

# Measuring Bahamian lionfish impacts to marine ecological services using habitat equivalency analysis

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**Abstract** Marine ecological services provide goods, amenities, food resources, and economic benefits to millions of people globally. The loss of these services, attributed to the infiltration of marine invasive species such as the Indo-Pacific lionfish (*Pterois volitans/miles*), is measurable. The highly successful lionfish now flourishes in great densities in the US Gulf of Mexico and Atlantic waters and the entire Caribbean, yet the loss of ecological services attributed to the invader has not yet been assessed. In this study, we employ a derivative of a well-utilized method of ecosystem valuation known as habitat equivalency analysis to measure the time-value-adjusted loss of biomass- and recruitment-related ecosystem services brought by lionfish to Bahamian reefs. Drawing upon the literature examples of tangible lionfish damages in the Bahamas, we (1) quantitatively evaluate the loss of ecosystem services instigated by lionfish by measuring the total service-year losses partitioned over yearly time steps, (2) provide a metric by which ocean managers may value the remunerations of Bahamian lionfish controls when weighed against removal costs, and

(3) deliver a tool to quantify changes in ecosystem services as a consequence of invasive species impacts and control. We found that the invader imposed losses of 26.67 and 21.67 years to recruitment and biomass services per km<sup>2</sup> of Bahamian reef if left uncontrolled. In the same accord, the most conservative Bahamian lionfish removal regime modeled, i.e., which produced a 50 % recovery of pre-lionfish ecosystem function over 10 years, provided service gains of 9.57 and 4.78 years per km<sup>2</sup>. These data deliver a platform upon which to quantify present and future fiscal costs of the lionfish invasion and also to value lionfish control efforts.

## Introduction

The environmental and economic losses caused by invasive species are staggering (Pimentel et al. 2005), and island nations, such as the Bahamas, are particularly susceptible to the threat of these invaders. This susceptibility results from the intrinsic geographic isolation of oceanic islands, limiting species composition to fewer, less vagile biotas which are more sensitive to disturbance than their mainland counterparts (Reaser et al. 2007). The non-native predatory lionfish (*Pterois volitans/miles*) has been documented from the Atlantic since the year 1985 (USGS-NAS 2014), and they have subsequently and swiftly infiltrated the entire Caribbean Sea, Gulf of Mexico, and tropical Western Atlantic. Invasive lionfish in the Bahamas are found in densities far greater than lionfish populations in their native Indo-Pacific (Green and Côté 2009). Lionfish were likely introduced via the aquarium trade and feed heavily on juvenile bony fishes, crustaceans, and mollusks, though small teleosts comprise the largest percentage of adult lionfish diets (Semmens et al. 2004; Morris and Akins 2009). Much work

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has focused on classifying and quantifying the prey species chosen by invasive lionfish and also evaluating the impacts on native prey fish on the reefs in which lionfish reside and feed. For instance, Green et al. (2012) documented a sharp increase in Bahamian lionfish numbers to 40 % of total predatory fish biomass spanning the years 2004–2010. The thriving lionfish population was linked to a 65 % reduction (conservatively, as lionfish were abundant prior to the study) in the biomass of lionfish prey fishes on reefs containing the invader spanning the years 2008–2010. Lionfish densities in the same Bahamian location were reported to be  $>390$  fish  $\text{ha}^{-1}$  by Green and Côté (2009). Albins and Hixon (2008) found a 79 % recruitment reduction in all teleost species on reefs artificially introduced with lionfish over a 5-week time period; however, they did not report on lionfish densities observed at the study sites. A more recent Bahamian study by Albins (2015) found a 43.6 % reduction in total density, a 31.9 % decrease in biomass, and 21.4 % decline in species richness of small ( $<10$  cm) prey fish on large coral reefs (1400–4000  $\text{m}^2$ ) that contained resident lionfish near Lee Stocking Island, Bahamas.

There is little evidence in the literature to suggest that lionfish prey heavily or exclusively on commercially valuable reef species in the Caribbean, such as the yellowtail snapper (*Ocyurus chrysurus*) and the graysby (*Cephalopholis cruentata*), as these species are sparsely found in lionfish gut contents (Morris and Akins 2009; Valdez-Moreno et al. 2012). More commonly, lionfish prey upon grammatids, apogonids, labrids, and gobiids, filling a similar trophic niche as native predators and therefore directly competing for food resources with these native fishes (Albins and Hixon 2008; Morris and Akins 2009; Valdez-Moreno et al. 2012). It is also probable that lionfish compete with native Atlantic species for shelter (Barbour et al. 2011). Large quantities of lionfish now occupy the western Atlantic, Caribbean, and Gulf of Mexico, and given that lionfish feed heavily on the same prey items as native predators and the abundant lionfish population, this invader has the capacity to significantly reduce the quantity and quality of food items available for native fish. This reduction may induce a trophic cascade effect to ecosystems spanning the entire introduced range of lionfish by reducing the fitness and survivorship of native predator and also prey fish populations.

Despite extensive study of the feeding ecology of invasive lionfish, the realized short- and long-term loss of reef ecosystem services attributed to lionfish has not yet been quantified. Simply defined, marine reef ‘ecosystem services’ are vital ecological functions that provide a vast array of goods, amenities, and food, therefore delivering economic benefits to millions of people globally (Peterson and Lubchenco 1997; Holmlund and Hammer 1999). Worm et al. (2006) showed that a loss of reef system biodiversity

impacts ecosystem services and has a direct and exponentially negative relationship with ecosystem stability, water quality, and recovery potential from disturbances. Given the pronounced prey species biomass, recruitment, and biodiversity damages to Bahamian reef fish populations seen by Green et al. (2012), Albins and Hixon (2008) and Albins (2015), the supposition can be made that the incurred services lost due to lionfish in the Bahamas is pronounced. Motivated by this lack of knowledge, the purpose of this study was to measure the loss of reef ecosystem services instigated by lionfish and also to forecast future service losses if lionfish control measures fail or are slow to curb the invasive population. To meet our goals, we quantified Bahamian lionfish prey fish biomass (simply referred to going forward as ‘biomass’) and reef fish recruitment losses initiated by lionfish by employing a permutation of an ecosystem valuation method known as habitat equivalency analysis (HEA) (Dunford et al. 2004).

