch exclusively after sunset causing a flux of yolk sac larvae in the plankton during early evening hours (Robertson, 1991).

Most of the postflexion fishes observed near Palace Bar reef are within the size range for demersal naked gobies described by Breitburg (1989, 1991; 6 to 14 mm SL). Demersal gobies are immediately pre-settlement and commonly aggregate near possible settlement substrates and structures (Breitburg, 1989, 1991, 1998; Brogan, 1994; Breitburg et al., 1995). Settlement for many larval coral reef fishes occurs nocturnally (Sale, 1970; Victor, 1986; Sweatman and St. John, 1990; Leis, 1991) and larvae actively move onto reefs when they are ready to settle (Sale, 1970). The abundance of post-flexion naked goby larvae greater than 6 mm SL (87% of all post-flexion gobies collected) around Palace Bar reef at night may be due to nocturnal settlement behavior by these fish. Kobayashi (1989) demonstrated that older Hawaiian gobiid larvae were significantly more abundant over the reef slope than away from the reef during bright moon and daylight hours and that these distribution differences disappeared on dark (no moon) nights. He concluded that gobiid larvae use visual cues to maintain near-reef distribution and suggested that post-flexion gobiid larvae that encounter reef structures during passive drift or active swimming will orient to the reef and avoid further dispersal (Kobayahsi, 1989). Similar structure-oriented behavior has been observed in larval fishes from rocky intertidal habitats. Marliave (1986) observed schools of blennoid and cottid larvae hovering within 2.0 m of the substrate by day and 0.5 m of the substrate at night usually near rocky features regardless of local current

strength and wave action. These larval fishes moved closer to the substrate at twilight when schools became disorganized (Marliave, 1986).

Bottom light levels from dawn to dusk at Palace Bar reef are within the 3 to 20  $\mu\text{E m}^{-2} \text{ s}^{-1}$  light range (Figure 25). Lara (1999) estimated the visual range of presettlement Labrids in coral reef habitats during daylight hours as less than 100 m or about the visual range of a human diver under optimal conditions. If the comparison with human vision field holds for larval naked gobies and striped blennies, a rough estimate of the vision range for larval fishes in conditions common near Palace Bar reef would be 0.5 m or less (J. Harding, personal observation). Presettlement larval reef fishes in the Piankatank River probably cannot see the reef at a distance and orient to it but if local circulation patterns bring them into proximity with the reef during daylight, they may use visual cues to stay near it until settlement per Marliave (1986; see above). Presettlement visual orientation to the reef and schooling behavior would be facilitated by ontogenic development of cone and rod photoreceptors and subsequent increase of visual acuity (see Fuiman and Delbos, 1998). Successful settlement by these goby and blenny larvae may be more a function of encounter with suitable habitat than active searching behavior because of the low-visibility conditions in the estuary. This pattern would fit with the behavior of presettlement schools of naked gobies observed during daylight hours by Breitburg (1989, 1991) as well as the observed diel abundance of gobies and blennies in relation to Palace Bar reef. When oysters and oyster reefs were dominant features of the Bay's shallow water habitats, water filtration and particle biodeposition by oysters may have resulted in very low turbidity levels (Newell, 1988) in proximity to oyster communities. Increased water clarity combined with increased settlement habitat probably increased encounter rate with suitable settlement habitat and subsequent settlement success.

Under natural conditions, post-flexion naked goby larvae have been observed schooling near the substrate at sizes in excess of 6 mm (Breitburg, 1991). Studies of other larval fishes have shown that the swimming ability of larval fishes at sizes in excess of 5 to

6 mm SL is sufficient to resist moderate estuarine currents and maintain vertical distribution in the water column (see Weinstein et al., 1980; Fortier and Leggett, 1983). The maximum speed of tidal currents in the Piankatank River near Palace Bar reef is approximately  $0.12 \text{ m s}^{-2}$  (Chen et al., 1977). Assuming a cruising speed of 2 to 3 body lengths per second (per Blaxter, 1986) for goby and blenny larvae; most larvae would be unable to maintain position during maximum tidal flow unless they took advantage of low flow zones e.g., around substrate (Breitburg et al., 1995) and in the reef's tidal wake. However, during periods of reduced tidal flow, a 6 mm SL larvae would be able to move from near-bottom habitat (maximum of 3 m near Palace Bar reef) to the surface in approximately 5 minutes of sustained swimming at cruising speeds. Most of the post-flexion fishes observed near Palace Bar reef were greater than 6 mm SL (Figures 21B and 22B) and should be able to actively move through the water column to take advantage of optimum light levels or prey concentrations for at least a portion of each day.

Breitburg et al. (1995) observed that demersal naked gobies aggregate in low-flow areas on the down-current sides of physical structure and that larger aggregations of goby larvae were found in down-current positions at rocks that created larger low-flow zones. Palace Bar reef may create a large area or zone of reduced tidal flow on its east and west perimeter, depending upon the direction of tidal flow, because of its parallel orientation to tidal flow that demersal naked gobies use to their advantage (Figure 17). Although the role of this tidal wake zone in the distribution of planktonic and demersal larval fishes around the reef was confounded in this study by the overlap of diurnal and tidal factors in that the tide was ebbing during evening hours on June 27, 1996, the possibility that reef fish larvae use the tidal wake to enhance feeding or settlement habitat bears further investigation. If positive effects on larval fish survival and settlement can be demonstrated for reef wake zones across diurnal and tidal scales, orientation of reef structures in relation to tidal flow may be an important consideration for subsequent oyster reef community restoration efforts.

**Reefs oriented normal to tidal flow would theoretically have larger flow wakes and would create more low-flow habitat adjacent to suitable settlement sites for larval reef fishes and reef-dwelling invertebrates such as oyster larvae.**



## SYNTHESIS

The preceding chapters describe field collections and laboratory experiments designed to quantitatively assess the role of the larval oyster - larval fish interaction on the development of oyster reef communities post-restoration. The current Palace Bar reef structure was built in 1993 on the footprint of a historic reef. The related ecological community has been allowed to develop naturally since the construction of the three-dimensional shell habitat. By 1996, Palace Bar reef supported densities of adult oysters similar to those observed on Palace Bar, a two dimensional natural oyster bar within 1 km of Palace Bar reef (Harding and Mann, 1999), as well as benthic invertebrates (e.g., polychaetes, barnacles, mud crabs, grass shrimp, and blue crabs), benthic fishes (e.g., naked gobies, striped blennies, oyster toadfish, and clingfish), and transient pelagic fishes (e.g., striped bass, bluefish, spot, Atlantic croaker, and weakfish) (Mann and Harding, 1997, 1998; Harding and Mann, 1999).

Observed densities of oysters, naked gobies, and striped blennies from Palace Bar reef were used to generate estimates of larval settlement for oysters and benthic fishes to assess the relative stability of these populations on the reef; i.e., do these populations have the potential to be self-sustaining? Oyster larval production estimates were made by combining observed densities and length-frequency distributions of adult oysters on Palace Bar reef with published size:fecundity relationships for oysters (Cox and Mann, 1992; Rainer and Mann, 1992; Thompson, et al. 1996; Mann and Evans, 1998) derived from James River, Virginia oyster populations. The Piankatank River is geographically close to the James River and is exposed to similar temperature conditions (Annual spatfall reports, VIMS, 1970-1999). Salinity conditions at Palace Bar reef were similar to those observed in the James River during collection of the material used for development of the size:fecundity

relationships (approximately 13.5 ppt; per Mann and Evans, 1998). The resulting density-based estimate of larval oyster production for Palace Bar reef was combined with estimates of larval oyster mortality and stage duration to make an estimate of oyster settlement.

Larval oyster mortality rates were derived from hatchery data at conditions similar to those in the James and Piankatank Rivers (per Mann and Evans, 1998) in the absence of reliable field estimates. The daily planktonic mortality rate (0.07) used for these calculations as well as Mann and Evans (1998) is within the range of average larval mortalities reported for other planktonic invertebrate larvae by Morgan (0.01 to 1.01; 1995). In practice, this mortality rate is paired with an estimate of larval development time (21 d) to estimate survivorship to settlement. Veligers that develop more quickly may be able to sustain a relatively higher mortality rate because they are exposed to planktonic sources of mortality for a shorter time window. For example, in Chapter 1 a 7% daily mortality function is applied for 21 days yielding an average of 76 spat per m<sup>2</sup>. If a 10% daily mortality function is applied for 14 days the resulting estimate is 80 spat per m<sup>2</sup>. At development times longer than 21 days, this mortality function is “gradually but increasingly insensitive to change in number of days above 21” (Mann and Evans, 1998). These larval mortality rates do not distinguish between sources of larval mortality and make no accommodations for larval behavior. Larval mortality due to advection away from favorable settlement substrate is not considered in these calculations. In reality, oyster larvae are able to aggregate and/or stay in proximity to favorable settlement habitat. Cohorts of oyster larvae that develop quickly and stay near settlement habitat would be able to sustain mortality rates higher than 7% and still produce settlement estimates that are similar to those obtained using a lower mortality rate for a longer period of time. Even with these inherent sources of variability, estimates of oyster settlement for Palace Bar reef generated using a daily mortality of 7% for 21 days are of the same order of magnitude as the observed densities of recently settled oysters (spat).

