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Abstract

Invasive species have caused widespread economic and environmental disruption, which have been widely studied. However, their potential benefits have received much less attention. If invasive species contribute to livelihoods, their eradication may negatively impact wellbeing. Failing to value these benefits may lead to an undervaluation of invaded ecosystems. We assess the potential economic benefits of an invasive species within an artisanal fishery in Jamaica. We monitored catches over 259 fisherman-days, and conducted 45 semi-structured interviews, with 76 fishermen. We show that the invasive Australian Red Claw crayfish (*Cherax quadricarinatus*) is an important source of income for fishermen within the Black River Lower Morass of Jamaica and supplement incomes during periods when native shrimp (*Macrobrachium spp.*) catches decline. We also show that full-time fishermen and those who have no alternative occupations expend the greatest fishing effort. We use the intra-annual variation of fishermen's harvest effort between seasons (when catch per unit effort changes) as a proxy for dependence. Using this measure, we found that the least wealthy appear to be the most dependent on fishing, and consequently benefit the most from the invasive crayfish. Our results demonstrate the importance of considering the potential benefits of invasive species within integrated landscape management.

Keywords: Invasive alien species. Invaded ecosystems. Small-scale fishery. Ecosystem services. Wild-harvest products.

1. Introduction

There is strong evidence that invasive alien species (IAS) have damaged ecological and economic systems around the world (McGeoch *et al.* 2010; Pejchar & Mooney 2009; Sala *et al.* 2000). Yet, there is little research investigating the potential economic benefits of IAS (Young 2010; Pejchar & Mooney 2009). Of the few studies that have explored the economic benefits of IAS (e.g. Shackleton *et al.* 2006; de Neergaard *et al.* 2005; Geesing *et al.* 2004; Jakubowski *et al.* 2001) even fewer have quantified the income that they generate (Schlaepfer *et al.* 2011, but see: Shackleton, Kirby & Gambiza (2011); Pascual *et al.* 2009; Ackefors 1999; Southwick & Southwick 1992). It is unclear whether this is because IAS are near-universally destructive or because of a bias within the academic community (Stromberg *et al.* 2009; Gurevitch & Padilla 2004).

A lack of appreciation of the potentially positive role of some IAS in human livelihoods may lead to a number of undesirable outcomes. First, undervaluing the benefits of IAS may lead to excessive investment in their removal. For instance, *Lantana camara L*. is a widely studied invasive shrub (van Wilgen *et al.* 2004), considered to be among the top ten worst invasive species in the world (GISIN 2012). The majority of studies conducted to determine the economic and ecological costs and benefits of removal have not quantified the positive role this species can play as a harvestable resource for communities, such as a source of firewood or craft materials (e.g. Marais & Wannenburgh 2008; Le Maitre *et al.* 2002, but see Patel 2011). The costs associated with *Lantana* probably still exceed the benefits of its presence. However, incorporating the benefits that accrue to local communities may change the optimal distribution of removal effort across the landscape. Second, this lack of awareness of the potential positive economic value of IAS may lead to underestimation of the value of invaded ecosystems, which may bias spatial conservation planning.

Pimentel *et al.* (2001) estimate that 20-30% of IAS in the US, UK, Australia, India, South Africa and Brazil are considered pests and only a minority of these are likely to be serious pests (also see Lodge 1993). It is possible that among the remaining species, an important portion may be socially and economically beneficial. Whether an IAS is beneficial depends on characteristics of the IAS, and of the ecosystems and social groups that are affected by it (García-Llorente *et al*. 2008). In Northern Ethiopia, invasive eucalyptus is used and sold as a building material and to construct farming tools; this species performs better in water- and nutrient-poor soils than indigenous species, and as a result is commonly grown in farmers' woodlots (Jagger & Pender 2003). However, in South Africa, eucalyptus is being removed from riparian areas to help restore natural water resources and increase the availability of potable water to communities (Marais & Wannenburgh 2008). It follows that the impact and role of IAS, and therefore control measures, are context specific. Part of this context relates to the socioeconomic factors that influence the relationships between IAS and communities.

Similarly, the benefits of IAS vary within human communities as well as between them. The link between individuals' socioeconomic characteristics and their non-timber forest product harvesting behaviour has been well studied (e.g. Gavin & Anderson 2007; Lacuna-Richman 2002; McSweeney 2002; Barham *et al.* 1999). For instance, although it was once believed that those living in extreme poverty are particularly dependent on wild foods for subsistence (Scoones *et al.* 1992), the relationship is often more complex (e.g. Wilkie *et al.* 2001). In some situations, wealthier households have greater capacity to hunt, consume and sell wild products (de Merode *et al.* 2004). The same complexities may also apply to the use of IAS, making the economic implications of removing an invasive species unclear. For example, communities bordering the Chitwan National Park in Nepal use a number of invasive species, including the plant *Mikania micrantha.* Rai *et al.* (2012) found that household socioeconomic characteristics influence *M. micratha's* perceived value. Those families that were more dependent on forest products incurred more of both the costs and benefits associated with *M. micrantha* than less forest-dependent families. The value of ecosystem services often varies spatially and temporally; the management of invasive species that contribute to ecosystem services should therefore reflect this variability (Hershner & Havens 2008).

