The Role of Larval Diet in Anuran Metamorphosis[1]

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SYNOPSIS. Focus on tadpole diet and foraging behavior offers potential for integrating ecological and endocrinological approaches to understanding anuran metamorphosis. Natural larval diets vary widely in relative amounts of protein, carbohydrate and lipid, factors known to influence thyroid hormone function, which in turn is essential for metamorphosis to occur. Previous work has shown that tadpoles fed high protein diets grow and develop quickly. This pattern is consistent with findings from other classes of vertebrates that some aspects of thyroid function, *e.g.*, activity of 5'D monodeiodinase, an enzyme that converts thyroxine (T_4) to the more potent metamorphosis-inducer 3,5,3'-triiodothyronine (T_3), are proportional to availability of dietary protein. In field experiments at a northern California river, I found that nutritional variation among algal taxa routinely consumed by tadpoles (chlorophytes, diatoms, cyanobacteria, etc.) influenced metamorphosis several ways. Growth rate was positively correlated with percent protein content of a food type. Tadpoles fed filamentous green algae with epiphytic diatoms developed more quickly and metamorphosed at larger sizes than tadpoles raised on other diets. The dominant diatoms in this system are high in protein because they host nitrogen fixing cyanobacterial endosymbionts. Resource quality also mediated the effects of competition and predation. Changes in abundance of high quality algae caused by invading bullfrog (*R. catesbeiana*) tadpoles explained most of their competitive effects on metamorphosis of native tadpoles (*Hyla regilla* and (*Rana boylii*). In choice experiments, tadpoles foraged selectively on the algal foods that promoted most rapid growth and development. In the presence of garter snake predators, however, tadpoles avoided such patches thus decreasing growth. Direct examination of thyroid hormone production in tadpoles consuming different diets may reveal a proximate mechanism linking diet quality to size at and time to metamorphosis.

INTRODUCTION

The basic premise of this review is that an examination of tadpole diet and foraging behavior can reveal links between what ecologists and endocrinologists know about anuran metamorphosis. Ecologists have examined external influences on metamorphosis including food quantity (Wilbur, 1977*a*, *b*; Berven and Chadra, 1988), changes in growth history (Travis, 1984; Alford and Harris, 1988), food quality (Steinwachser and Travis, 1983; Ahlgren and Bowen, 1991; Pfennig *et al.*, 1991; Kupferberg *et al.*, 1994), diet composition (Crump, 1983, 1990; Pfennig, 1990), and competition for food resources (Brockelman, 1969; DeBenedictis 1974; Wilbur, 1980; Travis, 1984; Kupferberg 1996). Variables directly influenced by diet, *e.g.*, consumption rate ($J g^{-1} \cdot day^{-1}$) and size specific growth rate ($g \cdot day^{-1} \cdot g^{-1}$ tadpole), have been identified as key predictors in physiological (Pandian and Marian, 1985*a*) and ecological (Wilbur and Collins, 1973) models of amphibian metamorphosis. Other environmental factors which can vary independently of food availability, *e.g.*, temperature, may indirectly influence metamorphosis by altering feeding rates (Calef, 1973; Pandian and Marian, 1985*b*; Warkentin, 1992*a*, 1992*b*). Interactions between food availability and temperature have also been shown to affect expression of genes controlling levels of paedomorphosis in the Mexican axolotl (Voss, 1995).

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Endocrinologists, on the other hand, have primarily examined internal influences on metamorphosis, identifying thyroid hormone (TH) as essential to this transformation (reviewed by Galton, 1988), and prolactin (PRL) as essential to maintaining larval structures and promoting growth (White and Nicoll, 1981; Delidow 1989; Tata 1991). Molecular biologists have identified nuclear TH receptors as transcription factors that regulate cascades of gene expression governing specific cell death, proliferation, and differentiation (reviewed by Shi, 1994). External stressors, such as pond drying and crowding, can affect neurotransmittors important in the thyroid axis, such as the stress hormone corticosterone, which in turn affect TH (Denver, 1997). The external factor influencing TH function that I will focus on is the food ingested by tadpoles.

In this paper, I review the effects of diet quantity and composition on thyroid and prolactin function in mammals, birds, and fish, because there is no research directly addressing diet effects on thyroid or prolactin in larval amphibians. The patterns observed from the general vertebrate literature, however, are consistent with the results of many investigations of diet effects on anuran metamorphosis. I argue that a focus on diet composition is pertinent to understanding metamorphosis because the various foods consumed by larval anurans vary widely in ratios of protein, carbohydrate, and lipid, factors shown to influence thyroid function in other vertebrates. I then present some of my published and unpublished results on the ways in which interactions among algae, larval anuran grazers, and garter snake predators influence survival to, time to, and size at metamorphosis. I show that independent of quantity (because tadpoles were fed *ad libitum*), protein content of diverse algal taxa correlates with rapid growth and metamorphosis; that tadpoles feed selectively on the algae that promote growth and development; and, that this selectivity changes in the presence of predators. I also show that the effects of tadpoles on the composition of algal assemblages can explain the competitive interactions among tadpoles. Finally, I end with sugges-

tions for future research which could directly address the effects of diet on thyroid function in larval anurans.

