Letters to the Editor

Linking removal targets to the ecological effects of invaders: a predictive model and field test

To the Editor:

Green et al. (2014) presented a model of Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) predation that can be used to estimate target densities for the control of invasive lionfish on Western Atlantic coral reefs. The model produces estimates of two annual, site-specific rates: biomass production by lionfish prey, $\bar{P}$ (g·ha^{-1}·yr^{-1}), and the rate of prey consumption by lionfish, $\bar{C}$ (g·ha^{-1}·yr^{-1}). The difference between the two is the net rate of biomass production ($\bar{N}_p$) by the prey fish assemblage at a site. The model then assumes that native prey fish biomass will decline if lionfish consume prey at a rate that exceeds the rate of prey production (i.e., $\bar{N}_p < 0$). The lionfish target density can then be computed as that density under which prey consumption by lionfish equals production of prey biomass.

Unfortunately, the authors seem to have selected incorrect values for some of the coefficients in their Eq. 4, which is used to estimate the rate of prey fish production $\bar{P}$ by an individual prey fish (the site-specific $\bar{P}$ corresponds to the summation of all individual $\bar{P}$ in the site; see Eq. 2 in the article). In Eq. 4, the mortality rate Z scales as an allometric function of body mass B with constants j and q, which approximates the P/B ratio widely used in fisheries ecology, that is, the ratio of production rate of biomass (g·ha^{-1}·yr^{-1}) to standing biomass (g ≠ ha)

$$Z \approx \frac{P}{B} = \frac{jB^q}{e^{E/kT}}. \tag{4}$$

The denominator in the right-hand side of Eq. 4 describes the effect of environmental temperature on prey fish production rates, where E is the activation energy, k is Boltzmann's constant, and T is ambient water temperature in degrees Kelvin. This term was introduced by Brown et al. (2004) as a temperature-correcting factor for their metabolic theory of ecology.

Green et al. (2014) assume a value of −0.25 (not 0.25, as shown erroneously in Table 1) for the scaling exponent q, as empirically validated by Brown et al. (2004), while the value of j is assumed to be 3.08, as

validated by Lorenzen (1996). In fact, Lorenzen had also estimated q for marine tropical fish taxa as −0.21 (Table II in Lorenzen). The problem is that Lorenzen estimated both parameters j and q in the context of the model $Z = jB^q$, that is, disregarding the correcting factor $e^{E/kT}$ introduced by Brown et al. (2004). Because E, k, and T are assumed to be 0.65 eV, 8.617 × 10^{-5} eV≠K, and 299.25 K (26°C), respectively, the annual mortality rates Z computed from Eq. 4 are unrealistically low. For example, the annual mortality rate for prey fish measuring 7 cm and weighing approximately 8.14 g turns out to be 2.041 × 10^{-11} (zero, in practical terms), while Lorenzen's equation indicates that mortality rate Z would be 1.98, implying an annual survival of 13.8%. Remember here that Z is the instantaneous rate of mortality in a model of exponential decay and not the probability of dying as erroneously indicated by Green et al. (2014:1313).

It is unclear how Green et al. (2014) were able to compute the lionfish target densities ($\bar{d}$), given the extremely low mortality rates for prey fish suggested by the coefficient values summarized in their Table 1. It is important to understand how these densities were derived because the model could potentially be used to estimate site-specific target densities across the Caribbean. In fact, Hackerott (2014) recommends discontinuing manual removal of lionfish in Belize, as lionfish abundance is currently below the target densities estimated by Green et al. (2014).

It is also important to note that the Brown et al. (2004) correcting factor was intended to adjust the mortality–biomass relationship by accounting for differences in ambient water temperatures across latitudes. However, Lorenzen (1996) explicitly addressed the effects of temperature by developing separate estimates of j and q for tropical, temperate, and polar regions. Because the ecosystems affected by the invasive lionfish are predominately tropical, the corresponding set of coefficients reported by Lorenzen (3.08 and −0.21) should suffice to estimate rates of prey mortality and prey fish production. The correcting factor $e^{E/kT}$ is then superfluous.

