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Trait-based diet selection: Prey behaviour and morphology predict vulnerability to predation in reef fish communities

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Summary

1. Understanding how predators select their prey can provide important insights into community structure and dynamics. However, the suite of prey species available to a predator is often spatially and temporally variable. As a result, species-specific selectivity data are of limited use for predicting novel predator-prey interactions because they are assemblage-specific.

2. We present a method for predicting diet selection that is applicable across prey assemblages, based on identifying general morphological and behavioural traits of prey that confer vulnerability to predation independent of species identity. We apply this trait-based approach to examining prey selection by Indo-Pacific lionfish (*Pterois volitans*), an invasive predator that preys upon species-rich reef fish communities and is rapidly spreading across the Western Atlantic.

3. We first generate hypotheses about morphological and behavioural traits recurring across fish species that could facilitate or deter predation by lionfish. Constructing generalised linear mixed-models that account for relatedness among prey taxa, we test whether these traits predict patterns of diet selection by lionfish within two independent data sets collected at different spatial scales: 1) *in situ* visual observations of prey consumption and availability for individual lionfish, and (2) comparisons of prey abundance in lionfish stomach contents to availability in invaded reefs at large.

4. Both analyses reveal that a number of traits predicted to affect vulnerability to predation, including body size, body shape, position in the water column and aggregation behaviour, are important determinants of diet selection by lionfish. Small, shallow-bodied solitary fishes found resting on or just above reefs are the most vulnerable. Fishes that exhibit parasite cleaning behaviour experience a significantly lower risk of predation than non-cleaning fishes, and fishes that are nocturnally active are at significantly greater risk. Together, vulnerable traits heighten the risk of predation by a factor of nearly 200.

5. Our study reveals that a trait-based approach to studying diet selection yields insights into predator-prey interactions that are robust across prey assemblages. Importantly, *in situ* observations of selection yield similar results to broad-scale comparisons of prey use and availability, which are more typically gathered for predator species. A trait-based approach could therefore be of use across predator species and ecosystems to predict the outcomes of changing predator-prey interactions on community dynamics.

Key-words foraging behaviour, predator-prey interactions, prey characteristics, resource use and availability, selective predation, stomach contents analysis, *in situ* observations, *Pterois volitans/miles*

Introduction

Predation affects the demographic rates of species in most ecosystems (Caley et al. 1993; Carr and Hixon 1995, Arcese et al. 1996, Lima et al. 2001, Creel et al. 2007). Understanding the process by which predators select their prey can therefore provide key insights into the structure and function of communities (Gilinsky 1984, Holt 1984, Kotler 1984, Karanth and Sunquist 1995, Juanes et al. 2001, Almany and Webster 2004). Optimal foraging theory predicts that predators should select prey items in a manner that maximizes energetic gain while minimizing the energy expended in locating, handling and processing the item (Pyke *et al.* 1977). If all prey types are equally profitable, then predators should consume prey in proportion to their abundance in the environment, so diet composition will track changes in prey community composition across space and time (e.g., Beukers-Stewart & Jones 2004). However, predators often consume some prey in quantities disproportionate to their availability (i.e., dietary preference or selective predation; e.g.Green and Osborne 1981, Scott and Murdoch 1983, Donázar and Ceballos 1989, Hambright 1991, Hernández 1995, Almany et al. 2007; Nunn et al, 2012).

Identifying prey species that are selectively consumed (or, conversely, avoided) has been the aim of much foraging ecology research, with a large number of studies focussed on which species predators choose in experimental settings (e.g. Main 1985, Wahl & Stein 1988, 1989, Wahl 1995, Einfalt & Wahl 1997; Nilsson & Bronmark 2000; Heinonen & Auster 2013; Provost et al. 2006), and a smaller number focussed on species selection *in situ* (e.g. Cunningham et al. 1999; Wen et al. 2012; Isaac et al 2013). However, the assemblage of prey available to a given predator is spatially and temporally variable, owing both to natural processses (e.g., gradients in prey assemblage across the predator's range [e.g., Holt 1984, Steele 1989, Bost et al. 2002, Phillips et al. 2009, Jaeger et al. 2010]), and, increasingly, anthropogenically mediated species additions (i.e., through invasion; e.g. [Caut et al. 2008]) and removals (e.g. through exploitation; e.g. [Crooks and Soulé 1999]), limiting the utility of experimental and assemblage-specific findings for predicting selection from varying sets of prey.

The heterogeneous nature of predator-prey interactions necessitates an approach to predicting diet selection that can be applied across changing community compositions. Selective predation is thought to occur when prey types vary in one or more morphological or behavioural characteristics that affect their encounter rate and handling time (Pyke et al. 1997). It therefore follows that diet selection should be predictable across prey assemblages if vulnerability to predation is conferred by morphological and/or behavioural traits of prey that recur across species assemblages. Thus, the strength of interactions when a predator is exposed to new prey types could be predicted by identifying traits associated with vulnerability to predation, independently from species identity. A functional, or trait-based approach has been advocated as a means to make community ecology more predictive (McGill et al. 2006), but we are not aware of studies that have tested this idea in the context of predator–prey interactions.

