

# Potential effects of climate change on a marine invasion: The importance of current context

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**Abstract** Species invasions threaten marine biodiversity globally. There is a concern that climate change is exacerbating this problem. Here, we examined some of the potential effects of warming water temperatures on the invasion of Western Atlantic habitats by a marine predator, the Indo-Pacific lionfish (*Pterois volitans* and *P. miles*). We focussed on two temperature-dependent aspects of lionfish life-history and behaviour: pelagic larval duration, because of its link to dispersal potential, and prey consumption rate, because it is an important determinant of the impacts of lionfish on native prey. Using models derived from fundamental metabolic theory, we predict that the length of time spent by lionfish in the plankton in early life should decrease with warming temperatures, with a concomitant reduction in potential dispersal distance. Although the uncertainty around change in dispersal distances is large, predicted reductions are, on average, more than an order of magnitude smaller than the current rate of range expansion of lionfish in the Caribbean. Nevertheless, because shorter pelagic larval duration has the potential to increase local retention of larvae, local lionfish management will become increasingly important under projected climate change. Increasing temperature is also expected to worsen the current imbalance between rates of prey consumption by lionfish and biomass production by their prey, leading to a heightened decline in native reef fish biomass. However, the magnitude of climate-induced decline is predicted to be minor compared to the effect of current rates of lionfish population increases (and hence overall prey consumption rates) on invaded reefs. Placing the predicted effects of climate change in the current context thus reveals that, at least for the lionfish invasion, the threat is clear and present, rather than future [*Current Zoology* 58 (1): 1–8, 2012].

**Keywords** Non-indigenous species, Coral reefs, Dispersal, Ecological impacts of invasion

## 1 Introduction

Marine environments are globally threatened by a multitude of stressors of human origin. Some of the largest ecological impacts have been caused by introductions of exotic species into novel habitats where they have become invasive (Carlton, 2000). Invasive species can compete with, displace or prey on native species, resulting in reductions in abundance, local extirpations and endangerment of indigenous taxa as well as impacts on local economies (Ruiz et al., 1999; Grosholz, 2002). Much effort has been devoted to identifying the features of both species and environments that make invasions likely (e.g., Carlton, 1996; Miller et al., 2002), in order to predict and prevent their occurrences.

One phenomenon that can make predictions about the spread and impact of invasions more uncertain is climate change. For example, increasing sea temperatures, which have already been noted across most of the world's oceans (IPCC, 2007), influence in a predictable manner growth and reproduction of marine fish and

invertebrates, two factors directly implicated in population increase (Brown et al., 2004). Populations of marine invaders may therefore grow more quickly following establishment, but so may populations of recipient native species. Moreover, warmer temperature can also have direct impacts on habitats, for example through bleaching of corals (Hughes et al., 2003) or impairment of photosynthesis and reduced growth in kelp (Wernberg et al., 2010). Degraded habitats may be more or less invasible by non-indigenous species, depending on the mechanism of invasion (Richardson and Pysek, 2006). Nevertheless, the common consensus appears to be that climate change is more likely to exacerbate than to slow down marine invasions.

A unique invasion of shallow-water marine habitats is currently occurring in the Western Atlantic. Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) were introduced to the Florida coast via the aquarium trade in the late 1980s (Morris and Whitfield, 2009). In 2004, lionfish were found on coral reefs of the Bahamian archipelago, and they are now in the process of colonizing

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the entire Caribbean basin, occupying coral reef, seagrass and mangrove habitats. The generalist diet of lionfish (Morris and Akins, 2009), combined with their relatively large size (up to ~ 50 cm length in the introduced range [Morris and Whitfield, 2009]), is generating grave concern about their impacts on native biodiversity and fish production (Albins and Hixon, 2008; Morris and Whitfield, 2009; Sutherland et al., 2010).

Our aim was to examine some of the potential effects of warming water temperatures on the lionfish invasion. Many aspects of lionfish life-history and behavior are expected to be temperature-dependent. We therefore focussed on two, namely pelagic larval duration, because of its link to dispersal potential, and prey consumption rate, because it is an important determinant of the impacts of lionfish on native prey. We predicted that temperature increases would shorten larval duration, perhaps also shortening dispersal distances, and increase prey consumption rates, thus accelerating negative impacts on native prey. Most importantly, we place these predicted effects of climate change in the context of current rates of spread and depletion of native prey biomass by lionfish to evaluate the likely consequences of ocean warming on this invasion.