Estimates of larval reef fish production were made by combining observed densities of adult naked gobies and striped blennies with estimates of numbers of eggs per nest, nest mortality, and time to hatching derived from the literature (Hildebrand and Cable, 1938; Massmann et al., 1963; Dahlberg and Conyers, 1973; Nero, 1976) and laboratory observations (Harding, 1999 [See Chapter 3 this volume]; J. Harding, unpublished data) resulting in species-specific estimates of numbers of planktonic larvae. Estimates of larval growth rates and stage duration were based on laboratory culture of both species (Houde and Zastrow, 1993; Harding and Mann, 2000 [See Chapter 2 of this volume]) in the absence of field estimates. A generalized larval mortality rate for marine fishes from Houde (1989) incorporating species-specific growth rates and stage duration was used. The resulting daily mortality rates (0.22 for naked gobies and 0.20 for striped blennies) are similar to previous estimates of estuarine larval fish mortality (Houde, 1989; Houde and Zastrow, 1993). The estimates of larval fish growth, mortality, and stage duration are potential sources of large variability in these calculations given the consequences of small changes in any of these variables on resulting recruitment levels (see Houde, 1987, 1989). Despite these limitations, the resulting estimates of larval reef fish settlement are within one order of magnitude of the observed adult densities and of the same order of magnitude as previous estimates of recruitment for naked gobies in Chesapeake Bay (Breitburg, 1999).

Estimates of larval production and settlement for both oysters and benthic fishes are complicated by a lack of knowledge regarding the effects of advection from the reef on larval densities available to settle on the reef, as well as the assumption made in both cases for a single release of reproductive products: eggs or sperm (oysters) and nests hatching (gobies and blennies). Ongoing restoration activities in the Piankatank River include additional reef construction and shell planting at sites upstream and downstream of Palace Bar reef. Larvae produced on Palace Bar reef may be carried to the recently added habitat structures by the local gyre system, resulting in a net loss of larvae on Palace Bar reef. Oysters may spawn multiple times in any given year (Kennedy, 1996); Virginia oyster

populations commonly spawn from June through September (Andrews, 1979). Adult females of both fish species may spawn multiple times within a season (Nero, 1976; Fritzche, 1978).

The zooplankton community around Palace Bar reef was sampled intensively across temporal and spatial scales during both 1996 and 1997. Temporal factors including day of the year, time of day and tidal stage were sources of statistically significant variability in zooplankton abundance for the overall community as well as individual taxa. Although there was no difference in abundance of zooplankton (either individual taxa or total number of animals) between north and south sides of the reef, zooplankton taxa were distributed patchily within a location regardless of the temporal scale. Zooplankton samples were collected by towing a plankton net on the edges of the reef structure (north and south) as opposed to over the reef itself because of navigational and gear hazards posed by the reef structure. This integrative method lends itself to a description of the plankton community near the reef on the scale of tens of meters; resolution of spatial patterns on smaller scales requires a different approach and may be more sensitive to taxa that are found exclusively over the reef and can resist advection off-reef (e.g., harpacticoid copepods, mysid shrimp).

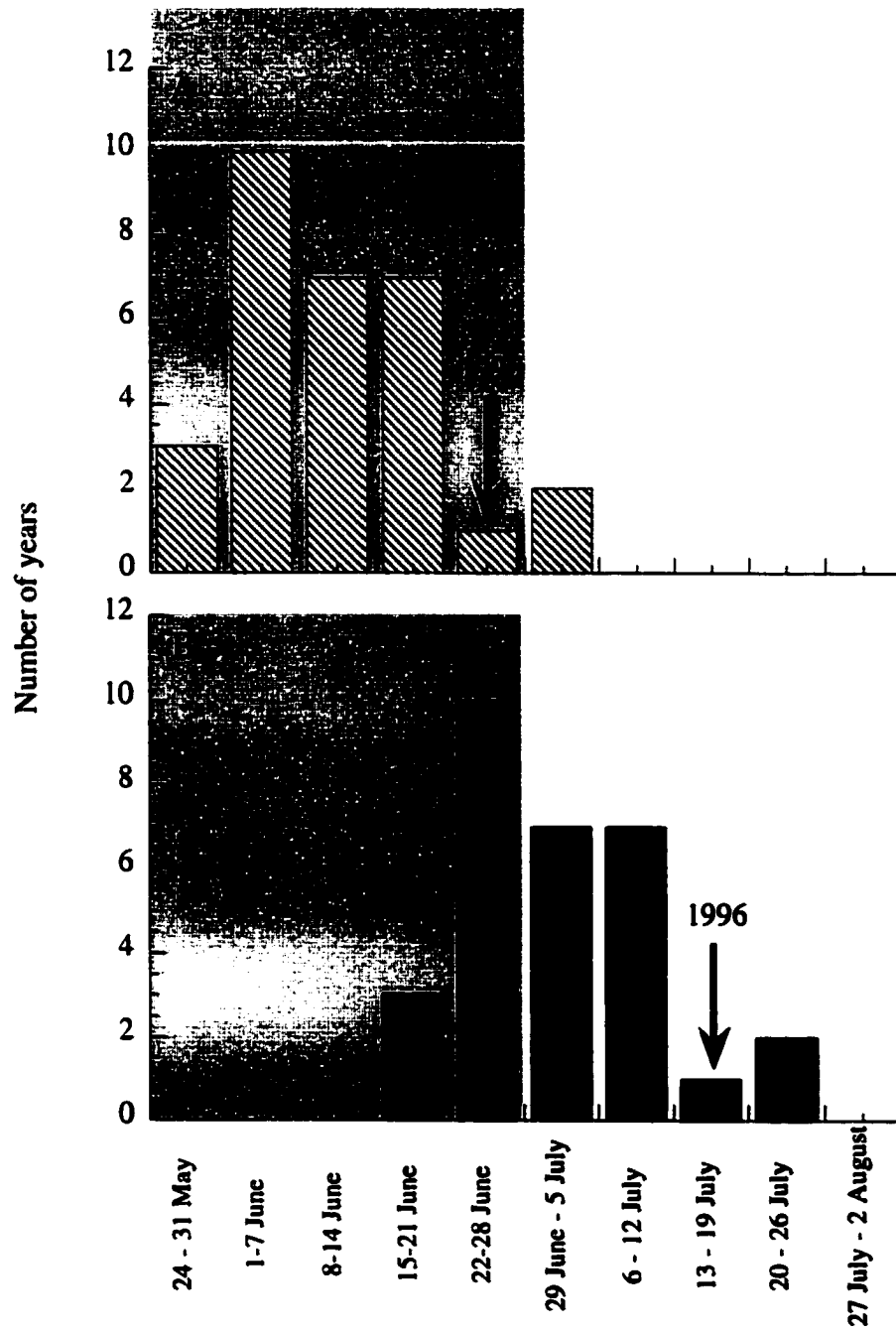
Field collections of larval gobies and blennies indicate a strong influence of diurnal factors on fish abundance around the reef. These estimates of reef fish abundance and habitat use may be compromised by sampling methods and differences in behavior of fish life history stages. Preflexion reef fishes, which are primarily passive and move with the water because their swimming abilities are too poorly developed to move independently, are more vulnerable to a bongo net towed in the upper portion of the water column. As the fish grow both swimming ability and visual acuity develop increasing maneuverability and sensitivity to ambient light levels. Not only are post-flexion fishes capable of avoiding a bongo net, they may also migrate vertically in relation to light levels. Older larvae orient to structure and aggregate near the reef surface in low-flow zones created by the reef (Breitburg et al., 1995) almost certainly removing them from the range of any towed net. A complete description of habitat use by larval reef fishes would include surface and bottom samples as

well as specialized collection methods for specific lifehistory stages.

Field estimates of prey availability for larval naked gobies and striped blennies relied on zooplankton tows that were spatially and temporally offset from the fish collections. Initial attempts to nest the zooplankton nets in the bongo nets resulted in a loss of steerage on the vessel and were deemed unsafe given the proximity of the reef structure. Although both types of tows were conducted along approximately the same tow paths, bongo tows were usually offset from zooplankton tows by 45 minutes to an hour. While it was assumed that the zooplankton community or prey field did not vary substantially between zooplankton and bongo tows, tidally mediated plankton transport, vertical migration by individual taxa, or local predation by schools of planktivorous fishes (e.g., Atlantic menhaden *Brevoortia tyrannus*) may have resulted in variations between the actual and estimated prey field available to larval gobies and blennies.

Larval naked gobies and striped blennies consumed bivalve veligers selectively in laboratory feeding experiments. Previous field studies have described selective feeding on veligers by seaboard gobies (Olney, 1996) and gobiids from Biscayne Bay (Houde and Lovdal, 1984). However, bivalve veligers were completely absent in the diets of larval gobies and blennies collected from Palace Bar reef during 1996! During late May and June, 1996, the seasonal time period when larval fish abundance was the highest, the species of interest did not co-occur. Temporally, the absence of overlap between larval forms of oysters and fishes during 1996 could not be controlled. The historical data on oyster recruitment in the Piankatank River (Annual spatfall reports, VIMS Molluscan Ecology Program, 1970-1999), indicates interannual variability in the initiation of spat settlement ranging from the third week of June through the fourth week of July (Figure 26). Oyster veligers are planktonic for two to three weeks prior to settlement. Approximate estimates of the onset of oyster spawning were made by subtracting three weeks from the first observed oyster settlement. During 28 of the 30 years for which data were examined (1970-1999), the estimated temporal window for onset of oyster spawning and veliger production overlaps the period of highest

**Figure 26:** Frequency histogram describing temporal patterns of oyster spawning (A.) and settlement (B.) in the Piankatank River, Virginia from 1970 - 1999. The week with first recorded settlement in each year (B.) was used to estimate the time of first spawning (A.) by subtracting 3 weeks. The grey area in both panels indicates the temporal window when naked goby and striped blenny larval densities were the highest during 1996. Data on oyster settlement are from annual spatfall reports produced by the VIMS Molluscan Ecology Program under assorted titles and authors.



observed larval reef fish densities (late May through June; Figure 26). These historical data provide strong evidence to support temporal co-occurrence of larval oysters and larval reef fishes. Interannual stochastic variability in habitat conditions, primarily temperature as related to seasonal spawning cues for oysters (Shumway, 1996), resulted in a failure to address the primary question (larval oyster - larval reef fish interactions) with quantitative field data.

