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INVASION NOTE

A stage-based matrix population model of invasive lionfish with implications for control

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Abstract The rapid invasion of lionfish into the Western North Atlantic and Caribbean will undoubtedly affect native reef fishes via processes such as trophic disruption and niche takeover, yet little is known about the dynamics of this invasion. We constructed a stage-based, matrix population model in which matrix elements were comprised of lower-level parameters. Lionfish vital rates were estimated from existing literature and from new field and laboratory studies. Sensitivity analysis of lower-level parameters revealed that population growth rate is most influenced by larval mortality; elasticity analysis of the matrix indicated strong influence of the adult and juvenile survival elements. Based on this model, approximately 27% of an invading adult lionfish population would have to be removed monthly for abundance to decrease. Hierarchical modeling indicated that this point estimate falls within a broad uncertainty interval which could result from imprecise estimates of life-history parameters. The model demonstrated that sustained removal efforts could be substantially more effective by targeting juveniles as well as adults.

Keywords Lionfish · *Pterois* · Matrix model · Invasive · Nonindigenous

Introduction

Invasive lionfish, *Pterois miles* and *P. volitans*, are now established along the southeast coast of the United States and parts of the Caribbean (Morris et al. 2009; Schofield et al. 2009). Lionfish represent the first marine reef fish invader to this region and are thought to have been released intentionally by aquarists over many years (Courtenay 1995; Morris and Whitfield 2009). The rapidity of the lionfish invasion in the Western North Atlantic and Caribbean is unprecedented among marine fishes. Not only are invasive lionfish now widely distributed geographically, in some locations that are one of the most abundant reef fishes (Green and Côté 2009).

Lionfish have the potential to significantly affect the trophic structure of reef communities (Albins and Hixon 2008). As generalist piscivores (Morris and Akins 2009), lionfish could compete with native reef

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fishes of the snapper-grouper complex, a group of fishes that have been heavily exploited (Coleman et al. 1999). This competition could hamper current efforts to rebuild overfished stocks.

To better understand the dynamics of this invasion, we synthesized existing information on lionfish, including data not previously published, and constructed a stage-based, matrix population model. Elements of the matrix were estimated from life-history characteristics such as fecundity and instantaneous mortality rates (i.e., lower-level parameters). Our specific objectives were to assess the sensitivity of lionfish population growth rate (λ) to matrix elements and to lower-level parameters. We also assessed the magnitude of control efforts required to reduce λ below the level required to sustain an invading population of lionfish.

Methods

Matrix model

A stage-based, matrix model (Lefkovitch 1965; Crouse et al. 1987; Caswell 2001) of female lionfish was constructed using three life stages: larvae (L), juveniles (J), and adults (A). Lionfish vital rates were assessed by stage rather than age because of the lack of ageing studies. The matrix model accounts for survival, growth, and reproduction to describe monthly transitions among life stages,

$$\begin{bmatrix} L_{t+1} \\ J_{t+1} \\ A_{t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & R_A \\ G_L & P_J & 0 \\ 0 & G_J & P_A \end{bmatrix} \begin{bmatrix} L_t \\ J_t \\ A_t \end{bmatrix} \qquad (1)$$

where G is the probability of surviving and growing to the next stage; P is the probability of surviving and remaining in the same stage; and R is reproductive contribution. All model runs were performed using a 1-month time-step based on the shortest stage duration, i.e., the larval stage.

Parameter values

To calculate the matrix elements (Table 1), we obtained estimates of vital rates from existing literature and from new field and laboratory studies (Table 2). The transition of larvae to juveniles (G_L) depended on larval mortality rate and duration of the larval stage. The instantaneous larval mortality (M_L) was the median larval mortality rate from McGurk (1987) for pelagic fish larvae, conditional on mean water temperature $\geq$10°C. We used the value of 10°C as the cutoff, because it represents the chronic lethal minimum for lionfish (Kimball et al. 2004). Larval duration (D_L) was determined through analysis of settlement marks and daily increments in the otoliths of juvenile lionfish collected in the Bahamas (Ahrenholz and Morris 2010).

