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# VIRGINIA RECREATIONAL FISHING DEVELOPMENT FUND
# SUMMARY PROJECT APPLICATION*

| **NAME AND ADDRESS OF APPLICANT:** | **PROJECT LEADER (name, phone, e-mail):** |
|---|---|
| Department of Biological Sciences<br>Virginia Institute of Marine Sciences<br>PO Box 1346<br>Gloucester Point, VA 23062-1346 | J. Emmett Duffy (804-684-7369, jeduffy@vims.edu)<br>Robert J. Latour (804-684-7312, latour@vims.edu)<br>Jacques van Montfrans (804-684-7391, vanm@vims.edu) |
| **PRIORITY AREA OF CONCERN:** | **PROJECT LOCATION:** |
| Research | Lower Chesapeake Bay, VIMS |

**DESCRIPTIVE TITLE OF PROJECT:**

**Submerged Aquatic Vegetation (SAV) as essential fish habitat in lower Chesapeake Bay: Linking variation in SAV, forage animal production, and sportfish abundance**

**PROJECT SUMMARY:**

Seagrass habitats are widely recognized as providing essential fish habitat. In Virginia, seagrass beds provide food and shelter for several important sportfishes, including (among others) spotted seatrout, Atlantic croaker, red drum, summer flounder, striped bass, and grey trout. Yet the reasons for this habitat value are known only vaguely. This project will employ intensive field sampling, diet analysis, and statistical modeling to quantify food-chain links from seagrass or algae, through benthic invertebrates and small fishes, to recreationally and commercially important predatory fishes, and to characterize seasonal and among-bed variation in these interactions. Clarifying the critical but poorly understood role of small invertebrate communities in channeling primary production to predatory fishes is central to understanding how and why SAV habitats are essential to fish production. These data will help understand why SAV beds vary in fish productivity, and enable resource managers to make informed decisions related to ecosystem-based management of SAV habitats and their associated fish populations in the Chesapeake Bay.

**EXPECTED BENEFITS:**

This research will benefit recreational fisheries for several species in Virginia estuarine and coastal waters by providing a more complete mechanistic understanding of the widely recognized, but poorly understood, link between submerged aquatic vegetation, epifaunal invertebrate communities, and fish production. A novel aspect of this work is its focus on identifying the mechanisms behind previously documented, strong variation in fish production among superficially similar seagrass beds in Chesapeake Bay.

**COSTS:**

**VMRC Funding: $69,268**
**Recipient Funding: $32,616**
**Total Costs: $101,884**

**Detailed budget is included with proposal.**

**Proposal: RFAB 2006**
PIs: Duffy, Latour, van Montfrans

## Submerged Aquatic Vegetation (SAV) as essential fish habitat in lower Chesapeake Bay: Linking variation in SAV, forage animal production, and sportfish abundance

| | RFAB | VIMS | TOTAL |
|---|---|---|---|
| **A. SENIOR PERSONNEL** | | | |
| PI: Duffy (12%) | 4,463 | 4,463 | 8,927 |
| PI: Latour (9%/3%) | 4,456 | 1,127 | 5,583 |
| PI: van Montfrans (12%) | | 6,134 | 6,134 |
| **B. OTHER PERSONNEL** | | | |
| Graduate student (1) | 8,450 | | 8,450 |
| Technician: Duffy (6 mo) | 18,000 | | 18,000 |
| Technician: van Montfrans (4 mo - hrly) | 6,000 | | 6,000 |
| **C. FRINGE BENEFITS** | 8,535 | 3,517 | 12,052 |
| **TOTAL, PERSONNEL COSTS** | **49,904** | **15,242** | **12,052** |
| **D. EQUIPMENT** | 0 | | 0 |
| **E. TRAVEL** | 750 | | 750 |
| VIMS truck (mileage, tolls) for field sampling | | | |
| **G. OTHER DIRECT COSTS** | | | |
| 1. Materials and supplies | 1,500 | | 1,500 |
| 2. stable isotope analysis (250 @$8) | 2,000 | | 2,000 |
| 4. Vessels (14 days @ $90/d) | 1,260 | | 1,260 |
| **H. TOTAL DIRECT COSTS** | **55,414** | **15,242** | **70,656** |
| **I. INDIRECT COSTS** | **13,854** | **17,375** | **31,228** |
| **J. TOTAL DIRECT & INDIRECT** | **69,268** | **32,616** | **101,884** |