## 2 Predicted Effect of Warming Temperature on Lionfish Pelagic Larval Duration and Dispersal

Like the majority of reef fish, lionfish are broadcast spawners with external fertilization (Fishelson, 1975). Lionfish larvae therefore spend time in the plankton before settling onto the substratum. On the basis of otolith rings and the clear mark left by the transition from planktonic to benthic life, Ahrenholz and Morris (2010) estimated that the pelagic larval duration (PLD) of lionfish collected in the Bahamas ranged from 20 to 35 days, with a modal PLD of 25 days.

Much of the variation in lionfish PLD is undoubtedly linked to variation in temperature during the pelagic phase, since the relationship between temperature and larval development in marine organisms is well established (O'Connor et al., 2007). Across 69 marine species (6 fish, 62 invertebrates), this relationship was described as:

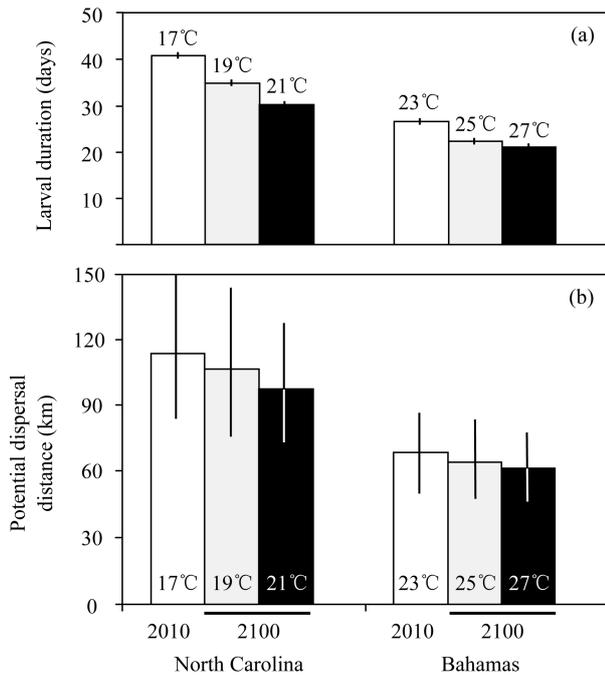
$$PLD = e^{\beta_0} * (T/T_c)^{-1.4-0.27*\ln(T/T_c)} \quad (1)$$

where PLD is the larval duration in days, T is the ambient water temperature (in °C), and T<sub>c</sub> is used as a centering factor and set to 15°C. The slope of the relationship was similar across taxa, latitudes and oceans, but

the intercept  $\beta_0$  varied widely among species (O'Connor et al., 2007). Lionfish was not included in this analysis, which preceded the publication of lionfish PLD estimates. However, we solved equation (1) for  $\beta_0$  and used Monte Carlo simulation to generate a lionfish-specific distribution for  $\beta_0$  which incorporated variation in both lionfish PLD, as provided by Ahrenholz and Morris (2010) ( $26.2 \pm 3.49$  days; mean  $\pm$  SD), and temperature of Bahamian waters ( $27 \text{ }^\circ\text{C} \pm 2 \text{ }^\circ\text{C}$  [NOAA, 2010]; see online supplement). We estimated  $\beta_0$  for lionfish as  $3.89 \pm 0.13$  (mean  $\pm$  SD). This value is higher than the average  $\beta_0$  reported by O'Connor et al. (2007) ( $\beta_0 = 3.17$ ), indicating slower than average larval development by lionfish for a given temperature.

This lionfish-specific scaling factor allows the prediction of lionfish PLDs for a range of temperatures. Of specific interest are temperatures predicted to occur as a result of carbon-driven atmospheric warming. Fig. 1a shows that lionfish PLD for populations near the northern edge of their range (i.e. North Carolina) is expected to decrease, on average, by 6 and 10 days compared to current PLD if winter sea temperatures rise by 2 and 4 °C, respectively, by 2100, which are the increases predicted according to the most optimistic and most pessimistic climate change scenarios (IPCC, 2007). For the same temperature increases, the change in PLD is expected to be more modest at lower latitudes of the introduced range, ranging from 3- to 5-day reductions, on average, in PLD in the Bahamas. The errors around our estimated PLDs are small compared to that of Ahrenholz and Morris (2010) because their estimate of PLD was obtained from a sample of lionfish taken from across multiple months and years, and hence likely from a wide range of temperatures. By contrast, each of our estimates was calculated for a single temperature of interest. Nevertheless, although our estimates are clearly subject to many assumptions, they serve to illustrate the fact that changes in PLD are likely to be uneven across the introduced range of lionfish owing to temperature effects as well as variation in, for example, nutritive content of yolk and parental fish condition.

