Ecosystem Services 8 (2014) 1–15

Contents lists available at ScienceDirect

Ecosystem Services

journal homepage: www.elsevier.com/locate/ecoser

Comparison of methods for quantifying reef ecosystem services: A case study mapping services for St. Croix, USVI

Susan H. Yee*, John A. Dittmar, Leah M. Oliver

US Environmental Protection Agency, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Gulf Ecology Division, Gulf Breeze, FL 32561, USA

ARTICLE INFO

Article history:
Received 9 January 2013
Received in revised form
26 October 2013
Accepted 6 January 2014
Available online 31 January 2014

Keywords:
Coral reef
Ecological integrity
Fishing
Natural products
Recreation
Shoreline protection

ABSTRACT

A key challenge in evaluating coastal and watershed management decisions is that monitoring efforts are largely focused on reef condition, yet stakeholder concerns may be more appropriately quantified by social and economic metrics. There is an urgent need for predictive models to quantitatively link ecological condition of coral reefs to provisioning of reef ecosystem goods and services. We investigated and compared a number of existing methods for quantifying ecological integrity, shoreline protection, recreational opportunities, fisheries production, and the potential for natural products discovery from reefs. Methods were applied to mapping potential ecosystem services production around St. Croix, U.S. Virgin Islands. Overall, we found that a number of different methods produced similar predictions. Furthermore, areas predicted to be high in ecological integrity also tended to be high in other ecosystem services, including the potential for recreation, natural products discovery, and fisheries production, but this result depended on the method by which ecosystem services supply was calculated. Quantitative methods linking reef condition to ecosystem goods and services can aid in highlighting the social and economic relevance of reefs, and provide essential information to more completely characterize, model, and map the trade-offs inherent in decision options.

Published by Elsevier B.V.

1. Introduction

Ecosystem function and services are inextricably linked to human well-being, yet are often overlooked or taken for granted in social and economic decision-making (MEA (Millennium Ecosystem Assessment), 2005). A key challenge is that environmental assessments typically focus on ecological endpoints, failing to consider the social and economic values of stakeholders (Arvai and Gregory, 2003). A key to bridging ecological and socio-economic concerns is the concept of ecosystem goods and services (Wainger and Boyd, 2009).

In particular, coral reef ecosystems provide the ecological foundation that supports multi-billion dollar reef fishing and tourism industries vital to coastal and island economies (Burke and Maidens, 2004; C. I. (Conservation International), 2008; Pendleton, 2008). However, reef ecosystem goods and services are threatened by a rapidly growing regional human population, climate change, and serial over-exploitation (Waddell and Clarke, 2008; Wilkinson, 2008). Policies to protect coastal resources will be more effective if they account for the social and economic concerns of stakeholders in the watershed, and are responsive to potential tradeoffs among coastal resources or with other economic sectors such as agriculture or industry (Productivity Commission, 2003; Roebeling, 2006; Thomas et al., 2012). A key challenge is that reef monitoring efforts are largely focused on indicators of reef condition, such as coral cover and diversity, yet stakeholder concerns may be more appropriately quantified by health, social, or economic measures of factors such as subsistence from fisheries, opportunities for tourism or recreation, or coastal protection of property or lives during storm events (Cesar et al., 2003; Burke and Maidens, 2004). A quantitative link between attributes of reef condition and potential supply of ecosystem services will help identify meaningful indicators to compare decisions or monitor the success of their implementation, contribute to a conceptual link between coral condition and socio-economic relevance, and provide greater clarity in decision-making, including being able to estimate the potential consequences of alternative decisions on key stakeholder objectives (Yee et al., in press).

Insufficient scientific information can make it challenging to be able to estimate the consequences of potential management options. Coral reef modeling efforts to date have typically focused on the link between stressors and ecosystem condition, modeling a limited number of stressors such as land-based activities (Wolanski and De'ath, 2005), fishing pressure (Ault et al., 2005), or climate change (Buddemeier et al., 2008), and a few components of the ecosystem, such as reef fish or stony coral (e.g., McClanahan et al. (2007), Wakeford et al. (2008)). Other models

* Corresponding author. Tel.: +1 850 934 9397.
E-mail address: yee.susan@epa.gov (S.H. Yee).

2212-0416/$ - see front matter Published by Elsevier B.V.
http://dx.doi.org/10.1016/j.ecoser.2014.01.001

have included more ecosystem interactions, including interactions between coral, algae, herbivorous fish, and mangroves (Ault et al., 2003; McClanahan and Branch, 2008; Mumby and Hastings, 2008) and incorporate multiple stressors (Melbourne-Thomas et al., 2011). To be useful for decision-makers, however, the ecological endpoints of these models must be linkable to things stakeholders and decision-makers recognize as valuable (Wainger and Boyd, 2009). For coral reefs, development and application of production function methods is an essential step in the integration of models describing threats, coral reef dynamics, ecosystem services production, and socio-economic benefits (e.g. van Cesar (2004), Chang et al. (2008), Thomas et al. (2012)).

Two types of functional relationships are required to translate ecosystem state into human benefits: ecological production functions (EPF) and ecosystem services valuation functions (Wainger and Boyd, 2009; Compton et al., 2011). EPFs quantify the relationships between metrics of ecosystem condition and the supply of ecosystem goods and services. While ecosystem production functions describe the supply or provisioning of ecosystem services, the realized value of these benefits will depend on human demand for them (Wainger and Boyd, 2009). Ecosystem services valuation functions (EVF) relate characteristics of society, such as demand, accessibility, or substitutability, to derive value for ecosystem services (Compton et al., 2011). Numerous studies have developed and applied methods for estimating economic values for benefits received from coral reefs (reviewed in C. I. (Conservation International) (2008), Pendleton (2008)). Here, we evaluate methods for translating reef ecosystem condition into potential production of ecosystem goods and services.

A number of methods have been developed for linking biophysical attributes of reef condition, such as reef structural complexity, fish biomass, or species richness, to provisioning of ecosystem goods and services (Principe et al., 2012). We investigated the feasibility of using existing methods and data for mapping production of reef ecosystem goods and services. We applied these methods toward mapping potential ecosystem goods and services production in St. Croix, U.S. Virgin Islands (USVI). Spatially explicit methods are needed to quantify ecosystem services because supply and demand for ecosystem services are inherently spatially explicit and may differ geographically, such that mapping becomes a useful tool for communicating and supporting decision-making (Crossman et al., 2013).

Although coral reefs provide numerous economic benefits, to maximize the potential for transferability between locations, we focused on four categories of ecosystem services that are commonly identified as the four most valuable economic benefits: shoreline protection, tourism and recreation opportunities, fisheries production, and natural products potential (Principe et al., 2012). These were also key objectives of stakeholders identified in workshop discussions in the U.S. Virgin Islands, Florida, and Puerto Rico (Rehr et al., 2013; Carriger et al., 2013; Yee et al., In review). In addition to direct and indirect economic benefits from reefs, stakeholders also identified maximizing reef ecosystem integrity as a key objective (Carriger et al., 2013). Therefore, we also investigated metrics of reef ecosystem integrity, or how well the ecosystem is functioning, which may contribute to non-use values such as existence value, cultural value, or option value (Cesar, 2000; Principe et al., 2012). Finally, we examined the overall suite of ecosystem goods and services metrics to evaluate comparability across the different methods and to assess the extent to which different categories of ecosystem services produce similar spatial patterns.

2. Methods

Methods for linking reef condition to provisioning of ecosystem services have been described in a number of ways, including anecdotally, statistical analysis, bio-physical models, and surveys of stakeholder preferences (reviewed in Principe et al. (2012)). For each of the five categories of ecosystem services, we chose a suite of models and indices for estimating potential production based on relative ease of implementation, consisting of well-defined parameters, and likely availability of input data, to maximize potential for transferability to other locations. For each method, we assembled the necessary reef condition and environmental data as spatial data layers for St. Croix (Table 1). The coastal zone surrounding St. Croix was divided into 10×10 m grid cells, and production functions were applied to quantify ecosystem services provisioning in each grid cell.

2.1. Ecosystem services production functions

2.1.1. Ecosystem integrity

A number of indicators have been proposed for measuring reef integrity, defined as the capacity to maintain healthy function and retention of diversity (Turner et al., 2000). The Simplified Integrated Reef Health Index (SIRHI) combines four attributes of reef condition into a single index:

$$\mathrm{SIRHI} = \sum_i G_i \tag{I1}$$

where G_i are the grades on a scale of 1 to 5 for four key reef attributes: percent coral cover, percent macroalgal cover, herbivorous fish biomass, and commercial fish biomass (Table 2; Healthy Reefs Initiative, 2010). An alternative, but similar, indicator for reef ecological integrity (van Beukering and Cesar, 2004) defines the state of the reef as

$$\text{State of the Reef} = \sum_i w_i R_i \tag{I2}$$

where the R_i are the relative quantity of coral cover, macro-algal cover, fish richness, coral richness, and fish abundance, standardized to reflect the range of conditions at the location being evaluated (in this case, St. Croix). The w_i give the weighted contribution of each attribute to reef condition based on expert judgment, originally developed for Hawaii, which were $w_{\mathrm{coral\_cover}}=0.30$, $w_{\mathrm{algae\_cover}}=0.15$, $w_{\mathrm{fish\_richness}}=0.15$, $w_{\mathrm{coral\_richness}}=0.20$, and $w_{\mathrm{fish\_abundance}}=0.20$ (van Beukering and Cesar, 2004). Ideally, these values would be developed to reflect local knowledge and concerns for the Caribbean or St. Croix. Changes in the state of the reef are expected to have consequences for dive and snorkeling tourism, the value of homes and hotels in the vicinity of the reef, the reef's existence value or scientific value, and the probability of a bio-prospecting discovery (van Beukering and Cesar, 2004).

2.1.2. Shoreline protection

Shoreline protection as an ecosystem service has been defined in a number of ways including protection from shoreline erosion, storm damage, or coastal inundation during extreme events (UNEP-WCMC (United Nations Environment Programme, World Conservation Monitoring Centre), 2006; WRI (World Resources Institute), 2009), but is often quantified as wave energy attenuation, an intermediate service that contributes to shoreline protection by reducing rates of erosion or coastal inundation (Principe et al., 2012). Perhaps the simplest method to estimate shoreline protection is by defining the relative contribution of different habitat types to wave energy attenuation (Mumby et al., 2008). For each grid cell, we estimated the contribution of coral reefs to wave energy dissipation as the overall weighted average of the magnitude of wave energy dissipation across habitat types within that grid cell:

$$\text{Relative wave energy dissipation} = \sum_i c_i M_i \tag{S1}$$

where c_i is the fraction of area within each grid cell for each habitat type i (dense, medium dense, or sparse seagrass, mangroves, sand,

Table 1
The different methods applied to estimate ecological integrity, shoreline protection, recreation, fisheries, and natural products potential, and the reef condition attributes needed as input data for each. Methods for each include individual metrics (*M*), weighted indexes based on expert opinion (*I*), statistical models derived from field or survey data (*S*), and bio-physical process models (*P*).

