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Functional response metrics explain and predict high but differing ecological impacts of juvenile and adult lionfish.

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Acknowledgments

Abstract

Recent accumulation of evidence across taxa indicates that the ecological impacts of invasive alien species are predictable from their Functional Response (FR; e.g., the maximum feeding rate) and Functional Response Ratio (FRR; the FR attack rate divided by handling time). Here, we experimentally derive these metrics to predict the ecological impacts of both juvenile and adult lionfish (*Pterois volitans*), one of the world's most damaging invaders, across representative and likely future prey types. Potentially prey-population destabilising Type II FRs were exhibited by both life stages of lionfish towards four prey species: *Artemia salina*, *Gammarus oceanicus*, *Palaemonetes varians* and *Nephrops norvegicus*. FR magnitudes revealed ontogenetic shifts in lionfish impacts where juvenile lionfish displayed similar if not higher consumption rates than adult lionfish towards prey, apart from *N. norvegicus,* where adult consumption rate was considerably higher. Additionally, lionfish FRR values were very substantially higher than mean FRR values across known damaging invasive taxa. Thus, both life stages of lionfish are predicted to contribute to differing but high ecological impacts across prey communities, including commercially important species. With lionfish invasion ranges currently expanding across multiple regions globally, efforts to reduce lionfish numbers and population size structure, with provision of prey refugia through habitat complexity, might curtail their impacts. Nevertheless, the present study indicates that management programmes to support early detection and complete eradication of lionfish individuals when discovered in new regions is advised.

Introduction

Invasive species are predicted to continue to increase in number and severity of ecological impacts (Seebens et al. 2021; IPBES 2023). However, species-specific impacts are difficult to predict with surety and can vary considerably among invaded ecosystems due to a plethora of biotic and abiotic interactions (e.g., Dickey et al. 2021; Coughlan et al. 2022). Also, invaders with highly similar morphological and behavioural traits, and even congeneric species, may differentially impact invaded regions (e.g., Števove & Kováč 2013). Thus, we require robust metrics that are both explanatory and predictive of ecological impact across habitats and trophic and taxonomic groups (Dick et al. 2014, 2017).

The red lionfish, *Pterois volitans*, is currently considered one of the most invasive and ecologically harmful marine fish worldwide (Goodbody-Gringley et al. 2019), with populations spreading across the Western Atlantic Ocean, Caribbean (Schofield, 2010), and Mediterranean Seas (Bariche et al. 2013). Both *P. volitans* and its sister species, *Pterois miles*, are also currently establishing themselves across the Mediterranean. Due to the significant impact of *P. miles* and the extensive invasion by *P. volitans*, we use *P. volitans* in this study as a proxy when referring to lionfish. As generalist and opportunistic predators, lionfish show dietary plasticity for prey items (Côté et al. 2013) and demonstrate clear negative impacts on some prey species (del Rio et al. 2022). Although adult lionfish are primarily piscivorous, they have also been recorded to predate on a variety of invertebrates (e.g., Morris and Akins 2009). Most lionfish dietary studies have been completed on adult individuals due to ease of capture compared to juveniles (i.e. <15 cm; see Dahl et al. 2014; Muñoz et al. 2011; Mizrahi et al. 2017; Dahl et al. 2017; Zannaki et al., 2019; Acero et al. 2019; Batjakas et al. 2023; Samourdani et al. 2024), therefore juvenile lionfish predation is data limited, however, information available suggests a predominance of small crustaceans and larval fish (Cure *et al.* 2012; Eddy et al. 2016; Dahl et al. 2017). As a consequence of culling programmes, selective removal of large individuals tends to occur in invaded areas, with the remaining population being largely composed of juveniles and smaller sized individuals which are cryptic, fast moving and avoid culling activity by spear fishers (Morris et al. 2011; Frazer et al. 2012). Accordingly, a predictive assessment of lionfish invasion impacts thus requires dual examination of juvenile and adult feeding rates on representative and future likely prey communities.