Changes in pelagic larval duration are important in the context of invasion ecology because PLD is believed to be a correlate of dispersal capacity. There is often a general positive association between PLD and dispersal distance, measured either directly (e.g., from moving invasion fronts) or indirectly (e.g., inferred from genetic differences) (Siegel et al., 2003; Shanks et al., 2003; Kinlan et al., 2005; but see Shanks, 2009). Shanks (2009) suggested that variability in this relationship



**Fig. 1 Predicted pelagic larval durations (a) and potential dispersal distances (b) of invasive lionfish at current and warmer winter sea temperatures at two locations within their introduced range: North Carolina and the Bahamas**

The two predictions for 2100 correspond to optimistic (+2°C) and pessimistic (+4°C) scenarios of climate change. Medians are shown with parametric bootstrapped 95% confidence intervals (see online supplement for method).

arises owing to the existence of discrete, functionally divergent dispersal strategies among marine taxa. Therefore, to estimate the relationship between PLD and dispersal distance in a manner relevant to lionfish, we compiled information on both characteristics for marine organisms that share with lionfish the features of having feeding larvae that remain pelagic for at least one week and adults that inhabit either shallow coastal waters and deeper waters (i.e., strategy types 3 and 4 in Shanks 2009) (see online supplement). The relationship between dispersal distance ( $D_d$ , in km) and pelagic larval duration (PLD, in hours) for the 45 marine species included (31 invertebrates, 14 fish) was significant ( $F_{1,43} = 5.33$ ,  $P = 0.026$ ) and described as:

$$D_d = 22.5 * (PLD)^{0.43} \quad (2)$$

However, pelagic larval duration explained only 11% of variation in dispersal distance in this assemblage of species. The remaining variation is likely accounted for by other variable environmental and life history parameters, such as current strength and larval swimming ability. The uncertainties around the slope and intercept

of this relationship were propagated through the calculations of dispersal distances under different climate warming scenarios using Monte Carlo simulations (see online supplement).

If lionfish conform to the relationship described by equation (2), then the shorter PLDs predicted in warmer conditions should result in reduced dispersal distances. Thus, in North Carolina, a 6-day decrease in PLD resulting from a 2-degree increase in sea temperature, as estimated above, might lead to a ~5% reduction (or ~5.5 km), on average, in potential dispersal distance by lionfish propagules. A 4° increase in temperature might lower potential dispersal distance by ~15 km (or 13%), on average, in each generation (Fig. 1b). By contrast, the smaller reductions in PLD at lower latitudes (3 and 6 days, at 2°C and 4°C warmer than present in the Bahamas) might lead to smaller reductions in dispersal distance (i.e., ~5% or ~4 km and 9% or ~6 km, respectively, per generation) (Fig. 1b). Note that our predictions are associated with relatively large uncertainties (Fig. 1) and thus the magnitude of these predicted changes should be viewed with caution. However, the qualitative patterns suggest heterogeneous effects across the Atlantic range of lionfish.

Any temperature-induced reduction in dispersal distance may be perceived as desirable consequence of climate change if it results in a slowing of the spread of invasive species. However, an objective assessment needs to contrast this apparent benefit with the current rate of spread. The lionfish invasion is arguably the best ever documented spread of a marine invader (see Schofield et al., 2011). Approximate tracking of the lionfish invasion front between 2004 and 2009 shows a southward, linear rate of spread of 250 to 300 km per year. This is considerably higher than the rate of spread predicted solely on the basis of larval duration (Fig. 1b). This discrepancy may be explained by the influence of life history characteristics and specific oceanographic conditions on dispersal rate (Cowen et al., 2006). The reductions in annual dispersal distances predicted as a result of faster development rates of eggs and larvae in warming seas are, on average, more than one full order of magnitude smaller than the realized annual lionfish range extension. Thus, even if climate change slows the spread of lionfish, it is unlikely to do so appreciably.

A decrease in time spent as planktonic larvae, however small, could nevertheless affect connectivity among reefs, which may be important from a management perspective. Shorter PLDs due to warmer waters

might reduce the maximum dispersal range downstream from any given reef, thus effectively interrupting connectivity between distant sites. This might make the success of control efforts at one site slightly less dependent on control efforts at sites far upstream. By contrast, shorter planktonic life is also expected to increase larval retention near, and even promote spread upstream of, spawning sites, allowing invasive populations to establish and grow in areas from which they might have otherwise drifted (Byers and Pringle, 2006). If the latter effect (i.e., local retention) is more important than the former (i.e., disrupted connectivity), climate change would make local management of invasive species, such as lionfish, even more important than it currently is.