To illustrate a trait-based approach to studying diet selection, we evaluate whether morphological and behavioural characteristics of Caribbean coral reef fishes affect vulnerability to predation by the Indo-Pacific lionfish (*Pterois volitans* and *P. miles*). Lionfish have rapidly become established on coral reefs across the western Atlantic, Caribbean and Gulf of Mexico, and the invasion continues to spread southward (Betancur-R *et al.* 2011; Côté et al. 2013). Predation by invasive lionfish has been implicated in the significant decline of reef fish biomass in the northern Caribbean (Albins and Hixon 2008; Green *et al.* 2012; Green et al. *in press*). Given that reef fish assemblages differ across this large region, elucidating prey trait variants that are most susceptible to predation will aid in forecasting prey declines as the invasion spreads to areas with novel fish assemblages. To do this, we generated hypotheses about prey traits that could facilitate or deter predation by lionfish, and assessed whether selective predation on specific trait variants occurs from data collected at two spatial scales. At the smallest scale, during underwater visual observations we simultaneously recorded prey available to and prey consumed by individual lionfish hunting. At a larger scale, we compared the abundance of prey items in lionfish stomach contents to prey abundance on invaded reefs at large.

Materials and methods

PREY TRAIT HYPOTHESES

To simultaneously examine the effects of prey morphology and behaviour on lionfish diet selection, we compiled information on a suite of traits that are likely to influence vulnerability to predation (Table 1), and generated hypotheses for each. We then assigned a score or value for each trait to each fish species encountered on our study reefs (Appendix S1), based on published descriptions of each species (Böhlke & Chaplin 1993; Deloach 1999; FAO 2002a,b; Humann & Deloach 2002).

Behaviour

Lionfish are visual predators that employ a stalking strategy, in which they approach their prey by hovering slowly over the substrate (Côté & Maljković 2010; Green *et al.* 2011). Several aspects of prey behaviour should confer variable vulnerability to this hunting style. We predicted that demersal (i.e. living < 2 m from the bottom) fishes would be more vulnerable to predation than benthic species (i.e. those living on or in the benthos), which may be less visible, and that pelagic fishes occupying the water column above reefs (i.e. > 2 m above the benthos) would be least accessible. While many studies suggest that schooling behaviour is an effective anti-predator strategy because aggregations can dilute individual risk of predation (Pitcher 1993), we hypothesized that lionfish, whose slow movements afford them a close approach to potential prey, may in fact target schooling fish species because the conspicuousness of schools may reduce predator search time. We recognised three categories of aggregation behaviour: solitary, shoaling and schooling. We defined shoaling as an intermediate state, based on the observation that many fish species tend to form loose feeding aggregations as juveniles (e.g. wrasses and parrotfishes). We also hypothesized that fishes that are nocturnally active and whose emergence from sheltered reef habitats overlaps with the timing of lionfish foraging behaviour at crepuscular times (Green *et al.* 2011) would be more vulnerable to lionfish predation than their diurnal counterparts because this strategy may result in increased encounters with hunting lionfish (Hobson 1973; Fishelson 1975; Green *et al.* 2011). Finally, we anticipated that fishes that exhibit cleaning behaviour, either facultatively (i.e. only as juvenile) or obligately (i.e. throughout their lifespan), may be less readily consumed by lionfish, because such species often experience lower mortality rates from predation, possibly because of recognition by fish predators of the service cleaners provide (e.g. Côté 2000; Colin 1975).

Morphology

We considered three major aspects of prey morphology that may affect vulnerability to predation by lionfish. For gape-limited predators, the costs of prey consumption (in terms of energy and time for capture and handling) increase with prey body depth (Hambright 1991; Nilsson & Brönmark 2000). We thus anticipated that prey body shape plays an important role in prey selection by gape-limited lionfish, with vulnerability to predation decreasing with increasingly deep-bodied (i.e. increasingly round) shapes. We quantified shape as the ratio of TL to maximum body depth, such that higher values indicate less round (i.e. more elongate), and hence more vulnerable, shapes. We calculated the average ratio of fish TL to body depth (in cm), measured as the linear distance from the pelvic girdle to the dorsal ridge, as in Hambright (1991), from lateral images of 3-5 specimens (available in Humann & Deloach [2002] and on FishBase [www.fishbase.org]) of each fish species encountered on the study reefsimages were only used for specimens that were with a size range that could be consumed by lionfish (i.e. <15cm TL; Green et al. 2012). Second, we hypothesized that fishes possessing a chemical or physical defense (e.g. a toxic or distasteful compound, sharp spine(s) or barb) would be less vulnerable to predation compared with their undefended counterparts (e.g. Hoogland *et al.* 1956; Caley and Schluter 2003; Schubert *et al.* 2003). Finally, the average size of prey (total length) relative to the size of their lionfish predator across several studies of lionfish stomach contents is ~15% (much smaller than the maximum of ~48% (Morris & Akins 2009; Munoz *et al.* 2011; Côté *et al.* 2013). It is unclear whether this result simply reflects the abundance of various prey sizes on invaded reefs. However, there is ample experimental evidence that gape-limited predators tend to selectively consume prey that are far smaller than their maximum gape limits, likely because larger prey are better at evading predators and smaller prey are less costly to capture and handle by predators (Einfalt & Wahl 1997; Nilsson & Brönmark 2000). We therefore hypothesized that vulnerability to predation would decrease with increasing prey size, quantified as body mass (in g), which we obtained by converting estimates of total length (TL to the nearest 1 cm) to weight using the allometric scaling function Mass (g) = $a*TL(cm)^b$, where a and b are species-specific constants that relate length to weight obtained from FishBase (www.fishbase.org). .

