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A NEW *IN SITU* METHOD FOR MEASURING SESTON UPTAKE BY SUSPENSION-FEEDING BIVALVE MOLLUSCS

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ABSTRACT The most commonly used methods for measuring the amount of seston removed from the water column (uptake) by populations of suspension-feeding bivalve molluscs involve taking discrete water samples followed by laboratory analyses. Here we describe a new method based on *in situ* fluorometry that provides rapid measurement of seston removal rates. The new system is comprised of two identical units, each consisting of an *in situ* fluorometer, data logger and peristaltic pump with plastic tube attached to a deployment device. The deployment device allows precise placement of the fluorometer probe and intake end of the plastic tube so that *in situ* fluorescence (chlorophyll *a*) can be measured and water can be sampled for seston analyses in the laboratory from the same height. The typical setup involves placing one unit upstream and the other downstream of the study area and sampling the water at periodic intervals. Changes in seston concentration are revealed in the field by the fluorometers, and the sampled water can be analyzed in the laboratory for various seston parameters. Comparisons of the *in situ* data with data from laboratory analyses of pumped water samples were made for three species at four study sites: the eastern oyster (*Crassostrea virginica*), hard clam (*Mercenaria mercenaria*), and blue mussel (*Mytilus edulis*). Comparisons of measured upstream versus downstream seston concentrations indicated significant (*t*-tests, $P < 0.05$) differences (uptake) for six of eight trials based on *in situ* fluorometry, but only marginally significant ($P < 0.10$) differences at two of the four trials using laboratory chlorophyll *a* measurements. These data demonstrate that compared with sampling methods requiring laboratory analyses, the new *in situ* method provides much more rapid quantitative assessments and may provide more accurate estimates.

KEY WORDS: bivalve, fluorometry, seston uptake, suspension-feeding, *Crassostrea*, *Mercenaria*, *Mytilus*

INTRODUCTION

Empirical and theoretical research demonstrates that populations of suspension-feeding bivalve molluscs can remove substantial amounts of suspended particulates (seston) from the overlying water column by their feeding activities (Ulanowicz & Tuttle 1992, Dame 1996, Newell, et al. 2005, Haamer & Rodhe 2000, Cressman et al. 2003, Nelson et al. 2004). This has important implications for shellfish aquaculture and more recently for water quality management associated with shellfish restoration projects (Luckenbach et al. 1999, 2005, Thayer et al. 2005). Field studies on seston uptake typically involve laboratory analysis of discrete water samples obtained manually or by pumps (Dame & Libes 1993, Newell & Shumway 1993, Cressman et al. 2003, Nelson et al. 2004). This approach is effective and it allows the measurement of multiple water parameters. However, there is a need to develop *in situ* approaches that have the potential to greatly increase the spatial and temporal resolution of measurements of the feeding/seston uptake process.

A major impetus for development of the new method is the need for quantitative success metrics for constructed shellfish (mainly oysters) reefs that are part of ongoing restoration programs in many areas. These projects often emphasize the ecological functions of oysters, instead of or at least in addition to, their historical role as a commercial resource (Luckenbach et al. 1999, 2005, Brumbaugh et al. 2000, Coen & Luckenbach 2000). One of the major ecological functions of oyster reefs is their potential influence on water quality because of their filtration capacity (Dame 1996, Dame et al. 2001, French McCay 2003, Peterson et al. 2003). Field studies, however, typically have not demonstrated measurable seston removal by natural (Dame & Libes 1993, Wilson-Ormond et al. 1997) or restored (Nelson et al. 2004) oyster reefs. Cressman et al. (2003) is the only study we are aware of that measured substantial (up to 25%) removal of seston by small intertidal reefs. Hence, there is a need to critically assess this often-cited reason for restoring shellfish reefs (Coen & Luckenbach 2000, Luckenbach et al. 2005). How much of an impact on water quality should be expected from restored shellfish reefs?

Previous research has used *in situ* fluorometry to assess food availability to cultured bivalves (Grant & Bacher 1998) and phytoplankton biomass as part of broader ecological studies (Gregor et al. 2005). However, we are not aware of previous attempts to use *in situ* fluorometry to measure seston uptake by benthic organisms in the field. Here we describe a novel method for directly measuring uptake rates, and the results of field trials involving three bivalve species that compare measurements using the new *in situ* method with laboratory analysis of pumped water samples.