In the absence of field data describing the larval oyster - larval reef fish interaction, are there other ways of addressing this question? Yes, estimates of larval oyster production may be combined with estimates of larval fish feeding rates, feeding period, and field densities to predict the potential grazing abilities of larval fishes that co-occur with larval veligers near Palace Bar reef. Dagg and Govoni (1996) used a similar approach to evaluate potential effects of larval fish predation on copepod mortality in the northern Gulf of Mexico. A second method, relying on an energy balance derived from estimates of fish weights, growth efficiency, and veliger weights may also be used.

#### **Method 1:**

Estimates of average larval oyster production for Palace Bar reef derived in Chapter 1 (349 embryos or early stage veligers per  $m^{-2}$ ) were converted to concentrations of oyster larvae in the water column directly above the reef assuming a uniform depth of 1.5 m over the entire reef area (300 m x 30 m). Thus, oyster veliger concentrations above the reef within 24 h of spawning were estimated at  $7.14 \times 10^6$  veligers  $m^{-3}$ . Dilution effects resulting from advection of veligers were not considered.

Larval fish feeding rates of 8 veligers  $h^{-1}$  were estimated from laboratory feeding experiments (Chapter 3). Naked gobies and striped blennies were assumed to have equal feeding rates and gut evacuation times (4 to 5 h, based on Chapter 3 data). Since larval gobies and blennies collected around Palace Bar reef were feeding across diurnal temporal scales, 15 h was used as a conservative estimate of the time available for larval fish feeding in a single day. Thus, a single fish larvae could consume a maximum of 120 oyster veligers



day<sup>-1</sup>. Lateral advection of fish larvae and veligers above the reef was assumed to affect both equally and functionally make no difference in encounter rate because both predators and prey were moving with a water parcel.

Average larval naked goby and striped blenny densities observed near Palace Bar reef at 2200 on June 27, 1996 were used to estimate the numbers of larval fishes available to consume veligers. Assuming densities of 14 fish m<sup>-3</sup> available in each of the 13,500 m<sup>3</sup> of water present above the reef, a total of 189,000 larval fish predators would be present near the reef. This number of larval gobies and/or blennies could consume  $2.27 \times 10^7$  oyster veligers per day<sup>-1</sup> or 317% of estimated larval oyster production on any given day.

Larval fish feeding abilities may be limited by mouth size, visual conditions, and swimming ability. For most of their planktonic developmental period, oyster veligers are small enough to be consumed by all but very recently hatched naked gobies and striped blennies. These fishes should be able to feed in light conditions (as assumed here) from hatch onward. As goby and blenny larvae age, their visual acuity will increase as cones develop and rods proliferate contributing to scotopic vision appropriate to feed in low light conditions. Oyster veliger swimming speeds range from 0.7 and 3.1 mm s<sup>-1</sup> (Mann and Rainer, 1990; Kennedy, 1996). Larval fish cruising speeds range from 1 to 3 body lengths s<sup>-1</sup> (Blaxter, 1986) but this estimate may be conservative for demersally hatched larvae such as gobies and blennies that enter the plankton at a more advanced developmental stage than larvae that hatch from pelagic eggs (Johannes, 1978). A 4 mm fish larvae swimming at approximately 8 mm s<sup>-1</sup> is clearly capable of catching an oyster veliger.

Encounter rates between larval fish predators and oyster veliger prey will be affected by small scale aggregations or patchiness that result in the concentration of predators and/or prey in relatively small areas. Consumption by a fish larvae encountering an aggregation or patch of veligers (as observed in this study [Chapter 2] and others [Pritchard, 1953; Vecchione, 1987]) would be limited only by the fish's capture success and handling time of each prey. Fish larvae may not need to successfully consume veligers to reduce overall veliger survival;

unsuccessful capture events may still result in damage to prey that may place them at increased mortality risk from other predators, advection, or starvation.

These scenarios suggest that larval oyster production estimates based on current oyster densities from Palace Bar reef are insufficient to feed the observed densities of larval fishes. Larval fishes are capable of completely cropping the relatively dilute veliger resource several times daily. In the absence of an abundant veliger resource, larval fishes consume other plankton taxa including copepods and polychaete larvae. The existing Palace Bar reef oyster population contains a higher percentage of smaller individuals than historic populations must have contained simply due to disease-related mortality at 2 to 3 years. Fecundity in oysters is closely related to size and populations with a large proportion of larger (older) animals would produce more larvae than younger (smaller) populations such as the existing Palace Bar reef oyster population.

Current average oyster densities on Palace Bar reef are low (34 adults  $m^{-2}$ ) in relation to densities observed on extant natural reefs in the James River and, presumably, historic oyster densities. For example, Point of Shoals reef in the James River currently supports 128 adult oysters  $m^{-2}$  (Mann and Evans, 1998; R. Mann, VIMS, unpublished data). Estimates of embryo or early-stage veliger production for the Point of Shoals oyster population are  $6.31 \times 10^6$  larvae  $m^{-2}$  (Mann and Evans, 1998). If Point of Shoals larval production estimates are combined with the estimated volume of water over Palace Bar reef (13,500  $m^3$ ), the resulting estimate of early-stage veliger abundance over the reef within 24 hr of spawning is  $1.29 \times 10^{11}$  oyster veligers  $m^{-3}$ . Application of the same larval fish feeding estimates described above yields a total daily larval fish consumption estimate of 2% of the oyster veliger production. Thus a reef's oyster population structure (density, length-frequency) influences both lower and intermediate trophic levels in that older oyster populations with higher densities may produce enough veligers to accommodate the probable grazing of veligers by larval fishes. This balance or equilibrium is lacking in younger, less dense oyster populations and larval oyster - larval fish interactions are probably much more influential. Oyster

populations on constructed reefs may be more vulnerable to the influences of larval fish grazing because the habitat structure that was historically created by adult oysters has been artificially created providing habitat for adult fishes in the absence of the oyster fecundity and density relationships inherent in natural reef communities.

#### Method 2:

Estimates of naked goby weights at hatch (20 µg) and metamorphosis (1,821 µg) from Houde and Zastrow (1993) were used for both naked goby and striped blenny larvae. Larvae of both species were assumed to gain 1,801 µg during planktonic development.

Growth efficiencies in the literature (Laurence, 1977, winter flounder, *Pseudopleuronectes americanus*; Houde and Schekter, 1981; bay anchovy, *Anchoa mitchilli*, sea bream *Archosargus rhomboidalis*, lined sole, *Achirus lineatus*) range from 5 to 52% depending upon the ration size, species, and temperature. A growth efficiency of 20% was used estimate a required ingestion of 9,005 µg per fish during planktonic development for naked gobies and striped blennies.

Veliger weights were estimated using the relationship between dry mass (DM, in µg) and veliger shell length (SL, in µm) described by Widdows et al. (1989):

$$DM = (2.48 \times 10^{-5}) SL^{2.073}$$

Assuming a required ingestion of 9,005 µg for development from hatch through metamorphosis, each larval fish would need to eat approximately  $6.16 \times 10^3$  200 µm SL veligers to reach settlement. At densities of 189,000 larval fish above the reef, collectively these fish could consume  $1.17 \times 10^9$  200 µm veligers or more than 100 times the reef's estimated veliger production prior to settlement. If only half of the weight gain from hatching through metamorphosis is due to consumption of veligers (4,502 µg), each fish might consume  $3.98 \times 10^3$  200 µm SL veligers and the total goby/blenny population would need to consume  $5.83 \times 10^8$  veligers or approximately 80 times the reef's estimated veliger production. If Point of Shoals veliger production estimates combined with Palace Bar reef volume are applied to this approach, larval fishes relying exclusively on veligers from hatch

through metamorphosis would consume 0.9% of the veligers produced and larval fishes relying on veligers for half of their developmental weight gain would consume 0.45% of veliger production.

Given existing oyster and fish demographics on Palace Bar reef, if larval oysters and larval reef fishes co-occur, larval fishes have the capacity to drastically reduce, perhaps eliminate, local veliger populations. The strength of this interaction is directly related to the demography of resident oyster populations and the resulting veliger production. Restored reefs provide habitat for adult fishes but lag behind established natural oyster reef communities in ecological function until oyster populations achieve densities and length-frequency distributions that can produce enough veligers to balance consumption by larval fishes. In the absence of abundant veliger resources, larval gobies and blennies use other planktonic food sources (copepod adults and nauplii, polychaete larvae, barnacle nauplii). The larval oyster - larval fish interaction is a trophic interaction that is directly related to habitat issues.

Oyster reef restoration addresses physical habitat reconstruction (structure) and the renewal of a keystone species (per Paine, 1969). The idea that the relationship between oysters (keystone species) and other reef community members may be a combination of both trophic and habitat issues bears further examination. If this is the case, the habitat issue becomes one that may not be controlled by the food relationship between early life history stages (larval oyster - larval fish) alone but by something much more complex (e.g., competition for space, shelter, or other foods). Historic reef communities offered adult reef fishes structural shelter (habitat), a supply of clean articulated oyster shells from recent mortality for use as nesting sites (habitat), and relatively high habitat heterogeneity that increased predation refuges (habitat) and surface area (habitat) available for colonization by benthic macrofauna and subsequent grazing by adult fishes (food). Current reef populations of adult gobies and blennies may be limited by shelter and nest site availability due to low oyster densities and the fact that few oysters survive beyond their second summer

yielding smaller shells for fish habitat.

