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REVIEW PAPER

Comparison of snail density, standing stock, and body size between Caribbean karst wetlands and other freshwater ecosystems

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Abstract Synthesizing data from multiple studies generates hypotheses about factors that affect the distribution and abundance of species among ecosystems. Snails are dominant herbivores in many freshwater ecosystems, but there is no comprehensive review of snail density, standing stock, or body size among freshwater ecosystems. We compile data on snail density and standing stock, estimate body size with their quotient, and discuss the major pattern that emerges. We report data from 215 freshwater ecosystems taken from 88 studies that we placed into nine categories. Sixty-five studies reported density, seven reported standing stock, and 16 reported both. Despite the breadth of studies, spatial and temporal sampling scales were limited. Researchers used 25 different sampling devices ranging in area from 0.0015 to 2.5 m^2. Most ecosystem categories had similar snail densities, standing stocks, and body sizes suggesting snails shared a similar function among ecosystems. Caribbean karst wetlands were a striking exception with much lower density and standing stock, but large body size. Disparity in body size results from the presence of ampullariids in Caribbean karst wetlands suggesting that biogeography affects the distribution of taxa, and in this case size, among aquatic ecosystems. We propose that resource quality explains the disparity in density and standing stock between Caribbean karst wetlands and other categories. Periphyton in Caribbean karst wetlands has high carbon-to-phosphorous ratios and defensive characteristics that inhibit grazers. Unlike many freshwater ecosystems where snails are key grazers, we hypothesize that a microbial loop captures much of the primary production in Caribbean karst wetlands.

Keywords Cross-system comparison · Energy flow · Body size · Biomass · Everglades · Food webs · Grazing · Microbial loop

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Introduction

Combining data from multiple ecosystems generated by many different studies is a powerful tool for producing hypotheses about processes that govern the distribution and abundance of species in nature. Many studies have compared the relative importance of top-down and bottom-up processes among ecosystems with meta-analysis (e.g., Shurin et al., 2002; Gruner et al., 2008). Few comparative studies have used the data on density, standing stock, and body size available for many taxa. These three measures provide insight into the influence of taxa on the communities and ecosystems where they occur. Density and standing stock are fundamental measures describing the distribution and abundance of species across space and time. Body size and standing stock both contain information on mass, but body size provides a size distribution of individuals within ecosystems and yields information on growth rate and reproductive status of individuals (Peters, 1983; Brown et al., 2004). These data are often used in time-series analyses (density, standing stock) and studies of population dynamics and biogeography (body size) between ecosystems within studies, but are rarely compared among studies. Synthesizing the copious data on density, standing stock, and body size available should aid the generation and testing of specific hypotheses related to understanding the distribution and abundance of species in nature.

Freshwater gastropods occur worldwide and are important components of many freshwater ecosystems and water chemistry largely determines their regional distributions (Dillon, 2000). Most freshwater snails are excluded from soft-water ecosystems that have less than 5 mg/l of water-born calcium (Lodge et al., 1987). Above this lower bound, snails occur in a diversity of lentic and lotic ecosystems including wetlands, ponds, lakes, canals, streams, and rivers. Snail grazing reduces periphyton standing crop, alters periphyton assemblages, and can produce strong positive feedbacks (e.g., nutrient regeneration) by freeing space and redistributing nutrients (Power et al., 1988; Brönmark, 1989; McCormick & Stevenson, 1989; McCormick & Stevenson, 1991; Hill, 1992; Rosemond, 1994; Feminella & Hawkins, 1995; Hillebrand et al., 2002). In many freshwater ecosystems, snails are prey to invertebrate and vertebrate taxa including sciomyzid flies, belostomatids, dragonfly larvae, crayfish, fish, and birds (Eckblad, 1976; Brown & Devries, 1985; Brönmark & Malmqvist, 1986; Kesler & Munns, 1989; Alexander & Covich, 1991; Reed & Janzen, 1999). Surveys and experiments confirm the strong linkage between periphyton, snails, and their predators. Brönmark & Weisner (1996) surveyed 44 ponds and found abundant snails but little periphyton in fishless ponds, while ponds with molluscivorous fishes were depauperate of snails but periphyton was abundant. Numerous experimental studies demonstrate reduced snail growth and activity in the presence of molluscivores that cascades to positively affect overall periphyton growth (Underwood & Thomas, 1990; Brönmark et al., 1992; Lodge et al., 1994; Bernot & Turner, 2001; Lewis, 2001). Therefore, snails are integral components of many freshwater ecosystems as important primary consumers in ecosystems without molluscivores and are key links in the flow of energy from primary producers to upper trophic levels in ecosystems with molluscivores.

