



## Predicted impact of the invasive lionfish *Pterois volitans* on the food web of a Caribbean coral reef

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### ABSTRACT

The invasion of lionfish in the Caribbean is causing grave concern because of its deleterious impacts on coral reef food-webs. We have used an Ecosim-with-Ecosim model to predict the impacts of lionfish invasion on a coral reef community based on pre-invasion fish community data. Forty-six groups were defined, and an initial Ecosim model was balanced with a near-zero biomass of lionfish. In Ecosim, the near-zero biomass was eradicated by applying a very high fishing pressure in the first year of simulation. We subsequently (re-)introduced lionfish with a very low biomass, and allowed them to increase to very high abundance. With a near-zero lionfish biomass, the great majority of mesocarnivorous/omnivorous coral reef fish were predicted to be dominant while sharks were predicted to be the apex predators. Different management scenarios were established in the ecosystem to explore the eradication and resilience of lionfish. The management scenarios showed that if all adult lionfish were exploitable it will in theory be possible to fish the lionfish to a very low level, but the fishing pressure will have to be maintained, or the lionfish will recover. If the largest individuals are unexploitable it will be much more difficult to control the lionfish population.

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### 1. Introduction

In three decades, since the first documented Atlantic occurrence in the mid-1980s, the invasive lionfish species (*Pterois volitans*), a voracious fish predator, has spread from the North Western North Atlantic to the Caribbean and Campeche Bank (Morris et al., 2008; Morris and Akins, 2009; Schofield, 2009; Ahrenholz and Morris, 2010; Aguilar-Perera and Tuz-Sulub, 2010; Schofield, 2010; USGSa, 2011a,b). The invasion is assumed to be due to accidental or intentional releases from aquaria (Whitfield et al., 2002; Semmens et al., 2004; Ruiz-Carus et al., 2006; Hamner et al., 2007). Originally uncommon, this species is now one of the most well-known and abundant predators in the center of origin of the invasion (Florida) and is now abundant in the Bahamian archipelago off Florida (Albins and Hixon, 2008) and the Caribbean (USGSa, 2011a,b; NCCOS, 2011). Average density estimates on Bahamian coral reefs of 390 lionfish  $\text{ha}^{-1}$  (Green and Côté, 2009) place Bahamian lionfish at several times higher than on its native ranges, from 2.2 lionfish  $\cdot \text{h}^{-1}$  in Palau (Grubich et al., 2009) to 80 lionfish  $\text{ha}^{-1}$  in the Red Sea

(Fishelson, 1997). Off the coast of North Carolina, mean densities of 21 lionfish  $\cdot \text{ha}^{-1}$  were reported in 2004 (Whitfield et al., 2007), which have increased to over 400 lionfish  $\cdot \text{ha}^{-1}$  in some locations in 2007 (Morris and Whitfield, 2009). No other published density estimations are available, but the lionfish is becoming a common species in the Caribbean (Schofield, 2009, 2010). Thus, 260 lionfish were caught during July 2010–February 2011 on Alacranes Reef, in the southern Gulf of Mexico, (Aguilar-Perera and Tuz-Sulub, 2011). Lionfish are the first marine fish known to invade the western Atlantic Ocean and Caribbean Sea, and have the potential to add additional stress to an environment already compromised by over-fishing, pollution and climate change (Schofield, 2010).

The extremely rapid expansion of lionfish represents a potentially major threat to coral reef food webs in the Caribbean region by decreasing the survival of a wide range of native animals via predation (Albins and Hixon, 2008). Individual lionfish can be very efficient hunters (Côté and Maljković, 2010), and have been shown to reduce fish recruitment by 79% on Bahamian coral reefs (Albins and Hixon, 2008). The style of lionfish predation (i.e., ambush predator) is not unique in Caribbean coral reefs, (e.g., red grouper, frog fish and scorpion fish), but the lack of experience of prey species with lionfish specifically may increase its predation efficiency (Hare and Whitfield, 2003). Lionfish in the Bahamian archipelago largely prey upon teleosts (78% volume) and crustaceans (14% volume) (Morris and Akins, 2009). Twenty-one families and 41 species of teleosts were

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represented in the diet of the lionfish; the top 10 families of dietary importance were Gobiidae, Labridae, Grammatidae, Apogonidae, Pomacentridae, Serranidae, Blenniidae, Atherinidae, Mullidae and Monacanthidae.

In addition to high densities, the impact of the invasive species on fish communities increases as individual lionfish have been shown to have a considerably higher predation rate on Bahamian coral reefs than lionfish from the Gulf of Aqaba, Red Sea (Fishelson, 1997; Côté and Maljković, 2010). Some calculations given for the Bahamian coral reefs result in  $13 \text{ g d}^{-1}$  for lionfish that were on average ( $\pm \text{SE}$ )  $25 \pm 6 \text{ cm TL}$  (or  $\sim 340 \text{ g}$ ) (Côté and Maljković, 2010). This predation rate is higher than that reported by Fishelson (1997) for larger *Pterois* spp (300–400 g body weight), which consumed approximately  $8.5 \text{ g d}^{-1}$ . A bioenergetic model of the daily consumption of a Bahamian population of 393 lionfish predicted a daily consumption of 2.124–2.186 kg of prey from June to October when mean temperatures are greater than  $28^\circ \text{C}$  (Cerino, 2010). The daily average consumption by lionfish was 5.5 g, a value only half of what was found in the field.

The dramatic density increases, and spread of lionfish throughout the Caribbean coral reefs, its wide diversity spectrum of fish prey and high consumption rates are probably having an extensive trophic impact on Caribbean food webs. Since the invasion is relatively new, it is unclear how lionfish will affect Atlantic coral reef ecosystems. Invasive species are considered one of the greatest disturbances to affect community and food web structure (Carlton and Geller, 1993; Ruiz et al., 1997; Streftaris et al., 2005; Pine et al., 2007). Predatory invasive species may have potential effects on native fish via predation or competition (Mercado-Silva et al., 2009; Zambrano et al., 2010), they may reduce trophic positions, modify, have indirect effects on food webs (VanderZanden et al., 1999, 2003; Hovius et al., 2007) and produce cascade effects altering the entire ecosystem (Carpenter et al., 1985; Moyle and Light, 1996a). Thus, it is important to predict the potential impact of lionfish invasion on Caribbean food webs and generate possible control scenarios.

