

The interplay between resource supply and demand determines the influence of predation on prey body size¹

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Abstract: Predation has been shown to either increase or decrease the body mass of fish, as well as cause variable changes in growth rate. The mechanisms underlying these contrasting responses are not well understood. Here we compared intraspecific body size and growth responses to predation against a backdrop of 2006 estimates of asymptotic mass and growth constants (i.e., von Bertalanffy parameters) across species. We show that intraspecific responses can be quite large relative to interspecific variation and confirm that the magnitude and direction of body size responses is variable. We then employed the supply-demand (SD) model of body mass evolution to explore how predator-induced changes in resource demand or supply could alter body mass. The SD model predicts that any combination of increasing or decreasing body mass and increasing or decreasing growth rate is possible when predation risk is increased, which is consistent with the literature. Finally, we use three case studies to illustrate how the interplay of resource supply and resource demand determines the actual body mass and growth rate response to predation.

Résumé : Il a été démontré que la prédation peut accroître ou réduire la masse corporelle des poissons, tout en modifiant le taux de croissance de manière variable. Les mécanismes qui sous-tendent ces réactions divergentes ne sont pas bien compris. Nous comparons les réactions intraspécifiques à la prédation en termes de taille du corps et de croissance par rapport à 2006 estimations de constantes asymptotiques de masse et de croissance (c.-à-d. paramètres de Bertalanffy) pour différentes espèces. Nous démontrons que les réactions intraspécifiques peuvent être très importantes comparativement aux variations interspécifiques et confirmons que l'ampleur et la direction des réactions de la taille du corps sont variables. Nous utilisons ensuite un modèle d'offre et de demande (OD) de l'évolution de la masse corporelle pour examiner comment les changements de la demande ou de l'offre de ressources induits par les prédateurs peuvent modifier la masse corporelle. Le modèle OD prédit que toutes les combinaisons de masse corporelle croissante ou décroissante et de taux de croissance croissant ou décroissant sont possibles quand le risque de prédation augmente, ce qui concorde avec les études déjà publiées. Enfin, nous utilisons trois études de cas pour illustrer comment la combinaison de l'offre et de la demande de ressources détermine les réactions réelles à la prédation de la masse corporelle et du taux de croissance. [Traduit par la Rédaction]

Introduction

Body mass is related to many natural processes and patterns (Peters 1983; Calder 1996; Brown et al. 2004). As a result, body mass ties together many aspects of the ecology and evolution of natural communities (Bonner 2006). Body mass is also highly responsive to environmental gradients, including temperature (Atkinson 1994), land area (Lomolino 2005), latitude (Blackburn et al. 1999), resources (Kimmance et al. 2006), and predation risk (Kozłowski 1996a; Riessen 1999). Because of the links between body mass and processes and between environmental gradients and mass, body mass may play an important role in mediating how communities respond to environmental change. It is thus crucial to understand the evolution of and plasticity in body mass.

Many studies have explored the connections between environmental gradients and body size. Despite evidence that a particular body mass can maximize fitness (Roff 1986; Kozłowski 1992), associations between environmental gradients and body size often lack generality. For example, body mass often declines with warming for ectotherms (the temperature–size rule; Atkinson 1994), but there are many counterexamples in which body mass gets larger with warming (Atkinson 1995; DeLong and Hanson 2011). Similarly,

body mass is often smaller on islands than on the nearby mainland, but sometimes, it is the reverse (Bromham and Cardillo 2007), and body mass may increase or decrease with latitude (Blanckenhorn and Demont 2004). Complicating the picture, many organisms show changes in growth rate in response to the same environmental gradients that are influencing body mass (e.g., Riessen 1999; DeLong 2012). Because growth rate and body mass may be functionally connected (Beverton and Holt 1959; Kozłowski 1992; Charnov 1993; Elliott and Hurley 1995), the joint response of growth rate and body mass to various environmental signals may be more informative than either response alone.

