

**Alien invasions and livelihoods: Economic benefits of invasive Australian Red Claw crayfish in Jamaica**

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Alien invasions and livelihoods: economic
benefits of invasive Australian Red Claw crayfish
in Jamaica

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Abstract

1 Invasive species have caused widespread economic and
2 environmental disruption, which have been widely
3 studied. However, their potential benefits have received
4 much less attention. If invasive species contribute to
5 livelihoods, their eradication may negatively impact
6 wellbeing. Failing to value these benefits may lead to an
7 undervaluation of invaded ecosystems. We assess the
8 potential economic benefits of an invasive species within
9 an artisanal fishery in Jamaica. We monitored catches
10 over 259 fisherman-days, and conducted 45 semi-

11 structured interviews, with 76 fishermen. We show that
12 the invasive Australian Red Claw crayfish (*Cherax*
13 *quadricarinatus*) is an important source of income for
14 fishermen within the Black River Lower Morass of
15 Jamaica and supplement incomes during periods when
16 native shrimp (*Macrobrachium spp.*) catches decline. We
17 also show that full-time fishermen and those who have no
18 alternative occupations expend the greatest fishing effort.
19 We use the intra-annual variation of fishermen's harvest
20 effort between seasons (when catch per unit effort
21 changes) as a proxy for dependence. Using this
22 measure, we found that the least wealthy appear to be
23 the most dependent on fishing, and consequently benefit
24 the most from the invasive crayfish. Our results
25 demonstrate the importance of considering the potential
26 benefits of invasive species within integrated landscape
27 management.

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

31

32 **1. Introduction**

33 There is strong evidence that invasive alien species (IAS)
34 have damaged ecological and economic systems around
35 the world (McGeoch *et al.* 2010; Pejchar & Mooney 2009;
36 Sala *et al.* 2000). Yet, there is little research investigating
37 the potential economic benefits of IAS (Young 2010;
38 Pejchar & Mooney 2009). Of the few studies that have
39 explored the economic benefits of IAS (e.g. Shackleton *et*
40 *al.* 2006; de Neergaard *et al.* 2005; Geesing *et al.* 2004;
41 Jakubowski *et al.* 2001) even fewer have quantified the
42 income that they generate (Schlaepfer *et al.* 2011, but
43 see: Shackleton, Kirby & Gambiza (2011); Pascual *et al.*
44 2009; Ackefors 1999; Southwick & Southwick 1992). It is
45 unclear whether this is because IAS are near-universally
46 destructive or because of a bias within the academic
47 community (Stromberg *et al.* 2009; Gurevitch & Padilla
48 2004).

49

50 A lack of appreciation of the potentially positive role of
51 some IAS in human livelihoods may lead to a number of

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

72

73 Pimentel *et al.* (2001) estimate that 20-30% of IAS in the
74 US, UK, Australia, India, South Africa and Brazil are
75 considered pests and only a minority of these are likely to
76 be serious pests (also see Lodge 1993). It is possible that

77 among the remaining species, an important portion may
78 be socially and economically beneficial. Whether an IAS
79 is beneficial depends on characteristics of the IAS, and of
80 the ecosystems and social groups that are affected by it
81 (García-Llorente *et al.* 2008). In Northern Ethiopia,
82 invasive eucalyptus is used and sold as a building
83 material and to construct farming tools; this species
84 performs better in water- and nutrient-poor soils than
85 indigenous species, and as a result is commonly grown in
86 farmers' woodlots (Jagger & Pender 2003). However, in
87 South Africa, eucalyptus is being removed from riparian
88 areas to help restore natural water resources and
89 increase the availability of potable water to communities
90 (Marais & Wannenburg 2008). It follows that the impact
91 and role of IAS, and therefore control measures, are
92 context specific. Part of this context relates to the
93 socioeconomic factors that influence the relationships
94 between IAS and communities.

95
96 Similarly, the benefits of IAS vary within human
97 communities as well as between them. The link between
98 individuals' socioeconomic characteristics and their non-
99 timber forest product harvesting behaviour has been well
100 studied (e.g. Gavin & Anderson 2007; Lacuna-Richman
101 2002; McSweeney 2002; Barham *et al.* 1999). For

102 instance, although it was once believed that those living
103 in extreme poverty are particularly dependent on wild
104 foods for subsistence (Scoones *et al.* 1992), the
105 relationship is often more complex (e.g. Wilkie *et al.*
106 2001). In some situations, wealthier households have
107 greater capacity to hunt, consume and sell wild products
108 (de Merode *et al.* 2004). The same complexities may also
109 apply to the use of IAS, making the economic implications
110 of removing an invasive species unclear. For example,
111 communities bordering the Chitwan National Park in
112 Nepal use a number of invasive species, including the
113 plant *Mikania micrantha*. Rai *et al.* (2012) found that
114 household socioeconomic characteristics influence *M.*
115 *micratha's* perceived value. Those families that were
116 more dependent on forest products incurred more of both
117 the costs and benefits associated with *M. micrantha* than
118 less forest-dependent families. The value of ecosystem
119 services often varies spatially and temporally; the
120 management of invasive species that contribute to
121 ecosystem services should therefore reflect this variability
122 (Hershner & Havens 2008).