DESCRIPTION OF *IN SITU* FLUOROMETRY APPARATUS

Each apparatus consists of a fluorometer (Seapoint Sensors Model SCF,) with multimeter/datalogger (Extech Model 383,274), and peristaltic pump (Masterflex Model 7533) with 1-cm ID plastic tube attached to a custom-made deployment device (Fig. 1A, B, C). The fluorometer probe is placed within a 5-cm ID PVC pipe that is attached to the bottom plate. The probe and light shield are held in position by a hose clamp on the outside of the PVC pipe; loosening of the clamp allows the light shade and probe to be moved up and down on the pipe and secured at any height above the bottom plate. The bottom plate is designed to rest on the bottom so the fluorometer probe remains at the same height

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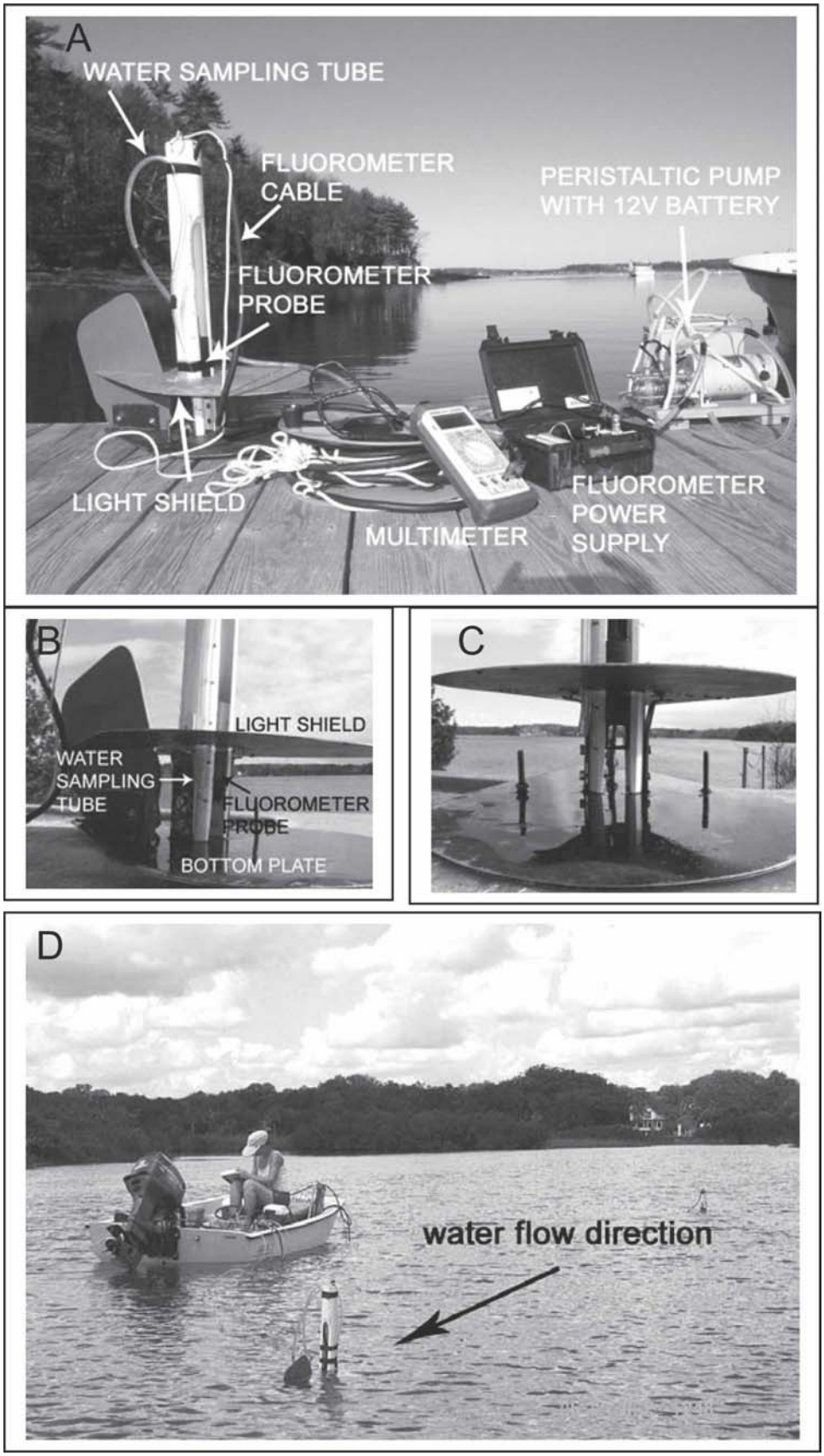

Figure 1. New *in situ* fluorometer and water sampling apparatus. (A) Complete apparatus (one of two identical units); (B) close up oblique view of fluorometer probe in deployment device; (C) close up face-on view; (D) deployment of two identical units over intertidal oyster reef in Florida.

throughout the measurement period, but the entire apparatus can be suspended at any height and moved up and down in the water column as needed. A tail fin attached to the bottom plate orients the probe so that water flows directly through the sensing chamber as it is lowered to the bottom (Fig. 1C). The bottom plate is constructed of 2-mm thick stainless steel sheet material and provides sufficient weight to hold the apparatus in position under most flow conditions. The fluorometer probe and the end of the water intake tube are placed at the same height so that comparisons can be made between *in situ* fluorescence (chlorophyll *a*) and laboratory analysis of pumped water. Total cost of each unit is about $5,000 (2006 US$).