DIRECT OBSERVATIONS OF PREY SELECTION

To quantify lionfish prey selection *in situ*, we conducted detailed visual observations of lionfish on shallow coral patch reefs off Eleuthera Island, The Bahamas (22º22.500 N, 76º49.000 W), in

September 2008 and December 2009. On invaded reefs, lionfish exhibit bold behaviour and have little fear of divers, which facilitates a close approach without altering behaviour (Côté & Maljković 2010; Green *et al.* 2011). They hunt prey via a slow, hovering, stalking strategy, which affords observers easy view of the target prey, as well as the success of strikes at prey (Côté & Maljković 2010; Green *et al.* 2011). Individual lionfish were observed continuously for 30 min by a SCUBA diver from a distance of 2-3 m (as per Green *et al.* 2011). Only individuals that were actively hunting (i.e. oriented with head down, pectoral fins spread and actively stalking prey fishes) and consumed at least 1 prey item during the 30 min. observation period were included in this study. At the onset of observations, we estimated the size of the focal lionfish (total length [TL] to the nearest 1 cm). During each observation period, we recorded the identity, abundance and size (total length [TL] to the nearest 1 cm) of all fishes within a 1 m radius of the hunting lionfish every 5 min (hence, six point counts per observation). The large number of fish precluded continuous tabulation of prey across the 30 min period. We also recorded the identity and size of all prey items consumed by lionfish during the 30 min. period, as well as the fishes within a 1 m radius of the focal lionfish immediately following each prey capture. Lionfish are visual predators that primarily hunt in the open over the top of coral reefs or sand/seagrass beds. We thus assumed that only prey within visual sight of the lionfish (i.e. not those in crevices or under ledges) were available for consumption. We classified all fishes of less than 15 cm TL as potential prey items, based on physiological limits on predator: prey size ratio set by gape size (Nilsson & Brönmark 2000).

INDIRECT OBSERVATIONS OF PREY SELECTION

We also inferred lionfish prey selection by comparing the abundance of prey items in the stomachs of lionfish collected from eight sites along a continuous coral reef system off southwest New Providence Island, Bahamas (24º59.072 N, 77 º 32.207 W), to the abundance of prey identified during visual surveys of the same sites. Lionfish collections and prey visual surveys were conducted at depths of 10-20 m between May and July 2008. Lionfish were collected using hand nets, and euthanized in a clove oil and seawater solution at the surface. We then measured TL to the nearest 1 cm, extracted stomach contents from each specimen and identified all fish prey items visually to the lowest taxonomic resolutions possible. For whole fish prey (i.e. items for which TL could be estimated) that could not be identified to species because of degradation of key skin pigments and colouration, we obtained species identity via DNA barcode analysis (Côté *et al.* 2013). To minimize potential identification bias, we only included in our analyses lionfish stomachs from which all of the fish items could be identified to species (either visually or via DNA barcoding).

To estimate the abundance of prey available to lionfish, we conducted detailed surveys of prey-sized fishes (i.e. <15 cm TL) on 6-12 belt transects (30 m x 2 m) at each of the eight lionfish capture locations. Along each transect a trained observer carefully searched in all holes and crevices for cryptic fishes, using a dive light as needed. The identity and TL of all fishes were recorded to the nearest 1 cm. We assumed that any prey hidden within the reef framework and not recorded in our visual surveys would not be available to lionfish to consume.

Transect surveys of prey-sized fishes were conducted immediately prior to lionfish collections at each site. We assumed that the assemblage of prey-sized fishes observed on our transect surveys matched the assemblage of prey fishes available to lionfish during hunting bouts at the sites within ~24 h of capture, based on lab-derived times to digestion for lionfish prey (J.A. Morris, unpublished data) and preliminary results from external tagging and tracking of lionfish that suggested limited movement on the study reefs (S.J. Green, unpublished data).

STATISTICAL ANALYSIS

In the absence of prey selection, our null expectation was that lionfish should consume prey types in proportion to their abundance. Our analyses of direct and indirect observations of lionfish predation tested whether the consumption by lionfish of prey types varying in morphology and behaviour deviated significantly from this null expectation. Specifically, we used generalised linear mixed-effects models (GLMMs) to assess the effects of prey morphology and behaviour on lionfish prey selection from our direct and indirect observations of predation. We created models for each data set (i.e. direct and indirect observations) using the glmer() function in the package lme4 for the statistical software R (Bates et al. 2012; R Core Team 2012). Because morphological and behavioural traits can be shared among related species, and are thus not statistically independent (e.g. Jennings *et al.* 1999), we accounted for phylogenetic relatedness among prey fishes by specifying family as a nested random effect in our models (Sodhi *et al.* 2012). In the absence of a complete molecular phylogeny for the reef fishes in our study region, we classified species based on their most recent taxonomic groupings obtained from FishBase (www.fishbase.org), cross-checked with the World Registry of Marine Species (www.marinespecies.org).

