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Consuming Costly Prey: Optimal Foraging and the Role of Compensatory Growth

Randall Brian Langerhans[1]*, Taylor R. Goins[1], Kenzi M. Stemp[2], Rüdiger Riesch[3], Márcio S. Araújo[4] and Craig A. Layman[5]†

[1] Department of Biological Sciences, W. M. Keck Center for Behavioral Biology, North Carolina State University, Raleigh, NC, United States, [2] Department of Biology, Appalachian State University, Boone, NC, United States, [3] Department of Biological Sciences, Centre for Ecology, Evolution and Behaviour, Royal Holloway, University of London, Egham, United Kingdom, [4] Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, Brazil, [5] Department of Applied Ecology, North Carolina State University, Raleigh, NC, United States

Some prey are exceptionally difficult to digest, and yet even non-specialized animals may consume them—why? Durophagy, the consumption of hard-shelled prey, is thought to require special adaptations for crushing or digesting the hard shells to avoid the many potential costs of this prey type. But many animals lacking specializations nevertheless include hard-bodied prey in their diets. We describe several non-mutually exclusive adaptive mechanisms that could explain such a pattern, and point to optimal foraging and compensatory growth as potentially having widespread importance in explaining costly-prey consumption. We first conducted a literature survey to quantify the regularity with which non-specialized teleost fishes consume hard-shelled prey: stomach-content data from 325 teleost fish species spanning 82 families (57,233 stomach samples) demonstrated that non-specialized species comprise ∼75% of the total species exhibiting durophagy, commonly consuming hard-shelled prey at low to moderate levels (∼10–40% as much as specialists). We then performed a diet survey to assess the frequency of molluscivory across the native latitudinal range of a small livebearing fish, *Gambusia holbrooki*, lacking durophagy specializations. Molluscivory was regionally widespread, spanning their entire native latitudinal range (>14° latitude). Third, we tested for a higher frequency of molluscivory under conditions of higher intraspecific resource competition in Bahamian mosquitofish (*Gambusia* spp.). Examining over 5,300 individuals, we found that molluscivory was more common in populations with higher population density, suggesting that food limitation is important in eliciting molluscivory. Finally, we experimentally tested in *G. holbrooki* whether molluscivory reduces growth rate and whether compensatory growth follows a period of molluscivory. We found that consumption of hard-shelled gastropods results in significantly reduced growth rate, but compensatory growth following prior snail consumption can quickly mitigate growth costs. Our results suggest that the widespread phenomenon of costly-prey consumption may be partially explained by its relative benefits when few alternative prey options exist, combined with compensatory growth that alleviates temporary costs.

Keywords: durophagy, food web, growth compensation, niche partitioning, predator-prey interactions, prey choice, resource competition, trophic ecology

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J. Jaime Zúñiga-Vega,
National Autonomous University of Mexico, Mexico

Reviewed by:
Regina Vega Trejo,
Stockholm University, Sweden
Geoff Smith,
Denison University, United States

****Correspondence:***
Randall Brian Langerhans
langerhans@ncsu.edu

†Present address:
Craig A. Layman,
Department of Biology, Center for Energy, Environment, and Sustainability, Wake Forest University, Winston-Salem, NC, United States

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INTRODUCTION

Competition for food resources serves as one of the most important factors driving major ecological and evolutionary patterns (e.g., Tilman, 1982; Schluter, 2000; Chase and Leibold, 2003; Morin, 2011; Pfennig and Pfennig, 2012). This fact has led to an array of adaptations, where particular species have evolved different resource specializations for acquiring and consuming certain types of foods. For instance, animals have evolved specialized means of feeding on potentially costly prey, such as those characterized by toxins, thorns, spines, and hard shells (e.g., Savitzky, 1983; Benkman, 1993; Coley and Barone, 1996; Brodie, 1999; Wainwright, 2006). Nevertheless, many animals exhibit a broad diet, opportunistically feeding on a variety of organisms, and appear to regularly include the consumption of seemingly costly prey (Westoby, 1978; Rex et al., 2010).

Throughout, we refer to "costly prey" as those prey whose acquisition and consumption can cause reduced fitness relative to feeding on most other prey regularly available and consumed by a given species (e.g., decreased survival, fecundity, mating success, parental care). Reduction in fitness can result from impacts such as reduced growth, condition/health, egg/embryo development, and age/size at maturity. Natural selection should generally favor diets comprising more easily acquired and consumed prey having higher net energy intake, i.e., more beneficial cost-to-benefit ratios (MacArthur and Pianka, 1966; Schoener, 1971; Pyke et al., 1977; Pyke, 1984; Stephens and Krebs, 1986). But then what might explain the widespread consumption of costly prey?

We suggest four adaptive, non-mutually exclusive mechanisms might explain the phenomenon of eating costly prey items (**Box 1**). The four mechanisms represent two categories of explanation: (1) consumption of costly prey could reflect adaptive feeding strategies (mechanisms I-III), and (2) costs can potentially be offset through evolved mechanisms that provide a delayed compensation for the costs (mechanism IV). In this study, we seek to explain why so many animals consume prey items that not only seem relatively less profitable than other options, but seem particularly costly. That is, we are specifically concerned with the consumption of especially costly prey in non-specialized taxa, and not merely the inclusion of poor-quality or low-cost prey in diets, or the very rare (perhaps inadvertent) consumption of moderate- to high-cost prey. We suggest that two particular mechanisms, optimal foraging, and compensatory growth, seem especially likely to prove important in explaining this phenomenon in nature, as the conditions conducive for their operation are common: decades of literature have revealed strong support for optimal foraging theory, and compensatory growth is widespread throughout the animal kingdom (see **Box 1**). In essence, costly-prey consumption may be largely explained by animals making the best of a bad situation (optimal foraging) and having the ability to offset its negative impacts by rapidly achieving a body size or condition associated with high fitness after the resumption of a high-quality diet (compensatory growth; **Figure 1**).

Here we test the predictions of optimal foraging and compensatory growth to evaluate their role in explaining durophagy in fishes. Durophagy describes the consumption of hard-shelled prey, including snails, bivalves, crabs, and urchins. This type of diet is typically thought to demand distinctive adaptations for crushing the hard shells, such as blunt teeth and strong jaws (Liem, 1986; Wainwright, 1988; Grubich, 2003; Hulsey et al., 2008). So why would animals lacking such specializations consume hard-bodied prey that will likely result in fitness costs? Durophagy can induce costs such as reduced growth of somatic or reproductive tissue owing to the large proportion of indigestible material consumed, spatial constraints within the gut as hard prey slowly evacuate (restricting entry, digestion, and evacuation of other prey, and potentially constraining available space for eggs or developing embryos), and possible injuries during consumption or excretion. Yet previous work on fish diets suggests that many fish lacking specializations might commonly include hard-shelled prey in their diet (see literature survey below). In this study, we (1) conduct a literature survey to quantify the regularity with which non-specialized teleost fishes consume hard-shelled prey, (2) perform a non-invasive diet survey to assess the frequency of molluscivory across the native latitudinal range of a wide-ranging, small, livebearing fish, *Gambusia holbrooki*, (3) test optimal foraging predictions of higher frequency of molluscivory under conditions of higher intraspecific resource competition in Bahamian mosquitofish (*Gambusia* spp.), and (4) conduct an experimental test in *G. holbrooki* for a cost of molluscivory (i.e., reduced growth rate) and the occurrence of compensatory growth following a period of molluscivory.

MATERIALS AND METHODS

Literature Survey of Durophagy in Teleost Fishes

To estimate the occurrence of hard-shelled prey in the diet of wild teleost fishes, we conducted a literature search of diet studies that employed stomach-content analysis. Rather than attempt to provide an exhaustive review of fish diets, we limited our search to the first 100 studies we encountered that matched the criteria described below. In this way, our search should provide a representative sample of fish diets, approximating what an exhaustive literature review might find. Using Google Scholar, we searched for studies of fish diets that directly examined stomach contents of wild-caught teleost fish, and provided quantitative information relevant to determining the inclusion of hard-shelled prey in the diets. Quantitative diet information was gathered for five different estimates of hard-shelled prey consumption: (1) percent occurrence (number of stomachs with hard-shelled prey / total number of stomachs that contained prey items), (2) percent by number (number of hard-shelled prey items / total number of prey items), (3) percent by weight (weight of hard-shelled prey / weight of all prey), (4) percent by volume (volume of hard-shelled prey / volume of all prey), and (5) percent index of relative importance. This latter metric is a commonly employed compound index of fish diets, and incorporates occurrence, bulk, and amount: percent occurrence × (percent volume + percent by number), expressed as a percentage of the sum of all index of relative importance values for all prey items [for details, see Pinkas et al. (1971), Cortes (1997)]. This large set of studies

BOX 1 | Why animals consume costly prey

We describe and evaluate four adaptive explanations for the consumption of costly diet items in non-specialized animals (**Table I**).

TABLE I | Four adaptive, non-mutually exclusive mechanisms to explain the consumption of costly prey in non-specialized taxa.

Mechanism	Description
I. Direct benefits	Costly prey provide direct advantages that result in net fitness benefit, such as essential limiting nutrients or buffer effects of toxic compounds.
II. Individual specialization	Some individuals possess specialized traits that reduce the costs of costly prey.
III. Optimal foraging	Costly prey are relatively less costly than alternative prey or no prey at all.
IV. Compensatory growth	Mitigate negative effects of costly-prey consumption by later exhibiting accelerated growth of somatic or reproductive tissue following consumption of higher-quality resources.

Mechanism I–Direct benefits: Animals could attain a net fitness gain from consuming particularly difficult-to-eat prey because they confer important benefits. Despite substantial costs, certain prey might provide important limiting nutrients, aid in detoxifying compounds derived from other foods, support mechanical digestion, or facilitate the removal of obstructions, parasites, or harmful microbiota (Bernays et al., 1994; Provenza et al., 2003; Simpson et al., 2004; Voigt et al., 2008). While consumption of some inedible items, such as clay or soil, might offer some important benefits at low to moderate cost, this "direct benefits" mechanism seems unlikely to commonly explain the consumption of prey that induce considerable costs, as the gains would need to be quite large to overcome the costs—unless the costly prey was only infrequently consumed in small amounts. Thus, although theoretically possible, and potentially important in combination with other mechanisms, we doubt that this mechanism alone can explain frequent or moderate levels of consumption of particularly costly prey.

Mechanism II–Individual specialization: Competition for food can drive intraspecific resource partitioning to reduce the intensity of competition, where individuals within a population differ in their ranked preferences of prey items. That is, some individuals rank costly prey items higher than others due to frequency-dependent competition (Bolnick, 2001) and specialized phenotypes that reduce costs of acquiring and consuming those prey resources (Bolnick et al., 2003). For instance, individuals might possess certain behaviors, morphologies, or physiologies that enhance foraging or feeding performance for costly prey, and thus more readily consume those prey than other individuals less equipped to contend with these resources (Olsson et al., 2007). This scenario results in individual diet specialization (e.g., Bolnick et al., 2003; Svanbäck and Persson, 2004; Svanbäck and Bolnick, 2007; Araujo et al., 2011), with certain individuals consistently feeding on costly prey more frequently than other individuals. Certain cases of intraspecific resource polymorphisms provide one source of known examples of this scenario, where phenotypically-specialized subsets of populations consume costly prey items, such as snail-feeding within several cichlid fishes and hard-seed consumption within some finches (e.g., Smith and Skúlason, 1996; Swanson et al., 2003). However, for individual specialization to account for the widespread consumption of costly prey in "non-specialized" species, there must be considerable cryptic phenotypic variation within populations that has so far gone undetected. While the occurrence of individual diet specialization appears pervasive across many taxa (e.g., Bolnick et al., 2003; Araujo et al., 2011), whether or not such specialization often comprises specialized phenotypes that reduce the impact of costly-prey consumption is currently unknown.

Mechanism III–Optimal foraging: Animals might adaptively consume costly prey when the net energetic gain associated with that particular prey type is greater (or when the net energetic loss is smaller) than alternative prey options. This comprises a fundamental prediction of optimal foraging theory (e.g., Stephens and Krebs, 1986), where animals should increase consumption of suboptimal prey as higher-quality resources become more difficult to acquire. Specifically, if individuals rank prey resources largely based on net energy intake, and include different resources in their diet according to this criterion, then situations can arise where consumption of costly prey represents an adaptive foraging behavior because these prey become relatively less costly in comparison with other available prey. For instance, this might occur in cases of reduced abundance or absence of higher-quality resources, reduced access to higher-quality resources (e.g., interference competition, predation), increased abundance of costly prey, or increased encounter rates with costly prey within less risky foraging areas. This might be most prevalent during particular seasons, times of drought, in the face of strong resource competition, when particular individuals or species guard high-quality resources, or when elevated predation risk confines individuals to regions without higher-quality resources. Put simply, this mechanism provides a means by which animals can make the best of a bad foraging situation. This mechanism could prove common for suboptimal prey resources of moderate costliness, while particularly severe conditions might be required for this mechanism to wholly explain moderate levels of consumption of highly costly prey. Thus, the importance of this mechanism depends on the balance between the costliness of the prey and the severity of the alternative option of not eating the costly prey (e.g., starving, eating lower-quality resources, suffering a high risk of injury or death in attempting to acquire higher-quality resource).

Mechanism IV–Compensatory growth: Animals might endure temporary costs of consuming difficult-to-eat items, but exhibit compensatory growth that offsets these costs once they subsequently obtain higher-quality food. Compensatory growth describes a phase of accelerated growth when high-quality nutrition is restored after a period of growth depression (Osborne and Mendel, 1916; Bohman, 1955; Hornick et al., 2000), and is widespread in animals after diet/nutrient restriction and in plants following herbivory (Wilson and Osbourn, 1960; Tanner, 1963; McNaughton, 1983; Ryan, 1990; Ali et al., 2003; Hector and Nakagawa, 2012; Won and Borski, 2013). Because body size often has a strong link to fitness (Roff, 2002), compensatory growth has been thought to represent an adaptation to avoid negative consequences of reduced body size caused by episodes of reduced growth. Thus, animals might more readily accept costs of suboptimal prey consumption partially because elevated growth later will compensate for these costs, resulting in little to no net reduction in fitness. Natural selection might often favor such a strategy in systems that meet two criteria: (1) temporally or spatially patchy distributions of high-quality food resources, occasionally requiring consumption of costly prey (e.g., via mechanism III), and (2) high likelihood of acquiring higher-quality food within a relatively short period after costly-prey consumption. The latter criterion implies a low mortality risk during the compensatory growth phase, as an individual cannot offset fitness costs at a later date if it cannot survive until that time. These two criteria are often met in natural populations, and combined with both the pervasiveness of compensatory growth and the ability of compensatory growth to minimize fitness costs, this mechanism might play an important, previously unrecognized role in explaining the common phenomenon of costly-prey consumption in natural animal populations. Whether animals initially consume costly prey because of direct benefits, to reduce intraspecific competition via individual specialization, or through optimal foraging strategies, compensatory growth might provide a common solution for offsetting costs. That is, complete elimination of costs is unlikely through any of the three mechanisms described above, and thus selection should often favor an additional mechanism that can largely offset those costs. Based on our current knowledge, compensatory growth seems to hold considerable promise as a widespread, influential factor in permitting costly-prey consumption.