Body mass may be linked to predation risk via plastic responses to predator exposure (e.g., Riessen 1999; Basolo and Wagner 2004) or evolutionary responses to increased predator-induced mortality (Walsh and Reznick 2008; Reznick et al. 1990). The optimal body mass of prey in response to predation risk, however, may be complicated by the indirect effects of predators on food resources (Wootton 1994). For example, predators may inhibit foraging in prey (Lima and Dill 1990), reducing food intake, or increase the food available to survivors, increasing food intake. Thus, it is likely that the observed body size under predation risk may arise

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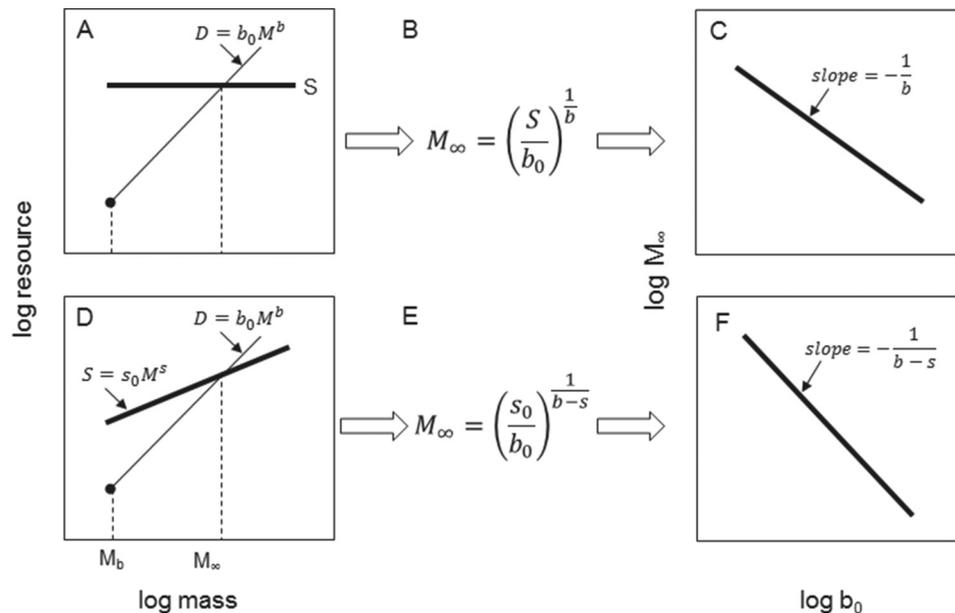
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Fig. 1. Schematic of the supply–demand (SD) model. (A) and (D) show graphically how the supply and demand curves (S and D , respectively) intersect to determine asymptotic body size, both with a horizontal supply curve (A) and a nonhorizontal supply curve (D). (B) and (E) show the derived equations for asymptotic size under the assumptions in (A) and (D), respectively. (C) and (F) show the predicted relationship between the log of asymptotic mass and the log of demand under the assumptions in (A) and (D), respectively. M_∞ is asymptotic mass and M_b is mass at the beginning of independent life.



through the interaction of a life history or activity strategy shift and a change in food availability.

In this study, we use a recent model for understanding and predicting optimal body mass to assess whether apparently idiosyncratic responses of fish to predation risk can be understood as outcomes of a general process. Our approach will be to illustrate variation in the response of asymptotic mass and the growth constant for von Bertalanffy parameters for a range of fish that exhibit plasticity or evolved differences in response to predator-induced mortality or risk (Belk and Hales 1993; Bell et al. 2011; Billman et al. 2011; Herczeg et al. 2012). We show that these responses can be quite large relative to interspecific variation and that the responses are qualitatively variable. We then employ the supply–demand (SD) model of optimal body mass (DeLong 2012) to illustrate how all of the observed responses can arise through a general process.

The supply–demand model

The SD model (DeLong 2012; DeLong and Hanley 2013; DeLong et al. 2014) proposes that the optimal body mass is that which matches resource demand to the expected environmental supply of resources (Fig. 1). This makes sense because an organism that is not large enough to use all of the available resources is competitively inferior to an organism that is large enough to do so, whereas an organism that is so large that it cannot meet its nutritional needs will suffer costs associated with low survival or reproduction. Thus, the most fit body mass is one that maximizes total resource use given the supply constraint (Lotka 1922). This optimization principle is akin to maximizing the production function in resource allocation models (e.g., Kozłowski 1992, 1996b), with the idea being that maximizing production maximizes the opportunity to allocate toward reproduction and survival, given the environment. The SD model applies to changes in body mass through phenotypic plasticity and through genetic change, and because there are no taxon-specific assumptions, the model applies in principle to all living things.