Food webs are excellent macrodescriptors of ecosystem perturbation (Wootton et al., 1996; Vander-Zanden et al., 1999) and could be used as a representation of ecosystem response to invasive predatory species. The information obtained by the food web characterization including lionfish species can be used to generate a better understanding of the impact within Caribbean coral reef communities, which has potential implications for on-going management efforts in the area.

We have simulated the effect of lionfish invasion on a Caribbean food web using the Ecopath with Ecosim (EwE, <http://www.ecopath.org>) modeling approach. EwE is a powerful and widely used tool for investigating food web structure and for exploring the ecosystem impacts of policy decisions—it primarily focuses on fishing regulations, but also models the impact of nutrients regimes and regulations on ecosystems (Christensen and Walters, 2004). Several hundred models have been published to date, which combined with its popularity as a management tool has resulted in a dramatic increase in policy simulations in recent years (Christensen and Walters, 2004). Recently EwE has been used to investigate the impact of functional groups and species additions into aquatic ecosystems, such as parasites (Arias-González and Morand, 2006) and apex predators (Pine et al., 2007). Functional groups include all species of a community, which share a certain number of qualities linked to ecological functions, and are normally defined according to the way in which they use and compete for any kind of resources (Raghukumar and Anil, 2003; Arenas et al., 2006). Species comprising one functional group typically have comparable requirements with regard to resources (e.g., food) or provide similar tasks (Raghukumar and Anil, 2003; Arenas et al., 2006). Effects of invasive species have also been modeled using EwE (Pine et al., 2007); however this is the first application modeling a species that has only recently invaded the ecosystem.

Here, a food web model was constructed to predict the potential impact of lionfish on coral reef communities and possible management strategies of the lionfish population. We developed the food web model based on extensive empirical data prior to the lionfish invasion in Alacranes Reef, a relatively isolated Caribbean coral reef system. Our model is a good way of making predictions regarding the community level effects of predation, which is likely to be a primary driver of this invader's impacts because of its position as an apex predator. The food web model suggests that lionfish will have severe direct and indirect impacts on coral reef communities. Therefore lionfish must be the object of intense local and regional management, and our research could potentially guide such efforts.

## 2. Material and methods

### 2.1. Alacranes Reef

Recently several individuals of the invasive lionfish have been reported in different areas of Campeche Bank (CB) (USGSa, 2011a), suggesting that the lionfish is invading different coastal and coral reef systems in this area. The first two

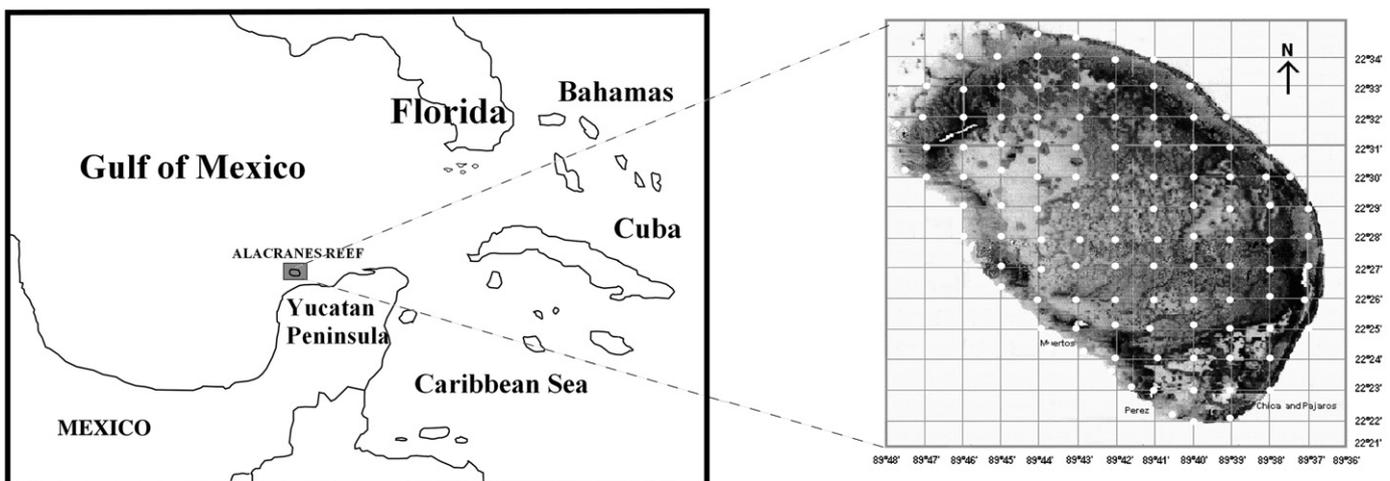


Fig. 1. Study area and distribution of field sampling sites of fish assemblages within Alacranes Reef, Campeche Bank.

records of the presence of lionfish in CB were in 2010 in a coral reef patch in the southern Gulf of Mexico (Aguilar-Perera and Tuz-Sulub, 2010). Recently, in Alacranes Reef, approximately 40 fishermen have caught 260 lionfish between July 2010 and February 2011 (Aguilar-Perera and Tuz-Sulub, 2011). Based on the NOAA's invasion phases established for the Florida Keys National Marine Sanctuary, lionfish invasion in Alacranes Reef is in an intermediate-advanced invasion (> 200 in one year) (Aguilar-Perera and Tuz-Sulub, 2011).

Alacranes Reef, an atoll type reef located in Campeche Bank, contains a large coral reef system with a high variety of relatively well-conserved habitats (Fig. 1) (González-Gándara et al., 1999). Since this system is 72 miles from the coast, it provides an excellent "recent or before lionfish invasion" treatment because of the low anthropogenic impact on the reef and low fishing pressure.

Alacranes Reef has a semi-elliptic shape with an extension of approximately 27 km in length and a width of 15 km (Fig. 1). It is a coral reef system with a great number of coral patches and microatolls in the reef lagoon consisting mainly of corals, sponges and macroalgae. The geomorphology of the reef is highly complex; to the windward side it possesses a conspicuous reef crest and within the reef lagoon several reticulate habitats are present (González-Gándara et al., 1999). We developed a food web model for all of the area defined by the reef.

