TROPICAL ECOLOGY

Allometric Scaling of Morphological Feeding Adaptations and Extreme Sexual Dimorphism in Energy Allocation in Invasive Lionfish

A Study of Pterois Volitans

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Lionfish (*Pterois volitans*) are a rapidly spreading invasive marine species in the Western Atlantic. High feeding success and reproductive output are potential mechanisms that allow lionfish to be such successful invaders. In order to better understand these mechanisms, we studied the allometry of morphological features involved in lionfish feeding ecology (specifically pectoral fin length and gape area), using fat mass as a metric of feeding success. We expected shorter lionfish to have longer pectoral fins, larger gape areas, and more fat stored than expected for their length. This allometric pattern would give smaller lionfish a feeding advantage, allowing them to grow to a large size quickly and outcompete other reef piscivores. Since we expected increased pectoral fin length and gape area to increase feeding success, we expected lionfish with longer pectoral fins and larger gape areas relative to length to have relatively more fat. We found that 1) shorter fish have longer pectoral fins, larger gape areas, and more fat mass than expected for their size, 2) lionfish with longer pectoral fins and larger gape areas for their length do not have more fat than expected for their length, and 3) females of a given body size had significantly lower fat mass than males. Our results indicate that compensatory allometric scaling of morphological features involved in feeding may give shorter lionfish a competitive advantage over native piscivores. We also found that fat mass is not necessarily indicative of feeding success. Finally, adult females may be investing more energy in reproduction than in growth or fat storage. Because lionfish reproduce continually while other reef piscivores reproduce seasonally, this intense allocation of energy into reproduction may play a critical role in the invasive success of lionfish in the Caribbean.

Introduction

Biological invasions are homogenizing the world and occurring more frequently as human activity increases on an international scale (1). Despite the overall increase in non-native introductions, introductions of marine fish species are surprisingly rare (2). Lionfish (*Pterois volitans*) are the first non-native marine fish species to invade the Western Atlantic (3, 4). This lionfish invasion represents one of the most rapid marine fish invasions in documented history (5). Anecdotal evidence blames the introduction of lionfish on releases from aquaria in South Florida (4). Since introduction in the 1990s, lionfish have spread north to Bermuda and south to Jamaica (4, 6). Albins and Hixon (2008) performed the first experimental study investigating the impact of this invasion, demonstrating that lionfish predation decreased native coral reef fish recruitment by 79%. This study showed that lionfish feeding ecology is a vital factor in understanding the success of their invasion. Previous studies have documented that lionfish use their long pectoral fins to corral fish and benthic invertebrates into their mouths (5). Lionfish also blow a jet stream of bubbles to mimic a current, tricking fish into swimming headfirst into their mouths (7). Such novel predation strategies potentially allow lionfish to grow rapidly and outcompete other piscivorous fish for prey and resources, contributing to their success.

To investigate which characteristics of lionfish contribute to their feeding success in invaded communities, we measured two feeding-related morphological features: pectoral fin length and gape area. Additionally, we assumed that the mass of fat stores in a lionfish would serve as a metric of feeding success. If these morphological features and fat stores follow an allometric growth pattern where smaller fish have longer pectoral fins, larger gape areas, and/or larger fat stores than expected for their size, this would indicate that selection has favored greater prey-capture ability in smaller lionfish. Because this allometric pattern would give smaller lionfish a feeding advantage, lionfish could grow to a large size quickly outcompeting other reef piscivores. If lionfish feeding success is directly related to feeding morphological features, we would expect lionfish with longer pectoral fins and larger gape areas for their size to have more fat stores than expected for their size. Alternatively, sex may be a better predictor of fat stores than morphological features. Unlike most piscivorous Caribbean fish, lionfish do not spawn once or twice a year. Instead, studies suggest that lionfish reproduce during all seasons (8) and may be capable of reproducing every four days (3). Thus, if sex is a better predictor of fat than morphology, we would expect females to have less fat than males due to allocation of energy to reproduction instead of growth.

Methods

On 1 March 2012, lionfish (*n* = 41) were culled at the Rock House Bay dive site off Little Cayman Island. The fish were speared by divers at a depth of approximately 55 feet. On 2 March 2012, additional lionfish (*n* = 4) were obtained at approximately the same depth from the Locher’s dive site off Little Cayman.

On 2-3 March 2012, we dissected the lionfish, measuring mass, total length, gape height, gape width and pectoral fin length. Total length (TL) was measured as the distance from the front of the mouth to the end of the caudal fin. Gape length and width were measured from the inside edges of the mouth. Pectoral fin length (PFL) was measured from the base of the fin to its longest point. Fish mass was measured...
Statistical Analyses

Fat mass was square root transformed and GA was log transformed for normality. A multiple regression was used to determine which morphological characteristics (PFL, GA, TL, or sex) best predicted fat mass. To analyze various pairwise relationships, we regressed TL on PFL, GA, and fat mass, separately for male (n = 29) and female (n=16) lionfish.

To account for the effect of fish length on PFL, GA, and fat mass, we took the residuals of each of the regressions mentioned above regardless of statistical significance. For the remainder of this paper, we will refer to these residuals as relative PFL, relative GA, and relative fat mass. We performed two linear regressions with relative PFL and relative GA as predictors of relative fat mass. These regressions were performed separately for males and females. We also calculated residuals of fat mass by length regardless of sex and performed a t-test to determine if this relative fat mass differed between males and females. All statistical analyses were performed using JMP 9 software (SAS Institute, Cary, NC).