Table 1 Matrix elements, values, computation, and elasticities

Element	Value	Computation	Elasticity
P_A	0.949	e^{-M_A}	0.508
P_J	0.777	$(11/12)e^{-M_J}$	0.210
G_L	0.00003	$e^{-M_L D_L}$	0.094
G_J	0.071	$(1/12)e^{-M_J}$	0.094
R_A	35,315	$\rho f e^{-M_E D_E}$	0.094

See Table 2 for definitions of parameters used in computations

Juvenile transition rates (P_J and G_J) depended on the juvenile mortality and maturation rates. Instantaneous juvenile mortality (M_J) was computed from the weight-mortality function provided by Lorenzen (1996). To derive a typical juvenile mortality estimate, we used the mid-point of estimated weights from a weight-length log-linear regression of field collected specimens from 20 to 174 mm total length (TL). The lower limit (20 mm TL) is the smallest juvenile observed, and the upper limit (174 mm TL) is the size at 50% maturity (Morris 2009). Lionfish mature at about 1-year old (Ahrenholz and Morris 2010), and thus 1/12 of surviving juveniles transitioned monthly to the adult stage.

Adult survivorship (P_A) depended on the instantaneous adult mortality rate (M_A), computed from the Lorenzen (1996) weight-mortality function. The mid-point of estimated weights from a weight-length log-linear regression of field collected specimens from 175 to 390 mm total length (maximum size in field collections) was used to obtain a typical adult weight, and thus a typical adult mortality value.

Adult reproductive contribution (R_A) depended on egg mortality, egg production, and sex ratio. The instantaneous egg mortality (M_E) was the median egg mortality rate reported by McGurk (1987) for pelagic eggs of fishes, conditional on mean water temperature $\geq$10°C. Egg duration (D_E) was assumed to be similar

Table 2 Values of lower-level parameters, their sources, and the sensitivity of λ to each of them

Parameter	Value	Units	Reference	Sensitivity
Larval mortality M_L (G_L)	0.350	days^{-1}	McGurk (1987)	-3.17
Adult mortality M_A (P_A)	0.052	months^{-1}	Lorenzen (1996)	-0.57
Juvenile mortality M_J (P_J, G_J)	0.165	months^{-1}	Lorenzen (1996)	-0.34
Proportion female ρ (R_A)	46%	–	Ahrenholz and Morris (2010)	0.23
Larval duration D_L (G_L)	30	days	Ahrenholz and Morris (2010)	-0.04
Egg mortality M_E (R_A)	0.310	days^{-1}	McGurk (1987)	-7.50×10^{-7}
Fecundity f (R_A)	194,577	Eggs months^{-1} female^{-1}	Morris (2009)	5.43×10^{-7}
Egg duration D_E (R_A)	3	days	Morris (2009)	-7.75×10^{-8}

The matrix element in which the lower-level parameter was used is in parentheses. Mortality terms are expressed as instantaneous rates in units of per month or per day

to that of most teleosts with pelagic eggs (J. Morris, personal observation). Batch fecundity estimate (24,630 eggs per batch) was estimated by counting the number of eggs in newly released egg balls from lionfish held in captivity (Morris 2009). Based on gonadal histology of specimens collected from the Atlantic ($n = 1{,}674$), lionfish spawn throughout the year about every 3.85 days, and the proportion of female lionfish (ρ) is 46% (Morris 2009). Monthly fecundity (f) was derived by multiplying batch fecundity by the number of spawning events per month (7.9 spawns per month).

Sensitivity and elasticity

Population growth rate (λ) was calculated as the dominant eigenvalue of the matrix model (Caswell 2001). Sensitivities of λ to matrix elements (a_{ij}) were computed from partial derivatives,

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \boldsymbol{w}, \boldsymbol{v} \rangle} \tag{2}$$

where $\boldsymbol{v}$ is the left eigenvector associated with λ, $\boldsymbol{w}$ is the right eigenvector associated with λ, and $\langle \boldsymbol{w}, \boldsymbol{v} \rangle$ is the scalar product. These sensitivities were subsequently used to compute elasticities of matrix elements and sensitivities of lower-level parameters.

We used standard methods (Caswell 2001) to compute elasticities (e_{ij}) of λ with respect to matrix elements,

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}. \tag{3}$$

Elasticities represent proportional contributions to λ and are often considered easier to interpret than sensitivities, particularly when matrix elements are measured in different units or operate on different scales (e.g., survival and fecundity) (de Kroon et al. 1986).

Sensitivities of λ to lower-level parameters (x) were also investigated. These sensitivity values were computed by application of the chain rule,

$$\frac{\partial \lambda}{\partial x} = \sum_{ij} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x} \tag{4}$$

as described by Caswell (2001).