CONNECTIONS BETWEEN DIET AND THYROID FUNCTION

Food quantity

Food quantity and patterns of nutrient intake affect several aspects of thyroid function in a variety of vertebrates (reviewed by Eales, 1988). In mammals (most studies done on humans and rats) starvation leads to decreased levels of triiodothyronine (T_3) and thyroxine (T_4) in the blood, decreased production of thyroid stimulating hormone (TSH), and decreased activity of 5'D, the monodeiodinase enzyme which converts T_4 to T_3 in the liver. The starvation response can be triggered by a decrease in carbohydrates, and the carbohydrates eaten in a single meal after starvation stimulate the hypothalamo-pituitary-thyroid axis. Decreasing caloric intake decreases the binding capacity of T_3 receptors. Overfeeding, on the other hand, increases plasma T_3 because of increased conversion of T_4 to T_3. In birds and fish similar responses have been observed. Starvation leads to decreased production of T_4 from the thyroid and decreased conversion of T_4 to T_3, and carbohydrates in feedings after starvation cause plasma T_4 levels to surge (Himick *et al.*, 1991).

Effects of food quality

Most investigations of food quality and thyroid function have focused on varying the proportions of carbohydrates, lipids, and proteins in rations. Dietary protein appears to be central in triggering diet-induced changes in thyroid function. In humans, protein deprivation leads to decreases in serum T_3 by altering the 5' monodeiodination of T_4 (Marine *et al.*, 1991). In rats, elimination of protein from the diet is sufficient to reduce hypothalmic thyroid releasing hormone (TRH) and pituitary TSH gene expression, leading to decreased plasma T_3 (Shi *et al.*, 1993). In trout *(Oncorhyncus mykiss)*, low amounts of dietary protein depress T_3, and the activity of 5'D is proportional to the amount of dietary protein

(Eales *et al.*, 1992). When the ratio of protein to lipid is increased in artificial rations for trout, the amount of T_3 increased (Eales *et al.*, 1990), whereas when protein was held constant and carbohydrates and lipids varied, no effects on TH were observed. Not only is the proportion of protein important, but the amino acid composition of the protein also influences thyroid function (Riley *et al.*, 1993).

Because conversion of T_4 to T_3 is a key step in the TH induction of amphibian metamorphosis and maximal conversion occurs at mid-metamorphic climax (Buscaglia *et al.*, 1985), I will speculate that effects of food quantity and quality on metamorphosis observed in the ecological experiments reviewed below may be mediated through this pathway.

ECOLOGICAL STUDIES ON TADPOLE DIETS

Effects of food quantity on growth and timing of metamorphosis

The amount of food available is often the cause for density dependent effects on anuran life history traits and survivorship (Brockelman, 1969; DeBenedictis, 1974; Wilbur, 1980; Travis, 1984). Diet manipulations have confirmed that food quantity (Wilbur, 1977*a, b;* Alford and Harris, 1988, Berven and Chadra, 1988) can determine tadpole growth and timing of metamorphosis. These results are consistent with the pattern in other vertebrates, described above, that level of food ration can determine up-regulation of TH and TH receptors.

In addition to quantity *per se,* the sequence of food abundance and scarcity during larval ontogeny influences the tradeoffs between growth and differentiation (Alford and Harris, 1988; Tejedo and Reques, 1994; Audo *et al.*, 1995). In these experiments, tadpoles starved, or on low rations early in ontogeny, caught up with high food control tadpoles to metamorphose at a similar size, but at a later time. This result is predicted by Wilbur and Collins' (1973) model that tadpoles optimally delay metamorphosis by decreasing development rate when size-specific growth rate is above a certain threshold, as in an improving food

environment. My hypothesis suggests that if high food level up-regulates TH, then increasing resource abundance would accelerate development and tadpoles would metamorphose promptly. Because nutrition is likely to influence secretion of many hormones other than TH (*e.g.,* growth hormone, insulin, insulin-like growth factor, and PRL), which have a range of positive, negative, or unknown effects on metamorphosis, a diet based endocrine explanation of this phenomenon is potentially very complex. PRL is of particular interest because it clearly inhibits metamorphosis, but its response to feeding and/or fasting is highly variable. If PRL concentration were to increase as a result of feeding in tadpoles, as has been reported for humans (Carlson, 1989), cattle (McAttee and Trenkle, 1971) and horses (DePew *et al.*, 1994; Sticker *et al.*, 1995), then metamorphosis would be delayed. Conversely, diet restriction decreases PRL in rats (Atterwill *et al.* 1989) and goats (Kloren *et al.*, 1993). In tilapia, a teleost fish, fasting appears to have the opposite effect, causing augmentation of PRL release by pituitary cells *in vitro* (Rodgers *et al.*, 1992). Other studies report no effect of food manipulation on PRL (sheep: Landefeld *et al.*, 1989; Thomas *et al.*, 1990; rat: McGuire *et al.*, 1995). For amphibians, I have found no evidence on how diet affects PRL. An alternative endocrine explanation for delayed metamorphosis in an improving food environment has been suggested by Wassersug (1997). High rates of ingestion may result in tadpoles dosing themselves with a metamorphic inhibitor, *i.e.,* epidermal growth factor, that is secreted in their oral mucus (Lee *et al.*, 1993).