The relationship between biodiversity and ecosystem services is complex (Cameron 2002). However, higher biodiversity is generally positively correlated with higher ecosystem service value in warm climates (Cardinale *et al.* 2012; Naeem *et al.* 2009; Costanza *et al.* 2007 Balvanera *et al.*, 2006). The effect of IAS species on biodiversity and habitat function is also complex (Hector and Bagchi, 2007; Schwartz *et al*., 2000). Although the majority of the literature investigating the ecological impact of invasive species concludes that they are detrimental to native biodiversity, there are some examples where IAS assist native species, for instance through positive habitat modification (Rodriguez 2006). Similarly, the impact of IAS can change over time (Strayer *et al.* 2006). The invasive fire ant *Solenopsis invicta* in southern USA initially reduced the populations of other insects when first introduced in the 1980’s. However, 12 years later *S. invicta* populations substantially declined and native arthropod species recovered to pre-invasion levels (Orrison & Loyd 2002). In this case, total arthropod biodiversity appears to have increased without compromising the population sizes of native species over the long term. It is plausible to suggest that in some instances, perhaps where there are empty niches (e.g., on some islands), the addition of IAS may increase biodiversity, ecosystem function & resilience and the value of ecosystem services (Young 2012; Young 2010; Hershner & Havens 2008). The absolute socioeconomic costs and benefits of invasive species are hard to estimate because of the complex impact that they have on invaded ecosystems and species. However, arguably, this applies equally to the valuation of native species within wider ecosystems.

In order to explore these issues, we studied the economic benefits of the invasive Australian Red Claw crayfish, *Cherax quadricarinatus* (von Martens), within fishing communities of the Black River Lower Morass (BRLM) of southwest Jamaica (Figure 1). This study aims to answer three questions: a) can this invasive alien species provide an economically significant source of gross revenue, b) how are the economic benefits distributed over time and c) who within these communities benefits the most?

Increased household revenue is expected to contribute to increased consumption. Additional earnings may be particularly important for those that subsist on relatively low incomes, who are anticipated to have greater marginal utility from income (Ellis 1994). The temporal distribution of household liquidity is also important, especially in the absence of precautionary saving or functioning credit markets. Temporary or seasonal fluctuations in income may lead to corresponding changes in consumption. This may lead to periods of cyclical poverty (Dercon and Krishnan 2000). Finally other socioeconomic characteristics may influence the capacity for individuals to mobilize resources or otherwise influence harvesting behaviour. Identifying the distribution of economic benefits across different groups is also useful for contextualising the benefit of additional revenue. For example, those with no alternative occupations would have a higher opportunity cost from not engaging in harvesting, than those that do. As a result, they may be the most dependent on the income derived from harvesting activity.

The study does not determine if there is a net economic benefit associated with the invasive crayfish to the communities within the BRLM. Instead it seeks to encourage landscape managers to consider possible economic benefits, as well as costs, within invaded ecosystems and compared to more pristine ecosystems. Accounting for the possible benefits, as well as costs, may improve conservation resource allocation within landscape management and improve the accuracy of ecosystem valuation.

1.1 Study site

The Black River Lower Morass is situated within the parish of St. Elizabeth. The parish is described by Campbell, Barker and McGregor (2011) as the ‘breadbasket of Jamaica’, owing to its importance as a domestic source of agricultural produce. The agricultural sector is dominated by small-scale farmers, which are deemed to be relatively prosperous relative to national living standards (McGregor, Barker and Campbell 2009). Fishing, using traditional gear, is a common occupation in the BRLM Ramsar site. Although a few individuals specifically target either native shrimp (*Macrobrachium spp.*) or invasive crayfish (*C. quadricarinatus)* with specialist gear, the vast majority catch both using the same harvesting equipment: homemade shrimp pots. Fishing is one of the most common occupations in the four target communities of the BRLM who operate from two landing stages in Community 1 and Community 2 (Figure 1). Village names, and details that could be used to identify those villages, were kept anonymous because of the sensitive nature of some activities, including Marijuana cultivation. Fishermen from another village, further south in the BRLM, often use wire mesh traps that specifically target the invasive crayfish as opposed to traditional shrimp pots for native shrimp, and were not included in the study. All caught shrimp and crayfish are sold to local women who then cook and sell them along roadsides throughout the country. The fishery requires relatively low capital inputs and has few barriers to entry. Of these barriers the most significant appear to be the purchasing of fish pots at c. USD$1.20 per pot, for those unable to construct their own, and the construction and maintenance or borrowing of dugout canoes.

Low flow and drought events, such as those found during the dry season within the BRLM (Figure 1), reduce hydrological connectivity and pool volumes. They also lower water quality (reduced dissolved O_2 as the result of decomposing organic matter) and increase salinity, all of which negatively impact *Macrobrachium spp.* abundance (Covich & Crowl 2006; Jayachandran 2001; Bowles *et al.* 2000).

The invasive crayfish (*C. quadricarinatus)* are native to rivers and streams of north Australia and Papua New Guinea (Carpentaria 2008) - areas that experience seasonal drought (Riek 1969). They have diverse feeding habits that vary between habitats (Jones 1989), are physically robust (Ruscoe 2002), tolerant of anoxic environments, and a wide range of salinities and temperatures (Meade & Watts 2002; Meade *et al.* 1994). It is these characteristics, combined with their large size and edibility that make them ideal candidates for aquaculture. It also makes them successful invasive species, and they have established feral populations in Singapore, South Africa, Israel, Mexico, Jamaica and Puerto Rico (often escaping from aquaculture, Ahyong & Yeo 2007).

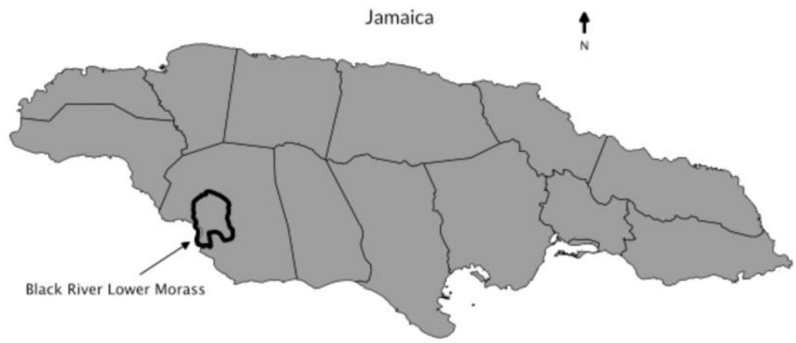

Figure 1. The Black River Lower Morass (thick line) in the Saint Elizabeth Parish, in southwest Jamaica.