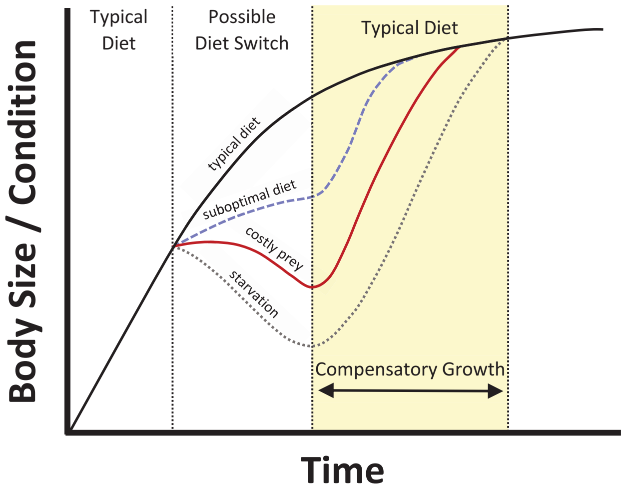

FIGURE 1 | Illustration of possible negative consequences of costly-prey consumption, and the rapid offsetting of costs via compensatory growth. Costly-prey consumption might often entail strong fitness costs relative to other prey items (especially in the absence of mechanisms I or II, **Box 1**), but still offer more energetic return than starvation, with compensatory growth providing a generalized response to counteract periods of growth depression.

should provide reasonable estimates of our parameters of interest (see Results for species diversity and sample size). All studies included in this review, and their associated data, are presented in **Appendix 1** in the **Supplementary Material**.

To avoid ambiguities and maintain consistency across studies, we only included molluscs and crabs in our category of "hard-shelled prey" even though some other prey may have shells or other dense parts (e.g., ostracods). For mollusc prey, unequivocal quantitative data for hard-shelled molluscs must have been provided in the study for inclusion in our dataset. For some studies, we could not obtain estimates of hard-shelled prey consumption even though quantitative data were provided; we excluded those studies. For instance, we excluded studies that only provided percent occurrence data separately for different mollusc species because this did not allow us to determine the overall percent occurrence of all molluscs (i.e., stomachs could have contained multiple mollusc species). Inclusion of crab prey data followed the same criteria, with the exception that if a study only provided values for the entire group of "crustaceans" or "decapods," we ignored those values and assumed the groups did not contain crabs. This conservative approach likely biased our estimates downward only slightly, as this only occurred in three studies, and in all these cases it was unlikely that crabs comprised a substantial part of the diet owing to the habitat use and diet of these species.

We classified each fish species included in the dataset as either a "specialist" or "non-specialist" based on the presence or absence of specialized morphological features for crushing and consuming hard-shelled prey. This classification was straightforward and unambiguous in all cases, as species with durophagous specializations are well-known. Typically, durophagous specialists possess specialized pharyngeal jaw morphologies accompanied by large, strong epaxial muscles (e.g., Liem, 1986; Wainwright, 1988; Meyer, 1990; Grubich, 2003; Hulsey et al., 2008). We further classified each species as either exhibiting durophagy or not, based on the presence or absence of hard-shelled prey in their diet. Because durophagy can be rare in non-specialists, low sample sizes might fail to detect durophagy within populations where it is present at low frequency. To test whether the detection of durophagy depended on sample size in our dataset, we conducted logistic regression for non-specialists with the presence of durophagy as the dependent variable (0 vs. 1) and $\log_{10}$-transformed sample size (number of stomachs examined) as the independent variable. We did not include specialists in this test because durophagy was detected in all specialists, regardless of sample size (see below). If sample size affected the detection of durophagy, then we would exclude species with low sample sizes (either <5 or 10 individuals, using separate analyses) where durophagy was not detected, and re-perform the logistic regression to determine whether the sample-size dependence of durophagy detection could be eliminated by excluding species with particularly small sample sizes. If so, then we would exclude those species with small sample sizes for all analyses. All analyses in this study were performed in the programs SAS v.7.15 and JMP v. 14.2 (SAS Institute Inc., Cary, NC, USA).

Field Survey of Molluscivory in *Gambusia holbrooki*

Gambusia fishes are small, livebearing fish (family Poeciliidae) that exhibit wide-ranging diets (Meffe and Snelson, 1989; Pyke, 2005), occasionally consuming hard-shelled molluscs by swallowing them whole (Bay and Anderson, 1966; Hubbs et al., 1978; Walters and Legner, 1980; Hubbs, 1990; Pen and Potter, 1991; Araujo et al., 2014). We selected *G. holbrooki* for detailed investigation because of its broad diet, extensive geographic range, lack of any adaptive specializations for durophagy, potential for substantial costs of molluscivory in terms of both growth and reproduction, and ability to exhibit compensatory growth (Kahn et al., 2012; Livingston et al., 2014).

We collected *G. holbrooki* in August 2011 from 10 natural populations along the eastern coast of the United States, spanning their entire native latitudinal range (**Figure 2A**, **Supplementary Table 1**). Specimens were immediately euthanized and preserved in 95% ethanol upon collection. We used digital x-ray imaging to examine the presence/absence of molluscs in gut contents of preserved adult *G. holbrooki* (261 females, 170 males). We captured a digital x-ray of each fish in the lateral perspective using a custom-built digital x-ray unit comprising a micro-focus x-ray source (Hamamatsu L6731-01) and a digital x-ray detector (PaxScan 2520E) housed in a lead-shielded cabinet. We inspected each image for the occurrence (presence/absence) and number of molluscs within the stomach. Previous work demonstrated the feasibility of this technique for detection of hard-shelled prey, such as molluscs (Beckmann et al., 2015). Because direct stomach-content analysis of a subset of fish revealed that snails smaller than 1 mm shell

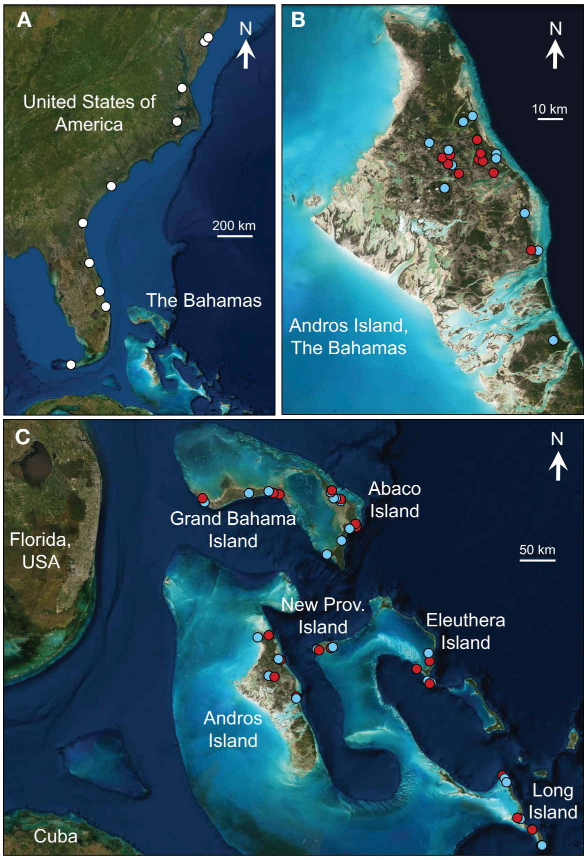

FIGURE 2 | Map of collection localities for the field studies of molluscivory in **(A)** *Gambusia holbrooki*, **(B)** *G. hubbsi* in blue holes, and **(C)** three species of Bahamian mosquitofish in tidal creeks. Blue symbols: high density/low predation; red symbols: low density/high predation.

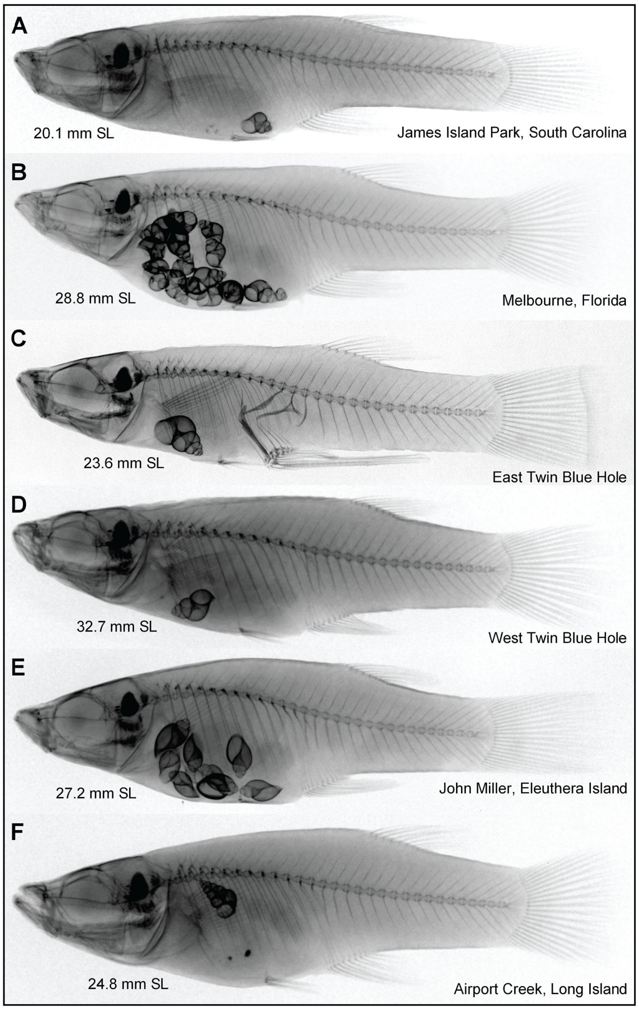

FIGURE 3 | Representative x-ray images of wild-caught **(A,B)** *Gambusia holbrooki*, **(C,D)** *Gambusia hubbsi*, and **(E,F)** *Gambusia manni* that had consumed snails (standard length of each fish provided).

length were rarely detected by x-ray imaging, our estimates provide lower bounds for the frequency of molluscivory in *G. holbrooki*, capturing cases of particularly dense mollusc shells (see **Figure 3**). Moreover, because x-ray imaging could not unequivocally determine which stomachs were empty and which contained prey items (Beckmann et al., 2015), our estimate of percent occurrence of molluscivory was calculated as the number of fish with snails in their stomachs divided by the total number of fish examined (rather than the total number of fish with prey items in their stomach).

Molluscivory and Resource Competition in Bahamian Mosquitofish

To test whether increased levels of resource competition are associated with molluscivory, as predicted by optimal foraging theory, we examined endemic livebearing fish in The Bahama Archipelago. Bahamian *Gambusia* were selected for study for reasons similar to *G. holbrooki*, with the added feature that they inhabit environments known to vary substantially in population density, with prior work finding multiple lines of evidence indicating stronger resource competition in populations with higher densities (Heinen et al., 2013; Riesch et al., 2013, 2015; Araujo et al., 2014; Heinen-Kay et al., 2016; Langerhans, 2018). We conducted our tests in two separate systems: (1) *Gambusia hubbsi* in inland blue holes on Andros Island and (2) three *Gambusia* species in tidal creeks across six islands. In all cases, we immediately euthanized and preserved individuals in 95% ethanol upon collection.

During the past ∼15,000 years (Fairbanks, 1989), *G. hubbsi* colonized many inland blue holes (water-filled, vertical caves) and have subsequently undergone adaptive diversification in a large number of traits [reviewed in Langerhans (2018)] and evolved varying levels of reproductive isolation among populations (e.g., Langerhans et al., 2007; Langerhans and Makowicz, 2013). A primary driver of evolutionary divergence in this system stems from the fact that in some blue holes *G. hubbsi* experience a relatively predator-free environment devoid of any piscivorous fish, and consequently exhibit high population densities with elevated competition for food resources. In other blue holes, *G. hubbsi* are heavily preyed upon by the much larger bigmouth sleeper (*Gobiomorus dormitor*) and have much lower population densities (e.g., Langerhans et al., 2007; Heinen et al., 2013; Martin et al., 2015). Because these two categories of blue holes do not systematically differ in abiotic environmental variables (Langerhans et al., 2007; Heinen et al., 2013; Riesch et al., 2013; Björnerås et al., 2020), this system provides a remarkable opportunity to test for the role of altered predatory and competitive environment on diet.

For *G. hubbsi* inhabiting blue holes on Andros Island, we tested for increased frequency of molluscivory under scenarios of higher resource competition by examining x-ray radiographs of 2,248 adult fish collected from 21 populations (11 with high density and no predators, 10 with low density and predatory fish present; **Figure 2B**, **Supplementary Table 2**). For each site, we calculated the overall proportion of fish with molluscs in their guts. For statistical analysis, we conducted a one-way analysis of variance (ANOVA) using arc-sin square-root transformed proportional molluscivory as the dependent variable and the dichotomous factor "predation regime" (high-density/low-predation vs. low-density/high-predation) as the independent variable.

Bahamian tidal creeks are shallow, tidally influenced estuaries typically having a relatively narrow creek mouth that broadens landward. Water flux largely arises from tidal exchange (freshwater input only provided via rainfall and aquifer percolation), so salinities in unfragmented systems are typically around 35 ppt and the biotic communities comprise marine taxa (Layman et al., 2004; Valentine-Rose et al., 2007a,b; Araujo et al., 2014; Riesch et al., 2015). Three species of Bahamian mosquitofish (*G. hubbsi*, *G. manni*, and *G.* sp.) inhabit tidal creeks across the archipelago, with each species within these systems found on different islands (Heinen-Kay et al., 2014). Fragmentation of Bahamian tidal creeks—the process by which connectivity with the ocean is restricted or cut off entirely—is principally caused by road construction, and results in strong and persistent ecological change. Most road construction that fragmented tidal creeks occurred during the 1960s and 1970s. Fragmentation dramatically reduced tidal exchange (tidal amplitude ∼0–10 vs. ∼40–80 cm in unfragmented creeks), leading to increased sedimentation rates, reduced animal biomass, reduced species diversity, and changes in the community composition of fishes, macroinvertebrates, plants, and macroalgae (Layman et al., 2004; Valentine-Rose et al., 2007a,b, 2011; Valentine-Rose and Layman, 2011; Araujo et al., 2014; Riesch et al., 2015). Key among these changes are markedly reduced densities of piscivorous fishes (e.g., great barracuda, *Sphyraena barracuda*; needlefish, *Strongylura* spp.) and increased densities of Bahamian mosquitofish. Previous work suggests that these drastic changes in intraspecific resource competition and predation represent the drivers of rapid phenotypic change in Bahamian mosquitofish in these systems (Araujo et al., 2014; Heinen-Kay et al., 2014; Giery et al., 2015; Riesch et al., 2015).