HEA was adopted in the USA in 1987 to address the government’s ‘no net loss’ policy. The policy was inspired by the need to mitigate destruction in wetlands caused by anthropogenic development by restoring replacement systems with equal ecosystem function as to the habitat that was injured, hence providing a ‘no net loss’ (Sibbing 2005). The base quantitative metric of an HEA is a service unit year (SUY). One SUY is defined as the total quantity of an ecosystem service or function provided by one area unit (set to 1  $\text{km}^2$  in this study) of that ecosystem for one full year. Inherently, SUYs are monetarily unit-less and must be multiplied by the perceived yearly value of the service per unit of area in order to arrive at the fiscal value of one SUY (see Sect. “Quantifying ecosystem losses from lionfish” for a full discussion of SUY calculations). A HEA computes the loss and gain of all past and future ecosystem services (going forward referred to as ‘services’) in relation to pre- and post-injury service levels of the injured (i.e., damaged) and compensatory resource. The net service losses incurred by the damaged system are offset by gains of services in a replacement habitat (i.e., ‘compensatory action’). Services lost and gained are discounted over time by a fixed percentage—typically a value which reflects the contemporary rate of inflation. The discount rate assures that services lost are deemed more economically valuable in the preliminary years of damage, and equally, services gained via mitigation are also more valued if performed immediately rather than at a later date. Moreover, and from an ecological perspective, the immediate loss of services in the early years of damage may have a greater long-term and compounding effect (i.e., fish lost in the present are unable to breed to replenish future generations) than those services lost at a later date. Service losses and gains are measured in discounted service unit years (DSUYs), with one DSUY equivalent to the entire quantity of services provided by

one area unit of the damaged or replacement system for a given year. The net metric of a standard HEA is a quantity of replacement habitat required to offset the losses brought about by the injury.

Though developed for terrestrial applications, the HEA method has broad multidisciplinary applications in marine conservation and a track record of valuing coral reef restoration efforts (Jaap 2000; Milon and Dodge 2001; Viehman et al. 2009). There are, however, many differences between invasions and the simple destruction of habitat, such as intraspecific competition for food and living space brought by the invaders. If discrete impacts can be quantitatively measured, such as competition for living space, then an output of HEA—cumulative DSUYs lost due to these impacts—can be used to value many of the issues associated with invasive species. One such example of competition for space exists in the Florida Keys, USA, where lionfish are often caught as bycatch in lobster trap fisheries (Akins et al. 2012). As the second most abundant finfish caught in these lobster traps, Akins et al. (2012) noted a negative correlation between the presence of lionfish in the traps and lobster catches. Though the reduction in catch rates was not explicitly documented, this lionfish impact logically is not a result of direct predation as adult lobsters are not food sources for lionfish. Should this negative relationship be quantified, however, measuring the cumulative DSUYs lost could be helpful to evaluate the lobster fishery losses instigated by lionfish. This is but one example of how data derived from a HEA may be applied to measure injuries caused by invasive species.

In addition to measuring lionfish-related service losses (the primary objective here), net DSUYs gained can also be useful to estimate the recovery of services facilitated by lionfish controls. Valuing these controls, however, necessitates appraising the benefits to reef ecosystems that removals may provide. Ecosystem recovery directly attributed to lionfish removals has not yet been assessed on a broad scale; however, a small-scope study in the Cayman Islands evidenced that reducing the abundance of large lionfish, such as occurs during lionfish culls, can shift predation from juvenile economically valuable reef fish to smaller crustaceans such as shrimps (Frazer et al. 2012). Furthermore, Green et al. (2014) found that reducing lionfish densities on Bahamian patch reefs produced a 50–70 % rise in native prey fish biomass, comprising an increase of 10–65 % of species economically important to fisheries, over 18 months. We posit that system recovery may be linked to varied levels of lionfish removals and resultant differences in lionfish abundance, and so graduated scenarios of ecosystem recovery times attributed to lionfish control efforts, partitioned over yearly time steps, were modeled in this study (i.e., sensitivity testing). One case study itemizing lionfish service losses and also the cost of lionfish

controls for a subregion of the Bahamas was computed to provide a sample application of the study data. It is hoped this effort will (1) quantitatively assess the service losses instigated by Bahamian lionfish, founded on previous studies that measured ecosystem losses, and (2) provide a metric by which ocean managers can estimate the actual fiscal damages wrought by lionfish should the monetary value of services provided by impacted Bahamian species and reefs be enumerated in the future. The study is useful to estimate the net future benefits of lionfish control efforts, when considering potential removal costs, and also provides a tool in order to quantify changes in ecosystem services as a consequence of invasive species impacts and control.

## Materials and methods

HEA calculations can be performed either manually or with the help of automated software tools such as the Visual\_HEA computer program. Visual\_HEA, created by the National Coral Reef Institute (NCRI), provides a consistent and robust way for ocean managers to implement a standard HEA (Kohler and Dodge 2006). Visual\_HEA was therefore used here to perform our analysis as the software automates repetitive and tedious computations which are otherwise prone to human error. Additional information about the software can be obtained from the NCRI Visual\_HEA web site: [http://www.nova.edu/ocean/visual\\_heal/](http://www.nova.edu/ocean/visual_heal/).

### Visual HEA input parameters

To use Visual\_HEA, values that represent the quantity of habitat loss due the injury, the inflation-adjusted valuation of money over time, and also the expected future gains for any compensatory action (i.e., lionfish control) are input by the analyst. The outputs from Visual\_HEA comprise a graph and also tabular values of damage and recovery at the damaged site and also any gains achieved as a result of a compensatory action.