## Supply list for Duffy et al RFAB proposal

| | |
|---|---|
| **Normalin (10 gal.) for preserving stomachs:** | **$220** |
| **Gut bags for fish stomachs (500 ea):** | **$132** |
| **5 gal buckets and lids (10 @ 2.50ea)** | **$ 25** |
| **YSI Oxygen sensor membrane kit:** | **$ 22** |
| **Whirlpacs (500 for otoliths; fish aging):** | **$ 46** |
| **5 slide boxes (hold 100 slides each)** | **$ 60** |
| **Case of slides (fish aging)** | **$150** |
| **Isomet saw blades (3” and 4” blades, 1/3 cost, shared)** | **$266** |
| **Crystal bond 509 clear (2 sticks; $30/stick; fish aging)** | **$ 60** |
| **RE pipette cap (replacement)** | **$ 35** |
| **Glass fiber filters (chlorophyll analysis; 200 @ $45/100)** | **$ 90** |
| **Acetone (chlorophyll analysis)** | **$ 40** |
| **Acrodiscs (chlorophyll analysis; 20 ea)** | **$100** |
| **Shell vials for isotope analysis (case of 500):** | **$120** |
| **Misc field and lab supplies (Ziploc bags, coolers, mesh bags, batteries etc.)** | **$134** |

Proposal Submission to

Virginia Recreational Fishing Advisory Board

By

THE VIRGINIA INSTITUTE OF MARINE SCIENCE
COLLEGE OF WILLIAM AND MARY

**SUBMERGED AQUATIC VEGETATION (SAV) AS ESSENTIAL FISH HABITAT IN LOWER CHESAPEAKE BAY: LINKING VARIATION IN SAV, FORAGE ANIMAL PRODUCTION, AND SPORTFISH ABUNDANCE**

J. Emmett Duffy
Co-Principal Investigator

Robert Latour
Co-Principal Investigator

Jacques van Montfrans
Co-Principal Investigator

J. Emmett Duffy
Chair, Department of Biological Sciences

John Graves
Chair, Department of Fisheries Science

Jane A. Lopez
Director, Sponsored Programs

Roger L. Mann
Director for Research and Advisory Services

15 June 2006

**Submerged Aquatic Vegetation (SAV) as essential fish habitat in lower Chesapeake Bay: Linking variation in SAV, forage animal production, and sportfish abundance**

## Need

A crucial issue in fishery ecology is the role of habitat quality in the population dynamics of recreationally, commercially, or ecologically valuable species. Many fish species rely on specific habitats during some phase of their life cycle because these habitats enhance survival, growth and/or reproduction. In estuarine and coastal marine systems, seagrass beds and other submerged aquatic vegetation (SAV) provide such essential fish habitat to a variety of commercially and recreationally important predatory fish species. The high fishery production in seagrass beds results from complex interactions of target species with the invertebrates and fishes at lower trophic levels that make up the food web. Yet these interactions are understood only in broad, qualitative outline. Identifying and quantifying the food-chain links by which seagrass or algae and invertebrates support production of recreationally, commercially, and ecologically important predators is critical to explaining known variation among SAV beds in fish production, and the responses of important fisheries to environmental disturbances mediated through the food web. Such understanding will enable resource managers to make informed decisions related to ecosystem-based management with specific relevance to SAV habitats.

## Background

The widely recognized value of seagrass habitats for fishery production stems from both high primary production by algae and seagrasses, which provide food for higher trophic levels, and from the physical structure of seagrasses, which provides shelter that allows fishes to escape their own predators during vulnerable juvenile stages (Thayer et al. 1978, Heck and Orth 1980, Klumpp et al. 1989, Heck et al. 2003). Numerous studies in recent decades have shown that the primary food sources of fishes associated with submerged vegetation are small crustaceans, including amphipods, isopods, shrimp, and small crabs (e.g., Adams 1976, Klumpp et al. 1989).

