Provision of ecosystem services by human-made structures in a highly impacted estuary

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Abstract
Water filtration is one of the most important ecosystem services provided by sessile organisms in coastal ecosystems. As a consequence of increased coastal development, human-made shoreline structures (e.g., docks and bulkheads) are now common, providing extensive surface area for colonization by filter feeders. We estimate that in a highly urbanized sub-tropical estuary, water filtration capacity supported by filter feeding assemblages on dock pilings accounts for 11.7 million liters of water h⁻¹, or ~30% of the filtration provided by all natural oyster reef throughout the estuary. Assemblage composition, and thus filtration capacity, varied as a function of piling type, suggesting that the choice of building material has critical implications for ecosystem function. A more thorough depiction of the function of coastal ecosystems necessitates quantification of the extensive ecosystem services associated with human-made structures.

Keywords: ecosystem services, estuary, filtration, oysters, urbanization

1. Introduction
Coastal ecosystems have been fundamentally altered by human activities, resulting in substantial decay in provisioning of ecosystem services that we value (Worm et al 2006, Barbier et al 2011). Of the myriad of human impacts on coastal systems, habitat alteration is one of the most problematic (Lotze et al 2006). Habitat alteration takes many forms, with the most obvious being conversion of natural shoreline to artificial structures. Docks, breakwaters, bulkheads, and jetties are common in urbanized coastal areas, and are often the dominant intertidal and subtidal habitat type (Bulleri and Chapman 2010). The associated loss of natural ecosystems, such as mangroves and salt marshes, results in coastal water bodies with a fundamentally different structure and function (Barbier et al 2011).

Concomitant with shoreline conversions have been drastic declines in populations of many estuarine organisms (Lotze et al 2006). Of particular importance have been declines in benthic filter feeders, organisms that capture substantial amounts of suspended matter, and thus influence water column primary production, control water clarity, and generate direct linkages between pelagic and benthic environments (Beck et al 2011). For instance, in US coastal waters between the early 1900s and early 2000s, oyster extent declined by 64% and biomass by 88% (zu Ermgassen et al 2012). This has resulted in estuary-wide filtration capacity declines of 85% (median value) across 13 US estuaries (zu Ermgassen et al 2013). In Chesapeake Bay (USA), a water volume equivalent to that of the upper and middle Bay was once filtered every ~3.6 days; declines in oyster populations have increased this same filtration time to several hundred days (Kemp et al 2005).

Oysters and other filter feeding organisms require stable substrates for settlement. In many urbanized estuaries,
human-made structures create a vast amount of hard surface area available for colonization of sessile organisms, i.e., ‘fouling’ communities (Hughes et al. 2005). Assemblages that develop on human-made structures are extremely diverse, and often may have different composition from assemblages on natural substrates such as mangrove roots and rocky outcroppings (Connell and Glasby 1999, Connell 2001). From an ecological perspective, fouling communities on human-made structures have provided an excellent template to test basic population- and community-level questions, e.g., regarding invasive species biology (Byrnes and Stachowicz 2009). Yet our understanding of the broader ecological role of organismal communities on human-made structures remains in its infancy (Bulleri and Chapman 2010), especially with respect to their role in mediating large-scale ecosystem processes.

A thorough understanding of ecosystem function in estuaries necessitates quantification of those processes associated with human-made structures. Here we focus on water filtration capacity, one of the most critical functions provided by filter feeding organisms (Beck et al. 2011). In an urbanized subtropical estuary, we surveyed dock piling fouling communities, and coupled these abundance data with previously published taxon-specific equations for water filtration rates, to estimate the fouling communities’ water filtration capacity. The study was framed around three questions:

1. At the scale of an entire estuary, what is the water filtration capacity of dock piling fouling communities?
2. Does piling material type affect the composition of fouling communities, and thus filtration capacity?
3. How does the filtration capacity of human-made structures compare with natural oyster reefs in the river?