Following is a review of the values required to parameterize Visual\_HEA, using the software syntax as denoted in italics, for reproducibility. Section "[Quantifying ecosystem losses from lionfish](#)" details the specific application of the method and parameters define here as they pertain to the lionfish damages documented by Green et al. (2012) and Albins and Hixon (2008) and also simulated lionfish control (see also Table 1 for a summary of values used in this study). The *pre-injury service level* represents the level of services provided by the injured site before the damage occurred—i.e., before the Bahamian lionfish invasion—and is expressed as a percentage. *Pre-restoration service level*, also a percentage, measures the service level before compensatory action was implemented (i.e., after lionfish

**Table 1** Values used to parameterize the analysis

Parameter	Value
Pre-injury service level	100 %
Pre-restoration service level	0 %
Time unit	1 year
Discount rate	3 %
Claim year	2008
Units	km <sup>2</sup>
Number of injured area units	1
Gain perpetuity	Yes
Loss perpetuity	Yes
Biomass losses (spanning 2008–2010)	65 %
Recruitment losses (spanning 2008–2010)	80 %

establishment but before lionfish removal efforts have been initiated). A *time unit*, set to 1 year, is the incremental step over which lionfish damages (losses) and lionfish controls (gains) were calculated. The *discount rate* is a percentage rate per *time unit* by which the values of losses and gains were decremented as time lapsed over the lifetime of the analysis. The *discount rate* used in this study reflects the typical 3 % rate of inflation, given that one monetary unit provides less ‘buying power,’ or value, in the future than in the present. The *claim year* is the year that the damage occurred and was set to 2008 in this study. Service gains and losses are measured annually per area *unit* (1 km<sup>2</sup>), and the *number of injured area units* represents the extent of the injured area. In this study, the *number of injured area units* was set to one in order to provide a per km<sup>2</sup> evaluation of losses and gains. *Service losses at the injured area* comprise the level and duration of service loss spanning the time of injury until the conclusion of the analysis. *Service gains from compensatory action* defines the expected level of gained services as a result of compensatory action (i.e., lionfish controls in this study) spanning the analysis time frame. If the *gain* and *loss perpetuity* options are marked, losses and gains are calculated annually until those values fall to zero owing to the *discount rate* over time.

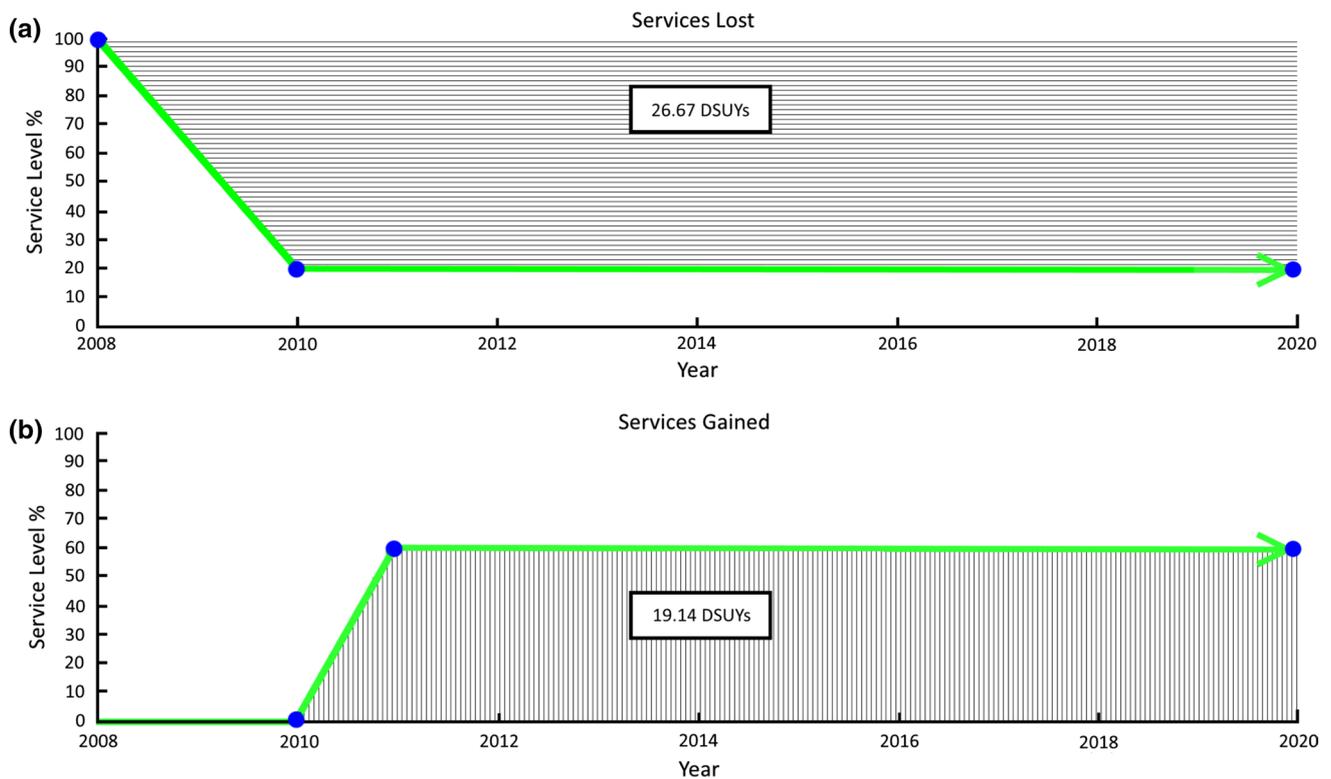
### Quantifying ecosystem losses from lionfish

A standard HEA typically draws upon DSUYs lost and gained in order to calculate the total area of replacement habitat that that will compensate for the injury at the damaged site. An equitable restoration, however, is not requisite to measure net DSUY losses if repair is not done. For this study, we simply quantified the damages incurred by lionfish by measuring the total net loss of DSUYs per km<sup>2</sup>. Accordingly, DSUYs lost resulting from lionfish damages and DSUYs gained (i.e., recovery—defined as natural replenishment of fish stocks to pre-injury levels) from

simulated lionfish control measures (i.e., the compensatory action) were calculated and then subtracted, leaving a net loss of DSUYs per km<sup>2</sup>. The DSUYs gained and lost delivered here can be used to calculate monetary values of impacts and lionfish control by multiplying the perceived value of biomass and recruitment functions per km<sup>2</sup> by the total area impacted and also the DSUYs lost or gained. The valuation of services provided by global coral reef systems and their inhabitants, however, is complex and not well quantified in the literature. As such, we limit our analysis here to measuring the total DSUYs lost per km<sup>2</sup> owing to lionfish. We also provide a hypothetical example to guide future valuation studies of lionfish impacts using this method.