2. Methods

Two main methods of data collection were used: recording catches at landing stages and one-off semi-structured interviews. Additionally, informal observations and interviews were also conducted throughout the study period. Catch data included the weights of native shrimp and invasive crayfish and the number of pots hauled per fisherman per day. Semi-structured interviews collected a range of variables that were used to model predictors of harvesting behaviour (Table 1).

2.1. Catch data collection

The target population was all shrimp fishermen (estimated c. 95) from the four target communities who use the landing stages in Community 1 and Community 2. Because of the low absolute number of fishermen, we aimed to collect a complete census of all fishermen’s harvesting activities. There are no accurate records of the number of fishermen within the four communities. However, evidence of shrimp harvesting was only found in areas accessible from the two landing stages. Forest and swamp patches adjacent to other accessible areas were not found to contain shrimp harvesting gear. The fishermen targeted within the study were the main resources users within the morass and of the invasive crayfish. Seventy-six out of an estimated ninety-five fishermen agreed to participate (54 and 22 from communities 1 and 2 respectively).

A sampling framework, in which catch data were collected on alternate days from each landing stage for six days, followed by two days of no catch data collection, was implemented. Catch data were collected between

07:30h and 14:30h when the majority of fishermen returned to landing stages. The catches were separated into native shrimp and crayfish (one species, *Macrobrachium rosenbergii*, was not included in the analyses because it was harvested using different fishing gear), then weighed using an electronic hanging scale (ElectroSamson™ Digital Hanging Scales, 25 kg ± 0.02 kg). The number of pots hauled that day was also recorded. We conducted a pilot study in September 2010. Changes were made to the protocol and so pilot data was not included in the study. Data were collected between October 2010 and August 2011. A local fisherman was hired as a research assistant to help collect catch data, assist in conducting semi-structured interviews and act as a key informant and guide to the community. The research assistant had worked as a fisherman his entire life, as well as serving as an assistant on other research projects, and was well respected within the communities. The research assistant also provided information about the standard (universal across all fishermen-buyer transactions) seasonal price change between the wet and dry seasons, which was confirmed by other community members during frequent, informal discussions throughout the study period. Informal discussions with other community members were routinely used to triangulate qualitative data provided by the research assistant and across participants.

2.2. Semi-structured interviews

During March 2011, 50 interviewees were randomly selected (using a random number generator in R (R Development Core Team 2005)) from the 76 participating fishermen from whom we collected catch data; 36 from the landing stage in Community 1 and 14 from the landing stage in Community 2. Semi structured interviews were conducted primarily at the landing stages or in private residences. Interviews were often conducted during wider informal discussions. An interview guide (see Supplementary Material 3) was used to ensure that all questions were answered during the interview whilst allowing the delivery of the questions to remain flexible. This was necessary to both aid comprehension, and because of participant’s hesitancy to answer questions that they perceive could be used to identify them as cultivating marijuana or for taxation purposes. To this effect, no audio recording equipment was used. Instead data were recorded in a notebook. This data were subsequently coded and the relevant quantitative data were extracted.

We asked respondents which community landing stage they used, the number of family members who were dependent on them and their total fishing experience in years (or fractions of years). We also asked if participants had other sources of income and to indicate their perceived standards of living according to a self-ranked wealth scale. This self-ranked wealth scale asked participants to rank their financial security relative to their community. Although this did not provide absolute data on individuals' wealth, it did provide an indicator of participants' perceived relative wealth, which appeared to be an important determinant of harvesting behaviour. Although using self-ranked measures of wealth can be problematic, Bodegom *et al.* (2009) found a significant correlation ($p>0.001$) between the in-depth Demographic Health Survey (DHS) wealth index and self-reported wealth measures. Similarly, self-ranked measures of wealth have been successfully used by others including Williams *et al.* (2012).

Opportunistic informal questioning of fishermen during the whole study provided valuable qualitative data regarding behaviour and incentives under varying catch conditions. This contextual data was vital for developing a set of candidate models as detailed below (section 2.3). It also allowed the validity of inferences observed in the data to be evaluated and questioned based on a qualitative understanding of the community and fishing system. No information that could identify individuals was retained because of the sensitivity of some of the fishermen's illegal activities.

2.3. Analysis

Data were converted from JA$ to US$ (JA$84.7= US$1 (XE Currency Converter 2010)) and imperial to metric weights where appropriate. Using the catch data, we calculated the gross revenues from crayfish and native shrimp harvesting by fishermen and investigated the seasonality of catches (weight per fishermen day) and catch value (total value per fishermen day). To do this we used the Köppen climate classification system to determine dry months (following Peel, Finlayson & McMahon 2007). For tropical wet/dry forests and savannah, the pronounced dry season contains months with precipitation of less than 60 mm or less than (100 − [total annual precipitation {mm}/25]). Total rainfall over the study period was 1072 mm; therefore the 60 mm value was higher than the 57 mm value (calculated using the stated formula) used to determine dry months. As such, months with < 60 mm rainfall (total for the month) were considered dry months. Each month was designated as a dry or a wet month, depending on the total rainfall calculated for each month (using data from the Meterological Service of Jamaica). The designated wet and dry months were used as different levels (wet vs. dry) of a factor (season) and the individual times when the fishermen were interviewed were used as replicates for each month. We used a generalised linear mixed model (GLMM; with the communities as the random factor) with a gamma distribution and reciprocal link function (if the data did not include a zero value) to assess the effects of the seasons on the average yield of native shrimp, and invasive crayfish, the average number of pots hauled, and the average value of the native shrimp and invasive crayfish and the value of the combined yields. If the data included a zero value, we used a normal distribution with a reciprocal or a log link function (depending on an assessment of the residuals). We then used a one-way ANOVA to assess the differences between seasons for each site, the differences between each site, and the differences between each site for a particular season for average yield, pots hauled and value (total and average). Following an assessment of the residuals, we found that the assumptions of this analysis were not upheld. Therefore yield and value data were first transformed using $\log_{10}(x + 1)$ before analysis. Average number of pots hauled data was not transformed because an assessment of the residuals indicated that the assumptions of the ANOVA were not violated. These statistical tests were performed using the GenStat Discovery Edition 4.0 (VSN International, Hemel Hempstead, UK) statistical package.