Functional Response (FR) metrics (described as Type I, II, and Type III) have been used successfully to assess the ecological impact of current, future and emerging invasive species,

123   through consideration of resource consumption (i.e., the amount of a resource utilised, such as

124   prey) as a function of resource density (Dick et al. 2014; Dickey et al. 2021; Coughlan et al.

125   2022). The Type I response is a linear response, characteristic of filter feeders which are not

126   constrained by handling times (Hoxha et al. 2018); density-dependent Type II responses are

127   characterised by a plateauing of consumption as prey density increases (Hassell 1978); Type

128   III responses are represented by a sigmoidal curve due to a reduction of consumption at low

129   prey densities, often providing low density refugia to rare prey species and sometimes related

130   to learned predator avoidance behaviour in prey populations (Colton, 1987; Kalinkat et al.

131   2023). Deriving the Type of FR, plus the attack rates, handling times and maximum feeding

132   rates, has been successful across taxa in explaining and predicting invader impacts (Dick et al.

133   2014; South et al. 2017; Coughlan et al. 2022). However, while high attack rates and low

134   handling times predict high impact (Dick et al. 2017), predictions based on either parameter

135   alone can be contradictory (e.g., when handling times are low, but attack rates are also low;

136   Cuthbert et al. 2019). To resolve this, Cuthbert et al. (2019) proposed a composite metric, the

137   Functional Response Ratio (FRR), that is, attack rate divided by handling time. The FRR has

138   a clear pattern of high values predicting high ecological impact, where the worst invaders have

139   an FRR ratio mean of 83.36. This benchmarking allows comparison of newly derived FRRs,

140   and hence likely ecological impact, in studies such as the present regarding lionfish (see

141   Cuthbert et al. 2019). FRR however is applicable for Type II and Type III comparison as Type

142   I FR is devoid of a handling time.

143

144   We thus assessed the predatory impacts of both juvenile and adult *P. volitans* on four prey

145   species by employing the FR metrics approach. The selected prey species were used to mimic

146   a host of similar prey found across the invaded and future ranges of lionfish, namely the brine

147   shrimp (*Artemia salina*), marine gammarid (*Gammarus oceanicus*), dwarf white shrimp

148   (*Palaemonetes varians*), and finally Dublin Bay prawn (*Nephrops norvegicus*), as the lionfish

149   range is currently expanding across the Mediterranean (albeit predominantly *P. miles*) into

150   areas where commercially and ecologically valuable *N. norvegicus* are located (Lolas and

151   Vafidis, 2021). Given that morphological and metabolic changes may affect diet, leading to

152   variations in preferred prey types, as well as possible restricted ability of juvenile lionfish to

153   predate larger prey due to the size relationship between predator and prey. We hypothesised

154   that juvenile and adult lionfish will display FR metrics consistent with high ecological impact,

155   with ontogenetic shifts in these metrics due to predator/prey size.

156

Materials and Methods

Animal collection and maintenance

Experiments were undertaken at Queen's University Marine Laboratory (QML), Portaferry, UK, between January and October 2019. Juvenile *P. volitan* lionfish ($n = 8$) and adult *P. volitan* lionfish ($n = 8$) were obtained from Seahorse Aquarium, Dublin. Juveniles had a total body length (mean ± SE) of 102.80 ± 3.18mm, with a pectoral fin diameter of 57.89 ± 4.80mm, as measured across the widest point when elongated. Adults measured 305.51 ± 3.73mm in length with a pectoral fin diameter of 265.51 ± 6.37mm. Juveniles were kept in a holding tank (W: 32cm ×L: 152cm ×H: 45cm, 218L) with external filtration containing UV- and sand-filtered recirculated Strangford Lough seawater. Adult holding tanks separately employed the same filtration set up, while two adults were housed per tank (W: 82cm ×L: 227cm ×H: 61cm, 1130L). Up to 10% of the tank water was changed daily, monitoring temperature, and conditions including pH and ammonium. Seawater was maintained at 25.0 ± 1.0°C using an aquarium heater under a natural light regime. Lionfish were maintained daily *ad libitum* on frozen anchovy to avoid predator learning behaviour of the experimental prey species. Feeding experiments were conducted within glass tanks (juveniles: W: 33cm ×L: 46cm ×H: 30cm, 45L; adults: W: 51cm ×L: 132cm ×H: 38cm, 250L) maintained at 25.0 ± 1.0°C to ensure lionfish welfare. Experimental tanks were scaled to reflect the difference between juvenile and adult lionfish when pectoral fins were fully elongated during feeding trails, where adults were approximately five times the size of juvenile lionfish. All fish were acclimated in the experimental arenas for a 30-minute period immediately prior to experimentation.