### 3 Predicted Effect of Warming Temperature on Lionfish Predation Rate and Native Prey Depletion

In the invaded Western Atlantic, lionfish are generalist predators capable of consuming prey up to half their total length (Morris and Akins, 2009). More than 50 species of native Caribbean reef fish have been documented in the stomachs of lionfish to date (Morris and Akins, 2009; Green et al., *in press*). This number will continue to increase as additional diet studies are conducted. The rapid rate at which lionfish consume Caribbean reef fishes is generating concern about their predatory impacts on native communities (e.g., Albins and Hixon, 2008; Côté and Maljković, 2010). These concerns were confirmed by Green et al. (*in press, in review*), who recently quantified the cumulative impact of predation by invasive lionfish on native Caribbean reef fishes. They compiled data on population parameters of lionfish and their fish prey, lionfish bioenergetics and diet to create a probabilistic model that evaluates the balance between rates of lionfish prey consumption and the production of their prey on invaded Bahamian reefs. They found that lionfish populations are currently consuming native reef fishes at rates far greater than prey populations can replace themselves on Bahamian reefs and that significant reductions in lionfish abundances are required at the majority of reef sites to prevent further reductions in native fish biomass (Green et al., *in review*).

How will climate change affect lionfish predation rates, and thus the impact of lionfish on Caribbean fish communities? For most fishes, there is an intrinsic relationship between environmental temperature and me-

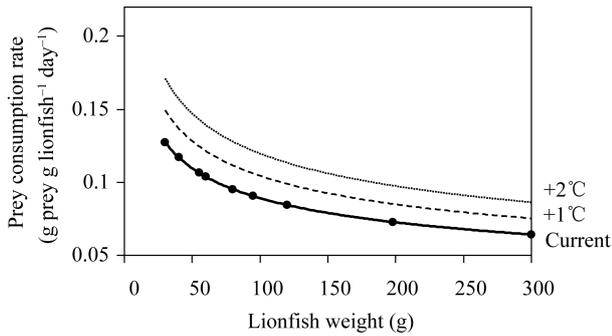
tabolism, with metabolic rate increasing in a predictable fashion as temperature rises (Brown et al., 2004). This fundamental link, which affects pelagic larval duration as described earlier, also has major consequences for food consumption (i.e., energy requirement) and growth rate (i.e., the rate at which energy is converted to new biomass), which both vary in response to ambient water temperature (e.g., Fonds et al., 1992). As climate change increasingly affects the tropical Western Atlantic, warming water temperatures will cause a rise in both the rate at which lionfish consume prey and the rates at which their prey produce new biomass.

We used the mass-balance model of Green et al. (*in review*) to re-examine the inequality between lionfish prey consumption and prey fish production under increasing temperature conditions. If lionfish prey consumption increases more rapidly for a given temperature rise than the production of their prey, then climate change will exacerbate the rate at which lionfish are currently depleting Caribbean fish populations. Alternatively, if the converse occurs, then climate change could in fact mitigate the impacts of lionfish on native fishes.

To derive the relationship between prey consumption rate and temperature for lionfish, we drew on *in situ* observations of prey consumption by invasive lionfish in the Bahamas conducted by Green et al. (2011) and Côté and Maljković (2010) over multiple seasons (and hence multiple temperatures, 23°C, 25 °C and 28°C). Using these data, we derived the relationship between prey consumption rate, temperature and body mass for lionfish as:

$$C_{xa} = 0.006e^{0.16T_a}M_x^b \quad (3)$$

where  $C$  is the mass-specific prey consumption (g prey g lionfish<sup>-1</sup> day<sup>-1</sup>) by lionfish  $x$  at ambient water temperature  $a$ ,  $T_a$  is the ambient water temperature (°C),  $M$  is the body mass (g) of lionfish  $x$ , and  $b$  is the constant slope for the relationship between lionfish body mass and mass-specific rate of prey consumption, estimated as  $-0.291$  (Fishelson, 1997). As expected, mass-specific prey consumption rate declines with lionfish size but, more importantly, increases with temperature. Fig. 2 illustrates this effect for temperature increases that are 1 °C and 2°C above current annual temperatures for Bahamian lionfish. Thus, for example, for a 1°C increase in temperature over the current average annual temperature in the Bahamas (27°C, NOAA 2010), we predict a ~17% percent increase, on average, in daily prey consumption for a 150 g lionfish.