Green et al. (2012) reported a 65 % reduction in biomass of prey fish species on lionfish-dominated Bahamian reefs spanning the years 2008–2010. This percentage, therefore, was used to parameterize prey fish biomass losses on Bahamian reefs. To measure recruitment losses for all reef teleosts, we established our analysis upon the 79 % decrease (rounded to 80 %) in recruitment of all reef fish as reported by Albins and Hixon (2008). For both decreases, we summarized these losses per km<sup>2</sup> for the purposes of our analysis. It is unknown whether the lionfish damages seen by Green et al. (2012), Albins and Hixon (2008), and more recently, Albins (2015) in the Bahamas are representative of similar injury throughout the entire Caribbean—few broad-scale and non-Bahamian studies are available by which to quantify lionfish-induced loss of services. It should also be noted that the studies by Green et al. (2012) and Albins and Hixon (2008) were conducted on patch reefs and the scalability of such studies to entire reef tracts should be made with caution. Nevertheless, these three studies can serve as worst-case scenarios and also guide investigations that quantify lionfish impacts in similar lionfish-dense Bahamian locations. As we measured annual DSUYs lost per km<sup>2</sup>, the results from this study are applicable to any constituency similarly affected by lionfish as the example study locations where the total reef area deplete of natural reef fish stocks owing to lionfish is known.

The protracted decrease in recruitment and biomass functions attributed to lionfish was set to span the years 2008–2010, founded on biomass decreases spanning this timeframe as reported by Green et al. (2012). In the analysis, recovery, attained by lionfish control (assumed to be 0 % at the start of the simulation), succeeded lionfish damages through the year 2020 (Table 1). As service levels on damaged reefs will probably never attain their pre-invasion baseline levels of service due to the difficulties associated with lionfish control, and lionfish removals will also continue to yield services beyond the year 2020, both losses and gains were also calculated ‘in perpetuity’ beyond the year 2020. By doing so, a perpetuity calculation implies



**Fig. 1** Sample analysis. Graphical depiction of 80 % recruitment losses spanning the years 2008–2010, shown unto the year 2020 (a). Service gains of 60 %, achieved by lionfish control, reach full effect

by the year 2011 and are illustrated through the year 2020 (b). Both measures are calculated in perpetuity to account for all future gains and losses

that service losses or gains extend annually until the discount factor effectively reaches zero as a result of the incremental and yearly loss of value owing to the discount rate. Given this, the total DSUYs lost per km<sup>2</sup> delivered here are permanent and net losses when considering lionfish damages and also lionfish control. Realistically, it is not likely that all lionfish are able to be permanently removed from a Bahamian reef due to constant propagule pressure from distant locations (e.g., Johnston and Purkis 2014). Consequently, we assumed that recovery of lionfish-damaged reefs to a 100 % pre-invasion level is likely unattainable. Reflecting this reality, 80 % was conjectured as a more realistic rate of recovery for biomass and recruitment functions and was therefore used as a baseline recovery rate in order to quantify damages.

### DSUY calculations

In this study, one SUY represented the total quantity of recruitment or biomass function as provided by one area unit (A—1 km<sup>2</sup>) of a Bahamian reef for one full year. Using the calculation of recruitment losses as an example, each A of Bahamian reef provided 100 % of recruitment services spanning 1 year pre-lionfish invasion, and so, one A of this

reef was valued at one SUY annually. Accordingly, one DSUY lost was equivalent to the quantity of SUYs per A of lionfish-damaged patch reef for one full year, discounted annually and post-invasion by the rate of monetary inflation. In this analysis, the total recruitment of all reef fish to one A of patch reef was assumed to decrease linearly by 80 % spanning the years 2008–2010 (Fig. 1; Table 2). Subsequent to the year 2010, and unto perpetuity, one A of patch reef only provided a 20 % recruitment service function annually as a result of lionfish predation. In order to compute the total quantity of DSUYs lost per A and per year due to the lionfish damages, a discount factor ( $p_t$ ), computed annually, was multiplied by the raw service unit years (RSUY) lost per year spanning the analysis timeframe. RSUY losses were defined as the yearly mean quantity of SUY service losses per A. The calculation of  $p_t$  can be summarized by the equation

$$p_t = 1/(1+r)^{(t-C)} \quad (1)$$

where  $r$  is the discount rate,  $t$  is the start year of the analysis (i.e., 0), and  $C$  is the zero-based year subsequent to the date of damage. We assumed that the quantity of SUYs lost was not discounted over the first year, and as such, 0.200 SUYs per A were lost during the year 2008 (i.e.,  $0.200 \times 1$ ) for

**Table 2** Sample analysis

Year	Beginning service level lost (%)	End service level lost (%)	Mean service level lost (%)	Raw SUYs lost	Discount factor	Discounted SUYs lost
2008	0.00	40.00	20.00	0.200	1.000	0.200
2009	40.00	80.00	40.00	0.600	0.971	0.583
2010	80.00	80.00	80.00	0.800	0.943	0.754
2011	80.00	80.00	80.00	0.800	0.915	0.732
2012	80.00	80.00	80.00	0.800	0.888	0.711
2013	80.00	80.00	80.00	0.800	0.863	0.690
2014	80.00	80.00	80.00	0.800	0.837	0.670
2015	80.00	80.00	80.00	0.800	0.813	0.650
2016	80.00	80.00	80.00	0.800	0.789	0.632
2017	80.00	80.00	80.00	0.800	0.766	0.613
2018	80.00	80.00	80.00	0.800	0.744	0.595
2019	80.00	80.00	80.00	0.800	0.722	0.578
2020	80.00	80.00	80.00	0.800	0.701	0.561
Beyond						18.703
Total discounted service unit years (DSUYs) lost						26.672
Year	Beginning service level gained (%)	End service level gained (%)	Mean service level gained (%)	Raw SUYs gained	discount factor	Discounted SUYs gained
2010	0.00	60.00	30.00	0.300	0.943	0.283
2011	60.00	60.00	60.00	0.600	0.915	0.549
2012	60.00	60.00	60.00	0.600	0.888	0.533
2013	60.00	60.00	60.00	0.600	0.863	0.518
2014	60.00	60.00	60.00	0.600	0.837	0.502
2015	60.00	60.00	60.00	0.600	0.813	0.488
2016	60.00	60.00	60.00	0.600	0.789	0.474
2017	60.00	60.00	60.00	0.600	0.766	0.46
2018	60.00	60.00	60.00	0.600	0.744	0.446
2019	60.00	60.00	60.00	0.600	0.722	0.433
2020	60.00	60.00	60.00	0.600	0.701	0.421
Beyond						14.028
Total discounted service unit years (DSUYs) gained						19.135
Net discounted service unit years (DSUYs) lost						7.54