Eq.	Ecosystem service metric	Method type	Wetland cover	Macroalgae cover	Reef type	Coral cover	Coral abundance	Coral richness	Coral rugosity	Fish biomass	Fish abundance	Fish richness	Sponge richness	Distance to shore	Reef depth
Ecosystem integrity															
(I1)	Simplified Reef Health Index	I		X		X				X					
(I2)	State of the Reef Index	I		X		X					X	X			
Shoreline protection															
(S1)	Relative wave dissipation	I	X	X	X	X									
$(S1)_{reef}$[a]	Relative wave dissipation by reef	I			X	X									
(S2)	Coral Reef Protection Index	I			X	X								X	
(S3)	Wave height attenuation	P		X		X								X	X
(S4)	Wave energy attenuation	P		X		X								X	X
$(S4)_{reef}$[b]	Wave energy attenuation by reef type	P			X	X								X	X
$(S4)_{height}$[b]	Wave energy attenuation	P				X			X					X	X
(S6)	Decrease in erosion	P		X		X								X	X
(S7)	Decrease in wave runup	P		X		X								X	X
Recreational opportunities															
(R1)	Relative ease of access	I	X	X	X	X									
(R2)	Relative sand generation	I	X	X	X	X									
(R3)	Relative density of *Epinephelus striatus*	I	X	X	X	X									
(R4)	Relative snorkeling opportunity	I	X	X	X	X									
$(R1)_{reef}$[a]	Relative ease of access to reef	I			X	X									
$(R2)_{reef}$[a]	Relative sand generation by reef	I			X	X									
$(R3)_{reef}$[a]	Relative density of *E. striatus* on reef	I			X	X									
$(R4)_{reef}$[a]	Relative snorkeling opportunity in reef	I			X	X									
(R5)	Value of a dive	S					X	X			X	X			
(R6)	Dive site favorability	S				X		X	X		X	X			
(R7)	Visitation to dive sites	S				X								X	
$(R7)_{topo}$[c]	Visitation to dive sites	S				X			X					X	
Fisheries production															
F1	Relative density of *Panulirus argus*	I	X	X	X	X									
(F2)	Relative density of *Strombus gigas*	I	X	X	X	X									
(F3)	Relative density of *E. striatus*	I	X	X	X	X									
(F4)	Relative presence of *Euchema*	I	X	X	X	X									
(F5)	Relative value of finfish	I	X	X	X	X									
(F6)	Relative curios/jewelry production	I	X	X	X	X									
$(F1)_{reef}$[a]	Relative density of *P. argus* on reef	I			X	X									
$(F2)_{reef}$[a]	Relative density of *S. gigas* on reef	I			X	X									
$(F3)_{reef}$[a]	Relative density of *E. striatus* on reef	I			X	X									
$(F4)_{reef}$[a]	Relative presence of *Euchema* on reef	I			X	X									
$(F5)_{reef}$[a]	Relative value of finfish on reef	I			X	X									
$(F6)_{reef}$[a]	Relative curios/jewelry production by reef	I			X	X									
(F7)	Mangrove connectivity	I	X			X									
(F8)	Key commercial fish biomass	M								X					

Table 1 (*continued*)

Eq.	Ecosystem service metric	Method type	Wetland cover	Macroalgae cover	Reef type	Coral cover	Coral abundance	Coral richness	Coral rugosity	Fish biomass	Fish abundance	Fish richness	Sponge richness	Distance to shore	Reef depth
Natural products															
(N1)	Bioprospecting potential	I		X		X					X	X			
(N2)	Sponge richness	M											X		
(N3)	Relative pharmaceutical product potential	I	X	X	X	X									
$(N3)_{reef}$[a]	Relative pharm. product potential by reef	I			X	X									

[a] Relative magnitudes of ecosystem service production were also calculated using only the contribution of coral reef habitats (patch reef, dense or sparse gorgonians, *Acropora palmata*, and *Montastraea*).
[b] Wave attenuation models were also calculated using estimates of reef friction based on broad classes of coral reef habitat (SLD, SHD, DLD, DHD; subscript "reef") or coral colony heights (Eq. (S5); subscript "height").
[c] Visitation to dive sites was also calculated estimating topography by standard deviation in depth.

macroalgae, *Acropora palmata*, *Montastraea* reef, patch reef, and dense or sparse gorgonians), and M_i is the relative magnitude of wave energy dissipation associated with each habitat type on a scale of 0–3 (Table 3).

Reef habitat alone, however, fails to consider other key factors including reef continuity and distance from shore that influence the degree of wave energy dissipation (WRI (World Resources Institute), 2009). An alternative index has been developed specifically for coral reefs, the Coral Reef Protection Index (CRPI), that accounts for the continuity of the reef and distance from shore in addition to reef habitat type (Burke et al., 2008):

$$\mathrm{CRPI} = \frac{\text{Reef type} + \text{Reef distribution} + \text{Reef distance}}{10} \times 4 \qquad \text{(S2)}$$

where the scaled magnitude of coastal protection due to each factor ranges from 0 (no protection) to 4 (very high protection; Table 2).

An alternative to weighted indices (Eqs. (S1) and (S2)) is to use bio-physical process models to more rigorously describe wave energy dissipation over a reef (Gourlay and Colleter, 2005). From earlier models Gourlay (1996, 1997), Sheppard et al. (2005) developed a tool that can be used to estimate the percent attenuation in wave energy or wave height due to the presence of the reef. The decay in wave heights over the reef is described by

$$\frac{dH_{rs}}{dx} = -\frac{f_w}{3\pi}\frac{{H_{rs}}^2}{(\overline{\eta}_r + h_r + \eta_w)^2} \qquad \text{(S3a)}$$

where H_{rs} is significant wave height, f_w is friction over the reef top, h_r is water depth over the reef flat, and η_w is meteorological surge. Wave set-up on the reef-flat, $\overline{\eta}_r$, is estimated iteratively using

$$\overline{\eta}_r = \frac{3}{64\pi}K_p\frac{g^{1/2}H_0^2T}{(\overline{\eta}_r + h_r + \eta_w)^{3/2}}[1 - 0.16S^2] \qquad \text{(S3b)}$$

where K_p is the reef profile, g is the gravitational acceleration constant ($9.81\ \mathrm{m\ s^{-2}}$), H_0 is the wave height offshore, T is the wave period offshore, and S is the relative submergence of the reef, given by $(\overline{\eta}_r + h_r)/H_0$. The energy in a moving wave (E) can then be calculated by

$$E = \frac{1}{8}\rho g H^2 \qquad \text{(S4)}$$

where ρ is the density of seawater ($1025\ \mathrm{kg\ m^{-3}}$) and H is wave height. The reef profile factor, K_p, is related to the angle of the slope of the reef face (Sheppard et al., 2005) and can be determined from the angle between adjacent grid cells, oriented from seaward to shore, determined by the difference in reef height (or water depth) between adjacent cells. As modeled waves travel toward shore, each grid cell makes some contribution to overall wave height or energy attenuation reaching the shoreline.

Reef friction (f_w), associated with the degree of topography over the reef flat, is a strong determinant of the degree of wave energy attenuation, with reefs producing as much as 10 times the amount of drag as sandy bottoms (Monismith, 2007). We explore three options for calculating friction. First, the percent cover of benthic habitat within each cell, in particular live coral or uneroded dead coral, can be used to define f_w from 0.08 to 0.20 (Sheppard et al., 2005). Dead, or partially dead, coral colonies are assumed to have a comparable ability to attenuate waves as live coral, as long as dead coral are uneroded. Second, coral reef habitat can be categorized into four broad classes to assign values to parameters and estimate wave energy attenuation by reef type (Table 2; van Beukering et al., 2011): shallow, low density habitat (SLD; $f_w = 0.14$, $h_r = 1.8$ m); shallow, high density habitat (SHD; $f_w = 0.18$, $h_r = 2.5$ m); deep, low density habitat (DLD; $f_w = 0.14$, $h_r = 15$ m); deep, high density habitat (DHD; $f_w = 0.18$, $h_r = 15$ m). Third, estimates of reef rugosity or variability in coral heights along the reef can be used to more directly estimate f_w (Lowe et al., 2005). Wave energy attenuation (Eqs. (S3) and (S4)) is calculated but with f_w estimated by measures of coral rugosity,

Table 2
Relative weightings of different reef characteristics toward provisioning of ecosystem service metrics (SIRHI weightings from Healthy Reef Initiative 2010; CRPI weightings from Burke et al. (2008)).

Eq.	Ecosystem service metric Input variable	Magnitude				
		Very good (5)	Good (4)	Fair (3)	Poor (2)	Critical (1)
(I1)	SIRHI score					
	Coral cover (%)	≥ 40	20.0–39.9	10.0–19.9	5.0–9.9	< 5
	Fleshy macroalgal cover (%)	0–0.9	1.0–5.0	5.1–12.0	12.1–25	> 25.0
	Key herbivorous fish (g/100 m^2)	≥ 3480	2880–3479	1920–2879	960–1919	< 960
	Key commercial fish (g/100 m^2)	≥ 1680	1260–1679	840–1259	420–839	< 420
		Very high (4)	High (3)	Medium (2)	Low (1)	None (0)
(S2)	CRPI score					
	Reef type	Barrier	Patch	Fringe	Other	No reef present
	Reef distribution	N/A	N/A	Continuous	Discontinuous	No reef present
	Reef distance (m)	< 250	250–500	500–1000	> 1000	No reef present
		Very high (95.5%)	High (90.0%)	Medium (38.0%)	Low (32.0%)	None (0%)
$(S4)_{reef}$	Wave energy attenuation by reef type					
	Reef type	High density	Low density	High density	Low density	No reef present
	Reef depth (m)	≤ 8	≤ 8	> 8	> 8	No reef present
	Reef distance (m)	≤ 1750	≤ 1750	≤ 1750	≤ 1750	> 1750

Notes: For SIRHI weightings (source: Healthy Reefs Initiative (2010)), key herbivorous fish included only parrotfish and surgeonfish; key commercial fish included only snapper and grouper. For CRPI weightings (source: Burke et al. (2008)), barrier reefs were defined by linear reefs in NOAA benthic habitat maps; patch reefs were defined as aggregated patch reefs or spur and groove reefs; fringe reefs were defined as reef habitat with 1 km of shore; and other reefs were all other reef habitats; No reef was present if predicted hardcoral cover was less than 10%; continuous reefs were assumed to have coral cover greater than 50%. For wave energy attenuation (source: van Beukering et al. (2011)), high density coral reefs were defined by linear or spur and groove reefs; low density reefs were defined by colonized bedrock or pavement, aggregated patch reef, or scattered coral rock; offshore wave height assumed $H_0 = 27.36$ m; offshore wave period assumed $T = 11.19$ s; swell assumed $\eta_w = 4$ m; reef profile assumed $K_p = 1$.

Table 3
Relative weightings of the contribution of different habitat types from 0 (none) to 3 (highest) toward provisioning of ecosystem services (from Mumby et al. (2008)).

Eq.	Ecosystem service metric	Mangroves	Dense sea grass	Medium density sea grass	Sparse sea grass	Sand	Macroalgal dominated	Patch reef	*A. palmata*	Dense gorgonians	Sparse gorgonians	*Montastraea* reef
(S1)	Wave energy dissipation	3	0	0	0	0	0	0	3	2	2	2
(R1)	Ease of access for education	3	3	3	1	1	1	3	2	1	1	1
(R2)	Sand generation	0	0	0	0	0	2	1	3	1	1	3
(R3) and (F3)	Density of *E. striatus*	3	1	1	0	0	3	0	0	2	3	3
(R4)	Opportunity for snorkeling	0	0	0	1	3	1	3	2	1	1	3
(F1)	Density of *P. argus*	3	3	2	0	0	3	3	1	1	1	3
(F2)	Density of *S. gigas*	0	3	3	3	3	1	1	1	0	1	0
(F4)	Presence of *Euchema*	0	2	3	3	1	0	1	0	0	0	0
(F5)	Value of finfish	1	1	1	2	1	2	1	3	1	1	3
(F6)	Production of curios and jewelry	0	2	3	2	0	1	3	1	1	1	3
(N3)	Pharmaceutical products	3	1	1	0	0	1	1	1	1	1	3

namely the standard deviation in colony heights (σ_r) as

$$f_w = \exp\left[5.5\left(\frac{A}{k_w}\right)^{-0.2} - 6.3\right], \; k_w \approx 4\sigma_r \tag{S5a}$$

where k_w is the hydraulic roughness length. The wave orbital diameter, A, is calculated as

$$A = \frac{H}{2\sinh((\bar{\eta}_r + h_r + \eta_w) \times (2\pi/L))} \tag{S5b}$$

where L, the wavelength, is estimated by

$$L = \frac{gT^2}{2\pi}\sqrt{\tanh\left(\frac{4\pi^2(\bar{\eta}_r + h_r + \eta_w)}{T^2 g}\right)} \tag{S5c}$$

where T is wave period.