Models derived to explain patterns observed in coral reef fish assemblages may have some applicability to oyster reefs, particularly if oyster reef habitat is a limiting factor for naked goby and striped blenny populations. Sale (1977, 1980) used a "lottery" model to discuss the recruitment of individuals to a community where "allocation of space between species was due more to chance patterns of recruitment by individuals rather than to systematic partitioning by specialized species of the resources available". In this view, the recruitment "lottery" determines the composition of the fish assemblage because multiple ecologically-similar species compete for resources (Mapstone and Fowler, 1988). Thus, reef residents are generalists with broad niche requirements rather than specialists with finely partitioned, narrow niches (*sensu* Bakus, 1969). "Lottery"-derived assemblages have similar numbers of fishes over time but show temporal variations in species composition that is primarily due to stochastic variability in recruitment events (Sale, 1977, 1980; Mapstone and Fowler, 1988). Oyster reefs in trap type estuaries, like the Piankatank River, benefit from circulation patterns that retain and recirculate planktonic larvae locally. Larval oysters and reef fishes in these habitats are recirculated and kept in proximity to suitable settlement habitat. Reefs in shallow estuaries may be easier for presettlement larval fishes to find and orient to prior to settlement. Possible reductions in turbidity around oyster reefs from oyster filtration may make it easier for larval fishes to locate and recruit to reef habitat.

Phylogenetically, gobies and blennies are tropical invaders of temperate habitats. These species, as with similar coral reef species, have broad niche requirements and are opportunistic fishes that take advantage of the habitat and food resources offered by oyster reefs. The generalist tendencies of these fishes are indicated by the continued presence of adults and larvae in Chesapeake Bay in the absence of abundant natural oyster reefs and reef fields. Although, neither fish is restricted exclusively to oyster reef habitat (Nero, 1976; Fritzche, 1978), oyster reefs are widely acknowledged as optimal habitat (e.g., Wells, 1961; Dahlberg and Conyers, 1973) for adults of these species. Although larval reef fishes

selectively consume oyster veligers when they encounter them (Chapter 3; Harding, 1999), these larval fishes also consume other, more abundant prey items (copepod adults and nauplii, polychaete larvae, barnacle nauplii) and are thus generalist predators rather than specialists. In the context of optimal habitat, the oyster's role as a keystone species as portrayed by Baird and Ulanowicz (1989) is justifiable.

Although the assertion that oyster reefs are essential fish habitat is not applicable for generalists such as naked gobies and striped blennies, the EFH concept may be related to oyster reefs in a limited fashion. Neither the keystone species nor the related community members are restricted to oyster reef habitats but, as demonstrated by Minello (1999), densities of naked gobies and striped blennies are higher on oyster reefs than other estuarine intrahabitat types including submerged aquatic vegetation, *Spartina alterniflora* marsh edge, mixed-vegetation marsh edge, inner marsh, and shallow nonvegetated bottom. Oyster reef habitat may be optimal fish habitat for many estuarine species but it is not essential habitat. Broad niche width and flexibility between ecologically similar species have probably enabled oyster reef fauna to survive drastic reductions in habitat quantity and quality over the last two centuries.

By definition, oyster reef restoration activities increase habitat and, over time, the related ecological functions. The conceptual model for larval oyster - larval reef fish interactions presented in Figure 1 is supported by laboratory observations and the calculations described above even in the absence of field data confirming co-occurrence. If larval oysters and larval reef fishes co-occur, the resulting predator-prey interaction provides an important link between oysters and oyster reef fish assemblages including upper level predators that feed on gobies and blennies. Reef restoration will facilitate the development and progression of related ecological communities by providing optimal habitat conditions for ubiquitous estuarine species such as naked gobies and striped blennies.

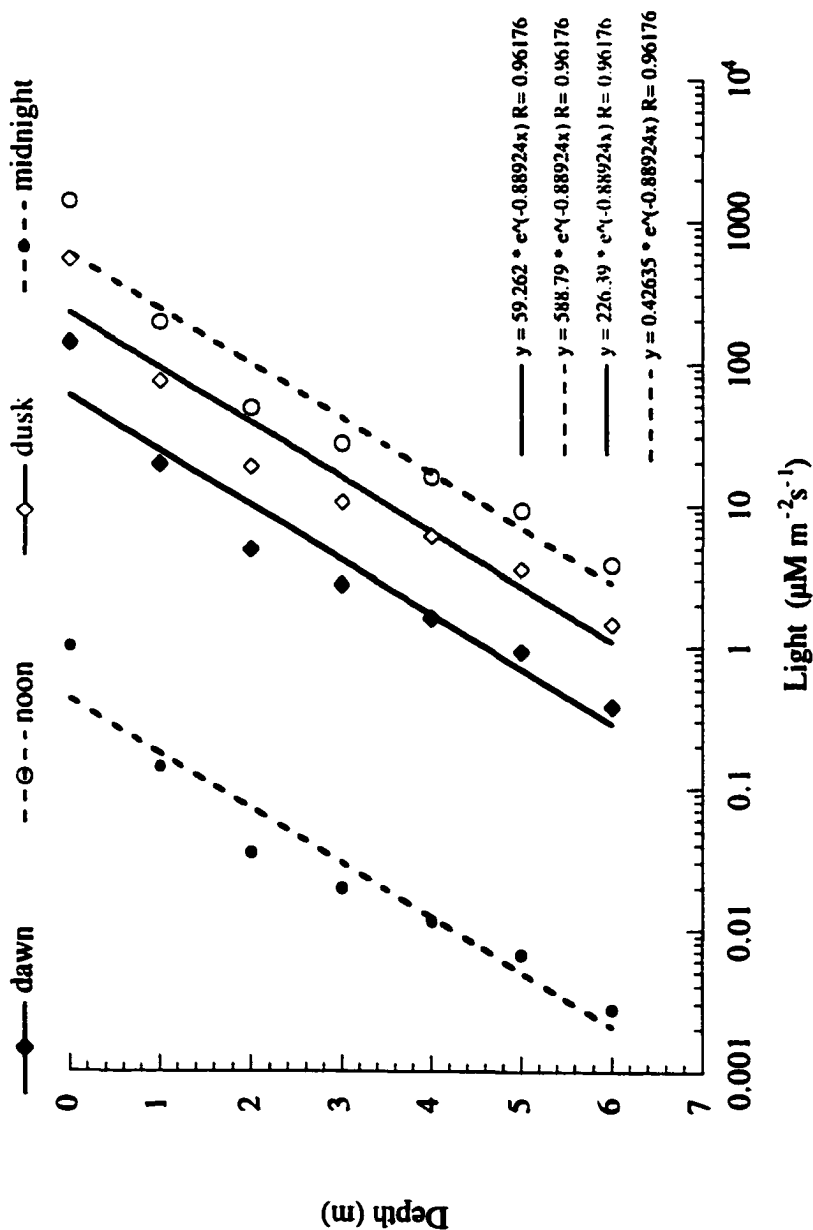
**APPENDIX 1**

**Derivation of light attenuation profile for Palace Bar reef, Piankatank River, Virginia.**

Solar radiation data (photosynthetically active radiation (PAR);  $\mu\text{E m}^{-2} \text{s}^{-1}$ ) for the Piankatank River was obtained from the Chesapeake Bay Program web site (<http://www.chesapeakebay.net/data/index.htm>). Seasonal radiation data obtained from the VIMS Byrd Hall data logging station via the VIMS Scientific Data Archive ([http://www.vims.edu/data\\_archive](http://www.vims.edu/data_archive)) was used to estimate surface light levels at different times of day in the absence of on-site measurements at various times. The site-specific solar radiation readings at depth were used to calculate light attenuation coefficients ( $K_D$ ) for each depth as close to the seasonal window when sampling occurred as possible. Piankatank River data used to calculate a site specific  $K_D$  values were from June 12, 1996. Seasonal radiation data from June 27-28, 1996 (the actual date of sampling in the Piankatank River) were used to estimate surface radiation ( $I_0$ ) values at particular times of the day (06:00, 12:00, 18:00, 24:00) for the Piankatank River. Radiation levels at particular times of the day were combined with site and depth specific attenuation coefficients to estimate the light attenuation profiles (Figure A1:  $R^2 = 0.92$ , at dawn (06:00), noon (12:00), dusk (18:00) and midnight (24:00). Time-specific light attenuation profiles were combined with data on goby and blenny feeding patterns (percentage of fish examined feeding at a particular depth at a particular time) to create Figure 25.



Figure A1: Light attenuation data for Piankatank River (Chesapeake Bay Program station LE3.7) for June 12, 1996.