## 2.2. Model approach

### 2.2.1. Model

The Ecopath with Ecosim (EwE) software contains several key routines for the study of aquatic ecosystems: the Ecopath, originally developed by Polovina and Ow (1983) and Polovina (1984, 1985), and operationalized by Christensen and Pauly (1992); network analysis (Ulanowicz, 1986); Ecoranger and sensitivity analysis (Christensen and Walters, 2004); Ecospace and Ecosim (Walters et al., 1999, 2000); keystone species (Libralato et al., 2006) among others. The Ecopath food web model of Alacranes Reef employs biomass estimations of 140 coral reef fish species in 24 trophic groups and their prey and predators in order to establish an instantaneous mass balance description of the food web linkages in the coral reef system. The Ecopath food web model was constructed directly from field data, using similar criteria to models for the Caribbean (Opitz, 1996; Arias-González, 1998; Arias-González et al., 2004) and following the methods of Christensen and Walters (2004). Ecopath initially employed assumptions of steady-state but now base parameters on an assumption of mass balance over a period of time, in this case a year.

Ecopath parameterization is integrated into two master equations. The first describes how the production term for each group or compartment (*i*) can be split into components (Christensen and Walters, 2004):

$$B_i(P/B)_i EE_i - \sum_{j=1}^n B_j(Q/B)_j DC_{ji} - Y_i - BA_i - E_i = 0$$

where  $B_i$  is the mean biomass of functional group *i*;  $P/B_i$  is its production/biomass ratio;  $EE_i$  is the ecotrophic efficiency (i.e., the fraction of a prey species' annual production that is consumed by the predator);  $Q/B_i$  is its food consumption per biomass unit;  $DC_{ji}$  is the fraction of Prey *i* consumed by Predator *j*;  $Y_i$  is the total fishery catch rate of *i*;  $E_i$  is the net migration rate (emigration-immigration); and  $BA_i$  is the biomass accumulation rate for *i*. Ecopath requires the input of diet and catches and at least three of the four basic parameters for each functional group in the model.

The second master equation is designed to balance the energy flows of a biomass pool, i.e., consumption (*Q*) equals the sum of production (*P*), unassimilated food (*UAF*) and respiration (*R*). Ecopath links the production of each group with the consumption of all groups, using these links to estimate missing parameters. Once the missing parameters are estimated, the energy balance is ensured within each group using the equation (Christensen and Walters, 2004):

$$Q = P + R + UAF$$

We have estimated the role of the lionfish biomass in structuring the modeled coral reef food web. Ecopath utilizes an approach for estimating the keystone of the functional groups (species or group of species) of food web models (Libralato et al., 2006). The keystone is calculated through the analysis of the mixed trophic impacts, which is implemented in Ecopath, and allows to rank functional groups by their impact on the different elements of the ecosystem resulting from a small change to the biomass (Libralato et al., 2006). We estimated the keystone of the functional groups of the food web model after lionfish invasion. We have used current lionfish biomass on Bahamas coral reefs for the post-invasion estimation.

We modeled the impact of lionfish-derived invasion on the mass balance model of the coral reef food web for Alacranes Reef using Ecosim. The Ecosim model, based on a series of coupled differential equations, describes a dynamic simulation of the changes in biomass and flow within the system over time by accounting for changes in predation, consumption rate and fishing (Walters and Christensen, 2007). The rate of change of biomass of group *i* ( $B_i$ ) is given as

$$\frac{dB_i}{dt} = g_i - \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i)B_i$$

where  $dB_i/dt$  represents the growth rate during the time interval *dt* of group *i* in terms of its biomass,  $B_i$ ;  $g_i$  is the net growth efficiency;  $Q_{ji}$  and  $Q_{ij}$  are the consumption rates of group *j* by group *i* and the consumption rate of group *i* by group *j*, respectively;  $I_j$  is the immigration flow in tonnes · km<sup>-2</sup>;  $MO_i$  is non-predation mortality;  $F_i$  is fishing mortality; and  $e_i$  is emigration rate (Christensen and Walters, 2004).

## 2.3. Data and models

### 2.3.1. Data

We have used an extensive database on coral reef fish produced for this site since 1999 (González-Gándara et al., 1999; González-Gándara and Arias-González, 2001a,b). The fish species, abundance and lengths were based on the visual censuses study carried out in 131 sites throughout the reef with visual transects of 50 × 2 m (Fig. 1). The fish lengths recorded were converted to biomass using an isometric growth equation:  $W = aL^b$ , where *W* is the wet weight, *L* is the standard length, *a* the intercept and *b* the slope if the relationship between the length and the weight is calculated through a logarithmic transformation. The constants for each fish species were obtained from observations made in this area (González-Gándara et al., 2003) and Fishbase (Froese and Pauly, 2010). Biomass was estimated from the biomass of each individual fish averaged across replicate transects at a site. A diet matrix was developed for fish species from published data (Opitz, 1996; Froese and Pauly, 2010). Fish were grouped into 24 major functional categories obtained by Opitz (1996) (Appendix A). The unknowns in this study were sessile invertebrate feeders, and the non-fish group biomasses. The  $P B^{-1}$  and  $Q B^{-1}$  values for the fish groups were obtained from Fishbase (Froese and Pauly, 2010).  $P B^{-1}$  and  $Q B^{-1}$  values and diet for non-fish groups were obtained from Opitz (1996) (Appendix B). A great majority of the information comes from Opitz (1996) based on the analysis of a hypothetical Virgin Island/Puerto Rico reef ecosystem. This author obtained biomass, diet composition of the various consumers and consumption and production rates for different invertebrate organisms using relevant published data and appropriate ecological efficiencies. The diet matrix for the model is shown in Appendix C.

Harvest rates for different species in Alacranes Reef are relatively low, and are focused on few species, principally because it is a remote reef and it is at present a marine protected area. Harvest occurs exclusively for certain species of groupers, snappers, sharks, octopus and lobster. Harvest data on these groups on Alacranes Reef were obtained directly from statistical fisheries of the National Fisheries Institute located in Yucalpetén, Yucatán, México. Fishery data include a time series of 7–8 years of exploitation, depending on the species (Appendix D).