Although the importance of crustaceans to high fish productivity seems clear, the trophic pathways mediating this transfer are understood only in broad outline. The small grazing invertebrates that dominate intermediate trophic levels are among the least understood components of aquatic food webs, and can be considered the "black box in the middle" of the food web. Several lines of evidence support the central role of small invertebrate grazers in both community dynamics and flow of energy and materials in aquatic ecosystems. First, energetic analyses of seagrass beds (Kikuchi 1974, Edgar and Shaw 1995) and rocky reef communities (Taylor 1998) indicate that production by small crustaceans is the most important predictor of fish production in vegetated aquatic systems. Second, epifaunal and infaunal invertebrates are the most highly connected trophic group in food webs of the Chesapeake Bay (Lipcius et al. 2005), and in many other aquatic food webs. Third, epifaunal crustaceans have been found packing the stomachs of normally piscivorous apex predators such as striped bass in Chesapeake Bay (van Montfrans and Latour, unpublished). Finally, certain grazing amphipod species have disproportionately high biomass-specific impacts on their algal resource, potentially qualifying them as ecologically important "keystone species" (Duffy and Hay 2000) and hinting that changing predation pressure on them may have important ripple effects through the remaining community (e.g., Duffy et al. 2005). All of these considerations indicate that small crustaceans form the critical intermediate link between submerged aquatic vegetation and fish production, and that trophic interactions involving these intermediate trophic levels will strongly influence how environmental impacts propagate through the food web to influence fish production (Valentine and Duffy 2006).

Aquatic food-web studies often lump lower and intermediate trophic levels into a few broad groups such as "benthos" and "plankton" (e.g., Fisheries Ecosystem Plan). Yet species composition of these animals varies considerably among sites and through the seasons. Moreover, field research and experimental studies show that common epifaunal crustaceans of Chesapeake eelgrass beds differ strongly in grazing rate, population productivity, and vulnerability to predation (Fredette et al. 1990, Duffy et al. 2001, 2003, 2005). These data suggest that variation among seagrass beds, and through the seasons, in species composition of epifauna may strongly influence the abundance and productivity of fishes. Indirect evidence for the importance of particular forage species comes from stable isotope studies by van Montfrans et al. (unpublished) in coastal bays of the Eastern Shore, who showed that the seagrass-associated isopod *Erichsonella* sp., along with amphipods and mud crabs, was an important dietary source for many fishes, including silver perch (*Bairdiella chrysoura*), pig fish (*Orthopristes chrysoptera*), tautog (*Tautoga onitus*), and Northern pipe fish (*Syngnathus fuscus*), which in turn are important links to recreationally important predators such as spotted seatrout (*Cynoscion nebulosus*) and striped bass (*Morone saxatilis*). Thus, the factors determining abundance of these small crustaceans may have important consequences for fish production and fisheries management.

The importance of spatial variation in food web interactions and epifaunal community composition is illustrated by recent findings that spotted trout can be traced via otolith chemistry to specific seagrass beds separated by as little as 15 km (Dorval et al. 2005 a,b). This tracer approach holds strong promise for determining which specific seagrass habitats contribute most to production of spotted seatrout, and in turn to uncovering what characteristics of those particular habitats are responsible. In this proposal, we focus on critical intermediate links in the food chain as one important such characteristic and address how variation in community composition and abundance of these lower trophic levels may influence variation among beds in fish production and population dynamics. The results of this study will contribute directly to ecosystem-based approaches to fisheries management by providing valuable information on the food web dynamics of fishes in Chesapeake Bay across temporal (i.e., seasonal) and spatial (i.e., habitat-specific) scales.

## Objectives

The goal of the proposed study is to conduct field and modeling research to identify and rigorously quantify the links from seagrass habitat, through benthic invertebrate communities, to production of recreationally, commercially, and ecologically important fishes in the Chesapeake Bay. By focusing on the poorly studied invertebrates that form the "black box in the middle" of the food chain, this research will begin to forge the missing mechanistic link between the comparatively well studied submerged aquatic vegetation and recreational fishes, both of which are subjects of important long-term monitoring programs.  Specific goals of the research are to:

1) Intensively characterize spatial and seasonal variation among two selected eelgrass beds in biomass, community composition, and productivity of lower trophic levels.

2) Characterize the diets of seagrass-associated fishes to determine their dependence on small invertebrates and forage fishes, using gut content and stable isotope analyses.

3) Use statistical modeling approaches to identify the role of individual invertebrate species in supporting growth and production of recreationally important predatory fishes and their forage species.