2. Materials and methods

The Loxahatchee River and estuary (hereafter referred to as river), is located on the southeast Atlantic coast of Florida, US (26°56’N, 80°05’W), draining a 620-km² watershed and connecting to the ocean through Jupiter Inlet. The lower 6.5 km of the river are highly urbanized with almost no natural shoreline remaining (figure 1). Historical fringing red mangrove (Rhizophora mangle) forests have been replaced by residential lands, and contemporary shorelines are largely dominated by docks and bulkheads. Although shoreline habitats have been greatly disturbed by development, the river still supports ∼60 000 m² of natural subtidal oyster reefs. An additional 24 000 m² of oyster restoration reefs were constructed in the river in 2010, as part of a NOAA-funded American Recovery and Reinvestment Act project. Benthic faunal composition at the restoration reefs has converged with that of natural reefs (Jud and Layman 0000), and the constructed reefs support extensive live oyster growth (Howard 2011).

In addition to natural and restored oyster reefs, abundant filter feeding communities are found on structures such as dock pilings, bridge pilings, bulkheads, boat hulls, and riprap piles in the Loxahatchee River. In this letter, we focused on dock piling fouling communities, as these had the most standardized shapes and sizes that provided for most straightforward quantification of filter feeding organisms. Pilings were constructed from one of four materials: pressure-treated wood (hereafter wood), pressure-treated wood wrapped in a high density polyethylene material (pile wrap), round polyvinyl chloride (PVC) pipe filled with concrete, and square steel-reinforced concrete beams (example piling types in figure 2). To account for potential spatial differences in dock piling community composition, we divided the shoreline of the estuary into seven sections (figure 1). We counted the total number of pilings in each section of river (categorized by material type) by snorkeling and from a boat.

Within each river section, 5–15 docks with each piling type were randomly selected for community composition analysis (smaller sample sizes when a specific dock type was rare in a given river section). On each of these docks, we haphazardly selected a single piling for sampling.
filter feeding communities that occurred on dock pilings, we visually examined (with mask and snorkel when submerged) the entire surface of each piling, from the mean high water mark (delineated by the highest barnacle on the piling) to the benthos. When possible, organisms were identified to the species level; however, certain taxa were combined into functional groups (e.g. encrusting sponges, see table 1). Two distinct approaches were used to quantify organism abundance (identified in table 1). For solitary organisms, we counted the number of individuals from each taxon (broken down by size class for most taxa) on the surveyed pilings. For encrusting and colonial organisms, we estimated total area covered (cm² per piling) for each taxon over the entire piling, using a plastic mesh grid with 25 mm square openings as a reference.

Since most clearance rates for filter feeding organisms in the literature are reported as a rate per dry mass (table 2), we converted our field survey measurements to dry mass per taxon per piling. To calculate mass per individual for solitary taxa, we weighed replicate field-collected samples of individual organisms (dried at 60 °C). For encrusting and colonial taxa, we scraped square patches of colonies (of a known surface area) off of pilings using chisels. These pieces were then dried and weighed to obtain mass cm⁻² for all encrusting taxa. Field data (counts per piling and area covered per piling) were then converted to dry mass per piling for each taxon.

Filtration capacity (l H₂O h⁻¹) of dock piling fouling communities was estimated using Monte Carlo simulations with 10000 iterations. Each iteration consisted of four hierarchical steps. First, a filter feeding community was assigned to all dock pilings in the river by randomly selecting, with replacement, from the observed communities within the appropriate river section and piling type. Second, the filtration capacity of each individual or organism group on each dock piling was estimated using previously published equations for each taxonomic group (table 2). For organisms with filtration rate equations based on dry weight or volume, a value was assigned to each individual by randomly selecting, with replacement, from the observed dry weights or volumes for that organism and size class. Third, filtration capacity was summed across taxa to get an estimated filtration capacity for each dock piling. Finally, filtration capacities were summed by piling type within each section of river. Variation surrounding our filtration rate estimate was generated by the random assignment of community composition to dock pilings, as well dry weights to individual organisms.

For comparative purposes, we also estimated filtration capacity of natural and restored oyster reefs (separately). Filter feeder densities on oyster reefs were estimated by quantifying organismal abundance within randomly selected 0.09 m² quadrats (n = 46 for natural reef, n = 19 for restoration reefs) across the entire distribution of reef sites in the river. We modeled filtration capacity on oyster reefs using Monte Carlo simulations (10000 iterations) similar to that described above, using quadrat samples as the unit of replication rather than individual dock pilings.