Results

The mean TL was 304 ± 8.8 mm for males and 261.3 ± 5.2 mm for females (mean ± 1 S.E.). TL ranged from 138 to 366 mm for males and from 222 to 306 mm for females. Since lionfish reach sexual maturity at lengths of 100 mm for males and 180 mm for females (9), all lionfish included in our study were adults.

The multiple regression analysis indicated that sex was the only significant predictor of fat mass (t = -2.97, df = 40, P = 0.005). None of the other main effects significantly predicted fat mass (TL: t = 1.70, df = 40, P = 0.098; GA: t = -0.60, df = 40, P = 0.554; PFL: t = 1.58, df = 40, P = 0.123).

For univariate analyses, PFL significantly increased with TL for males ($r^2 = 0.40$, df = 27, $P < 0.001$, Fig. 2) but not for females ($r^2 = 0.15$, df = 14, $P = 0.132$, Fig. 2). The slope of this regression for males (m=0.18) was less than 1. GA significantly increased with TL for both males and females ($r^2 = 0.93$, df = 27, P < 0.001; $r^2 = 0.62$, df = 14, P < 0.001, respectively; Fig. 3). The slope of these regressions for both males (m = 0.009) and females (m = 0.008) was less than 1. Fat mass significantly increased with TL for males ($r^2 = 0.41$, df = 27, P < 0.001, Fig. 4), but not for females ($r^2 = 0.01$, df = 14, $P = 0.7278$, Fig. 4). The slope of this regression for males (m = 0.01) was less than 1.

Relative PFL did not significantly predict relative fat mass for either males ($r^2 = 0.06$, df = 27, $P = 0.209$) or females ($r^2 = 0.11$, df = 14, $P = 0.1995$). Relative GA did not significantly predict relative fat mass for either males ($r^2 = 0.03$, df = 27, $P = 0.367$) or females ($r^2 = 0.05$, df = 14, $P = 0.416$). Relative fat mass regardless of sex was significantly greater in males than females ($t = 5.06$, df = 40.1, P < 0.001).

Discussion

Our results indicate significant differences in growth allometries between male and female lionfish. However, since the slopes of all allometric relationships were less than 1 or not significantly different from 0, smaller fish, regardless of sex, have longer pectoral fins, larger mouths, and more fat stores relative to their length. This suggests either that shorter lionfish may be compensating for their small size, or that shorter lionfish have been selected to have larger feeding features that could increase their feeding success. It is not known whether their piscivorous competitors (such as groupers, jacks, and snappers) exhibit similar allometric scaling of morphological features that are important for feeding. If lionfish are the only reef piscivores to display these compensatory patterns, shorter lionfish may be able to use their relatively longer pectoral fins and larger mouths to grow at a faster rate than their competitors.

Despite this potential compensatory mechanism, the fact that lionfish of both sexes with relatively longer pectoral fins and larger mouths do not have relatively more fat suggests that these morphological characteristics may be less important to feeding success than we had hypothesized. Feeding success could depend more on diet or behavioral adaptations than on morphological features. Since small lionfish primarily eat crustaceans and large lionfish are primarily piscivores (5), diet may affect fat stores in differently sized lionfish. Also, predation pressure may play a greater role than feeding success in selecting for relatively longer pectoral fins in shorter lionfish. Alternatively, prey may not be limiting lionfish in the Western Atlantic. A lack of interspecific competition for food could explain why lionfish with relatively longer pectoral fins and larger mouths do not have more fat than their less well-endowed conspecifics.

Fat stores may not be a good indicator of feeding success in lionfish and could be influenced more by energy allocation than by feeding success. The fact that TL does not predict PFL or fat mass in females suggests that female lionfish are allocating energy differently than males. Females may switch from investing energy in somatic growth and fat storage to investing
in reproduction once they reach sexual maturity, as occurs seasonally in other fish species that spawn once or twice a year (10). Lionfish reproduction is not well studied, but it is estimated that lionfish can produce between 20,000 and 30,000 eggs as often as every 4 days, year-round (3). This would require a relatively constant energy allocation to egg production in females, which would explain why females have significantly lower fat stores than males.

Given the fitness trade-off between investing in reproduction and survival, it is surprising that female lionfish do not face extremely high mortality in exchange for allocating so much energy towards reproduction. Release from predation, disease, and parasites in the Western Atlantic post-introduction could allow female lionfish to invest high amounts of energy into reproduction without incurring survival costs (6).

Feeding ecology and reproductive success are vital components in understanding how non-native species invade certain ecosystems. Compensatory allometry of morphological features in smaller size classes could give lionfish a competitive advantage over other coral reef predators, contributing to their success as invaders. The apparent switch in energy allocation from growth and fat stores to reproduction in adult females warrants future studies including both juveniles and adults. In female lionfish, the apparent intense energy allocation into reproduction without decreased survival likely contributes to the incredible success of lionfish as an invasive species in the Caribbean. Future studies should investigate the trade-off between reproduction and survival in lionfish in their native environment to see how it compares to Western Atlantic populations. The combination of abnormally high reproductive success with morphological adaptations that could give smaller lionfish a feeding advantage over other reef piscivores may play a crucial role in the invasive success of lionfish in the Caribbean.

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References