Brine shrimp (*Artemia salina*), marine gammarid (*Gammarus oceanicus*), dwarf white shrimp (*Palaemonetes varians*), and Dublin Bay prawn (*Nephrops norvegicus*) were used as live prey. *Artemia salina* were obtained from Seahorse Aquariums, Dublin, Ireland, while *G. oceanicus* and *P. varians* were obtained from Grosvenor Tropicals, Lisburn, UK. *Nephrops norvegicus* were caught in fishing grounds off the western Irish Sea, by the FV Fulmar, an 11.33m trawler using a SELTRA in single-rig configuration. Once samples were landed, they were immediately brought to QML. *Artemia salina*, *G. oceanicus* and *P. varians* were maintained under identical conditions to the predators in separate holding tanks (W: 15cm × L: 20cm × H: 18cm, 10L), whereas *N. norvegicus* were housed in a dark outdoor holding tank (H: 94cm × W: 142cm × L: 211cm, 2800 L), which included tunnels for refuge. All prey species were acclimated to lionfish maintenance temperature of 25.0 ±1.0°C before being introduced to the testing tank. *Artemia salina*, *G. oceanicus*, and *P. varians* were kept at 22.0 ± 1.0°C, which

191   was then raised to 25.0 ± 1.0°C sixty minutes before introduction. In contrast, *N. norvegicus*

192   was initially kept at 18.0 ± 1.0°C and gradually exposed to a temperature change in the testing

193   tank over sixty minutes until reaching 25.0 ± 1.0°C. Intraspecific prey size was standardised

194   throughout all trials. Total length (mean±SE): *A. salina*, (6.2 ± 0.8mm); *G. oceanicus*, (10.7 ±

195   0.9mm); *P. varians*, (11.3 ± 0.5mm), and total carapace length for *N. norvegicus* (20.1 ±

196   3.1mm).

197

198   Selected prey species mimic those that are commonly found in lionfish stomachs across their

199   invaded and potential future regions and have been used in previous lionfish FR experiments

200   using similar laboratory set-ups to the present study (Morris and Akins 2009; Layman and

201   Allgeier, 2012; Layman et al. 2014; Ortiz et al. 2015; Dahl et al. 2017, South et al. 2017;

202   McCard et al. 2021). The present study represented the first comparative assessment of juvenile

203   and adult lionfish, as well as the first assessment of lionfish impact on *N. norvegicus,* which

204   are a valuable commercial fishery species across the United Kingdom and European Union that

205   will likely be threatened by the expanding lionfish invasion (Smith and Papadopoulou, 2003;

206   Bell et al. 2006; Nikolic et al. 2015). Furthermore, *N. norvegicus* can be used as a proxy for

207   juveniles of other large crustacean species such as the Caribbean spiny lobster (*Panulirus*

208   *argus*), the European lobster (*Homarus gammarus*) and Anomurans (squat lobsters).