The wide distribution of freshwater snails and their prominence in many ecosystems make them good candidates for comparisons among ecosystems. Despite their prominence in many freshwater ecosystems, snails appear to be relatively rare in Caribbean karst wetlands. The Everglades, the most well-studied Caribbean karst wetland, is distinguished from other freshwater ecosystems because standing stocks of decapods, fishes, and macroinvertebrates are low, but periphyton standing crop is exceptionally high (Vymazal, 1995; Goldsborough & Robinson, 1996; Turner et al., 1999). Preliminary research in other Caribbean karst wetlands indicates they are similar (Trexler et al., unpublished data). Our motivation for this study was to review the literature on snail density (no./m^2), standing stock (g/m^2), and body size (g/ind.) to establish how rare snails are in Caribbean karst wetlands compared to a diversity of other freshwater ecosystems. We review sampling protocols and devices used for quantitatively collecting snails and address the potential for bias from collecting snails with devices of different sizes. We report the prevalence of the three measures in the literature and discuss the importance of standing stock and body size for understanding ecological and biogeographic patterns. We establish a rank distribution of snail density, standing stock, and body size among ecosystems to facilitate comparisons of Caribbean karst wetlands to other freshwater ecosystems and use these data to generate hypotheses on the mechanisms responsible for the pattern that emerges.

Methods

Literature review

We used Web of Science to identify studies that reported freshwater snail density and standing stock on an areal basis (area^{-1}) and mined the literature-cited sections of these studies for additional studies to generate our database. We extracted data from tables, the text, and figures. In addition, we recorded specific information from each study to facilitate ecosystem comparisons and assess sampling methods among ecosystems. We documented the year of publication, the type and location of each ecosystem within a study, the number of sites sampled in each ecosystem, the number of times data were collected at each site, the months data were collected, and the device or method used to collect data. We bolstered the data mined from the published literature with four unpublished datasets (Trexler; Trexler et al.; Turner; Uzarski et al.); details on the sampling protocols and the ecosystems sampled are in Online Resource 1.

Sampling methods and protocols

With the information on sampling protocols and devices gleaned from the methods sections of papers, we summarized the sampling methods and protocols among ecosystems to assess the variety of techniques used to quantify snail density and standing stock among freshwater ecosystems. We generated frequency distributions to illustrate the number of times ecosystems were sampled and the number of sites sampled within ecosystems. A third frequency distribution revealed the seasonal changes in sampling effort for each ecosystem. We used Pearson correlations to examine the relationship between the area sampled by a device and the resulting density and standing stock estimates for an ecosystem because strong relationships might indicate bias in sampling techniques. For these correlations, area, density, and standing stock were natural log transformed to normalize the data.

A common currency

We used total snail wet-tissue mass and total snail count scaled to 1 m^2 as a common metric for standing stock and density comparisons. Mass reported in other units (e.g., ash-free dry mass) was converted to wet mass by assuming an 85% loss for dried, and a 90% loss for ashed samples. These loss estimates were based on data collected from the *Haitia cubensis* (Pfeiffer, 1839), *Planorbella duryi* (Weatherby, 1879), and *Pomacea paludosa* (Say, 1829) that represent the size range of snails encountered among all ecosystems (CBR unpublished data).

Studies from the literature review and the unpublished datasets generated density and standing stock data at multiple spatial and temporal scales within and between ecosystems. Data reported within ecosystems (multiple plots or sites or multiple events) were averaged across space (plots then sites) and then time (years then months). We aggregated data on multiple species separately within ecosystems and then summed the values for each species to calculate the total snail standing stock or density for that ecosystem. We treated each ecosystem (e.g., multiple streams) within a study separately. Different studies that reported data on the same ecosystem were averaged together after within study samples were aggregated.

We estimated standing stock from density and individual size data for seven studies. Hunter (1975), Eversole (1978), Crowl (1990), and Costil & Daguzan (1995) provided snail-size information that allowed us to calculate a mean individual wet mass with species or genera level (for similarly shaped species, e.g., planospiral) size-to-weight regressions. We multiplied individual mass estimates by density to provide an estimate of standing stock for those ecosystems. A. D. Rosemond (personal communication, University of Georgia) provided an average shell size for *Elimia clavaeformis* (Lea, 1841) in streams located at Oak Ridge National Laboratories, Tennessee. We used the average shell size to calculate wet mass with a size-to-weight regression (Rosemond et al., 1993) that allowed us to estimate standing stock for Rosemond (1994), Hill et al. (1995), and Hill (1992).