## LITERATURE CITED

- Able, K. 1999. Measures of juvenile fish habitat quality: examples from a National Estuarine Research Reserve. pp. 134-147. In: L. Benaka (ed) Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Symposium 22, Bethesda, Maryland.
- Able, K. and M. Fahay. 1998. The first year in the life of estuarine fishes of the Middle Atlantic Bight. Rutgers University Press, Piscataway, NJ.
- Allen, J., T. Kinsey, and M. James 1976. Abundances and production of copepods in the Rhode River subestuary of Chesapeake Bay. Chesapeake Science 17: 86-92.
- Allen, D. and L. Barker. 1990. Interannual variations in larval fish recruitment to estuarine epibenthic habitats. Marine Ecology Progress Series 63: 113-125.
- Amundsen, P., H. Gabler and F. Staldvik. 1996. A new approach to graphical analysis of feeding strategy from stomach content data - modification of the Costello (1990) method. Journal of Fish Biology. 48:607-614.
- Andrews, J.D. 1979. Pelecypoda: Ostreidae. pp. 293-341. In: A.C. Geise and J.S. Pearse (eds.) Reproduction of Marine Invertebrates Volume V. Molluscs: Pelecypods and Lesser Classes. Academic Press, Inc., New York, NY.
- Bahr, L. 1974. Aspects of the structure and function of the intertidal oyster reef community at Sapelo Island, Georgia (U.S.A.). Doctoral Dissertation. University of Georgia, Athens.
- Baird, D. and R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay Ecosystem. Ecological Monographs 59: 329 - 364.
- Bakus, G. 1969. Energetics and feeding in shallow marine waters. Int. Rev. gen. exp. Zool., 4: 275-369.

- Bartol, I. and R. Mann. 1997. Small-scale settlement patterns of the oyster *Crassostrea virginica* on a constructed intertidal reef. *Bulletin of Marine Science* 61: 881-897.
- Bartol, I and R. Mann. 1999a. Small scale patterns of recruitment on a constructed intertidal reef: the role of spatial refugia. pp. 159-170 In: M.Luckenbach, R. Mann, and J. Wesson, editors. *Oyster reef habitat restoration: a synopsis and synthesis of approaches*. Virginia Institute of Marine Science Press, Gloucester Point, VA.
- Bartol, I., R Mann, and M. Luckenbach. 1999b. Growth and mortality of oysters (*Crassostrea virginica*) on constructed intertidal reefs: effects of tidal height and substrate level. *Journal of Experimental Marine Biology and Ecology*. 237: 157-187.
- Batty, R. 1987. Effect of light intensity on activity and food searching of larval herring, *Clupea harengus*: a laboratory study. *Marine Biology*. 94: 323-27.
- Batty, R., J. Blaxter and J. Richard. 1990. Light intensity and feeding behavior of herring, *Clupea harengus*.. *Marine Biology*. 107: 383-388.
- Benaka, L. 1999. Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Symposium 22, Bethesda, Maryland.
- Blaber, S. and T. Blaber. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology*. 17: 143-162.
- Blaxter, J. 1969. Visual thresholds and spectral sensitivity of flatfish larvae. *Journal of Experimental Biology*. 51: 221-230.
- Blaxter, J. 1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society*. 115: 98-114.
- Boehlert, G. and J. Morgan. 1985. Turbidity enhances feeding abilities of larval Pacific herring, *Clupea harengus pallasii*. *Hydrobiologia*. 123: 161-170.
- Breitburg, D. 1988. Oxygen fluctuations and fish population dynamics in a Chesapeake Bay oyster bed. In: M.P. Lynch and E. C. Krome (eds.) *Understanding the estuary: Advances in Chesapeake Bay Research*, Publication 129, Chesapeake Research

Consortium, Gloucester Point, Virginia.

- Breitburg, D. 1989. Demersal schooling prior to settlement by larvae of the naked goby. *Environmental Biology of Fishes* 26: 97 - 103.
- Breitburg, D. 1991. Settlement patterns and presettlement behavior of the naked goby, *Gobiosoma boscii*, a temperate oyster reef fish. *Marine Biology* 109: 213-221.
- Breitburg, D. 1999. Are three dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community. pp. 239-250. In: M.W. Luckenbach, R. Mann, and J.A. Wesson (eds.). *Oyster reef habitat restoration. A synopsis and synthesis of approaches.* Virginia Institute of Marine Science Press. Gloucester Point, Virginia.
- Breitburg, D., M. Palmer, and T. Loher 1995. Larval distributions and the spatial patterns of settlement of an oyster reef fish: responses to flow and structure. *Marine Ecology Progress Series* 125:45-60.
- Brogan, M. 1994. Distribution and retention of larval fishes near reefs in the Gulf of California. *Marine Ecology Progress Series.* 115:1-13.
- Brookins, K. and C. Epifanio 1985. Abundance of brachyuran larvae in a small coastal inlet over six consecutive tidal cycles. *Estuaries* 8: 60-67.
- Buskey, E. 1993. Annual pattern of micro- and mesozooplankton abundance and biomass in a subtropical estuary. *Journal of Plankton Research* 15: 907-924.
- CANOCO for Windows 4.0 1998. Center for Biometry, CPRO-DLO, Wageningen, The Netherlands.
- Checkley, D.M. Jr. 1982. Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. *Marine Ecology Progress Series.* 9: 245-253.
- Chen, H., P. Hyer, A. Kuo, and C. Fang 1977. Hydrography and hydrodynamics of Virginia estuaries XI. Mathematical model studies of water quality of the Piankatank estuary. Special report No. 124 in *Applied Science and Ocean Engineering*, Virginia Institute of Marine Science, Gloucester Point, Virginia, 80 p.

- Chesney, E.J. Jr. 1989. Estimating the food requirements of striped bass larvae, *Morone saxatilis*: effects of light, turbidity, and turbulence. Marine Ecology Progress Series. 53: 191-200.
- Chesson, J. 1978. Measuring preference in selective predation. Ecology. 59: 211-215.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology. 64: 1297-1304.
- Coen, L., E. Wenner, D. Knott, B. Stender, N. Hadley, M. Bobo, D. Richardson, M. Thompson, and R. Giotta. 1997. Intertidal oyster reef habitat assessment and restoration: evaluating habitat use, development and function. Journal of Shellfish Research. 16:262.
- Coen, L., M. Luckenbach, and D. Breitburg. 1999. The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. pp. 438-454. In: L.R. Benaka (ed.) Fish habitat: Essential fish habitat and rehabilitation. American Fisheries Society, Symposium 22, Bethesda, Maryland.
- Coen, L. and M. Luckenbach. 1999. Developing success criteria and goals for evaluating shellfish habitat restoration: Ecological function or resource exploitation? Ecological Engineering.
- Confer, J., G. Howick, M. Corzette, S. Kramer, S. Fitzgibbon, R. Landesberg. 1978. Visual predation by planktivores. Oikos. 31:27-37.
- Conley, W. and J. Turner 1991. Phytoplankton and zooplankton of the Westport River estuary Massachusetts (USA). Hydrobiologia 210: 225-232.
- Connaughton, V. 1994. Selective feeding by larval weakfish, *Cynoscion regalis*: The influence of prey characteristics and larval behavior. Doctoral Dissertation. University of Delaware, Newark, Delaware. 142 p.
- Connaughton, V. and C. Epifanio. 1993. Influence of previous experience on the feeding habits of larval weakfish, *Cynoscion regalis*. Marine Ecology Progress Series. 101: 237-41.

- Costello, M. 1990. Predator feeding strategy and prey importance: a new graphical analysis. *Journal of Fish Biology*. 36:261-63.
- Cowan, J. and R. Birdsong. 1985. Seasonal occurrence of larval and juvenile fishes in a Virginia Atlantic coast estuary with emphasis on drums (Family Sciaenidae). *Estuaries* 8: 48 - 59.
- Cox, C. and R. Mann. 1992. Fecundity of oysters, *Crassostrea virginica* (Gmelin), in the James River, Virginia, U.S.A. *Journal of Shellfish Research* 11: 49 - 54.
- Crabtree, R. and D. Middaugh. 1982. Oyster shell size and the selection of spawning sites by *Chasmodes bosquianus*, *Hypleurochilus geminatus*, *Hypsoblennius ionathus* (Pisces, Blenniidae) and *Gobiosoma bosc* (Pisces, Gobiidae) in two South Carolina estuaries. *Estuaries* 5: 150 - 155.
- Cronin, L. J. Daiber, and E. Hulbert 1962. Quantitative seasonal aspects of zooplankton in the Delaware River estuary. *Chesapeake Science* 3: 63-93.
- Currie, W., M. Claereboudt, and J. Roff 1998. Gaps and patches in the ocean: a one dimensional analysis of planktonic distributions. *Marine Ecology Progress Series* 171: 15-21.
- Dagg, M. and J. Govoni. 1996. Is ichthyoplankton predation an important source of copepod mortality in subtropical coastal waters? *Marine and Freshwater Research*. 47: 137-44.
- Dahlberg, M. and J. Conyers. 1973. An ecological study of *Gobiosoma bosc* and *G. ginsburgi* (Pisces, Gobiidae) on the Georgia coast. *Fisheries Bulletin, U.S.* 71: 279 - 287.
- Dovel, W. 1971. Fish eggs and larvae of the upper Chesapeake Bay. *Nat. Res. Inst., Univ. of Maryland Contrib. No. 460*. 71 p.
- Durbin, A. and E. Durbin 1981. Standing stock and estimated production rates of phytoplankton and zooplankton in Narrangsett Bay, Rhode Island. *Estuaries* 4: 24-41.