Direct observations

To identify the drivers of lionfish prey selection from our direct observations of lionfish hunting on Eleuthera reefs, we first quantified the abundance of potential prey types (species and TL [in 1 cm bins] combination) within 1m of focal hunting lionfish, and then calculated the proportion of each type that were consumed (i.e. proportional response variable). As potential predictors of prey selection (proportion consumed), we included individual prey size (mass in g), species-specific body shape (quantified as the ratio of body length to depth), position in the water column, whether the prey species was nocturnal, physically or chemically defended, and a cleaner (either obligate or facultative) (fixed effects; Table 1). In addition to fish order and family, we specified three nested random effects, so that each potential prey was nested within the point count on which it was observed, the focal lionfish that was being observed, and the body length of the lionfish (TL to the nearest 1cm). Parameter estimates for each fixed and random effect were obtained using the Laplace approximation with a binomially distributed error and cloglog-link function because the proportion of zeros in our dataset greatly exceeded the proportion of ones (Bolker *et al.* 2009; Zuur *et al.* 2009). We conducted multiple Bonferroni-corrected Wald Z tests to obtain pair-wise comparisons of the relative selection probabilities for all levels of all categorical variables.

Indirect observations

To identify the drivers of lionfish prey selection from our indirect observations of lionfish stomach contents and prey availability on New Providence reefs, we first calculated the proportion of each fish prey type (species and length class [in 1-cm bins] combination) consumed by lionfish by dividing the abundance of each type, summed across the stomach contents of all lionfish, by its abundance estimate from our visual surveys of availability on the reefs. Next, we constructed a GLMM where the proportion of each prey type consumed (i.e. proportional response) was predicted by its morphological and behavioural characteristics (fixed effects; Table 1), and weighted by its abundance in surveys of the study area (following Zuur *et al.* 2009). Again, we conducted multiple Bonferroni-corrected post-hoc Wald Z tests to obtain pair-wise comparisons of the relative selection probabilities for each categorical predictor.

Model selection and multi-model averaging

For both of our analyses (direct and indirect observations), we evaluated the relative strength of support for predictions about the effect of prey morphological and behavioural traits and incorporated model uncertainty using AICc (for small sample sizes) model selection and averaging, respectively (Burnham and Anderson 2002). AICc values represent the trade-off between model complexity (i.e., the number of parameters) and model fit within a candidate set of models. In order to compare relative effect sizes we standardized our data by centering (subtracting the mean) and dividing by two standard deviations (Gelman 2008). We calculated average parameter estimates for each prey trait variable from its weights in the set of top models (i.e. those with ΔAICc < 4) in the MuMIn package (Barton 2013) for R Statisical Software, using the “Natural Average” method (Grueber et al. 2011; Burnham and Anderson 2002).

Results

PREY SELECTION FROM DIRECT OBSERVATIONS

On Eleuthera reefs we observed 22 hunting lionfish capture a total of 32 prey fishes from12 species and 6 families (Appendix S1). Lionfish size ranged from 10-36 cm TL (26 ± 6 cm; mean ± SD), while their captured prey ranged from 2- 7 cm TL (4 ± 1 cm; mean ± SD). The maximum number of prey consumed by a single lionfish during our observations was 4; twelve lionfish consumed a single prey fish. There were 32 species from 16 families recorded in point counts of fish prey availability (i.e. all individuals within 1 m radius of the focal lionfish and less than 15 cm TL; Appendix S1).

In line with our predictions, vulnerability to predation, measured as the probability of being consumed, decreased significantly with prey size and with increasingly deep body shapes (Table 2; Fig. 1, Fig 2a and b). Prey living solitarily or forming ephemeral feeding shoals were more likely to be consumed by lionfish than schooling prey, as were prey living on or in the benthos (Table 2). We also found some evidence that fishes which exhibit cleaning behaviour were less vulnerable to predation than their non-cleaning counterparts (Table 2; Figure 1). We observed no instances of predation on nocturnal, physically defended or pelagic prey however very few individuals of each of these types were observed within the vicinity of hunting lionfish on Eleuthera reefs (Table 2; Fig. 1).

PREY SELECTION FROM INDIRECT OBSERVATIONS

In total 637 lionfish were collected in New Providence and 108 contained whole fish prey that could be identified to species, either visually or through DNA barcode analysis. From these specimens, we documented a total of 258 prey fishes from 33 species and 15 families (Appendix S1). The lionfish examined ranged in sizes from 10 – 38 cm TL (25 ± 5 cm; mean ± SD) and their fish prey ranged from 2-13 cm TL (4 ± 2 cm; mean ± SD). The maximum number of prey fishes observed in a single lionfish stomach was 15; more than half (57 of 108) of the lionfish stomachs contained only one prey fish. We recorded 103 species from 30 families during the visual surveys of potential prey (i.e., all fishes < 15cm TL; Appendix S1).