Population control

To examine possible control of an invading lionfish population in its new environment, we systematically varied matrix elements P_J and P_A (the two elements found to have the highest values of elasticity), and recomputed λ as well as elasticities. We further identified a threshold adult survivorship, below which the population could not sustain itself ($\lambda < 1$). To estimate additional mortality required to achieve $\lambda < 1$, we applied the Baranov catch equation (Baranov 1918);

$$\frac{C}{N} = \frac{F}{Z}\left(1 - e^{-Z}\right) \tag{5}$$

where C is the catch (fishing removals), N represents abundance of adult lionfish, F is the instantaneous fishing mortality, and Z is the total instantaneous mortality ($F + M_A$). The ratio C/N represents the proportion of adults removed per month (i.e., the exploitation rate), as might be applied in an eradication program. This ratio was applied over a range of similarly computed exploitation rates of juvenile lionfish.

Uncertainty in the estimate of catch required for population control was investigated using a hierarchical modeling approach (Jiao et al. 2009). We generated $n = 1{,}000$ matrices in which each lower-level parameter was drawn independently from a normal distribution with mean equal to the original point estimate and variance determined by a coefficient of variation (CV) of 5%. The distributions were truncated to exclude outliers beyond the 95% confidence interval. Matrices were then used to compute 1,000 values of λ over a range of fishing intensity. The choice of CV = 5% was arbitrary, as no empirical estimates of variance were available. Thus these results do not provide actual confidence intervals on λ or catch; rather, they illustrate sensitivity to misspecification of parameter values.

Results

Lionfish growth rate was $\lambda = 1.12$, with the matrix elements P_A and P_J exhibiting the highest values of elasticity (Table 1; Fig. 1a). Analysis of lower-level parameters indicated that λ was most sensitive to larval mortality, M_L (Table 2).

Given the point estimate of P_J, values of $P_A < 0.68$ were required to achieve negative population growth, i.e., $\lambda < 1$ (Fig. 1a). If P_J were also reduced, negative growth could be achieved with more modest reduction of adult survivorship (Fig. 1a). For example, a simultaneous reduction of ~15% in P_J and P_A would lead to $\lambda < 1$. Elasticity of P_A decreased with reductions in P_A but increased with reductions in P_J (Fig. 1b). Similarly, elasticity of P_J decreased with reductions in P_J but increased with reductions in P_A (Fig. 1c). Together, these results indicate that an eradication program targeting juveniles and adults jointly would be far more effective than one targeting either life stage in isolation.

Assuming that an additional source of mortality could be fishing or removal efforts, approximately 27% of the adult lionfish population would have to be harvested monthly to reduce λ below a sustainable level (Fig. 2a). This point estimate, however, fell within a broad uncertainty interval that could result from imprecise estimates of life-history parameters (Fig. 2a). The same result of negative population growth could be achieved with lower than 27% adult removal, if juveniles were simultaneously targeted (Fig. 2b).

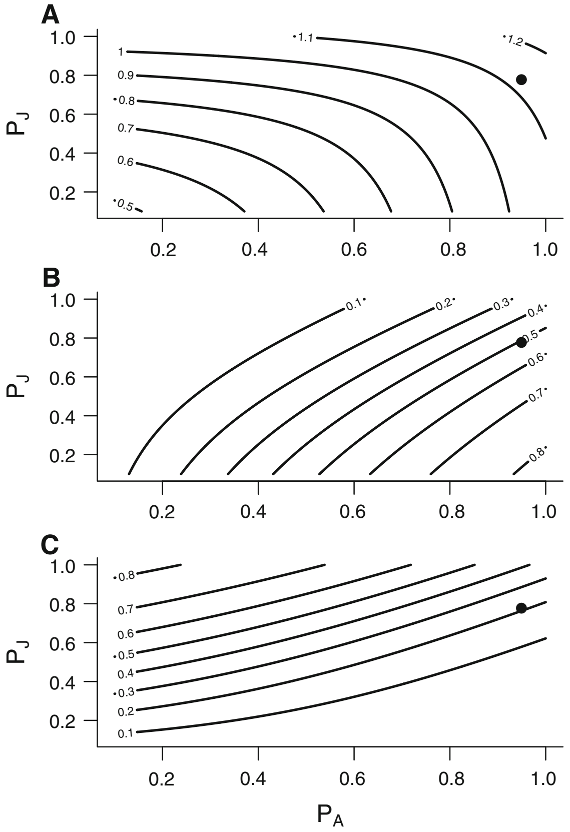

Fig. 1 **a** Population growth rate λ, **b** elasticity of P_A, and **c** elasticity of P_J for theoretical values of matrix elements P_J and P_A. In *each panel*, the *solid circle* represents baseline estimates from the matrix model of Table 1