**Fig. 2 Relationship between mass-specific prey consumption rate and body weight of invasive lionfish at three temperatures**

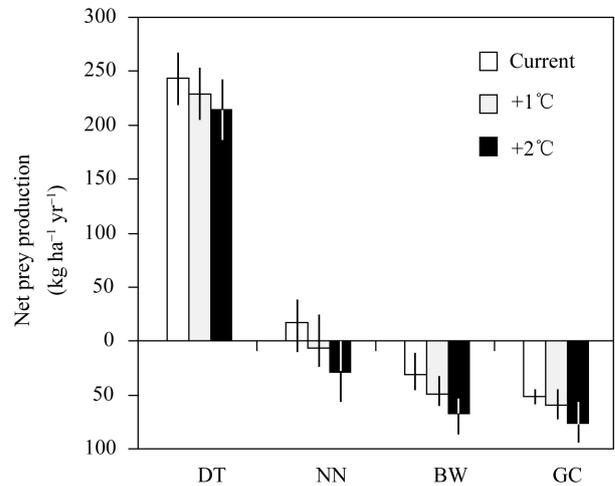
To quantify the relationship between prey fish biomass production and temperature, we drew on the theoretically derived and empirically validated metabolic scaling relationship between fish biomass production, body size and temperature. Brown et al. (2004) evaluated the parameters of this general relationship with empirical data for 175 fish stocks as:

$$\ln((P_M/M)M^{1/4}) = -0.45T + 19.24 \quad (4)$$

where  $P_M$  is the rate of whole-organism production of new biomass ( $\text{g ha}^{-1} \text{yr}^{-1}$ ) by an organism of mass  $M$  (in g) and  $T$  is absolute temperature ( $^{\circ}\text{K}$ ). We used this relationship to calculate the percent change in prey production ( $P_M$ ) as a function of increasing temperature ( $^{\circ}\text{C}$ ), and found that as temperature rises, increases in rates of new biomass production per degree Celsius will diminish. However, this effect is fairly minor within the range of temperatures experienced by tropical Western Atlantic fishes (i.e.,  $21\text{--}30^{\circ}\text{C}$  [NOAA 2010]). For Bahamian fishes, which experience average water temperatures of  $\sim 27^{\circ}\text{C}$  (NOAA 2010), a  $1^{\circ}\text{C}$  increase in average annual temperature should therefore elicit a  $\sim 6\%$  increase, on average, in production.

Finally, we incorporated the relationships between temperature and both lionfish prey consumption and prey biomass production into the mass-balance model of Green et al. (*in review*) to examine the impact of lionfish on Caribbean fish populations under two scenarios of modest climate change (i.e., a  $1^{\circ}\text{C}$  or  $2^{\circ}\text{C}$  increase in average water temperature) at four of the sites studied by Green et al. (*in review*), which are representative of the range of invaded Bahamian coral reefs. Current variation in net prey biomass production (i.e. prey biomass produced through growth and reproduction minus prey biomass consumed by lionfish) (white bars in Fig. 3) can be explained by variation in current lionfish size and density as well as variation in prey productivity.

Thus, sites DT and NN show positive current net prey biomass production rates because at the time of the study, they were inhabited by fewer lionfish and had a larger prey base than the other two sites. Our analysis revealed that under anticipated ocean warming, lionfish prey consumption should increasingly outstrip the production of their prey on each reef. On two of the four reefs (BW and GC), native fish populations should be depleted (i.e., net prey production will be negative) by lionfish at a higher rate than they are currently (Fig. 3). On one reef (NN), an increase in water temperature of  $2^{\circ}\text{C}$  is predicted to cause lionfish consumption to exceed the production of their prey – an imbalance not currently observed at this site (Fig. 3). The impacts of ocean warming are therefore again expected to be variable, but this time on a smaller reef-scale.