### 2.3.2. Ecopath model

The mass balance model of Alacranes Reef was created to determine whether or not the presence of lionfish biomass quantitatively alters the coral reef food web. The model was created using a top-down simulation based on the original fish visual census data collected to estimate the necessary fish biomass to maintain the biomass of predators. In the model it was assumed that, using an ecotrophic efficiency of 0.95, natural predation consumed a large portion of fish production, including the fishing impact. The model was originally constructed in EwE 5.1 and later transferred to EwE version 6.0.1. In the EwE 5.1-version of the model, the input data of each Ecoranger model were balanced and the annual mean of  $B$ , the  $P B^{-1}$  ratio,  $Q B^{-1}$  ratio and  $EE$  were estimated. In order to avoid bias in the estimated values of different parameters, the preliminary data were introduced into the Ecoranger routine of EwE (version 5.1) and ranges based on a 10% coefficient of variation were introduced. Random input variables were drawn from a normal distribution for each basic parameter. The process was repeated in order to generate a theoretical frequency distribution for each parameter using Monte Carlo simulations. 10,000 models were run and from the 200 fitting models for each one of the scenarios, the model with parameters closest to the overall mean was used for further analysis.

The Ecopath model was validated prior to running the simulations of lionfish invasion using Ecosim. We used the prebalance (PREBAL) diagnostics (Link, 2010) including biomasses and rates (Appendix E). PREBAL provides a set of guidelines presented as a form of "checklist" to ensure that potential problems are captured before network model outputs are used to address research or management questions (Link, 2010).

### 2.3.3. Simulating the invasion

The initial Ecopath model was balanced with a near-zero biomass of lionfish (0.01 t km<sup>-2</sup>), so that its impact on the system defined as the 'current state' was insignificant. In Ecosim, the near-zero biomass was then "fished out" immediately at the start of the simulations by applying a high fishing mortality. After five years, the lionfish were (re-)introduced by forcing the biomass of the 10–35 month age group to 0.01 t km<sup>-2</sup> for one time step. The biomass of lionfish would then build up to a total biomass of around 10.5 t km<sup>-2</sup>, which is comparable to post-invasion biomasses observed in the Bahamas (Green and Côté, 2009; Côté and Maljković, 2010). The results were then compared with historical information on coral reef

fish communities prior to lionfish invasion in Alacranes Reef and used as an indicator of model performance following the criteria of Pine et al. (2007).

#### 2.3.4. Modeling lionfish eradication

At present there is strong concern regarding the best control strategies of the rapid invasion of lionfish in the Caribbean and Gulf of Mexico. Control of the lionfish invasion is needed to mitigate its impacts. We examined the response of the ecosystem to the population increase in lionfish, and also evaluated four scenarios to eliminate lionfish through intensive removal after the lionfish populations had levelled off after the invasion:

- (1) Applying a fishing mortality of  $10 \text{ y}^{-1}$  on all adult lionfish for five years (Fig. 5a).
- (2) Applying a fishing mortality of  $1 \text{ y}^{-1}$  on all adult lionfish continuously (Fig. 5b).
- (3) Applying a fishing mortality of  $10 \text{ y}^{-1}$  on the smaller spawners (10–35 months) for five years (Fig. 5c).
- (4) Applying a fishing mortality of  $1 \text{ y}^{-1}$  on the smaller spawners (10–35 months) continuously (Fig. 5d).

The two last scenarios were designed to evaluate the scenario that the largest lionfish are in deep water and inaccessible to divers (who may be needed for the eradication; NCCOS, 2011, pers. observations).

The scenarios are inspired by the criterion used by Pine et al. (2007) for the eradication simulation of an apex predator on a Coastal Riverine Fish Community. In contrast with Pine et al. (2007), since there is no information on lionfish exploitation in the area, it was necessary to investigate the harvest effort by which the lionfish population could be eradicated and the ecosystem reaches equilibrium.

#### 2.4. Lionfish parameterisation

Records of lionfish densities and predation rates obtained from two recent studies carried out in New Providence on Bahamian coral reefs (Green and Côté, 2009; Côté and Maljković, 2010) were used to calculate the biomass ( $B$ ) and consumption to biomass ratio ( $QB^{-1} \text{ y}^{-1}$ ).  $QB^{-1} \text{ y}^{-1}$  was obtained by multiplying average densities ( $393.3 \pm 144.4 \text{ lionfish ha}^{-1}$ ; mean  $\pm 1 \text{ SD}$ ) obtained by Green and Côté (2009) by the ratio of clear of 13.1 kills  $\text{d}^{-1}$ , or  $\sim 13 \text{ g d}^{-1}$  for lionfish for overcast days obtained by Côté and Maljković (2010), amounting to a consumption rate ( $Q$ ) of  $5109 \text{ g d}^{-1} \text{ ha}^{-1}$ ; resulting in a total  $Q$  of  $186 \text{ g m}^{-2} \text{ y}^{-1}$  and a  $QB^{-1}$  ( $186 \text{ g y}^{-1} \text{ m}^{-2} / 13.36 \text{ g wet weight m}^{-2}$ ) of  $13.95 \text{ y}^{-1}$ . According to Cerino (2010) the daily consumption estimates of lionfish populations may vary greatly with temperature and population density. Consumption estimates increased nearly eight fold from 14 to  $30 \text{ }^\circ\text{C}$ , and increased in direct proportion to population density. A bioenergetic model performed by the same author of a New Province population of

393 lionfish  $\cdot \text{ha}^{-1}$  predicted a daily consumption of 2.124–2.186 kg of prey from June to October when mean temperatures are greater than  $28 \text{ }^\circ\text{C}$ . The cumulative annual consumption was  $680 \text{ kg ha}^{-1}$ . From Cerino's value we calculated a  $QB^{-1} \text{ y}^{-1}$  ratio of  $5.8 \text{ y}^{-1}$  ( $68 \text{ g m}^{-2} \text{ y}^{-1} / 13.36 \text{ g wet weight m}^{-2}$ ).

The  $PB^{-1}$  (production to biomass ratio) value for the lionfish was obtained from Fishbase ( $M \sim PB^{-1}$  per year: 0.41) in the Indo-Pacific (Froese and Pauly, 2010). This value must be taken as an approximation due to the potential change in natural mortality of lionfish in the Caribbean Sea, which can vary, as was the case for the predation rate (Côté and Maljković, 2010). A diet matrix was developed for lionfish species from published data on Bahamian coral reefs (Albins and Hixon, 2008; Morris and Akins, 2009). Each item identified in the diets of lionfish by Morris and Akins (2009) was assigned (based on the percentages obtained) to one of the major functional categories acquired by Opitz (1996).