The typical setup involves placing one apparatus upstream and another downstream of the study population and sampling the water at periodic intervals (Fig. 1D). To be sure the downstream apparatus is exposed to the same water mass as the upstream apparatus, a floating object is released periodically from the upstream position to show the ambient water flow path across the reef. Adjustments in location of either device, including raising the apparatus to allow the tail fin to reorient the probe with respect to water flow direction, can be made as needed. Changes in seston concentration caused by bivalve feeding ("seston uptake") are revealed immediately by differences in the two fluorometer readings (upstream vs. downstream), and the sampled water can be analyzed for various parameters to verify the fluorometry and provide additional data on changes in seston characteristics.

MATERIALS AND METHODS

Populations of bivalve molluscs were studied at sites in New Hampshire (a blue mussel, *Mytilus edulis*, reef), Virginia (hard clam, *Mercenaria mercenaria*, beds at an aquaculture farm), South Carolina (a restored eastern oyster, *Crassostrea virginica*, reef), and midAtlantic Florida (several natural eastern oyster reefs). Table 1 summarizes the environmental characteristics of the study sites, and the measured seston uptake rates. Sites were chosen because they met two criteria: (1) water less than ~1.5 m deep and (2) water flow constrained laterally, or width-to-length ratio sufficient to minimize lateral transport across the width of the sampled area. Meeting these criteria would likely result in environmental conditions (e.g., well mixed water column) that would allow sampling at one height to be representative of the entire flow field.

The general protocol for field studies consisted of making repeated measurements of environmental conditions and changes in seston concentration upstream and downstream of each population of bivalves based on *in situ* fluorometry and laboratory analysis of pumped water samples (Table 1; Fig. 1C). Each of the fluorometer probes and water intake tubes were set at 5–10 cm above the bottom (either the top of the reef for mussels and oysters or the sediment surface for clams). A set of measurements (each consisting of 10–20 fluorometry readings recorded at 10-s intervals) was made at 10-min intervals for the duration of each deployment at each site (except for the South Carolina study, which consisted of single readings recorded at 5–15-min intervals). The peristaltic pumps required about 5 min to obtain each sample. Readings from the two fluorometers also were compared side-by-side at the beginning of each deployment and again after the last set of readings was taken to be sure they gave similar readings.

Pumped water samples were stored in the dark on ice and returned to the laboratory for filtration (Whatman GF/C or Gelman GF/F filters) within 6 h of collection; the filters were further pro-

TABLE 1.

Summary of environmental characteristics, bivalve population data, and other information for all study sites.

Species	Bivalve Density (#/m^2)	Mean Shell Size (mm)	Location	Site	Date	Tide	Sampling Duration (hr)	# of Samples		Water Depth Range (m)	Flow Length (m)	Flow Speed Range (cm/s)	*In situ* Fluoro (% uptake)	Laboratory Chl *a* (% uptake)
								In situ Fluoro	Pumped Water					
Mytilus edulis	526	45.0	New Hampshire	Albacore Channel	11/13/01	Ebb	1.4	4	4	0.32–0.47	63	12.6–27.8	27.8	11.8
Mercenaria mercenaria	285	19.4	Virginia	Clam Bed 1	6/5/02	Flood	0.8	5	4	0.35–0.42	9	10.0–13.0	35.3	16.1
Mercenaria mercenaria	285	19.4	Virginia	Clam Bed 2	6/6/02	Ebb	0.4	3	0	0.61–0.65	44	3.0–5.0	62.3	
Crassostrea virginica	61	36.8	Florida	CANA Reef 1	6/10/02	Flood	1.0	7	0	0.28–0.34	12	12.0–17.0	11.4	
Crassostrea virginica	122	54.9	Florida	CANA Reef 2	6/10/02	Ebb	0.7	4	0	0.18–0.19	20	3.0–4.0	37.4	
Crassostrea virginica	76	50.5	Florida	CANA Reef 3	6/11/02	Ebb	1.8	8	6	0.40–0.50	20	4.0–6.0	10.7	11.9
Crassostrea virginica	134	47.0	Florida	CANA Reef 4	6/12/02	Flood	1.3	4	0	0.17–0.18	17	8.0	26.3	
Crassostrea virginica	2538	26.7	South Carolina	Palmetto Reef 1	10/18/04	Flood	1.7	11	3	1.0–1.5	6	3.5–11.5	−2.7	−5.3

cessed immediately in most cases, or frozen until processed. The New Hampshire, Florida and Virginia samples were analyzed spectrophotometrically using acetone extraction and standard techniques (APHA 1992). The South Carolina samples were analyzed fluorometrically following a modified EPA Method 445.0 procedure (Arar 1997, Rev. 1.2).