The degree of wave energy and wave height attenuation over the reef has important consequences for the degree of wave run-up onto shore (Hughes, 2004; Wielgus et al., 2010). The proportional change in rates of sand transport, or erosion, from a beach is roughly equivalent to a power of the proportional increase in wave height (Dean and Galvin, 1976; CETS (Commission on Engineering and Technical Systems of the National Research Council), 1987), and can thus be estimated as

$$\%\ \text{Decrease in erosion due to reef} = 1 - \left(\frac{H_0}{H}\right)^{2.5} \tag{S6}$$

where H_0 is the attenuated wave height due to the presence of the reef and H is wave height in the absence of the reef. The probability of flooding during extreme storm events will depend on the degree of wave run-up onto shore, as well as the slope and porosity of the shoreline (FEMA (Federal Emergency Management Agency), 2007; Hughes, 2004). Wave run-up, R, can be estimated as

$$\frac{R}{H}=1.0\frac{\tan\ \alpha}{\sqrt{H/H_0}} \tag{S7}$$

where H is the wave height nearshore, H_0 is the deepwater wave height, and α is the angle of the beach slope. R may be corrected by a multiplier depending on the porosity of the shoreline surface (FEMA (Federal Emergency Management Agency), 2007). The relative reduction in wave run-up is then $(1-R_{reef}/R_{no\ reef})\times 100\%$, where R is calculated in either the presence or the absence of the reef. The contribution of each grid cell to reduction in wave run-up would depend on its contribution to wave height attenuation (Eq. (S3)).

2.1.3. Recreational opportunities

A number of recreational activities are associated directly or indirectly with coral reefs including scuba diving, snorkeling, surfing, underwater photography, recreational fishing, wildlife viewing, beach sunbathing and swimming, and beachcombing (Principe et al., 2012). Non-natural factors, such as income and crowding, also influence recreational (Brander et al., 2007), however here we focus on the contribution of reef habitats and biota. Synthesis of scientific literature and expert opinion can be used to estimate the relative potential for recreational opportunities across different benthic habitat types (Mumby et al., 2008). For each grid cell, we estimated the contribution of coral reefs to recreational opportunities as the overall weighted average of relative magnitudes of contribution across habitat types within that grid cell:

$$\text{Relative recreational opportunity } j=\sum_i c_i M_{ij} \tag{R1–R4}$$

where c_i is the fraction of area within each grid cell for each habitat type i (dense, medium dense, or sparse seagrass, mangroves, sand, macroalgae, *A. palmata*, *Montastraea* reef, patch reef, and dense or sparse gorgonians), and M_{ij} is the magnitude associated with each habitat for a given metric j: (1) ease of access for education, (2) sand generation, (3) density of the grouper *Epinephelus striatus*, and (4) opportunities for bonefishing, snorkeling, and swimming (Table 3).

Another method to quantify recreational opportunities is to use survey data of tourists and recreational visitors to the reefs to generate statistical models to quantify the link between reef condition and production of recreation-related ecosystem services. Wielgus et al. (2003) used interviews with SCUBA divers in Israel to derive coefficients for a choice model in which willingness to pay for higher quality dive sites was determined in part by a weighted combination of factors identified with dive quality:

$$\text{Relative value of dive site} = 0.1227(S_{coral}+S_{fish}+A_{coral}+A_{fish})+0.0565V \tag{R5}$$

where S_{coral}, S_{fish} are coral and fish richness, A_{coral}, A_{fish} are abundances of fish and coral per square meter, and V is water visibility (meters). A number of survey studies have found water visibility, living coral, fish and sea life variety (Leeworthy et al., 2004), as well as sponges, unusual or large fish or coral, and reef structure (Williams and Polunin, 2002) to be important to reef visitors and recreational divers. However, where metrics used in surveys were not clearly defined (e.g., unusual fish), we could not include them in this study.

In lieu of surveys of diver opinion, recreational opportunities can also be estimated by actual field data of coral condition at preferred dive sites. A few studies have directly examined links between coral condition and production of recreational opportunities through field monitoring in an attempt to validate perceptions of recreational quality (Pendleton, 1994; Williams and Polunin, 2002; Leeworthy et al., 2004; Leujak and Ormond, 2007; Uyarra et al., 2009). Uyarra et al. (2009) used surveys to determine reef attributes related to diver perceptions of most and least favorite dive sites. Field data was used to narrow down the suite of potential preferred attributes to those that reflected actual site condition. We combined these attributes to form an index of dive site favorability:

$$\text{Dive site favorability}=\sum_i p_i R_i \tag{R6}$$

where p_i is the proportion of respondents indicating each attribute i that affected dive enjoyment positively. R_i is the mean relative magnitude of measured variables used to quantify each descriptive attribute i, including 'fish abundance' ($p_i=0.803$), quantified by number of fish schools and fish species richness, and 'coral condition' ($p_i=0.746$), quantified by percent live coral, percent rubble, coral species richness, and structural complexity, which were standardized to reflect the range of conditions for St. Croix.

Pendleton (1994) used field observations of dive sites to model potential impacts on local economies due to loss of dive tourism with reef degradation. A key part of the diver choice model is a fitted model of visitation to dive sites described by

$$\text{Visitation to dive sites}=2.897+0.0701\ c_{reef}-0.133D+0.0417\tau \tag{R7}$$

where c_{reef} is percent coral cover, D is the time in hours to the dive site, which we estimate using distance from reef to shore and assuming a boat speed of 5 knots or 2.57 m s^{-1}, and τ is a dummy variable for the presence of interesting topographic features. We interpret τ as dramatic changes in bathymetry, quantified as having a standard deviation in depth among grid cells within 30 m that is greater than the 75th percentile across all grid cells. Because our interpretation of topography differed from the original usage of "interesting features", we also calculated dive site visitation assuming no contribution of topography ($\tau=0$). Unsightly coastal development, an additional but non-significant variable in the original model, was assumed to be zero for St. Croix.

2.1.4. Fisheries production

We broadly consider fisheries production to include harvesting of aquatic organisms as seafood for human consumption (NOAA (National Oceanic and Atmospheric Administration), 2009; Principe et al., 2012), as well as other non-consumptive uses such as live fish or coral for aquariums (Chan and Sadovy, 2000), or shells or skeletons for ornamental art or jewelry (Grigg, 1989; Hourigan, 2008). The density of key commercial fisheries species and the value of finfish can be associated with the relative cover of key benthic habitat types on which they depend (Mumby et al., 2008). For each grid cell, we estimated the contribution of coral reefs to fisheries production as the overall weighted average of relative magnitudes of contribution across habitat types within that grid cell:

$$\text{Relative fisheries production } j=\sum_i c_i M_{ij} \tag{F1–F6}$$

where c_i is the fraction of area within each grid cell for each habitat type i (dense, medium dense, or sparse seagrass, mangroves, sand, macroalgae, *A. palmata*, *Montastraea* reef, patch reef, and dense or sparse gorgonians), and M_{ij} is the magnitude associated with each habitat for a given metric j: (1) density of the spiny lobster *Panulirus argus*, (2) density of the queen conch *Strombus gigas*, (3) density of grouper (*E. striatus*), which was also associated with recreational opportunity (Eq. (R1)–(R5)), (4) density of *Euchema* sp. seaweed, (5) value of finfish, and (6) production of curios and jewelry associated with each habitat (Table 3).

An alternative method to estimate potential fisheries production is to quantify not just the percent coverages of key habitats (F1)–(F6), but the degree of connectivity among those habitats. Many species that utilize coral reef habitat as adults are dependent on mangrove or seagrass nursery habitats as juveniles (Nagelkerken et al., 2000; Dorenbosch et al., 2006). In the Caribbean, the community structure or adult biomass of more than 150 reef fish species was affected by the presence of mangroves in the vicinity of reefs (Mumby et al., 2004). The value of habitat for fish production will therefore depend on the degree of connectivity between reefs and nearby mangroves (Mumby, 2006) and can be estimated as

$$C_{ij} = D - \sqrt{(|m_{ix} - r_{ix}|)^2 + (|m_{jy} - r_{jy}|)^2} \quad \text{(F7)}$$

where C_{ij} is the connectivity between each reef cell i and nearby mangrove cell j, and D is the maximum migratory distance between mangroves and reefs (assumed to be 10 km), weighted by the distance between cells (x,y coordinates) such that shorter distances result in greater connectivity. The row sums then give the total connectivity of each reef cell to mangroves.

In lieu of quantifying potential fish habitat (Eqs. (F1)–(F6) and (F7)), fish production is often assessed more directly through monitoring of commercially important fish species populations over time (Ault et al., 2005; McField and Kramer, 2007; Paddack et al., 2009). A number of indicators of fisheries production are directly monitored as attributes of reef condition, including fish abundance, fish size, conch abundance, lobster abundance, or the biomass of commercially important species (McField and Kramer, 2007). Assessments of commercial fish biomass have been considered an important indicator of reef health (Healthy Reefs Initiative, 2010) and can be quantified as

$$\text{Key commercial fish biomass} = \sum_i B_i \quad \text{(F8)}$$

where B_i is the biomass of two commercial fish groups, snappers and groupers.

2.1.5. Natural products

Coral reef ecosystems are the source for a large number of pharmaceuticals, biochemicals, and biomaterials (Fenical, 1997; Gerwick, 2008; Principe et al., 2012). A healthy reef with high biodiversity may increase the probability that any given species could be the source of a marketable product. As such, the probability of a bio-prospecting discovery may be represented as directly proportional to the state of the reef (van Beukering and Cesar, 2004):

$$\text{Potential for bioprospecting} = \sum_i w_i R_i \quad \text{(N1)}$$

where R_i are the relative quantity of coral cover, macro-algal cover, fish richness, coral richness, and fish abundance, standardized to reflect the range of conditions at St. Croix, and the w_i give the weighted contribution of each attribute to reef condition based on expert judgment (see Eq. (I2)).

An alternative to quantifying bioprospecting potential by reef quality (N1) is to specifically target faunal groups that are more likely to provide biochemical sources. Among marine phyla, sponges (Porifera) and their symbiont bacteria have contributed more than 60% of marine secondary metabolites with pharmaceutical potential (Hunt and Vincent, 2006). Consequently, sponge diversity and abundance may be a good indicator of the potential for pharmaceutical products:

$$\text{Sponge richness} \propto \text{Pharmaceutical product potential} \quad \text{(N2)}$$

When data on sponge diversity is unavailable, benthic habitat coverages may be used to estimate relative magnitudes of sponge diversity and abundance as an indicator of potential pharmaceutical production (Mumby et al., 2008). For each grid cell, we estimated the contribution of coral reefs to potential pharmaceutical production as the overall weighted average of relative magnitudes of contribution across habitat types within that grid cell:

$$\text{Pharmaceutical product potential} = \sum_i c_i M_i \quad \text{(N3)}$$

where c_i is the fraction of area within each grid cell for each habitat type i (dense, medium dense, or sparse seagrass, mangroves, sand, macroalgae, *A. palmata*, *Montastraea* reef, patch reef, and dense or sparse gorgonians), and M_i is the relative magnitude of sponge diversity associated with each habitat.