We employed two methodological approaches to test for consistent differences in molluscivory of Bahamian mosquitofish between the high-competition conditions of fragmented tidal creeks and the low-competition scenarios of unfragmented tidal creeks. First, we used x-ray radiographs of 2,463 adults from 44 populations across six Bahamian islands (two islands for each of three species; 1,466 females, 997 males; **Figure 2C**, **Supplementary Table 3**) to measure the proportion of fish with molluscs in their guts at each site. Again, the limitations of this method mean that our estimates provide a lower bound, likely underestimating the frequency of molluscivory because small molluscs (<1 mm shell length) can go undetected and because all fish, not only those with prey items in their stomachs, were used as the denominator in the percent occurrence calculation. We conducted a general linear model with arc-sin square-root-transformed proportional molluscivory as the dependent variable to test for effects of fragmentation regime, species, the interaction between species and fragmentation regime, island nested within species, and the interaction between fragmentation and island nested within species. Second, we complemented this non-invasive method with direct examination of stomachs because this could reveal smaller, less dense snail, and bivalve shells than detectable with x-rays. For this reason, and to additionally examine individuals particularly vulnerable to costly growth reductions caused by molluscivory, we included juveniles in our stomach-content analyses. We examined stomachs of 625 *G.* sp. on Abaco Island (373 females, 122 males, 130 juveniles) from 13 tidal creeks that span wide, continuous variation in population density (**Supplementary Table 4**). Some of these fish (156 females) were previously examined in Araujo et al. (2014), which can be consulted for details, but overall mollusc consumption has never previously been examined for these fish. Briefly, we removed the stomach of each individual in the laboratory and analyzed the gut contents under a stereo microscope, counting and identifying all prey items to the lowest feasible taxonomic level. To estimate the frequency of molluscivory, we calculated the average proportion of molluscs in the stomachs of each sex-age class for each population (number of molluscs divided by total number of prey items present in each stomach). We tested for greater molluscivory in populations with higher densities using an analysis of covariance (ANCOVA) with arc-sin square-root transformed proportion of molluscs as the dependent variable, and sex-age class and $\log_{10}$-transformed density as independent variables (interaction between sex-age class and $\log_{10}$-transformed density was excluded due to non-significance, $P = 0.93$).

Experimental Test of Cost of Molluscivory and Compensatory Growth in *G. holbrooki*

We experimentally tested whether molluscivory induces a cost in terms of growth in *G. holbrooki* and whether these fish can exhibit compensatory growth after snail consumption to reduce costs. Because our field survey found that females consumed snails more frequently than males (see Results), and because males exhibit minimal growth after sexual maturity in *G. holbrooki* (reducing our ability to detect growth-rate changes), we only examined adult females in this experiment. We collected adult fish from a single population in Cary, North Carolina. We first confirmed the presence of molluscivory in this population through fecal examination of live fish (i.e., expelled whole shells), and verified willingness to consume molluscs for all fish before experimentation by feeding live *Physa acuta* snails to the fish. All fish were maintained in the lab several months prior to experimentation. Although pregnancy status varied among fish used in the experiment (15 of 24 fish were determined to be pregnant by examination after the experiment), none of the fish gave birth during the experiment, and pregnancy status was highly non-significant when included as a covariate in analyses described below (main effect and all interaction terms: $P > 0.65$). Thus, we did not include pregnancy status in our final analyses.

We conducted a 17-day feeding experiment examining 24 female *G. holbrooki* [32.5–47.0 mm standard length (SL)]. The experiment was conducted in two temporal blocks, where we applied all the same experimental procedures twice, separated by 6 months (194 days), with 12 females examined within each block. For each block, each fish was individually placed in a 4.5-L container with an aerator on day 1, starved for 48 h, and then received a single feeding of a prescribed treatment per day until day 17. We housed tanks side-by-side on two shelves within a single room, and assigned a feeding treatment, hard-bodied prey vs. soft-bodied prey, alternately to each tank to avoid any potential confounding of treatment with spatial location or shelf effects. Fish in the hard-bodied prey treatment were fed two *P. acuta* snails with shells intact per day for 8 days (days 3–10), and then received Tetra-min Pro flakes for 6 days (days 11–16). Fish in the soft-bodied prey treatment were fed two *P. acuta* snail bodies removed from their shells per day for 8 days (days 3–10), and then received a similar 6 days of Tetra-min Pro flakes (days 11–16). Thus, the only difference between prey treatments involved the inclusion/exclusion of the shell along with the snail body during the snail-feeding period of the experiment—i.e., nutritional value remained constant across treatments, assuming no nutritive content of the hard shell itself for *Gambusia* fishes. We weighed (g) and measured standard length (mm) of each fish on four occasions: days 3, 7, 11, and 17. Fish of relatively similar size were selected for experimentation, and body size did not differ between treatments (*t*-test, initial mass: $P = 0.58$; initial SL: $P = 0.79$), nor did the average amount of snail mass fed to fish ($P = 0.82$). Fish mass changed considerably during the experiment, but length did not. Thus, we used initial SL as a potential covariate when examining variation in growth rate (g/day) during the experiment. To confirm low measurement error in our estimates of body size, we weighed and measured six similarly sized adult female *G. holbrooki* three times each and calculated repeatability as the intraclass correlation coefficient. Even though overall variation in body size was not high in this test (coefficient of variation = 0.14 and 0.07 for mass and SL, respectively), we found that repeatability was extremely high in both cases (mass: $r > 0.999$, SL: $r > 0.998$), supporting our use of these estimates of body size.

We collected all *P. acuta* snails from the same locality as the *G. holbrooki* used in the experiment, and prepared snails for feeding in advance of the experiment by weighing and freezing each individual (thawed immediately prior to feeding). We assigned each snail to be fed to a particular fish in a manner that maintained consistency throughout the experiment in the average mass of snails fed per day to a given fish. We prepared the Tetra-min Pro flakes in advance by weighing the flakes to ensure that each fish received flakes weighing twice the average mass of snails fed to each particular fish. During the experiment, tanks were vacuumed of debris and fecal waste every other day. Tanks were checked periodically throughout each day to note any feces or passed snail shells, which were removed once sighted.

We calculated the average daily growth rate (g/day) of each fish during both feeding periods (snail-feeding and flake-feeding periods) using the mass data collected during the experiment and conducted a repeated-measures general linear mixed model to test for effects on growth rate for the following terms: feeding period (snails vs. flakes), prey treatment (hard vs. soft), the interaction between feeding period and prey treatment, fish SL, and snail mass (average daily snail mass fed to each fish). The latter two variables were included as covariates to control for potential effects of body size or the amount of prey consumed on growth rate. We also initially included all two-way interactions between main effects and covariates and excluded all highly non-significant interaction terms ($P > 0.4$) from our final model. We included individual and block as random effects. We were especially interested in the interaction between feeding period and prey treatment, as we hypothesized that fish in the hard-bodied prey treatment would suffer reduced growth rate during the snail-feeding period, but subsequently exhibit elevated (compensatory) growth during the flake-feeding period.

To visualize changes in mass throughout the experiment, we plotted the relative mass of *G. holbrooki* over time (the 17 days of the experiment, with four measurement periods), and used cubic regression to summarize growth trajectories within each treatment. We estimated relative mass as back-transformed residuals of a linear regression of mass on SL (residuals + mean), which resulted in values of mass for each fish for each measurement period, controlling for body length, in g units. To provide an intuitive metric of recovery in the hard-prey treatment, we calculated the "compensatory index" following Wilson and Osbourn (1960). This index expresses the magnitude of compensatory mass gain as a percentage of the maximal mass differential between treatments, with a value of 100% indicating full recovery. We calculated the compensatory index as the difference in mass between treatments at the end of the snail-feeding period minus the difference in mass between treatments at the end of the flake-feeding period, divided by the mass difference at the end of the snail-feeding period.

RESULTS

Literature Survey of Durophagy in Teleost Fishes

We accumulated a dataset of 366 teleost fish species from 23 orders and 84 families, comprising stomach-content data from a total of 57,511 individual fish (**Supplementary Appendix 1**). Fifty one species from 18 families within this dataset were "durophage specialists," possessing adaptive morphological modifications for crushing and consuming hard-shelled prey—all of these species exhibited durophagy in our dataset. Within non-specialists, we detected a strong, positive effect of sample size on the detection of durophagy ($\chi^2 = 19.32$, $P < 0.0001$). Thus, the detectability of durophagy within non-specialists depended on the sample size of stomachs examined. Excluding species with <5 stomach samples did not eliminate this sample-size dependency ($\chi^2 = 7.08$, $P = 0.0078$), but excluding species with <10 stomach samples did ($\chi^2 = 1.20$, $P = 0.2731$). This resulted in a reduced dataset of 325 species from 22 orders and 82 families, comprising 57,233 stomach samples (48,579 for non-specialists, 8,654 for specialists). The reduced dataset did not remove any study completely from the analysis, as all excluded species derived from three studies that reported diets for multiple species, including some with large sample sizes (Randall, 1967; Winemiller and Ponwith, 1998; Lopez-Peralta and Arcila, 2002). We used this reduced dataset for all results presented here.

We found that over 63% of the species in our dataset exhibited durophagy (206 of 325 species). These 206 species spanned 14 orders (63.6%) and 60 families (73.2%). The majority of fish species that included hard-shelled prey in their diet did not possess specialized features for processing these prey: non-specialists represented ~75% of the species (155 of 206 species). Despite potential costs for consuming hard-shelled prey, non-specialists typically consumed 10–40% as much hard-shelled prey as specialists, depending on the estimate of durophagy (**Table 1**). Even for specialized fishes, hard-shelled prey tended to comprise less than half of the diet on average (**Table 1**), consistent with broadly opportunistic foraging in most fishes, with partial reliance on specialized prey.

Field Survey of Molluscivory in *G. holbrooki*

We observed molluscivory in 8 of the 10 *G. holbrooki* populations examined, spanning their entire latitudinal range (**Supplementary Table 1**). While molluscivory appears widespread in *G. holbrooki* at the regional scale (especially in females), it was always locally uncommon within populations (3.3–13.3% occurrence; based on all fish examined, not only those with prey items present), at least based on x-ray images, which likely failed to detect consumption of small molluscs (<1 mm). Overall, we detected molluscs in the stomachs of 13 of 261 females (5.0%) and 2 of 170 males (1.2%). For fish with mollusc shells apparent within their stomachs in x-ray images, we found 1–20 shells present within a single stomach (**Figures 3A,B**), with a total of 56 shells observed. Individuals with molluscs in their stomach spanned a range of body size (18.2–33.8 mm SL, mean = 26.5 mm SL), suggesting that adults of any body size might consume molluscs in the wild. All shells appeared to be gastropods (primarily *Physa* spp.), except for two bivalves.

Molluscivory and Resource Competition in Bahamian Mosquitofish

In blue holes on Andros Island, we detected molluscivory in *G. hubbsi* within all 11 blue holes having high population density and no predatory fishes, but detected molluscivory in only 4 of 10 blue holes with low population density and predatory fish present (**Supplementary Table 2**). Overall, we found a much higher frequency of molluscivory in high-density/low-predation blue holes compared to low-density/high-predation blue holes ($F_{1,19} = 14.48$, $P = 0.0012$; **Figure 4A**), consistent with the prediction from optimal foraging theory for a higher frequency of costly-prey consumption in populations experiencing stronger resource competition. Our lower-bound estimate of molluscivory indicated that it was generally rare, with an average of 3% of fish examined having molluscs in their guts for populations where molluscivory was detected. When molluscs were observed, between 1 and 18 shells were present within stomachs (**Figures 3C,D**). Again, individuals with molluscs in their stomach spanned a large range of body size (17.0–49.2 mm SL, mean = 28.4 mm SL).

In Bahamian tidal creeks across six islands, we detected molluscivory using x-ray radiographs in 18 of 44 populations (41%), 47 of 1,466 females (3.2%), and 7 of 997 males (0.7%) (**Supplementary Table 3**). Consistent with the prediction from optimal foraging theory, we observed a higher frequency of molluscivory in the high-density scenarios of fragmented tidal creeks compared to unfragmented tidal creeks ($F_{1,\,32} = 6.80$, $P = 0.0137$; **Figure 4B**). We found no differences between the three species in molluscivory ($F_{2,\,32} = 0.42$, $P = 0.66$), nor any effects of the interaction between species and fragmentation status ($F_{2,\,32} = 1.41$, $P = 0.26$). Similarly, we found no significant variation among islands within species ($F_{3,\,32} = 0.96$, $P = 0.42$) or for the interaction between fragmentation status and island ($F_{3,\,32} = 1.28$, $P = 0.30$). Fish with mollusc shells in their guts again spanned the full range of adult body size (14.1–36.9 mm SL, mean = 22.4 mm SL), and had between 1 and 10 shells within their stomachs (**Figures 3E,F**).

Using direct examination of stomach contents for Bahamian mosquitofish in 13 tidal creeks on Abaco Island, we found a much higher frequency of molluscivory than when using x-ray methodology. Our observations indicated that this derived from smaller molluscs being detected using direct stomach-content analysis. In all, we detected molluscivory in 12 of the 13 populations, with an average percent by number of

TABLE 1 | Summary of average quantitative diet information for the 206 fish species exhibiting durophagy within our dataset derived from our literature survey.

Durophage specialization	*N*	% O	% N	% W	% V	% IRI	Stomachs
Non-specialized	155	7.68	8.64	12.61	19.99	4.53	34,273
Specialized	51	39.83	28.07	42.14	43.67	39.96	8,654

% O, percent occurrence; % N, percent by number; % W, percent by weight; % V, percent by volume; % IRI, percent index of relative importance.

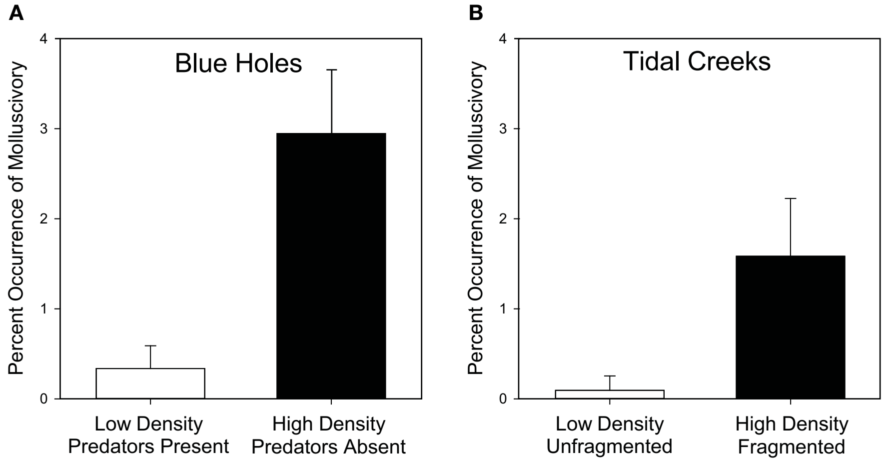

FIGURE 4 | Higher frequency of molluscivory associated with higher densities in Bahamian mosquitofish inhabiting **(A)** inland blue holes on Andros Island and **(B)** tidal creeks across six Bahamian islands. Back-transformed means ± SE depicted.