Bivalve densities were determined at most sites by sampling 5 to 10 of 0.16 m^2 quadrats, counting and measuring shell length or height of all live bivalves collected to the nearest mm using calipers. For the South Carolina oyster reef, data on bivalve size and density available from previous samples taken at that site were used. Flow length was the distance between the two fluorometers. Water depth was measured at 10-min intervals using a marked rod. Water flow speed was measured at the same height as the fluorometer probes were placed (5–10 cm above the bottom) with a Marsh-McBirney Model 201 electromagnetic current meter, with 10–20 replicate speeds recorded at 10-s intervals every 10 min for the duration of the measurement period. Near-surface water speed and flow direction were also estimated by releasing an orange at the upstream site and recording travel time to the downstream site. This provided a measurement of near-surface water flow speed to compare with the near-bottom measurements and insured that the sampling units were placed properly.

Data analysis consisted of comparisons of chlorophyll *a* concentrations, based on field data (*in situ* fluorometry) with laboratory analysis of pumped water samples. Data were analyzed graphically (scatterplots), and statistically (*t*-tests, regression and correlation) using SYSTAT version 10 (2000) software. For the *in situ* fluorometry data only, the *t*-tests were done using the means of the mean values for each 10-min observation period.

RESULTS AND DISCUSSION

A total of eight trials of paired upstream versus downstream *in situ* fluorometry measurements were taken at the four study areas; pumped water samples were taken for laboratory chlorophyll *a* analysis during four of the eight trials (Table 1). T-tests indicated significant differences between mean upstream and downstream fluorometry readings for six of the eight trials (Fig. 2), but only marginally significant ($P < 0.10$) differences at two of the four trials for laboratory measurements (Fig. 3). Both approaches, however, showed instances of seston uptake rates exceeding 25%.

A scatterplot of the full dataset comparing each *in situ* flurorometry reading with its corresponding laboratory chlorophyll measurement showed two distinct groupings (Fig. 4). Overall, this assessment indicated that the two measurement techniques yield comparable data, but their relationship is not simple.

Using In situ *Fluorometry to Provide Rapid Measurement of Seston Uptake*

As already noted, field studies on seston uptake typically have involved laboratory analysis of discrete water samples obtained manually or by pumps using various sampling protocols (e.g., Dame & Libes 1993, Judge et al. 1993, Newell & Shumway 1993, Cressman et al. 2003, Nelson et al. 2004). We obtained pumped water samples for laboratory analysis as means of "ground truthing" the *in situ* fluorometry data because in the long-term our goal is to rely as much as possible on the latter. Most applications of *in situ* fluorometry to date have been in the area of water quality monitoring (e.g., Gregor et al. 2005), in some cases (e.g., Grant & Bacher 1998) related to bivalve aquaculture. Our application essentially represents an ecological extension of the method, but it required some important modifications to off-the-shelf fluorometers. Ambient sunlight can strongly interfere with the sensor, so a large aluminum plate was added to shade the probe (Fig. 1). It was also necessary to construct a deployment apparatus that allowed precise placement of the probe vertically, and it automatically oriented the probe so the predominant water flow was directly through the sensor chamber. These modifications have resulted in an apparatus that is simple to deploy and appears to consistently yield reliable data.

In situ fluorometry could become a fast, effective and nondestructive approach to quantifying the impacts of shellfish populations on seston removal but it needs further development, including more comparisons with laboratory analysis of pumped water samples. One of the issues that will need to be settled for some applications concerns the relationship between the *in situ* fluorometry data and laboratory-determined chlorophyll *a* concentrations. Our data from four different areas showed two distinct groups, with substantial disparity between the two in the relationship between fluorescence and chlorophyll *a* concentrations determined by wet chemistry techniques (Fig. 4). Grant and Bacher (1998) also reported substantial disparities between the two approaches. Gregor et al. (2005) noted that differences between *in situ* fluorometric methods and laboratory methods should be expected when different analytical techniques (e.g., ethanol vs. acetone extraction) are compared and phytoplankton taxonomic composition varies. For our data, the pumped water samples were a composite taken over about 5 min, as compared with multiple fluorometry reading taken over about 2 min (see Methods section). Hence, although both types of samples were taken at approximately the same time, some of the differences (Fig. 4) could represent actual temporal variability in seston concentrations.

Another potential limitation of *in situ* fluorometry is that it does not provide data on components of the seston other than phytoplankton that can be important food items for bivalves. However, if chlorophyll *a* data alone are sufficient then *in situ* fluorometry represents a much more effective approach compared with analysis of pumped water samples because it provides rapid results, and if fluorometers are deployed at multiple heights in the water column, spatial variations in seston removal that are related to hydrodynamical factors can be assessed. For example, a fully mixed water column is not necessary for estimating uptake rates.