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Response to Valderrama and Fields: effect of temperature on biomass production in models of invasive lionfish control

To the Editor:

The aim of our study "Linking removal targets to the ecological effects of invaders: a predictive model and field test" was to provide a general method for estimating target densities to guide the control of predatory invasive lionfish (*Pterois volitans* and *P. miles*) across their Western Atlantic range, as Valderrama and Fields (2015, hereafter VF) acknowledge. However, contrary to the assertion of VF, management of the invasion is not limited to tropical regions; invasive lionfish are now distributed across a wide range of habitats varying in temperature from 10°C to more than 30°C (U.S. Geological Survey Nonindigenous Aquatic Species Database, *available online*).[1] In addition, lionfish forage at temperatures as low as 16°C (Kimball et al. 2004), making it crucial to explicitly account for the effects of temperature on both rates of prey consumption by lionfish and rates of biomass production by their prey base. Here, we (1) clarify the parameter values used in the analyses of Green et al. (2014) to estimate rates of biomass production by fishes consumed by invasive lionfish (Table 1); (2) compare estimates from our modeling approach with the alternative method for estimating biomass production proposed by VF (Table 2); and (3) evaluate the consequences for target densities used in management (Table 3). We find that the VF model greatly overestimates fish community biomass production below a narrow range of warm temperatures, resulting

[1] http://nas2.er.usgs.gov/viewer/omap.aspx?SpeciesID=963

TABLE 1. Corrected parameter values for Eq. 4 and 6 in Green et al. (2014).

Equation	Parameter
4	$j = e^{26.25}$ (Brown et al. 2004)
4	$q = -0.25$ (Brown et al. 2004)
6	Replace 0.006 with 9×10^{-22} (value for T in Kelvin, with a log normal distribution)

in less conservative (i.e., higher) targets for lionfish control, which increases the risk of ecological impacts due to overconsumption of native prey. This is because the VF model relies on an equation from Lorenzen (1996) that does not explicitly characterize the effects of temperature on production. Consequently, we recommend that readers continue to use the method outlined in Eq. 9 here and in Green et al. (2014), which allows for the explicit incorporation of local environmental temperature. We elaborate further in the following sections.

Testing alternative approaches to estimating prey fish biomass production

Green et al. (2014) incorporated the effect of temperature on both prey biomass production and lionfish biomass consumption rates into their estimates of threshold densities for lionfish control. Specifically, individual prey fish biomass production (*P*) was estimated via the relationship

$$Z \approx \frac{P}{B} = \frac{jB^q}{e^{E/kT}} \qquad \text{(Eq. 4 in Green et al. 2014)}$$

where the scaling exponent (*q*) has been theoretically proposed as −0.25, and *j* empirically validated as $e^{26.25}$ (Brown et al. 2004; see Table 1). The equation $e^{E/kT}$ describes the effect of environmental temperature on prey fish production rates, where *E* is the activation energy, *k* Boltzmann's constant, and *T* is ambient water temperature, expressed in degrees Kelvin. The body mass (*B*) of each individual *v* of prey fish species *i* (B_v) was estimated using the allometric scaling function

$$B = a_i L^{b_i}. \qquad \text{(Eq. 5 in Green et al. 2014)}$$

TABLE 2. Individual prey fish biomass production rates (g·individual⁻¹·yr⁻¹) estimated for a range of fish body sizes (via Eq. 4.1), and body sizes and temperatures (via Eq. 4).

	Biomass production (g·individual⁻¹·yr⁻¹)			
	Eq. 4			
Fish mass (g)	296.15 K	299.15 K	302.15 K	Eq. 4.1
0.82	1.9	2.4	3.1	2.6
4.10	6.3	8.1	10.4	9.4
6.847	8.8	11.4	14.7	13.5
18.80	19.7	25.4	32.6	31.3

TABLE 3. Rates of prey fish production ($g \cdot m^{-2} \cdot yr^{-1}$) estimated for the prey fish community at study sites from Green et al. (2014) via Eqs. 2 and 2.1, and accompanying target lionfish densities estimated via Eqs. 9 and 9.1.

Site number	Mean prey fish production ($g \cdot m^{-2} \cdot yr^{-1}$)		Median target lionfish density (fish/reef)	
	Eq. 2	Eq. 2.1	Eq. 9	Eq. 9.1
55	14.5	17.1	3	4
70	15.4	18.0	4	5
71	13.8	16.2	4	5
72	12.8	15.0	4	4

Individual biomass production rates (P from Eq. 4) were summed across prey sizes and species, and averaged across transect surveys at each study site to give average site-specific prey productions rates

$$\bar{P} = \frac{1}{z}\sum_{\forall_z}\sum_{\forall_i}\sum_{\forall_v} P_{v,i,z}. \qquad \text{(Eq. 2 in Green et al. 2014)}$$