209

Functional response (FR) procedure

211   Each prey species was separately supplied at 15 densities (2, 4, 6, 8, 12, 16, 20, 25, 30, 35, 40,

212   45, 50, 55, 60; experiment replication $n = 8$ per density for each of the four prey species) in a

213   randomised pattern of both prey species and densities. This was achieved with the re-use of the

214   available lionfish in the following manner: Following the addition of the allotted prey to the

215   experimental tanks that contained an individual predator, functional response experiments were

216   initiated. Lionfish were allowed to feed for 3 h before being removed for enumeration of prey

217   consumed. In a one-month period there were eight experiment days, with all lionfish being

218   used on each experiment day (adult $n = 8$; juvenile $n = 8$). This facilitated a three-day recovery

219   period between experiment days. Re-use of individuals was essential due to the limited number

220   of lionfish available, hence the recovery period (see Alexander et al. 2014). The entire

221   experiment was conducted over a 10-month period, with all lionfish being systematically

222   exposed to all prey items at all densities, in a randomly allocated order. Controls consisted of

223   one replicate of each prey type across all densities in the absence of lionfish predators.

224

Statistical analyses

Statistical analyses were undertaken using the 'frair' package in R (R Core Development Team, 2018). Logistic regression was used to derive FR types based on analyses of proportional prey consumption across prey densities, with 'prey density' included as a continuous variable (Pritchard et al. 2017). To model the FRs, data were fit using Rogers' random predator equation, as prey were not replaced once consumed (Rogers, 1972):

$$N_e = N_0(1 - exp(a(N_e h - T))) \qquad (1)$$

Wherein N_e represents the amount of prey consumed, N_0 is initial prey density, a is the attack rate parameter, h is the handling time and T is the total time available. Data of prey eaten were then non-parametrically bootstrapped ($n = 2000$) to produce 95% confidence intervals using initial maximum likelihood estimates of a and h. The handling time parameter was used to determine maximum feeding rates ($1/h$) of lionfish across prey groups. Additionally, the Functional Response Ratio (FRR) was calculated for each prey species using the parameter estimates of a and h derived from the FR curve from eqn (1):

$$FRR = a / h \qquad (2)$$

Results

Across all control groups (i.e., no predator) for all prey species, survival of the prey exceeded 99% in the absence of lionfish, therefore, all mortality of prey in experimental groups was assumed to be due to predation by lionfish.

Functional responses (FRs)

First order terms were significantly negative as per Juliano (2001), indicating Type II FRs by all lionfish towards all prey species (Table 1; Figure 1).

Juvenile Lionfish

The attack rates and handling times of juvenile lionfish towards the four prey species resulted in FR magnitudes greatest for *A. salina*, lowest for *N. norvegicus* and intermediate for *G. oceanicus* and *P. varians* (Table 1; Figure 1). FRR values for juvenile lionfish were greatest

258   for *A. salina* (564.29), followed by *P. varians* (350.14), *G. oceanicus* (158.54), and *N.*

259   *norvegicus* (57.62: Table 1). The first three FRR values are markedly higher than the mean

260   FRR value of 83.36 that was found for highly damaging invaders across taxa (see Cuthbert et

261   al. 2019), by factors of 7, 4.5 and 2, predicting high ecological impacts of juvenile lionfish on

262   prey with similar traits to *A. salina*, *P. varians* and *G. oceanicus*.

263

264   *Adult lionfish*

265   The attack rates and handling times of adult lionfish result in quite different FR magnitudes

266   compared to juveniles, with adult FRs ordered greatest for *N. norvegicus* followed by *A. salina*,

267   *P. varians* and *G. oceanicus* (Table 1; Figure 1). FRR values for adult lionfish were greatest

268   for *N. norvegicus* (310.91), then *A. salina* (237.74), *P. varians* (207.76) and *G. oceanicus*

269   (122.61; Table 1). All these FRR values are substantially higher than the mean FRR value of

270   83.36 found by Cuthbert et al. (2019) by factors of 3.8, 3, 2.6 and 1.5, predicting high ecological

271   impacts of adult lionfish on such crustacean prey.

272

273   **Discussion**

274   The observed consumption patterns and Functional Response (FR) metrics predict that both

275   juvenile and adult lionfish can exert damaging impact on a range of crustacean prey where

276   larger individuals show size dependent preferences for larger prey items compared to the gape

277   limited juveniles (Morris and Akins, 2009; Mihalitsis and Bellwood, 2017; Rojas-Velez et al.