Seston Uptake by Oyster Reefs

As discussed earlier, the need to estimate the potential impact of constructed or restored oyster reefs on water quality has driven the development of the *in situ* fluorometers. The potential for bivalve shellfish to control phytoplankton populations in coastal areas such as San Francisco Bay was proposed over 20 y ago (Cloern 1982, Officer et al. 1982). Subsequent studies in the Bay documented a variety of ecological effects, including seston depletion, attributable to dense infaunal bivalve populations (e.g., Alpine & Cloern 1992). In a widely cited paper, Newell (1988) hypothesized that the historical depletion of oyster populations in Chesapeake Bay has been a major factor in water quality degradations and other ecological changes in the Bay (also see Heck 1987). Subsequent studies support this notion (Ulanowicz & Tuttle 1992, Newell 2004). Similar water quality impacts in some areas of the Great Lakes by the invasive zebra mussel have also been documented (Budd et al. 2001, Ackerman et al. 2001). Recent research in mesocosms has further characterized the role that sus-

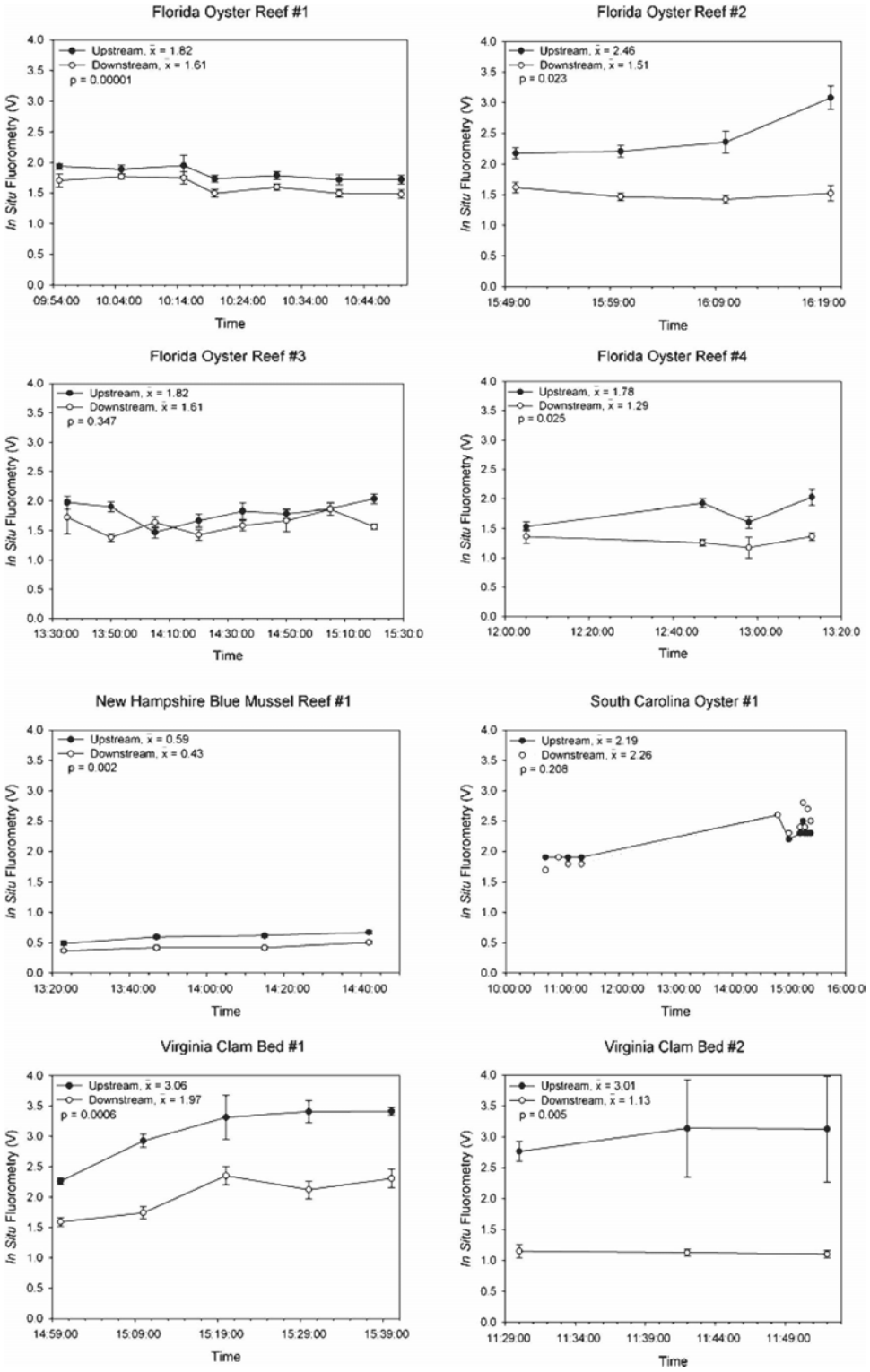

Figure 2. Upstream and downstream *in situ* fluorometry measurements for all study sites. *P* values from *t*-tests; error bars show 1 SD.