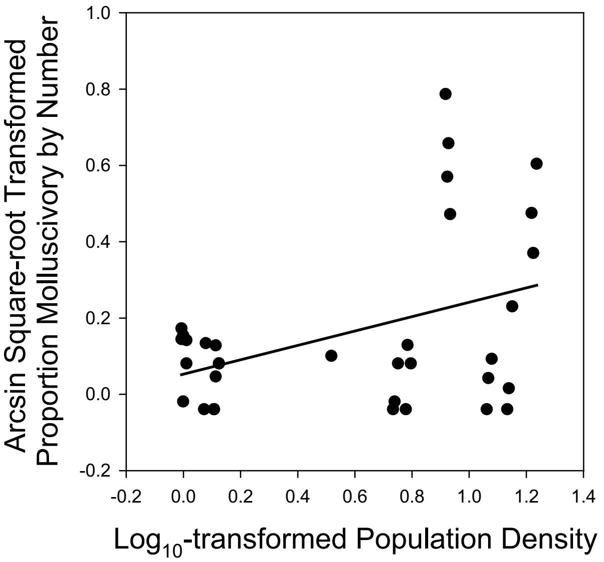

FIGURE 5 | Increased proportion of molluscs in the diet in sites with higher conspecific densities based on stomach-content analyses of male, female, and juvenile Bahamian mosquitofish inhabiting tidal creeks on Abaco Island, The Bahamas (see **Supplementary Table 4**) based on our general linear model (see text).

16.9% (molluscs as a percent of total prey items in the stomach). Consumption of molluscs was positively associated with population density ($F_{1,\,30} = 5.58$, $P = 0.0248$; **Figure 5**), while variation among sex/age classes was not significant ($F_{1,\,30} = 0.82$, $P = 0.45$).

Experimental Test of Cost of Molluscivory and Compensatory Growth in *G. holbrooki*

During the experiment, fish consumed the majority of prey given to them (184 of 192 snails in hard-prey treatment, 178 of 192 snail bodies in soft-prey treatment). For the hard-prey treatment, all snail shells were likely swallowed whole, as intact and empty shells of 94% of the snails consumed by *G. holbrooki* were found on the bottom of the aquarium (remaining shells were not found), and no case of shell crushing has ever been documented for any *Gambusia* fish.

TABLE 2 | Results of repeated-measures general linear mixed model examining variation in *Gambusia holbrooki* growth rate in the feeding experiment.

Source	*F*	*df*	*P*
Feeding period	16.37	1.48	0.0002
Prey treatment	0.07	1.48	0.7964
Standard length	2.26	1.48	0.1393
Snail mass	2.94	1.48	0.0929
Prey treatment × Feeding period	8.70	1.48	0.0049
Snail mass × Feeding period	5.20	1.48	0.0271

In our repeated-measures general linear mixed model, we found significant effects of two key terms on *G. holbrooki* growth rate: the prey treatment-by-feeding period interaction term and the snail mass-by-feeding period interaction term (**Table 2**). The clearest result from the experiment indicated that fish in the hard-prey treatment exhibited a reduced growth rate during the snail-feeding period relative to the soft-prey treatment, but elevated growth rate during the flake-feeding period (**Figure 6A**). This reflects a growth-rate cost of consuming hard-shelled prey, but also the presence of compensatory growth in fish receiving a high-quality diet after a period of consuming costly prey items. The second effect revealed by this experiment indicated that snail mass only influenced *G. holbrooki* growth rate during the snail-feeding period (not the flake-feeding period), with lower growth rates in fish fed larger snails on average—a trend primarily evident in the hard-prey treatment (**Figures 6B,C**).

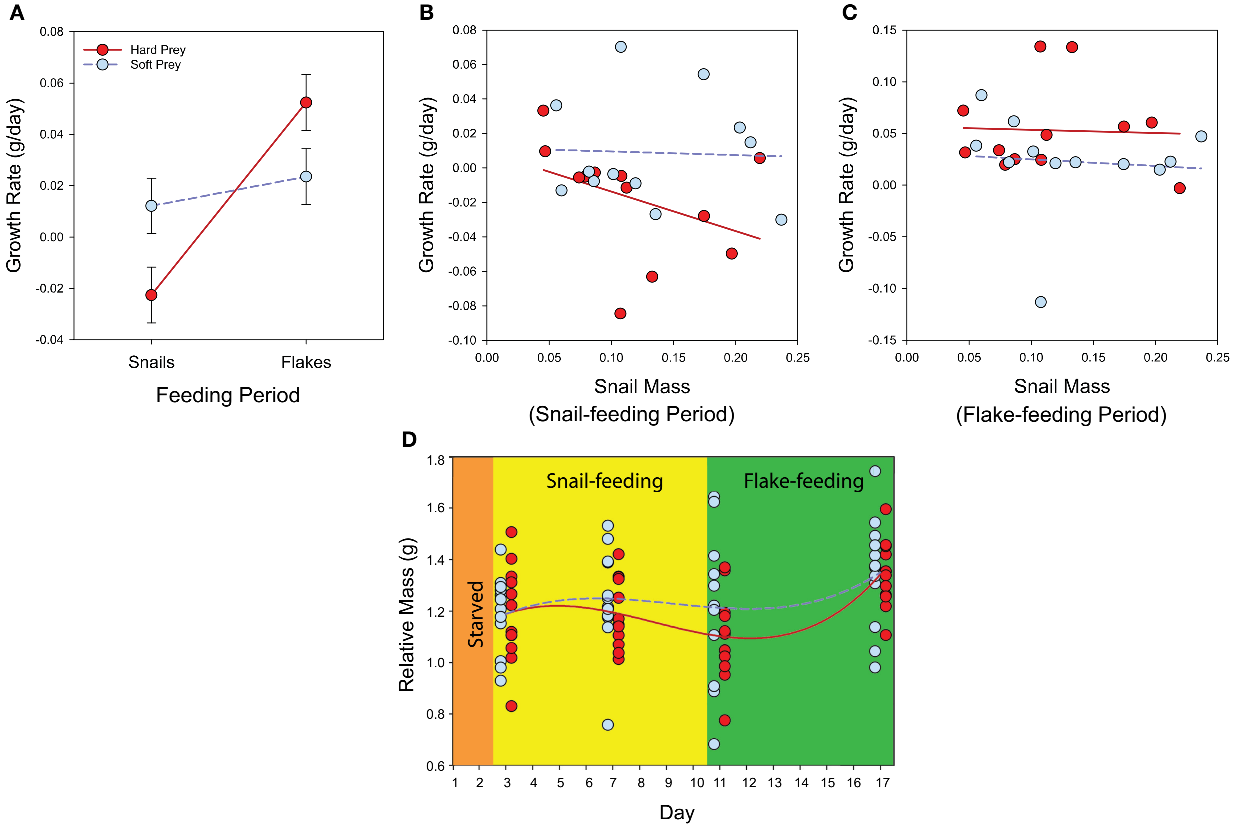

FIGURE 6 | Feeding experiment results in *Gambusia holbrooki* illustrating **(A)** differences in growth rate between hard- and soft-prey treatments during both snail-feeding and flake-feeding periods (least-squares means ± 1 standard error), **(B,C)** relationship between snail weight fed to fish and growth rate for both hard- and soft-prey treatments during **(B)** the snail-feeding period and **(C)** the flake-feeding period, and **(D)** overall pattern of mass change (relative to body length) during the experiment.

Overall, growth trajectories of the two treatments tended to diverge early in the experiment, reaching the maximal difference around the end of the snail-feeding period, but then converged by the end of the experiment due to compensatory growth during the flake-feeding period (**Figure 6D**). The estimated compensatory index was 93%, indicating a robust recovery of mass loss for fish in the hard-prey treatment via compensatory growth during the 6-day flake-feeding period.

DISCUSSION

Many animals eat a wide variety of prey, including items that likely elicit energetic, health, or reproductive costs, such as highly toxic or hard-shelled prey. Here we demonstrated that (1) durophagy is widespread in teleost fishes and that the majority of species that consume hard-shelled prey lack any relevant feeding specializations, (2) low levels of durophagy are prevalent throughout the range of *G. holbrooki* even though it results in reduced growth, (3) higher incidence of durophagy occurs under conditions of higher intraspecific competition for resources in Bahamian mosquitofish, and (4) compensatory growth can mitigate growth-related costs of durophagy. Overall, our results suggest that animals consume costly prey at a non-negligible frequency, increasing their consumption of these prey when high-quality prey become relatively scarce, and cope with the growth-depressing impacts of costly prey by exhibiting compensatory growth that offsets costs if alternative prey can be later acquired.

Costly Prey

While few would dispute the notion that many animals often consume suboptimal prey, an important question concerns the frequency with which animals consume truly *costly* prey in nature. To date, we have little relevant data to directly address this question, but much anecdotal evidence. Here we focused on durophagy, which is not only widely thought to entail considerable costs (see Introduction), but we experimentally confirmed a cost in terms of growth rate in the non-specialized fish *G. holbrooki* after eating molluscs for only 8 days. Our experimental design, which compared consumption of snails with intact shells to the consumption of only the snail bodies, allowed us to explicitly reveal growth-related costs of shell consumption *per se*, revealing the cost of consuming the hard, indigestible component of hard-shelled prey. Moreover, growth costs manifested rapidly even in adults, suggesting growth costs for juveniles or during longer-term durophagy would likely be more severe. In small livebearing fish, like *Gambusia* spp., gastropod shells can take up a significant portion of the gut, restricting the space available for other food or, in the case of pregnant females, for developing offspring within the body cavity. Therefore, molluscivory might affect growth, reproduction, and survival in *Gambusia* fishes. Hard-bodied prey are generally swallowed whole in non-specialized taxa, with little-to-no nutrition gained from the dense material. Thus, many, perhaps most, non-specialized animals likely experience a cost in terms of growth or fecundity when consuming hard-shelled prey relative to a soft-prey diet.

Regularity of Consumption of Costly Prey

Despite the apparent disadvantages, we found that costly-prey consumption appears widespread in nature. A majority of non-specialized species examined in our literature review exhibited durophagy, consuming ∼30–45% as much hard-shelled prey as specialists based on number, weight, and volume of diet items. Moreover, durophagy occurred throughout much of the native ranges of *G. holbrooki*, *G. hubbsi*, *G. manni*, and *G.* sp.—small, viviparous taxa that seem particularly vulnerable to durophagy-induced costs. Combined with previous work, this suggests that *Gambusia* fishes may regularly consume molluscs in the wild, sometimes at moderate to high frequencies [e.g., *G. affinis*: 58% occurrence (Walters and Legner, 1980), *G. nobilis*: 29% occurrence (Hubbs et al., 1978)]. Consumption of costly prey thus does not appear restricted to episodes of severe environmental harshness, but instead occurs, at least at low to moderate levels, throughout the year across many regions.

The apparent trend observed using x-ray methods where female *Gambusia* fishes often showed a higher frequency of molluscivory than males probably reflects the larger body size of females in these species, and their subsequent consumption of larger molluscs that are more dense and detectable with radiography. Indeed, our direct examination of stomach contents revealed more frequent consumption of smaller molluscs across all age and sex classes, with no differences between the sexes. That said, livebearing females may more regularly consume larger and denser snails than males due to their greater energy requirements—a pattern that could lead to considerable costs, as our experiment showed that consumption of larger snails had more negative consequences for growth. Interestingly, even though stomach-content analyses revealed higher absolute estimates of molluscivory than the x-ray methods, both methodological approaches pointed to the same associations with resource competition (see below). This suggests that x-ray methods underestimate total molluscivory, but provide reliable *relative* estimates of molluscivory, and reveal cases with strong likelihoods of fitness costs owing to the size and density of detectable shells. To determine the generality of our findings, future work should investigate the frequency of consumption of other types of costly prey, examine other taxa, and experimentally confirm the costliness of consumption of particular prey.

Costly Prey and Optimal Foraging Theory

According to optimal foraging theory, as high-quality foods become more difficult to acquire, animals should incorporate more suboptimal prey in their diet. Consistent with this prediction, the frequency of durophagy in our focal species appears related to resource competition—Bahamian *Gambusia* exhibited increased molluscivory in populations with higher density. This pattern was evident across three species spanning six islands inhabiting two different types of ecosystems (blue holes and tidal creeks), regardless of whether we used x-rays to detect molluscivory or stomach contents to quantify relative consumption of molluscs. This suggests that increased competition for food resources in these high-density populations elicits increased utilization of costly prey that provide little benefit relative to starving. While most of the mollusc species observed within *Gambusia* diets are present within nearly all study sites (RBL pers. obs.), and preliminary examination within a subset of these sites has found no covariation between mollusc abundance and *Gambusia* population density (RBL unpubl. data), future work should directly examine this topic. In the present study, predation risk may provide an additional contributing factor, as prey could alter activity levels or utilize alternative habitats with varying mollusc abundances in the presence of predators, and thus encounter mollusc prey at different frequencies in high-predation/low-density environments compared to low-predation/high-density environments. Regardless, swallowing whole snail shells that occupy considerable space in the digestive tract and body cavity, and eventually expelling them whole, poses a range of risks and potential costs with comparatively little energetic gain from the snail body. Thus, molluscivory should presumably be exceedingly rare except in extreme circumstances—but our findings in the literature survey and across the range of four *Gambusia* species indicate that it is not as rare as one might expect, suggesting an additional mechanism that mitigates its costs may be prevalent.

Costly Prey and Compensatory Growth

Compensatory growth is widespread across animal taxa (see **Box 1** and references therein) and could represent a common means of offsetting growth costs caused by eating costly prey. Compensatory growth has traditionally been viewed as an evolved mechanism that (at least partially) offsets fitness costs imposed by food shortage or a reduced growing season, but perhaps compensatory growth is more profitably viewed as a generalized life-history strategy to buffer adult body size against a wide range of environmental perturbations that could potentially reduce body size. Thus, compensatory growth might not only occur in response to food restriction or time constraints but also to generalized cues of a reduced probability of achieving an optimal body size. This means it might represent an important, previously unrecognized means of counteracting growth-depressing effects of the widespread phenomenon of costly-prey consumption.

The magnitude and rate of compensatory growth that we observed in *G. holbrooki* suggests this mechanism might greatly reduce, or even eliminate, potential fitness costs in the wild under a range of scenarios of low to moderate consumption of costly prey. Whether compensatory growth might vary with age, sex, stage of pregnancy, or duration of durophagy is currently unknown, but previous work has found some of these factors can influence the degree of compensatory growth [e.g., see Wilson and Osbourn (1960)]. Because the adaptive benefit of compensatory growth depends on the likelihood of surviving until high-quality food is re-acquired, this suggests that animals inhabiting environments with especially high mortality rates following costly-prey consumption should exhibit reduced levels of compensatory growth compared to organisms in low-mortality environments. Future work could test this hypothesis using comparative data across populations or species.