2.2. Environmental and biological condition data

2.2.1. Environmental and habitat data

A total of 41 production function methods were identified for translating attributes of coral reef condition into ecosystem services provisioning for St. Croix (Table 1). Spatial data layers on habitat and environmental data needed to apply each method were assembled for St. Croix and corresponding values extracted for each 10 × 10 m grid cell. Bathymetry data, obtained from NOAA National Geophysical Data Center (10 × 10 m resolution), was used to characterize reef height and slope for shoreline protection models (K_p, h_r; Eqs. (S3a), (S3b)–(S5a), (S5b), (S5c)) and topography for estimating recreational quality (Eq. (R7)). Daily estimates of offshore significant wave height and period were obtained from NOAA Wavewatch III model predictions (4 arc minute grid), and used to estimate the wave height and period (H_0, T; Eqs. (S3a), (S3b)–(S5a), (S5b), (S5c)) as the average of the highest 1% of all waves in order to estimate attenuation under an extreme 100-year storm event (FEMA (Federal Emergency Management Agency), 2007; van Beukering et al., 2011). The contribution of wave height by swell during an extreme event (η_W; Eqs. (S3a), (S3b)–(S5a), (S5b), (S5c)) was estimated by assuming frequencies less than $0.9 \times 1.25/U_{10}$ were swell (Gilhousen and Hervey, 2001), where U_{10} is windspeed (m/s), also obtained from NOAA Wavewatch III. Water visibility was estimated by converting the diffuse attenuation coefficient Kd_{490}, obtained from NASA Ocean Color Web (1 × 1 m resolution), to meters of visibility assuming $Kd_{490} = 1.44 \times (1/SD)$, where SD is observed Secchi depth (Schaeffer et al., 2011). Reef type (Eq. (S2), $(S4)_{reef}$; Table 2) was characterized from NOAA benthic habitat maps (NOAA, 2001).

2.2.2. Predictive models of reef condition

For a number of coral reef condition attributes, including fish richness, coral richness, and reef structural complexity, available data were point surveys from field monitoring by the US Environmental Protection Agency (see Oliver et al. (2011)) or the NOAA Caribbean Coral Reef Ecosystem Monitoring Program (see Pittman et al. (2008)). To generate continuous maps of coral condition for St. Croix, we fitted regression tree models to point survey data for St. Croix and then used models to predict reef condition in non-sampled locations (Fig. 1). In general, we followed the methods of Pittman et al. (2007) which generated predictive models for fish richness using readily available benthic habitat maps and bathymetry data. Because these models rely on readily available data (benthic habitat maps and bathymetry data), the models have the potential for high transferability to other locations where monitoring data may be sparse.

We fitted regression tree models (Venables and Ripley, 2002) to point survey data using a number of predictor variables. Regression trees are an effective technique when there are potential nonlinearities or collinearities in data, and provide a set of decision rules to classify data. Regression trees use an algorithm to split the

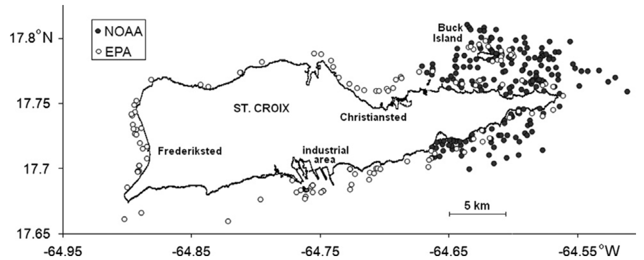

Fig. 1. Locations of NOAA and EPA point survey data for coral reef condition metrics.

response data into groups based on association with a predictor variable. To compensate for overfitting, the optimal tree size should include only the most significant predictor variables. A sequence of trees were generated using 10-fold cross validation (Venables and Ripley, 2002), and the final model was selected as the smallest tree within one standard error of the tree with the minimum error rate. Regression trees were run using the library "tree" in *R* (www.r-project.org).

We examined a number of environmental predictor variables likely to contribute to attributes of reef ecosystem condition, including bathymetry, habitat rugosity, and percent cover of benthic habitat types (Pittman et al., 2007). Data were examined at a spatial resolution of 10 × 10 m. Mean bathymetry, standard deviation of bathymetry, and percent cover of benthic habitat types were estimated in a series of increasing spatial extents around each point survey location (cells = 1 × 1 [100 m^2]; 3 × 3 [900 m^2]; 5 × 5 [2500 m^2]; 9 × 9 [8100 m^2]; 17 × 17 [28,900 m^2]; 33 × 33 [108,900 m^2]; 65 × 65 [422,500 m^2]). In addition, mean field estimates of rugosity for each habitat type (e.g., seagrass, sand, scattered coral, linear reef, patch reef) were used to estimate mean habitat rugosity in each spatial extent (Pittman et al., 2007). Mean rugosity values of soft sediment habitats or hardbottom habitats were used to fill in habitat types (e.g., mangroves, spur and groove reefs) not quantified by Pittman et al. (2007). In addition to bathymetry and habitat, we also included predictor variables related to human disturbance: the landscape development intensity index in the coastal zone of the survey (Oliver et al., 2011) and a binary variable as to whether or not the survey was located within a marine protected area, for which delineations were obtained from NOAA MPA Inventory. We also included the Euclidian distance from the survey site to the nearest point on the shoreline and to the shelf edge where the shallow water steeply declines to deep ocean. These metrics reflect across-shelf location and are known to be predictive of fish distribution (Pittman and Brown, 2011). Finally, because fish abundance and richness may be related to coral condition (Gratwicke and Speight, 2005; Wilson et al., 2007), once models were developed for hard coral cover, abundance, richness, and height variability, we included predicted estimates of these variables at each survey location as additional predictor variables to estimate fish density, biomass, and richness.

Where possible, EPA's 2006–2007 St. Croix field survey data was used to develop models because of its broader spatial extent (Fig. 1; Table 4). To test for spatial autocorrelations, we calculated Moran's index and visually assessed semi-variograms (Pittman et al., 2007). Spatial autocorrelation was relatively low, with high co-variances among surveys only at short distances. Predictive accuracy was first assessed by using coefficients of determination (R^2) to measure the strength of the association between observed data and predicted data. Second, we constructed receiver-operating characteristic curves for each class predicted by regression tree models, and calculated the area under the curve (AUC) to calculate predictive performance (Pittman et al., 2007). Finally, we used fitted models to predict reef condition at locations in an independent data set and calculated the AUC to quantify the ability of models to predict the observed class of data. Models fit to EPA 2006–2007 data were validated using NOAA 2010 data, and models fit to NOAA 2010 data were fit using NOAA 2006–2007 data, which was collected only around Buck Island.

Table 4
Results from regression trees fitted to EPA or NOAA survey data, including the number of nodes in the most parsimonious tree, goodness of model fit (R^2), and classification accuracy (AUC) for both the data used to fit the model and an independent data used for model validation.

Variable	Data source	Fitted model			Validation data
		Nodes	R^2	AUC	AUC
Sand + fine sediments (% cover)	NOAA	6	0.811	0.752	0.715
Rubble (% cover)	NOAA	3	0.250	0.793	0.695
Hardbottom (% cover)	NOAA	2	0.167	0.694	0.650
Turf algae (% cover)	NOAA	6	0.829	0.835	0.656
Seagrass (% cover)	NOAA	4	0.758	0.918	0.944
Macroalgae (% cover)	NOAA	5	0.516	0.799	0.713
Gorgonians (% cover)	NOAA	4	0.466	0.759	0.670
Hardcoral (% live cover)	EPA	6	0.644	0.749	0.678
Live hardcoral cover/total hardcoral cover	EPA	2	0.138	0.847	–
Montastraea cover/total hardcoral cover	EPA	3	0.445	0.786	0.534
A. palmata cover/total hardcoral cover	EPA	2	0.192	0.964	0.951
Sponge (% cover)	NOAA	4	0.553	0.779	0.672
Sponge richness/m^2	NOAA	4	0.604	0.779	0.718
Coral abundance/100 m^2	EPA	6	0.667	0.687	0.716
Coral richness/100 m^2	EPA	6	0.657	0.682	0.721
Standard deviation in coral heights	EPA	4	0.376	0.749	–
Fish richness/100 m^2	NOAA	5	0.738	0.732	0.658
Fish abundance/100 m^2	NOAA	5	0.628	0.805	0.682
Fish schools	NOAA	4	0.630	0.830	0.685
Key herbivorous fish biomass (g/100 m^2)	NOAA	6	0.500	0.728	0.631
Key commercial fish biomass (g/100 m^2)	NOAA	4	0.315	0.872	0.814

Because EPA 2006–2007 survey data and NOAA 2010 survey data were collected using different metrics and at different spatial resolutions, we implemented some correction factors to allow comparability between datasets where possible. We developed a scaling factor to translate coral species richness at 1 m^2 (S_1) to larger areas (S_A) so that we could compare coral richness at 1 m^2 (NOAA) to 25.1 m^2 (EPA) to 100 m^2 (10 × 10 m spatial resolution for model predictions). The scaling factor was developed by fitting a species-area curve, $S_A/S_1 = A^z$ (Scheiner et al., 2000), to a hierarchical subset of the EPA coral richness data from 2006, collected at 12.5 m^2, 25.1 m^2, and 50.2 m^2 (fitted model: $z = 0.509$; $R^2 = 0.856$). Estimates of coral density (numbers per m^2) and percent cover were assumed to be linearly scalable from 1 m^2 to 25.1 m^2 to 100 m^2. For EPA data, we generated estimates of hard coral cover by using measured coral colony diameters to estimate coral colony area (Area = π × radius^2), and summing over the total number of measured colonies. Percent hard coral cover was then estimated as total colony area/25.1 m^2. Percent live coral cover was similarly generated using colony diameters, except estimates of percent live tissue for each colony were used to estimate live coral colony area.

2.3. Mapping and comparing ecosystem services methods

We applied production functions to produce maps of ecosystem services provisioning by reefs surrounding St. Croix. Specifically, for each identified method (Table 1) we used spatial data layers on attributes of reef condition (Table 4) and environmental variables to quantify ecosystem services provisioning in each 10×10 m grid cell in the coastal waters surrounding St. Croix. The statistical package *R* (www.r-project.org) was used for all calculations and maps were produced using function 'spplot' in package 'sp'.

To evaluate consistency across the different ecosystem services methods, we took a random subsample of 5% of grid cells and calculated Spearman rank correlation coefficients among metrics within each of the five ecosystem service categories, as well as across categories. We used principal components analysis (PCA) on the subsample of grid cells to evaluate whether ecosystem services metrics were responding in a similar, opposite, or independent manner across space. PCA is a multivariate ordination technique that can be used to convert a set of potentially correlated variables into a set of uncorrelated principal component factors (Quinn and Keough, 2002). Metrics were normalized (mean=0, standard deviation=1) prior to analysis because of the wide range in values across metrics. Analyses were run using the "rda" function of package "vegan" in *R*.

2.4. Validating predictions of ecosystem services methods

Evaluating the predictive accuracy of production function methods is challenging because in general there is little available data on production of ecosystem services at reef sites. However, observational data on human use of the reef can provide some insight as to whether methods are giving reasonable predictions (Fig. 2). To assess accuracy of methods quantifying recreational opportunities (Eqs. (R1)–(R4) to R7), we mapped the locations of popular dive and snorkeling locations (www.stcroixtourism.com). Accuracy of fisheries production methods ((F1)–(F6) to (F8)) was assessed by comparing to major fishing areas for dive fishing, currently the dominant method around St. Croix (NMFS (National Marine Fisheries Service), 2007; Valdés-Pizzini et al., 2010). Natural products potential ((N1)–(N3)) was evaluated by comparing survey locations for which known sources of natural products, including sponges, tunicates, the coral *Erythropodium caribaeorum*, red algae of the genus *Laurencia*, sharks, or gorgonians (Principe et al., 2012), had been observed, compiled using the Ocean Biogeographic Information System (IOBIS, www.iobis.org). Recent data in IOBIS (2000–2010) was almost exclusively derived from the NOAA Caribbean Coral Reef Ecosystem Monitoring Program (Pittman et al., 2008), so to reduce confounding presence/absence with sampling effort, we limited our comparisons to presence/absence of key source species within the NOAA 2010 survey data. Ecosystem integrity (Eqs. (I1) and (I2)) was expected to be higher in areas protected from fishing, vessels, and anchoring, namely Buck Island National Monument. For shoreline protection (Eqs. (S1)–(S7)), we compared the predictions of our relatively simple models to estimates of wave attenuation between adjacent grid cells in the high resolution Simulating Waves Nearshore (SWAN) model, obtained for 2010–2011 from the Caribbean Coastal Ocean Observing System (www.caricoos.org). Wave height attenuation between grid cells for the SWAN model was estimated assuming a trajectory perpendicular to shore and calculating the maximum observed attenuation for each grid cell as the percent reduction in wave height between adjacent grid cells. We expected a correspondence between cells with a high percentage decrease in wave height predicted by the SWAN model, and cells predicted to have high shoreline protection as estimated by the production function methods.