The decision of when to cease allocating towards somatic growth is a key determinant of adult mass (Kozłowski 1992;

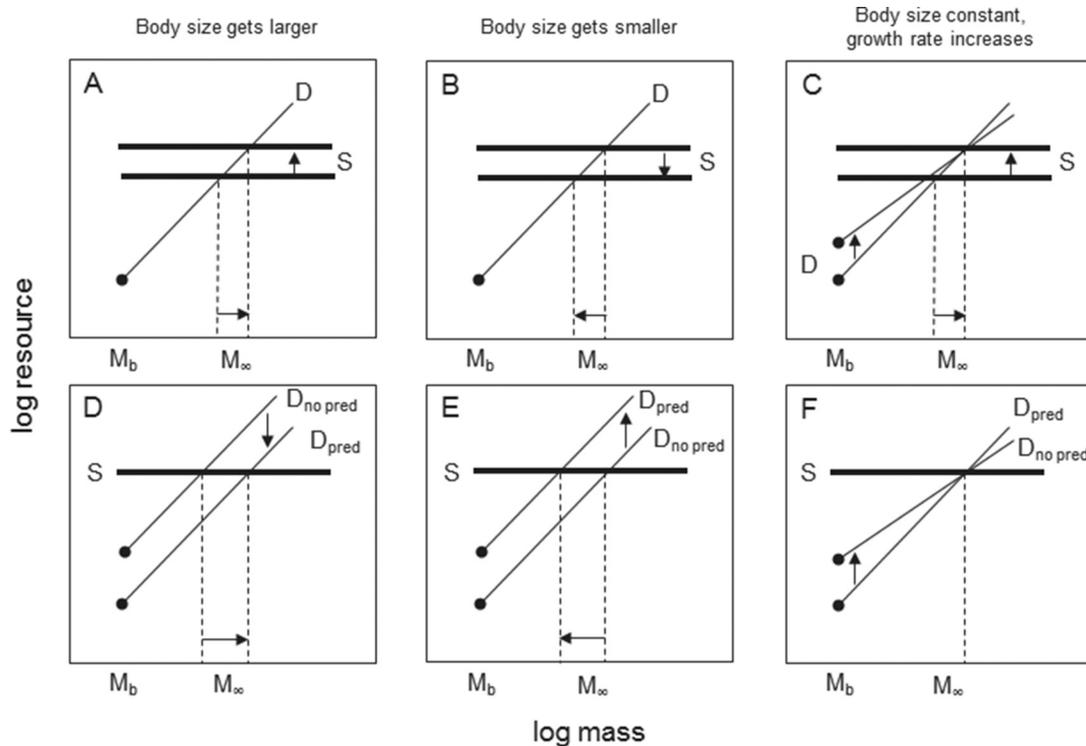
Davidowitz and Nijhout 2004). To develop the SD model, then, we first assume that an organism begins life with mass M_b (birth mass) and begins to grow. As it grows, the individual requires more resources. In the SD model, the curve that describes the relationship between the required resources and body mass is called the demand curve (D). The demand curve is assumed to be a power law function of mass, along the lines of a metabolic scaling function, although other functions may work as well. The SD model proposes that the mass at which the individual should stop growing (the optimum) is where the D curve intersects the supply curve (S), which indicates the amount of resource that an individual expects to get at any particular mass (Fig. 1A). If $D = b_0 M^b$, where b_0 is the demand at unit mass, M is mass, and b is a scaling parameter, and assuming that the asymptotic mass occurs where $S = D$ and the supply curve is horizontal (i.e., independent of body mass), we arrive at a simple, explicit expression for asymptotic mass (M_∞ ; Fig. 1B):

$$(1) \quad M_\infty = \left(\frac{S}{b_0}\right)^{\frac{1}{b}}$$

This model predicts that the optimal mass should increase with resource supply and decrease with increasing demand. In log space, eq. 1 predicts a linear relationship between asymptotic mass and metabolic demand with a slope of $-1/b$ (Fig. 1C).