278   2023). These findings are in line with *in-situ* stomach content analyses (e.g., Muñoz et al. 2011;

279   Eddy et al. 2016; Dahl et al. 2017).

280

281   The Type II FRs by both juveniles and adults suggests potential destabilising effects on

282   invertebrate prey species populations, although lionfish may switch prey preference for species

283   that are more abundant in the environment, which provides a low-density prey refuge, and

284   complex habitat structure can mitigate impacts (McCard et al. 2021; Kalinkat et al. 2023).

285   These mitigating drivers may explain the difference in field impact between the Bahamas

286   (high) and Belize (low) (Green et al. 2012; Hackerott et al. 2017). Habitat structure can offer

287   refuges for prey, reducing predator search success at low prey densities, leading to sigmoid

288   Type III functional responses (Rickers and Scheu, 2005; Birkhofer et al. 2008). In contrast, the

289   absence of habitat structure and the effects of arena size often result in Type II functional

290   responses (Vucic-Pestic et al. 2010). Our comparative laboratory study used standardised

291   conditions for all organisms without additional habitat complexity. Despite this, FR analyses

292 and related impact assessment metrics are highly predictive of *per capita* impacts and simple

293 laboratory settings of FR analyses are predictive of actual field impacts (Dick et al. 2014, 2017;

294 Dickey et al. 2018). While lionfish use the entire water column to hunt, benthic and pelagic

295 prey can attempt escape in both the upward and downward direction, which adds additional

296 complexity to *in situ* foraging by lionfish in nominal 2-dimensional benthic and 3-demensional

297 pelagic environments.

298

299 Further predictive confidence of high lionfish impact is their remarkable Functional Response

300 Ratio (FRR) values, that were up to seven times higher than the mean FRR across known

301 damaging invasive taxa (Cuthbert et al. 2019). The benchmark FRRs values of Cuthbert et al.

302 (2019) indicate that, overall, mean FRRs of 83.36 typify high impact invaders, since attack

303 rates are high and handling times are low. The FRR values found here for lionfish were

304 distinctively high, indicating an ecologically damaging ability of lionfish to find, subdue,

305 consume and digest prey, which is clearly commensurate with actual field impacts of lionfish.

306

307 Lionfish pose a threat to commercial crustacean fisheries and can disturb benthic food webs in

308 both current and potential invasion areas (Ballew et al. 2016; Savva et al. 2020). Lionfish have

309 been observed at varying depths in regions they have infiltrated: surpassing 100 meters in the

310 Bahamas (Lesser and Slattery, 2011), reaching depths of 250 meters in Honduras (Gress et al.

311 2017), and descending as far as 304 meters in Bermuda (Gress et al. 2017) where dense lionfish

312 populations have been identified at specific locations, particularly at or below 60 meters, in

313 select Bermuda sites (Eddy, 2016; Andradi-Brown et al. 2017). The potential for high

314 consumption rates of *N. norvegicus* by adult lionfish is a cause for concern considering that

315 lionfish range expansions will overlap with commercially important fishing grounds. While

316 juveniles also fed on *N. norvegicus*, they did so in smaller numbers, which may be due to

317 limitations in gape and their inability to efficiently predate the hard exoskeleton (Björnsson

318 and Dombaxe 2004; Rojas-Velez et al. 2023). *Nephrops norvegicus* are generally a deep-water

319 species which reside in mud-flat burrows at depths of 20-800 meters, given that lionfish have

320 been found at mesophotic depths this suggests that deep water populations could be sustained

321 on *N. norvegicus* (Andradi-Brown et al. 2016). Furthermore, high FRR values on *P. varians*

322 indicates high potential for consumption of functional analogue species such as *Pandalus*

323 *montagui* and *Cragon crangon*, both of which form a high percentage of diet for native fish

324 predators (Myers and Worm, 2003). The full and pernicious impacts of lionfish invasion may

325 be further revealed if prey depletion leads to trophic cascades through loss of prey for native
326 predators (Moll et al. 2017; Palmer et al. 2022).