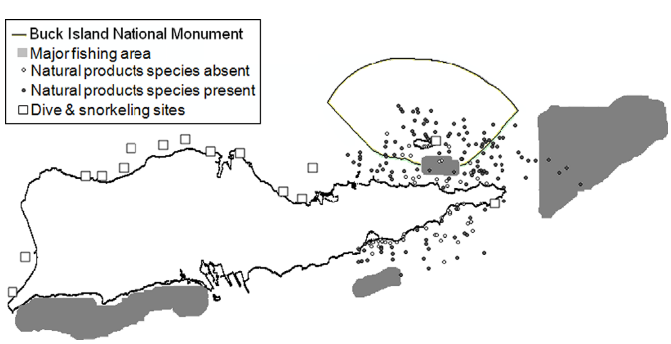

Fig. 2. Maps of popular dive and snorkeling locations (squares), surveys in which known sources for natural products were either present (filled circles) or absent (open circles), major areas for fishing (grey areas), and spatial delineation of Buck Island National Monument (line), used for validating ecosystem service production function methods for recreational opportunities, natural products potential, fisheries production, and ecological integrity. Refer to text for source data.

For each ecosystem services production function method, we tested whether predicted values of ecosystem service production were significantly higher in areas of human use using one-tailed *T*-tests. In other words, we tested whether predicted values of ecosystem integrity, recreational opportunities, fisheries production, or natural products potential were significantly higher in, respectively, marine protected areas, popular dive locations, major fishing areas, and surveys in which natural products sources were present. For metrics of shoreline protection, we used Spearman rank correlation coefficients to evaluate whether predictions of our methods were significantly correlated with predictions of the high resolution SWAN model.

2.5. Application of ecosystem services mapping

To demonstrate a potential application of ecosystem services mapping, we assessed whether potential ecosystem services provisioning declined in correspondence with observed declines in reef condition along a human disturbance gradient (Fisher et al., 2008). Three locations around St. Croix are known to have visible human activity on the adjacent land and near-shore environment: (1) the city of Frederiksted in the west, which generates potential stresses from a sewage overflow line, small boat traffic, and intermittent cruise ship activity, (2) urban development around Christiansted in the north, including small boat traffic and point and non-point source disturbances, and (3) the industrial area in the south, which included a dredged commercial ship channel, airport, and a number of industries (Fig. 1).

We randomly subsampled 5% of grid cells and calculated the distance to the nearest point of disturbance. Locations within 2 km of Buck Island National Monument, northeast of St. Croix, were also targeted for comparison due to the relative absence of direct human disturbance. For each location, we calculated the potential ecosystems services production for each metric, scaled from 0 to 1, so that we could combine them to calculate a grand total production value across all methods for each location.

3. Results

3.1. Correspondence among ecosystem service metrics

Predictive regression tree models were used to produce maps of characteristics of reef condition in each 10×10 m grid cell around St. Croix (Table 4). In general, regression tree models had relatively good fit ($R^2 > 0.5$) and accuracy in replicating data (AUC > 0.7). Spatial data layers on reef condition, as well as environmental data such as bathymetry and offshore waves, were applied as input data to estimate ecosystem services production for the 41 identified methods (Table 5). Example maps for each ecosystem services category are shown in Fig. 3. Principal components analysis reduced the 41 different methods into 3–5 PC

Table 5
Predicted mean and standard deviation across all spatial grid cells around St. Croix for ecosystem services estimated by each method (see Table 1), and statistical comparison by either *T*-test or Spearman correlation coefficient (*R*) comparing model predictions to observational data.

Eq.	Ecosystem service metric	Min	Mean	Max	*T*-statistic	*R*
Ecosystem integrity						
(I1)	Simplified Reef Health Index	1.00	2.27	4.00	33.1***	
(I2)	State of the Reef Index	0.00	0.41	0.87	19.4***	
Shoreline protection						
(S1)	Relative wave dissipation	0.00	0.10	1.70		−0.32NS
$(S1)_{reef}$	Relative wave dissipation by reef	0.00	0.10	0.50		−0.32NS
(S2)	Coral Reef Protection Index	0.00	0.77	3.60		0.05***
(S3)	Wave height attenuation (%)	0.00	0.70	70.3		0.52***
(S4)	Wave energy attenuation (%)	0.00	0.60	88.4		0.51***
$(S4)_{reef}$	Wave energy attenuation by reef type (%)	0.00	12.7	95.5		0.28***
$(S4)_{height}$	Wave energy attenuation (%)	0.00	0.80	88.9		0.54***
(S6)	Decrease in erosion (%)	0.00	1.70	95.2		0.52***
(S7)	Decrease in wave runup (%)	0.00	0.40	45.5		0.52***
Recreational opportunities						
(R1)	Relative ease of access	0.20	0.70	2.50	5.8***	
(R2)	Relative sand generation	0.10	0.30	1.50	0.8NS	
(R3)	Relative density of *E. striatus*	0.10	0.30	2.10	−2.1NS	
(R4)	Relative snorkeling opportunity	0.30	1.20	2.80	17.3***	
$(R1)_{reef}$	Relative ease of access to reef	0.10	0.30	2.20	6.6***	
$(R2)_{reef}$	Relative sand generation by reef	0.00	0.20	1.00	16.7***	
$(R3)_{reef}$	Relative density of *E. striatus* in reef	0.00	0.10	0.80	25.8***	
$(R4)_{reef}$	Relative snorkeling opportunity in reef	0.10	0.40	2.30	9.7***	
(R5)	Value of a dive	6.36	28.9	63.5	−31.1NS	
(R6)	Dive site favorability	0.00	0.41	0.90	−2.5NS	
(R7)	Visitation to dive sites (boats/site)	3.17	3.74	6.35	7.6***	
$(R7)_{topo}$	Visitation to dive sites (boats/site)	3.17	3.73	6.31	6.4***	
Fisheries production						
(F1)	Relative density of *P. argus*	0.20	0.60	2.50	27.4***	
(F2)	Relative density of *S. gigas*	0.20	1.00	2.80	45.7***	
(F3)	Relative density of *E. striatus*	0.10	0.30	2.10	−47.8NS	
(F4)	Relative presence of *Euchema*	0.10	0.40	2.20	61.7***	
(F5)	Relative value of finfish	0.20	0.60	1.70	36.5***	
(F6)	Relative curios/jewelry production	0.20	0.60	2.50	−4.3NS	
$(F1)_{reef}$	Relative density of *P. argus* on reef	0.10	0.40	2.30	53.4***	
$(F2)_{reef}$	Relative density of *S. gigas* on reef	0.00	0.10	0.70	42.2***	
$(F3)_{reef}$	Relative density of *E. striatus* on reef	0.00	0.10	0.80	−32.6NS	
$(F4)_{reef}$	Relative presence of *Euchema* on reef	0.00	0.10	0.70	64.8***	
$(F5)_{reef}$	Relative value of finfish on reef	0.00	0.20	1.00	27.4***	
$(F6)_{reef}$	Relative curios/jewelry production by reef	0.10	0.40	2.30	10.0***	
(F7)	Mangrove connectivity	0.00	836.2	5299.4	−33.0NS	
(F8)	Key commercial fish biomass (g/100 m^2)	23.6	103.3	1080.0	34.3***	
Natural products						
(N1)	Bioprospecting potential	0.00	0.41	0.87	5.5***	
(N2)	Sponge richness (numbers/m^2)	0.34	1.35	1.80	10.9***	
(N3)	Relative pharmaceutical product potential	0.10	0.30	1.80	−3.0NS	
$(N3)_{reef}$	Relative pharmaceutical product potential by reef	0.00	0.20	1.00	−1.8NS	

factors, which explained 67.0–80.0% of the variability (Fig. 4). Ordination plots can be used to identify methods that produced maps with similar patterns (arrows in the same direction), opposite patterns (arrows in opposite direction), or independent (perpendicular arrows).

The two methods for ecological integrity (Eqs. (I1) and (I2)) produced similar spatial patterns around St. Croix (Fig. 3a), both loading negatively on PC2 (Fig. 4) and highly correlated with one another ($r=0.67$, $p<0.001$). In general, predicted integrity was highest northeast of Buck Island and lowest off the southwest coastline of St. Croix. Both methods produced significantly higher predictions of integrity within Buck Island National Monument (Table 5).

In general, methods for estimating potential shoreline protection (Eqs. (S1)–(S7)) produced two distinct spatial patterns. Methods based solely on habitat coverages (Eq. (S1)), tended to produce similar maps to ecological integrity (Fig. 3a), loading in close proximity to integrity metrics in PCA (Fig. 4). Methods based on biophysical models (Eqs. (S3a) and (S3b)–(S7)), in contrast, clustered as a distinct group, loading strongly on PC3. Biophysical models predicted highest potential shoreline protection along shallow, high density reefs (Fig. 3b). Spatial patterns of wave energy attenuation (Eq. (S4)), percent reduction in erosion (Eq. (S6)), and percent reduction in wave run-up (Eq. (S7)) produced similar patterns to predicted metrics of wave height attenuation (Eqs. (S3a) and (S3b); $r>0.97$, $p<0.001$ for all pairwise comparisons). Furthermore, methods in which friction in biophysical models was calculated by coral cover (Eq. (S4)), coral rugosity (Eq. $(S4)_{height}$), or broad reef habitat classes (Eq. $(S4)_{reef}$) were highly correlated (S4, $S4_{height}$: $r=0.86$, $p<0.001$; S4, $S4_{reef}$: $r=0.28$, $p<0.001$; $S4_{height}$, $S4_{reef}$ $r=0.27$, $p<0.001$) and produced only minor differences in spatial patterns around St. Croix (Fig. 3b), though perhaps overestimated percent attenuation when categorizing reefs into broad habitat classes (Table 5). The Coral Reef Protection Index produced maps that were a blend of habitat-based methods (Eq. (S1)) and biophysical models (Eqs. (S3a) and (S3b)–(S7)), and were significantly correlated with all methods ($r>0.22$, $p<0.001$ for all pairwise comparisons). Unlike the