It is possible, however, that the supply curve can be nonlinear. In particular, it is plausible that the supply curve increases with body mass such that organisms have access to more food as they grow (Fig. 1D). Such an increase may be common with many fish that exhibit ontogenetic niche shifts and switch from smaller invertebrates to successively larger prey as they grow (e.g., Sherwood et al. 2002; De Roos and Persson 2013). If we account for this by writing S as a power law, $S = s_0 M^s$, where s_0 is the supply at unit mass and s is a scaling parameter, we obtain a slightly more general expression for asymptotic mass (Fig. 1E):

Fig. 2. Many possible patterns of change in asymptotic size can arise from different directions of change in the supply (S) and the demand (D) curves. In (A), body size increases as supply is increased. In (B), body size decreases as supply is reduced. In (C), a change in the demand curve, for example, becoming steeper, can interact with a change in supply, altering the magnitude of the body size change. In (D), a decrease in demand under predation risk (a conservative, predator-avoiding strategy) can allow growth to larger size, whereas in (E), an increase in demand under predation risk will cause a reduced body size. Finally, in (F), changes in the slope of the demand curve that leave the intersection of supply and demand in the same location may not result in a change in body size. M_∞ is asymptotic mass and M_b is mass at the beginning of independent life.



$$(2) \quad M_\infty = \left(\frac{s_0}{b_0} \right)^{\frac{1}{b-s}}$$

Equation 2 predicts a linear relationship in log space between asymptotic mass and metabolic demand with a slope of $-1/(b-s)$. The slope is steeper than if the S curve was horizontal if the scaling parameter s is positive and shallower if it is negative (Fig. 1F).

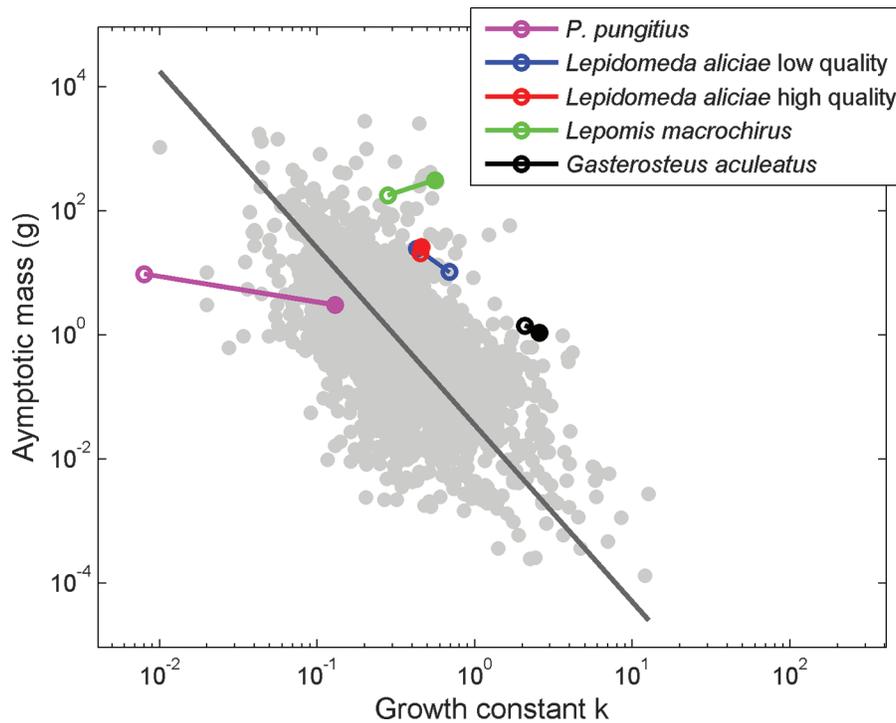
The SD model illustrates how asymptotic body mass and metabolic demands can respond to environmental gradients in multiple ways. For example, body mass can increase with resource levels (Fig. 2A), without a concomitant change in metabolic demand, but a lowering of metabolic demand can also lead to larger body mass if the supply is held constant (Fig. 2D). The converse is also true: body mass can get smaller if resources become less abundant or also if metabolic demands increase while holding supply constant (Figs. 2B, 2E). This latter pattern is what appears to happen when body mass gets smaller in response to warming (DeLong 2012). If shifts in the metabolic scaling slope occur (e.g., the slope gets steeper with predation risk; Glazier et al. 2011), changes in metabolic demands can appear decoupled from body mass changes, depending on how the shift alters the intersection of the supply and demand curves (Figs. 2C, 2F). Finally, if the supply and demand curves both shift in response to an environmental gradient, then any combination of increasing or decreasing body mass or increasing or decreasing metabolic demands are possible, and then the intersection of the supply and demand curves can move in any direction (Figs. 2C, 2F).