328 While *A. salina* and *P. varians* are generally pelagic with high mobility (Ward-Booth and
329 Reiss, 1988; Harding et al. 2023), *G. oceanicus* and *N. norvegicus* tend to be epibenthic with a
330 relatively lower rate of mobility (Maynou and Sarda, 2001; Navarro-Barranco et al. 2020;
331 Coughlan et al. 2021). It appears that both lionfish life stages can exploit pelagic and epibenthic
332 prey (Green and Côté, 2014; Green et al. 2019), with utilisation of prey items being linked to
333 body type (McCleery, 2011; Muñoz, Currin & Whitfield, 2011), size (Green and Côté, 2014;
334 Kindinger and Anderson, 2016; Navarro-Martínez et al. 2022) and digestibility (Steell et al.
335 2019; Trehern et al. 2024) rather than mobility (Trehern et al. 2024) for juvenile lionfish, while
336 adults appeared to better utilise the largest prey and least mobile prey. Previous studies have
337 shown lionfish may specialise on small prey species that are solitary, nocturnal, and bottom
338 dwelling (Layman and Allgeier, 2012; Green and Côté, 2014), however, the adult lionfish in
339 this study showed a reduced consumption of small epibenthic species (*G. oceanicus*) compared
340 to the larger *N. norvegicus* and the pelagic species. This may indicate some difficulty in
341 consumption within the tank confines due to spatial limitations on manoeuvrability.

343 The current geographical spread and increased growth in abundance of lionfish in the Atlantic
344 has made eradication impossible (Johnston and Purkis, 2015). While the data in this study were
345 collected in a laboratory setting, with prey being presented in isolation from other prey
346 resources, this work provides a basis for estimates of consumption rates of both juvenile and
347 adult lionfish on representative and future prey types. Further, current management strategies
348 for lionfish populations rely on the removal of adults (Barbour et al. 2011; Johnston and Purkis,
349 2015), however, our data indicate that juvenile lionfish can have a greater impact on native
350 prey species than adult lionfish. This increased predation pressure reduces prey availability for
351 native predators. Therefore, populations composed of juveniles and adults will have wide
352 ranging impacts across multiple prey species, potentially driven by ontogenetic shifts in
353 functional morphology, since juveniles have traits associated with a mechanical advantage
354 during prey capture, whereas adult morphology is more associated with locomotion and
355 sustained swimming but a lower suction velocity (Rojas-Velez et al. 2023). Accordingly,
356 management strategies will need to be developed to efficiently control all life stages, rather
357 than adults alone. Finally, whilst culling might reduce lionfish impacts through reduced
358 numbers of individual predators, imaginative strategies to alter FR metrics might also be

employed; for example, Type III FRs and lowered FRRs may result from increased habitat complexity such as artificial reefs. The present study demonstrates both juvenile and adult lionfish can have a considerable impact on prey populations if allowed to establish and persist in regions at risk of invasion. Ultimately, early detection and eradication remain the best, if least utilised, strategies for invasive species management.