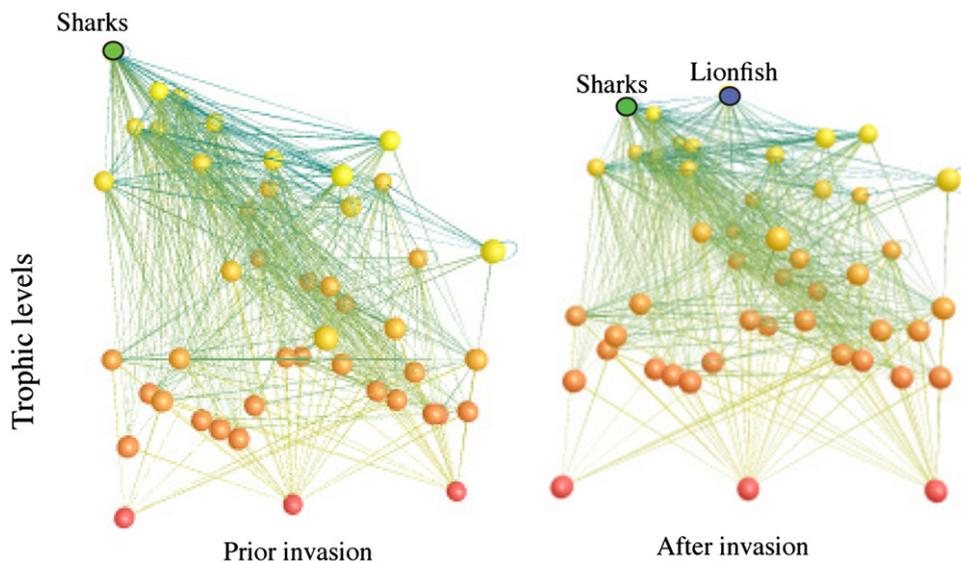
Based on the sources above, we modeled lionfish using an age-structured model nested within the biomass-structured Ecopath model (Walters et al., 2010). The lionfish were thus described with four age stanza (0–1, 2–10, 11–35 and 36+ months). The corresponding mortality rates for the stanza were set to 30, 1.98, 0.62 and  $0.32 \text{ year}^{-1}$ , while the  $QB^{-1} \text{ y}^{-1}$  were to 197, 35, 14 and  $9.3 \text{ y}^{-1}$ , for the four age groups, respectively. The model was initialized with a biomass for the oldest age group of  $0.01 \text{ t km}^{-2}$ . The VBGF growth parameter,  $K$ , was set to  $0.55 \text{ y}^{-1}$ , while the recruitment power was 0.8.

### 3. Results

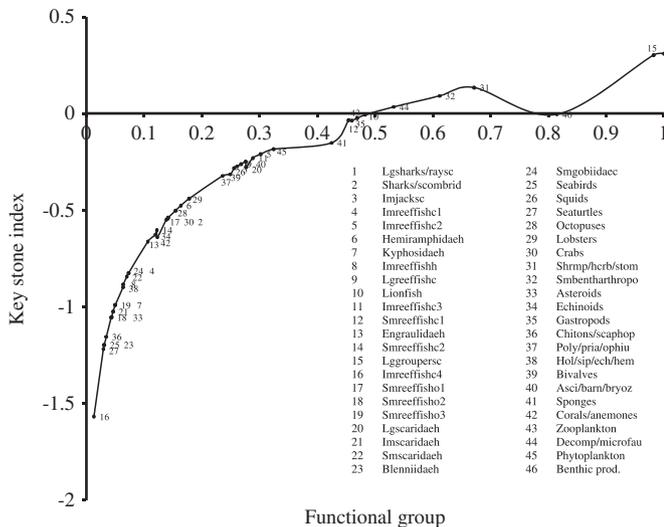
#### 3.1. Food web structure

The lionfish model presented a complex food web structure with a high number of pathways within the food web (Fig. 2). The food web structure changed with the invasion of lionfish appearing as a top predator, above sharks and groupers. Maximum trophic levels were thus associated with sharks, rays, groupers and lionfish.

Sharks and groupers were classified as the most important functional groups in terms of relative total impact and keystone-ness (Fig. 3). Other groups that had the highest relative total impact and keystone-ness were the shrimps, arthropods, decomposers, lionfish and small carnivorous reef fishes. Benthic producers also had a high relative total impact, but due their high biomass it cannot be considered a keystone group.



**Fig. 2.** Food web scheme of the Alacranes Reef system prior to and after invasion by lionfish (blue node). The flow diagram and web structure in the image is organized vertically in function of trophic levels, with node color representing trophic level. Red nodes represent basal species, such as primary producers and detritus; orange nodes represent intermediate species; yellow nodes represent top species or primary predators. Green node represents sharks. Note that sharks represent apex predators prior lionfish invasion while after invasion lionfish become the apex predator. Links characterize the interaction between two nodes. Image produced with FoodWeb3D, written by R.J. Williams and provided by the Pacific Ecoinformatics and Computational Ecology Lab ([www.foodwebs.org](http://www.foodwebs.org), Yoon et al., 2004). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 3.** Keystone index and relative total impact of each functional group of the model.

### 3.2. Invasion simulation

The predation of lionfish produced a negative impact on several fish functional groups of the system (Fig. 4). Lionfish had a direct negative impact on small carnivorous and omnivorous fish, intermediate carnivorous and herbivorous fish, octopuses, lobster, crabs and shrimps. All other functional groups presented a positive response to lionfish interaction, particularly intermediate jacks, reef fishes, hemiramphids, engraulids, large groupers, scarids, blenniids, seabirds, squids, crabs, arthropods, polychaetes, etc. (Fig. 4). Lionfish together with sharks, jacks and groupers had a very strong impact on coral reef fish functional groups. Positive interactions may denote strong links within functional groups and negative interactions may be the result of predation and competition. Positive and negative interactions may be direct and indirect.

The initial removal of lionfish as part of the model initialization resulted at the most in a 3% change in biomass for other groups in the models (and for most the change was much less than 1%). We can thus conclude that the initialization did not have any notable impact on any other groups in the system.