**Fig. 3 Net annual rate of native fish prey production (i.e. rate of prey production minus rate of lionfish prey consumption) at current and two warmer sea temperatures for four study coral reefs in the Bahamas**

Positive values indicate that prey are replacing themselves at rates that exceed the rate of predation by lionfish, thus prey biomass on these reefs can remain stable at current lionfish densities. Negative values indicate that lionfish are consuming prey at a faster rate than prey can replace themselves, leading to loss of native prey fish biomass. Means are shown with 95% parametric bootstrapped confidence intervals

Again, it is important to view the predicted impact of climate change on lionfish predation in the context of the magnitude of the invasion itself. A  $1^{\circ}\text{C}$  increase in average Bahamian water temperature should cause lionfish populations to consume, on average, an additional  $8\text{--}24 \text{ kg ha}^{-1} \text{yr}^{-1}$  in excess of prey production across the four reefs (Fig. 3). Such a temperature-mediated increase is approximately equivalent to adding  $1\text{--}4$  lionfish  $\text{ha}^{-1}$  (each consuming on average between  $\sim 6.5$  and

8 kg ha<sup>-1</sup> yr<sup>-1</sup> [Green et al., 2011]) to the sites under current conditions, which represents site-specific population increases of, on average, 7%–14% over the next 50–100 years. However, lionfish have reached densities of more than 400 individuals ha<sup>-1</sup> on many Bahamian reefs in only 5 years since their establishment (Green and Côté, 2009). Their densities are currently increasing similarly rapidly across the Caribbean. Lionfish are therefore likely to have severely depleted their prey base owing to natural population growth before any climate-enhanced impacts affecting prey consumption occur.

## 4 Conclusions

Warmer ocean conditions are expected to facilitate the establishment and spread of invasive species (e.g., Harris and Tyrell, 2001; Stachowicz et al., 2002; Agius, 2007; Saunders and Metaxas, 2007). This facilitation will occur through a variety of mechanisms. For example, previously thermally inhospitable habitats may become suitable for invaders at higher temperatures. Such expansions of the potential range of invasive species are almost certain to be realized if invaders have unconstrained access to all suitable areas. As such, one of the most concrete ecological consequences of climate change will be distribution ranges which are larger than they are today for a number of current invasive species (e.g., Raitsos et al., 2010).

The consequences of climate-facilitation of invasion through other mechanisms are less certain and more likely to be species-specific. Differences in the extent to which invaders and native species benefit from warmer conditions, for example in terms of growth and reproduction, will alter interactions among species and ultimately determine the direction of community shifts and the speed of spread of invaders. The weight of current evidence suggests that marine invaders will generally benefit more than indigenous species from warming temperatures (e.g., Stachowicz et al., 2002; Sorte et al., 2010), leading to predictions of exacerbated ecological trauma in the future.

Using lionfish as a model system, we considered three potential impacts of warming sea temperatures on an on-going invasion. All three features – pelagic larval duration, potential dispersal distance, and the balance of prey consumption and production – are predicted to change with temperature. Although the exact magnitude of change is more uncertain for some features than for others, spatial variation in temperature-driven change is highly likely. The three aspects of lionfish life-history

and behaviour we focused on are obviously not the only parameters that will be affected by sea warming. The limits of the lionfish's introduced range, currently determined by the 10°C isotherm (Morris and Whitfield, 2009), is set to expand as the isotherm shifts north and south in the two hemispheres. Whether lionfish can colonize habitats that are currently too cold in the southern hemisphere portion of this range will depend largely on their ability to cross the low salinity barrier of the Orinoco River. Temperature increases should also affect generation time and fecundity of both invaders and their prey, with potentially significant repercussions for future invasion dynamics.

Although the potential effects of warming oceans are numerous, and predictable in some cases, we show the importance of placing any predicted consequences of climate change for invasive species in the context of current invasion dynamics. Thus, for lionfish, as for any marine species with a pelagic larval phase, the length of time spent in the plankton in early life is expected to decrease with warming temperatures, with a concomitant reduction in potential dispersal distance. However, for lionfish, this reduction is more than an order of magnitude smaller than the current annual rate of range expansion in the Caribbean. Similarly, increasing temperature is expected to exacerbate the current imbalance between lionfish consumption and prey production rates, but the extent to which it will do so is minor in comparison to current rates of lionfish population increases (and hence overall predation rates) on invaded reefs. Placing the predicted effects of climate change in the current context reveals that, at least for the lionfish invasion, the threat is clear and present.

Our conclusions are perhaps very specific to lionfish, an admittedly unusual marine invader (i.e., a predator) with behavioral and life history traits (e.g., early age at maturity, high fecundity, year-round breeding) that allow very rapid population growth and drastic impacts on recipient communities. However, this is difficult to confirm because predicted consequences of climate change for invasions are rarely contrasted to current invasion characteristics. There is no doubt that climate change, with its many manifestations, will have profound effects on marine ecosystems, but in some cases, it is warranted to be more concerned about the present than about the future.

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