pension-feeding bivalves can play in controlling phytoplankton populations (Cerrato et al. 2004, Porter et al. 2004). It seems reasonable to expect measurable water quality effects from restored oyster reefs, but empirical studies of the effects are needed.

Several field studies involving bivalves such as clams, mussels and other taxa have demonstrated substantial seston uptake and in some cases longer-term water quality changes caused by bivalve feeding and filtration (e.g., Alpine & Cloern 1992, Haamer 1996, Coen et al. 2000, Haamer & Rodhe 2000, Ackerman et al. 2001; see reviews by Dame 1996 and Dame et al. 2001). Field studies on oysters, however, typically have shown no measurable uptake or very little (Dame & Libes 1993, Wilson-Ormond et al. 1997, Nel-

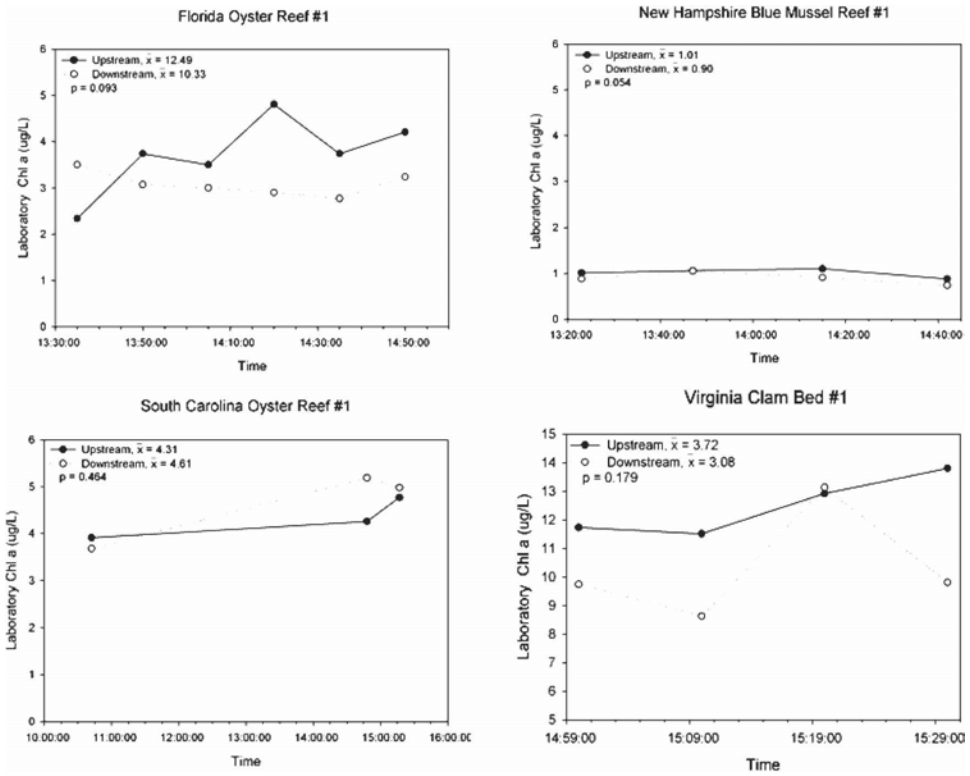

Figure 3. Upstream and downstream laboratory measurements of chlorophyll *a* concentrations from pumped water samples for all study sites. *P* values from *t*-tests.

son et al. 2004); Cressman et al. (2003) is the only field demonstration of substantial seston removal (up to 25% decreases in chlorophyll *a*) we are aware of for oyster reefs. In the present study, maximum measured seston uptake rates for the three bivalve species ranged from 27.8% for *Mytilus*, 37.4% for *Crassostrea*, to 62.3% for *Mercenaria*. The differences in rates mainly reflected differences in bivalve size and densities relative to water flow and water depth (Table 1). Hence, it seems reasonable to conclude that field studies on oysters should consistently yield quantitative measures of seston depletion if they are properly scaled. In any case, our new *in situ* device would allow rapid assessments for future studies on restored and natural oyster reefs.