The proliferation of lionfish had ecological impact on many other groups in the model. The initial biomass of fish groups in a near-zero lionfish biomass simulation resulted in increases by about 40–69% in small and intermediate carnivorous and omnivorous coral reef fish (1, 2, 3 and 4) groups (Fig. 4a), and by about 28–35% in sharks, rays, scombrids, jacks, small scarids and gobiids groups, for a period of 15 years (Fig. 4b). The biomass of blenniids, groupers, large scarids, engraulids, small and intermediate scarids declined by about 14–47% (Fig. 4c). With a near-zero lionfish biomass, the great majority of small and intermediate/omnivorous coral reef fish were predicted to be the dominant fish group species while jacks, sharks, rays and scombrids were predicted to be the apex predators. After 15 years, lionfish invasion produced an inverse interaction with all the species groups described above and the ecosystem remained stable for 50 years (Fig. 4a–c).

### 3.3. Eradication and resilience simulation

Once the invasion was established in the ecosystem, we ran different management scenarios to explore the eradication and resilience of lionfish. For this we used four scenarios as described above. In the first scenario we used a very high fishing mortality ( $F=10\text{ y}^{-1}$ ) for all adult lionfish for five years (Fig. 5a), and this

resulted in a drastic and rapid reduction in lionfish abundance. Once fishing pressure was relieved, the lionfish would, however, bounce back within a few years, and eventually reach their carrying capacity again.

In the second scenario, we applied a continuous, lower fishing mortality ( $F=1\text{ y}^{-1}$ ), also on all adult lionfish (Fig. 5b). This resulted in a more gradual reduction in abundance of adult lionfish, while the production of eggs, larvae and juvenile were maintained at a fairly high level for a decade, for then to decline to low levels. The scenario thus indicates that lionfish abundance in theory can be reduced to a very low level, but this calls for a continuous, long-term commitment to control through directed fisheries.

In the last two scenarios we repeated the first two, but fishing was only on the intermediate age group of lionfish spawners (ages 10–35 months)(Fig. 5c). This was done due to observations (NCCOS, 2011, pers. observations) that the largest (and very fecund) lionfish tend to occur at depths where they largely are inaccessible for divers. In these scenarios the strong, but short-term (five years) eradication program (Fig. 5c) as expected would cause the younger spawners to be reduced to a very low level, while the oldest lionfish would only gradually decrease over a ten-year period for then to recover once fisheries were stopped.

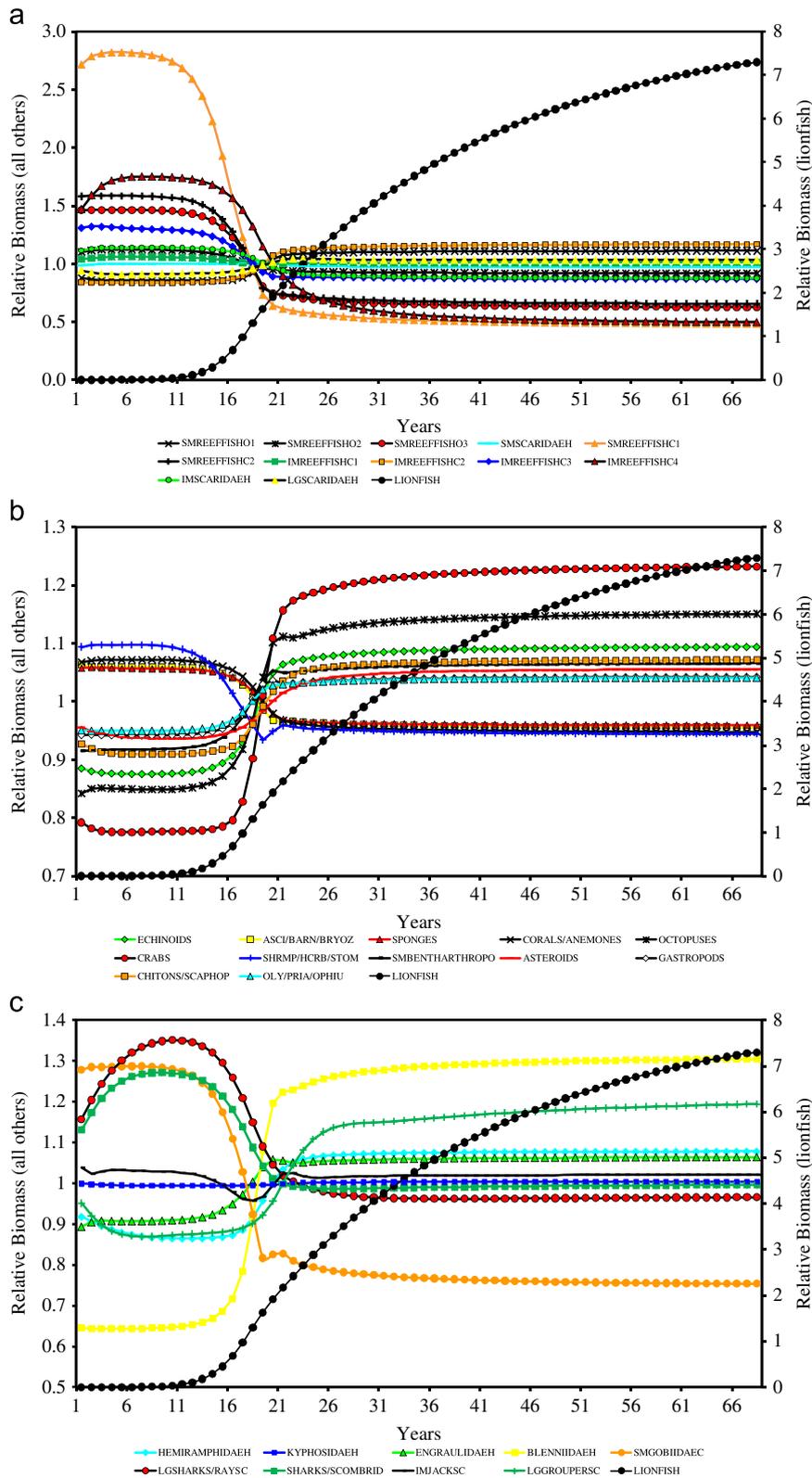
The final scenario applied a continuous, lower ( $F=1\text{ y}^{-1}$ ) fishing mortality to the younger spawners only, and resulted in a gradual reduction of the biomass of the spawners, but to a level considerably higher than if all adults were fished (Fig. 5d).