123

124 The relationship between biodiversity and ecosystem
125 services is complex (Cameron 2002). However, higher
126 biodiversity is generally positively correlated with higher

127 ecosystem service value in warm climates (Cardinale *et*
128 *al.* 2012; Naeem *et al.* 2009; Costanza *et al.* 2007
129 Balvanera *et al.*, 2006). The effect of IAS species on
130 biodiversity and habitat function is also complex (Hector
131 and Bagchi, 2007; Schwartz *et al.*, 2000). Although the
132 majority of the literature investigating the ecological
133 impact of invasive species concludes that they are
134 detrimental to native biodiversity, there are some
135 examples where IAS assist native species, for instance
136 through positive habitat modification (Rodriguez 2006).
137 Similarly, the impact of IAS can change over time
138 (Strayer *et al.* 2006). The invasive fire ant *Solenopsis*
139 *invicta* in southern USA initially reduced the populations
140 of other insects when first introduced in the 1980's.
141 However, 12 years later *S. invicta* populations
142 substantially declined and native arthropod species
143 recovered to pre-invasion levels (Orrison & Loyd 2002).
144 In this case, total arthropod biodiversity appears to have
145 increased without compromising the population sizes of
146 native species over the long term. It is plausible to
147 suggest that in some instances, perhaps where there are
148 empty niches (e.g., on some islands), the addition of IAS
149 may increase biodiversity, ecosystem function &
150 resilience and the value of ecosystem services (Young
151 2012; Young 2010; Hershner & Havens 2008). The

152 absolute socioeconomic costs and benefits of invasive
153 species are hard to estimate because of the complex
154 impact that they have on invaded ecosystems and
155 species. However, arguably, this applies equally to the
156 valuation of native species within wider ecosystems.

157

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

167

168 Increased household revenue is expected to contribute to
169 increased consumption. Additional earnings may be
170 particularly important for those that subsist on relatively
171 low incomes, who are anticipated to have greater
172 marginal utility from income (Ellis 1994). The temporal
173 distribution of household liquidity is also important,
174 especially in the absence of precautionary saving or
175 functioning credit markets. Temporary or seasonal
176 fluctuations in income may lead to corresponding

177 changes in consumption. This may lead to periods of
178 cyclical poverty (Dercon and Krishnan 2000). Finally
179 other socioeconomic characteristics may influence the
180 capacity for individuals to mobilize resources or otherwise
181 influence harvesting behaviour. Identifying the distribution
182 of economic benefits across different groups is also
183 useful for contextualising the benefit of additional
184 revenue. For example, those with no alternative
185 occupations would have a higher opportunity cost from
186 not engaging in harvesting, than those that do. As a
187 result, they may be the most dependent on the income
188 derived from harvesting activity.

189

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

200

201 **1.1 Study site**

202 The Black River Lower Morass is situated within the
203 parish of St. Elizabeth. The parish is described by
204 Campbell, Barker and McGregor (2011) as the
205 'breadbasket of Jamaica', owing to its importance as a
206 domestic source of agricultural produce. The agricultural
207 sector is dominated by small-scale farmers, which are
208 deemed to be relatively prosperous relative to national
209 living standards (McGregor, Barker and Campbell 2009).
210 Fishing, using traditional gear, is a common occupation in
211 the BRLM Ramsar site. Although a few individuals
212 specifically target either native shrimp (*Macrobrachium*
213 *spp.*) or invasive crayfish (*C. quadricarinatus*) with
214 specialist gear, the vast majority catch both using the
215 same harvesting equipment: homemade shrimp pots.
216 Fishing is one of the most common occupations in the
217 four target communities of the BRLM who operate from
218 two landing stages in Community 1 and Community 2
219 (Figure 1). Village names, and details that could be used
220 to identify those villages, were kept anonymous because
221 of the sensitive nature of some activities, including
222 Marijuana cultivation. Fishermen from another village,
223 further south in the BRLM, often use wire mesh traps that
224 specifically target the invasive crayfish as opposed to
225 traditional shrimp pots for native shrimp, and were not

226 included in the study. All caught shrimp and crayfish are
227 sold to local women who then cook and sell them along
228 roadsides throughout the country. The fishery requires
229 relatively low capital inputs and has few barriers to entry.
230 Of these barriers the most significant appear to be the
231 purchasing of fish pots at c. USD\$1.20 per pot, for those
232 unable to construct their own, and the construction and
233 maintenance or borrowing of dugout canoes.