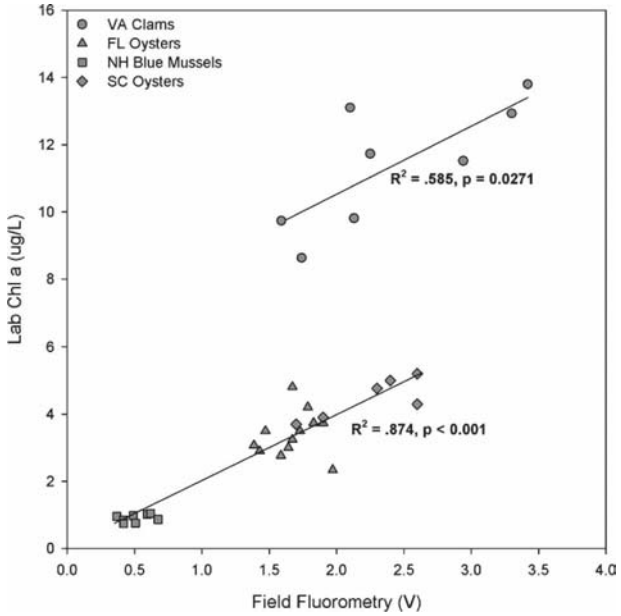

Figure 4. *In situ* fluorometry compared with laboratory analysis of pumped water samples for all study sites.

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LITERATURE CITED

Ackerman, J. D., M. R. Loewen & P. F. Hamblin. 2001. Benthic-pelagic coupling over a zebra mussel bed in the western basin of Lake Erie. *Limnol. Oceanogr.* 46:892–904.

Alpine, A. E. & J. E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnol. Oceanogr.* 37:946–955.

APHA. 1992. Standard methods for the examination of water and wastewater, 18th edition. Method 10200 H, Chlorophyll. American Public Health Association, Washington, DC.

Arar, E. J. 1997. Method 447.0, Determination of chlorophylls *a* and *b* and identification of other pigments of interest in marine and freshwater algae using high performance liquid chromatography with visible wavelength detection. Cincinnati, Ohio: National Exposure Research Laboratory, Office of Research and Development, US Environmental Protection Agency. 20 pp.

Brumbaugh, R. D., L. A. Sorabella, C. O. Garcia, W. J. Goldsborough & J. A. Wesson. 2000. Making a case for community-based oyster restoration: an example from Hampton Roads, Virginia, USA. *J. Shellfish Res.* 19:467–472.

Budd, J. W., T. D. Drummer, G. L. Fahnenstiel & T. Nalepa. 2001. Remote sensing of biotic effects: Zebra mussels (Dreissena polymorpha) influence on water clarity in Saginaw Bay, Lake Huron. *Limnol. Oceanogr.* 46:213–223.

Cerrato, R. M., D. A. Caron, D. J. Lonsdale, J. M. Rose & R. A. Schaffner. 2004. Effect of the northern quahog *Mercenaria mercenaria* on the development of blooms of the brown tide alga *Aureococcus anophagefferen. Mar. Ecol. Prog. Ser.* 281:93–108.

Cloern, J. E. 1982. Does the benthos control phytoplankton biomass in south San Francisco Bay? *Mar. Ecol. Prog. Ser.* 9:191–202.

Coen, L. D. & M. W. Luckenbach. 2000. Developing success criteria and goals for evaluating oyster reef restoration: ecological function or resource exploitation? *Ecol. Eng.* 15:323–343.

Coen, L. D., M. Judge, C. Moncreiff & K. Hammerstrom. 2000. Hard clam (*Mercenaria mercenaria*) mariculture in US waters: evaluating the effects of large-scale field growout practices on clam growth, nutrition and inshore estuarine creek communities. Final Project Report to Saltonstall-Kennedy, NMFS. 38 pp.

Cressman, K. A., M. H. Posey, M. A. Mallin, L. A. Leonard & T. D. Alphin. 2003. Effects of oyster reefs on water quality on a tidal creek estuary. *J. Shellfish Res.* 22:753–762.

Dame, R. 1996. Ecology of marine bivalves: an ecosystem approach. Boca Raton, FL: CRC Marine Science Series. 254 pp.

Dame, R. & S. Libes. 1993. Oyster reefs and nutrient retention in tidal creeks. *J. Exp. Mar. Biol. Ecol.* 171:251–258.

Dame, R., D. Bushek & T. Prins. 2001. The role of suspension feeders as ecosystem transformers in shallow coastal environments. In: K. Reise, editor. Springer-Verlag, Berlin: The ecology of sedimentary coasts. pp. 11–37.

French McCay, D. P., C. H. Peterson, J. T. DeAlteris & J. R. Catena. 2003. Restoration that targets function as opposed to structure: replacing lost bivalve production and filtration. *Mar. Ecol. Prog. Ser.* 264:197–212.

Grant, J. & C. Bacher. 1998. Comparative models of mussel bioenergetics and their validation at field culture sites. *J. Exp. Mar. Biol. Ecol.* 219:21–44.