## 4. Discussion

Our modeling exercise suggests that lionfish may have a strong impact on the magnitude of biomasses and fluxes in Caribbean coral reef food webs. Small and intermediate carnivorous–omnivorous fish showed strong decreases in biomass following lionfish invasion (Fig. 4a–c). The change in biomass (Fig. 4a–c) and fluxes (Fig. 2) in the Alacranes Reef food web model is consistent with that observed in other aquatic ecosystems (Moyle and Light, 1996a,b; Hovius et al., 2007; Miller et al., 2010; Zambrano et al., 2010). The model suggests that lionfish can impact the ecosystem in different ways: by releasing competition and producing greater predation mortality among species (Pine et al., 2007), and by producing direct competition for fish resources. The slight increase in some small and intermediate carnivorous and omnivorous fish, as well as scarids, followed by the increase in biomass of the lionfish, demonstrates possible competition for resources among these different groups of fish. The decrease in large sharks, sharks, rays, jacks, and scombrids followed by the increase in lionfish biomass demonstrates the potential competition for resources among these groups (Fig. 4a–c).

Invaders spread rapidly and have a strong impact on species by displacing or preying on them (Moyle and Light, 1996a,b). Invaders can also induce large indirect changes to communities through direct predation effects (Hovius et al., 2007). Perhaps among the most important potential indirect food web effects of the lionfish invasion is the decrease in large and small sharks, turtles and corals (Fig. 4a–c). The indirect effects of lionfish as mediated through the food web are unknown in the Caribbean, but our results suggest that they are likely to be as extreme as the direct impacts.

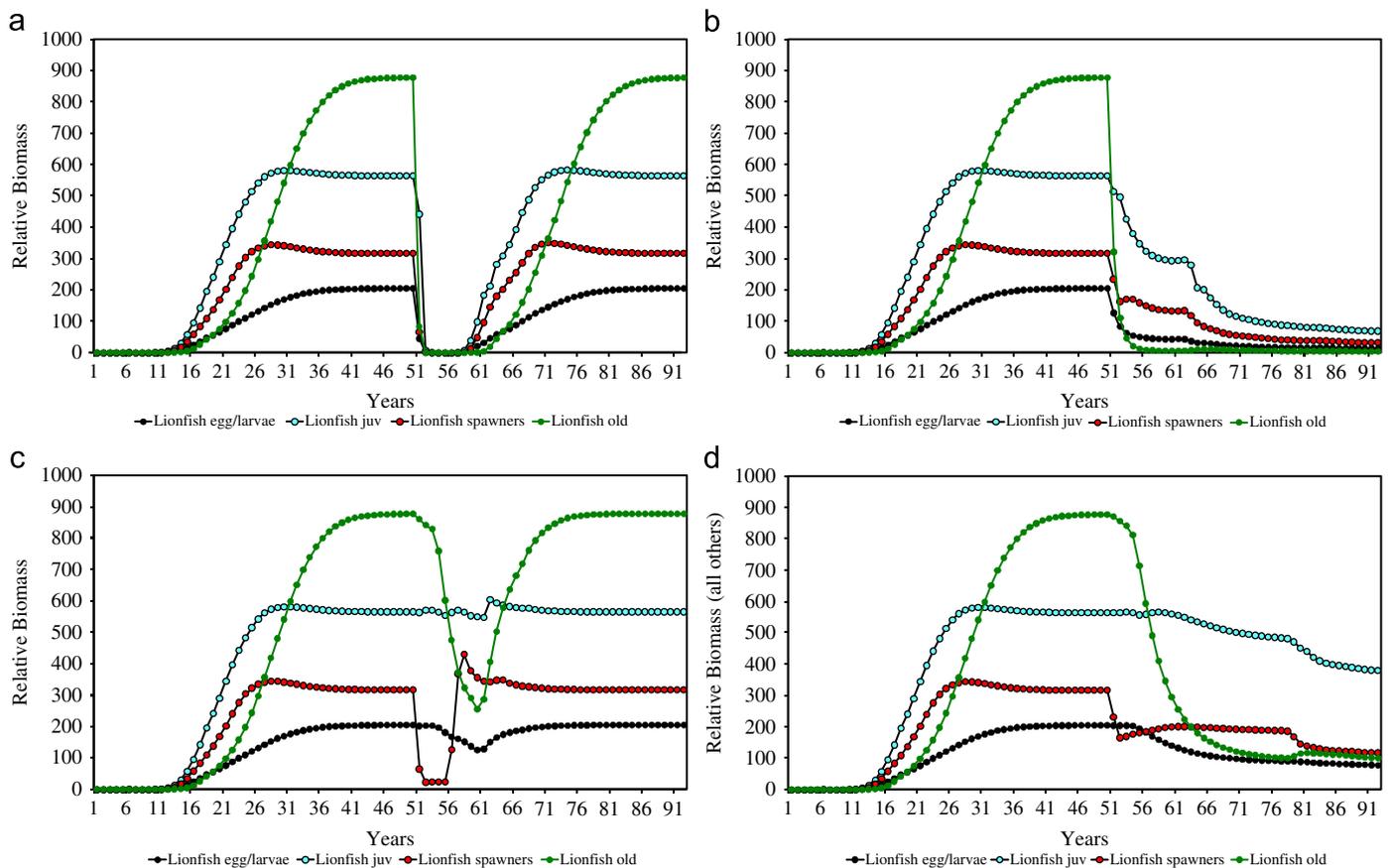
Piscivores are the most successful fish invaders (Moyle and Light, 1996a,b). This pattern is based on observations in different aquatic systems that prey species are naïve in terms of recognizing the predator and predation style of the predator (Moyle and Light, 1996a). Another important aspect is that in the same way,



**Fig. 4.** Simulation responses to the invasion of lionfish in a coral reef system by small and intermediate coral reef fish species (a), other coral reef fishes (b) and birds, turtles and macroinvertebrate trophic groups (c) over a 50-year period. Responses are measured as the changes in the relative biomass of the various functional groups. The initial lionfish biomass in this simulation is near-zero. See Appendix A for a description of the coral reef fish species names that compose each functional group.

native piscivorous may not be capable of recognizing the lifestyle of the new piscivorous invaders, reducing the possibilities of being preyed upon. These two characteristics are critical in the lionfish invasion within Atlantic coral reef ecosystems.