Discussion

Given that lionfish reproduce monthly throughout the year, the time that they survive as adults affects λ substantially. Our model simulations demonstrate the magnitude of removal efforts (e.g., fishing mortality) required to reverse lionfish population growth under density independence, as may occur during the early phase of the invasion. For expansive regions of the lionfish's new habitat, such as the hardbottom communities off the southeast US coast, monthly removal of 27% of adult lionfish might not be feasible, or else would require substantial resources to achieve. For smaller regions, however, where lionfish habitat is more distinctly defined (e.g., near some Caribbean islands), lionfish control using fishing mortality and targeted removal could be an effective management approach. Exploiting lionfish as food for humans, as in

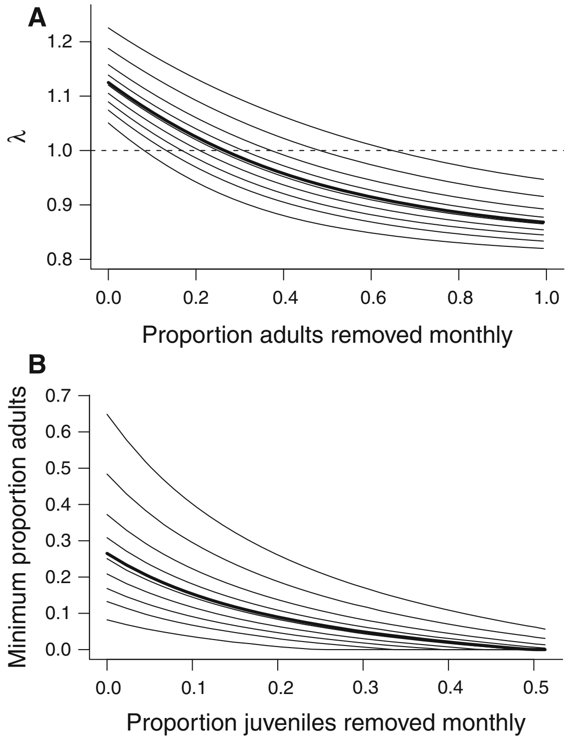

Fig. 2 **a** Population growth rate λ as a function of the proportion adults removed monthly, assuming no juveniles removed. **b** The minimum proportion adults required for removals to achieve negative population growth rate, as a function of proportion juveniles removed. Thus, the horizontal slice at $\lambda = 1$ in *panel* **a** would correspond to the *vertical slice* at proportion juveniles removed of 0.0 in *panel* **b**. In *both panels*, *thick curves* represents baseline estimates, and *thin curves* represent 10th, 20th, …, 90th percentiles from $n = 1{,}000$ stochastic variations of the baseline model

its native range, could provide a significant source of sustained mortality needed to reduce lionfish populations, especially in otherwise protected areas.

The point estimate for lionfish control—monthly removal of 27% of adults—depends on the interacting effects of all parameters. In our analyses, as adult survival was decreased, the elasticity of adult survival also decreased, indicating reduced efficiency of removal efforts. However, if juveniles were simultaneously targeted, efficiency could be maintained even with reduced (i.e., lower than 27%) exploitation rate of adults.

The width of our uncertainty intervals surrounding exploitation rates relied on the assumption of $CV = 0.05$ of lower-level parameter estimates. In truth, precision of those estimates is unknown and undoubtedly differs across parameters. As we learn more about lionfish life-history parameters, uncertainty intervals surrounding exploitation rates can become empirically based.

Lionfish population growth was most sensitive to the lower-level parameter of larval mortality. Because natural mortality is not reported for any larval tropical scorpaenid, we assumed that lionfish larval mortality is similar to that reported for many other pelagic marine fishes. This assumption could result in an overestimate. For example, scorpaenid larvae are defended by large cranial spines possibly resulting in relatively low larval predation mortality. Similarly, juvenile and adult natural mortality values derived from Lorenzen's meta-analysis (Lorenzen 1996) could be overestimates. Lionfish are novel prey to native predators of the Atlantic and Caribbean and are equipped with venomous spines for defense, thus predation on lionfish may be low compared with native reef fishes (Morris 2009). For these reasons, the estimated fishing effort required to reduce lionfish λ during the invasion could be underestimated.