On New Providence reefs, the vulnerability of prey fishes to lionfish predation again decreased with prey size and increasingly deep body shapes (Table 2; Fig. 1, Fig 2c and d). We found that cleaning behaviour predicted consumption by lionfish, with cleaners being selected relatively less frequently than non-cleaners (Table 2; Fig. 1). Aggregation behaviour and nocturnal activity also strongly influenced lionfish prey selection on New Providence reefs (Table 2; Fig. 1). As on Eleuthera reefs, schooling fishes were significantly less vulnerable than their solitary and shoaling counterparts, with solitary fishes most vulnerable to predation by lionfish (Table 2; Fig. 1). The presence of physical defense did not affect fish vulnerability to lionfish predation. Again we observed no instances of predation on pelagic prey, despite their prevalence within our environmental surveys of New Providence reefs (Table 2; Fig. 1). When these traits are considered in combination, fishes that exhibit vulnerable forms of each morphological and behavioural trait are ~200 times more likely to be consumed by lionfish than their 'invulnerable' counterparts of the same size and body shape on New Providence reefs (Fig. 2).

Discussion

The majority of our predictions about the behavioural and morphological features of reef fishes that affect selection by lionfish predators were confirmed by data collected at two very different spatial scales, demonstrating that vulnerability to predation can be conferred by traits that recur across species within prey assemblages. In particular, our analyses of both *in situ* behavioural observations and *ex situ* stomach contents reveal that prey size, body shape, aggregation size and cleaning behaviour are important determinants of vulnerability to predation, with small, solitary and shallow-bodied fishes that do not engage in parasite removal consumed selectively. Water column position also strongly influenced vulnerability to predation; prey occurring on and in the benthos most vulnerable to predation on Eleuthera reefs, and pelagic prey occupying the water column >2m above reefs were never selected by lionfish in our study. Nocturnality also predicted lionfish prey selection in our large-scale analysis of New Providence reefs.

Counter to our prediction, we found that schooling behaviour decreased the vulnerability of fish prey to lionfish predation on New Providence reefs, and that solitary behaviour increased vulnerability on Eleuthera reefs, supporting the hypothesis that schooling behaviour can be effective anti-predator strategy (Pitcher 1993). While our observations indicate that, on the whole, solitary species are more vulnerable than schooling species, the success of schooling behaviour as an anti-predator strategy has been shown to depend on a combination school size, prey vigilance and predator detection strategy, which are thought to be species- and context-dependent (Bednekoff & Lima 1998). Further work is needed to tease apart the effects of school size and prey vigilance on vulnerability to lionfish predation. Another prey feature that unexpectedly had little influence on vulnerability to lionfish predation was the presence of a physical or chemical defense. One possible explanation is that the manner in which prey use physical defenses (e.g. spines or barbs) may be ineffective against the hunting strategy of lionfish. During many of our direct observations, prey appeared largely unaware of stalking lionfish immediately prior to a capture. Alternatively, the defenses of small-bodied prey may simply be ineffective against relatively large-bodied lionfish predators; prey were on average only 15% of the lionfish's length.

We show that mortality from lionfish predation will be greatest for prey possessing a specific suite of behavioural and morphological characteristics on invaded Atlantic coral reefs (e.g. Figure 2). As lionfish can reach densities that allow the rapid depletion of prey biomass (Green *et al.* 2012), prey types that are selectively consumed may post more rapid and substantial declines over time, with potentially serious implications for local population persistence. Time-series data documenting the relative change in biomass of prey types over time, in relation to lionfish predation pressure, are needed to test this prediction. Moreover, selective predation by lionfish may have repercussions on invaded marine food webs if vulnerability to lionfish predation correlates with functional role of prey. For example, herbivorous fishes grow through size classes vulnerable to lionfish predation, and many species are of a body shape (body depth ratio range: 4-7) that is vulnerable to predation by lionfish (Figure 2C; Appendix S1). Thus, high rate of lionfish-induced mortality on juveniles stages could impair the process of herbivory, which suppresses algal growth on coral reefs (Mumby *et al.* 2006), in the long term. Because our analyses focus on prey characteristics and not species identity, our findings may provide useful insight into the potential effects of lionfish predation on fish communities elsewhere in the invaded region; data on fish assemblages from before and early in the invasion of a region may be used to establish spatial priorities for management action. For example, locations where native fish communities are composed of a high proportion of vulnerable individuals (i.e. small-bodied, shallow-bodied, benthic or demersial, and nocturnal species) could be targeted for lionfish culling.

Predicting the strength of novel predator-prey is essential for understanding how ecological patterns and processes will be affected by the ongoing process of human-mediated species exchange. In particular, biological invasions are a major consequence of species exchange that are occuring at an increasing rate (Mooney and Cleland 2001). The expansion of the Burmese python (*Python molurus bivittatus*) northward from the Florida Everglades (Rodda et al. 2009), recent spread of Asian tiger prawn (*Penaeus monodon*) into the Gulf of Mexico and Western Atlantic (USGS 2013) and progression of snakehead fishes (Channidae) throughout North American freshwater systems (Herborg *et al*. 2007) are just a few examples of non-native predators that are rapidly expanding into new areas, where they encounter and consume novel prey items. Low trophic level species are also invading non-native ranges at an increasing rate, where they alter the diet of native predators (e.g. the consumption of invasive gypsy moth [*Lymantria dispar*] by native cuckoos [*Coccyzus erythrpthalmus* and *C. americanus*] (Barber et al. 2008). Using our approach of identifying general prey traits that confer vulnerability to predation will aid in forecasting changes to predator-prey relationships, and ultimately consequences for community structure, in each of these systems. The only requirements to apply a trait-based approach are that: 1) the predator's diet consistent of multiple species, 2) prey species share at least 1 trait that is predicted to affect vulnerability to predation, and 3) information on prey consumption and availability be obtained, either through *in situ* observation of predation or by pairing broad-scale diet information from guts or tissues with surveys of environmental prey abundance.