Tadpoles facing food deprivation late in development metamorphose generally at the same time as high food controls but at a smaller size (Alford and Harris, 1988; Tejedo and Reques, 1994; Audo *et al.*, 1995). A possible reason for this lack of plasticity in metamorphic timing is that once tadpoles reared on abundant foods reach a certain developmental stage, developmental rate becomes fixed (Travis, 1984; Hensley, 1993). If starvation decreases production of TH in tadpoles as it does in the

vertebrate examples reviewed above, the question remains how does differentiation continue? Perhaps internal stores of energy and nutrients replace the reduced rations to allow TH synthesis to occur.

Effects of food quality on growth and metamorphosis

Larval anuran diets are diverse and vary widely across taxa and environments. The foods consumed by tadpoles include vascular plants (Storre, 1994), vascular plant based detritus (Diaz-Paniagua, 1985), attached algae or periphyton, a combination of filamentous green algae, cyanobacteria, diatoms, bacteria, and desmids (Dickman, 1968; Kupferberg *et al.,* 1994), ultraplankton (Wassersug, 1972), planktonic green algae (Seale, 1980) and cyanobacteria (Seale and Beckvar, 1980), precipitates of dissolved organic matter (Ahlgren and Bowen, 1991), protozoans (Nathan and James, 1972), pollen (Wagner, 1986), mosquito larvae (Pimm and Kitching, 1987; Blaustein and Kotler, 1993), fairy shrimp (Pfennig, 1990; Pfennig *et al.,* 1991), other tadpoles (Crump, 1983, 1986; Polis and Meyers, 1985; Pfennig, 1990), and other amphibian eggs (Polis and Meyers, 1985; Lannoo *et al.,* 1987; Jungfer and Schiersari, 1995). The differences in nutritional quality among the above foods are obvious when one considers the differences between plant and animal tissues. Plant tissue is generally higher in carbohydrates and lower in lipids and protein than animal matter. Less obviously, there is also substantial variation in the nutrient content of primary producers. For example, filamentous green algae store excess photosynthate as carbohydrate whereas diatoms store excess photosynthate as lipid (Bold and Wynne, 1985). Aquatic and terrestrial primary producer nutrient content is also determined by growing conditions, such that food quality is lowest when plants grow under nutrient shortage (Goldman *et al.,* 1979; Chapin *et al.,* 1990). A growing body of literature is showing that aquatic herbivores can be limited by the mineral (*e.g.,* nitrogen or phosphorous) content of their food (Sterner, 1993, and references cited therein).

Are tadpole growth and development protein limited? Several lines of evidence suggest that they are. Laboratory studies in which tadpoles were fed diets in which both carbohydrate and protein were varied, either in terms of lab rations or in amounts of animal protein included in diet, demonstrate that increased protein enhances either growth or development. Steinwachser and Travis (1983) found that growth and development of *Hyla chrysoscelis* tadpoles was proportional to the ratio of protein to carbohydrate in the diet, not overall ration quantity. For *Rana clamitans* tadpoles, growth was proportional to percent protein, but the tadpoles did not develop (*i.e.,* change Gosner stage) during the one week feeding trial. Pandian and Marian (1985a) found that *Rana catesbeiana* tadpoles whose rations were supplemented with tubifex worms had shorter larval periods and grew faster than tadpoles fed *ad libitum* non-animal diets. Nathan and James (1972) found that addition of protozoans to a boiled lettuce diet decreased time to metamorphosis in *Bufo* tadpoles. Although tadpoles fed only lettuce also successfully metamorphosed, the addition of live protozoans in mud or of sterilized mud increased size at, and decreased time to metamorphosis. In the sterilized mud treatment, tadpoles were seen swimming upside down at the water's surface consuming surface films, which the authors suggested were high in protein and lipids. Additional support for this protein limitation hypothesis will be presented in the section below describing results from feeding trials I conducted in a northern California river.