While compensatory growth can provide important benefits that mitigate costs of eating certain prey resources, it can also entail costs of its own, explaining why animals don't always exhibit the high growth rates observed during phases of compensatory growth (Arendt, 1997; Mangel and Stamps, 2001; Metcalfe and Monaghan, 2001; Johnsson and Bohlin, 2006; Royle et al., 2006; De Block and Stoks, 2008; Dmitriew, 2011; Hector and Nakagawa, 2012; Kahn et al., 2012). Faster than optimal growth can involve a range of costs, such as reductions in cell functioning efficiency, immune function, resistance to physiological stressors, fecundity, dominance rank, body size, locomotor performance, mating attractiveness, and lifespan. As long as the benefits outweigh the costs, compensatory growth provides an adaptive strategy for contending with costly prey. Considering that many of the purported costs of compensatory growth are delayed until later in life, often after (at least initial) reproduction (Metcalfe and Monaghan, 2001; Yearsley et al., 2004; Stoks et al., 2006; Ab Ghani and Merilä, 2014), combined with the ubiquity of compensatory growth in animals (e.g., Wilson and Osbourn, 1960; Tanner, 1963; Ali et al., 2003; Hector and Nakagawa, 2012), it may be that the fitness benefits indeed typically outweigh the costs in many natural systems. Nevertheless, to better understand the evolution of compensatory growth and its role in coping with the consumption of costly prey, future work should examine the potential costs of compensatory growth and their fitness consequences.

One area that seems to warrant future attention is how costly-prey consumption and compensatory growth might influence reproductive strategies. For instance, whether compensatory growth might often involve reproductive tissue, as opposed to somatic growth, has not yet been explored. Costly-prey consumption might affect reproductive traits such as egg development, yolk content, nutrient transfer to embryos, and embryo abortion. Moreover, while large body size often enhances fitness (Roff, 2002), elevated somatic growth can sometimes have smaller fitness consequences than reproductive traits that directly increase fecundity. Thus, we might expect to find compensatory *reproduction* following costly-prey consumption in some taxa. That is, if compensatory growth represents a life-history adaptation to achieve high fitness in the face of costly-prey consumption through rapid attainment of appropriate body size, then compensatory reproduction might represent an alternative, non-mutually exclusive strategy to maintain high reproductive output, especially later in life when somatic growth has less importance for fitness and future reproductive output is at a premium [essentially a special case of the terminal-investment hypothesis, (Charlesworth and Leon, 1976; Clutton-Brock, 1984)]. Therefore, animals might exhibit compensatory growth of reproductive tissues, such as larger or more numerous eggs or embryos, or invest more in reproductive behaviors, to compensate for lost reproductive output or mating opportunities. Future work should examine how costly-prey consumption might influence reproductive strategies.

CONCLUSION

Our results, combined with both the established predictive power of optimal foraging theory and the pervasiveness of compensatory growth in animals, point to these two mechanisms as factors of general importance in explaining why animals may regularly include costly prey in their diet. Thus, it appears that a profitable avenue for future investigation would center on optimal foraging and compensatory growth as major explanations for costly-prey consumption in nature.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Materials**, and available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mkkwh70z4 (Langerhans et al., 2020).

ETHICS STATEMENT

Animal research was reviewed and approved by the Institutional Animal Care and Use Committee of North Carolina State University (protocol 13-101-O).

AUTHOR CONTRIBUTIONS

RL conceived and coordinated the study, analyzed the data, and prepared the original manuscript. TG and KS performed the literature survey and laboratory experiment. RR led the field survey of *G. holbrooki*. RR, MA, and CL assisted with Bahamian mosquitofish components. RL and TG collected molluscivory data using x-rays. MA conducted the stomach-content analyses of Bahamian mosquitofish. CL made intellectual contributions to the work. All authors contributed significant edits to the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.603387/full#supplementary-material

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Online Supplementary Material for *Consuming costly prey: optimal foraging and the role of compensatory growth*

R.B. Langerhans, T.R. Goins, K.M. Stemp, R. Riesch, M.S. Araújo, C.A. Layman

Table S1 | Sample-size and molluscivory information based on x-ray imaging for the 10 populations of *G. holbrooki* collected along the eastern coast of the U.S.A. Numbers in parentheses denote the number of fish observed with mollusc shells in their stomachs.

Locality	Females	Males
Cape West May, New Jersey	34 (2)	6
Rehoboth Beach, Delaware	30 (1)	11
Suffolk, Virginia	30 (1)	9
Hyde County, North Carolina	31	20
James Island Park, South Carolina	30 (1)	20
St. Simons, Georgia	20	27
Daytona Beach, Florida	26 (1)	20 (1)
Melbourne, Florida	30 (4)	20
Port St. Lucie, Florida	24 (3)	16
Zachary Taylor State Park, Florida	6	21 (1)

Table S2 | Sample sizes and percent occurrence of molluscivory for Bahamas mosquitofish (*Gambusia hubbsi*) in 21 inland blue holes on Andros Island, The Bahamas. Numbers in parentheses depict the number of individuals with molluscs observed in their stomachs via x-ray radiographs.

Predation Regime	Population	N	% Mollusc.	Females	Males
Predators Absent	Archie's	161	1.86	97 (1)	64 (2)
	Douglas Christopher	60	1.67	30 (1)	30
	East Twin	96	3.13	32 (1)	64 (2)
	Gabbler	104	3.85	84 (3)	20 (1)
	Gollum	158	6.96	95 (10)	63 (1)
	Hubcap	124	4.03	65 (4)	59 (1)
	Ken's	85	1.18	43 (1)	42
	Little Frenchman	107	5.61	61 (6)	46
	Pigskin	81	1.23	40 (1)	41
	Rainbow	247	4.05	169 (10)	78
	Voy's	64	1.56	39 (1)	25
Predators Present	Cousteau	216	0.00	71	145
	Gibson	81	1.23	41	40 (1)
	Goby Lake	32	0.00	17	15
	Hard Mile	56	0.00	26	30
	Murky Brown	56	3.57	26 (2)	30
	Rivean	123	0.00	68	55
	Runway	76	0.00	36	40
	Shawn's	42	0.00	39	47
	Stalactite	151	0.66	74 (1)	77
	West Twin	128	3.91	64 (4)	64 (1)

Table S3 | Sample sizes and percent occurrence of molluscivory for three species of Bahamian mosquitofish in 44 tidal-creek populations across six islands in The Bahamas. Numbers in parentheses depict the number of individuals with molluscs observed in their stomachs via x-ray radiographs.

Species	Island	Fragmentation	Site Name	N	% Mollusc.	Females	Males
Gambusia sp.	Abaco	Fragmented	Crossing Rocks	19	0.00	10	9
			Double Blocked Down	60	1.67	34 (1)	26
			Double Blocked Up	55	9.09	28 (3)	27 (2)
			Indian River East	116	3.45	64 (2)	52 (2)
			Loggerhead Creek	41	2.44	21 (1)	20
			Sandy Point	146	0.68	64 (1)	82
			Stinky Pond	202	0.99	123 (2)	79
		Unfragmented	Blue Holes Creek	19	0.00	10	9
			Cherokee Creek	61	0.00	29	32
			Sand Bar	31	0.00	24	7
			Treasure Cay	55	1.82	30	25 (1)
			Twisted Bridge	87	2.30	51 (1)	36 (1)
	Grand Bahama	Fragmented	Crumbling Road	71	0.00	46	25
			Jellyshell West	50	0.00	37	13
			Rainy Blocked	25	0.00	10	15
		Unfragmented	Blue Holes Creek	26	0.00	10	16
			Empty House	33	0.00	18	15
			Expansive Creek	65	1.54	38 (1)	27
Gambusia hubbsi	Andros	Fragmented	Fresh Creek Back Up	48	10.42	35 (5)	13
			Independence Park	21	0.00	7	14
			Red Bays Pond	34	0.00	19	15
			Thompson/Scott	116	3.45	88 (4)	28
		Unfragmented	Cargill Creek	54	3.70	33 (1)	21 (1)
			Davey Creek	24	0.00	10	14
			Fresh Creek Twin Lakes	50	0.00	30	20
			Stafford Creek North	30	0.00	10	20

	New Providence	Fragmented	Adelaide Up	64	0.00	46	18
			Fox Hill Creek Up	55	7.27	31 (4)	24
		Unfragmented	Defense Creek	50	0.00	33	17
			Fox Hill Creek Down	32	0.00	18	14
Gambusia manni	Eleuthera	Fragmented	John Miller	53	24.53	39 (13)	14
			Princess Cay	47	6.38	31 (3)	16
			Tarpum Bay	63	0.00	46	17
		Unfragmented	Airport Eleuthera	43	0.00	20	23
			Cape Eleuthera	46	0.00	31	15
			Cruise Ship	40	0.00	20	20
	Long Island	Fragmented	Airport Creek	36	2.78	19 (1)	17
			Gordon's Beach	100	0.00	50	50
			Stella Maris	64	0.00	43	21
			Two Sisters	64	4.69	53 (3)	11
		Unfragmented	Clarence Creek	38	0.00	20	18
			Cliff Creek	25	0.00	10	15
			Glinton's Creek	47	2.13	35 (1)	12
			Gordon's Creek	57	0.00	42	15

Table S4 | Sample sizes and percent by number molluscivory based on stomach-content analysis of Bahamian mosquitofish in 13 tidal-creek populations on Abaco Island, The Bahamas.

	Density	Females		Males		Juveniles	
Site Name	(#/m2)	N	% by Num.	N	% by Num.	N	% by Num.
Blue Holes Creek	0.3	18	0.43	7	0.00	7	0.00
Cherokee Sound	0.3	27	2.15	3	0.00	2	0.00
Crossing Rocks	7.6	25	22.27	6	41.27	0	
Double Blocked Down	4.5	26	0.00	6	0.00	1	0.00
Double Blocked Up	10.7	38	0.38	9	0.00	72	0.01
Indian River East	12.8	31	0.12	6	0.00	22	2.23
Indian River West	2.3	14	1.43	0		0	
Loggerhead Creek	7.4	21	30.91	3	54.08	0	
Sand Bar	0.0	39	0.00	30	3.36	4	0.37
Sandy Point	15.8	64	14.43	38	24.25	8	25.00
Stinky Pond	5.1	18	2.18	6	0.00	9	0.00
Treasure Cay	0.2	28	2.32	5	0.00	0	
Twisted Bridge	0.0	24	2.99	3	4.44	5	0.00

Appendix 1. Literature Review of Durophagy in Teleost Fishes

Table A1 | Total dataset accumulated in our review of durophagy in teleost fishes based on 100 studies, comprising 366 species from 23 Orders and 84 Families, and a total of 57,511 individual stomachs. % O: percent occurrence, % N: percent by number, % W: percent by weight, % V: percent by volume, % IRI: percent index of relative importance. When a single species was represented by multiple studies, values within each dietary column depict mean values across the multiple studies. When no hard-bodied prey was observed in any stomachs for a given species, then a value of zero was assigned to all dietary metrics. However, when hard-shelled prey was observed within the diet of a given species, then values for only the measured metrics were recorded. Thus, blank cells indicate that while the value is non-zero, the exact value is unknown.

Order	Family	Species	Durophage Specialist	% O	% N	% W	% V	% IRI	# Stomachs	Reference(s)
Acipenseriformes	Polyodontidae	*Polyodon spathula*	N	0.0	0.0	0.0	0.0	0.0	20	Sampson et al. 2009
Anguilliformes	Anguillidae	*Anguilla anguilla*	N	>16	75.0	22.7			623	Hynes 1950, de Nie 1982
Anguilliformes	Congridae	*Taenioconger halis*	N	0.0	0.0	0.0	0.0	0.0	12	Randall 1967
Anguilliformes	Muraenidae	*Echidna catenata*	Y				96.3		11	Randall 1967
Anguilliformes	Muraenidae	*Gymnothorax moringa*	N	0.0	0.0	0.0	0.0	0.0	26	Randall 1967
Anguilliformes	Muraenidae	*Gymnothorax vicinus*	N				25.0		11	Randall 1967
Anguilliformes	Ophichthidae	*Myrichthys acuminatus*	N	0.0	0.0	0.0	0.0	0.0	8	Randall 1967
Anguilliformes	Ophichthidae	*Myrichthys ocellatus*	N				61.2		22	Randall 1967
Anguilliformes	Ophichthidae	*Ophichthus ophis*	N	0.0	0.0	0.0	0.0	0.0	5	Randall 1967
Atheriniformes	Atherinidae	*Allanetta harringtonensis*	N	0.0	0.0	0.0	0.0	0.0	23	Randall 1967
Atheriniformes	Atherinidae	*Atherinomorus stipes*	N	0.0	0.0	0.0	0.0	0.0	20	Randall 1967
Atheriniformes	Atherinidae	*Labidesthes sicculus*	N	0.0	0.0	0.0	0.0	0.0	45	Keast 1978
Aulopiformes	Synodontidae	*Synodus foetens*	N	0.0	0.0	0.0	0.0	0.0	9	Randall 1967
Aulopiformes	Synodontidae	*Synodus intermedius*	N	0.0	0.0	0.0	0.0	0.0	38	Randall 1967
Aulopiformes	Synodontidae	*Synodus saurus*	N	0.0	0.0	0.0	0.0	0.0	224	Esposito et al. 2009
Aulopiformes	Synodontidae	*Synodus*	N	0.0	0.0	0.0	0.0	0.0	4	Randall 1967

		synodas								
Beloniformes	Belonidae	*Platybelone argalus*	N	0.0	0.0	0.0	0.0	0.0	15	Randall 1967
Beloniformes	Belonidae	*Strongylura timucu*	N	0.0	0.0	0.0	0.0	0.0	20	Randall 1967
Beloniformes	Belonidae	*Tylosurus acus*	N	0.0	0.0	0.0	0.0	0.0	13	Randall 1967
Beloniformes	Belonidae	*Tylosurus crocodilus*	N	0.0	0.0	0.0	0.0	0.0	19	Randall 1967
Beloniformes	Hemiramphidae	*Hemiramphus balao*	N	0.0	0.0	0.0	0.0	0.0	16	Randall 1967
Beloniformes	Hemiramphidae	*Hemiramphus brasiliensis*	N	0.0	0.0	0.0	0.0	0.0	39	Randall 1967
Beryciformes	Holocentridae	*Holocentrus ascensions*	N				74.3		31	Randall 1967
Beryciformes	Holocentridae	*Holocentrus coruscus*	N				27.3		24	Randall 1967
Beryciformes	Holocentridae	*Holocentrus marianus*	N				30.6		13	Randall 1967
Beryciformes	Holocentridae	*Holocentrus rufus*	N				64.7		55	Randall 1967
Beryciformes	Holocentridae	*Holocentrus vexillarius*	N				52.0		55	Randall 1967
Beryciformes	Holocentridae	*Plectrypops retrospinis*	N				50.0		10	Randall 1967
Characiformes	Alestidae	*Brycinus nurse*	N	1.1					980	Saliu 2002
Characiformes	Characidae	*Astyanax bimaculatus*	N	0.0	0.0	0.0	0.0	0.0	88	Esteves 1996
Characiformes	Characidae	*Astyanax fasciatus*	N	0.0	0.0	0.0	0.0	0.0	94	Esteves 1996
Characiformes	Characidae	*Astyanax schubarti*	N	1.6					126	Esteves 1996
Clupeiformes	Clupeidae	*Alosa pseudoharengus*	N	0.0	0.0	0.0	0.0	0.0	48	Keast 1978
Clupeiformes	Clupeidae	*Dorosoma cepedianum*	N	0.0	0.0	0.0	0.0	0.0	279	Sampson et al. 2009
Clupeiformes	Clupeidae	*Harengula clupeola*	N	0.0	0.0	0.0	0.0	0.0	21	Randall 1967
Clupeiformes	Clupeidae	*Harengula humeralis*	N	0.0	0.0	0.0	0.0	0.0	24	Randall 1967
Clupeiformes	Clupeidae	*Jenkinsia lamprotaenia*	N	0.0	0.0	0.0	0.0	0.0	28	Randall 1967
Clupeiformes	Clupeidae	*Nematalosa*	N	0.0	0.0	0.0	0.0	0.0	61	Sternberg et al. 2008