Because the SD model can make quantitative predictions about the magnitude of changes, it is possible to set up strong tests of

the model. Two such tests have been conducted. First, eq. 1 predicts that an increase in metabolic demand due to temperature should drive down body size if the supply is held constant, providing a simple mechanistic explanation for widespread declines in body size with temperature (the temperature-size rule; Atkinson 1994). DeLong (2012) exposed the predatory protist *Actinosphaerium* to three temperatures and measured the resulting changes in cell volume and biomass production rate (demand). In this experiment, a horizontal supply curve (an essential mathematical assumption in eq. 1) was maintained by manually normalizing prey levels across all replicates. Using eq. 1 with an independent estimate of b at 1.06 (DeLong et al. 2010), the predicted slope between the log of cell volume and the log of production was -0.94 , and the observed value was -0.91 . This close quantitative agreement of theory and data lend strong support to the SD model.

Equation 1 similarly predicts that variation in metabolic demand due to any other kind of process, e.g., inherent genetic variation or predation risk, could drive similar changes in body size. DeLong and Hanley (2013) studied cross-individual variation in growth rate (a proxy for metabolic demand, given by the von Bertalanffy growth constant) and asymptotic mass in genetically different *Daphnia ambigua*. In *Daphnia*, the metabolic scaling slope is, on average, 0.96 under good food conditions and, on average, 0.83 for low food conditions, which suggests that the slope of the relationship between the log of asymptotic mass and the log of the growth constant should shift from about -1.04 in high food to about -1.21 in low food. In this study, daphnids were grown under high and low food levels, and the slopes were exactly as predicted (-1.0 in high food and -1.25 in low food). Both the quantitative agreement between predicted and observed slopes and the shift in slopes given a change in the demand curve provide strong support

Fig. 3. The von Bertalanffy asymptotic mass and growth constant for ray-finned fishes from FishBase (Froese and Pauly 2014) and for four species experiencing variation in predation risk. Open circles represent no predation; solid circles represent predation. Sources: *Pungitius pungitius*, Herczeg et al. 2012; *Lepidomeda aliciae*, Billman et al. 2011; *Gasterosteus aculeatus*, Bell et al. 2011; *Lepomis macrochirus*, Belk and Hales 1993. The solid gray line is a reduced major axis fit to the FishBase data with a slope of -2.85 .



for the model. Yet this study also reveals that a good estimate of b is important and that one might need to be aware of potential changes in b under varying conditions. For example, under higher predation risk, the amphipod *Gammarus minus* shows a shallower metabolic scaling slope, which would alter the predicted changes in mass (Glazier et al. 2011).

In this study, our objective is to explore predation-induced variation in growth and asymptotic mass of teleost fish within the context of the SD model. Specifically, we (i) assess the overall relationship between asymptotic mass and growth constant across teleost fishes to provide a backdrop for the predation-induced changes, (ii) compare changes in asymptotic mass and growth constant induced by predation risk to this broad cross-species pattern, and (iii) illustrate how divergent responses to predation can be unified within the SD framework.

Methods

The SD model explains changes in body mass as an interactive response to changes in the environmental supply of resources and the bodily demand for those resources. To consider the effect of predation risk on changes in demand and body size in fish, then, we need estimates or proxies of mass and metabolic demand. We used parameters from the von Bertalanffy growth model: asymptotic length (l_{inf}) converted to mass and the growth constant (k) as a proxy for demand. The growth constant reflects growth rate and is clearly responsive to environmental drivers for metabolic demand (Charnov 1993). Although k is an imperfect proxy for growth and total metabolic demand (Rennie et al. 2005), the requirement of metabolic fuel for growth and the fact that faster growing organisms will show a higher k , all else being equal, indicates that k can serve as a useful surrogate for metabolic demand (DeLong and Hanley 2013).