3. Results

A total of 13554 dock pilings were counted that supported fouling assemblages, and composition of 208 pilings was quantified. To explore potential differences in community composition among piling types and river section, we created a NMDS ordination from a Bray–Curtis similarity matrix using presence–absence data from each piling (Primer v.6.1.16; figure 3). Downstream pilings supported the most diverse fauna, including numerous species of sponge, tunicate, bryozoan, polychaete worm and mollusk (see figure 2 for image of a representative piling). Pilings further from the inlet typically just supported oysters and barnacles. A 2-way nested ANOSIM (Primer v.6.1.16) suggested community composition varied both as a function of river section (Global R = 0.57, p = 0.001) and piling type (R = 0.2, p = 0.001). Filtration capacity of the dock pilings was not distributed as would predicted by the number of dock pilings in each river section and structure type ($\chi^2_{18} = 247.5,$ $p-value < 0.0001,$ figure 4). River section 1 contributed more than expected, accounting for 53% of total piling filtration capacity while containing only 5% of the dock pilings. Across all sections of the river, concrete pilings supported 68% of total filtration, despite accounting for 7% of all pilings (note especially river section 6 in figures 3(a) and (b)). Pile wrap was the most common dock piling type (69% of all dock pilings in the river), yet these pilings supported only 10% of all filtration.
Table 1. Organisms and size categories used in survey protocol for dock pilings. Symbols indicate which taxa were included for natural and restoration oyster reef surveys.

| Organism group                        | Size category | Information recorded |
|---------------------------------------|---------------|-----------------------|
| Eastern oysters                       | <25 mm        | Number of individuals  |
| Eastern oysters                       | 25–50 mm      | Number of individuals  |
| Eastern oysters                       | >50 mm        | Number of individuals  |
| Tree oysters                          | <25 mm        | Number of individuals  |
| Tree oysters                          | 25–50 mm      | Number of individuals  |
| Tree oysters                          | >50 mm        | Number of individuals  |
| Scorched mussels                      | <10 mm        | Number of individuals  |
| Scorched mussels                      | 10–25 mm      | Number of individuals  |
| Scorched mussels                      | >25 mm        | Number of individuals  |
| Barnacles                             | NA            | Number of individuals  |
| Solitary tunicates; erect clusters    | NA            | Number of individuals  |
| Encrusting tunicates                  | NA            | Area (cm$^2$)          |
| Solitary erect sponges                | NA            | Volume (cm$^3$)        |
| Encrusting sponges                    | NA            | Area (cm$^2$)          |
| Encrusting bryozoans                  | NA            | Area (cm$^2$)          |
| Vermetid worm-snails                  | NA            | Number of individuals  |
| Feather duster worms                  | <25 mm        | Number of individuals  |
| Feather duster worms                  | >25 mm        | Number of individuals  |
| Erect bryozoans                       | NA            | Area (cm$^2$)          |
| Encrusting bryozoans                  | NA            | Area (cm$^2$)          |

a Enumerated on natural and restored oyster reefs.
b Subsequently converted to volume assuming a standard thickness of 0.4 cm.

Table 2. Equations used to estimate filtration rates, along with initial literature citation. Dry weights were used in calculations.