Finally, our study shows that a functional traits approach has value for generating predations about the effects of prey selection on the structure of ecological communities (i.e. McGill et al. 2006). Current thinking about predator-prey interactions can be broadly characterized into two prevailing paradigms: a species-based view, in which food webs are constructed by quantifying the interaction strength between pairs of predators and prey (Paine 1980, Polis and Strong 1996), and a size-based view, which classifies predator-prey interactions based on body size, largely ignoring species identity (Jennings 2005, Blanchard *et al.* 2011). Our study is the first identify general traits of prey that predict vulnerability to predation, and indicates that a trait-based view of predator-prey interactions, in which variation in morphology and behaviour confer prey selection, also has significant influence on species interactions within ecological communities (e.g., Hartvig *et al.* 2011). It is also, to our knowledge, the first to examine diet selection simultaneously at two spatial scales. Importantly, both our *in situ* observations of predation and broad-scale analyses of stomach contents identified the same prey traits as important drivers of diet selection. However, directly observing prey capture *in situ* is challenging for many predatory species and information on diet composition is commonly gathered via methods similar to our broad-scale analyses, with 'snapshots' of diet obtained by examining gut content (as we did) or scat composition. The similarity of traits identified by both analyses suggests that diet selection can be well estimated from these broad-scale analyses when direct observation of predation is not logistically feasible.

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Data accessibility

Data used in analyses: species data uploaded as online supporting information (Appendix S1) and available through Fig Share pending acceptance of the study for publication.

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Table 1. Morphological and behavioural traits of prey fish predicted to influence vulnerability to predation by invasive lionfish (*Pterois volitans/miles*)

	Prey attribute	**Data type**	**Units/Levels**	**Predictions of vulnerability to predation**
Morphology	Body shape	Continuous	Body length to depth ratio: Higher values indicate increasingly linear shapes	↑ ratio (i.e. ↑shallow bodied) = ↑ vulnerability
	Body size	Continuous	Mass (g)	↑ mass = ↓ vulnerability
	Physical or chemical defense	Binary	yes/no = 0/1	+ defense = ↓ vulnerability
Behaviour	Cleaning behaviour	Binary	Yes/no = 0/1	+ cleaning behaviour = ↓ vulnerability
	Aggregation size	Categorical	Solitary, shoaling, schooling	Solitary < shoaling < schooling
	Nocturnally active	Binary	Yes/no = 0/1	+ nocturnality = ↑ vulnerability
	Water column position	Categorical	Benthic, demersal, pelagic	Pelagic < benthic < demersal

Table 2. Top generalised linear mixed-effects models (GLMMs) of lionfish diet selection from **A.** *in situ* observations of lionfish predation on coral reefs off Eleuthera, Bahamas, and **B.** inferred from lionfish stomach contents and visual surveys of reef fish on coral reefs off New Providence, Bahamas. Δ AICc is the difference in AICc values between model i and the best model of those considered, and w_i is the probability that model is the best of the set. The top models considered with those with Δ AICc < 4.
Relative variable importance is the sum of the weights of all models that contain that particular variable.

		Morphology				**Behaviour**							
Response variable	**Rank**	**Body shape**	**Body size**	**Cleaner**	**Defense**	**Aggregation size**	**Nocturnality**	**Water column position**	**logLik**	**AICc**	**Δ AICc**	**Weight**	**df**
***In situ* feeding observations**	1	✓	✓			✓			-69.41	157.90	0.00	0.19	9
	2	✓	✓			✓	✓		-69.09	159.50	1.60	0.09	10
	3	✓	✓		✓	✓			-69.14	159.60	1.72	0.08	10
	4		✓			✓		✓	-69.24	159.90	1.92	0.07	10
	5	✓	✓	✓		✓			-69.29	159.90	2.02	0.07	10
	6	✓	✓						-72.67	160.00	2.08	0.07	7
	7		✓			✓			-71.58	160.00	2.12	0.07	8
	8		✓		✓	✓			-70.73	160.60	2.64	0.05	9
	9		✓						-74.04	160.60	2.66	0.05	6
	10	✓	✓		✓	✓	✓		-68.80	161.30	3.32	0.04	11
	11		✓		✓	✓		✓	-68.90	161.50	3.52	0.03	11

	12		✓	✓		✓		✓	-68.92	161.50	3.56	0.03	11
	13		✓					✓	-72.33	161.50	3.61	0.03	8
	14	✓	✓	✓		✓	✓		-69.00	161.70	3.72	0.03	11
Stomach contents analysis	1	✓	✓	✓		✓	✓	✓	-370.78	762.00	0.00	0.32	10
	2	✓	✓	✓	✓	✓	✓	✓	-369.91	762.30	0.33	0.27	11
	3	✓	✓	✓		✓	✓		-374.08	764.40	2.44	0.10	8
	4		✓	✓		✓	✓		-375.27	764.80	2.76	0.08	7
	5	✓	✓	✓	✓	✓	✓		-373.25	764.90	2.86	0.08	9
	6	✓	✓		✓	✓	✓	✓	-372.45	765.30	3.33	0.06	10
	7	✓	✓		✓	✓	✓		-374.74	765.80	3.76	0.05	8
	8		✓	✓	✓	✓	✓		-374.82	765.90	3.92	0.05	8
Relative variable importance (direct/indirect)		***0.63/0.87***	***1/1***	***0.16/0.89***	***0.23/0.5***	***0.85/1***	***0.18/1***	***0.2/0.65***					