Does the addition of animal protein to tadpole diet enhance growth and development or is the consumption of animal hormones the proximate mechanism? Recent experiments on the effects of tadpole-tadpole cannibalism, which has been documented in at least 11 anuran species (Polis and Meyers, 1985), offer some insight regarding this question. *Hyla pseudopuma* tadpoles fed conspecifics grow faster and are larger at metamorphosis than tadpoles fed isocaloric diets of heterospecifics, but do not reach metamorphosis in significantly shorter periods of time (Crump,

1990). Carnivorous morphs of spadefoot toad tadpoles *(Scaphiopus bombifrons, S. intermontanus,* and *S. multiplicatus),* however, do develop and metamorphose more rapidly than omnivorous morphs that consume a combination of algae, detritus, and fairy shrimp (Pfennig, 1990). The larger carnivore morph is triggered by ingestion of shrimp or other tadpoles. Bragg (1956) postulated that the enhanced development observed among cannibals is due to either iodine or thyroxine in the prey. Pfennig (1992) confirmed that exposure to exogenous thyroid hormone indeed produces carnivore morphs. He concluded that ingestion of other tadpoles, which contain T_4, or shrimp, which contain diiodotyrosine (T_2), could be the proximate mechanism for stimulating the development of the carnivore morph. It is not clear from his investigation, however, if the quantity of T_2 in the shrimp eaten by tadpoles was equivalent to the amount of exogenous T_4 required to produce the carnivorous morphology. It would be interesting to offer early stages of spadefoot toad tadpoles a choice between algae and anastrocans to determine whether they selectively ingest high TH foods that induce the carnivorous morphology. The observation that thyroxine causes the same results as a shrimp diet, however, does not rule out the possibility of an indirect causal pathway through protein or other limiting nutrients contained in the prey affecting the cannibal's rate of TH production. Crump (1986) also hypothesized that cannibals receive a perfect balance of nutrients when she observed premetamorphic Cuban treefrogs, *Osteopilus septentronalis,* preying on older individuals with four limbs. As a possible mechanism, she cited the increased protein conversion efficiency (ratio of the amount of amino acids in a tadpole's food to the amount of amino acid in its whole carcass) when tadpoles are fed conspecifics as opposed to other high protein food sources such as fish meal (Nagai *et al.,* 1971). To definitively separate protein effects from exogenous TH effects, further experiments in which tadpoles are fed isoproteinaceous diets and TH metabolism is directly measured are needed.

INTERACTIONS BETWEEN TADPOLES AND ALGAE IN A NORTHERN CALIFORNIA RIVER: EXAMPLES OF DIET IMPACTS ON METAMORPHOSIS

Natural history and study system

My hypothesis regarding protein limitation as a connection between the endocrine and nutritional controls of anuran metamorphosis stems, in part, from manipulations of algal diets and tadpole competition conducted in the South Fork of the Eel River (Angelo Coast Range Reserve, Mendocino Co., California (39°44′N, 123°39′W). The river has a winter flood/summer drought hydrograph typical of rivers in Mediterranean climates. Like most western rivers, with limited deciduous canopy cover, the rock bedded river is sun lit, and most productivity comes from algae which bloom during the low flows of spring and summer. Nitrogen is one of the important factors limiting algal growth in this system (Hill and Knight, 1988; Power, 1992). During the low flow period, the river is used for breeding by three species of anurans: yellow legged frogs, *Rana boylii,* Pacific treefrogs, *Hyla regilla,* and non-indigenous bullfrogs, *Rana catesbeiana.* Despite their hundred year history in California, bullfrogs are only presently invading the study reach.

The available food resources for tadpole consumers include the dominant filamentous green alga, *Cladophora glomerata,* and the diatoms that grow as epiphytes on *Cladophora.* The epiphytes can completely cover the filaments of the host algae with mean ($\pm$ 1 SE) diatom biovolume of 180,238 $\pm$ 18,353 μ^3/mm of algae (Kupferberg, 1997). Tadpoles, *R. boylii* in particular, can effectively remove diatoms from *Cladophora,* decreasing average epiphyte biovolume to 78,526 $\pm$ 13,343 μ^3/mm of algae. Diatoms increase the nutritional value of *Cladophora* for two reasons. The most common epiphytes, *Epithemia* spp., contain nitrogen fixing cyanobacterial endosymbionts, so the protein content of *Cladophora* with epiphytes is 11.3% vs. 5.8% without (nutritional data from Kupferberg *et al.,* 1994). Epiphytes store excess photosynthate as lipid rather than carbohydrate so *Cladophora* with epiphytes has 1%
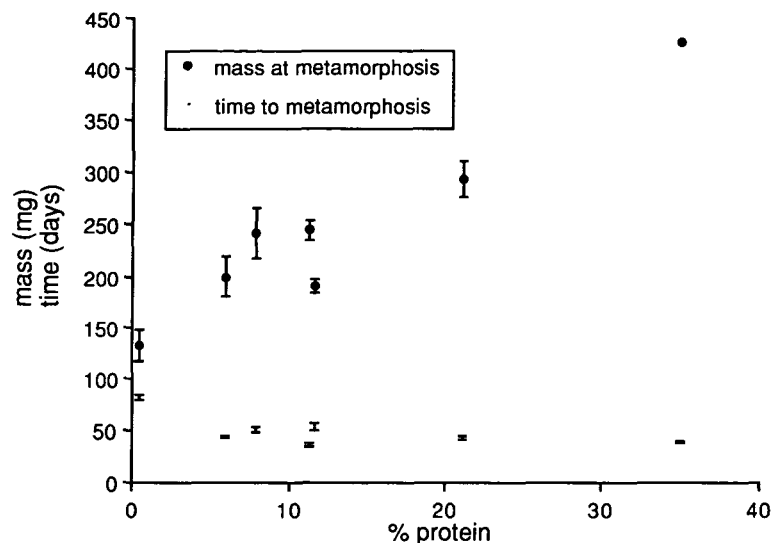
FIG. 1. Size at, and time to, metamorphosis of *Hyla regilla* tadpoles fed diets of varying protein content. Each point represents the mean for a diet treatment (n = 6 replicates/treatment and 5 tadpoles/replicate). Error bars indicate ± 1 SE.