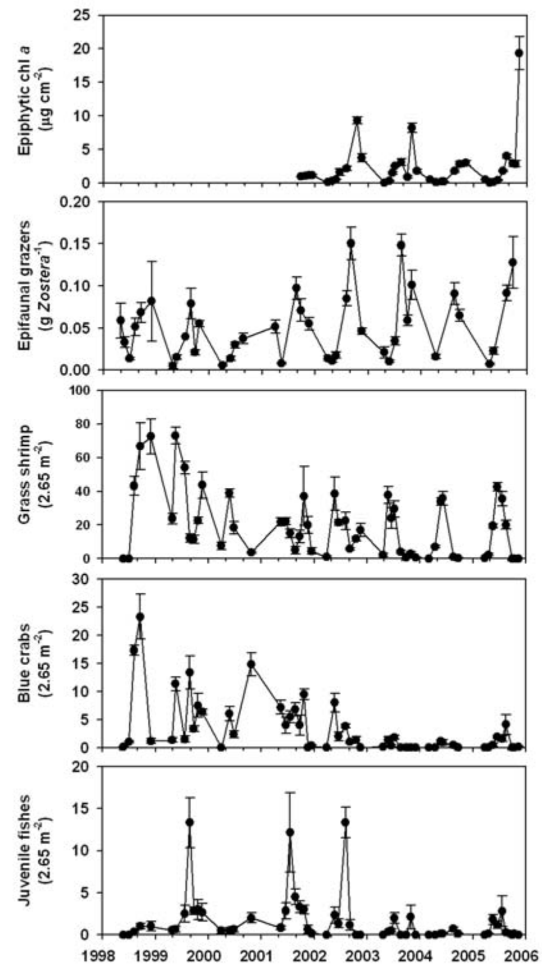

Figure 1.  Time series of three trophic levels at the Goodwin Islands eelgrass bed.

To maximize our power to quantify these links, we will focus on two Chesapeake eelgrass beds that differ strongly in predatory fish abundance. By measuring variation among beds in the abundance, species composition, and productivity of the intermediate links in the food chain, we can evaluate how they mediate variation in abundance and production of recreationally important predatory fishes.

The project will join two ongoing, complementary research programs: one focusing on species composition, abundance/biomass, age- and size-structure, and trophic interactions of larger predatory fishes (Latour and van Montfrans) and the other focusing on these same variables at the lower end of the food web, among invertebrate grazers, small predators, and the algae that support them (Duffy, see Figure 1). Joining these two efforts will allow description of the food web and community dynamics of seagrass-associated fishes in unprecedented detail, and will ultimately provide important components for development of ecosystem-based fisheries management plans.   Intensive field sampling will be conducted in April – June 2007, with processing of samples and analysis of epifaunal community structure, gut contents, stable isotopes, and modeling completed by April 2008, at which time a final project report will be submitted.

**Expected Results or Benefits**

This research will benefit recreational fisheries for several species in Virginia estuarine and coastal waters by providing a more complete mechanistic understanding of the widely recognized, but poorly understood, link between submerged aquatic vegetation, epifaunal invertebrate communities, and fish production. A novel aspect of this work is its focus on identifying the mechanisms behind previously documented, strong variation in fish production among superficially similar seagrass beds in Chesapeake Bay.

**Approach**

1. *Variation in biomass, community composition, and productivity of lower trophic levels*

In each of two SAV beds we will sample SAV cover and biomass as measures of habitat quantity and quality, biomass of epiphytic algae as an estimate of primary production supporting the food chain, and the abundance, species composition, and diets of animals ranging from small epifaunal invertebrates through adult fishes. Samples will be collected twice each month at each site between April, when juvenile and adult fishes begin to enter the estuary, through June. Lower levels of the food web (SAV, epiphytic algae, epifaunal herbivores, carnivorous crustaceans and small fishes) will be sampled using methods used in Duffy's group for several years (see Figure 1). Briefly, we sample each of two 50-m transects parallel to shore, one near the offshore margin and one near the inshore margin of a bed, and measure the following parameters. *Seagrass cover* (N=25 +/- points per transect) and *seagrass biomass* (5 cores/transect) are measured on each date. *Epiphyte biomass* is sampled as chl *a* at N=5 points per transect. *Epifaunal invertebrates* are sampled at five randomly selected locations per bed on each of the inshore and offshore transects, using a mesh-paneled box that closes around the upright seagrass blades and traps associated epifauna inside (e.g. Duffy et al. 2001). Mobile epifauna are further sorted into size classes by passing through a series of nested sieves; empirically derived equations are then used to convert abundance by size class into biomass and, with inclusion of water temperature, to production of these small forage invertebrates (Edgar 1990). *Resident (sedentary) small predators* are sampled quantitatively using standardized dipnet sweeps (5 m long sweep x 0.53 m opening width = 2.65 $m^2$ sampled), 3 sweeps per inshore and offshore transect, for a total of 6 predator samples on each date; small fishes, blue crabs (*Callinectes sapidus*), grass shrimp (*Palaemonetes* spp.), and sand shrimp (*Crangon septemspinosa*), are counted, measured, and all predators are then released.