234

235 Low flow and drought events, such as those found during
236 the dry season within the BRLM (Figure 1), reduce
237 hydrological connectivity and pool volumes. They also
238 lower water quality (reduced dissolved O₂ as the result of
239 decomposing organic matter) and increase salinity, all of
240 which negatively impact *Macrobrachium spp.* abundance
241 (Covich & Crowl 2006; Jayachandran 2001; Bowles *et al.*
242 2000).

243

244 The invasive crayfish (*C. quadricarinatus*) are native to
245 rivers and streams of north Australia and Papua New
246 Guinea (Carpentaria 2008) - areas that experience
247 seasonal drought (Riek 1969). They have diverse feeding
248 habits that vary between habitats (Jones 1989), are
249 physically robust (Ruscoe 2002), tolerant of anoxic
250 environments, and a wide range of salinities and

251 temperatures (Meade & Watts 2002; Meade *et al.* 1994).
252 It is these characteristics, combined with their large size
253 and edibility that make them ideal candidates for
254 aquaculture. It also makes them successful invasive
255 species, and they have established feral populations in
256 Singapore, South Africa, Israel, Mexico, Jamaica and
257 Puerto Rico (often escaping from aquaculture, Ahyong &
258 Yeo 2007).

259



260

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

263

264 **2. Methods**

265 Two main methods of data collection were used:
266 recording catches at landing stages and one-off semi-
267 structured interviews. Additionally, informal observations
268 and interviews were also conducted throughout the study
269 period. Catch data included the weights of native shrimp
270 and invasive crayfish and the number of pots hauled per

271 fisherman per day. Semi-structured interviews collected a
272 range of variables that were used to model predictors of
273 harvesting behaviour (Table 1).

274 **2.1. Catch data collection**

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

291

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

296 07:30h and 14:30h when the majority of fishermen
297 returned to landing stages. The catches were separated
298 into native shrimp and crayfish (one species,
299 *Macrobrachium rosenbergii*, was not included in the
300 analyses because it was harvested using different fishing
301 gear), then weighed using an electronic hanging scale
302 (ElectroSamson™ Digital Hanging Scales, 25 kg ± 0.02
303 kg). The number of pots hauled that day was also
304 recorded. We conducted a pilot study in September 2010.
305 Changes were made to the protocol and so pilot data was
306 not included in the study. Data were collected between
307 October 2010 and August 2011. A local fisherman was
308 hired as a research assistant to help collect catch data,
309 assist in conducting semi-structured interviews and act as
310 a key informant and guide to the community. The
311 research assistant had worked as a fisherman his entire
312 life, as well as serving as an assistant on other research
313 projects, and was well respected within the communities.
314 The research assistant also provided information about
315 the standard (universal across all fishermen-buyer
316 transactions) seasonal price change between the wet and
317 dry seasons, which was confirmed by other community
318 members during frequent, informal discussions
319 throughout the study period. Informal discussions with
320 other community members were routinely used to

321 triangulate qualitative data provided by the research
322 assistant and across participants.

323

324 **2.2. Semi-structured interviews**

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

345

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

365

366 Opportunistic informal questioning of fishermen during
367 the whole study provided valuable qualitative data
368 regarding behaviour and incentives under varying catch
369 conditions. This contextual data was vital for developing a
370 set of candidate models as detailed below (section 2.3). It

371 also allowed the validity of inferences observed in the
372 data to be evaluated and questioned based on a
373 qualitative understanding of the community and fishing
374 system. No information that could identify individuals was
375 retained because of the sensitivity of some of the
376 fishermen's illegal activities.

377 **2.3. Analysis**

378 Data were converted from JA\$ to US\$ (JA\$84.7= US\$1
379 (XE Currency Converter 2010)) and imperial to metric
380 weights where appropriate. Using the catch data, we
381 calculated the gross revenues from crayfish and native
382 shrimp harvesting by fishermen and investigated the
383 seasonality of catches (weight per fishermen day) and
384 catch value (total value per fishermen day). To do this we
385 used the Köppen climate classification system to
386 determine dry months (following Peel, Finlayson &
387 McMahon 2007). For tropical wet/dry forests and
388 savannah, the pronounced dry season contains months
389 with precipitation of less than 60 mm or less than $(100 -$
390 $[\text{total annual precipitation } \{\text{mm}\}/25])$. Total rainfall over
391 the study period was 1072 mm; therefore the 60 mm
392 value was higher than the 57 mm value (calculated using
393 the stated formula) used to determine dry months. As
394 such, months with < 60 mm rainfall (total for the month)
395 were considered dry months. Each month was