Sample analysis for recruitment (i.e., scenario 1 in Table 3) showing an initial service loss of 80 % (from a 100 % pre-service level, resulting in a remnant 20 % service level) (top) and 60 % subsequent recovery rate due to lionfish removals (bottom). A net recovery rate of 80 % is attained within 1 year in this example

recruitment (Table 2). For the year 2009, and using equation one, the value of  $p_t$  was 0.971 [i.e.,  $1/(1 + 0.03)^{(0-1)}$ ]. The RSUY loss for the year 2009 was then multiplied by  $p_t$ —i.e.,  $0.600 \times 0.97$ —resulting in a loss of 0.583 DSUYs per  $A$  for 2009. DSUYs lost per  $A$  were similarly calculated annually through the year 2020 and in perpetuity (denoted as ‘Beyond’ in Table 2). Finally, DSUYs for all years and in perpetuity were summed, delivering the total recruitment losses for 1 km<sup>2</sup> of patch reef.

The total quantity of DSUYs gained for 1 km<sup>2</sup> of patch reef supplied by lionfish control was computed using the identical methodology as measuring DSUY losses. In the analysis, lionfish removals were expected to provide a

60 % return of recruitment services during the year 2010 for a total service value of 80 % of pre-lionfish invasion function (i.e., 20 % existing function plus 60 % recovery owing to lionfish removal), assuming a linear rate of recovery. Using the calculation of DSUY losses as a template, the total DSUYs gained per  $A$  for the year 2010 equals the RSUYs gained during 2010 (0.300) multiplied by the discount factor (0.943) to arrive at 0.283. Likewise, in the year 2011, 0.549 DSUYs were gained ( $0.600 \times 0.915$ ). DSUYs gained per  $A$  were similarly calculated per year in perpetuity and summed. Finally, net DSUY losses per  $A$  were computed by subtracting the total quantity of DSUYs gained from those lost. In the same way, lionfish losses and also

gains due to lionfish control were calculated for biomass using a 65 % reduction rate (e.g., from Green et al. 2012) spanning the years 2008 to 2010 and assuming an 80 % cumulative rate of recovery.

### Sensitivity testing

In order to quantify a range of losses and gains that may be realistically expected, should control efforts be more or less successful, the 80 % recovery scenario used as a baseline was sensitivity tested by varying the rate from 50 to 100 % in 10 % increments. Protracted rates of lionfish removals over time will lead to variable lionfish densities, and these different densities will produce different mean rates of biomass and recruitment losses and ecosystem function. In order to quantify these variances, we modeled all recovery scenarios in 1-year increments beginning 2 years post-invasion (i.e., the year 2010) until the year 2020 and in perpetuity, for a total of 60 model runs.

### Valuing losses

As SUYs are monetarily unit-less, the total DSUYs either gained or lost must be multiplied by the perceived annual value provided by the resource per  $A$  in order to arrive at a monetary value (MV) either gained or lost. As an arbitrary example, if one  $A$  of undamaged reef contributes \$1000 per year in value ( $V$ ) to recruitment function, and given a total reef area of  $10 \text{ km}^2$  ( $T$ ), the total value of the reef to recruitment is \$10,000 per year. This calculation can be summarized by the equation:

$$MV = (DSUYs)(V)(A)(T) \quad (2)$$

Over 10 years, therefore, the total value of recruitment function is \$100,000, assuming the reef provides 100 % of this service spanning the entire 10 years. Similarly, if we assume lionfish damages to the  $10 \text{ km}^2$  reef instigated a loss of 20.00 DSUYs and lionfish control delivered a gain of 6.00 DSUYs, the net loss is 14.00 DSUYs. It follows that the cost of the lionfish damages is \$20,000, the value of services gained from lionfish control is \$6000, and the net overall monetary loss is \$14,000 for the  $10 \text{ km}^2$  reef. For a more detailed evaluation of the equations used by the Visual HEA software, we direct the readers to Kohler and Dodge (2006).

Finally, using the DSUY losses obtained from our analysis, and in order to guide future application of the method and values obtained here, a purely hypothetical case study was modeled that estimated the service losses imposed by lionfish to Bahamian reefs fringing New Providence Island (NPI)—the same location of study upon which we based estimates of biomass loss as documented by Green et al. (2012). To do this, we arbitrarily and individually valued

annual biomass and recruitment services at \$1000 per  $\text{km}^2$  for ease of calculation. To provide a more realistic assessment of how the cost of lionfish control influences the value of restored ecosystem services, we also chose to consider here the additive costs (in present day monies) of lionfish removal efforts. In order to do this, we hypothetically valued annual lionfish removal costs at \$100 per  $\text{km}^2$ , when removals were protracted over 10 years, and \$500 per  $\text{km}^2$  per year when control was swiftly, but more expensively, accomplished within 1 year. Should future studies quantitatively measure the true value of biomass and recruitment functions to Bahamian reefs (i.e., the service value of those fish whose reductions were witnessed), and also the costs of lionfish removal, these estimates can be substituted for our example valuations to arrive at a robust approximation of lionfish monetary impacts in the Bahamas.