fat and 2% non-structural carbohydrates by weight, compared to .56% fat and 2.9% carbohydrates in *Cladophora* without epiphytes. Additional resources are: other filamentous green algae, such as *Oedogonium* which supports only a small epiphyte community (7.8% protein); mucous producing taxa such as *Mougeotia* (11.6% protein) and *Zygnema* (21% protein) which have no epiphytes; and flocculent material containing detritus, algae, protozoa, and bacteria (.44% protein).

Algal quality affects growth and metamorphosis

The variation in resource quality among these foods influences tadpole growth, development, and survival to metamorphosis. In field diet studies with *H. regilla* (Kupferberg *et al.*, 1994) fed the above foods as well as a control food, Tetra Reptomin® (35% protein), size at metamorphosis was significantly correlated (Pearson's r = 0.96, P = 0.0006) with protein content (Fig. 1). Although tadpoles fed high protein diets metamorphosed sooner than tadpoles fed low protein diets (Fig. 1), the correlation was not significant (r = −0.59, P = 0.16). In these experiments total food quantity was not controlled, tadpoles were fed *ad libitum*. Tadpoles were thus free to compensate for

low protein content of a food by eating more of it. If compensation did occur the relationship between protein content and performance would be weakened. An *ad libitum* feeding regime therefore provides a conservative test of the effects of protein content.

R. boylii were raised in a similar experiment (Kupferberg, 1996), to determine if the relative profitabilities of foods were alike. Food treatments were *Cladophora* with a heavy growth of epiphytes, *Cladophora* without epiphytes, Zygnematales (including *Mougeotia* and *Spirogyra* spp.), and finely ground Reptomin®. Tadpoles from a single clutch of eggs were kept in the river in flow through enclosures (12.7 liter, 30 cm diameter plastic buckets with two windows, 23 × 31 cm, covered with 1 mm fiberglass mesh, five tadpoles per bucket (70/m²), ambient density = 29.4 ± 30.8/m², range = 0 − 112/m², n = 14). Tadpoles were weighed each week and mean per capita weight calculated for each replicate. Dead tadpoles were replaced with size matched individuals from extra replicates. Treatment effects on size were compared using profile analysis. High protein diets generated significant differences in tadpole growth rate and total size (Table 1). The significant interaction between date and

TABLE 1. *Profile analysis of* Rana boylii *growth trajectories fed different quality diets, and Bonferroni multiple comparison probabilities of logarithmically transformed sums of tadpole mass on days 14, 28, 36, 50, and 64.*

Source	Mean square	Wilks' lambda	df	F	P
Analysis of differences (MANOVA)					
Date		0.039	4, 13	80.34	0.49×10^{-8}
Date × Treatment		0.153	12, 34	2.59	0.014
Analysis of totals (ANOVA)					
Treatment	0.359		3	9.29	0.86×10^{-3}
Error	0.039		16		

Multiple comparisons				
Treatment	Reptomin	Epiphytized *Cladophora*	Clean *Cladophora*	Zygnematales
Reptomin	1			
epiphytized *Cladophora*	0.8	1		
clean *Cladophora*	0.0006	0.02	1	
Zygnematales	0.06	1	0.3	1

treatment indicates that the growth trajectories were not parallel (Fig. 2). The trajectories of tadpoles fed commercial food or algal food rich in epiphytic diatoms were steeper than trajectories of tadpoles fed algae either cleaned of epiphytes or not supporting an epiphyte assemblage. The significant date effect merely shows that tadpoles grew. The multiple comparisons of

mean total size indicate that *Cladophora* cleaned of its epiphytes is the worst algal food but that *Cladophora* with its diatom epiphytes is not significantly different from a high quality commercial food (Table 1).