This method for estimating individual prey fish biomass production was used to model threshold lionfish densities ($\bar{d}$) at which prey consumption equals prey production as

$$\bar{d} = \frac{\frac{1}{z}\sum_{\forall_z}\sum_{\forall_i}\sum_{\forall_v}\left(\frac{j(a_i L_{v,i,z}^{b_i})^q}{e^{\frac{E}{kT}}}\right)a_i L_{v,i,z}^{b_i}}{\frac{1}{m}\sum_{\forall_m}(a_l L_m^{b_l})\bar{p}\left(9\times10^{-22}e^{0.16T}\frac{1}{m}\sum_m (a_l L_m^{b_l})^h\right)}\pi r^2.$$

$$\text{(Eq. 9 in Green et al. 2014)}$$

Alternatively, as suggested by VF, individual prey fish biomass production rates (P) could be estimated via a scaling relationship between fish mortality rate and body size empirically derived for tropical fishes by Lorenzen (1996). A major difference between this method and that used by Green et al. (2014), which is based on Brown et al. (2004), is that the method of VF does not explicitly estimate the effect of temperature on mortality, and as a result greatly overestimates production in fish communities below a narrow range of warm temperatures. Using the method proposed by VF, Eq. 4 from Green et al. (2014) becomes

$$Z \approx \frac{P}{B} = jB^q \qquad \text{(Eq. 4.1)}$$

with $j = 3.08$ and $q = -0.21$, estimated empirically by Lorenzen (1996), and $B = a_i L^{b_i}$. As in Green et al. (2014), individual biomass production rates (P from Eq. 4.1) are summed across prey sizes and species, and averaged across transect surveys at each reef site to give average site-specific prey production rates

$$\bar{P} = \frac{1}{z}\sum_{\forall_z}\sum_{\forall_i}\sum_{\forall_v} P_{v,i,z}. \qquad \text{(Eq. 2.1)}$$

Replacing Eq. 4 with Eq. 4.1 in Eq. 9 of Green et al. (2014) yields

$$\bar{d} = \frac{\frac{1}{z}\sum_{\forall_z}\sum_{\forall_i}\sum_{\forall_v}\left(j(a_i L_{v,i,z}^{b_i})^q\right)a_i L_{v,i,z}^{b_i}}{\frac{1}{m}\sum_{\forall_m}(a_l L_m^{b_l})\bar{p}\left(9\times10^{-22}e^{0.16T}\frac{1}{m}\sum_m (a_l L_m^{b_l})^h\right)}\pi r^2.$$

$$\text{(Eq. 9.1)}$$

Comparing the two approaches

We compared these two approaches for estimating individual fish biomass production (P in Eqs. 4 vs. 4.1; measured as $g \cdot individual^{-1} \cdot year^{-1}$) for several body masses and temperatures (Table 2). We then evaluated how the two estimates of individual fish biomass production scaled up to affect median production estimates for the prey fish community at large ($\bar{P}$ in Eqs. 2 and 2.1) and mean target densities of lionfish ($\bar{d}$ in Eqs. 9 and 9.1; Table 3) for four study sites in Green et al. (2014).

Estimates of individual biomass production generated from Eqs. 4 and 4.1 are quite close, with those from Eq. 4.1 within the upper range of those generated by Eq. 4 across the temperatures experienced by fishes in Green et al. (2014), i.e., $26° \pm 3°C$ (or $299.15° \pm 3°K$) (Table 1). However, those relatively small differences in individual production resulted in greater estimates of mean community-wide fish production when using Eq. 4.1 compared with Eq. 4, which incorporated temperature variation (Table 3). For some of the study reefs, the higher estimates of community-wide prey fish production yielded higher median lionfish threshold densities at study reefs estimated by Eq. 9.1, compared with those from Eq. 9 (Table 3).

In light of these results, we recommend that readers continue to estimate target lionfish densities ($\bar{d}$) via Eq. 9 of Green et al. (2014) rather than the alternative Eq. 9.1, for two reasons. First, Eq. 9 uses a method for estimating prey production that explicitly accounts for the effects of temperature on biomass production (Eq. 4). This flexibility is important, given that lionfish occupy habitats that vary from as low as 10°C to more than 30°C. The parameters in Eqs. 4.1 were empirically derived estimates by Lorenzen (1996) for tropical fishes, and so the congruence of production estimates generated by Eq. 4.1 with Eq. 4 will only hold over a narrow range of warm temperatures. Second, Eq. 9 produces marginally more conservative estimates of prey biomass production over the range of temperatures experienced by fishes in Green et al. (2014), resulting in slightly more conservative (i.e., lower)

lionfish target densities for management, compared with Eq. 9.1.

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