## Results

### Lionfish service losses

Herein we found that the net DSUYs lost due to lionfish damages to recruitment on Bahamian patch reefs, using an 80 % reduction in recruitment as seen by Albins and Hixon (2008), spanned from a minimum of 7.54 per  $\text{km}^2$ , when recovery to 80 % function was restored within 1 year (Fig. 1), to a maximum of 9.86 when a gradual and extended rate of recovery (by the year 2020) was executed (Tables 2, 3). These quantities can be interpreted as the cumulative yearly loss of recruitment services associated with the lionfish invasion in the presence of 1- to 10-year control measures that increased recruitment function to 80 % of pre-invasion levels. When lionfish control was completely absent, and thus no recovery was realized, the total recruitment DSUYs lost inflated to 26.67. For biomass, a DSUYs loss of 7.32 per  $\text{km}^2$  was found when 80 % ecosystem function was achieved by the year 2011 and 9.06 when function reached 80 % by the year 2020 (Table 3). In the absence of lionfish control, 21.67 biomass DSUYs were lost.

Sensitivity testing (Table 3) showed a minimum DSUYs loss to recruitment of 1.16 per  $\text{km}^2$  (recovery to 100 % service level in 1 year) and maximum of 18.27 (recovery to 50 % service level after 10 years). For biomass, a minimum of 0.94 (100 % recovery in 1 year) and maximum of 17.47 (50 % recovery after 10 years) DSUY losses per  $\text{km}^2$  were calculated. It is important to note that all loss and gains for the stated values were calculated in perpetuity, inferring that the given losses represent the total net of all present and future lionfish losses and also all recovery of services provided by lionfish control efforts.

**Table 3** DSUYs lost and gained

Recovery rate (%)	Total loss	1-year gains	1-year net loss	10-year gains	10-year net loss	Mean loss per year
<b>Recruitment</b>						
0	26.67	–	–	–	–	–
50	26.67	9.57	17.11	8.41	18.27	0.13
60	26.67	12.76	13.92	11.21	15.46	0.17
70	26.67	15.95	10.73	14.01	12.66	0.22
<b>80</b>	<b>26.67</b>	<b>19.14</b>	<b>7.54</b>	<b>16.81</b>	<b>9.86</b>	<b>0.26</b>
90	26.67	22.32	4.35	19.61	7.06	0.3
100	26.67	25.51	1.16	22.42	4.26	0.34
<b>Biomass</b>						
0	21.67	–	–	–	–	–
50	21.67	4.78	16.89	4.2	17.47	0.06
60	21.67	7.97	13.7	7	14.67	0.11
70	21.67	11.16	10.51	9.81	11.86	0.15
<b>80</b>	<b>21.67</b>	<b>14.35</b>	<b>7.32</b>	<b>12.61</b>	<b>9.06</b>	<b>0.19</b>
90	21.67	17.54	4.13	15.41	6.26	0.24
100	21.67	20.73	0.94	18.21	3.46	0.28

Shown are 1- and 10-year DSUYs lost and gained and mean DSUYs lost per year for recovery rates varied from 50 to 80 %. Highlighted in bold are modeled values for an 80 % recovery of services

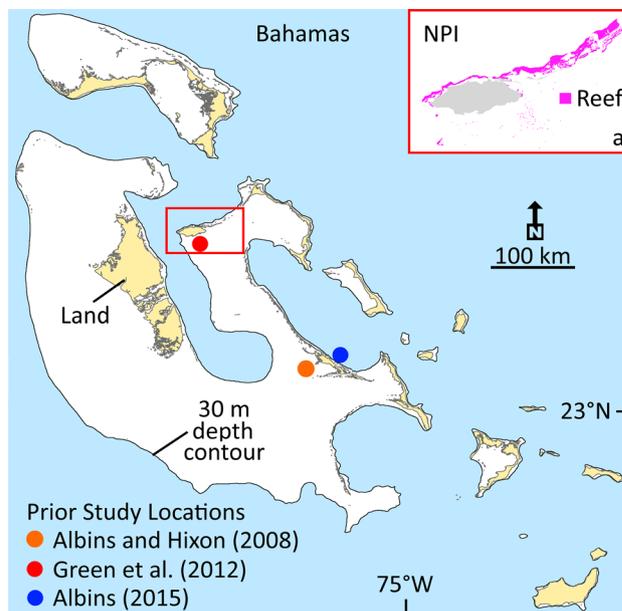
### Valuing lionfish control

The gain in services provided by lionfish control in this investigation was found to be a minimum (for a 1-year recovery rate) of 19.14 DSUYs per km<sup>2</sup> for recruitment and 14.35 for biomass given an 80 % recovery rate (Table 3). For every year that passed without repair to an 80 % pre-invasion service level, a mean recruitment loss of 0.26 DSUYs was realized, with the maximum loss from year 1 to 2 of 0.28 and a minimum of 0.24, given a 10-year recovery rate. For biomass, a mean service loss of 0.19 per km<sup>2</sup> was computed per year, with a minimum loss of 0.18 and a maximum loss of 0.21.

When varying the service recovery rate (i.e., sensitivity testing—see Table 3 for all tested values) from 50 to 100 % for both recruitment and biomass functions, a minimum DSUYs gain per km<sup>2</sup> provided by lionfish control of 4.20 for biomass and 8.41 for recruitment was seen, given a 50 % service level after 10 years. A maximum DSUYs gain of 20.73 for biomass and 25.51 for recruitment was calculated at a 100 % service level given a 1-year recovery rate.

### New Providence Island case study

The total reef coverage in waters surrounding NPI was estimated to be 83 km<sup>2</sup>, established on data obtained from Reefbase (Fig. 2) (Reefbase 2014). Using the minimum and maximum service losses calculated for 1- to 10-year recoveries at 50–100 % rates, and a hypothetical value of biomass and recruitment of \$1000 per km<sup>2</sup> each, we calculated



**Fig. 2** Prior lionfish studies in the Bahamas and also reef coverage in NPI. Reef coverage indicated in pink for New Providence Island (a). Data obtained from Reefbase. Prior locations of lionfish studies upon which the valuation was derived represented by pink (i.e., Albins and Hixon 2008), red (i.e., Green et al. 2012), and blue (i.e., Albins 2015) dots

total fiscal losses ranging from \$0.10 to \$1.52 million for recruitment and \$0.08 to \$1.45 million for biomass if lionfish control succeeds on NPI reefs. The additive costs of lionfish control to accomplish these recovery scenarios

ranged from \$0.04 million (1-year recovery) to \$0.08 million (10-year recovery). In the absence of lionfish removal, and calculated in perpetuity to encompass all present and future services lost, the monetary losses attributed to lionfish damages in this example increased to \$2.21 million for recruitment and \$1.80 million for biomass.