All subsequent data analyses were conducted using the statistics programme ‘R’ version 2.14.2 (R Development Core Team 2005). All socioeconomic variables were tested against each other for correlation using Spearman's rank correlation, one-way ANOVA, Kruskal-Wallis rank sum test and Pearson’s Chi-squared tests in R.

Next, we created two measures of dependence on fishing to determine which types of fishermen might be benefitting most from presence of the crayfish. Generally, it is challenging to measure dependence on resources directly, since this requires information on (hypothetical) alternatives to harvesting were the resources not to exist. In many developing countries, shadow wage rates are hard to estimate as labour markets are thinly developed and may not always be cash based. Using gross revenue as an indicator of harvester's *dependence* on native shrimp and invasive crayfish could be misleading, instead reflecting their individual capacity to mobilise resources or their effectiveness as fishermen. The distinction between the sizes of the gross revenue derived from harvesting activities, and the degree that individuals are dependent on that source of income, is due to several factors including the availability of alternative occupations and the opportunity cost of forgoing that revenue.

We therefore used two proxies for dependence. Firstly, i) mean daily harvest effort (mean number of pots hauled per fisherman per day across all days of data collection). Secondly, ii) intra-annual variation in harvesting effort (the change in harvest effort between the wet and dry season, for each fisherman).

We assumed that those harvesters who have the lowest mean harvest effort and who varied their harvesting effort the most in response to seasonal fluctuations in catches were less dependent on the resource than those who invest more effort into harvesting or maintain more consistent effort throughout the year, even when catches decline. We therefore investigated how socioeconomic variables (elicited during the semi-structured interviews) influenced i) daily mean harvesting effort and ii) intra-annual variation in harvesting effort. Equation (1) describes the means by which we calculated intra-annual variation in harvest effort (V) for each fisherman. P is the total recorded pots hauled per fisherman and D the total number of possible harvesting days, respectively, during the wet ($_w$) and dry ($_d$) seasons. Since monitoring effort was consistent across both seasons, this provides a combined indicator of changes in number of pots hauled per day and changes in the number of days fishermen are active in the fishery.

$$V = 100 * [(P\text{d} / D\text{d}) - (P\text{w}/D\text{w})]/(P\text{w}/D\text{w}) \qquad (1)$$

Within the two analyses, we used Generalised Linear Models (GLMs) to explore which socioeconomic characteristics predicted daily mean harvest effort and intra-annual variation in effort, with a Gaussian distribution and identity link function. The choice of explanatory variables was based on relevant literature, semi-structured interviews with fishermen and observations in the field (see Table 1 for a description of variables). Because eight explanatory variables were identified *a priori*, we fitted the global model and all possible combinations of variables. We then used an information-theoretic approach to avoid over-fitting, ranking our candidate sets of models using the corrected AIC (AICc) because of the small sample size (Akaike 1974). In both candidate sets there was no model with a ΔAICc >2 and so we averaged across all models following Anderson & Burnham (2002). For each analysis, the 10 models with the lowest AICc and the averaged models are detailed in the Supplementary Material 1. There was a strong positive relationship between years of experience and the capacity of fishermen to make their own pots ($F_{(43,1)}$= 6.65, p=0.013). Therefore, to avoid model redundancy, the pots variable was removed from the candidate set of both GLMs. The decision to drop this variable followed the reasoning that it was more likely that experienced fishermen would learn how to make pots than it was that those fishermen who know how to make pots would gain greater experience as a result.

Variable name	Variable type	Coding	Description	References	Overall		Community 1		Community 2	
					Mean	Std. error	Mean	Std. error	Mean	Std. error
community	binary	Community 1= 0 Community 2= 1	The landing stage that the fisherman operates from, which influences characteristics such as distance from markets.							
dependents	discrete		The number of dependents (spouses and children who are financially supported within the household) can either increase the constraints on, or availability of, labour.	(Mazera et al. 2007; McSweeney 2002; Barham et al. 1999)	3.55	0.37	4.39	0.75	3.14	0.62
experience	continuous		The number of years as a shrimp fisherman is an indicator of professional status and harvesting skill.	(Lacuna-Richman 2002)	28.00	2.59	30.69	2.92	22.07	5.08
occupation	binary	No alternative occupation= 0 Has one or more alternative occupations = 1	Fishermen with alternative occupations can re-distribute their effort in response to declining catches, thereby maximising incomes in ways that those who are solely reliant on shrimp harvesting cannot.	(Martin et al. 2013; Cinner et al. 2011; Ellis & Allison 2004; Mazera et al. 2007 Batterbury 2001; Ellis 2000)	0.93	0.03	0.97	0.03	0.86	0.10
wealth	ordinal	'I am living comfortably'= 4 'I am coping'=3 'I am living with some difficulty'=2 'I am living with extreme difficulty'=1	This scale is used as a rough proxy for wealth, whose impact on fishing behaviour, particularly when catches change, can be both positive or negative depending on other economic factors. Measuring wealth is challenging. We felt that a subjective measure of perceived standards of living was an adequate proxy for wealth in this study.	(Williams et al. 2012; Daw et al. 2012; Cinner et al. 2009; Takasaki et al. 2001; Cinner et al. 2011)	3.26	0.12	3.35	0.14	3.07	0.27
pots (not included)	binary	Yes=1, No=0	Do individuals use pots that they have constructed, as opposed to ones that have been purchased?		0.66	0.07	0.71	0.08	0.57	0.14
marijuana	binary	Yes=1, No=0	Do individuals cultivate marijuana alongside harvesting shrimp (which may be an alibi for being in the swamp)?		0.53	0.07	0.71	0.08	0.14	0.10
mean effort	scalar		Mean effort, as measured by the mean number of pots hauled per fisherman per day of data collection across the study period.		100.96	7.54	103.21	9.15	96.01	13.74
intra-annual variation in effort	continuous		A measure of an individual fisherman's change in harvest effort between the wet and dry season (%), defined according to fishermen's classification of the wet and dry seasons, to reflect traditional delineations.		11.3	14.7	12.0	19.7	9.8	18.6