396 designated as a dry or a wet month, depending on the
397 total rainfall calculated for each month (using data from
398 the Meteorological Service of Jamaica). The designated
399 wet and dry months were used as different levels (wet vs.
400 dry) of a factor (season) and the individual times when
401 the fishermen were interviewed were used as replicates
402 for each month. We used a generalised linear mixed
403 model (GLMM; with the communities as the random
404 factor) with a gamma distribution and reciprocal link
405 function (if the data did not include a zero value) to
406 assess the effects of the seasons on the average yield of
407 native shrimp, and invasive crayfish, the average number
408 of pots hauled, and the average value of the native
409 shrimp and invasive crayfish and the value of the
410 combined yields. If the data included a zero value, we
411 used a normal distribution with a reciprocal or a log link
412 function (depending on an assessment of the residuals).
413 We then used a one-way ANOVA to assess the
414 differences between seasons for each site, the
415 differences between each site, and the differences
416 between each site for a particular season for average
417 yield, pots hauled and value (total and average).
418 Following an assessment of the residuals, we found that
419 the assumptions of this analysis were not upheld.
420 Therefore yield and value data were first transformed

421 using $\log_{10}(x + 1)$ before analysis. Average number of
422 pots hauled data was not transformed because an
423 assessment of the residuals indicated that the
424 assumptions of the ANOVA were not violated. These
425 statistical tests were performed using the GenStat
426 Discovery Edition 4.0 (VSN International, Hemel
427 Hempstead, UK) statistical package.

428

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

436

437 Next, we created two measures of dependence on fishing
438 to determine which types of fishermen might be
439 benefitting most from presence of the crayfish. Generally,
440 it is challenging to measure dependence on resources
441 directly, since this requires information on (hypothetical)
442 alternatives to harvesting were the resources not to exist.
443 In many developing countries, shadow wage rates are
444 hard to estimate as labour markets are thinly developed
445 and may not always be cash based. Using gross revenue

446 as an indicator of harvester's *dependence* on native
447 shrimp and invasive crayfish could be misleading, instead
448 reflecting their individual capacity to mobilise resources or
449 their effectiveness as fishermen. The distinction between
450 the sizes of the gross revenue derived from harvesting
451 activities, and the degree that individuals are dependent
452 on that source of income, is due to several factors
453 including the availability of alternative occupations and
454 the opportunity cost of forgoing that revenue.

455

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

462

463 We assumed that those harvesters who have the lowest
464 mean harvest effort and who varied their harvesting effort
465 the most in response to seasonal fluctuations in catches
466 were less dependent on the resource than those who
467 invest more effort into harvesting or maintain more
468 consistent effort throughout the year, even when catches
469 decline. We therefore investigated how socioeconomic
470 variables (elicited during the semi-structured interviews)

471 influenced i) daily mean harvesting effort and ii) intra-
472 annual variation in harvesting effort. Equation (1)
473 describes the means by which we calculated intra-annual
474 variation in harvest effort (V) for each fisherman. P is the
475 total recorded pots hauled per fisherman and D the total
476 number of possible harvesting days, respectively, during
477 the wet (w) and dry (d) seasons. Since monitoring effort
478 was consistent across both seasons, this provides a
479 combined indicator of changes in number of pots hauled
480 per day and changes in the number of days fishermen
481 are active in the fishery.

$$482 \quad V = 100 * [(Pd / Dd) - (Pw/Dw)] / (Pw/Dw) \quad (1)$$

483

484

485 Within the two analyses, we used Generalised Linear
486 Models (GLMs) to explore which socioeconomic
487 characteristics predicted daily mean harvest effort and
488 intra-annual variation in effort, with a Gaussian
489 distribution and identity link function. The choice of
490 explanatory variables was based on relevant literature,
491 semi-structured interviews with fishermen and
492 observations in the field (see Table 1 for a description of
493 variables). Because eight explanatory variables were
494 identified *a priori*, we fitted the global model and all
495 possible combinations of variables. We then used an

496 information-theoretic approach to avoid over-fitting,
497 ranking our candidate sets of models using the corrected
498 AIC (AICc) because of the small sample size (Akaike
499 1974). In both candidate sets there was no model with a
500 $\Delta\text{AICc} > 2$ and so we averaged across all models
501 following Anderson & Burnham (2002). For each analysis,
502 the 10 models with the lowest AICc and the averaged
503 models are detailed in the Supplementary Material 1.
504 There was a strong positive relationship between years of
505 experience and the capacity of fishermen to make their
506 own pots ($F_{(43,1)} = 6.65$, $p = 0.013$). Therefore, to avoid
507 model redundancy, the pots variable was removed from
508 the candidate set of both GLMs. The decision to drop this
509 variable followed the reasoning that it was more likely that
510 experienced fishermen would learn how to make pots
511 than it was that those fishermen who know how to make
512 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

514 **3. Results**

515 All fishermen within the target group were male. In each
516 community 37.5% of catch days were recorded during the
517 11-month period. We weighed 4,909 catches during this
518 period. We attribute the disparity between participation
519 rates between the two communities (all 54 in Community
520 1 and 22 of 41 in Community 2) to greater suspicion
521 towards the objectives of the project in Community 2,
522 even though anonymity was assured and identities were
523 unspecified during publication (individuals were identified
524 using initials to allow data collection). Because of the
525 lower participation rates in Community 2 there may be
526 bias in our results, if the reasons for not participating are
527 linked to fishing activities. Of the 50 participants selected
528 for interview, 5 were unwilling to participate or did not
529 provide sufficiently detailed responses. We therefore
530 completed interviews with 31 individuals from Community
531 1, and 14 individuals from Community 2.