*Larger transient fish predators*. We will examine in detail the role of lower trophic levels in the food web dynamics of recreational fishes as the spring season progresses and fish enter these shallow habitats to feed. Fish predators will be sampled at high tide during the daytime and at night using a 600 foot long by 8 foot deep trammel net that will be deployed against the shoreline in the shape of an arc from a fast-moving, shallow-draft vessel. At least 2 - 3 net deployments will be made per seagrass bed, depending on bed size. GPS measurements will enable quantification of the area enclosed for deriving fish density estimates after adjusting for sampling efficiency. Sampling will occur around daytime and nocturnal high tide. Subsets of fish from each sample (approx. 10 – 15 randomly selected specimens per species or size-class within a species if necessary) will be processed for length, weight, sex and maturity-at-age determination, stomach contents and aging. Fish processing will occur as soon after capture as possible. Fish sex will be noted and age determined from otolith examination.

2. *Trophic relationships between invertebrates, forage fishes, and predators*

We will estimate trophic positions and diets by collecting and analyzing both gut contents from the most abundant species at all trophic levels, and stable C and N isotope data.

*Gut content analysis*. Immediately following collection (or gut evacuation), animals are frozen in liquid nitrogen. Gut contents of grazing invertebrates and shrimp are blotted on a microscope slide, and a point-count method is used to quantify remains of macroalgae, eelgrass, diatoms (periphyton), crustacean parts, mineral grains, and "detritus" (unidentifiable organic material). Blue crab guts will be analyzed according to Mansour (1992). For fishes, stomachs will be labeled, preserved in "normalin", and prey will be identified to the lowest possible taxon. Prey will be measured, and % number, wet weight and frequency of occurrence will be calculated by prey type.

*Stable isotope analysis*. Whereas gut contents provide a snapshot of an animal's most recent meal, stable isotopes of C,N, and S can provide a complementary time-integrated picture of certain aspects of diet, notably height in the food chain. Isotopic signatures (C and N) of benthic primary producers and seston will be measured to characterize the base of the food web. If these sources differ in $\delta^{13}C$ values, consumers may be traced to certain food sources, because the C isotope fractionation is generally conserved through successive trophic levels. The $\delta^{15}N$ signature allows determination of consumer trophic level, because $\delta^{15}N$ is enriched by a predictable factor (3.4 $\pm$ 1 ppt) with each trophic step (Peterson and Fry 1987). We will calculate consumer trophic level as $\delta + (\delta^{15}N_{organism} - \delta^{15}N_{base\ of\ food\ web})/3.4$, where δ is the trophic position of the base of the food web, i.e. δ =1 for primary producers (Post et al 2000). Formulae are available for determining trophic level of a consumer with multiple food sources that differ in $\delta^{15}N$ signatures (Post et al 2000). As basal food sources, we will sample seston, eelgrass, the most common macroalgal species, and epiphytic microalgae. $\delta^{13}C$, and $\delta^{15}N$ values for several of these food sources have been shown to differ significantly in other estuaries (Currin et al. 1995, Riera et al 1999, Kharlamenko et al. 2001). We will sample ~25 taxa/food web components (N=5 each), near the beginning and end of the sampling period, for a total of ~250 samples. Samples will analyzed by the Stable Isotope Facility, University of California, Davis, using a Europa Scientific Hydra 20/20 continuous flow isotope ratio mass spectrometer and Europa ANCA-SL elemental analyzer to convert organic C and N into CO2 and N2 gas.