3. Results

All fishermen within the target group were male. In each community 37.5% of catch days were recorded during the 11-month period. We weighed 4,909 catches during this period. We attribute the disparity between participation rates between the two communities (all 54 in Community 1 and 22 of 41 in Community 2) to greater suspicion towards the objectives of the project in Community 2, even though anonymity was assured and identities were unspecified during publication (individuals were identified using initials to allow data collection). Because of the lower participation rates in Community 2 there may be bias in our results, if the reasons for not participating are linked to fishing activities. Of the 50 participants selected for interview, 5 were unwilling to participate or did not provide sufficiently detailed responses. We therefore completed interviews with 31 individuals from Community 1, and 14 individuals from Community 2.

3.1. The monetary value of the invasive crayfish harvest

The mean market value of individual fishermen's daily catch over the 11 months (incorporating seasonal price changes) was US$22.81 with the invasive crayfish making up US$3.53 of that value. Informal discussions with fishermen indicate that the invasive crayfish is considered to be a by-catch of shrimp harvesting, as opposed to fishermen specifically targeting the invasive species. Additionally, other fishermen also catch the invasive species as by-catch using other fishing gear. Smaller invasive crayfish may not have been separated from the native shrimp catches. These results suggest that the total invasive crayfish catch values were probably lower than observed. From these figures, an approximate and illustrative gross annual revenue can be estimated; an ‘average’ fisherman, working the mean number of 5.95 days per week, hauling the mean value of 104.82 pots per day, would earn gross revenue of approximately US$7,077 per year. However, among individuals there is high variability in catch value, effort and gross value per unit effort. Effort varies from as little as 30 pots hauled per day to as many as 200 (including seasonal fluctuations in effort) and the maximum mean gross value per pot (across all pots hauled by one fishermen on one harvesting excursion) is nearly 520% greater than the minimum. Using the Köppen climate classification system analysis we determined that there were, in total, four dry months and seven wet months. Informal discussions with fishermen indicate that fishermen typically set more pots during the wet season. However, anecdotal evidence suggests the study period covered an unusually dry November, when fishermen normally set a high number of pots; it was subsequently classified as a dry season month, when it would typically be considered to be in the wet season. This may have skewed our results concerning the number of pots hauled. Consequently, we found that the average number of pots hauled across all fishermen was significantly higher in the dry season (dry = 111 (± 1.22 s.e.) vs. wet = 100.9 (± 1.75 s.e.) pots day^{-1}; $F_{(1,246)} = 24.53$, $p < 0.001$).

Market prices and catch sizes both varied between the wet and dry seasons. Native shrimp and invasive crayfish prices rose during the dry season, from US$6.44 to US$7.73 and US$3.86 to US$5.15 per kilogram respectively. We found that the native shrimp yield was significantly higher in the wet than the dry months (dry = 2.67 (± 0.07 s.e.) vs wet = 2.95 (± 0.09 s.e.) kg/ day^{-1}; $F_{(1,246)} = 6.8$, $p = 0.01$), when looking at all fishermen across the two communities, despite the lower effort, whilst the opposite was true for the invasive crayfish (dry = 1.11 (± 0.04 s.e.) vs. wet = 0.56 (± 0.05 s.e.) kg/ day^{-1}; $F_{(1,246)} = 49.22$, $p < 0.001$).

Across all fishermen, the gross revenue from the invasive crayfish was significantly higher during the dry months than the wet (dry = \$5.47 (± 0.2 s.e.) vs. wet = \$2.29 (± 0.23 s.e.) US\$ day^{-1}; $F_{(1,246)} = 54.85$, $p < 0.001$). The gross revenue of the native shrimp did not change over the seasons (dry = \$19.74 (± 0.56 s.e.) vs. wet = \$18.99 (± 0.85 s.e.) US\$ day^{-1}; $F_{(1,246)} = 1.13$, $p = 0.289$). The combined gross revenue of both the native shrimp and the invasive crayfish was higher during the dry season (dry = \$29.09 (± 0.07 s.e.) vs. wet = \$24.63 (± 0.07 s.e.) US\$ day^{-1}; $F_{(1,246)} = 25.97$, $p < 0.001$). However, we did not find any statistically significant differences in catches or number of pots hauled between the two communities.

During March (the height of the dry season), the invasive crayfish accounts for, on average, approximately one quarter to one third of the total catch value. Harvesting invasive crayfish appears to reduce the variability in fishermen's incomes during the year.

Catch weight, pots hauled and catch value for each community mirrored the overall trends between seasons. Exceptions to this were the absence of statistical significance in the average number of pots hauled and the average yield of native shrimp, between seasons, in

Community 1. Supplementary Material 2 describe the results from the one-way ANOVA used to assess seasonal effects on catches, number of pots hauled and catch value between the two communities across the seasons, and their means and standard errors.