Figure legends

Fig. 1 Model-averaged coefficients from the top generalised linear mixed-effects models (GLMMs; Δ AICc < 4 ; Table 2) of lionfish prey selection on Eleuthera coral reefs ('*in situ* observations') and on New Providence coral reefs (Stomach contents analysis). Points represent mean values bounded by 95% confidence intervals. Positive values (to the right of the line) indicate selective predation on prey displaying the trait, while negative values (to the left of the line) indicate avoidance. Levels 'Demersal' and 'Pelagic' are compared against the baseline level 'Benthic', and 'Schooling' and 'Solitary' are compared against 'Shoaling'. 'Body shape' is measured as the ratio of body length (cm) to depth (cm), and 'Body size' is measured as mass (in g) as per Table 1. Grey shading indicates trait forms that were not present in the corresponding data set. Numbers denoted with * are average parameter values, estimated with large uncertainty (i.e., standard error [SE] >100) because no individuals with that specific trait form were consumed by lionfish in the dataset.

Fig. 2 Example contour plots of predicted mean vulnerability to predation by lionfish for various combinations of prey size (mass in g) and body shape (quantified as the ratio of fish length to body depth; lower values indicate deeper-bodied shapes whereas higher values denote shallow-bodied shapes) for fishes on coral reefs off New Providence, Bahamas, displaying varying morphological and behavioural traits: A) shoaling demersal fishes such as *Scarus iserti* and the deeper-bodied *Acanthurus bahianus*, B) schooling pelagic fishes such as *Decapterus macarellus,* C) solitary nocturnal fishes such as *Apogon binotatius,* and D) benthic cleaning fishes such as *Elacatinus genie.* Black bands denote a change in probability of predation. Cooler colours denote the combinations of prey fish size and body depth ratio yielding low vulnerability to predation, while warmer colours denote scenarios in which vulnerability to predation is high. Species illustrations modified with permission from ReefNet (2007).