## Discussion

The 65 % biomass and 80 % recruitment decreases witnessed by Green et al. (2012) and Albins and Hixon (2008), and that are used in this analysis, cannot be transferred directly to measure fiscal losses without considering the declining monetary value of the damages over time. It follows that the benefit of applying the analysis method described here lies in the ability to measure, in contemporary and standardized units (i.e., DSUYs per area unit), protracted and varied rates of invasive species damages and recovery, provided by invasive species control, over time. The DSUYs delivered in such an analysis can then be used to assign monetary values to service losses and gains for whole ecosystems or individual species if data are available to both quantify the impacts of the invader and also the perceived monetary value of the impacted resource. Furthermore, the method presented is widely relevant not only for marine-invaded systems, but for any ecosystem, terrestrial or aquatic, where impacts by the invader, and also the recovery of services owing to removal of the invader, can be quantitatively measured and valued. As such, this study can functionally guide the application of this method to other invasion scenarios.

This study emphasizes how a complete lack of lionfish control, thus assuming no subsequent ecosystem recovery, imparts extensive service losses to Bahamian locations containing dense lionfish populations such as those sites surveyed by Green et al. (2012) and Albins and Hixon (2008). Without lionfish removals, total service losses to recruitment and biomass functions of 26.67 and 21.67 DSUYs per km<sup>2</sup> were seen in this analysis (Table 3). Considering the most conservative lionfish removal efforts in our sensitivity testing scenarios—those which provided a 15 % return of services (i.e., to a service level of 50 %) after 10 years—the loss of services imposed by lionfish was reduced to 18.27 DSUYs for recruitment and 17.47 for biomass. In the same accord, lionfish controls produced a gain of 8.41 and 4.20 DSUYs per km<sup>2</sup>; a 32 and 20 % increase over absent lionfish control. If removals succeeded to restore a 100 % pre-injury function level within 1 year, lionfish losses were reduced to 1.16 DSUYs per km<sup>2</sup> for recruitment and 0.94 for biomass and gains attributed to lionfish control were computed to be 25.51 and 20.73 DSUYs, respectively. Intrinsically, even a conservative effort to remove lionfish

holds important value as opposed to ignoring resident lionfish populations, while a more concerted effort brings a much greater rate of return than absent control.

The investigation also demonstrated that timely lionfish control, as opposed to delayed removals (i.e., 1-year recovery vs. 10-year recovery), reduced long-term losses given the same level of ecosystem recovery. This can be seen when examining the total DSUYs gained and lost given an 80 % recovery scenario spanning 1- to 10-year recoveries for recruitment—the total difference in DSUYs gained from a 1-year recovery to a 10-year recovery was 2.32 DSUYs per km<sup>2</sup>. Immediate efforts to contain lionfish, therefore, provide a greater rate of return than protracted and gradual efforts to control the fish and should be high priority.

In this study, we did not measure lionfish-mediated service losses or gains provided by recreational lionfish fisheries or tourism. The losses calculated here were also derived from studies in Bahamian locations that have already suffered degradation due to fishing pressure, coral bleaching, and pollution, among an elongated list of stressors to Bahamian coral reefs. Jackson et al. (2014) found, however, that the majority of this decline in coral reef cover due to these stressors occurred prior to the year 2000 and preclude the studies by Albins and Hixon (2008), Green et al. (2012), and Albins (2015) upon which lionfish damages for this study were derived (Fig. 2). Given this, we presumed the Bahamian damages calculated by the authors were solely attributed to lionfish. It is also probable that the reductions in biomass and recruitment observed by Albins and Hixon (2008) and Green et al. (2012) were directly linked to high lionfish densities; however, any potential relationship between lionfish damages and lionfish biomass has not yet been quantitatively evaluated. It is important that both studies were conducted in the Bahamas and additional work by Darling et al. (2011) found similarly high lionfish densities on Bahamian reefs surrounding NPI.

Changes in biomass and recruitment should be dependent on the abundance of the invader. This relationship is the basis of control programs that aim to reduce invasive species densities to levels where impacts, such as biomass loss, are minimized. Furthermore, varied levels of control success, measured by different densities of lionfish, will lead to uneven responses in biomass and recruitment function—a relationship that is, in all probability, not linear. Granular measurements of lionfish damages over time and also natural reef recovery after lionfish removal, however, have not been documented in the literature. Given this lack of available data, linear rates of damage and recovery were used in this analysis. As such, the derived DSUYs lost and gained documented here should therefore be interpreted as estimates in place of measured and variable rates of damage and recovery.

The study also based recruitment and biomass losses on assessments from lionfish-dense locations in the Bahamas and therefore we limit our interpretation of the results to locations showing similar concentrations of lionfish in the Bahamas. It follows that the ecosystem losses implied by the study must be taken with caution and, if interpreted austere, should be applied to Bahamian localities which harbor lionfish in similar numbers as to those in the study locations from which data were harvested for the analysis. Still, the study data are useful as a baseline to measure the service losses attributed to lionfish in similar ecosystems with great lionfish abundance and also locations that show similar reductions in recruitment and biomass of lionfish prey fish. Should the lionfish density-to-injury ratio become apparent, the study data can be scaled to other Caribbean locations which exhibit similar species composition and conditioning factors as the Bahamas but differing lionfish densities.