532

533 **3.1. The monetary value of the invasive crayfish** 534 **harvest**

535 The mean market value of individual fishermen's daily
536 catch over the 11 months (incorporating seasonal price
537 changes) was US\$22.81 with the invasive crayfish

538 making up US\$3.53 of that value. Informal discussions
539 with fishermen indicate that the invasive crayfish is
540 considered to be a by-catch of shrimp harvesting, as
541 opposed to fishermen specifically targeting the invasive
542 species. Additionally, other fishermen also catch the
543 invasive species as by-catch using other fishing gear.
544 Smaller invasive crayfish may not have been separated
545 from the native shrimp catches. These results suggest
546 that the total invasive crayfish catch values were probably
547 lower than observed. From these figures, an approximate
548 and illustrative gross annual revenue can be estimated;
549 an 'average' fisherman, working the mean number of 5.95
550 days per week, hauling the mean value of 104.82 pots
551 per day, would earn gross revenue of approximately
552 US\$7,077 per year. However, among individuals there is
553 high variability in catch value, effort and gross value per
554 unit effort. Effort varies from as little as 30 pots hauled
555 per day to as many as 200 (including seasonal
556 fluctuations in effort) and the maximum mean gross value
557 per pot (across all pots hauled by one fishermen on one
558 harvesting excursion) is nearly 520% greater than the
559 minimum. Using the Köppen climate classification system
560 analysis we determined that there were, in total, four dry
561 months and seven wet months. Informal discussions with
562 fishermen indicate that fishermen typically set more pots

563 during the wet season. However, anecdotal evidence
564 suggests the study period covered an unusually dry
565 November, when fishermen normally set a high number
566 of pots; it was subsequently classified as a dry season
567 month, when it would typically be considered to be in the
568 wet season. This may have skewed our results
569 concerning the number of pots hauled. Consequently, we
570 found that the average number of pots hauled across all
571 fishermen was significantly higher in the dry season (dry
572 = 111 (\pm 1.22 s.e.) vs. wet = 100.9 (\pm 1.75 s.e.) pots day⁻¹;
573 $F_{(1,246)} = 24.53$, $p < 0.001$).

574

575 Market prices and catch sizes both varied between the
576 wet and dry seasons. Native shrimp and invasive crayfish
577 prices rose during the dry season, from US\$6.44 to
578 US\$7.73 and US\$3.86 to US\$5.15 per kilogram
579 respectively. We found that the native shrimp yield was
580 significantly higher in the wet than the dry months (dry =
581 2.67 (\pm 0.07 s.e.) vs wet = 2.95 (\pm 0.09 s.e.) kg/ day⁻¹;
582 $F_{(1,246)} = 6.8$, $p = 0.01$), when looking at all fishermen
583 across the two communities, despite the lower effort,
584 whilst the opposite was true for the invasive crayfish (dry
585 = 1.11 (\pm 0.04 s.e.) vs. wet = 0.56 (\pm 0.05 s.e.) kg/ day⁻¹;
586 $F_{(1,246)} = 49.22$, $p < 0.001$).

587

588 Across all fishermen, the gross revenue from the invasive
589 crayfish was significantly higher during the dry months
590 than the wet (dry = \$5.47 (\pm 0.2 s.e.) vs. wet = \$2.29 (\pm
591 0.23 s.e.) US\$ day⁻¹; $F_{(1,246)} = 54.85$, $p < 0.001$). The
592 gross revenue of the native shrimp did not change over
593 the seasons (dry = \$19.74 (\pm 0.56 s.e.) vs. wet = \$18.99
594 (\pm 0.85 s.e.) US\$ day⁻¹; $F_{(1,246)} = 1.13$, $p = 0.289$). The
595 combined gross revenue of both the native shrimp and
596 the invasive crayfish was higher during the dry season
597 (dry = \$29.09 (\pm 0.07 s.e.) vs. wet = \$24.63 (\pm 0.07 s.e.)
598 US\$ day⁻¹; $F_{(1,246)} = 25.97$, $p < 0.001$). However, we did
599 not find any statistically significant differences in catches
600 or number of pots hauled between the two communities.