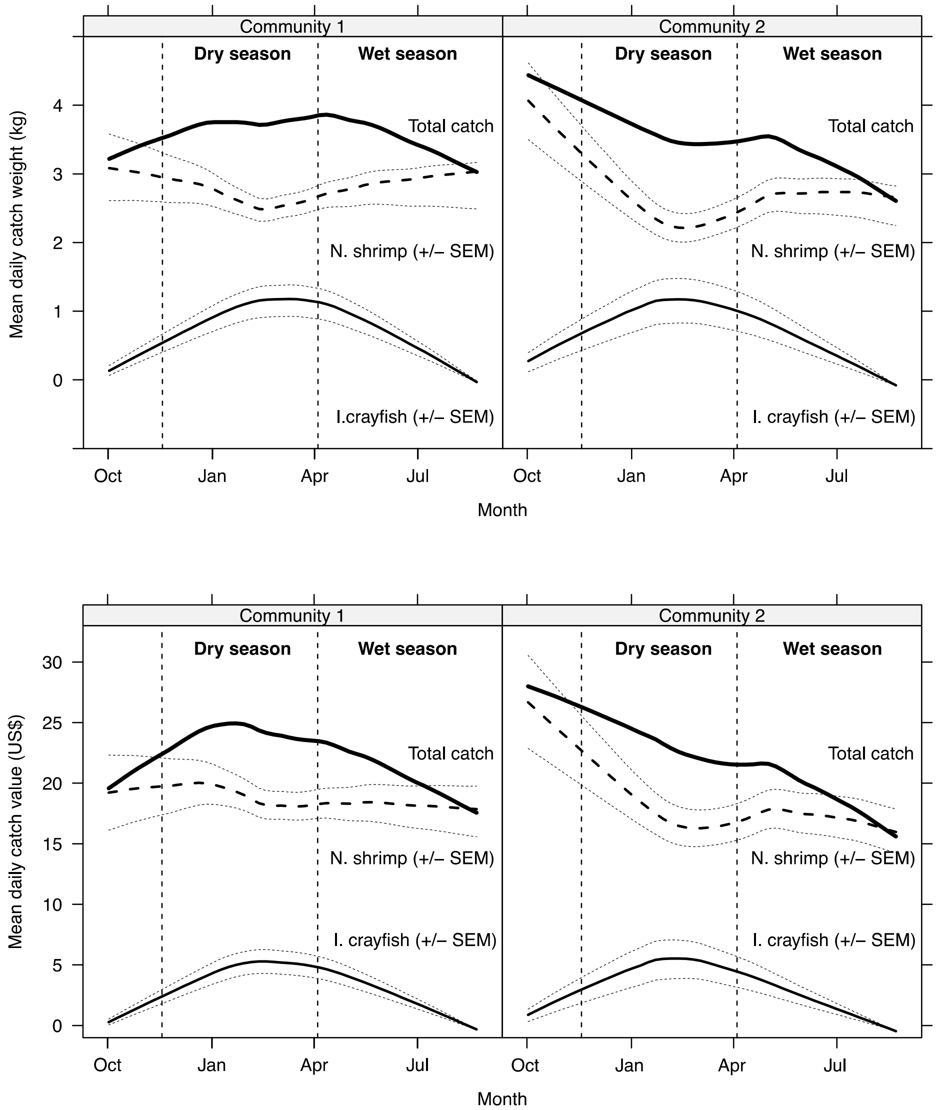

Figure 2. Smoothed seasonal trends in mean catch weight (top row) and mean catch value (bottom row) per trip for native shrimp (N. shrimp, dashed), invasive crayfish (I. crayfish, thin line) and total values (thick line) for the two communities including standard errors (+/-

SEM, thin dashed). Dry season is shown by vertical dashed lines.

During semi-structured interviews and informal interviews, fishermen unanimously reported that they had observed a decline in native shrimp catches during their lifetimes. They suggested that the primary drivers of this decline were reduced water quality and an increase in the number of fishermen; none mentioned the invasive crayfish as a likely contributor. Although there is no empirical evidence to substantiate these claims, our key informant and research assistant also held these opinions.

3.2. Socioeconomic predictors of harvesting effort

Marijuana cultivation was more common in Community 1 ($c^2_{(1,44)}$= 10.27, p= 0.0013), as was the likelihood of having an alternative occupation (aside from marijuana cultivation, $c^2_{(1,44)}$= 4.25, p= 0.0391). Those who cultivate marijuana are typically wealthier than those who do not ($H_{(3)}$= 5.66, p= 0.12).

Model averaging across all models in the candidate set (weighted by AICc, Burnham & Anderson 2002), we find that years of experience and having alternative occupations influence fishermen's mean harvest effort (Supplementary Material 1). It is estimated that on average those fishermen with alternative occupations set nearly 60 fewer pots per monitored day, than those with no alternative occupations (Figure 3). For each additional year of fishing experience, fishermen set on average 1.1 more pots per day. Wealth, number of dependents and marijuana cultivation all had positive effects on the number of pots set, but these relationships were weak. Those from Community 2 set around 22 fewer pots than those from Community 1. However, the relationship is only moderately strong, and according to the previous analysis (discussed above) is not statistically significant.

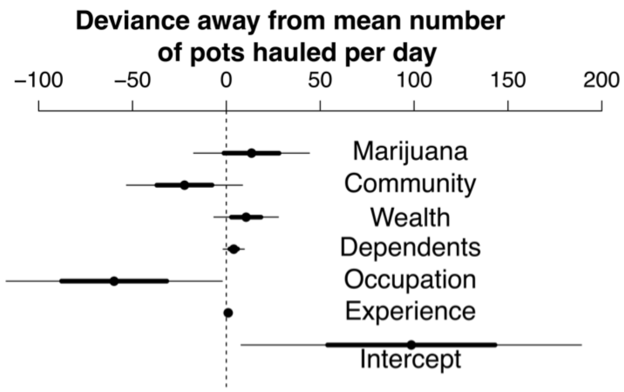

Figure 3. Model-averaged coefficients for socio-economic determinants of individual fishermen’s mean daily harvest effort, measured in number of pots hauled per day, across all days of data collection during the study period. The range shows the positive or negative impacts of the characteristics on the mean number of pots hauled across all fishermen. Points show the coefficient

estimates, thick lines indicate first confidence interval (68%) and thin lines indicate the second (95%).