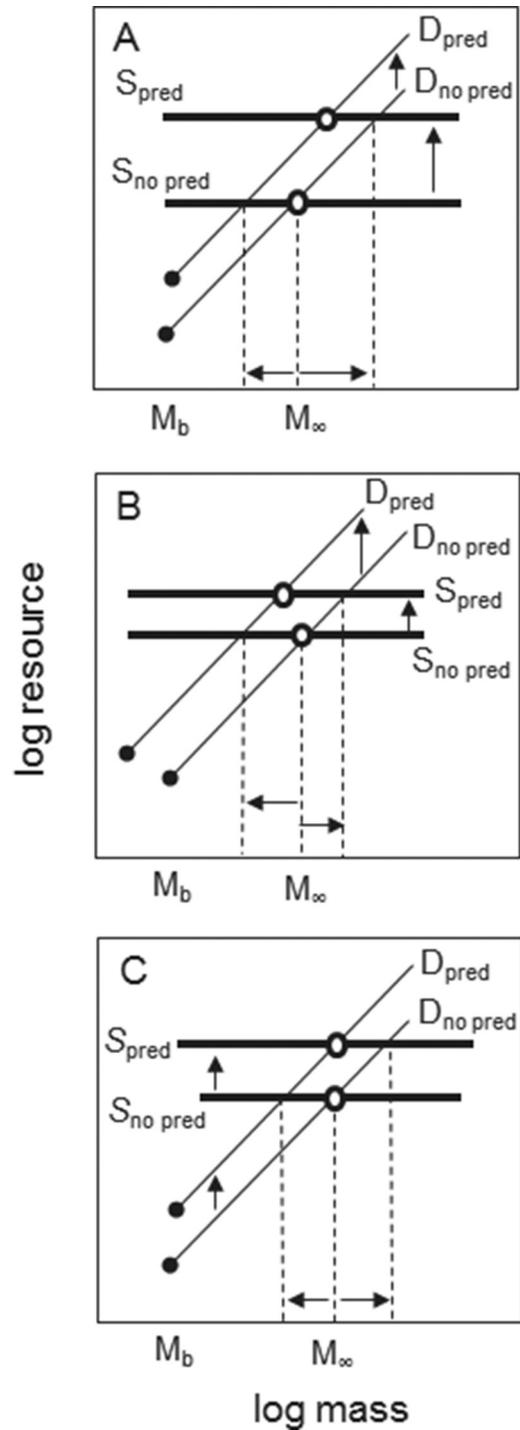
We searched the literature for papers on responses of fish to predation that reported growth constants or asymptotic lengths or that reported growth curves that we could fit to the von Berta-

lanffy equation (see below). Despite the broad interest in this problem, only four papers were found that had the requisite information (Belk and Hales 1993; Bell et al. 2011; Billman et al. 2011; Herczeg et al. 2012). We used parameters from these papers if they were reported, but where necessary, we digitized growth data from these studies and fit them to the three-parameter von Bertalanffy equation: $l_t = l_{inf} - (l_{inf} - l_0)e^{-kt}$, where l_t is length at time t , and l_0 is length at time 0. All lengths were in centimetres and time was in years. We used the nonlinear fitting tool in Matlab (The MathWorks Inc., Natick, Massachusetts) to obtain fits. We then acquired species-specific asymptotic length and the growth constant data for 2006 teleost fish species from FishBase (Froese and Pauly 2014) through the auximetric plotting tool. All lengths were converted to mass using the approximate average length-weight regression based on the ranges from Jellyman et al. (2013), which was $M = \exp(-11)l^3$. We logged the data and fit them to a power law using reduced major axis regression. Our results will be the same regardless of whether we show length or mass, but because the SD model is specifically about the evolution of mass, we will use mass instead of length.

Results and discussion

As expected, we found a negative relationship between asymptotic mass (M_{∞}) and growth constant (k) across fishes for data from FishBase (Froese and Pauly 2014; Fig. 3). The relationship appears linear in log space, and the slope (exponent of the power law) is -2.85 (95% CIs: -2.74 to -2.96). The SD model makes a prediction for this slope given an estimate of the metabolic scaling slope for fishes, which is around 0.8 (Clarke and Johnston 1999). Given eq. 1, where the supply is constant across species (i.e., the supply curve was horizontal), we would expect the relationship between asymptotic mass and growth constant to have a slope of $-1/b = -1/0.8 = -1.25$. The observed slope (-2.85), however, is significantly steeper than the predicted slope (-1.25). It is possible that across teleost fishes, larger species tend to have greater access to