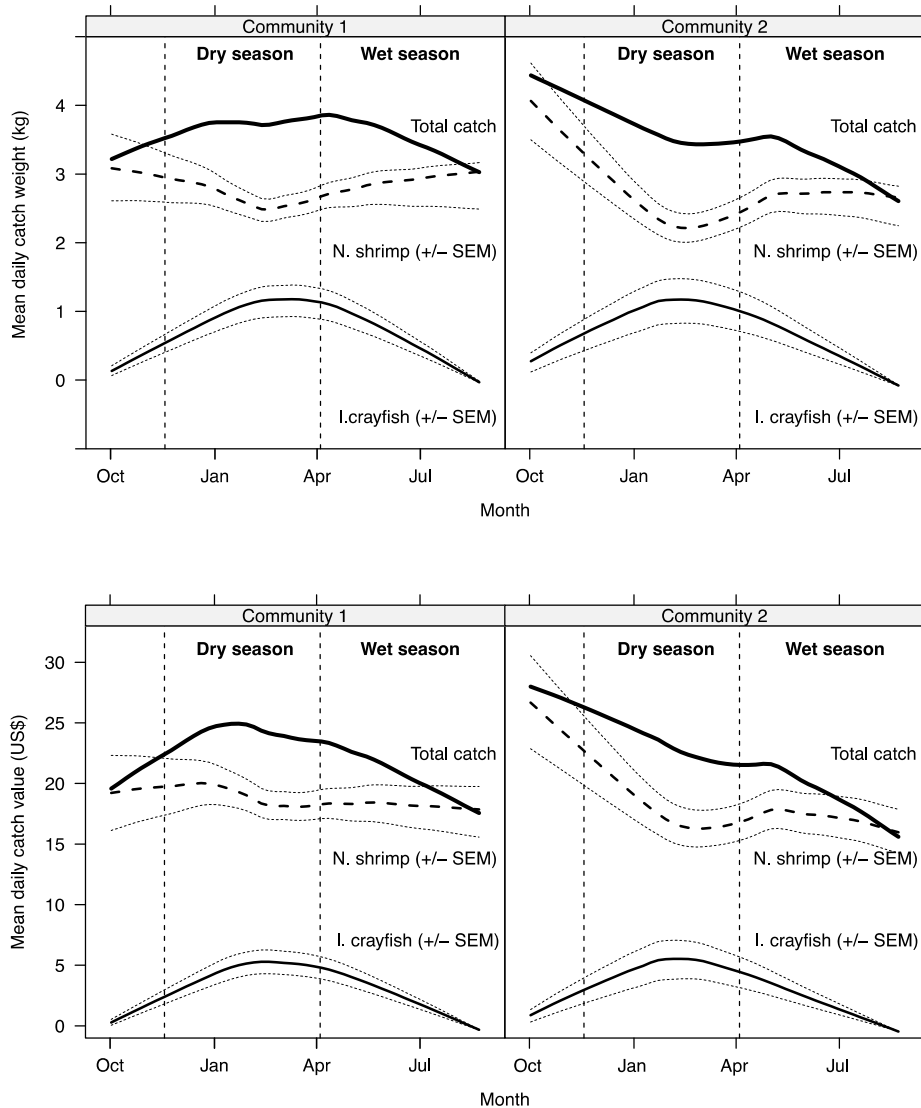
601

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

607

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

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



618
 619 Figure 2. Smoothed seasonal trends in mean catch
 620 weight (top row) and mean catch value (bottom row) per
 621 trip for native shrimp (N. shrimp, dashed), invasive
 622 crayfish (I. crayfish, thin line) and total values (thick line)
 623 for the two communities including standard errors (+/-

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

626

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

637

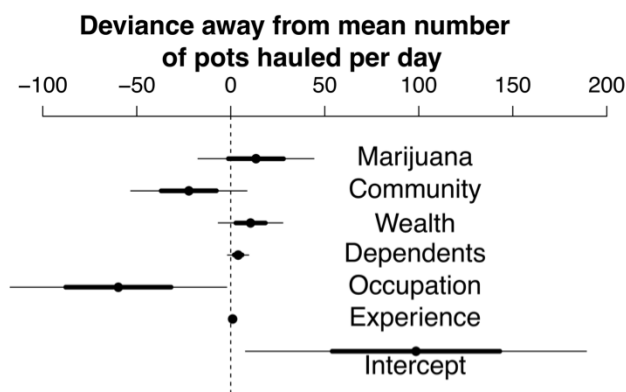
638 **3.2. Socioeconomic predictors of harvesting** 639 **effort**

640 Marijuana cultivation was more common in Community 1
641 ($\chi^2(1,44)= 10.27, p= 0.0013$), as was the likelihood of
642 having an alternative occupation (aside from marijuana
643 cultivation, $\chi^2(1,44)= 4.25, p= 0.0391$). Those who cultivate
644 marijuana are typically wealthier than those who do not
645 ($H(3)= 5.66, p= 0.12$).