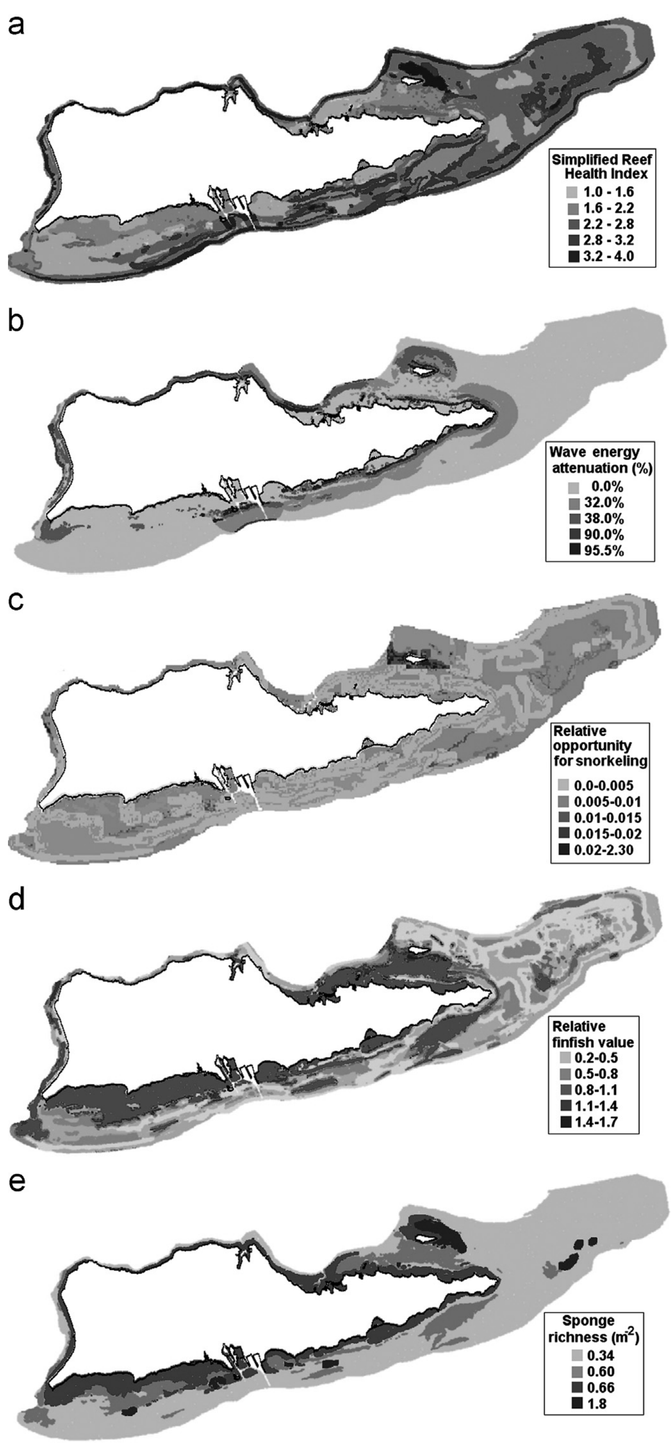

Fig. 3. Maps of ecosystem services provisioning for a representative subset of the calculated metrics: (a) ecosystem integrity (I1), (b) shoreline protection (S4), (c) recreational opportunity ($R4_{reef}$), (d) fisheries production (F4), and (e) natural products potential (N2).

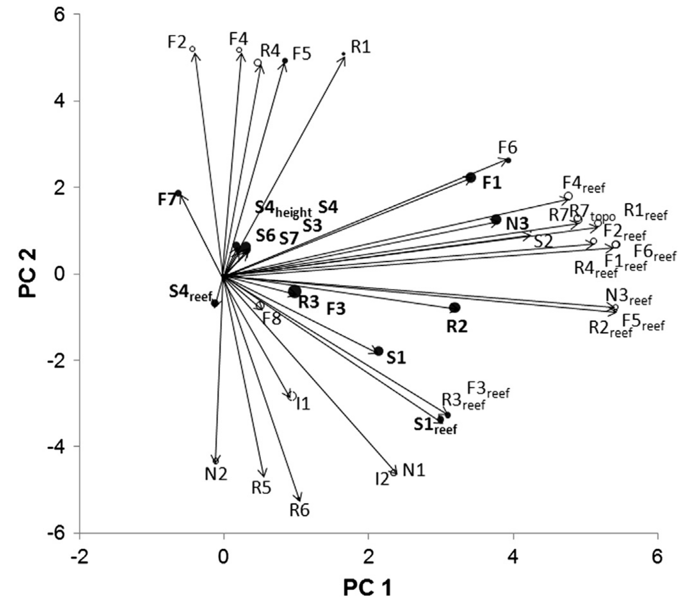

Fig. 4. Ordination plot for first two factors identified in the PCA. The direction of arrows indicates the metrics which are correlated with a given PC axis. Loadings along PC3 are indicated by the size of points, with negative scores in white, positive scores in grey, and metrics with scores >1 in bold. Ecosystem services metrics corresponding to each equation are described in Table 3.

habitat-based methods, the CRPI and the biophysical methods were significantly correlated with predictions of the high resolution SWAN model (Table 5), likely due to the inclusion of key physical metrics (e.g. distance from shoreline) in their calculation.

Principal components analysis reduced the 12 methods for estimating recreational opportunity into approximately three groups (Fig. 4). Methods based on coral reef habitat coverages (Eqs. $(R1)_{reef}$–$(R4)_{reef}$, (R7)) loaded positively along PC1 and predicted highest recreational potential in areas with high coral cover, particularly south of Buck Island and along the northwest coastline of St. Croix (Fig. 3c). Inclusion of topography (Eq. $(R7)_{topo}$) produced very similar spatial patterns to estimates without topography (Eq. (R7); $r=0.98$, $p<0.001$) and only slightly increased estimates of dive site visitation rates (Table 5). These methods, based primarily on coral reef habitat coverages, also had a high degree of accuracy, defined as being significantly higher at actual dive and snorkeling locations (Table 5). Methods that also included non-reef habitats, e.g. mangroves and seagrasses (Eqs. (R1) and (R4)), loaded positively along PC2 (Fig. 4) and expanded the area around St. Croix predicted to have high recreational potential (similar pattern to Eq. (F5), Fig. 3d). The inclusion of fish abundance or fish richness (Eqs. (R5) and (R6)) into estimates of recreational opportunity, produced different predicted spatial patterns of recreational potential that were more similar to maps of ecological integrity (Fig. 3a), with estimates of high dive value far offshore in contrast to actual dive and snorkeling locations (Table 5).

Similar to recreational opportunities, PCA reduced the methods for fisheries production into essentially three groupings: those based on reef habitat (Eqs. $(F1)_{reef}$–$(F6)_{reef}$; Fig. 4), those which also included wetland habitats (Eqs. (F1)–(F6) and (F7)), and those based on commercial fish biomass (Eq. (F8)). With the exceptions of predictions of relative *E. striatus* density (Eq. (F1)–(F6)) and predictions of fish habitat quality (Eq. (F7)), methods based on reef habitat or commercial fish biomass, and even most of those that included wetland habitats, predicted higher fisheries production in actual preferred dive-fishing areas (Fig. 3d, Table 5).

Predicted maps of natural products potential clustered into two groups (Fig. 4). Methods that estimated bioprospecting potential by either reef integrity (Eq. (N1)) or sponge richness (Eq. (N2)) produced predictions that significantly reflected survey locations where actual pharmaceutical source species had been observed (Fig. 3e, Table 5). In contrast, metrics based solely on habitat coverages (Eq. (N3)) tended to produce narrow spatial distributions of natural products potential (similar to Eq. $(R3)_{reef}$, Fig. 3c) that were not significantly related to presence/absence of source species at survey locations (Table 5).

High values of ecological integrity were not necessarily correlated with high values of other ecosystem service production (Fig. 4). In the ordination plot, methods which produced loadings opposite to (I1) and (I2), as indicated by an opposing direction of arrows and color of points, were strongly negatively correlated with (I1) and (I2). In particular, most estimates of potential shoreline protection from biophysical models (Eqs. (S3)–(S7)) were negatively correlated with estimates of ecological integrity (Eqs. (I1) and (I2); $r < -0.36$, $p < 0.001$ for all pairwise comparisons). Methods which included wetland habitat, including recreation (Eqs. (R1)–(R4); $r < -0.12$, $p < 0.001$ for all pairwise comparisons), fisheries production (Eqs. (F1)–(F6) and (F7); $r < -0.20$, $p < 0.001$ for all pairwise comparisons), and natural products potential (Eq. (N3); $r = -0.15$, $p < 0.001$), were also negatively correlated with reef ecological integrity.

Most other estimates of ecosystem services production were positively correlated with ecological integrity, producing loadings similar to (I1) and (I2) as indicated by the direction of the arrows and color of the points (Fig. 4). Estimates of ecosystem service production, including shoreline protection (Eq. (S1), $S1_{reef}$; $r > 0.44$, $p < 0.001$ for all pairwise comparisons), recreation (Eqs. $(R2)_{reef}$, $(R3)_{reef}$, (R5), (R6); $r > 0.29$, $p < 0.001$ for all pairwise comparisons), fishing (Eqs. $(F3)_{reef}$, $(F5)_{reef}$, (F8); $r > 0.19$; $p < 0.001$), and natural products (Eqs. (N1) and (N2), $N3_{reef}$; $r > 0.32$, $p < 0.001$) were strongly positively correlated with ecological integrity. For other methods, ecosystem integrity was weakly positively correlated or not significantly correlated with services production (Eqs. $(R1)_{reef}$, $(R4)_{reef}$, (R7), $(F1)_{reef}$, $(F2)_{reef}$, $(F4)_{reef}$, $(F6)_{reef}$;). Methods which were more strongly correlated with ecosystem integrity typically either included a combination of factors, such as species richness, biomass, or abundance (Eqs. (R5), (R6), (F8), (N1) and (N2)), or reflected a large contribution of Montastraea or gorgonians to ecosystem services provisioning (Eqs. $(S1)_{reef}$, $(R2)_{reef}$, $(R3)_{reef}$, $(F3)_{reef}$, $(F5)_{reef}$, $(N3)_{reef}$), both habitats of which tended to also be positively correlated with richness, biomass, and abundance.

3.2. Ecosystem services production along a disturbance gradient

To compare ecosystem services production by coral reefs along a disturbance gradient, we focused on the 29 metrics that specifically reflected reef condition, in particular excluding those methods that were dominated by mangrove cover. For almost all methods, estimates of ecological integrity, recreational opportunities, and natural products potential increased with increasing distance from centers of human activity (Fig. 5). Fisheries production was also predicted to increase with increasing distance from human disturbance, with the exception of predictions of fish habitat quality due to high connectivity with mangroves (Eq. (F7)), which have an extremely narrow distribution around St. Croix, including less than 2 km north of Christiansted and south of the industrial area. Estimates of shoreline protection were slightly higher near areas of disturbance than those further away. However, this is likely confounded with distance from shore and shallow reef depths, which are key determinants of shoreline protection. Nearshore reefs less than 2 km from Buck Island were generally estimated to provide greater shoreline protection than those less than 2 km from human disturbance centers, a pattern that was also true for ecological integrity, recreational opportunities, fisheries production, and natural products potential (Fig. 5).

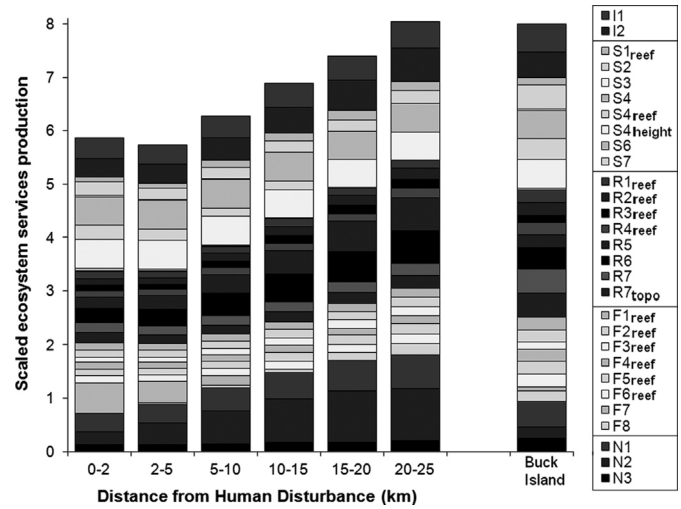

Fig. 5. Ecosystem service production by reef habitats, scaled from 0 to 1 for each method, along a human disturbance gradient and within 2 km of Buck Island.