		erebi								
Clupeiformes	Clupeidae	*Opisthonema oglinum*	N	0.0	0.0	0.0	0.0	0.0	23	Randall 1967
Cypriniformes	Catostomidae	*Ictiobus cyprinellus*	N	0.0	0.0	0.0	0.0	0.0	170	Sampson et al. 2009
Cyprinodontiformes	Cyprinodontidae	*Cyprinodon macularius*	N	13.3	6.0				75	Walters and Legner 1980
Cyprinodontiformes	Fundulidae	*Fundulus diaphanus*	N				4.0		114	Keast 1978
Cyprinodontiformes	Poeciliidae	*Gambusia affinis*	N	15.4	17.7	1.5			262	Walters and Legner 1980, Martin and Saiki 2009
Cyprinodontiformes	Poeciliidae	*Gambusia holbrooki*	N	0.2	0.02	1.1		0.01	909	Gkenas et al. 2012
Cyprinodontiformes	Poeciliidae	*Gambusia hubbsi*	N	19.4	9.3				534	Araujo et al. 2014
Cyprinodontiformes	Poeciliidae	*Poecilia latipinna*	N	0.0	0.0	0.0	0.0	0.0	222	Martin and Saiki 2009
Cyprinodontiformes	Poeciliidae	*Poecilia mexicana*	N	0.0	0.0	0.0	0.0	0.0	63	Martin and Saiki 2009
Cyprinodontiformes	Poeciliidae	*Poeciliopsis gracilis*	N	0.9		<0.1			235	Martin and Saiki 2009
Cyprinodontiformes	Poeciliidae	*Priapella chamulae*	N	1.8	0.4				55	Riesch et al. 2012
Cyprinoformes	Cyprinidae	*Hypophthalmichthys molitrix*	N	0.0	0.0	0.0	0.0	0.0	78	Sampson et al. 2009
Cyprinoformes	Cyprinidae	*Hypophthalmichthys nobilis*	N	0.0	0.0	0.0	0.0	0.0	228	Sampson et al. 2009
Cyprinoformes	Cyprinidae	*Leuciscus leuciscus*	N	0.0	0.0	0.0	0.0	0.0	237	Weatherly 1987
Cyprinoformes	Cyprinidae	*Notemigonus crysoleucas*	N	0.0	0.0	0.0	0.0	0.0	76	Keast 1978
Cyprinoformes	Cyprinidae	*Notropis heterodon*	N	0.0	0.0	0.0	0.0	0.0	52	Keast 1978
Cyprinoformes	Cyprinidae	*Pimephales notatus*	N	0.0	0.0	0.0	0.0	0.0	56	Keast 1978
Cyprinoformes	Cyprinidae	*Rutilus rutilus*	Y	25.6					1341	Hynes 1950, Weatherly 1987, Horppila 1999, Lappalainen et al. 2001
Cyprinoformes	Cyprinidae	*Tinca tinca*	N	0.0	0.0	0.0	0.0	0.0	188	Alas et al. 2010
Cyprinoformes	Cyprinidae	*Carasobarbus canis*	N	1.0					294	Spataru and Gophen 1985b
Elopiformes	Elopidae	*Megalops atlantica*	N	0.0	0.0	0.0	0.0	0.0	4	Randall 1967
Esociformes	Esocidae	*Esox*	N	0.0	0.0	0.0	0.0	0.0	302	Keast 1978, Kangur and Kangur 1998

		lucius								
Esociformes	Umbridae	*Umbra limi*	N				9.0		48	Keast 1978
Gasterosteiformes	Gasterosteidae	*Gasterosteus aculeatus*	N	10.1					1581	Hynes 1950
Gasterosteiformes	Gasterosteidae	*Pungitius pungitius*	N	5.0					656	Hynes 1950
Lophiiformes	Antennariidae	*Antennarius multiocellatus*	N				12.5		12	Randall 1967
Lophiiformes	Antennariidae	*Antennarius scaber*	N	0.0	0.0	0.0	0.0	0.0	11	Randall 1967
Lophiiformes	Ogcocephalidae	*Ogcocephalus nasutus*	N				33.4		9	Randall 1967
Mugiliformes	Mugilidae	*Mugil cephalus*	N	0.0	0.0	0.0	0.0	0.0	200	Eggold and Motta 1992
Mugiliformes	Mugilidae	*Mugil curema*	N	0.0	0.0	0.0	0.0	0.0	17	Randall 1967
Perciformes	Acanthuridae	*Acanthurus chirurgus*	N				0.1		20	Randall 1967
Perciformes	Acanthuridae	*Acanthurus coeruleus*	N	0.0	0.0	0.0	0.0	0.0	27	Randall 1967
Perciformes	Apogonidae	*Apogon conklini*	N	0.0	0.0	0.0	0.0	0.0	29	Randall 1967
Perciformes	Apogonidae	*Apogon maculatus*	N				23.7		22	Randall 1967
Perciformes	Blenniidae	*Blennius cristatus*	N				0.8		22	Randall 1967
Perciformes	Blenniidae	*Blennius marmoreus*	N	0.0	0.0	0.0	0.0	0.0	12	Randall 1967
Perciformes	Blenniidae	*Entomacrodus nigricans*	N	0.0	0.0	0.0	0.0	0.0	16	Randall 1967
Perciformes	Blenniidae	*Ophioblennius atlanticus*	N	0.0	0.0	0.0	0.0	0.0	50	Randall 1967
Perciformes	Branchiostegidae	*Malacanthus pluieri*	N				18.5		8	Randall 1967
Perciformes	Carangidae	*Alectis ciliaris*	N	0.0	0.0	0.0	0.0	0.0	4	Lopez-Peralta and Arcila 2002
Perciformes	Carangidae	*Carangoidea otrynter*	N			3.8			10	Lopez-Peralta and Arcila 2002
Perciformes	Carangidae	*Caranx bartholomaei*	N	0.0	0.0	0.0	0.0	0.0	7	Randall 1967
Perciformes	Carangidae	*Caranx fusus*	N				5.9		44	Randall 1967
Perciformes	Carangidae	*Caranx*	N	0.0	0.0	0.0	0.0	0.0	32	Hulsey et al. 2005

		hippos								
Perciformes	Carangidae	*Caranx latus*	N	3.0	0.3				39	Randall 1967, Silvano 2001
Perciformes	Carangidae	*Caranx lugubris*	N	0.0	0.0	0.0	0.0	0.0	6	Randall 1967
Perciformes	Carangidae	*Caranx ruber*	N				0.8		96	Randall 1967
Perciformes	Carangidae	*Chloroscombrus chrysurus*	N	0.0	0.0	0.0	0.0	0.0	297	Sanchez-Ramirez 2003
Perciformes	Carangidae	*Chloroscombrus orqueta*	N	0.0	0.0	0.0	0.0	0.0	7	Lopez-Peralta and Arcila 2002
Perciformes	Carangidae	*Decapterus macarellus*	N	0.0	0.0	0.0	0.0	0.0	2	Randall 1967
Perciformes	Carangidae	*Decapterus punctatus*	N	0.0	0.0	0.0	0.0	0.0	10	Randall 1967
Perciformes	Carangidae	*Oligoplites altus*	N	0.0	0.0	0.0	0.0	0.0	1	Lopez-Peralta and Arcila 2002
Perciformes	Carangidae	*Oligoplites saurus*	N	0.0	0.0	0.0	0.0	0.0	11	Randall 1967
Perciformes	Carangidae	*Selar crumenophthalmus*	N	0.0	0.0	0.0	0.0	0.0	215	Randall 1967, Lopez-Peralta and Arcila 2002
Perciformes	Carangidae	*Selene brevoortii*	N			15.2			33	Lopez-Peralta and Arcila 2002
Perciformes	Carangidae	*Selene oerstedii*	N			89.2			2	Lopez-Peralta and Arcila 2002
Perciformes	Carangidae	*Selene peruviana*	N	0.0	0.0	0.0	0.0	0.0	64	Lopez-Peralta and Arcila 2002
Perciformes	Carangidae	*Seriola dumerili*	N	0.0	0.0	0.0	0.0	0.0	8	Randall 1967
Perciformes	Carangidae	*Trachinotus carolinus*	Y			65.8			227	Hulsey et al. 2005
Perciformes	Carangidae	*Trachinotus falcatus*	Y				75.0		8	Randall 1967
Perciformes	Carangidae	*Trachinotus goodei*	Y				13.1		28	Randall 1967
Perciformes	Carangidae	*Trachurus declivis*	N	0.0	0.0	0.0	0.0	0.0	764	Young and Davis 1992
Perciformes	Carangidae	*Trachurus japonicus*	N	0.0	0.0	0.0	0.0	0.0	141	Sassa et al. 2008
Perciformes	Carangidae	*Trachurus trachurus*	N	0.8	2.9			2.3	2242	Jardas et al. 2004, Yankova et al. 2008
Perciformes	Centrarchidae	*Ambloplites rupestris*	N	0.0	0.0	0.0	0.0	0.0	44	Keast 1978
Perciformes	Centrarchidae	*Lepomis*	N	3.0					103	Etnier 1971

		cyanellus								
Perciformes	Centrarchidae	*Lepomis gibbosus*	Y	57.7		67.6	51.5		586	Etnier 1971, Keast 1978, Mittelbach 1984, Hulsey et al. 2005
Perciformes	Centrarchidae	*Lepomis macrochirus*	N	8.4		0.9	1.5		519	Gerking 1962, Etnier 1971, Keast 1978
Perciformes	Centrarchidae	*Lepomis microlophus*	Y				87.0		71	Hulsey et al. 2005
Perciformes	Centrarchidae	*Micropterus salmoides*	N	0.0	0.0	0.0	0.0	0.0	1320	Keast 1978, Olson 1996, Schindler et al. 1997, Huskey and Turingan 2001
Perciformes	Centrarchidae	*Pomoxis* sp.	N	0.0	0.0	0.0	0.0	0.0	73	Keast 1978
Perciformes	Chaetodontidae	*Centropyge argi*	N	0.0	0.0	0.0	0.0	0.0	5	Randall 1967
Perciformes	Chaetodontidae	*Chaetodon capistratus*	N	0.0	0.0	0.0	0.0	0.0	29	Randall 1967
Perciformes	Chaetodontidae	*Chaetodon sedentariuis*	N	0.0	0.0	0.0	0.0	0.0	3	Randall 1967
Perciformes	Chaetodontidae	*Chaetodon striatus*	N	0.0	0.0	0.0	0.0	0.0	16	Randall 1967
Perciformes	Chaetodontidae	*Holocanthus ciliaris*	N	0.0	0.0	0.0	0.0	0.0	26	Randall 1967
Perciformes	Chaetodontidae	*Holocanthus tricolor*	N	0.0	0.0	0.0	0.0	0.0	24	Randall 1967
Perciformes	Chaetodontidae	*Pomocanthus arcuatus*	N	0.0	0.0	0.0	0.0	0.0	34	Randall 1967
Perciformes	Chaetodontidae	*Pomocanthus paru*	N	0.0	0.0	0.0	0.0	0.0	23	Randall 1967
Perciformes	Chaetodontidae	*Prognathodes aculeatus*	N	0.0	0.0	0.0	0.0	0.0	8	Randall 1967
Perciformes	Cichildae	*Herichthys minckleyi*	Y	45.0			28.0		73	Hulsey et al. 2006
Perciformes	Cichlidae	*Astatoreochromis alluaudi*	N	0.0	0.0	0.0	0.0	0.0	52	Binning and Chapman 2008
Perciformes	Cichlidae	*Astatotilapia flaviijosephi*	Y	13.9					102	Spataru and Gophen 1985a
Perciformes	Cichlidae	*Cichlasoma urophthalmus*	Y	33.8					68	Bergmann and Motta 2005
Perciformes	Cichlidae	*Oreochromis mossambicus*	N	0.3		0.1			403	Martin and Saiki 2009
Perciformes	Cichlidae	*Oreochromis niloticus*	N	1.8					2570	Njiru et al. 2004, Peterson et al. 2006
Perciformes	Cichlidae	*Pseudocrenilabrus multicolor*	N	0.0	0.0	0.0	0.0	0.0	33	Binning and Chapman 2008
Perciformes	Cichlidae	*Tilapia*	N	3.7		1.2			107	Martin and Saiki 2009

		zillii								
Perciformes	Cirrhitidae	*Amblycirrhitys pinos*	N				12.1		16	Randall 1967
Perciformes	Clinidae	*Labrisomus guppyi*	N				77.5		6	Randall 1967
Perciformes	Clinidae	*Labrisomus kalisherae*	N	0.0	0.0	0.0	0.0	0.0	1	Randall 1967
Perciformes	Clinidae	*Labrisomus nuchipinnis*	N				43.7		22	Randall 1967
Perciformes	Echeneidae	*Echeneis naucrates*	N	0.0	0.0	0.0	0.0	0.0	12	Randall 1967
Perciformes	Echeneidae	*Remora remora*	N	0.0	0.0	0.0	0.0	0.0	7	Randall 1967
Perciformes	Eleotridae	*Dormitator maculatus*	N	0.0	0.0	0.0	0.0	0.0	222	Winemiller and Ponwith 1998
Perciformes	Eleotridae	*Eleotris amblyopsis*	N				1.5		625	Winemiller and Ponwith 1998
Perciformes	Eleotridae	*Eleotris pisonis*	N				3.1		156	Winemiller and Ponwith 1998
Perciformes	Eleotridae	*Gobiomorphus hubbsi*	N	0.0	0.0	0.0	0.0	0.0	720	Scimgeour and Winterbourn 1987
Perciformes	Eleotridae	*Gobiomorus dormitor*	N	19.8	13.3		0.4		367	Winemiller and Ponwith 1998, Martin et al. In Press
Perciformes	Eleotridae	*Gobiomorus guavina*	N	0.0	0.0	0.0	0.0	0.0	4	Winemiller and Ponwith 1998
Perciformes	Emmelichthyidae	*Inermia vittata*	N	0.0	0.0	0.0	0.0	0.0	3	Randall 1967
Perciformes	Ephippidae	*Chaetadipterus faber*	N	0.0	0.0	0.0	0.0	0.0	29	Randall 1967
Perciformes	Ephippidae	*Chaetodipterus zonatus*	N	0.0	0.0	0.0	0.0	0.0	2	Lopez-Peralta and Arcila 2002
Perciformes	Gerreidae	*Diapterus aureolus*	N			6.0			3	Lopez-Peralta and Arcila 2002
Perciformes	Gerreidae	*Diapterus peruvianus*	N			26.4			54	Lopez-Peralta and Arcila 2002
Perciformes	Gerreidae	*Eucinostomus argenteus*	N				15.9		19	Randall 1967
Perciformes	Gerreidae	*Eucinostomus gracilis*	N	0.0	0.0	0.0	0.0	0.0	4	Lopez-Peralta and Arcila 2002
Perciformes	Gerreidae	*Gerres cinereus*	Y				64.5		51	Randall 1967
Perciformes	Gobiidae	*Coryphopterus glaucofraenum*	N	0.0	0.0	0.0	0.0	0.0	4	Randall 1967
Perciformes	Gobiidae	*Gillichthys*	N	6.3		0.2			32	Martin and Saiki 2009