646

647 Model averaging across all models in the candidate set
648 (weighted by AICc, Burnham & Anderson 2002), we find
649 that years of experience and having alternative
650 occupations influence fishermen's mean harvest effort
651 (Supplementary Material 1). It is estimated that on
652 average those fishermen with alternative occupations set

653 nearly 60 fewer pots per monitored day, than those with
 654 no alternative occupations (Figure 3). For each additional
 655 year of fishing experience, fishermen set on average 1.1
 656 more pots per day. Wealth, number of dependents and
 657 marijuana cultivation all had positive effects on the
 658 number of pots set, but these relationships were weak.
 659 Those from Community 2 set around 22 fewer pots than
 660 those from Community 1. However, the relationship is
 661 only moderately strong, and according to the previous
 662 analysis (discussed above) is not statistically significant.
 663



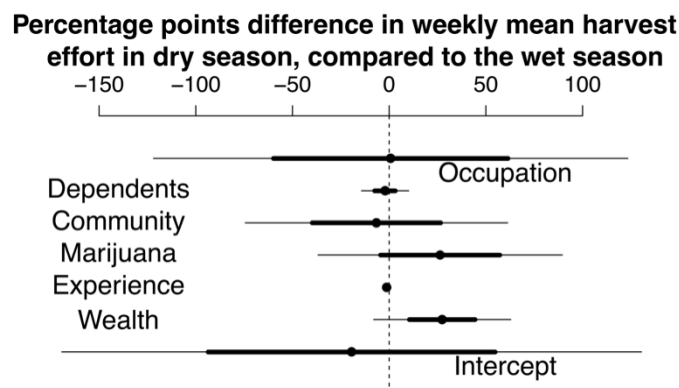
664
 665 Figure 3. Model-averaged coefficients for socio-economic
 666 determinants of individual fishermen's mean daily harvest
 667 effort, measured in number of pots hauled per day,
 668 across all days of data collection during the study period.
 669 The range shows the positive or negative impacts of the
 670 characteristics on the mean number of pots hauled
 671 across all fishermen. Points show the coefficient

672 estimates, thick lines indicate first confidence interval
673 (68%) and thin lines indicate the second (95%).

674 **3.3. Socioeconomic predictors of intra-annual** 675 **variation in harvest effort**

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

689



690

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

700

701 **4. Discussion**

702 **4.1. Can invasive alien species provide an** 703 **economically significant source of revenue?**

704 This study has quantified some of the gross economic
705 benefits of the IAS, the Australian Red Claw crayfish. Our
706 results suggest that the invasive crayfish provides an
707 economically significant portion of fishermen's gross
708 revenues, contributing approximately 15% of total catch
709 value across all fishermen during the study period.
710 However, this gross revenue does not occur evenly over
711 time or between individuals. Revenue derived from
712 harvesting invasive crayfish during the dry season
713 reduces the seasonal variability in incomes (income
714 smoothing). It was reported that the invasive crayfish's
715 mobility over land (something *Macrobrachium spp.* are

716 incapable of) lead to their congregation in residual water
717 bodies, making them easier to harvest. This may account
718 for the observed increase in crayfish harvests during the
719 dry season, as opposed to an absolute increase in their
720 population size.

721

722 The temporal distribution of incomes has been
723 recognised as an important factor in household
724 economics. Seasonal household liquidity constraints
725 suppress consumption and can lead to periods of cyclical
726 poverty (Dercon and Krishnan 2000). Weak or non-
727 existent credit markets, limited precautionary saving,
728 seasonal variance in prices and other factors can further
729 impede consumption smoothing (Baulch and Hoddinott
730 2000; Chaudhuri and Paxson 2001; Rosenzweig 2001).
731 According to Khandker (2009) 'when income smoothing
732 does not happen, a failure to smooth consumption may
733 result in food shortage and deprivation.'

734

735 Fishermen reported that during the dry season they had
736 less income from shrimp harvesting (supported by our
737 findings), and those that had alternative income
738 generating activities would refocus their efforts on those
739 activities. Our study did not explore the impact of
740 seasonal fluctuations in income on consumption

741 behaviour. Yet, fishermen reported that the dry season
742 was typically a more difficult period because of
743 constrained liquidity.