4. Discussion

We have presented a comparison of existing methods for quantifying ecosystem services provisioning from existing data on reef condition. Overall we found that many different methods for quantifying ecosystem services within a given category (e.g., fisheries production, recreational opportunities) produced similar patterns across space. This allows for some flexibility in the choice of methods, depending on the availability of condition or environmental data for a given region. Differences among methods for estimating shoreline protection suggested a need to include physical measures, such as distance from shore or reef depth. Similarly, methods that depended on fish abundance and richness tended to estimate recreational opportunities in far offshore areas where diving and snorkeling may be impractical. However, these methods could still be appropriate in decision-making for translation potential production into benefits, once social or economic considerations are taken into account.

By linking attributes of coral condition to ecosystem services, we have identified a number of ecosystem level indicators that may have greater socio-economic relevance than those typically monitored. Different suites of attributes were relevant for different categories of ecosystem services. For example, factors related to high quality recreational opportunities, such as coral or fish richness, were not necessarily factors that were indicative of high levels of shoreline protection, such as reef depth and distance from shore. Moreover, ecological integrity, was strongly correlated with many metrics of recreational opportunities, fisheries production, and natural products potential, which were based on multiple factors of reef condition, such as richness, biomass, and abundance. However, ecological integrity was negatively correlated with most estimates of potential shoreline protection. This likely reflects biophysical differences in reef condition at shallow sites or along the reef crest where shoreline protection is likely to be high. Methods which had a high contribution of wetland habitat to ecosystem services supply also tended to be negatively correlated with reef ecosystem integrity.

Reef attributes with indirect or direct socioeconomic relevance could be targeted for future monitoring. The methods we identified relied on metrics of reef condition that are not widely monitored (e.g., fish richness, fish biomass, variability in coral colony sizes) in standard reef monitoring methods (Fisher, 2007). Furthermore, a number of additional metrics are thought to be related to ecosystem services provisioning, such as presence of unique species or colorful invertebrates (Principe et al., 2012). However, until quantitative methods are developed to translate these attributes into ecosystem services provisioning, or monitoring data on such factors is more widely collected, such links are largely anecdotal or qualitative and difficult to implement in quantitative mapping or modeling applications.

Uncertainties in spatial ecological processes, such as dispersal, can also make it challenging to quantify the spatial distribution of marine ecological processes that contribute to ecosystem services (Leis, 2002; Kendall and Picquelle, 2003; Sale et al., 2005). Spatial areas that benefit from ecosystem services may be far distant from areas that provide them (Syrbe and Walz, 2012). This may be particularly true for mobile species or life stages, where the potential for recreation or fishery production may be far from the primary source habitat suitable for nursery or spawning aggregation. Spatially explicit decisions, such as the siting of a marine protected area or a recreational area, may alternatively target to protect key ecological processes, preserve ecosystem services supply, or modify demand. Therefore, mapping the spatial distribution of ecological processes and ecosystem services demand, in addition to supply as we have done here, may also be needed to inform decision-making (Crossman et al., 2013).

5. Conclusions

In coastal communities, landuse decisions can have major effects on the condition of nearshore coral reefs (Fisher et al., 2008; Oliver et al., 2011). Socio-economic gains on land, such as through housing or industrial development, often come at a cost to ecosystem services from the coastal zone. To better evaluate the potential socio-economic tradeoffs from coastal and watershed management decisions, there is an urgent need for predictive models to quantitatively link ecological condition of coral reefs to provisioning of reef ecosystem goods and services.

We have demonstrated that existing data and existing methods can be used to make relative comparisons of ecosystem services provisioning under different levels of reef condition—often with quite similar results. For many study areas, the data needed to estimate and map ecosystems service supply may simply not be available, but the existing methods presented here may atleast provide a qualitative link toward identifying indicators that are meaningful to decision-makers and stakeholders.

The existing methods reviewed here could undoubtedly be improved with additional field monitoring in areas with a paucity of data, particularly if monitoring targets key model variables such as coral richness, fish richness, or reef structural complexity. Furthermore, in reviewed studies (Principe et al., 2012), there was often a disconnect between key ecosystem service indicators, such as charismatic fauna for recreation or production of secondary metabolites for pharmaceutical potential, and environmental indicators that are typically monitored, such as coral cover, which limited our ability to apply potential methods. Development of new methods may be necessary to make more robust links between reef attributes and ecosystem goods and services, and to identify high priority indicators for future monitoring.

One of the goals of environmental and natural resource decision-making is to maximize social and economic benefits. Linking changes in reef condition to provisioning of ecosystem goods and services can aid in highlighting social and economic benefits derived from the coastal zone, providing more information to more completely characterize, map, and model the tradeoffs inherent in decision options (Tallis et al., 2011). Making these links and tradeoffs explicit will increase the likelihood that decisions have greater and longer-term benefits for both people and the ecosystems on which they depend.

Acknowledgments

We thank P. Principe, W. Fisher, P. Bradley, D. Campbell, A. Casper, J. Bousquin, and D. Santavy for ideas in the early stages of this manuscript, and L. Burke and R. Waite for comments. We thank B. Schaeffer for help processing remote sensing data. We are grateful to NIMBioS for support of the investigative workshop "Modeling sustainability of coral reef ecosystem services under multiple interacting stressors", co-led by S. Yee and J. Ault, from which a need for models linking reef condition to ecosystem services was identified.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.ecoser.2014.01.001.

References

Arvai, J., Gregory, R., 2003. Testing alternative decision approaches for identifying cleanup priorities at contaminated sites. Environ. Sci. Technol. 37, 1469–1476.
Ault, J.S., Luo, J., Wang, J.D., 2003. A spatial ecosystem model to assess fisheries risks from exploitation and environmental changes.. In: Bortone, S.A. (Ed.), Biology of Spotted Seatrout. CRC Press, Boca Raton, Florida, pp. 267–296
Ault, J.S., Bohnsack, J.A., Smith, S.G., Luo, J., 2005. Towards sustainable multispecies fisheries in the Florida, USA, coral reef ecosystem. Bull. Mar. Sci. 76, 595–622.
Brander, L.M., van Beukering, P., Cesar, H.S.J., 2007. The recreational value of coral reefs: a meta-analysis. Ecol. Econ. 63, 209–218.
Buddemeier, R.W., Jokiel, P.L., Zimmerman, K.M., Lane, D.R., Carey, J.M., Bohling, G. C., Martinich, J.A., 2008. A modeling tool to evaluate regional coral reef responses to changes in climate and ocean chemistry. Limnol. Oceanogr.—Methods 6, 395–411.
Burke, L., Maidens, J., 2004. Reefs at Risk in the Caribbean. World Resources Institute, Washington, D.C.
Burke, L., Greenhalgh, S., Prager, D., Cooper, E., 2008. Coastal Capital: Economic Valuation of Coral Reefs in Tobago and St. Lucia. World Resources Institute, Washington, D.C
Carriger, J.F., Fisher, W.S., Stockton , T.B., Sturm, P.E., 2013. Advancing the Guánica Bay (Puerto Rico) watershed management plan. Coast. Manage. 41, 19–38.
Cesar, H.S.J., 2000. Coral reefs: their functions, threats and economic value. In: Cesar, H.S.J. (Ed.), Collected Essays on the Economics of Coral Reefs. CORDIO. Department for Biology and Environmental Sciences, Kalmar University, Kalmar, Sweden, pp. 14–39
Cesar, H.S.J., Burke, L., Pet-Soede, L., 2003. The economics of worldwide coral reef degradation. Cesar Environmental Economics Consulting. The Netherlands, Arnhem
CETS (Commission on Engineering and Technical Systems of the National Research Council), 1987. Responding to Changes in Sea Level: Engineering Implications. National Academy Press, Washington, D.C
Chan, T.T.C., Sadovy, Y., 2000. Profile of the marine aquarium fish trade in Hong Kong. Aquarium Sci. Conserv. 2, 197–213.
Chang, Y.C., Hong, F.W., Lee, M.T., 2008. A system dynamic based DSS for sustainable coral reef management in Kenting coastal zone, Taiwan. Ecol. Modell. 211, 153–168.
C. I. (Conservation International). 2008. Economic Values of Coral Reefs, Mangroves, and Seagrasses: A Global Compilation. Conservation International, Center for Applied Biodiversity Science. Arlington, Virginia.
Compton, J.E., Harrison, J.A., Dennis, R.L., Greaver, T.L., Hill, B.H., Jordan, S.J., Walker, H., Campbell, H.V., 2011. Ecosystem services altered by human changes in the nitrogen cycle: a new perspective for US decision making. Ecol. Lett. 14, 804–815.
Crossman, N.D., Burkhard, B., Nedkov, S., Willeman, L., Petz, K., Palomo, I., Drakou, E. G., Martin-Lopez, B., McPhearson, T., Boynova, K., Alkemade, R., Egoh, B., Dunbar, M.B., Maes, J., 2013. A blueprint for mapping and modelling ecosystem services. Ecosyst. Serv. 4, 4–14.
Dean, R.G., Galvin, C.J., 1976. Beach erosion: causes, processes, and remedial measures. Crit. Rev. Environ. Sci. Technol. 6, 259–296.
Dorenbosch, M., Grol, M.G.G., Nagelkerken, I., van der Velde, G., 2006. Seagrass beds and mangroves as potential nurseries for the threatened Indo-Pacific humphead wrasse, Cheilinus undulatus and Caribbean rainbow parrotfish, Scarus guacamaia. Biol. Conserv. 129, 277–282.
FEMA (Federal Emergency Management Agency). 2007. Guidelines and Specifications for Flood Hazard Mapping Partners, Appendix D. FEMA, Washington, D.C.
Fenical, W., 1997. New pharmaceuticals from marine organisms. Trends Biotechnol. 15, 339–341.
Fisher, W.S. 2007. Stony Coral Rapid Bioassessment Protocol. U.S. Environmental Protection Agency. EPA/600/R-06/167.
Fisher, W.S., Fore, L.S., Hutchins, A., Quarles, R.L., Campbell, J.G., LoBue, C., Davis, W. S., 2008. Evaluation of stony coral indicators for coral reef management. Mar. Pollut. Bull. 56, 1737–1745.
Gerwick, W.H., 2008. Marine remedies. In: Walsh, P.J., Smith, S.L., Fleming, L.E., Solo-Gabriele, H.M., Gerwick, W.H. (Eds.), Oceans and Human Health: Risks and Remedies from the Seas. Academic Press, San Diego, pp. 425–429