Modeling lionfish demographics provides a valuable perspective on how life-history traits have facilitated the rapid establishment of lionfish in the Atlantic and Caribbean. Although the assumption of density independence is rarely met, it may be a reasonable approximation during the early phases of an invasion marked by exponential population growth. Often, sensitivity and elasticity analyses are considered to be the most practical results from matrix models (Caswell 2001). The high sensitivity of λ to lower-level mortality parameters (M_L, M_J, and M_A) indicates that relatively small adjustments in mortality can result in large changes in population growth, and thus lionfish-specific estimates of mortality would likely improve model results. The relatively low sensitivity of λ to the other lower-level parameters (ρ, D_L, M_E, F, and D_E) indicates that error in these parameter estimates would have little effect on the results. With further empirical studies and improved parameter estimates, more sophisticated modeling approaches will become possible.

The lionfish invasion provides a stark example of the ongoing need for prevention, early detection, and rapid response to marine invaders. This study demonstrates that extraordinary resources may be required to reduce or eradicate invasive fishes once established in marine systems.

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References

Ahrenholz D, Morris JA Jr (2010) Larval duration of the lionfish, *Pterois volitans* along the Bahamian Archipelago. Environ Biol Fish. doi:10.1007/s10641-010-9647-4

Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish (*Pterois volitans*) reduce recruitment of Atlantic coral-reef fishes. Mar Ecol Prog Ser 367:233–238

Baranov FI (1918) On the question of the biological basis of fisheries. Nauchn Issled Ikhtiolog Inst Izvest 1:81–128 (translated from Russian by W.E. Ricker)

Caswell H (2001) Matrix population models: constraints, analysis and interpretation, vol 2. Sinauer Associates, Sunderland

Coleman FC, Koenig CC, Eklund A, Grimes CB (1999) Management and conservation of temperate reef fishes in the grouper-snapper complex of the Southeastern United States. In: Musick JA (ed) Life in the slow lane. American Fisheries Society, Bethesda, pp 233–242

Courtenay WR (1995) Marine fish introductions in southeastern Florida. Am Fish Soc Introd Fish Sect Newsl 14:2–3

Crouse DT, Crowder LB, Caswell H (1987) A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423

de Kroon H, Plaisier A, van Groenendael J, Caswell H (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427–1431

Green SJ, Côté IM (2009) Record densities of Indo-Pacific lionfish on Bahamian coral Reefs. Coral Reefs 28:107

Jiao Y, Lapointe NWR, Angermeier PR, Murphy BR (2009) Hierarchical demographic approaches for assessing invasion dynamics of non-indigenous species: an example using northern snakehead (*Channa argus*). Ecol Modell 220:1681–1689

Kimball ME, Miller JM, Whitfield PE, Hare JA (2004) Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. Mar Ecol Prog Ser 283:269–278

Lefkovitch LP (1965) The study of population growth in organisms grouped by stages. Biometrics 21:1–18

Lorenzen K (1996) The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. J Fish Biol 49:627–647

McGurk MD (1987) Natural mortality and spatial patchiness: reply to Gulland. Mar Ecol Prog Ser 39:201–206

Morris JA Jr (2009) The biology and ecology of invasive Indo-Pacific lionfish. Dissertation, North Carolina State University, Raleigh, NC

Morris JA Jr, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. Environ Biol Fish 86:389–398

Morris JA Jr, Whitfield PE (2009) Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA Tech Memo NOS NCCOS 99, 57 pp

Morris JA Jr, Akins JL, Barse A, Cerino D, Freshwater DW, Green SJ, Muñoz RC, Paris C, Whitfield PE (2009) Biology and ecology of the invasive lionfishes, *Pterois miles* and *Pterois volitans*. Proc Gulf Caribb Fish Inst 29:409–414

Schofield PJ, Morris JA Jr, Langston JL, Fuller PL (2009). *Pterois miles/volitans* FactSheet. USGS Nonindigenous Aquatic Species Database, Gainesville, FL. http://nas.er.usgs.gov/taxgroup/fish/lionfishdistribution.htm. Cited 15 Sept 2009