3.3. Socioeconomic predictors of intra-annual variation in harvest effort

The second GLM found wealth to be an important determinant of intra-annual variation in harvest effort (the change in harvest effort for an individual fisherman between the wet and dry season) for some fishermen (Figure 4). Between those fishermen who have the highest and lowest wealth there is c.27 percentage points more variability between the wet and dry season; a fisherman who is ‘living comfortably’ (wealth category 4) reduces effort, on average, by 27 percentage points more than someone ‘living with extreme difficulty’ (wealth category 1). Having an alternative occupation was found to not have a clear effect on the variability between the wet and dry season.

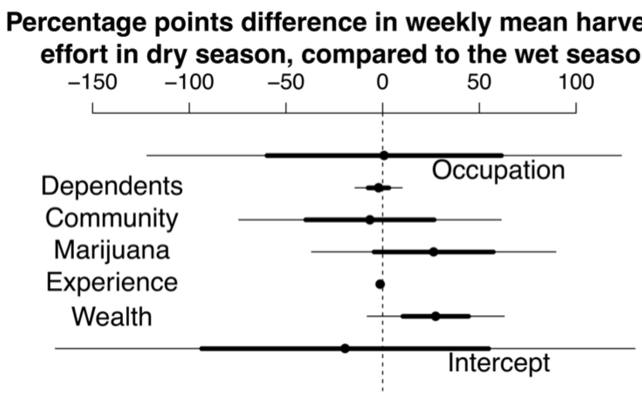

Figure 4. Model-averaged coefficients (in percentage points) for socio-economic determinants of intra-annual variation. 0 indicates no effect on seasonal changes in harvest effort, whereas an estimate of -10pp, for example, indicates that the factor is associated with an additional 10pp decline in harvest effort between the wet and dry season. Points show the coefficient estimates (as pp), thick lines indicate the first confidence interval (CI=68%), thin lines indicate the second (CI= 95%).

4. Discussion

4.1. Can invasive alien species provide an economically significant source of revenue?

This study has quantified some of the gross economic benefits of the IAS, the Australian Red Claw crayfish. Our results suggest that the invasive crayfish provides an economically significant portion of fishermen's gross revenues, contributing approximately 15% of total catch value across all fishermen during the study period. However, this gross revenue does not occur evenly over time or between individuals. Revenue derived from harvesting invasive crayfish during the dry season reduces the seasonal variability in incomes (income smoothing). It was reported that the invasive crayfish's mobility over land (something *Macrobrachium spp.* are incapable of) lead to their congregation in residual water bodies, making them easier to harvest. This may account for the observed increase in crayfish harvests during the dry season, as opposed to an absolute increase in their population size.

The temporal distribution of incomes has been recognised as an important factor in household economics. Seasonal household liquidity constraints suppress consumption and can lead to periods of cyclical poverty (Dercon and Krishnan 2000). Weak or non-existent credit markets, limited precautionary saving, seasonal variance in prices and other factors can further impede consumption smoothing (Baulch and Hoddinott 2000; Chaudhuri and Paxson 2001; Rosenzweig 2001). According to Khandker (2009) ‘when income smoothing does not happen, a failure to smooth consumption may result in food shortage and deprivation.’

Fishermen reported that during the dry season they had less income from shrimp harvesting (supported by our findings), and those that had alternative income generating activities would refocus their efforts on those activities. Our study did not explore the impact of seasonal fluctuations in income on consumption behaviour. Yet, fishermen reported that the dry season was typically a more difficult period because of constrained liquidity.

Within this context harvesting of the invasive crayfish during the dry season probably leads to less volatile incomes over the year. This increases income availability during the dry season, which is typically a period where incomes are constrained, and therefore may have an important consumption smoothing effect. This consumption smoothing may be particularly important for the poorest fishermen who may face seasonal deprivation if they cannot access credit markets and have no precautionary savings. An additional benefit can also be speculated. The invasive crayfish are more resilient to environmental fluctuations in temperature, salinity, and water chemistry. In this respect, they may also be more resistant to human induced environmental shocks. They may be more persistent in the face of environmental degradation than native shrimp species, and subsequently may become an increasingly important component of fishermen’s incomes.

This study did not seek to determine the impact of the invasive crayfish on the native shrimp population, and subsequently the incomes that might be derived from shrimp catches in the absence of the crayfish. Anecdotal evidence suggests that native shrimp catches had been declining since before the introduction of the invasive crayfish in Jamaica. The participating fishermen reported increasing numbers of fishermen and pollution as probable drivers of the decline. There have been few studies of the effects of *C. quadricarinatus* on invaded ecosystems, but invasive crayfish have caused significant global impacts, both ecologically and economically (Gherardi 2007). In the case of *M. micrantha* utilisation around the Chitwan National Park in Nepal, communities perceived the invasive shrub as an inferior forest product with associated economic costs as well as benefits (Rai *et al.* 2012). Rai *et al.* (2012) suggest "the farm household response to invasive plants is to make the best out of the worst situation". This might describe the situation in BRLM, but it also seems possible that the crayfish is exploiting otherwise unoccupied niches on the island, increasing aquatic diversity. Higher native biodiversity has been found to increase stability of ecosystems (Cardinale *et al.* 2012).