		mirabilis								
Perciformes	Gobiidae	*Gnatholepis thompsoni*	N	0.0	0.0	0.0	0.0	0.0	10	Randall 1967
Perciformes	Gobiidae	*Gobiosoma sp.*	N	0.0	0.0	0.0	0.0	0.0	4	Randall 1967
Perciformes	Gobiidae	*Neogobius melanostomus*	Y	22.0	4.1	6.5			30	Adamek et al. 2007, Pennuto et al. 2010
Perciformes	Gobiidae	*Neogobius fluviatilis*	N	22.0	0.4	2.0		0.5	11	Adamek et al. 2007
Perciformes	Gobiidae	*Neogobius gymnotrachelus*	N	2.2		0.4			46	Grabowska and Grabowski 2005
Perciformes	Gobiidae	*Neogobius kessleri*	N	0.0	0.0	0.0		0.0	33	Adamek et al. 2007
Perciformes	Gobiidae	*Proterorhinus marmoratus*	N	7.0	0.7	12.0		2.0	14	Adamek et al. 2007
Perciformes	Haemulidae	*Anisotremus surinamensis*	Y				25.9		62	Randall 1967
Perciformes	Haemulidae	*Anisotremus virginicus*	N				20.6		16	Randall 1967
Perciformes	Haemulidae	*Haemulon album*	N				10.8		57	Randall 1967
Perciformes	Haemulidae	*Haemulon aurolineatum*	N				11.8		28	Randall 1967
Perciformes	Haemulidae	*Haemulon carbonarium*	Y				53.5		30	Randall 1967
Perciformes	Haemulidae	*Haemulon chrysargyreum*	N				37.7		30	Randall 1967
Perciformes	Haemulidae	*Haemulon flavolineatum*	N				16.0		128	Randall 1967, Cocheret de la Moriniere 2003
Perciformes	Haemulidae	*Haemulon macrostomum*	Y				7.9		28	Randall 1967
Perciformes	Haemulidae	*Haemulon parra*	Y				41.2		33	Randall 1967
Perciformes	Haemulidae	*Haemulon plumieri*	Y				34.2		22	Randall 1967
Perciformes	Haemulidae	*Haemulon sciurus*	Y				26.7	26.7	140	Randall 1967, Cocheret de la Moriniere 2003
Perciformes	Haemulidae	*Plectorhinchus pictus*	N	33.3	10.9	19.9		20.0	56	Bachok et al. 2004
Perciformes	Haemulidae	*Pomadasys incisus*	N	7.5					463	Fehri-Bedoui and Gharbi 2008
Perciformes	Haemulidae	*Pomadasys panamensis*	N	0.0	0.0	0.0	0.0	0.0	5	Lopez-Peralta and Arcila 2002
Perciformes	Istiophoridae	*Istiophorus*	N	0.0	0.0	0.0	0.0	0.0	81	Vaske Junior et al. 2004

		albicans								
Perciformes	Istiophoridae	*Makaira nigricans*	N	0.0	0.0	0.0	0.0	0.0	24	Vaske Junior et al. 2004
Perciformes	Istiophoridae	*Tetrapturus albidus*	N	0.0	0.0	0.0	0.0	0.0	76	Vaske Junior et al. 2004
Perciformes	Istiophoridae	*Tetrapturus pfluegeri*	N	0.0	0.0	0.0	0.0	0.0	32	Vaske Junior et al. 2004
Perciformes	Kyphosidae	*Kyphosus incisor*	N	0.0	0.0	0.0	0.0	0.0	6	Randall 1967
Perciformes	Kyphosidae	*Kyphosus sectatrix*	N	0.0	0.0	0.0	0.0	0.0	19	Randall 1967
Perciformes	Labridae	*Bodianus rufus*	Y				42.8		31	Randall 1967
Perciformes	Labridae	*Clepticus parrae*	N	0.0	0.0	0.0	0.0	0.0	15	Randall 1967
Perciformes	Labridae	*Halichoeres bivittatus*	Y			41.5	44.8		192	Randall 1967, Wainwright 1988, Clifton and Motta 1998
Perciformes	Labridae	*Halichoeres garnoti*	Y			23.5	49.5		205	Randall 1967, Wainwright 1988, Clifton and Motta 1998
Perciformes	Labridae	*Halichoeres maculipinna*	Y			34.2	13.3		167	Randall 1967, Wainwright 1988, Clifton and Motta 1998
Perciformes	Labridae	*Halichoeres pictus*	N	0.0	0.0	0.0	0.0	0.0	14	Wainwright 1988
Perciformes	Labridae	*Halichoeres poeyi*	Y				57.5		61	Randall 1967, Wainwright 1988
Perciformes	Labridae	*Halichoeres radiatus*	Y				74.3		55	Randall 1967, Wainwright 1988
Perciformes	Labridae	*Hemipteronotus novacula*	Y				66.4		9	Randall 1967
Perciformes	Labridae	*Hemipteronotus splendens*	N				8.3		14	Randall 1967
Perciformes	Labridae	*Labroides dimidiatus*	N	0.0	0.0	0.0	0.0	0.0	24	Grutter 1997
Perciformes	Labridae	*Lachnolaimus maximus*	Y			51.6	45.8		95	Randall 1967, Clifton and Motta 1998
Perciformes	Labridae	*Thalassoma bifasciatum*	N			1.5	24.4		70	Randall 1967, Clifton and Motta 1998
Perciformes	Latidae	*Lates niloticus*	N	11.4			2.0		1138	Ogari and Dadzie 1988, Kishe-Machumu et al. 2012
Perciformes	Lutjanidae	*Hoplopagrus guntherii*	N			25.9			1	Lopez-Peralta and Arcila 2002
Perciformes	Lutjanidae	*Lutjanus analis*	N	16.4	3.7	4.7	60.2		194	Randall 1967, Duarte and Garcia 1999
Perciformes	Lutjanidae	*Lutjanus*	N				11.4		196	Randall 1967, Cocheret de la Moriniere 2003

		apodus								
Perciformes	Lutjanidae	*Lutjanus colorado*	N			70.6			1	Lopez-Peralta and Arcila 2002
Perciformes	Lutjanidae	*Lutjanus cyanopterus*	N	0.0	0.0	0.0	0.0	0.0	11	Randall 1967
Perciformes	Lutjanidae	*Lutjanus gibbus*	N	0.0	0.0	0.0	0.0	0.0	111	Bachok et al. 2004
Perciformes	Lutjanidae	*Lutjanus griseus*	N				23.4		112	Randall 1967, Cocheret de la Moriniere 2003
Perciformes	Lutjanidae	*Lutjanus guttatus*	N			10.1			34	Lopez-Peralta and Arcila 2002
Perciformes	Lutjanidae	*Lutjanus jocu*	N				19.0		92	Randall 1967
Perciformes	Lutjanidae	*Lutjanus jordani*	N	0.0	0.0	0.0	0.0	0.0	4	Lopez-Peralta and Arcila 2002
Perciformes	Lutjanidae	*Lutjanus mahogoni*	N				3.1		27	Randall 1967
Perciformes	Lutjanidae	*Lutjanus malabaricus*	N	0.0		0.0	0.0	0.0	125	Bachok et al. 2004
Perciformes	Lutjanidae	*Lutjanus sanguineus*	N	6.3	8.3	1.1		0.6	113	Bachok et al. 2004
Perciformes	Lutjanidae	*Lutjanus synagris*	N				50.0		6	Randall 1967
Perciformes	Lutjanidae	*Ocyurus chrysurus*	N				14.5		128	Randall 1967, Cocheret de la Moriniere 2003
Perciformes	Lutjanidae	*Pristipomoides filamentosus*	N	11.1	1.6	1.7		0.5	181	Bachok et al. 2004
Perciformes	Lutjanidae	*Rhomboplites aurorubens*	N	11.1	8.1	1.4	10.7	7.0	998	Johnson et al. 2010, Grimes 1979
Perciformes	Mullidae	*Mulloidichthys martinicus*	N				29.7		23	Randall 1967
Perciformes	Mullidae	*Mullus barbatus*	N		14.4	23.3			550	Labropoulous and Eleftheriou 1997
Perciformes	Mullidae	*Mullus surmuletus*	N		33.4	26.1			322	Labropoulous and Eleftheriou 1997
Perciformes	Mullidae	*Pseudopeneus maculatus*	N				37.7		27	Randall 1967
Perciformes	Opisthognathidae	*Opisthognathus aurifrons*	N	0.0	0.0	0.0	0.0	0.0	16	Randall 1967
Perciformes	Opisthognathidae	*Opisthognathus macrognathus*	N	0.0	0.0	0.0	0.0	0.0	1	Randall 1967
Perciformes	Opisthognathidae	*Opisthognathus maxillosus*	N	0.0	0.0	0.0	0.0	0.0	14	Randall 1967

Perciformes	Opisthognathidae	*Opisthognathus whitehurstii*	N				5.0		9	Randall 1967
Perciformes	Pempheridae	*Pempheris schomburgki*	N	0.0	0.0	0.0	0.0	0.0	19	Randall 1967
Perciformes	Percichthyidae	*Macquaria ambigua*	N	0.0	0.0	0.0	0.0	0.0	33	Sternberg et al. 2008
Perciformes	Percidae	*Morone americana*	N			24.5			204	Couture and Watzin 2008
Perciformes	Percidae	*Perca flavescens*	N	37.9		0.5	26.5		127	Keast 1978, Morrison et al. 1997, Pothoven et al. 2000
Perciformes	Percidae	*Perca fluviatilis*	N				0.8		1410	Lappalainen et al. 2001
Perciformes	Percidae	*Percina caprodes*	N				1.0		42	Keast 1978
Perciformes	Percidae	*Stizostedion lucioperca*	N	0.0	0.0	0.0	0.0	0.0	591	Kangur and Kangur 1998
Perciformes	Pinguipedidae	*Cheimarrichthys fosteri*	N	0.0	0.0	0.0	0.0	0.0	569	Scimgeour and Winterbourn 1987
Perciformes	Pinguipedidae	*Pinguipes chilensis*	N	>4	1.2		5.4	0.7	414	Gonzalez and Oyarzun 2003
Perciformes	Polynemidae	*Polydactylus approximans*	N	0.0	0.0	0.0	0.0	0.0	3	Lopez-Peralta and Arcila 2002
Perciformes	Polynemidae	*Polydactylus opercularis*	N			4.2			3	Lopez-Peralta and Arcila 2002
Perciformes	Pomacentridae	*Abudefduf taurus*	N				0.5		17	Randall 1967
Perciformes	Pomacentridae	*Chromis cyanea*	N	0.0	0.0	0.0	0.0	0.0	17	Randall 1967
Perciformes	Pomacentridae	*Chromis multilineata*	N	0.0	0.0	0.0	0.0	0.0	68	Randall 1967
Perciformes	Pomacentridae	*Microspathodon chrysurus*	N				0.1		45	Randall 1967
Perciformes	Pomacentridae	*Pomacenthus fuscus*	N				6.2		51	Randall 1967
Perciformes	Pomacentridae	*Pomacentrus leucostictus*	N				4.2		41	Randall 1967
Perciformes	Pomacentridae	*Pomacentrus planifrons*	N	0.0	0.0	0.0	0.0	0.0	18	Randall 1967
Perciformes	Pomacentridae	*Pomacentrus variabilis*	N				1.7		7	Randall 1967
Perciformes	Pomatomidae	*Pomatomus saltatrix*	N	1.0	1.0	2.4			628	Lucena et al. 2000, Harding and Mann 2001
Perciformes	Priacanthidae	*Priacanthus arenatus*	N				9.8		29	Randall 1967

Perciformes	Priacanthidae	*Priacanthus cruentatus*	N				15.6		32	Randall 1967
Perciformes	Rachycentridae	*Rachycentron canadum*	N	21.7	28.2	1.9	39.5	25.6	213	Randall 1967, Arendt 2001, Bachok et al. 2004
Perciformes	Scaridae	*Scarus coelestinus*	N	0.0	0.0	0.0	0.0	0.0	14	Randall 1967
Perciformes	Scaridae	*Scarus croicensis*	N	0.0	0.0	0.0	0.0	0.0	9	Randall 1967
Perciformes	Scaridae	*Scarus guacamaia*	N	0.0	0.0	0.0	0.0	0.0	15	Randall 1967
Perciformes	Scaridae	*Scarus taeniopterus*	N	0.0	0.0	0.0	0.0	0.0	8	Randall 1967
Perciformes	Scaridae	*Scarus vetula*	N	0.0	0.0	0.0	0.0	0.0	14	Randall 1967
Perciformes	Scaridae	*Sparisoma aurofrenatum*	N	0.0	0.0	0.0	0.0	0.0	11	Randall 1967
Perciformes	Scaridae	*Sparisoma chrysopterum*	N	0.0	0.0	0.0	0.0	0.0	6	Randall 1967
Perciformes	Scaridae	*Sparisoma radians*	N	0.0	0.0	0.0	0.0	0.0	5	Randall 1967
Perciformes	Scaridae	*Sparisoma rubripinne*	N	0.0	0.0	0.0	0.0	0.0	18	Randall 1967
Perciformes	Scaridae	*Sparisoma viride*	N	0.0	0.0	0.0	0.0	0.0	20	Randall 1967
Perciformes	Sciaenidae	*Aplodinotus grunniens*	Y	43.0			21.0		14	Morrison et al. 1997
Perciformes	Sciaenidae	*Argyrosomus japonicus*	N	0.0	0.0	0.0	0.0	0.0	413	Taylor et al. 2006
Perciformes	Sciaenidae	*Cynoscion arenarius*	N	0.0	0.0	0.0	0.0	0.0	108	Overstreet and Heard 1982
Perciformes	Sciaenidae	*Cynoscion guatucupa*	N			0.9			506	Lucena et al. 2000
Perciformes	Sciaenidae	*Cynoscion nebulosus*	N	0.3					373	Overstreet and Heard 1982
Perciformes	Sciaenidae	*Cynoscion nothus*	N	0.0	0.0	0.0	0.0	0.0	25	Overstreet and Heard 1982
Perciformes	Sciaenidae	*Equetus acuminatus*	N				5.3		35	Randall 1967
Perciformes	Sciaenidae	*Equetus lanceolatus*	N				6.2		5	Randall 1967
Perciformes	Sciaenidae	*Equetus punctatus*	N				49.5		28	Randall 1967
Perciformes	Sciaenidae	*Larimus pacificus*	N	0.0	0.0	0.0	0.0	0.0	12	Lopez-Peralta and Arcila 2002