Fig. 4. Three studies that illustrate the interactive effects of resource supply and changing demand on the resulting body size response to predation risk. (A) *Poecilia reticulata* from Reznick et al. (2001): an indirect increase in supply would cause an increase in size, but higher demand through faster growth would lower size. If both occurred but the supply increase was relatively larger than the demand increase, then a small increase in size could be accompanied by an increase in growth rate. (B) *Rivulus hartii* from Walsh and Reznick (2008): in contrast to the guppies, killifish got smaller in response to predation, even though food was more abundant, which could arise if the demand increase was larger than the supply increase, although growth was not reported in this study. (C) *Lepidomeda aliciae* from Billman et al. (2011): chub grew faster in high predation risk sites but showed limited increase in asymptotic size, perhaps due to a concomitant increase in supply. M_{∞} is asymptotic mass and M_b is mass at the beginning of independent life.



resources than smaller species, suggesting that eq. 2 is a better model for this comparison. Using the independent estimate of b (0.8) and the observed slope (obs; -2.85) and solving for s given the exponent in eq. 2, $s = b + (1/obs)$, this framework suggests that s is approximately 0.45 (this is a testable prediction). Because supply is not controlled across species, however, this result should not be construed as a test of the model. Rather, we use it as a backdrop to explore the magnitude and direction of change in growth and body mass due to predation risk.

Compared with this broad cross-species pattern, the shifts in asymptotic mass and growth constant caused by predation risk are, in most cases, remarkably large (Fig. 3). Most importantly, these shifts are not all in the same direction. Some species grow faster and get smaller under predation risk (*Pungitius pungitius* and *Gasterosteus aculeatus*), another grows faster and gets larger (*Lepomis macrochirus*), one species grows slower and gets larger (*Lepidomeda aliciae* in low-quality habitats), and finally one just gets larger (*Lepidomeda aliciae* in high-quality habitats). Only three of these shifts are even consistent with the overall negative relationship between asymptotic mass and growth constant across species that is predicted by theory (Charnov 1993; Kozłowski 1996b).

The SD model can help explain this variety of outcomes. Because predation risk can change access to resources and induce a variety of predator-avoidance strategies, the varied responses to predation risk are not surprising. For example, if predation risk causes prey to utilize a conservative, low-activity lifestyle to avoid encounters with predators, metabolic demands would decline, allowing the fish to grow larger under the same resources (Fig. 2D). In contrast, predation risk could induce a live fast – die young strategy. In this situation, a high demand for resources for growing quickly would require a smaller asymptotic mass under the same supply (Fig. 2E). However, if predators altered access to resources at the same time as inducing a change in strategy, the body mass change could be increased, eliminated, or even reversed. As a framework, then, the SD model has the ability to account for the varied responses to predation risk, which is an advance over earlier theory that makes narrower sets of predictions given the interplay of metabolic and environmental factors (e.g., Kozłowski 1992; Nakazawa et al. 2007; de Roos et al. 2006).

Three studies strongly implicate metabolic demand – resource supply interactions in generating body mass responses to predation risk in fish (Fig. 4). First, Trinidadian guppies (*Poecilia reticulata*) are located in streams that vary in predator-induced mortality (Reznick et al. 1996). They are found in “high predation risk” sites, where they co-occur with a diversity of piscivorous predators, and “low predation risk” sites that contain guppies and a gape-limited killifish. Research has shown that guppies suffer higher mortality in high predation risk sites and are, in turn, found at lower densities in these sites (Reznick et al. 2001). Reznick et al. (2001) showed that guppies grow faster and have a larger asymptotic

mass in high predation risk streams. If predation risk induced faster growth under a constant supply, then the guppies should get smaller not larger (Fig. 4A). However, if predation risk also indirectly increased access to resources, possibly by limiting the number of competing guppies (Wootton 1994), then the expected supply could have been raised. If the supply was raised more than the demand was raised, the direction of change in asymptotic body mass would be switched from declining to increasing. The lower abundances of guppies in high predation risk sites is consistent with this possibility (Reznick et al. 2001).