744

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

763

764

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

789

790 **4.2. Who benefits most from the fishery?**

791 In small-scale fisheries, fishermen are often found or
792 assumed to be the poorest within communities, and
793 fishing is a more frequent occupation in poor communities
794 (FAO 2012; Béné *et al.* 2007). Although there is no
795 economic data from communities within the BRLM with
796 which to compare fishing incomes, a wide degree of
797 socioeconomic heterogeneity within the fishing
798 communities was observed. Those who have no
799 alternative occupations tend to have higher average
800 harvest effort over the year. Individuals who have
801 alternative and more profitable occupations can distribute
802 their effort to maximise their income whilst managing risk.
803 This is supported by current economic and social theory
804 relating to subsistence livelihoods, where individuals
805 diversify their livelihoods to achieve higher and more
806 stable incomes (Martin *et al.* 2013; Ellis & Allison 2004;
807 Batterbury 2001; Ellis 2000). Our results are consistent
808 with Mazera *et al.* (2007) who found that greater non-
809 fishing income, derived from alternative occupations, was
810 associated with reduced fishing effort. Shackleton, Kirby
811 & Gambiza (2011) explore the role of the invasive prickly
812 pear (*Opuntia ficus-indica*) in incomes of poor trading
813 households in South Africa. They highlight the conflict of
814 interest between the South African Government, which is

815 concerned with the impact to the formal economy and
816 environment, and the income and nutritional needs of
817 local traders. They found that lower income traders were
818 most benefited by the presence of the invasive prickly
819 pear.

820

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

835

836 **4.3. Who benefits most from dry season** 837 **presence of crayfish?**

838 During the dry season, native shrimp catches decline and
839 invasive crayfish catches increase. In this study, we are

840 assuming that those with the least intra-annual variation
841 in harvest effort are choosing to maintain their harvesting
842 levels because they are most dependent on it. Again, as
843 a logical extension, they also derive the greatest benefit
844 from the invasive crayfish, which stabilises catches during
845 the dry season. Within the BRLM, those with low self-
846 reported wealth reduce their harvesting effort less during
847 the dry season relative to the wet, than do those who
848 consider themselves to be wealthier.

849

850 Although Cinner *et al.* (2011) found that fishermen
851 reported that they would increase their harvesting effort in
852 response to a decline in catches, Hoorweg *et al.* (2006)
853 observed that the wealthier fishermen on the Malindi-
854 Kalifi coast of Kenya were more inclined to reduce fishing
855 effort in response to a decline in catches. Similarly,
856 Hoorweg *et al.* (2006) found that those who had a range
857 of occupations generally had a more positive attitude
858 towards conservation of declining catch populations. This
859 suggests that the fishermen's response to changes in
860 catches is influenced by other socioeconomic
861 characteristics. Our study has found similar complexity in
862 behavioural responses to changing seasonal catch levels
863 within the community. Although there is an overall
864 increase in mean harvest effort during the dry season,

865 anecdotal evidence suggests this was atypical.
866 Additionally, despite statistical significance, it is unclear if
867 the observed mean change (an additional c.10 pots per
868 day) is socially and economically significant. As a result
869 this limits the wider conclusions that can be drawn
870 regarding behavioural responses to changes in catch
871 conditions. Pollnac *et al.* (2001) found that there are a
872 wide variety of income and non-income factors that affect
873 fishermen's readiness to leave fisheries in Southeast
874 Asia, including non-economic job satisfaction. Our study
875 differs in that it looks at seasonal changes in effort as
876 opposed to individuals permanently leaving a fishery.
877 Nevertheless, factors such as job satisfaction may also
878 play an important role in determining changes in seasonal
879 effort, though this was not explored in the present study.

880

881 Financial security is a reflection of other socioeconomic
882 characteristics, such as employment history and number
883 of dependents. The effects of wealth on wild product
884 harvesting behaviour are complex (Takasaki *et al.* 2001).
885 Some studies have found that less wealthy families
886 harvest more wild products, or are more reliant on them
887 (Shackleton *et al.* 2011). Others have found more
888 complex relationships, tied to land tenure and other
889 assets that allow individuals to invest resources that allow

890 them to increase returns on effort (Williams *et al.* 2012).

891 Gavin & Anderson (2007) suggest that the effects of

892 wealth on harvesting behaviour are confounded by other

893 socioeconomic and environmental factors.

894

895 The relationship between poverty and small-scale

896 fisheries in developing countries, once thought to be

897 close, is now understood to be more complex (Béné

898 2003). In some circumstances, where the opportunity

899 cost of time is low, the supply of available labour can

900 saturate open access fisheries, reducing incomes to the

901 level of the opportunity cost or shadow wage rate (Béné

902 2009). In short, incomes from small-scale or artisan

903 fisheries may be set exogenously (a function of labour

904 supply and alternative and more profitable occupations,

905 which have higher barriers to entry), and are normally the

906 least profitable activity within communities. Within the

907 BRLM we have not determined if this is the case.

908 However, those who are poorest are likely to remain in

909 the fishery when catches decline because of a lack of

910 capacity to adapt to changes in catch by mobilising

911 resources which would allow them to engage in

912 alternative occupations. In turn, this may allow them to

913 attain higher incomes and subsequently have greater

914 financial security (Badjeck *et al.* 2010). To the extent that

915 the invasive crayfish stabilises seasonal incomes and
916 possibly consumption, it is the poor who appear to benefit
917 most from its presence.

918

919 **5. Conclusion**

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

940 when considering the eradication of IAS and when
941 calculating the value of invaded ecosystems.

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