- Ebeling, A. W. and M. A. Hixon. 1991. Tropical and temperate reef fishes: a comparison of community structures. pp. 509 - 563. In: P. F. Sale (ed.) *The Ecology of Fishes on Coral Reefs*. Academic Press, Inc., San Diego, California.
- Epifanio, C., C. Valenti, and A. Pembroke 1984. Dispersal and recruitment of blue crab larvae in Delaware Bay, U.S.A. *Estuarine, Coastal and Shelf Science* 18: 1-12.
- Evans, D. and R. Mann. In review. Seasonally modulated growth functions. *Journal of Shellfish Research*.
- Fasham, M., M. Angel, and H. Roe 1974. An investigation of the spatial pattern of zooplankton using the Longhurst-Hardy plankton recorder. *Journal of Experimental Marine Biology and Ecology* 16: 93-112.
- Fortier, L. and W. Leggett 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. *Canadian Journal of Fisheries and Aquatic Science* 40: 1543-1555.
- Friedlander, A. and J. Parris. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* 224: 1-30.
- Fritzsche, R. 1978. Development of fishes of the Mid-Atlantic Bight- an atlas of larval and juvenile stages: Volume 5: Chaetodontidae through Ophidiidae. U.S. Fish and Wildlife Service, U.S. Department of the Interior. Washington, D.C. p. 214 - 218, 300 - 303.
- Fuiman, L. and B. Delbos. 1998. Developmental changes in visual sensitivity of red drum, *Sciaenops ocellatus*. *Copeia*. 4:936-943.
- Gallager, S, C. Davis, A. Epstein, A. Solow, and R. Beardsley. 1996. High-resolution observations of plankton spatial distributions correlated with hydrography in the Great South Channel, Georges Bank. *Deep Sea Research II*. 43: 1627-1633.
- Genin, A., C. Greene, L. Haury, P. Wiebe, G. Gal, S. Kaartvedt, E. Meir, C. Fey, and J. Dawson 1994. Zooplankton patch dynamics: daily formation over abrupt topography. *Deep Sea Research I*, 41: 941-951.

- Gladstone, W. and M. Westoby. 1988. Growth and reproduction in *Canthigaster valentini* (Pisces, Tetradontidae): a comparison of a toxic reef fish with other reef fishes. *Environmental Biology of Fishes*. 21:207-221.
- Govoni, J., D. Hoss, and A. Chester. 1983. Comparative feeding of three species of larval fishes in the Northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus*. *Marine Ecology Progress Series*. 13: 189-199.
- Govoni, J., P. Ortner, F. Al-Yamani, and L.Hill. 1986. Selective feeding of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae in the northern Gulf of Mexico. *Marine Ecology Progress Series*. 28: 175 -183.
- Harding, J. 1999. Selective feeding behavior of larval naked gobies (*Gobiosoma bosc*) and blennies (*Chasmodes bosquianus* and *Hypsoblennius hentzi*): preferences for bivalve veligers. *Marine Ecology Progress Series*. 179: 145 -153.
- Harding, J. and R. Mann. 1999. Fish species richness in relation to restored oyster reefs, Piankatank River, Virginia. *Bulletin of Marine Science*. 65(1): 289-300.
- Harding, J. and R. Mann. 2000. Estimates of naked goby (*Gobiosoma bosc*), striped blenny (*Chasmodes bosquianus*), and Eastern oyster (*Crassostrea virginica*) larval production around a restored Chesapeake Bay oyster reef. *Bulletin of Marine Science*. 66(1): 29 - 45.
- Hargis, W.J. Jr. 1999. The evolution of the Chesapeake oyster reef system during the Holocene epoch. pp. 5-23. In: M.W. Luckenbach, R. Mann, and J.A. Wesson (eds.). *Oyster reef habitat restoration. A synopsis and synthesis of approaches*. Virginia Institute of Marine Science Press, Gloucester Point, Virginia.
- Hargis, W.J. Jr. and D. Haven. 1988. The imperiled oyster industry of Virginia. VIMS Special Report Number 290 in *Applied Marine Science and Ocean Engineering*. 130 p.
- Hargis, W.J. Jr. and D. Haven. 1999. Chesapeake oyster reefs, their importance, destruction and guidelines for restoring them. pp. 329-358. In: M.W. Luckenbach, R. Mann, and



- J.A. Wesson (eds.). Oyster reef habitat restoration. A synopsis and synthesis of approaches. Virginia Institute of Marine Science Press. Gloucester Point, Virginia.
- Hartman, K. J. and S. B. Brandt. 1995a. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. *Transactions of the American Fisheries Society* 124: 520 - 537.
- Hartman, K.J. and S.B. Brandt. 1995b. Predatory demand and impact of striped bass, bluefish, and weakfish in the Chesapeake Bay: applications of bioenergetics models. *Canadian Journal of Fisheries and Aquatic Science*. 52: 1667-1687.
- Heinle, D 1966. Production of a calanoid copepod, *Acartia tonsa*, in the Patuxent River Estuary. *Chesapeake Science* 7: 59-74.
- Herman, S., J. Mihursky, and A. McErlean 1968. Zooplankton and environmental characteristics of the Patuxent River estuary 1963-1965. *Chesapeake Science* 9: 67-82.
- Hettler, W. and A. Chester. 1990. Temporal distribution of ichthyoplankton near Beaufort Inlet, North Carolina. *Marine Ecology Progress Series*. 68:157-168.
- Higgs, D. and L. Fuiman. 1998. Association between sensory development and ecology in three species of clupeoid fish. *Copeia*. 1998(1):133-144.
- Hildebrand, S. and L. Cable. 1938. Further notes on the development and life history of some teleosts at Beaufort, NC. *Bull. U.S. Bur. Fish.* 48: 505 - 642.
- Hill, A. 1998. Diel vertical migration in stratified tidal flows: implications for plankton dispersal. *Journal of Marine Research* 56: 1069-96.
- Hill, M. and H. Gauch 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47-58.
- Houde, E. 1987. Fish early life history dynamics and recruitment variability. *American Fisheries Society Symposium* 2: 17 - 29.
- Houde, E. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fisheries Bulletin, U.S.* 87: 471 - 495.

- Houde, E. and R. Schekter. 1980. Feeding by marine fish larvae: developmental and functional responses. *Environmental Biology of Fishes*. 5: 315-334.
- Houde, E. and R. Schekter. 1981. Growth rates, rations, and cohort consumption of marine fish larvae in relation to prey concentrations. *Rapp. P.-v. Reun. Cons. int. Explor. Mer.* 178:441-453.
- Houde, E. and J. Lovdal. 1984. Seasonality of occurrence, food, and food preferences of ichthyoplankton in Biscayne Bay, Florida. *Estuarine, Coastal, and Shelf Science* 18: 403 - 419.
- Houde, E. and J. Lovdal 1985. Patterns of variability in ichthyoplankton occurrence and abundance in Biscayne Bay, Florida. *Estuarine, Coastal and Shelf Science* 20: 79 - 103.
- Houde, E. and C. Zastrow. 1993. Ecosystem and taxon-specific dynamic and energetics properties of larval fish assemblages. *Bulletin of Marine Science* 53: 290-335.
- Houser, D. and D. Allen 1996. Zooplankton dynamics in an intertidal salt marsh basin. *Estuaries* 19: 659-73.
- Hunter, J.R. 1981. Feeding ecology and predation of marine fish larvae. pp. 33 - 77. In: Lasker, R. (ed) *Marine Fish Larvae: Morphology, Ecology, and Relation to Fisheries*. Washington Sea Grant Program, University of Washington, Seattle, Washington.
- Janssen, J. 1981. Searching for zooplankton just outside Snell's window. *Limnology and Oceanography*. 26: 1168-71.
- Jenkins, G. 1987. Comparative diets, prey selection, and predatory impact of co-occurring larvae of two flounder species. *Journal of Experimental Marine Biology and Ecology*. 110: 147-170.
- Jenkins, G. 1988. Micro- and fine-scale distribution of microplankton in the feeding environment of larval flounder. *Marine Ecology Progress Series* 43: 233-44.
- Johannes, R. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes*. 3:65-84.

- Kennedy, V. 1996. Biology of larvae and spat. pp. 371 - 421. In: Kennedy, V., Newell, R., and A. Eble (eds.) *The Eastern Oyster Crassostrea virginica*. Maryland Sea Grant, College Park, Maryland.
- Kennedy, V., Newell, R., and A. Eble. 1996. *The Eastern Oyster Crassostrea virginica*. Maryland Sea Grant, College Park, Maryland, 734 p.
- Kingsford, M. and J. Choat. 1989. Horizontal distribution patterns of presettlement reef fish: are they influenced by the proximity of reefs? *Marine Biology*. 101: 285-297.
- Kobayashi, D. 1989. Fine-scale distribution of larval fishes: patterns and process adjacent to coral reefs in Kaneohe Bay, Hawaii. *Marine Biology*. 100: 285-293.
- Laprise, R. and J. Dodson 1994. Environmental variability as a factor controlling spatial patterns in distribution and species diversity of zooplankton in the St. Lawrence estuary. *Marine Ecology Progress Series* 107: 67-81.
- Lara, M. 1999. Sensory development in settlement-stage larvae of Caribbean Labrids and Scarids - A comparative study with implications for ecomorphology and life history strategies. Doctoral Dissertation, College of William and Mary, Williamsburg, Virginia.
- Laurence, G. 1977. A bioenergetic model for the analysis of feeding and survival potential of winter flounder, *Pseudopleuronectes americanus*, larvae during the period from hatching to metamorphosis. *Fishery Bulletin, U.S.* 73(3): 529-546.
- Lassuy, D.R. 1980. Effects of "farming" behavior by *Eupomacentrus lividus* and *Hemiglyphidion plagiometopon* on algal community structure. *Bulletin of Marine Science*. 30: 304-312.
- Lechowicz, M. 1982. The sampling characteristics of electivity indices. *Oecologia*. 52:22-30.
- Lee, W.Y. and B. J. McAlice 1979. Sampling variability of marine zooplankton in a tidal estuary. *Estuarine and Coastal Marine Science* 8: 565 - 582.