| Organism                        | Equation/rate | Original units | Source                        |
|---------------------------------|---------------|----------------|-------------------------------|
| Eastern oysters                 | $6.79 \times g^{0.73}$ | l h$^{-1}$ | Riisgård (1988) |
| Tree oysters                    | $10.73 \times 0.617g$ | l h$^{-1}$ | Yukihira et al (1998) |
| Scorched mussels                | $6.15 \times g^{0.83}$ | l h$^{-1}$ | Riisgård (1988) |
| Barnacles                       | 0.1           | l h$^{-1}$ | Anderson (1981) |
| Solitary tunicates; erect clusters | $54.4 \times g^{1.05}$ | ml min$^{-1}$ | Randlov and Riisgård (1979) |
| Encrusting tunicates            | $46.4 \times g^{0.84}$ | ml min$^{-1}$ | Randlov and Riisgård (1979) |
| Sponges$^a$                     | 0.24          | 1 s$^{-1}$ L$^{-1}$ sponge | Vogel (1974) |
|                                | 0.08          | 1 s$^{-1}$ L$^{-1}$ sponge | Lynch and Philips (2000) |
|                                | 0.045         | 1 s$^{-1}$ L$^{-1}$ sponge | Riisgård et al (1993) |
|                                | 0.21          | 1 s$^{-1}$ L$^{-1}$ sponge | Reiswig (1974) |
|                                | 0.27          | 1 s$^{-1}$ L$^{-1}$ sponge | Reiswig (1974) |
| Vermetid worm-snails            | 396           | 1 g$^{-1}$ 20 min$^{-1}$ | Ribak et al (2005) |
| Feather duster worms            | $13.62 \times g^{0.24}$ | l h$^{-1}$ | Riisgård and Ivarsson (1990) |
| Erect bryozoans                 | 13.9          | ml mg$^{-1}$ h$^{-1}$ | Bullivant (1968) |
| Encrusting bryozoans            | 13.9          | ml mg$^{-1}$ h$^{-1}$ | Bullivant (1968) |

a Sponge pumping rates were allowed to vary by individual dock pilings in the model between all published rates for members of the identified genera.

Total estimated filtration capacity of dock pilings suggests that these human-made structures contribute significantly to estuarine-scale ecosystem processes in this system (figure 4(c)). Our estimates of 11.74 ($\pm$0.04) million 1 H$_2$O h$^{-1}$ represent $\sim$30% of the filtration capacity of the entire 60 000 m$^2$ extent of natural reef habitat (42.16 $\pm$ 0.003 million 1 H$_2$O h$^{-1}$). Dock piling filtration is roughly double the estimated filtration capacity supported by filter feeding organisms (oysters, mussels, and barnacles; 6.34 $\pm$ 0.001 million 1 H$_2$O h$^{-1}$) that inhabit new reef habitat resulting from the recent American Recovery and Reinvestment Act large-scale oyster restoration initiative.
Figure 3. Non-metric multi-dimensional scaling plot, with each point representing the composition of fouling organisms on a single dock piling. The closer two points are in the figure, the more similar the overall community composition (at a presence/absence level of resolution). Distribution of points is driven by decreasing taxonomic diversity from the Inlet (section 1) and adjacent river sections (sections 2 and 3) to upper sections of the river (e.g., sections 6 and 7).

Figure 4. (a) The number of dock pilings stratified by structure type and river section. (b) Filtration capacity on dock pilings stratified by structure type and river section. (c) Total filtration capacity on natural (N) and restored (R) oyster reefs compared to that supported by dock pilings (P).

4. Discussion

Our study highlights that in heavily urbanized estuaries, substantial ecosystem services may be supported by fouling communities on human-made structures. Although the filtration role of fouling communities is widely acknowledged (Hughes et al 2005), here we take a first step toward considering this service at the ecosystem scale. Importantly, the total filtration capacity provided by organisms on human-made structures in the Loxahatchee is vastly greater than the specific dock piling estimates herein, as bridge pilings, bulkheads, boat hulls, and riprap piles are extensive throughout the lower 6.5 km of the river. For example, there is 13,397 m of bulkhead shoreline (not including dock pilings, see image in figure 2) in the 7 sections of river we sampled (Nichols 2013), providing a vast surface area for colonization by filter feeders. Especially in the face of continued declines of once abundant filter feeding species such oysters (zu Ermgassen et al 2013), filtration capacity provided by fouling communities on human-made structures may make up a significant proportion of overall water filtration in urbanized estuaries.