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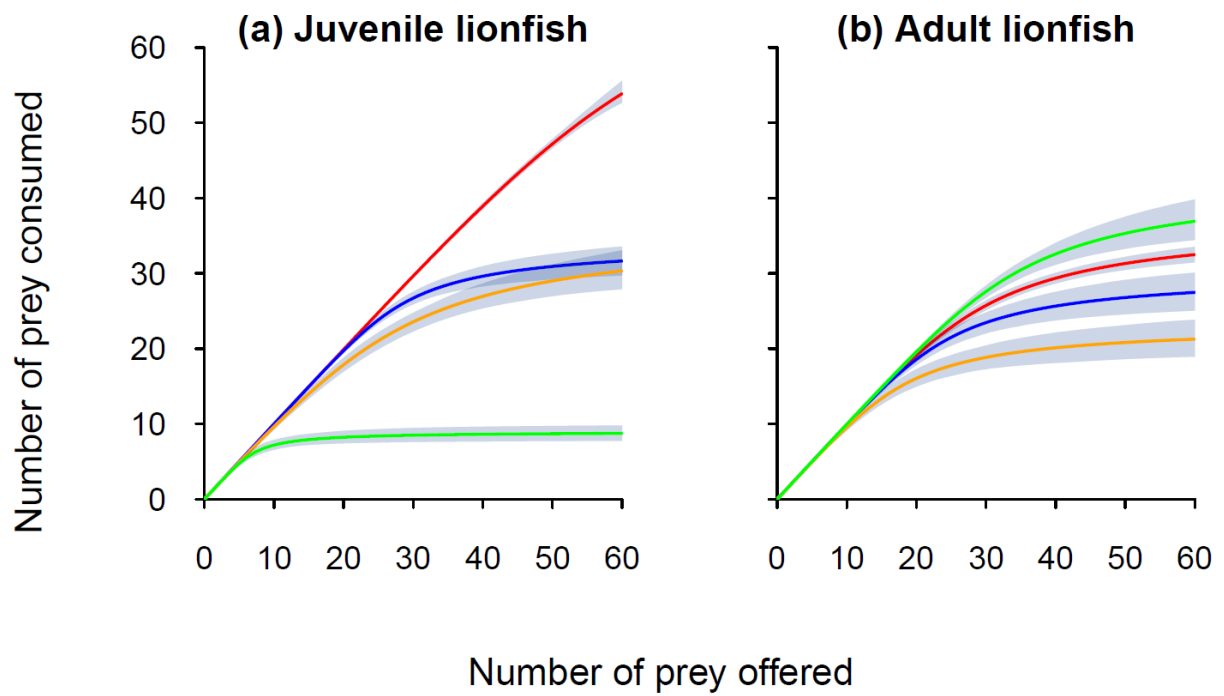
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613   **Table 1**: First order terms from logistic regression of prey consumed, alongside rounded initial

614   and bootstrapped (n = 2000; 95% CIs) functional response parameters (attack rates, handling

615   times, maximum feeding rates and FRRs), of juvenile and adult *Pterois volitans* with different

616   prey types.

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Predator	Prey	First Order Term, p	FR Type	a, 95% CIs	h, 95% CIs	Maximum feeding rate (1/h)	FRR (a/h)
Juvenile *P. volitans*	*Artemia salina*	-0.09 <0.001	II	7.11, 5.47 – 9.43	0.01, 0.01 – 0.02	79.37	564.29
Juvenile *P. volitans*	*Gammarus oceanicus*	-0.06 <0.001	II	4.44, 3.18 – 6.14	0.03, 0.02 – 0.03	35.71	158.54
Juvenile *P. volitans*	*Palaemonetes varians*	-0.08 <0.001	II	10.15, 7.22 – 14.55	0.03, 0.03 – 0.03	34.48	350.14
Juvenile *P. volitans*	*Nephrops norvegicus*	-0.06 <0.001	II	6.45, 3.85 – 11.84	0.11, 0.10 – 0.13	8.93	57.62
Adult *P. volitans*	*Artemia salina*	-0.07 <0.001	II	6.42, 5.19 – 7.94	0.03, 0.03 – 0.03	37.04	237.74
Adult *P. volitans*	*Gammarus oceanicus*	-0.06 <0.001	II	5.27, 3.61 – 7.83	0.04, 0.04 – 0.05	23.26	122.61
Adult *P. volitans*	*Palaemonetes varians*	-0.07 <0.001	II	6.86, 5.11 – 10.07	0.03, 0.03 – 0.04	30.30	207.76
Adult *P. volitans*	*Nephrops norvegicus*	-0.08 <0.001	II	7.15, 5.60 – 9.27	0.02, 0.02 – 0.03	43.48	310.91

618

Figure 1: Functional Responses showing the order of highest to lowest consumption of prey with both juvenile (a) and adult (b) *Pterois volitans* towards all prey types: *Artemia salina* (red), *Gammarus oceanicus* (orange)*, Palaemonetes varians* (blue) and *Nephrops norvegicus* (green). Shaded areas are bootstrapped (*n*=2000) 95% confidence intervals.