Fig. 1

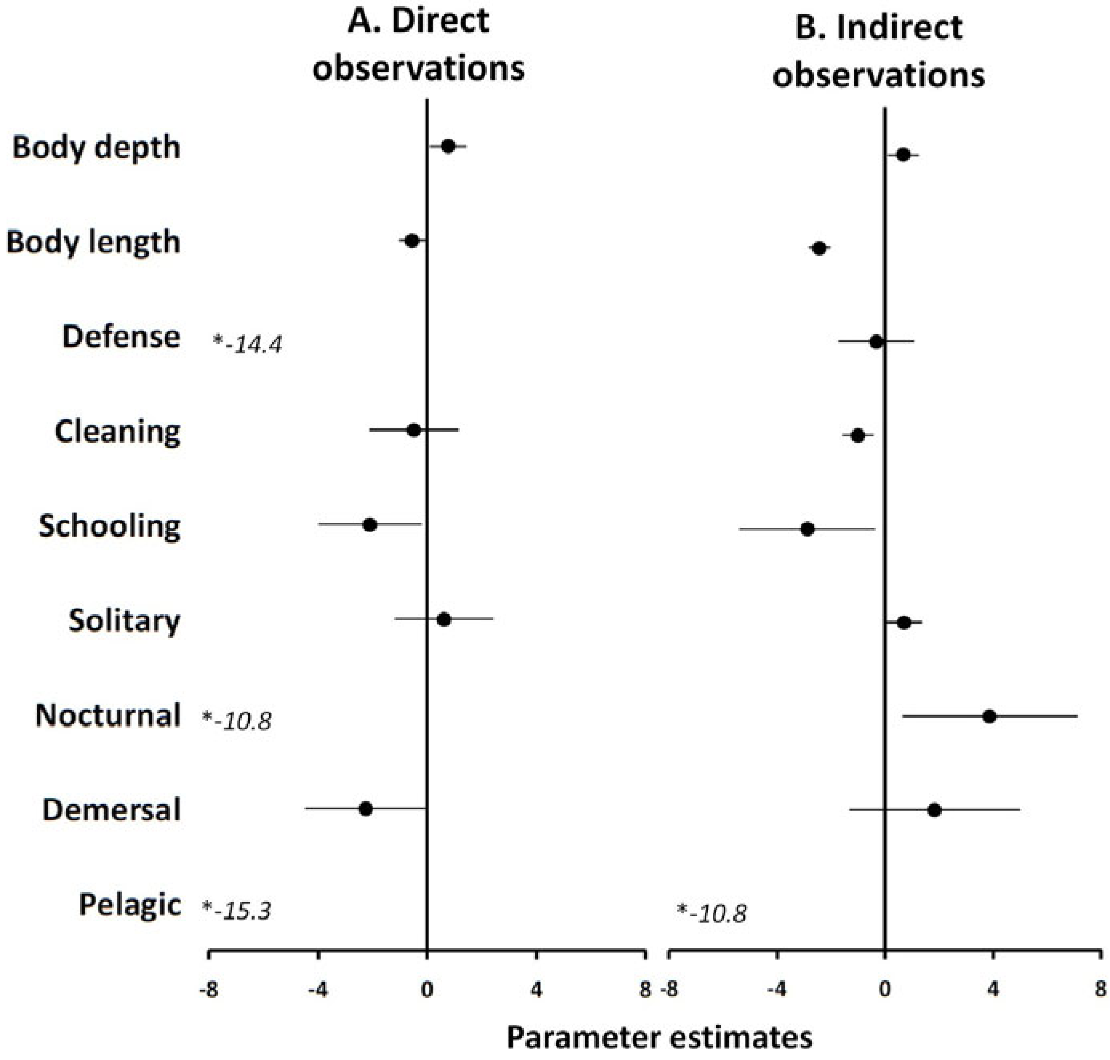
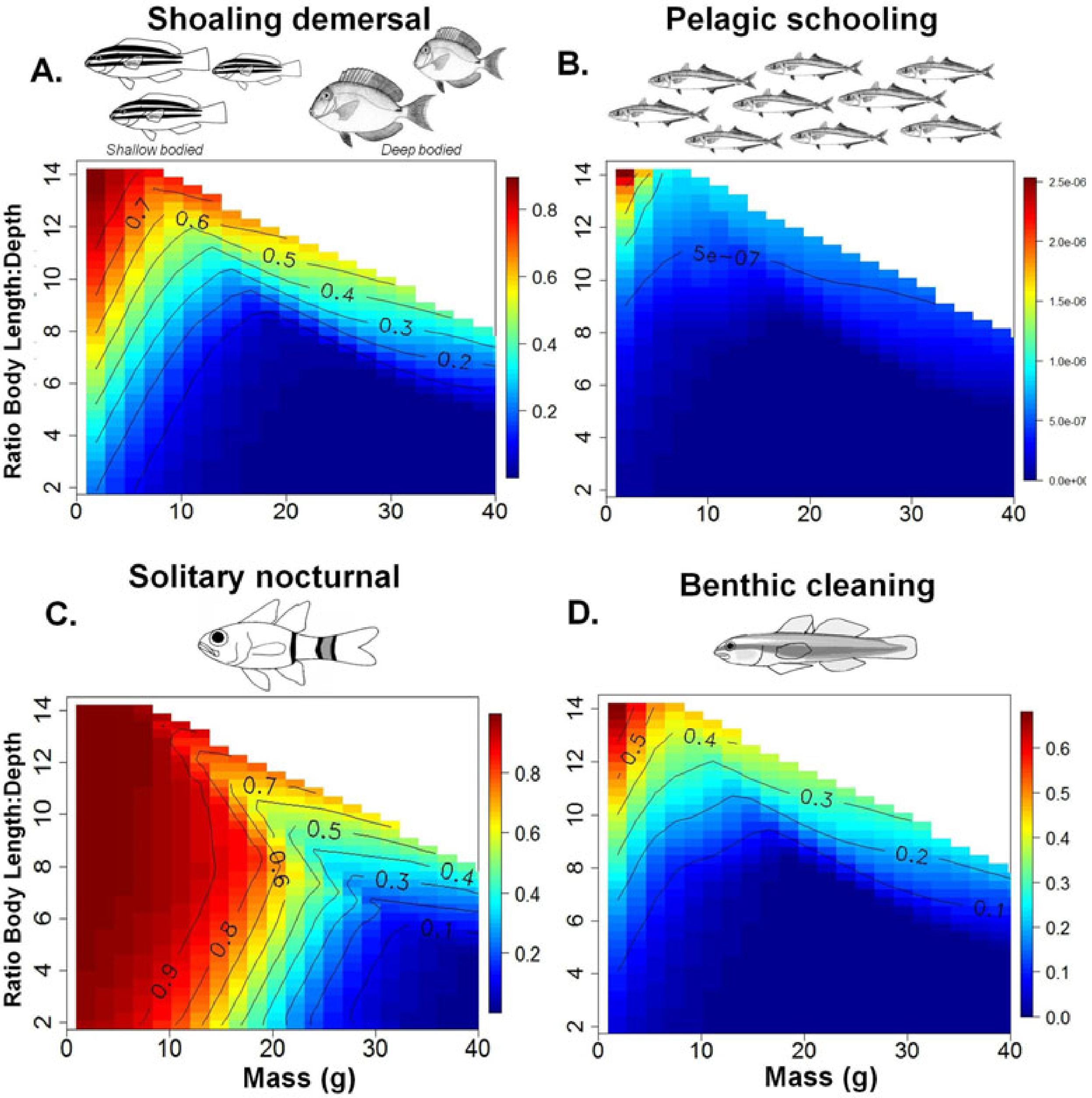


Fig. 2


Shoaling demersal
A.
Shallow bodied
Deep bodied
Pelagic schooling
B.
Solitary nocturnal
C.
Benthic cleaning
D.
Ratio Body Length:Depth
Mass (g)
0
10
20
30
40
2
4
6
8
10
12
14
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.8
0.9
5e−07
0.2
0.4
0.6
0.8
2.5e-06
2.0e-06
1.5e-06
1.0e-06
5.0e-07
0.0e+0
0.0