Gregor, J., R. Geris, B. Marsalek, J. Hetesa & P. Marvan. 2005. *In situ* quantification of phytoplankton in reservoirs using a submersible spectrofluorometer. *Hydrobiologia* 548:141–151.

Haamer, J. 1996. Improving water quality in a eutrophied fiord system with mussel farming. *Ambio* 25:356–362.

Haamer, J. & J. Rodhe. 2000. Mussel *Mytilus edulis* (L.) filtering of the Baltic Sea outflow through the Őresund—an example of a natural, large-scale ecosystem restoration. *J. Shellfish Res.* 19:413–421.

Heck, K. L., Jr. 1987. Benthos. In: Calvert Cliffs & K.L. Heck, Jr., editors. Ecological studies in the middle reach of Chesapeake Bay: lecture notes on coastal and estuarine studies #23 Berlin: Springer-Verlag. pp. 97–110

Judge, M. L., L. D. Coen & K. L. Heck, Jr. 1993. Does *Mercenaria mercenaria* encounter elevated food levels in seagrass beds? Results from a novel technique to collect suspended food resources. *Mar. Ecol. Prog. Ser.* 92:141–150.

Luckenbach, M. W., L. D. Coen, P. G. Ross, Jr. & J. A. Stephen. 2005. Oyster reef habitat restoration: relationships between oyster abundance and community development based on two studies in Virginia and South Carolina. *J. Coastal Res. Special Issue* 40:64–78.

Luckenbach, M. W., R. Mann & J. A. Wesson, editors. 1999. Oyster Reef Habitat Restoration. A synopsis and synthesis of approaches. Virginia Institute of Marine Science Press. Gloucester Point, VA: Virginia Institute of Marine Science Press. 358 pp.

Nelson, K. A., L. A. Leonard, M. H. Posey, T. D. Alphin & M. A. Mallin. 2004. Using transplanted oyster (*Crassostrea virginica*) beds to improve water quality in small tidal creeks: a pilot study. *J. Exp. Mar. Biol. Ecol.* 298:347–368.

Newell, C. R. & S. E. Shumway. 1993. Grazing of natural particulates by bivalve molluscs: a spatial and temporal perspective. In: R. Dame, editor. Bivalve filter feeders in coastal and estuarine ecosystem processes. Springer-Verlag, Berlin: NATO ASI Series G: Ecological Sciences. Vol. 33. pp. 85–148.

Newell, R. I. E. 1988. Ecological changes in Chesapeake Bay: are they the result of overharvesting the American oyster, *Crassostrea virginica*? In: M. P. Lynch & E. C. Krome, editors. Understanding the estuary: advances in Chesapeake Bay research. Gloucester Point, VA: Chesapeake Research Consortium, Publication 129 CBP/TRS 24/88. pp. 536–546.

Newell, R. I. E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *J. Shellfish Res.* 23:51–61.

Newell, R. I. E., T. R. Fisher, R. R. Holyoke & J. C. Cornwell. 2005. Influence of eastern oysters on N and P regeneration in Chesapeake Bay, USA. In: R Dame & S. Olenin, editors. The comparative roles of suspension feeders in ecosystems. Kluwer, Netherlands: NATO Science Series: IV—Earth and Environmental Sciences. pp. 93–120.

Officer, C. B., T. J. Smayda & R. Mann. 1982. Benthic filter feeding: a natural eutrophication control. *Mar. Ecol. Prog. Ser.* 9:203–210.

Peterson, C. H., R. T. Kneib & C. A. Manen. 2003. Scaling restoration actions in the marine environment to meet quantitative targets of enhanced ecosystem services. *Mar. Ecol. Prog. Ser.* 264:173–175.

Porter, E. T., J. C. Cornwall & L. P. Sanford. 2004. Effect of oysters *Crassostrea virginica* and bottom shear velocity on benthic-pelagic coupling and estuarine water quality. *Mar. Ecol. Prog. Ser.* 271:61–75.

Thayer, G. W., T. A. McTigue, R. J. Salz, D. H. Merkey, F. M. Burrows & P. F. Gayaldo (eds.). 2005. Science-based restoration monitoring of coastal habitats, Vol. 2: Tools for monitoring coastal habitats. Silver Spring, MD: NOAA Coastal Ocean Program Decision Analysis Series No. 23. NOAA National Centers for Coastal Ocean Science. 628 pp, plus appendices.

Ulanowicz, R. E. & J. H. Tuttle. 1992. The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. *Estuaries* 15:298–306.

Wilson-Ormond, E. A., E. N. Powell & S. M. Ray. 1997. Short-term and small-scale variation in food availability to natural oyster populations: food, flow and flux. *Mar. Ecol.* 18:1–34.