### Valuing losses

There is a pressing need for ocean managers to justify lionfish control costs when framed against the monetary impacts of the invader. In order to quantify the monetary damages done by Bahamian lionfish using the DSUY loss and gain values calculated here, it is first necessary to enumerate the monetary benefit streams provided by the species that lionfish have impacted in locations such as those surveyed by Albins and Hixon (2008) and Green et al. (2012). Regrettably, there is a distinct paucity of recent evaluations of the economic benefit streams of Caribbean reef systems and their inhabitants in order to do this. Cesar et al. (2003), however, estimated the total reef coverage in the Caribbean (excluding reefs in USA waters) to be 19,000 km<sup>2</sup> and the net total monetary benefit streams of all Caribbean coral reefs to be \$1.85 billion, translating to \$97.5 k per km<sup>2</sup>. Jackson et al. (2014) suggested that most of the degradation of Caribbean reefs occurred during the 1980s and 1990s before the appraisal tendered by Cesar et al. (2003). Given this, the assessment by Cesar et al. (2003) is one example of the perceived value of Bahamian reefs, such as those examined by Green et al. (2012) and Albins and Hixon (2008), at the time of this study. Still, the evaluation done by Cesar et al. (2003) is a very generalized estimate based on broad classifications of ecosystem services. Additionally, these ecosystem function values were derived from information derived from Hawaiian and Southeast Asian reef systems and not Bahamian reefs. It should be noted that there is great danger in transferring economic values of reefs from one location to another (Brander et al. 2007). In a meta-analysis of recreational values of coral reefs, Brander et al. (2007) found that the average transfer error was ~186 % and concluded that value transfers should simply not be done in

coral reef studies. As such, we have chosen to limit our evaluation to quantifying DSUYs lost per km<sup>2</sup> due to lionfish predation and gains from control efforts without assigning monetary values to either metric.

### The difficulties of lionfish control

Lionfish are now found in high densities in most Caribbean habitats. In an effort to reduce the impacts of the fish, removal programs have been implemented by many Caribbean nations to varying degrees of success (Barbour et al. 2011; de León et al. 2013). The most effective method of lionfish control is through manual removal, such as that accomplished by recreational spearfishing and hand-netting. Indeed, 'lionfish derbies' are held on a regular occasion in their invaded range and have proven an effective local control mechanism (Barbour et al. 2011). This fishery, however, is confined to waters shallower than recreational dive limits (30 m), is a laborious effort, and is not likely to produce complete eradication (Barbour et al. 2011). Moreover, local derbies do not target lionfish populations in distant and uninhabited regions. Also, being ambush predators which consume live prey, lionfish are not vulnerable to a traditional hook and line fishery. The most promising method to target deep lionfish that perhaps may serve as reservoirs for uncontrolled adult populations appears to be the bycatches of lionfish collected from reef traps (Morris and Whitfield 2009). Using traps to remove lionfish, however, will inevitably have short-term impacts on native biodiversity owing to native species bycatch. Development of a lionfish trap fishery, therefore, would necessitate gear that target lionfish singularly in order to reduce native catches. To date, such gear has not been developed. It also must be acknowledged that ongoing gains to Bahamian ecosystem functions obligate continuous lionfish culls, as evidenced by Barbour et al. (2011) who found that lionfish biomass recovered to 90 % of unfished biomass after only 6 years of non-removals. Even with wholesale removals, partial recovery is likely only where elimination rates are high (>50 %) and only on small spatial scales (Morris et al. 2011). Johnston and Purkis (2014, 2015) demonstrated long-distance connectivity between disparate Caribbean lionfish populations and that upstream 'source' populations provide recruits to distant 'sink' populations, further complicating lionfish control. Because of vast Caribbean connectivity, it is likely that limited-scope efforts alone cannot entirely regulate local populations (Johnston and Purkis 2015). Given these caveats, the prospect of successful and widespread lionfish eradication is daunting at best and perhaps un-attainable for the entire Caribbean. Still, this investigation demonstrates that even modest levels of lionfish control that successfully restore some ecosystem function provide value and should be continued.

Enumerating the variable costs to remove Bahamian lionfish by trapping, spear fishing, or other methods will be central going forward to determine the actual realized monetary value of lionfish removals and also the potential application of this analysis. Local eliminations demonstrate measureable gains (Frazer et al. 2012; de León et al. 2013; Green et al. 2014), and the results of this evaluation can be used in the future to quantify those successes in the Bahamas or other infected locations similar to the Bahamas containing high lionfish densities. It is widely acknowledged that invasive species control costs are extraordinarily high (Leung et al. 2002; Pimentel et al. 2005) and these extreme costs are especially relevant to eliminating lionfish which require a tedious manual removal regime. To date, the expenditures of such programs have not been quantified. An evaluation of lionfish control costs, however, is critical to justify lionfish eradication efforts when contrasted with damages done by the fish.

## Conclusion

In this study, losses to Bahamian recruitment and biomass measured 7.54 and 7.32 DSUYs per km<sup>2</sup> when recovery to 80 % of pre-invasion service levels was seen within 1 year. In the same accord, the gains produced by lionfish removal efforts were measured at 19.14 and 14.35 DSUYs per km<sup>2</sup> given the same rapid rate of ecosystem reclamation. Protracted rates of recovery were more costly; however, when Bahamian lionfish were left uncontrolled, losses as a result of lionfish damages increased to 26.67 and 21.67 DSUYs per km<sup>2</sup>, implying that even modest levels of control are better than none.

Though difficult to measure empirically, the studies used to parameterize this analysis (e.g., Green et al. 2012; Albins and Hixon 2008) have shown measureable reductions in biomass and recruitment on affected reefs, and it is likely that the continued presence of lionfish will further extend these ecosystem impacts if the invader is not controlled. Bahamian lionfish are likely to reduce the quantity and quality of prey items available to native predatory fish, such as snapper and grouper, and may induce cascading trophic effects caused by declines in prey and, perhaps, the predators themselves. This reduction is important for fisheries, which may witness lower catches as a result; however, fewer native species may also decrease the recreational value of Bahamian reefs to tourism—an industry upon which much of the Bahamian economy depends. Lionfish control, therefore, we deem compulsory in the Bahamas.

Going forward, quantifying the fine-grained monetary benefits of Caribbean reefs species to ecosystem services is necessary in order to fully leverage the results presented

here. These functional values are needed in order to enumerate lionfish monetary impacts and also to value lionfish control efforts in the Bahamas using the DSUY losses and gains offered in this analysis. Should the monetary remunerations to ecosystem function provided by the species impacted by lionfish become known, our evaluation can be used as a guide to appraise the true fiscal costs of lionfish in the Bahamas and elsewhere using the same methodology as used in this study.

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