Fouling communities are widely known to vary as a function of the colonized substrate (Connell and Glasby 1999, Connell 2001), and here we extend this to suggest important implications for ecosystem function. For instance, if all pile wrap pilings in the river were replaced with concrete, filtration capacity of docks would increase from 11.7 to 63.8 million l H$_2$O h$^{-1}$—a figure that substantially exceeds the filtering capacity of all existing natural oyster reefs in the system. Wood pilings are selected by homeowners because they may be cheaper to install than concrete, as well as for the fact that they can be designed to minimize colonization of fouling organisms (e.g., with pile wrap). But in a broader societal cost-benefit analysis, cement pilings may provide sufficient value, through provisioning of ecosystem services, that warrants consideration as the preferred dock piling material. For example, future tax incentives influencing choice of piling material may result in net societal benefit. It remains a difficult challenge to place a definitive monetary value on ecosystem services (such as preservation of water quality) and incorporate this into public policy (Barbier et al 2008). Yet our data suggest the sheer magnitude of ecosystem service that may be provided by artificial structures should not be ignored in policy making contexts.

Caveats to these filtration estimates are many. Filtration rate estimates (typically from laboratory studies) are not expected to map perfectly onto actual rates in the environment because of variation due to temperature, flow rate, salinity, vertical height in the water column and particle size/concentration, among many others (zu Ermgassen et al 2013). Lack of taxon-specific rates also limits specificity of filtration estimates, especially because different organisms filter different size particles from water (Stuart and Klump 1984), resulting in different ecosystem effects. Even estimating estuary-wide filtration by a single species is fraught with challenges (zu Ermgassen et al 2000, Fulford et al 2007, zu Ermgassen et al 2013), challenges compounded when considering diverse filter feeding taxa. As such, our data are intended more as a conceptual perspective than as precise in situ estimates. Despite such qualifications, simply the sheer amount of surface area of human-made structures suggests how important these must be in the context of ecosystem processes. We estimated that the river contained ∼42 000 m$^2$ of dock piling surface area that supported fouling organisms—a figure approaching that of the areal extent of natural oyster coverage in the river. This fact is impressive, especially when considering that we quantified filter feeding organisms on just one of the many types of human-made structures found in coastal systems.
Conveying these ideas to resource managers and stakeholders may be challenging, as data could be couched as evidence to actually justify conversion of natural shorelines to human-made structures. To the contrary, we categorically state that we are not equating dock pilings to healthy natural oyster reef. For example, it is important to remember that we only consider a single ecosystem service herein, and do not attempt a full assessment that would incorporate the numerous other ecosystems services that are compromised or lost with destruction of natural habitats (Barbier et al. 2008). Urbanization of coastal areas also may lead to other unwanted consequences, e.g., facilitating the spread of invasive species (Byrnes et al. 2007, Sheehy and Vik 2010). Conversely, creative architectural designs for human-made structures (e.g., ‘living’ seawall designs) can provide additional ecological benefits (Browne and Chapman 2011). Ignoring the numerous abiotic and biotic effects of artificial structures clearly hinders a complete and nuanced characterization of how coastal systems function (Bulleri and Chapman 2010). Although continued coastal development is inevitable, our findings emphasize the importance of creating human-made shoreline structures in such a way as to maximize their ecological benefits.

5. Conclusions

In many ways, the example in the present study is analogous to emerging ideas regarding the conversion of natural terrestrial habitats (e.g., primary and secondary forests) to what are regarded as more marginal lands (e.g., agricultural lands). But such marginal habitats are not ecological wastelands, as agricultural lands continue provide some level of ecosystem services, including maintenance of biodiversity, pollination, and carbon sequestration (Tscharntke et al. 2005). Likewise, the role of man-made habitats in urbanized coastal environments is essential to elucidate if we are to design and manage these habitats in a way that maximizes returns of the ecosystem services we highly value.