4.2. Who benefits most from the fishery?

In small-scale fisheries, fishermen are often found or assumed to be the poorest within communities, and fishing is a more frequent occupation in poor communities (FAO 2012; Béné *et al.* 2007). Although there is no economic data from communities within the BRLM with which to compare fishing incomes, a wide degree of socioeconomic heterogeneity within the fishing communities was observed. Those who have no alternative occupations tend to have higher average harvest effort over the year. Individuals who have alternative and more profitable occupations can distribute their effort to maximise their income whilst managing risk. This is supported by current economic and social theory relating to subsistence livelihoods, where individuals diversify their livelihoods to achieve higher and more stable incomes (Martin *et al.* 2013; Ellis & Allison 2004; Batterbury 2001; Ellis 2000). Our results are consistent with Mazera *et al.* (2007) who found that greater non-fishing income, derived from alternative occupations, was associated with reduced fishing effort. Shackleton, Kirby & Gambiza (2011) explore the role of the invasive prickly pear (*Opuntia ficus-indica*) in incomes of poor trading households in South Africa. They highlight the conflict of interest between the South African Government, which is concerned with the impact to the formal economy and environment, and the income and nutritional needs of local traders. They found that lower income traders were most benefited by the presence of the invasive prickly pear.

Individuals that are the most dependent on the fishery tend to be those with greater experience. It is these individuals who appear to benefit most from the presence of the invasive crayfish. Lacuna-Richman (2002) suggested that older members of communities in Leyte, in the Philippines, were more dependent on non-timber forest products because they had both fewer alternative livelihood options and greater harvesting skills than younger members. However, our study did not find a significant correlation between ‘experience’ and presence or absence of an alternative ‘occupation’, which indicates that older or more experienced fishermen did not necessarily have fewer livelihood options available to them.

4.3. Who benefits most from dry season presence of crayfish?

During the dry season, native shrimp catches decline and invasive crayfish catches increase. In this study, we are assuming that those with the least intra-annual variation in harvest effort are choosing to maintain their harvesting levels because they are most dependent on it. Again, as a logical extension, they also derive the greatest benefit from the invasive crayfish, which stabilises catches during the dry season. Within the BRLM, those with low self-reported wealth reduce their harvesting effort less during the dry season relative to the wet, than do those who consider themselves to be wealthier.

Although Cinner *et al.* (2011) found that fishermen reported that they would increase their harvesting effort in response to a decline in catches, Hoorweg *et al.* (2006) observed that the wealthier fishermen on the Malindi-Kalifi coast of Kenya were more inclined to reduce fishing effort in response to a decline in catches. Similarly, Hoorweg *et al.* (2006) found that those who had a range of occupations generally had a more positive attitude towards conservation of declining catch populations. This suggests that the fishermen's response to changes in catches is influenced by other socioeconomic characteristics. Our study has found similar complexity in behavioural responses to changing seasonal catch levels within the community. Although there is an overall increase in mean harvest effort during the dry season, anecdotal evidence suggests this was atypical. Additionally, despite statistical significance, it is unclear if the observed mean change (an additional c.10 pots per day) is socially and economically significant. As a result this limits the wider conclusions that can be drawn regarding behavioural responses to changes in catch conditions. Pollnac *et al.* (2001) found that there are a wide variety of income and non-income factors that affect fishermen's readiness to leave fisheries in Southeast Asia, including non-economic job satisfaction. Our study differs in that it looks at seasonal changes in effort as opposed to individuals permanently leaving a fishery. Nevertheless, factors such as job satisfaction may also play an important role in determining changes in seasonal effort, though this was not explored in the present study.

Financial security is a reflection of other socioeconomic characteristics, such as employment history and number of dependents. The effects of wealth on wild product harvesting behaviour are complex (Takasaki *et al.* 2001). Some studies have found that less wealthy families harvest more wild products, or are more reliant on them (Shackleton *et al.* 2011). Others have found more complex relationships, tied to land tenure and other assets that allow individuals to invest resources that allow them to increase returns on effort (Williams *et al.* 2012). Gavin & Anderson (2007) suggest that the effects of wealth on harvesting behaviour are confounded by other socioeconomic and environmental factors.

The relationship between poverty and small-scale fisheries in developing countries, once thought to be close, is now understood to be more complex (Béné 2003). In some circumstances, where the opportunity cost of time is low, the supply of available labour can saturate open access fisheries, reducing incomes to the level of the opportunity cost or shadow wage rate (Béné 2009). In short, incomes from small-scale or artisan fisheries may be set exogenously (a function of labour supply and alternative and more profitable occupations, which have higher barriers to entry), and are normally the least profitable activity within communities. Within the BRLM we have not determined if this is the case. However, those who are poorest are likely to remain in the fishery when catches decline because of a lack of capacity to adapt to changes in catch by mobilising resources which would allow them to engage in alternative occupations. In turn, this may allow them to attain higher incomes and subsequently have greater financial security (Badjeck *et al.* 2010). To the extent that the invasive crayfish stabilises seasonal incomes and possibly consumption, it is the poor who appear to benefit most from its presence.

5. Conclusion

Although IAS continue to pose significant ecological and economic causes for concern, our evidence suggests that to help achieve a more optimal allocation of both development and conservation effort, unbiased accounting of their benefits as well as their costs is required. Schlaepfer *et al.* (2011) argue that the benefits of introduced and invasive species to ecosystems and ecosystem functions are underestimated. Such non-native species may fill ecological niches that become vacant as the result of other anthropogenic factors (or are vacant because of island effects), foster habitat restoration and support ecosystem functions. Introduced species can also provide novel non-timber forest products, bushmeat or other wild harvest products. We share Shackleton, *et al.*'s (2011) conclusion that there is a need for a more nuanced approach towards the management of IAS that balances both local livelihood needs and wider environmental and social concerns. The positive contributions of IAS need to be recognised and incorporated into environmental management efforts, when considering the eradication of IAS and when calculating the value of invaded ecosystems.

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