Gilhousen, D.B., R. Hervey. 2001. Improved estimates of swell from moored buoys. In: Proceedings of the Fourth International Symposium: WAVES 2001. ASCE, Alexandria, VA.
Gourlay, M.R., 1996. Wave set-up on coral reefs. 2. Set-up on reefs with various profiles. Coastal Eng. 28, 17–55.
Gourlay, M.R., 1997. Wave set-up on coral reefs: some practical applications. In: Proceedings of the 13th Australian Coastal and Ocean Engineering Conference, Christchurch, pp. 959–964.
Gourlay, M.R., Colleter, G., 2005. Wave-generated flow on coral reefs: an analysis for two dimensional horizontal reef-tops with steep faces. Coastal Eng. 52, 353–387.
Gratwicke, B., Speight, M.R., 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. J. Fish Biol. 66, 650–667.
Grigg, R.W., 1989. Precious coral fisheries of the Pacific and Mediterranean. In: Caddy, J.F. (Ed.), Marine Invertebrate Fisheries: Their Assessment and Management. John Wiley, San Francisco, pp. 637–645
Healthy Reefs Initiative, 2010. Report Card for the Mesoamerican Reef. Smithsonian Institution, Washington, D.C
Hourigan, T., 2008. Deep Water Connections. NOAA Fisheries Management Service
Hughes, S.A., 2004. Estimation of wave run-up on smooth, impermeable slopes using the wave momentum flux parameter. Coastal Eng. 51, 1085–1104.
Hunt, B., Vincent, A.C.J., 2006. Scale and sustainability of marine bioprospecting for pharmaceuticals. Ambio 35, 57–64.
Kendall, A.W., Picquelle, S.J., 2003. Marine Protected Areas and the Early Life History of Fishes. Seattle, Wash, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center
Leeworthy, V.R., P.C. Wiley, J.D. Hospital. 2004. Importance-satisfaction Ratings Five-year Comparison, SPA & ER Use, and Socioeconomic and Ecological Monitoring Comparison of Results 1995–1996 to 2000–2001. National Oceanic and Atmospheric Administration (NOAA), Silver Spring, MD.
Leis, J.M., 2002. Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. Environ. Biol. Fishes 65, 199–208.
Leujak, W., Ormond, R.F.G., 2007. Visitor perceptions and the shifting social carrying capacity of South Sinai's coral reefs. Environ. Manage. 39, 472–489.
Lowe, R.J., Falter, J.L., Bandet, M.D., Pawlak, G., Atkinson, M.J., Monismith, S.G., Koseff, J.R., 2005. Spectral wave dissipation over a barrier reef. J. Geophys. Res. 110, C04001.
McClanahan, T., Graham, N.A.J., Calnan, J.M., MacNeil, M.A., 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecol. Appl. 17, 1055–1067.
McClanahan, T., Branch, G. (Eds.), 2008. Oxford University Press, Oxford
McField, M., Kramer, P.R., 2007. Healthy Reefs for Healthy People: A Guide to Indicators of Reef Health and Social Wellbeing in the Mesoamerican Reef Region. Smithsonian Institution, Washington, D.C
MEA (Millennium Ecosystem Assessment), 2005. Ecosystems and Human Well-being: Current State and Trends. Island Press, Washington, D.C
Melbourne-Thomas, J., Johnson, C.R., Fung, T., Seymour, R.M., Chérubin, L.M., Arias-González, J.E., Fulton, E.A., 2011. Regional-scale scenario modeling for coral reefs: a decision support tool to inform management of a complex system. Ecol. Appl. 21, 1380–1398.
Monismith, S.G., 2007. Hydrodynamics of coral reefs. Annu. Rev, Fluid Mech. 39, 37–55.
Mumby, P.J., 2006. Connectivity of reef fish between mangroves and coral reefs: algorithms for the design of marine reserves at seascape scales. Biol. Conserv. 128, 215–222.
Mumby, P.J., Edwards, A.J., Arias-Gonzalez, J.E., Lindeman, K.C., Blackwell, P.G., Gall, A., Gorczynska, M.I., Harborne, A.R., Pescod, C.L., Renken, H., Wabnitz, C.C.C., Llewellyn, G., 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427, 533–536.
Mumby, P.J., Broad, K., Brumbaugh, D.R., Dahlgren, C.P., Harborne, A.R., Hastings, A., Holmes, K.E., Kappel, C.V., Micheli, F., Sanchirico, J.N., 2008. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. Conserv. Biol. 22, 941–951.
Mumby, P.J., Hastings, A., 2008. The impact of ecosystem connectivity on coral reef resilience. J. Appl. Ecol. 45, 854–862.
Nagelkerken, I., van der Velde, G., Gorissen, M.W., Meijer, G.J., van't Hof, T., den Hartog, C., 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuarine Coastal Shelf Sci. 51, 31–44.
NMFS (National Marine Fisheries Service), 2007. Virgin Islands Fisheries Statistics and Price Data. Southeast Fisheries Science Center, Miami, FL
NOAA (National Oceanic and Atmospheric Administration). 2001. Benthic Habitats of Puerto Rico and the U.S. Virgin Islands. NOAA, National Ocean Service, National Centers for Coastal Ocean Science Biogeography Program, Silver Spring, MD.
NOAA. 2009. Fisheries of the United States 2008. Silver Spring, MD.
Oliver, L.M., Lehrter, J.C., Fisher, W.S., 2011. Relating landscape development intensity to coral reef condition in the watersheds of St. Croix, US Virgin Islands. Mar. Ecol. Prog. Ser. 427, 293–302.
Paddack, M.J., Reynolds, J.D., Aguilar, C., Appeldoorn, R.S., et al., 2009. Recent region-wide declines in Caribbean reef fish abundance. Curr. Biol. 19, 590–595.
Pendleton, L.H., 1994. Environmental quality and recreation demand on a Caribbean coral reef. Coastal Manage. 22, 399–404.
Pendleton, L. (Ed.), 2008. Coastal Ocean Values Press, Washington, D.C.
Pittman, S.J., Brown, K.A., 2011. Multi-scale approach for predicting fish species distributions across coral reef seascapes. PLoS One 6 (5), e20583.
Pittman, S.J., Christensen, J.D., Caldow, C., Menza, C., Monaco, M.E., 2007. Predictive mapping of fish species richness across shallow-water seascapes in the Caribbean. Ecol. Modell. 204, 9–21.
Pittman, S.J., S.D. Hile, C.F.G. Jeffrey, C. Caldow, M.S. Kendall, M.E. Monaco, Z. Hillis-Starr. 2008. Fish Assemblages and Benthic Habitats of Buck Island Reef National Monument (St. Croix, U.S. Virgin Islands) and the Surrounding Seascape: A Characterization of Spatial and Temporal Patterns. NOAA Technical Memorandum NOS NCCOS 71. Silver Spring, MD.
Principe, P., P. Bradley, S. Yee, W. Fisher, E. Johnson, P. Allen, D. Campbell. 2012. State of the Science on Linkages Among Coral Reef Condition, Functions, and Ecosystem Services. U.S. Environmental Protection Agency, Office of Research and Development, Research Triangle Park, NC. EPA/600/R-11/206.
Productivity Commission. 2003. Industries, Land Use and Water Quality in the Great Barrier Reef Catchment, Research Report, Canberra.
Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, New York
Rehr, A.P., Small, M.J., Bradley, P., Fisher, W.S., Vega, A., Black, K., Stockton, T., 2013. A decision support framework for science-based, multistakeholder deliberation: a coral reef example. Environ. Manage. 50, 1204–1218.
Roebeling, P.C., 2006. Efficiency in Great Barrier Reef water pollution control: a case study for the Douglas Shire. Nat. Resour. Model. 19, 539–556.
Sale, P.F., Cowen, R.K., Danilowicz, B.S., Jones, G.P., Kritzer, J.P., Lindeman, K.C., Planes, S., Polunin, N.V.C., Russ, G.R., Sadovy, Y.J., Steneck, R.S., 2005. Critical science gaps impede use of no-take fishery reserves. Trends Ecol. Evol. 20, 74–80.
Schaeffer, B.A., Sinclair, G.A., Lehrter, J.C., Murrell, M.C., Kurtz, J.C., Gould, R.W., Yates, D.F., 2011. An analysis of diffuse light attenuation in the northern Gulf of Mexico hypoxic zone using the SeaWiFS satellite data record. Remote Sens. Environ. 115, 3748–3757.
Scheiner, S.M., Cox, S.B., Willig, M., Mittelbach, G.G., Osenberg, C., Kaspari, M., 2000. Species richness, species-area curves and Simpson's paradox. Evol. Ecol. Res. 2, 791–802.
Sheppard, C., Dixon, D.J., Gourlay, M., Sheppard, A., Payet, R., 2005. Coral mortality increases wave energy reaching shores protected by reef flats: examples from the Seychelles. Estuarine Coastal Shelf Sci. 64, 223–234.
Syrbe, R.-U., Walz, U., 2012. Spatial indicators for the assessment of ecosystem services: Providing, benefiting and connecting areas and landscape metrics. Ecol. Indic. 21, 80–88.
Tallis, H.T., T. Ricketts, A.D. Guerry, E. Nelson, D. Ennaanay, S. Wolny, N. Olwero, K. Vigerstol, D. Pennington, G. Mendoza, J. Aukema, J. Foster, J. Forrest, D. Cameron, E. Lonsdorf, C. Kennedy, G. Verutes, C.K. Kim, G. Guannel, M. Papenfus, J. Toft, M. Marsik, J. Bernhardt. 2011. InVEST 2.0 beta User's Guide. The Natural Capital Project, Stanford.
Thomas, C.R., Gordon, I.J., Wooldridge, S., Marshall, P., 2012. Balancing the tradeoffs between ecological and economic risks for the Great Barrier Reef: a pragmatic conceptual framework. Hum. Ecol. Risk Assess.: Int. J. 18, 69–91.
Turner R.K., Brouwer R., Georgiou S., Bateman I.J. 2000. Ecosystem Functions and Services: An Integrated Framework and Case Study for Environmental Valuation. Norwich (UK): University of East Anglia, The Centre for Social and Economic Research on the Global Environment (CSERGE), CSERGE Working Paper GEC 2000-21, 32 pp.
UNEP-WCMC (United Nations Environment Programme, World Conservation Monitoring Centre). 2006. In the Front Line: Shoreline Protection and Other Ecosystem Services from Mangroves and Coral Reefs. Biodiversity Series, vol. 24. UNEP-WCMC, Cambridge, UK.
Uyarra, M.C., Watkinson, A.R., Cote, I.M., 2009. Managing dive tourism for the sustainable use of coral reefs: validating diver perceptions of attractive site features. Environ. Manage. 43, 1–16.
Valdés-Pizzini, M., J.J. Agar, K. Kitner, C. Garcia-Quijano, M. Tust, F. Forrestal. 2010. Cruzan Fisheries: A Rapid Assessment of the Historical, Social, Cultural and Economic Processes that Shaped Coastal Communities' Dependence and Engagement in Fishing in the Island of St. Croix, U.S. Virgin Islands. NOAA Technical Memorandum NMFS-SEFSC-597.
van Beukering, P., L. Brander, B. van Zanten, E. Verbrugge, K. Lems. 2011. The Economic Value of the Coral Reef Ecosystems of the United States Virgin Islands. Report R11/06, IVM Institute for Environmental Studies, Amsterdam.
van Beukering, P.J.H., Cesar, H.S.J., 2004. Ecological economic modeling of coral reefs. Pac. Sci. 58, 243–260.
Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S-PLUS. Springer, New York
Waddell, J.E., A.M. Clarke, (Eds.), 2008. The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States:2008. NOAA Technical Memorandum NOS CCOS 73. NOAA, Silver Spring, MD.
Wainger, L.A., Boyd, J.W., 2009. Valuing ecosystem services. In: McLeod, K., Leslie, H. (Eds.), Ecosystem-based Management for the Oceans. Island Press, Washington, D.C., pp. 92–111
Wakeford, M., Done, T.J., Johnson, C.R., 2008. Decadal trends in a coral community and evidence of changed disturbance regime. Coral Reefs 27, 1–13.
Wielgus, J., Chadwick-Furman, N.E., Zeitouni, N., Shechter, M., 2003. Effects of coral reef attribute damage on recreational welfare. Mar. Resour. Econ. 18, 225–237.
Wielgus, J., Cooper, E., Torres, R., Burke, L., 2010. Coastal Capital: Dominican Republic. Case Studies on the Economic Value of Coastal Ecosystems in the Dominican Republic. World Resources Institute, Washington, D.C

Wilkinson, C. (Ed.), 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Center, Townsville, Australia
Williams, I.D., Polunin, N., 2002. Differences between protected and unprotected reefs of the western Caribbean in attributes preferred by dive tourists. Environ. Conserv. 27, 382–391.
Wilson, S.K., Graham, N.A.J., Polunin, N.V.C., 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Mar. Biol. 151, 1069–1076.
Wolanski, E., De'ath, G., 2005. Predicting the impact of present and future human land-use on the Great Barrier Reef. Estuarine Coastal Shelf Sci. 64, 504–508.
WRI (World Resources Institute), 2009. Value of Coral Reefs and Mangroves in the Caribbean, Economic Valuation Methodology, v3.0. World Resources Institute, Washington, D.C
Yee, S.H., Carriger, J., Fisher, W.S., Bradley, P., Developing scientific information to support decisions for sustainable reef ecosystem services. Ecol. Econ. in press.