3. *Statistical analyses of links between invertebrate species and fish production*

As a first step, we will analyze relationships among taxa in the food web using generalized linear models (GLMs). This class of models is defined by the statistical distribution of the dependent variable (e.g., predatory abundance) and the nature by which a linear combination of a set of explanatory variables (e.g., prey type, water temperature, survey month, salinity, etc.) relate to the expected value of that dependent variable. The structure of a GLM is as follows:

$$g(\mu_i) = \sum_{1}^{p} \mathbf{x}_i \beta_i \qquad (1)$$

where $g$ is a differentiable and monotonic link function (e.g., identity function when the distribution of the response variable is normal, logit when the distribution is binomial, etc.), $\mu_i = E(y_i)$, which is the expected value of the $i^{th}$ dependent variable, $\mathbf{x}_i$ are the $p$ explanatory variables, and $\beta_i$ is the vector of parameters (McCullagh and Nelder 1989).

GLMs can be used to analyze data under a variety of designs, including those containing only categorical explanatory variables (e.g., prey type), those containing only continuous explanatory variables (e.g., water temperature), and those containing both categorical and continuous explanatory variables. Further, mixed-model designs where levels of categorical explanatory variables vary randomly can also be accommodated. We are opting for the GLM approach because this class of models is very powerful and general.

As a second step, we will analyze relationships among taxa in the food web using path analysis. Path analysis is based on multiple regression (Sokal and Rohlf 1981) and begins with a path diagram indicating (1) the potential, directional influences of each predictor variable (e.g., abundance or production of an invertebrate prey species) on the response variable (e.g., spotted seatrout abundance or growth), as well as (2) potential correlations among predictor variables. Path analysis uses a multiple regression approach to estimate a standardized path coefficient (i.e., correlation) for each arrow, allowing all path coefficients to be expressed in comparable, standardized units. The correlation between two variables can be visualized as the sum of the path coefficients between them. Thus, both the relative importance of different predictor variables and their direct vs. indirect influence can be distinguished.

By combining data on consumer field abundance, diet fraction in gut contents, and prey abundance, and making energetic assumptions based on body size and taxonomy, we will estimate interaction strengths (IS) from the field data (e.g., Bascompte et al. 2005). Interaction strength estimated from field data will be compared with our experimental measurements of IS in the corresponding season.

## Location

We will sample in two seagrass beds, one each on the western and eastern shore of the bay, respectively. These beds will be selected on the basis on published research by Dorval et al. (2005 a,b) and on discussions with C. Jones (unpublished data) who has documented habitat-specific growth rates for spotted seatrout in Chesapeake Bay. Sample processing and statistical modeling will occur at the Virginia Institute of Marine Science.

## Estimated Cost

Requested funds will go primarily to support salaries of two skilled technicians and a graduate student, who will conduct most of the labor-intensive work of sorting and processing samples of seagrass invertebrates and fishes, analyzing stomach contents, and preparing tissue samples for stable isotope analysis.

We request VIMS Facilities and Administrative Costs at the reduced rate of 25% of direct costs. VIMS will provide the difference between this figure and the standard institutional rate of 45%.

Salary funds are requested for one month of PI Latour's time, and half of the one month that PI Duffy intends to devote to this project. The remainder of Duffy's salary, all of van Montfrans' salary, and the differential indirect costs will be provided by VIMS as match.

**References Cited**


Adams, S.M. 1976. Feeeding ecology of eelgrass fish communities. *Transactions of the American Fisheries Society* 105:514-519.

Bascompte, J., C.J. Melian, and E. Sala. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences USA* 102:5443-5447.

Currin, C.A., S.Y. Newell, and H.W. Paerl. 1995. The Role of Standing Dead Spartina-Alterniflora and Benthic Microalgae in Salt-Marsh Food Webs - Considerations Based on Multiple Stable-Isotope Analysis. *Marine Ecology-Progress Series* 121:99-116.

Dorval, E., C.M. Jones, R. Hannigan R, et al. 2005. Can otolith chemistry be used for identifying essential seagrass habitats for juvenile spotted seatrout, *Cynoscion nebulosus*, in Chesapeake Bay? *Marine and Freshwater Research* 56: 645-653.