In this same study system in Trinidad, Walsh and Reznick (2008) explored the influence of the direct and indirect effects of preda-

tion on the evolution of body size in killifish (*Rivulus hartii*). *Rivulus* is found in the same high and low predation risk sites as guppies. *Rivulus* suffers higher rates of mortality in high predation risk streams (direct effect) and are less abundant and experience higher food availability in these sites (indirect effect of predation) (Walsh et al. 2011). Walsh and Reznick (2008) showed that *Rivulus* from high predation risk sites evolved smaller body masses (i.e., were smaller at maturation). Such changes parallel evolutionary shifts observed in guppies (Reznick et al. 1990). For a given food supply, getting smaller is consistent with faster growth and higher metabolic demands under predation risk (Fig. 4B). However, as part of this work, Walsh and Reznick (2008) reared multiple populations of *Rivulus* on food levels that match the known differences in growth mediated through food availability and found that the magnitude of the differences in body size between high and low predation risk sites depended on food levels. Although growth rate was not reported in this study, such results show that the body mass response cannot be predicted solely from a change in food supply or metabolic demand but from their interaction, which is the biological basis for the SD model.

The southern leatherside chub (*Lepidomeda aliciae*) is found in habitats that vary in quality (amount of channelization, altered hydrology, and water quality) and thereby growth. Billman et al. (2011) showed that chub grew faster in high-quality than low-quality habitats. This finding suggests that shifts in the demand curve in response to food levels are possible, so that resource supply influences the final mass more than just through supply. The chub also grew faster in habitats with predators than without predators, indicating higher demand (Fig. 4C). With faster growth in the predator habitats, under a constant supply rate, the chub should get smaller, but the growth curves suggest that asymptotic sizes were similar and possibly increasing. As above, this implicates an effect of predation risk on resource supply, in addition to the direct supply effect that was also observed.

These three studies show that body mass and growth rate changes may be a response to more than one environmental gradient at a time. Typically, changes in growth strategy generated by predation risk interact with either direct or indirect changes in food supply. Either by reducing competitors or by limiting access to resources, predators can alter both the supply and demand conditions for fish, altering the location of the optimal body mass. We argue that the apparently idiosyncratic responses across these studies can be understood using the SD framework.

An important caveat to our framework is that size may be under selection per se due to size-based predation risk (Brooks and Dodson 1965). Predators often take prey in preferred size ranges (Vucic-Pestic et al. 2010) such that low-risk prey sizes may come to dominate a population. Being small, for example, may reduce predation risk by lowering speeds of travel and thus encounter rates, by being harder to detect, or by yielding less energy (and thus being less preferred as prey). On the other hand, being large may generate a size refuge. Yet, selection on body size per se would not violate the SD model. Within-population variation in asymptotic size and growth constants occur within *Daphnia*, for example, that are at least in part genetic (DeLong and Hanley 2013) such that changes in body size would be accompanied by changes in growth rate. If growth rate and asymptotic size are not linked within populations, however, selection for a change in body mass per se could generate a surplus or a deficit of resources, which would lead to a change in population size. Such interactions between the consequences of energy budgets, body mass, and population dynamics have been extensively investigated elsewhere (De Roos and Persson 2013), but in principle, dynamic versions of the SD model also can begin to incorporate changes in body size into population and community dynamics (DeLong et al. 2014). Finally, both the Reznick et al. (1990) study, showing that asymptotic mass in guppies gets larger even though predators select larger guppies, and the Walsh and Reznick (2008) study, showing

the interaction of resource supply and predation risk, indicate that these responses cannot be attributed solely to size-based mortality but to an interaction of factors that may include changes in demand, changes in supply, and size-based selection.

In conclusion, we have illustrated how teleost fishes show variable responses of asymptotic mass and growth rate to predation risk. Some of this variation is quite large compared with cross-species patterns of variation. The apparent idiosyncratic nature of these responses, however, is easily understood to be part of a more general process described by the SD framework. Although the SD model is consistent with the full set of observations on the response of fish asymptotic mass and growth to predation risk, there have been no quantitative tests of the SD model yet with fish. The SD model may also be useful for understanding the combined effects of warming, food levels, and changing predation risk on body size. However, properly testing the SD model predictions in fish and other species is still needed, and this requires experiments that clearly control for resource supply and that measure both growth (or other index of metabolic demand) and asymptotic mass. We anticipate that the SD model will aid in understanding the causes of body mass evolution in fish, which will then pave the way for a broader understanding of how natural communities may respond to environmental change.

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