The conclusion from these growth studies is that if tadpoles just ate what was available, then seasonal and spatial variation in resources that vary in nutritional content
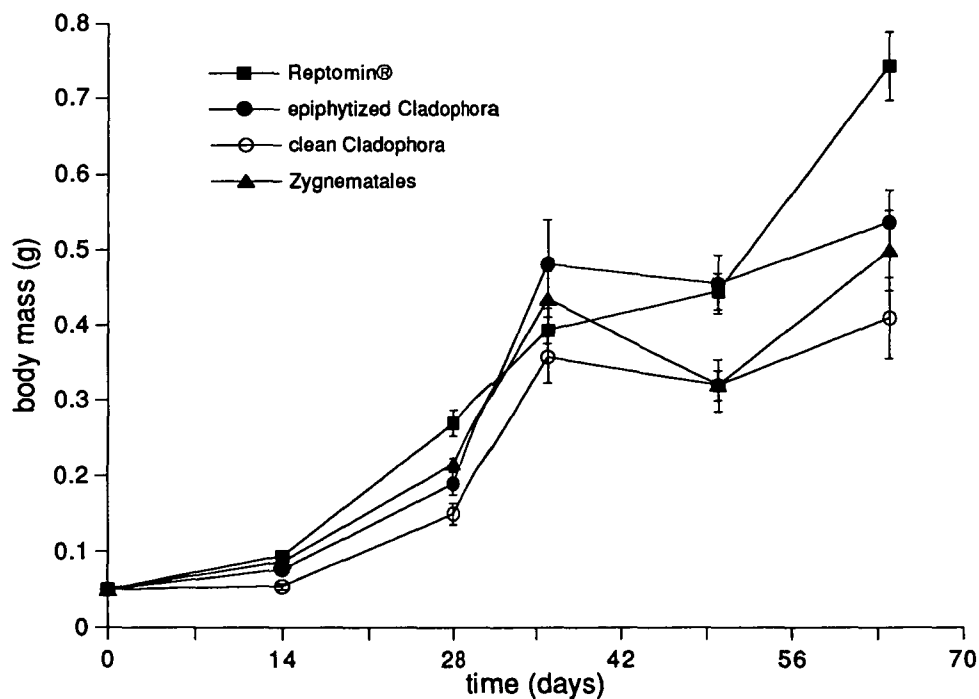
FIG. 2. Growth trajectories of *Rana boylii* tadpoles fed algal and control diets. See Table 1 for comparisons among treatments.
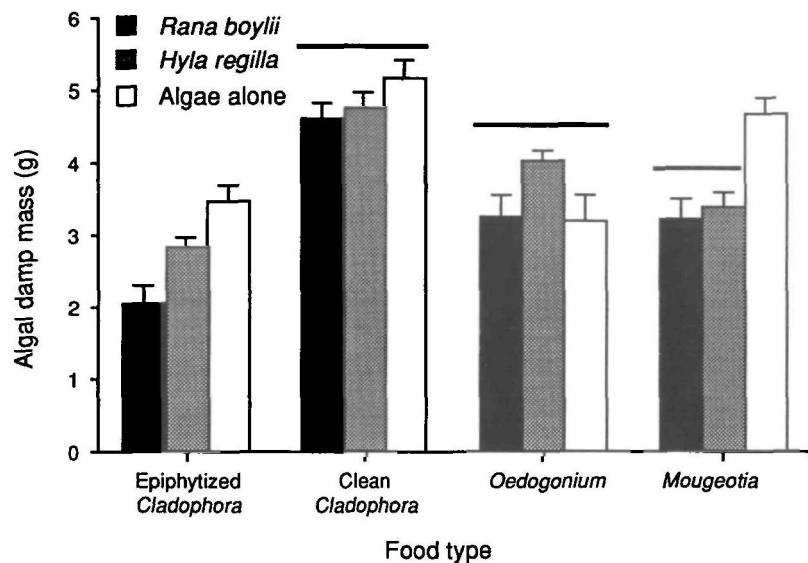
FIG. 3. Algal weights after 1 week in the presence or absence of *Hyla regilla* and *Rana boylii* tadpoles in a cafeteria food selectivity experiment. Histograms joined by horizontal bars are not significantly different from each other (Tukey's HSD $P > 0.05$).

could have a large effect on size and timing of metamorphosis. Selective foraging by tadpoles among these food types could further reinforce the importance of diet quality such that size at metamorphosis is maximized and time to metamorphosis minimized.

Effects of tadpole foraging behavior on metamorphosis: Food preference and predator avoidance

Do tadpoles feed selectively on the foods which promote early metamorphosis and large size at metamorphosis? Based on gut analyses of tadpoles in well mixed algal pond environments (Farlowe, 1928; Jenssen, 1967; Heyer, 1972, 1976; Nathan and James, 1972; Seale, 1980; Diaz-Paniagua, 1985; Loschenkohl, 1986), laboratory feeding trials on suspended particles (Wassersug, 1972; Seale and Beckvar, 1980), and on the morphological adaptations associated with suspension feeding (Wassersug, 1975), tadpoles have been considered indiscriminate feeders. In an environment where algal food resources are patchily distributed and grow attached to substrates, as in a river, there is the potential for selective foraging. I conducted field experiments

(Kupferberg, 1996) to determine whether tadpoles chose the foods they grew best on and how that behavior was changed by predators.