- Leis, J. 1986. Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. *Marine Biology*. 90: 505-516.
- Leis, J. 1991. The pelagic stage of coral reef fishes: the larval biology of coral reef fishes. pp. 183-230. In: Sale, P. (ed.). *The ecology of fishes on coral reefs*. Academic Press, Inc.
- Levitan, D. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biological Bulletin* 181: 261 - 268.
- Li-Cor, Inc. 1979. Radiation Measurements. RMR2-10284. Li-Cor, Inc./Li-Cor, Ltd.
- Lindberg, J. and S. Doroshov. 1986. Effect of diet switch between natural and prepared foods on growth and survival of white sturgeon juveniles. *Transactions of the American Fisheries Society*. 115: 166-171.
- Lonsdale, D. and B. Coull 1977. Composition and seasonality of zooplankton of North Inlet, South Carolina. *Chesapeake Science* 18: 272-283.
- Luckenbach, M., R. Mann, and J.A. Wesson. 1999. Oyster reef habitat restoration. A synopsis and synthesis of approaches. Virginia Institute of Marine Science Press.
- Mallin, M. 1991. Zooplankton abundance and community structure in a mesohaline North Carolina estuary. *Estuaries* 14: 481-88.
- Mann, R. 1988. Distribution of bivalve larvae at a frontal system in the James River, Virginia. *Marine Ecology Progress Series* 50: 29 - 44.
- Mann, R. 2000. Restoring The Oyster Reef Communities In Chesapeake Bay: A Commentary. *Journal of Shellfish Research*. In Press.
- Mann, R. and C.Wolf. 1983. Swimming behavior of larvae of the ocean quahog *Arctica islandica* in response to pressure and temperature. *Marine Ecology Progress Series*. 13: 211-218.

- Mann, R. and J. Rainer. 1990. Effect of decreasing oxygen tension on swimming rate of *Crassostrea virginica* (Gmelin, 1791) larvae. *Journal of Shellfish Research*. 9:323 - 327.
- Mann, R., B. Campos, and M. Luckenbach. 1991. Swimming rate and responses of larvae of three mactrid bivalves to salinity discontinuities. *Marine Ecology Progress Series*. 68: 257-269.
- Mann, R., Burreson, G., Evans, D., and D. Weiss. 1995. A stock recruit model of the James River oyster fishery. Final report submitted to the NOAA Oyster Disease Program, State, Federal and Constituent Programs Division, National Marine Fisheries Service, Northeast Region, Gloucester, MA.
- Mann, R. and J. Wesson. 1996a. Evaluation of oyster settlement and survival on large scale intertidal oyster reefs in Virginia. Final report submitted to the Virginia Department of Environmental Quality, Virginia Coastal Resource Management Program, Richmond, Virginia.
- Mann, R. and J. Wesson. 1996b. Fishery independent standing stock surveys of oyster populations in Virginia. Annual report submitted to NOAA, Chesapeake Bay Office, National Marine Fisheries Service, Annapolis, Maryland.
- Mann, R., Perkins, F., Wesson, J., and I. Bartol. 1996. Intertidal oyster reefs as a tool for estuarine rehabilitation and rejuvenation of the Virginia oyster fishery. Final report submitted to Department of Environmental Quality, Virginia Coastal Resource Management Program, Richmond, Virginia.
- Mann, R. and J. Harding. 1997. Trophic studies on "restored" oyster reefs. Annual report submitted to U.S. EPA Chesapeake Bay Program, Annapolis, Maryland.
- Mann, R. and J. Harding. 1998. Continuing trophic studies on "restored" oyster reefs. Annual report submitted to U.S. EPA Chesapeake Bay Program, Annapolis, Maryland.

- Mann, R. and D. Evans. 1998. Estimation of oyster, *Crassostrea virginica*, standing stock, larval production, and advective loss in relation to observed recruitment in the James River, Virginia. *Journal of Shellfish Research* 17: 239-253.
- Mapstone, B. and A. Fowler. 1988. Recruitment and the structure of assemblages of fish on coral reefs. *Trends Ecol. Evol.* 3(3): 72-77.
- Markle, D. F. and G.C. Grant. 1970. The summer food habits of young-of-the-year striped bass in three Virginia rivers. *Chesapeake Science* 11:50-54.
- Marliave, J. 1977. Substratum preferences of settling larvae of marine fishes reared in the laboratory. *Journal of Experimental Marine Biology and Ecology.* 27: 47-60.
- Marliave, J. 1986. Lack of planktonic dispersal of rocky intertidal fish larvae. *Transactions of the American Fisheries Society.* 115: 149-154.
- Massmann, W., Norcross, J. and E. Joseph. 1963. Distribution of larvae of the naked goby, *Gobiosoma bosc*, in the York River. *Chesapeake Science* 4: 120 - 25.
- Mathias, J. and S. Li. 1982. Feeding habits of walleye larvae and juveniles: comparative laboratory and field studies. *Transactions of the American Fisheries Society.* 111: 722-735.
- McGovern, J. and J. Olney 1996. Factors affecting survival of early life stages and subsequent recruitment of striped bass on the Pamunkey River, Virginia. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 1713-1726.
- McHugh, J. 1967. Estuarine nekton. pp. 581-620. In: G. Lauff (ed.) *Estuaries*. American Association for the Advancement of Science. Pub. No. 83.
- Mileikovsky, S. 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. *Marine Biology.* 23: 11-17.
- Mills, E., D. Widzowski and S. Jones. 1987. Food conditioning and prey selection by young yellow perch (*Perca flavens*). *Canadian Journal of Fisheries and Aquatic Science.* 44: 549-555.

- Minchin, P. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 67: 1167-1179.
- Minello, T. and G. Matthews 1981. Variability of zooplankton tows in a shallow estuary. *Contributions in Marine Science* 24: 81-92.
- Minello, T. J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. pp. 43-75. In: L. Benaka, (ed). *Fish habitat: essential fish habitat and rehabilitation*. American Fisheries Society, Symposium 22, Bethesda, Maryland.
- Minitab 10.5. 1995. Minitab 10Xtra user's guide. Minitab Inc., State College, PA. 298 p.
- Mohlenberg, F. 1987. A submersible net pump for quantitative sampling, comparison with conventional net sampling. *Ophelia* 27: 101-110.
- Montgomery, W.L. 1980. The impact of non-selective grazing by the giant blue damselfish, *Microspathodon dorsalis*, on algal communities in the Gulf of California, Mexico. *Bulletin of Marine Science*. 30: 290-303.
- Morales-Alamo, R. and R. Mann 1997. The status of Virginia's public oyster resource 1996. *Virginia Marine Resource Report 97-5*. Virginia Institute of Marine Science, Gloucester Point, Virginia. 46 p.
- Morales-Alamo, R. and R. Mann 1998. The status of Virginia's public oyster resource 1997. *Virginia Marine Resource Report 98-2*. Virginia Institute of Marine Science, Gloucester Point, Virginia. 49 p.
- Morgan, S. 1995. Life and death in the plankton: larval mortality and adaptation. pp 279-321. In : Larry McEdward (ed). *Ecology of marine invertebrate larvae*. CRC Press, Inc., Boca Raton, Florida.
- Munk, P. and T. Kiorboe. 1985. Feeding behavior and swimming activity of larval herring (*Clupea harengus*) in relation to density of copepod nauplii. *Marine Ecology Progress Series*. 24: 15-21.

- Munk, P., T. Kiorboe, and V. Christensen. 1989. Vertical migration of herring *Clupea harengus*, larvae in relation to light and prey distribution. *Environmental Biology of Fishes*. 26: 87 - 96.
- Musick, J. A. 1972. Fishes of the Chesapeake Bay and the adjacent coastal plain. pp. 175-212. In: M. Wass (ed.) A check list of the biota of Lower Chesapeake Bay. Virginia Institute of Marine Science Special Scientific Report No. 65. Gloucester Point, Virginia 23062.
- National Marine Fisheries Service (NMFS) 1997. Magnuson-Stevens Act provisions: essential fish habitat: interim final rule and request for comments. *Federal Register* [Docket 9610303007238-04; I.D. 120996A]: 66531-66559.
- Nero, L. 1976. The natural history of the naked goby *Gobiosoma bosc* (Perciformes: Gobiidae). M.S. Thesis, Old Dominion University, Norfolk, Virginia. 85 p.
- Newell, R. 1988. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica*? 536-546. In Lynch, M.P. and J.A. Mihursky (eds.). *Understanding the Estuary: Advances in Chesapeake Bay research*. Chesapeake Research Consortium Publication 129.
- O'Beirn, F., Luckenbach, M., Mann, R., Harding, J. and J. Nestlerode. 1999. Ecological functions of constructed oyster reefs along an environmental gradient in Chesapeake Bay. Annual report submitted to U.S. EPA Chesapeake Bay Program, Annapolis, MD 21043.
- Olney, J. 1983. Eggs and early larvae of the bay anchovy *Anchoa mitchilli* and the weakfish *Cynoscion regalis* in lower Chesapeake Bay with notes on associated ichthyoplankton. *Estuaries* 6:173 - 180.
- Olney, J. and G. Boehlert. 1988. Nearshore ichthyoplankton associated with seagrass beds in the lower Chesapeake Bay. *Marine Ecology Progress Series*. 45:33-43.