Perciformes	Sciaenidae	*Odontoscion dentex*	N				5.2		75	Randall 1967
Perciformes	Sciaenidae	*Pogonias cromis*	Y	37.5	31.5	21.6	42.5	22.5	229	Overstreet and Heard 1982, Cate and Evans 1994, Hulsey et al. 2005, Blasina et al. 2010
Perciformes	Sciaenidae	*Sciaenops ocellatus*	N	16.5		8.3	42.8		1398	Peters and McMichael 1987, Scharf and Schlicht 2000, Hulsey et al. 2005
Perciformes	Sciaenidae	*Seriphus polotus*	N	0.0	0.0	0.0	0.0	0.0	521	deMartini et al. 1984
Perciformes	Scombridae	*Euthynnus alletteratus*	N	0.0	0.0	0.0	0.0	0.0	29	Randall 1967
Perciformes	Scombridae	*Scomber* spp.	N	0.0	0.0	0.0	0.0	0.0	217	Sassa et al. 2008
Perciformes	Scombridae	*Scomberomorus cavalla*	N	0.0	0.0	0.0	0.0	0.0	22	Randall 1967
Perciformes	Scombridae	*Scomberomorus regalis*	N	0.0	0.0	0.0	0.0	0.0	116	Randall 1967
Perciformes	Scombridae	*Scomberomorus sierra*	N			1.5			12	Lopez-Peralta and Arcila 2002
Perciformes	Scombridae	*Thunnus maccoyii*	N	0.0	0.0	0.0	0.0	0.0	1219	Young et al. 1997
Perciformes	Serranidae	*Alphestes afer*	N				77.0		36	Randall 1967
Perciformes	Serranidae	*Centropristis striata*	N	2.9	0.3		0.4		313	Sedberry 1988
Perciformes	Serranidae	*Cephalopholis fulva*	N				17.2		58	Randall 1967
Perciformes	Serranidae	*Epinephelus adscensionis*	N				69.9		56	Randall 1967
Perciformes	Serranidae	*Epinephelus guttatus*	N				39.5		110	Randall 1967
Perciformes	Serranidae	*Epinephelus itajara*	N				12.2		9	Randall 1967
Perciformes	Serranidae	*Epinephelus morio*	N				33.3		5	Randall 1967
Perciformes	Serranidae	*Epinephelus striatus*	N				24.8		255	Randall 1967
Perciformes	Serranidae	*Hypoplectrus abberans*	N				18.7		25	Randall 1967
Perciformes	Serranidae	*Hypoplectrus chlorurus*	N				17.1		20	Randall 1967
Perciformes	Serranidae	*Hypoplectrus nigricans*	N				17.6		35	Randall 1967
Perciformes	Serranidae	*Hypoplectus puella*	N				21.1		38	Randall 1967

Perciformes	Serranidae	*Mycteroperca bonaci*	N	0.0	0.0	0.0	0.0	0.0	6	Randall 1967
Perciformes	Serranidae	*Mycteroperca interstitialis*	N	0.0	0.0	0.0	0.0	0.0	8	Randall 1967
Perciformes	Serranidae	*Mycteroperca tigris*	N	0.0	0.0	0.0	0.0	0.0	59	Randall 1967
Perciformes	Serranidae	*Mycteroperca venenosa*	N	0.0	0.0	0.0	0.0	0.0	127	Randall 1967
Perciformes	Serranidae	*Paranthias furcifer*	N	0.0	0.0	0.0	0.0	0.0	13	Randall 1967
Perciformes	Serranidae	*Petrometopon cruentatum*	N				7.6		75	Randall 1967
Perciformes	Serranidae	*Rypticus saponaceus*	N				9.6		27	Randall 1967
Perciformes	Serranidae	*Serranus cabrilla*	N		20.2	8.9			601	Labropoulous and Eleftheriou 1997
Perciformes	Serranidae	*Serranus hepatus*	N		17.3	33.1			583	Labropoulous and Eleftheriou 1997
Perciformes	Serranidae	*Serranus tabacarius*	N	0.0	0.0	0.0	0.0	0.0	4	Randall 1967
Perciformes	Serranidae	*Serranus tigrinus*	N				7.8		26	Randall 1967
Perciformes	Serranidae	*Serranus tortugarum*	N	0.0	0.0	0.0	0.0	0.0	2	Randall 1967
Perciformes	Sparidae	*Archosargus probatocephalus*	Y	21.0			23.8		193	Overstreet and Heard 1982, Cutwa and Turingan 2000
Perciformes	Sparidae	*Archosargus rhomboidalis*	Y	10.0		19.0	9.1		83	Randall 1967, Vaughan 1978
Perciformes	Sparidae	*Calamus bajonado*	Y				33.3		10	Randall 1967
Perciformes	Sparidae	*Calamus brachysomus*	Y			39.7			7	Lopez-Peralta and Arcila 2002
Perciformes	Sparidae	*Calamus calamus*	Y				21.1		15	Randall 1967
Perciformes	Sparidae	*Calamus leucosteus*	Y	>58.5	28.6		19.8		219	Sedberry 1989
Perciformes	Sparidae	*Calamus penna*	Y				100.0		3	Randall 1967
Perciformes	Sparidae	*Calamus pennatula*	Y				41.8		15	Randall 1967
Perciformes	Sparidae	*Diplodus caudimacula*	Y				18.0		5	Randall 1967
Perciformes	Sparidae	*Diplodus puntazzo*	Y	>62.5		4.0			16	Sala and Ballesteros 1997

Perciformes	Sparidae	*Diplodus sargus*	Y	>45.9	58.8	58.0		48.5	481	Sala and Ballesteros 1997, Osman and Mahmoud 2009
Perciformes	Sparidae	*Diplodus vulgaris*	Y	17.6	16.7	39.5		24.7	868	Sala and Ballesteros 1997, Pallaoro et al. 2006, Osman and Mahmoud 2009
Perciformes	Sparidae	*Lithognathus mormyrus*	Y	>47	26.4		32.1	37.3	120	Kallianiotis et al. 2005
Perciformes	Sparidae	*Oblada melanura*	N		0.1	4.9		0.1	926	Pallaoro et al. 2003
Perciformes	Sparidae	*Pagrus linnaeus*	Y	>59.2			39.9		779	Manooch 1977
Perciformes	Sparidae	*Pterogymnus laniarius*	Y	>60.9		63.5	52.5		302	Booth and Buxton 1997
Perciformes	Sphyraenidae	*Sphyraena barracuda*	N	0.0	0.0	0.0	0.0	0.0	104	Randall 1967
Perciformes	Sphyraenidae	*Sphyraena ensis*	N	0.0	0.0	0.0	0.0	0.0	5	Lopez-Peralta and Arcila 2002
Perciformes	Sphyraenidae	*Sphyraena jello*	N	0.0	0.0	0.0	0.0	0.0	17	Bachok et al. 2004
Perciformes	Sphyraenidae	*Sphyraena obtusata*	N	0.0	0.0	0.0	0.0	0.0	52	Bachok et al. 2004
Perciformes	Sphyraenidae	*Sphyraena picudilla*	N	0.0	0.0	0.0	0.0	0.0	13	Randall 1967
Perciformes	Trichiuridae	*Trichiurus lepturus*	N	0.0	0.0	0.0	0.0	0.0	836	Chiou et al. 2006
Pleuronectiformes	Bothidae	*Bothus lunatus*	N	0.0	0.0	0.0	0.0	0.0	11	Randall 1967
Pleuronectiformes	Bothidae	*Bothus ocellatus*	N				25.0		9	Randall 1967
Pleuronectiformes	Paralichthyidae	*Ancylopsetta dendritica*	N	0.0	0.0	0.0	0.0	0.0	1	Lopez-Peralta and Arcila 2002
Pleuronectiformes	Paralichthyidae	*Hippoglossina tetrophthalma*	N			1.5			1	Lopez-Peralta and Arcila 2002
Pleuronectiformes	Paralichthyidae	*Paralichthys dentatus*	N	1.0	0.3	0.6			137	Rountree and Able 1992
Pleuronectiformes	Paralichthyidae	*Paralichthys lethostigma*	N	0.0	0.0	0.0	0.0	0.0	212	Overstreet and Heard 1982
Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	N					0.9	815	Landingham et al. 1998
Salmoniformes	Salmonidae	*Oncorhynchus keta*	N					0.2	453	Landingham et al. 1998
Salmoniformes	Salmonidae	*Oncorhynchus kisutch*	N					0.0	543	Landingham et al. 1998
Salmoniformes	Salmonidae	*Oncorhynchus nerka*	N					0.2	361	Landingham et al. 1998

Salmoniformes	Salmonidae	*Oncorhynchus tshawytscha*	N	0.0	0.0	0.0	0.0	0.0	38	Landingham et al. 1998
Salmoniformes	Salmonidae	*Salmo clarkii*	N	1.0	1.0				120	Hynes 1950
Salmoniformes	Salmonidae	*Salmo gairdneri*	N	3.0	1.0				220	Hynes 1950
Salmoniformes	Salmonidae	*Salmo salar*	N	1.8	0.7				192	Hynes 1950
Salmoniformes	Salmonidae	*Salmo trutta*	N	1.3					577	Hynes 1950
Scorpaeniformes	Dactylopteridae	*Dactylopterus volitans*	N				61.7		7	Randall 1967
Scorpaeniformes	Scorpaenidae	*Pterois volitans*	N	1.1				0.2	1295	Morris and Atkins 2009, Munoz et al. 2011
Scorpaeniformes	Scorpaenidae	*Scorpaena brasiliensis*	N				7.1		13	Randall 1967
Scorpaeniformes	Scorpaenidae	*Scorpaena grandicornis*	N	0.0	0.0	0.0	0.0	0.0	15	Randall 1967
Scorpaeniformes	Scorpaenidae	*Scorpaena inermis*	N				0.6		28	Randall 1967
Scorpaeniformes	Scorpaenidae	*Scorpaena plumieri*	N				32.9		28	Randall 1967
Scorpaeniformes	Scorpaenidae	*Scorpaenodes caribbaeus*	N				17.3		21	Randall 1967
Scorpaeniformes	Triglidae	*Prionotus stephanophrys*	N			100			1	Lopez-Peralta and Arcila 2002
Siluriformes	Ariidae	*Arius oetik*	N	5.4	3.2	13.1		16.9	71	Bachok et al. 2004
Siluriformes	Bagridae	*Bagrus docmac*	Y	41.2					916	Okach and Dadzie 1988, Olowo and Chapman 1999
Siluriformes	Clariidae	*Clariallabes longicauda*	N		32.4	0.2		7.8	47	Wyckmans et al. 2007
Siluriformes	Clariidae	*Clariallabes melas*	N	3.9	3.2	2.0		0.9	51	Wyckmans et al. 2011
Siluriformes	Ictaluridae	*Ameiurus nebulosus*	N				9.0		49	Keast 1978
Siluriformes	Ictaluridae	*Pylodictis olivaris*	N	5.2	3.6	0.5			866	Weller and Robbins 1999
Siluriformes	Mochokidae	*Synodontis zambezensis*	Y	>25	30.4	50.1		80.1	441	Sanyanga 1998
Syngnathiformes	Aulostomidae	*Aulostomus maculatus*	N	0.0	0.0	0.0	0.0	0.0	80	Randall 1967
Syngnathiformes	Fistulariidae	*Fistularia commersonii*	N	0.0	0.0	0.0	0.0	0.0	841	Bariche et al. 2009

Syngnathiformes	Fistulariidae	*Fistularia tabacaria*	N	0.0	0.0	0.0	0.0	0.0	4	Randall 1967
Tetraodontiformes	Balistidae	*Balistes vetula*	Y	>69.2		33.4	13.5		106	Randall 1967, von Schiller and Garcia 2000
Tetraodontiformes	Balistidae	*Canthidermis sufflamen*	N	0.0	0.0	0.0	0.0	0.0	5	Randall 1967
Tetraodontiformes	Balistidae	*Melichthys niger*	N				6.1		17	Randall 1967
Tetraodontiformes	Diodontidae	*Chilomycterus antennatus*	Y				57.6		5	Randall 1967
Tetraodontiformes	Diodontidae	*Diodon holacanthus*	Y			96.9	71.4		7	Randall 1967, Lopez-Peralta and Arcila 2002
Tetraodontiformes	Diodontidae	*Diodon hystrix*	Y				52.1		42	Randall 1967
Tetraodontiformes	Monacanthidae	*Alutera schoepfi*	N				1.2		5	Randall 1967
Tetraodontiformes	Monacanthidae	*Alutera scripta*	N				0.6		8	Randall 1967
Tetraodontiformes	Monacanthidae	*Aluterus monoceros*	N			0.1			7	Lopez-Peralta and Arcila 2002
Tetraodontiformes	Monacanthidae	*Catherhines macrocerus*	N	0.0	0.0	0.0	0.0	0.0	10	Randall 1967
Tetraodontiformes	Monacanthidae	*Catherhines pullus*	N	0.0	0.0	0.0	0.0	0.0	27	Randall 1967
Tetraodontiformes	Monacanthidae	*Monacanthus ciliatus*	N				3.8		14	Randall 1967
Tetraodontiformes	Monacanthidae	*Monacanthus tuckeri*	N	0.0	0.0	0.0	0.0	0.0	4	Randall 1967
Tetraodontiformes	Ostraciidae	*Acanthostracion polygonius*	N				1.7		4	Randall 1967
Tetraodontiformes	Ostraciidae	*Acanthostracion quadricornis*	N				8.6		6	Randall 1967
Tetraodontiformes	Ostraciidae	*Lactophrys bicaudalis*	N				5.0		12	Randall 1967
Tetraodontiformes	Ostraciidae	*Lactophrys trigonus*	Y				47.4		21	Randall 1967
Tetraodontiformes	Ostraciidae	*Lactophrys triqueter*	N				14.2		17	Randall 1967
Tetraodontiformes	Tetraodontidae	*Canthigaster rostrata*	N				24.5		26	Randall 1967
Tetraodontiformes	Tetraodontidae	*Sphaeroides spengleri*	Y				30.9		31	Randall 1967

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