Tadpoles preferred algae with relatively high protein contents. Preferences among four types of algae, *Cladophora* with and without epiphytes, *Mougeotia*, and *Oedogonium*, were compared by placing 5 g damp mass of each type in flow through bucket enclosures. Enclosures were stocked with groups of 5 *R. boylii* or 5 *H. regilla* tadpoles (n = 10 enclosures/tadpole species) or algae only (n = 3). After 7 days, algae were harvested and reweighed after spinning the algae in a lettuce spinner 50 revolutions (Hay, 1986). For each alga the amount remaining in *Rana*, *Hyla*, and control replicates was compared with one-way ANOVA. Grazing treatments with *R. boylii* and *H. regilla* significantly reduced the mass of both *Cladophora* with epiphytes ($F_{2,20}$ = 7.1, $P = 0.005$) and *Mougeotia* ($F_{2,20}$ = 4.0, $P = 0.03$) relative to controls (Fig. 3). Tadpoles avoided the lower protein foods, with no significant differences observed between tadpole and algae only treatments: clean *Cladophora* ($F_{2,20}$ = 0.74, $P = .5$) or *Oedogonium* ($F_{2,20}$ = 3.3, $P = .06$).

I experimentally examined how predators, western aquatic garter snakes *(Thamnophis atratus,* formerly *T. couchii)* affected *H. regilla* tadpole numbers and selective foraging behavior (Kupferberg, 1996). In replicated (n = 24) fenced 1 m diameter pools dug into gravel bars, I observed whether tadpole patch choice follows the rule of minimizing the ratio of mortality risk, μ, to foraging gain, g (Werner and Gilliam, 1984; Werner, 1986). Enclosures were stocked with weighed tadpoles, 260 g *Cladophora* in a mat form, and 260 g of *Mougeotia* which took the shape of a floating cloud. Twelve randomly chosen ponds received a similarly sized garter snake. On day 9 tadpole feeding activity and location in *Cladophora, Mougeotia,* or sediment, was repeatedly spot checked. After the final spot check, tadpoles and algae were harvested and weighed. Response variables were the number of survivors, tadpole growth, proportion actively feeding, and proportion in each substrate type. Snake effects were evaluated with Bonferroni adjusted *t*-tests.

Garter snakes did not significantly reduce the number of tadpoles but did alter patch choice. Tadpoles spent significantly (t = 4.4, P = 0.002) more time in low food quality sediments when a snake was present (66 ± 3%) than when snakes were excluded (53 ± 1%). Avoidance of *Cladophora* in the presence of garter snakes significantly (t = −5.1, P = 0.0003) decreased tadpole growth by 28% (snake absent = 45.7 ± 1.5 *vs.* snake present 32.9 ± 2.1 mg/day). In mortality risk experiments, however, there were no significant differences in the numbers of tadpoles consumed among patch types, and garter snakes were not size selective. Therefore, patch choice did not follow the rule of minimizing μ/g. The change in patch choice was likely due to the sublethal effect of tadpoles being 56% less active in the presence of a snake, a common tadpole response to the presence of predators (Lawler, 1989; Werner, 1991; Skelly, 1994).

My observation that tadpoles moved less in the presence of snakes indicates that the trade-offs tadpoles make between mortality

and growth, which in turn determine the size at and time to metamorphosis (Werner, 1986), are manifest in activity level rather than habitat use *per se.* Tadpoles spent less time eating high quality algal foods, not because they were inherently risky places, but because feeding activity was risky. For negatively buoyant tadpoles, which *H. regilla* at the Eel River appear to be (S. Kupferberg, personal observation) decreased activity results in sinking away from floating algal resources. It is interesting to note that Anholt and Werner (1995) have found that food level and predator presence interact. At high food levels tadpoles adapt their behavior by decreasing activity and hence decreasing mortality, but at low food levels tadpoles must be more active to get food and thus suffer higher mortality. These predator effects on tadpoles relate to issues of hormonal control of metamorphosis via two pathways. Predators can influence food consumption, which in turn affects TH function. Predators could also directly increase the levels of corticoid stress hormones, which also influence TH.

Tadpole effects on algae: Basis for understanding effects of competition on metamorphosis

Because food quantity and quality have significant effects on tadpole growth and metamorphosis, the impact of tadpoles on the biomass and species composition of algal assemblages can determine the outcome of tadpole competition. Tadpole effects on standing stocks of algal biomass include depletion by consumption (Dickman, 1968; Seale, 1980; Brönmark *et al.,* 1991), enhancement by nutrient regeneration (Osborne and McLachlan, 1985), and facilitation of macroalgae via epiphyte removal (Kupferberg, 1997). Because tadpole mouth and feeding morphologies vary among taxa, interspecific differences in exploitative ability (Wassersug, 1972; Diaz-Paniagua, 1985; Kupferberg, 1997) lead to competitive interactions among tadpoles that are more complex than reduction of total food availability.