Dorval, E., C.M. Jones, and R. Hannigan. 2005b. Chemistry of surface waters: Distinguishing fine-scale differences in sea grass habitats of Chesapeake Bay. *Limnology and Oceanography* 50:1073-1083.

Duffy, J.E. and M.E. Hay. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs* 70:237-263.

Duffy, J. E., J. P. Richardson and E. A. Canuel. 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters* 6:637-645.

Duffy, J.E., J.P. Richardson, and K.E. France. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecology Letters* 8:301-309.

Duffy, J. E., K. S. Macdonald, J. M. Rhode and J. D. Parker. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82:2417-2434.

Edgar, G.J. 1990. The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *Journal of Experimental Marine Biology and Ecology* 137:195-214.

Edgar, G. J. and C. Shaw. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia. III. General relationships between sediments, seagrasses, invertebrates and fishes. *Journal of Experimental Marine Biology and Ecology* 194:107-131.

Fredette, T.J. et al. 1990. Secondary Production Within a Seagrass Bed (*Zostera marina* and *Ruppia maritima*) in Lower Chesapeake Bay. Estuaries 5:431-440.

Heck K.L., G. Hays, R.J. Orth. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253:123-136.

Heck, K. L., Jr., and R. J. Orth. 1980. Seagrass habitats: The roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages, p. 449-464, *In:* V. S. Kennedy (Ed.), *Estuarine perspectives*. Academic Press, NY.

Kharlamenko, V.I., S.I. Kiyashko, A.B. Imbs, and D.I. Vyshkvartzev. 2001. Identification of food sources of invertebrates from the seagrass Zostera marina community using carbon and sulfur stable isotope ratio and fatty acid analysis. *Marine Ecology Progress Series* 220:103-117.

Kikuchi, T. 1974. Japanese contributions on consumer ecology in eelgrass (*Zostera marina* L.) beds, with special reference to trophic relationships and resources in inshore fisheries. *Aquaculture* 4:145-160.

Klumpp, D. W., R. K. Howard, and D. A. Pollard. 1989. Trophodynamics and nutritional ecology of seagrass communities, p. 394-357, *In*: A.W. D. Larkum, A. J. McComb and S. A. Shepherd (eds.), *Biology of seagrasses*. Elsevier, Amsterdam.

Lipcius, R.N., D.B. Eggleston, K.L. Heck, Jr., R.D. Seitz and J. van Montfrans 2005. Post settlement abundance, survival, and growth of postlarvae and young juvenile blue crabs in nursery habitats. Chapter 13 *In:* Kennedy, V., J. Greer, E. Cronin (*Eds*.) Biology and management of the blue crab. Maryland Sea Grant Press, *in press*.

Mansour, R.A. 1992. Foraging ecology of the blue crab, Callinectes sapidus Rathbun, in lower Chesapeake Bay. Ph.D. Dissertation. Virginia Institute of Marine Science. College of William and Mary. Gloucester Point, Virginia

McCullagh, P. and J. A. Nelder. 1989. Generalized Linear Models. Chapman and Hall, 2nd edition.

Peterson, B.J., Fry, B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18: 293-320.

Post, D.M., Pace, M.L., Hairston, N.G. Jr. 2000. Ecosystem size determines food-chain length in lakes. *Nature* 405: 1047-1049

Riera, P, Stal, LJ, Nieuwenhuize, J., Richard, P., Blanchard, G. and Gentil, F. 1999. Determination of food sources for benthic invertebrates in a salt marsh (Aiguillon Bay, France) by carbon and nitrogen stable isotopes: importance of locally produced sources *Marine Ecology Progress Series* 187:301-307

Sokal, R.R. and F.J. Rohlf. 1981. *Biometry, 2nd edition*. W.H. Freeman and Company.

Thayer, G.W., P.L. Parker, M.W. LaCroix, and B. Fry. 1978. The stable isotope ratio of some components of an eelgrass, *Zostera marina*, bed. Oecologia 35:1-12.

Taylor, R. B. 1998. Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. *Marine Ecology Progress Series* 172:37-51.

Valentine, J.F. and J.E. Duffy. 2006. The central role of grazing in seagrass ecology. In: A.W.D. Larkum, R.J. Orth, and C.M. Duarte (eds). *Seagrasses: Biology, Ecology, and Conservation*. Springer, Amsterdam, pp. 463-501.