- Olney, J.E. 1996. Community structure, small scale patchiness, transport, and feeding of larval fishes in an estuarine plume. Doctoral Dissertation, University of Maryland, College Park, Maryland. 242 p.
- Owen, R. 1989. Microscale and finescale variations of small plankton in coastal and pelagic environments. *Journal of Marine Research* 47: 197 - 240.
- Paine, R. 1969. A note on trophic complexity and community stability. *American Naturalist*. 103: 91-93.
- Pankhurst, P. and P. Hilder. 1998. Effect of light intensity on feeding of striped trumpeter *Latris lineata* larvae. *Marine and Freshwater Research*. 49: 363-368.
- Pearre, S. 1982. Estimating prey preference by predators: use of various indices and a proposal of another based on chi-square. *Canadian Journal of Fisheries and Aquatic Science*. 39: 914-923.
- Poling, K. and L. Fuiman. 1997. Sensory development and concurrent behavior changes in Atlantic croaker larvae. *Journal of Fish Biology*. 51: 402-421.
- Pritchard, D. 1953. Distribution of oyster larvae in relation to hydrographic conditions. *Proc. Gulf Carib. Fish Instit.* 1952: 123-32.
- Rainer, J. and R. Mann. 1992. A comparison of methods for calculating condition in oysters (*Crassostrea virginica*, Gmelin) with commentary on the relative values of condition indices based on dry meat: shell cavity volumes and dry meat: dry shell weights. *Journal of Shellfish Research*. 11(1): 53 - 56.
- Raynie, R. and R. Shaw. 1994. Ichthyoplankton abundance along a recruitment corridor from offshore spawning to estuarine nursery grounds. *Estuarine, Coastal, and Shelf Science*. 39: 421-450.
- Rheinhardt, R. and R. Mann. 1990. Development of epibenthic fouling communities on a natural oyster bed in the James River, Virginia. *Biofouling* 2: 13 - 25.
- Roberts, C. M. and R. F. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series* 41: 1- 8.

- Robertson, R. 1991. The role of adult biology in timing of spawning of tropical reef fishes. pp. 356-386. In: Sale, P. (ed.). The ecology of fishes on coral reefs. Academic Press, Inc.
- Robichaud-LeBlanc, K.A., S.C. Courtenay, and J. M. Hanson 1997. Ontogenic diet shifts from age-0 striped bass, *Morone saxatilis*, from the Mirimichi River estuary, Gulf of St. Lawrence. *Canadian Journal of Zoology* 75: 1399-1309.
- Robinson, F. and J. Tash. 1979. Feeding by Arizona trout (*Salmo apache*) and brown trout (*Salmo trutta*) at different light intensities. *Environmental Biology of Fishes*. 4:363-368.
- Sale, P. 1970. Distribution of larval acanthuridae off Hawaii. *Copeia*. 1970(4): 765-766.
- Sale, P. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist*. 111: 337 - 359.
- Sale, P. 1980. The ecology of fishes on coral reefs. *Oceanogra. Mar. Biol. Ann. Rev.* 18: 367-421.
- Sameoto, D. 1975. Tidal and diurnal effects of zooplankton sample variability in a nearshore marine environment. *Journal of the Fisheries Research Board of Canada*. 32: 347-366.
- Schmitt, R. 1999. Essential fish habitat: opportunities and challenges for the next millennium. pp. 3-1. In: L. Benaka (ed). Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Symposium 22, Bethesda, Maryland.
- Shand, J. 1997. Ontogenetic changes in retinal structure and visual acuity: a comparative study of coral reef teleosts with differing post-settlement lifestyles. *Environmental Biology of Fishes*. 49: 307-322.
- Shenker, J., Hepner, D., Frere, P., Currence, L. and W. Wakefield. 1983. Upriver migration and abundance of naked goby (*Gobiosoma bosc*) larvae in the Patuxent River estuary, Maryland. *Estuaries* 6: 36 - 42.

- Shepherd, J. G. and D.H. Cushing. 1980. A mechanism for density dependent survival of larval fish as the basis for a stock-recruitment relationship. *J. Cons. Int. Explor. Mer.* 39: 160 - 67.
- Shumway, S. 1996. Natural environmental factors. pp.467 - 514. In: Kennedy, V., Newell, R., and A. Eble (eds.) *The Eastern Oyster Crassostrea virginica*. Maryland Sea Grant, College Park, Maryland.
- Similauer, P. 1998. CANODRAW version 3.1. Ceske Budejovice, Czech Republic.
- Smith, L., C. Miller, and R. Holton 1976. Small-scale horizontal distribution of coastal copepods. *Journal of Experimental Marine Biology and Ecology* 23: 241-253.
- Smith, W., J. Sibunka, and A. Wells. 1978. Diel movements of larval yellowtail flounder, *Limanda ferruginea*, determined from discrete depth sampling. *Fishery Bulletin, U.S.* 76:167178.
- Southworth, M. 1998. Oyster reef broodstock enhancement in the Great Wicomico River, Virginia. M.S. Thesis, Virginia Institute of Marine Science/School of Marine Science, College of William and Mary, Williamsburg, VA. 95 p.
- Southworth, M. and R. Mann. 1999. Oyster reef broodstock enhancement in the Great Wicomico River, Virginia. *Journal of Shellfish Research*. 17(4):1101-1114.
- Stoecker, D. and J. Govoni. 1984. Food selection by young larval gulf menhaden (*Brevoortia patronus*). *Marine Biology*. 80: 299-306.
- Stubblefield, C., C.Lascara, and M. Vecchione 1984. Vertical distribution of zooplankton in a shallow turbid estuary. *Contributions in Marine Science* 27: 93-104.
- Sweatman, H. and J. St. John. 1990. Effects of selective settlement and of aggression by residents on distribution of young recruits of two tropical damselfishes. *Marine Biology*. 105:247-252.
- ter Braak, C. 1995. Ordination. In: *Data analysis in community and landscape ecology*. R. Jongman, C. ter Braak, and O. Van Tongeren, editors. Cambridge University Press, Cambridge, England. p. 91-173.

- ter Braak, C. 1998. CANOCO software.
- Thayer, G., D. Hoss, M. Kjelson, W. Hettler, Jr., and M. Lacroix 1974. Biomass of zooplankton in the Newport River estuary and influence of postlarval fishes. *Chesapeake Science* 15: 9-16.
- Thompson, R., Newell, R., Kennedy, V., and R. Mann. 1996. Reproductive processes and early development. In: V. Kennedy, R. Newell, and A. Rosenfield (eds.). *Biology, culture and management of the American Oyster*. University of Maryland Sea Grant Press, College Park, Maryland.
- Townsend, C. and A. Risebrow. 1982. The influence of light level on the functional response of a zooplanktivorous fish. *Oecologia*. 53: 293-95.
- Turner, J. 1982. The annual cycle of zooplankton in a Long Island estuary. *Estuaries* 5: 261-274.
- Van Duren, L. and J. Videler. 1995. Swimming behavior of developmental stages of the calanoid copepod *Temora longicornis* at different food concentrations. *Marine Ecology Progress Series*. 126: 153-161.
- Van Guelpen, L., D. F. Markle and D. J. Duggan 1982. An evaluation of accuracy, precision, and speed of several zooplankton subsampling techniques. *J. Const. Int. Explor. Mer.* 40: 226 - 236.
- Vecchione, M. 1987. Variability in the distribution of late-stage oyster larvae in the Calcasieu Estuary. *Contrib. Mar. Sci.* 30: 77-90.
- Victor, B. 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecological Monographs*. 56(2): 145-160.
- Wells, H. 1961. The fauna of oyster beds, with special reference to the salinity factor. *Ecological Monographs* 31: 239 - 266.
- Weinstein, J. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fishery Bulletin, U.S.* 77(2): 339-357.

- Weinstein, M., S. Weiss, R. Hodson, and L. Gerry. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. *Fishery Bulletin, U.S.* 78: 419-435.
- Wenner, E., H. Beatty, and L. Coen. 1996. A method for quantitatively sampling nekton on intertidal oyster reefs. *Journal of Shellfish Research.* 15: 769-775.
- Whittaker, R. 1953. A consideration of climax theory: the climax as population and pattern. *Ecological Monographs.* 23: 41-78.
- Widdows, J., R. Newell, and R. Mann. 1989. Effects of hypoxia and anoxia on survival, energy metabolism, and feeding of oyster larvae (*Crassostrea virginica*, Gmelin). *Biological Bulletin.* 177:154-166.
- Wiebe, P. 1970. Small-scale spatial distribution in oceanic zooplankton. *Limnology and Oceanography* 15: 205-217.
- Woolridge, T. and T. Erasmus 1980. Utilization of tidal currents by estuarine zooplankton. *Estuarine and Coastal Marine Science* 11: 107-114.
- Zar, J. 1996. *Biostatistical Analysis*, 3rd edition. Prentice Hall, NJ. 662 p.

## VITA

- January 25, 1968**      **Born Melbourne, Florida**
- April 1986**            **Graduated from Martin Spalding High School, Severn, Maryland**
- **Marion Burke Knott Scholar**
- April 1990**            **B.S. (Biology), University of Dayton, Dayton, Ohio**
- **University Honors Program**
  - **Honors Thesis: Effects of season on rates of filter feeding in a northern population of the Asiatic clam, *Corbicula fluminea*.**
  - **Bro. Russell A. Joly Award, Class of 1990**
- April 1992**            **M.S. (Biology), University of Dayton, Dayton, Ohio**
- **Masters Thesis: Habitat preferences of Rainbow Darters (*Etheostoma caeruleum*) in a central Ohio river with regard to water column and benthic flow.**
  - **Teaching Assistant, Department of Biology**
- May 2000**             **Ph.D. (Marine Science), Virginia Institute of Marine Science/  
School of Marine Science, College of William and Mary,  
Williamsburg, Virginia**
- **Dissertation: Ecological interactions between benthic oyster reef fishes and oysters**
  - **Thatcher Award nominee, School of Marine Science**