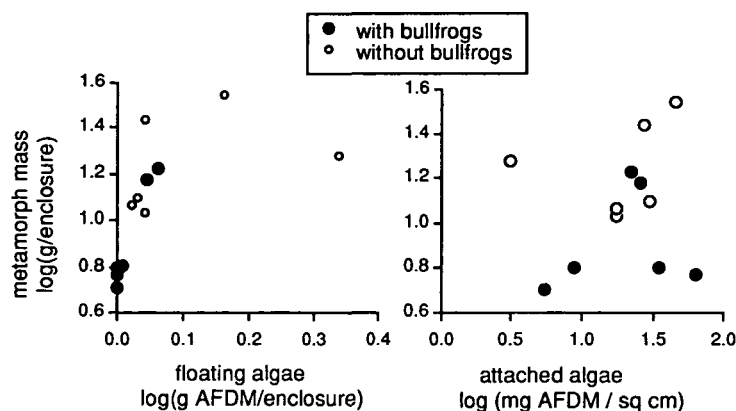For example, the impact of nonindigenous bullfrog tadpoles, *R. catesbei-*

FIG. 4. Relationship between the production of native frogs from pens enclosing or excluding bullfrog tadpoles and (a) high food quality floating algae, *Cladophora* with epiphytic diatoms and *Nostoc* ($r^2 = 0.79$, $P = 0.007$); and (b) low food quality attached algae, *Cladophora* with few epiphytes ($r^2 = 0.15$, $P = 0.67$).

ana, as novel grazers and competitors in the Eel River, was due to their effect on high protein algae rather than on total algal biomass. In 2 m² enclosures of natural river substrates and ambient densities of native tadpoles, bullfrog tadpoles caused a 48% reduction in survivorship of *R. boylii* to metamorphosis, and a 24% decline in mass at metamorphosis, relative to native only control enclosures. Bullfrog larvae had smaller impacts on *H. regilla,* causing 16% reduction in metamorph size, and no significant effect on survivorship. Four variables were tracked in this experiment. Production of each native frog was calculated as the sum of the masses of each species of native metamorph leaving an enclosure. An estimate of high food quality algal production was based on rank transformations of floating algal biomass consisting of senescing, heavily epiphytized *Cladophora,* and *Nostoc.* Production of lower food quality attached algae was based on biomass data from the midpoint of the experiment, indicating the bullfrog modified conditions that native grazers were experiencing.

Bullfrog impacts on algal food resources can explain the effects on metamorphosis of natives (Fig. 4), but differences in food quality among algae must be considered in order to understand the interactions. There was no significant correlation between native frog production and total algal biomass

(Table 2), but lumping all potential food into a pooled biomass category, although common, is not well justified (Mittelbach and Osenberg, 1994). When resources were partitioned into attached and floating algae, diminished food quality in the bullfrog enclosures is suggested by the decreased abundance of floating algae harvested in bullfrog enclosures (0.046 ± 0.026 g AFDM, mean $\pm$ SD) than in enclosures without bullfrogs (0.325 ± 0.182). Although the treatment effect on floating algae was not significant (Mann-Whitney U $= 2.56$, n $= 12$ enclosures, $P = 0.109$), there was a significant correlation between ranked floating algal mass and the total mass of *R. boylii* metamorphosing from the enclosures (Table 2). A small impact of bullfrogs on algal quality, thus resulted in a large impact on *Rana boylii* because there is such a strong correlation between algal quality and the biomass of *R. boylii* metamorphosing from the enclosures. Only a small portion of the variation in *Hyla* was explained. *Hyla* may be able to extract low quality or low availability resources not measured with my sampling regimes. For example, I observed *Hyla* tadpoles swimming on their backs at the surface grazing epineustic films of diatoms.

CONCLUSIONS

My research at the Eel River shows how food resources can influence anuran meta-

TABLE 2. *Observed correlations and descriptive statistics of variables in the bullfrog manipulations (n = 12 enclosures).*

	C	H	B	A	Q	Mean	S D.	S.S.
C = *Rana catesbeiana* presence *vs.* absence (1 *vs.* 0)	1					0.5	0.52	2.8
H = *Hyla regilla* total metamorph biomass (g)	−0.15	1				2.58	2.14	50.3
B = *Rana boylii* total metamorph biomass (g)	−0.63	0.53	1			11.7	7.9	688.6
A = Total algal standing stock ash free dry mass (g)	0.18	−0.12	0.07	1		24.7	16.7	3050.2
Q = Quality of algae as tadpole food (rank)	−0.48	0.51	0.75	−0.07	1	6.5	3.6	142.0

morphosis. In addition to abundance, the qualitative differences among food types, such as the amount of protein in different algae, can affect size at and time to metamorphosis. Tadpoles can select the foods they grow best on, and the presence of predators can induce changes in activity that alter selectivity. As grazers, tadpoles influence algal assemblages, thus changing food quality for competitors. Through my review of the literature I speculate that these food effects may be mediated through diet induced changes in thyroid function.

For future research I suggest that diet experiments be conducted in which tadpoles are fed different types of food with varying amounts of protein, carbohydrate, and lipid and are collected at similar stages for thyroid function assays. Specifically, does the amount of TH produced by tadpoles differ among treatments or does a tadpole require a specific amount of TH to reach a particular stage?

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