Few natural predators of lionfish are known in the Caribbean, but some documented evidence exists that demonstrates that lionfish are being preyed upon by groupers (Maljković and Van Leeuwen, 2008; Mumby et al., 2011). In our model, groupers



**Fig. 5.** Simulation responses by egg/larvae, juvenile, spawners and adult lionfish to attempt their eradication through intensive exploitation over a 91-year period: (a) applying a fishing mortality of  $10 \text{ y}^{-1}$  on all adult lionfish for five years; (b) applying a fishing mortality of  $1 \text{ y}^{-1}$  on all adult lionfish continuously; (c) applying a fishing mortality of  $10 \text{ y}^{-1}$  on the smaller spawners (10–35 months) for five years; (d) applying a fishing mortality of  $1 \text{ y}^{-1}$  on the smaller spawners (10–35 months) continuously.

increased in a similar way to lionfish due to the increased availability of lionfish as prey. Although there is little evidence of such relationship interactions between these two groups, groupers seem to benefit from lionfish increases. In the case of Alacranes Reef, despite the exploitation of groupers and sharks, they already play an important role in terms of their overall impact, since they strongly influence the biomasses of different functional groups (Fig. 3). Nevertheless, this is not the case for the majority of the coral reefs in the Caribbean and Gulf of Mexico because most piscivorous predators in the Atlantic coral reefs are overfished, especially sharks (Ward-Paige et al., 2010) and groupers; thus lionfish are believed to have few natural predators. Perhaps this is one of the reasons for the rapid dispersion of lionfish throughout the Caribbean and the Gulf of Mexico. Following groupers and sharks, lionfish had an important impact on the Alacranes coral reef food web model. The effect of a predator invasion can cascade through the entire ecosystem altering ecosystem processes (Carpenter et al., 1985; Moyle and Light, 1996a) as has been demonstrated by the model presented here.

The lesson from our eradication scenarios is that such programs will only be successful if all ages of the spawners can be targeted and if the program is long-term. A short eradication program is not likely to be successful. For this prediction to change, we would need to see the ecosystem develop alternate methods of control, e.g. through a build-up of potential predators, such as, e.g., large groupers (Mumby et al., 2011).

The lionfish has been documented throughout the Caribbean and Gulf of Mexico indicating that the lionfish population may be

highly connected and a continuous population, reducing the possibilities of complete eradication. Another important factor that reduces the possibilities of lionfish eradication is its depth distribution, as explored through our two last eradication scenarios. Different policy options could be applied to maintain the lionfish population to levels of low density in the Atlantic. One possible natural strategy is to restore and protect the stock of piscivorous fishes such as grouper, sharks, barracudas, etc., releasing pressure on native coral reef species (Mumby et al., 2011). Our modeling suggests that with the present abundance levels the predation pressure of piscivorous may not be intensive enough to decrease lionfish densities. There are some examples of invasive piscivorous in other ecosystems where a maintenance control of populations has been opted for rather than allowing populations to expand to large levels, and then attempting to reduce them (Lampo and De Leo, 1998; Pine et al., 2007). Aquatic plant managers have been using maintenance controls for invasive aquatic plant species rather than complete eradication (Pieterse and Murphy, 1990). This option has also been proposed to manage the invasion of a piscivorous fish in a coastal riverine fish community (Pine et al., 2007). These authors suggest that using maintenance control techniques keeps populations at low densities and reduces the time and financial resources required. Hence it is possible to establish local maintenance control programs of the lionfish population in conjunction with management and restoration strategies of piscivorous stocks.

Although our model suggests that reducing the lionfish through increased exploitation can directly and indirectly relax the pressure on the native species, there are still a number of

points that need to be considered. The main issue with ecosystem models, as with most models, is that they are difficult to validate, which brings into question their usefulness in the prediction of ecosystem responses and the management of resources (Pine et al., 2007). The predictions of our model are consistent with empirical observations made in other ecosystems: piscivorous invaders are most likely altering invaded communities, and their impact can cascade through the entire ecosystem (Carpenter et al., 1985; Moyle and Light, 1996a). At the theoretical level our model predictions are consistent with other models including piscivorous invaders in that they may suppress native fish community biomass in different proportions through both competition and predatory interactions (Pine et al., 2007). Even though our Ecopath model was validated to meet certain standardization requirements on the basis of PREBAL, certain parameterisation gaps exist, particularly for the lionfish. Much of the investigation performed on this species has been generated in the Bahamas, and we do not know how the rates of growth and predation, the values of biomass or diet, etc. vary throughout the Atlantic. Similarly, no information exists on the impact of fishery exploitation. It is true that a great concern with ecosystem models is that we will never have enough information to generate a “perfect” model, yet they may be useful (Pine et al., 2007). In coral reefs, this is evident. Ecopath was originally constructed to resolve questions concerning the productivity of coral reefs (Polovina, 1984). This approach and software contains information that can be integrated from different sources or be used to estimate missing information. Our observations of fish obtained directly from the field offer us estimations of the minimum observed biomass, in this case in the reef habitat, which in conjunction with bibliographic sources made it possible to construct a model that meets the basic balance requirements (Ma et al., 2010). This suggests that we are not overestimating biomass values throughout the food web.

The results obtained in the model highlight the need for immediate management actions to control lionfish populations. It is unlikely that it will be possible to eradicate this piscivorous invader from the reef systems of the Atlantic, but the model suggests that with an intensive, long term management control, the population of this species could probably be controlled.

## 5. Conclusions

Our results have important implications since they show that the impact of lionfish on Caribbean coral reef food webs may be extensive and have a very strong influence on coral reef fish communities and macroinvertebrates such as corals, shrimps, lobsters and octopuses. Lionfish may also have multiple indirect effects on the functional groups of coral reef fish by increasing or decreasing their biomass. Direct impacts were mainly shown by small carnivorous and herbivorous reef fish, which, based on our results, are keystone species of the Alacranes Reef ecosystem. The impact on these functional groups could be enormous since the model suggests an increase from 10 to 65% in small reef fish biomass in absence of lionfish. Without a maintenance control, lionfish may have a considerable impact on Caribbean coral reef food webs.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.envres.2011.07.008.

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