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References

Anderson D T 1981 Cirral activity and feeding in the barnacle Balanus perforatus brugiarei (Balanidae), with comments on the evolution of feeding mechanisms in thoracican-cirripedes Phil. Trans. R. Soc. B 291 411–49
Barbier E B, Hacker S D, Kennedy C, Koch E W, Sier A C and Silliman B R 2011 The value of estuarine and coastal ecosystem services Ecol. Lett. 12 830–41
Byrne J E, Reynolds P L and Stachowicz J J 2007 Invasions and extinctions reshape coastal marine food webs PLoS One 2 1–7
Byrnes J and Stachowicz J J 2009 Short and long term consequences of increases in exotic species richness on water filtration by marine invertebrates Ecol. Lett. 12 830–41
Connell S D 2001 Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs Mar. Environ. Res. 52 115–25
Connell S D and Glasby T M 1999 Do urban structures influence local abundance and diversity of subtidal epibiotic? A case study from Sydney Harbour, Australia Mar. Environ. Res. 47 373–87
Fulford R S, Breitburg D L, Newell R I E, Kemp W M and Luckenbach M 2007 Effects of oyster population restoration strategies on phytoplankton biomass in Chesapeake Bay: a flexible modeling approach Mar. Ecol. Prog. Ser. 336 43–61
Howard B 2011 Loxahatchee River oyster reef restoration monitoring summary 1–11 www.loxahatcheeriver.org/pdf/LRD_OysterMontiSummary2011.pdf
Hughes D, Cook E and Sayer M 2005 Biofiltration and biofouling on artificial structures in Europe: the potential for mitigating organic impacts Oceanogr. Mar. Biol.: Annu. Rev. 43 123–72
Jud Z R and Layman C A, Benthic fauna changes following large-scale oyster reef restoration in a subtropical estuary Estuar. Coast. Shelf Sci. in review
Kemp W M et al 2005 Eutrophication of Chesapeake Bay: historical trends and ecological interactions Mar. Ecol. Prog. Ser. 303 1–29
Lotze H K, Lemhan H S, Bourque B J, Bradbury R H, Cooke R G, Kay M C, Kidwell S M, Kirby M X, Peterson C H and Jackson J B C 2006 Depletion, degradation, and recovery potential of estuaries and coastal seas Science 312 1806–9
Lynch T C and Philips E J 2000 Filtration of the bloom-forming cyanobacteria Synechococcus by three sponge species from Florida Bay, USA Bull. Mar. Sci. 67 923–36
Nichols P 2013 unpublished data
Randlov A and Riisgård H U 1979 Efficiency of particle retention and filtration rate in 4 species of ascidians Mar. Ecol. Prog. Ser. 1 55–9
Reiswig H M 1974 Water transport, respiration and energetics of three tropical marine sponges J. Exp. Mar. Biol. Ecol. 14 231–49
Ribak C, Heller J and Genin A 2005 Mucus-net feeding on organic particles by the vermetid gastropod Dendropoma maximum in and below the surf zone Mar. Ecol. Prog. Ser. 293 77–87
Riisgård H U 1988 Efficiency of particle retention and filtration rate in six species of northeast American bivalves Mar. Ecol. Prog. Ser. 45 217–23
Riisgård H U and Ivarsson N M 1990 The column-filament pump of the suspension-feeding polychaete Sabella penicillus- Filtration, effects of temperature, and energy-cost Mar. Ecol. Prog. Ser. 62 249–57
Riisgård H U, Thomassen S, Jakobsen H, Weeks J and Larsen P S 1993 Suspension-feeding in marine sponges Halichondria-panicea and Haliclona-urceolus-effects of temperature on filtration-rate and energy-cost of pumping Mar. Ecol. Prog. Ser. 96 177–88
Sheehy D J and Vik S F 2010 The role of constructed reefs in non-indigenous species introductions and range expansions Ecol. Eng. 36 1–11

Bullivant J 1968 The method of feeding of lophophorates (Bryozoa, Phoronida, Brachiopoda) N. Z. J. Mar. Freshw. Res. 2 135–46
Byrnes J E, Reynolds P L and Stachowicz J J 2007 Invasions and extinctions reshape coastal marine food webs PLoS One 2 1–7
Byrnes J and Stachowicz J J 2009 Short and long term consequences of increases in exotic species richness on water filtration by marine invertebrates Ecol. Lett. 12 830–41
Connell S D 2001 Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs Mar. Environ. Res. 52 115–25
Connell S D and Glasby T M 1999 Do urban structures influence local abundance and diversity of subtidal epibiotic? A case study from Sydney Harbour, Australia Mar. Environ. Res. 47 373–87
Fulford R S, Breitburg D L, Newell R I E, Kemp W M and Luckenbach M 2007 Effects of oyster population restoration strategies on phytoplankton biomass in Chesapeake Bay: a flexible modeling approach Mar. Ecol. Prog. Ser. 336 43–61
Howard B 2011 Loxahatchee River oyster reef restoration monitoring summary 1–11 www.loxahatcheeriver.org/pdf/LRD_OysterMontiSummary2011.pdf
Hughes D, Cook E and Sayer M 2005 Biofiltration and biofouling on artificial structures in Europe: the potential for mitigating organic impacts Oceanogr. Mar. Biol.: Annu. Rev. 43 123–72
Jud Z R and Layman C A, Benthic fauna changes following large-scale oyster reef restoration in a subtropical estuary Estuar. Coast. Shelf Sci. in review
Kemp W M et al 2005 Eutrophication of Chesapeake Bay: historical trends and ecological interactions Mar. Ecol. Prog. Ser. 303 1–29
Lotze H K, Lemhan H S, Bourque B J, Bradbury R H, Cooke R G, Kay M C, Kidwell S M, Kirby M X, Peterson C H and Jackson J B C 2006 Depletion, degradation, and recovery potential of estuaries and coastal seas Science 312 1806–9
Lynch T C and Philips E J 2000 Filtration of the bloom-forming cyanobacteria Synechococcus by three sponge species from Florida Bay, USA Bull. Mar. Sci. 67 923–36
Nichols P 2013 unpublished data
Randlov A and Riisgård H U 1979 Efficiency of particle retention and filtration rate in 4 species of ascidians Mar. Ecol. Prog. Ser. 1 55–9
Reiswig H M 1974 Water transport, respiration and energetics of three tropical marine sponges J. Exp. Mar. Biol. Ecol. 14 231–49
Ribak C, Heller J and Genin A 2005 Mucus-net feeding on organic particles by the vermetid gastropod Dendropoma maximum in and below the surf zone Mar. Ecol. Prog. Ser. 293 77–87
Riisgård H U 1988 Efficiency of particle retention and filtration rate in six species of northeast American bivalves Mar. Ecol. Prog. Ser. 45 217–23
Riisgård H U and Ivarsson N M 1990 The column-filament pump of the suspension-feeding polychaete Sabella penicillus- Filtration, effects of temperature, and energy-cost Mar. Ecol. Prog. Ser. 62 249–57
Riisgård H U, Thomassen S, Jakobsen H, Weeks J and Larsen P S 1993 Suspension-feeding in marine sponges Halichondria-panicea and Haliclona-urceolus-effects of temperature on filtration-rate and energy-cost of pumping Mar. Ecol. Prog. Ser. 96 177–88
Sheehy D J and Vik S F 2010 The role of constructed reefs in non-indigenous species introductions and range expansions Ecol. Eng. 36 1–11
Stuart V and Klump D W 1984 Evidence for food-resource partitioning by kelp-bed filter feeders Mar. Ecol. Prog. Ser. 16 27–37

Tscharntke T, Klein A M, Kruess A, Steffan-Dewenter I and Thies C 2005 Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management Ecol. Lett. 8 857–74

Vogel S 1974 Current-induced flow through the sponge, Halichondria Biol. Bull. 147 443–56

Worm B et al 2006 Impacts of biodiversity loss on ocean ecosystem services Science 314 787–90

Yukihira H, Klumpp D W and Lucas J S 1998 Effects of body size on suspension feeding and energy budgets of the pearl oysters Pinctada margaritifera and P-maxima Mar. Ecol. Prog. Ser. 170 119–30

zu Ermgassen P S E, Gray M W, Langdon C J, Spalding M D and Brumbaugh R D, Quantifying the historic contribution of Olympia oysters to filtration in Pacific Coast (USA) estuaries and the implications for restoration objectives Aquat. Ecol. 47 149–61

zu Ermgassen P S E et al 2012 Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat Proc. R. Soc. B 279 3393–400

zu Ermgassen P S E, Spalding M D, Grizzle R E and Brumbaugh R D 2013 Quantifying the loss of a marine ecosystem service: filtration by the eastern oyster in US estuaries Estuaries Coasts 36 36–43