Six studies reported standing stock estimates that included the shell. Newbold et al. (1983), Huryn et al. (1995), and Stewart & Garcia (2002) reported ash-free dry mass (AFDM) with the shell. Hershey (1990) reported wet mass that included the shell. The published size-to-weight regression by Vaughn et al. (1993) that included the shell was used to estimate wet mass for Crowl (1990). Shell AFDM ranged between 12 and 30% of total snail AFDM for *P. paludosa*, *H. cubensis* and *P. duryi* from the Everglades; there was similar variability in the proportion between wet shell mass and total snail mass for these species based on data we collected for these species from the Everglades. Despite this variability, we include these standing stock estimates because they were similar to other ecosystems in the same category. Kushlan (1975) reported shell and tissue wet mass together for the *P. paludosa* in the Everglades and provided individual size data. We removed shell mass from snails in this study with species-specific regressions (CBR, unpublished data).

Ecosystem comparisons

Individual ecosystems served as the unit of observation, and we grouped ecosystems into nine general categories that represented the size range of lentic and lotic systems in nature for comparative purposes. Ecosystems were categorized based on information in the studies, or we contacted authors and searched other literature on a particular ecosystem when it was missing; otherwise, we used the most specific category reported in the study. We grouped lotic ecosystems into canals, small streams (1st order, 2nd order), medium streams (3rd and 4th order), and large streams (5th order and above). Ecosystems identified only as 'stream' were categorized as medium streams; creeks and springs were grouped with small streams, and rivers were categorized as large streams. The canal category included ditches. We divided lentic ecosystems into lakes, ponds, swamps, wetlands, and Caribbean karst wetlands. Borrow pits were categorized as ponds; reservoirs were included in the lake category. The wetland category included fluvial and isolated wetlands. Caribbean karst wetlands included four locations in the Caribbean basin: the Florida Everglades, Sian Ka'an Biopreserve, Mexico, New River Lagoon, Belize, and the Llanos, Venezuela. We report the mean and standard deviation among ecosystems within a category to compare density and standing stock among categories.

We compared individual snail size among categories by estimating the average size of an individual snail using the studies that reported snail density and standing stock and the studies that reported snail-size information that allowed us to estimate standing stock. Using these studies, we estimated individual snail size (g/ind.) as the quotient between snail standing stock (g/m^2) and density (no./m^2).

Results

We reviewed 88 studies that reported data from 215 ecosystems located in the northern temperate zone to the tropics. Ecosystems were located in the Americas, Africa, Spain, Russia, Europe, and New Zealand (Online Resource 2). Sixty-five studies reported just snail density, seven reported only standing stock, and sixteen reported both (Fig. 1). Overall, 81 studies reported snail density from 196 ecosystems. Thirty studies reported standing stock (or provided information to estimate standing stock) from 84 ecosystems; of these, 23 studies also reported density from 65 ecosystems.

Many researchers in the review sampled ecosystems once, at a single site. Studies in Caribbean karst wetlands, large streams, and wetlands all included multiple sites in their sampling protocols (Fig. 2). Sampling ecosystems multiple times at the same site was more common than sampling at multiple sites. Small- and medium-sized streams had the fewest number of repeated sampling events; researchers working in Caribbean karst wetlands, canals, and wetlands sampled ecosystems multiple times in their studies. Ecosystems studied at lower latitudes sampled throughout the year, while those at higher latitudes concentrated sampling effort during the warmer months (Fig. 2).

Researchers used 25 different sampling devices that varied in size by over two orders of magnitude for quantifying snail density or standing stock (Table 1). Quadrats, Surber samplers, and box samplers of various sizes were widely used among studies

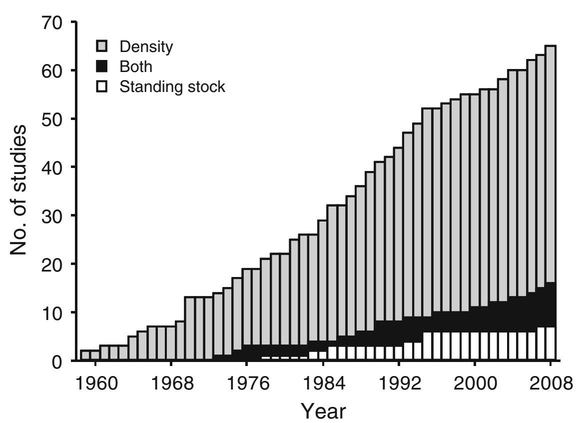

Fig. 1 The cumulative number of studies in the review ($n = 84$ published and 4 unpublished) that reported density (no./m^2, *gray*, $n = 65$), standing stock (g/m^2, *white*, $n = 7$), or both (*black*, $n = 16$). Standing stock was estimated for seven studies from density and size information presented; these studies were enumerated with those reporting density

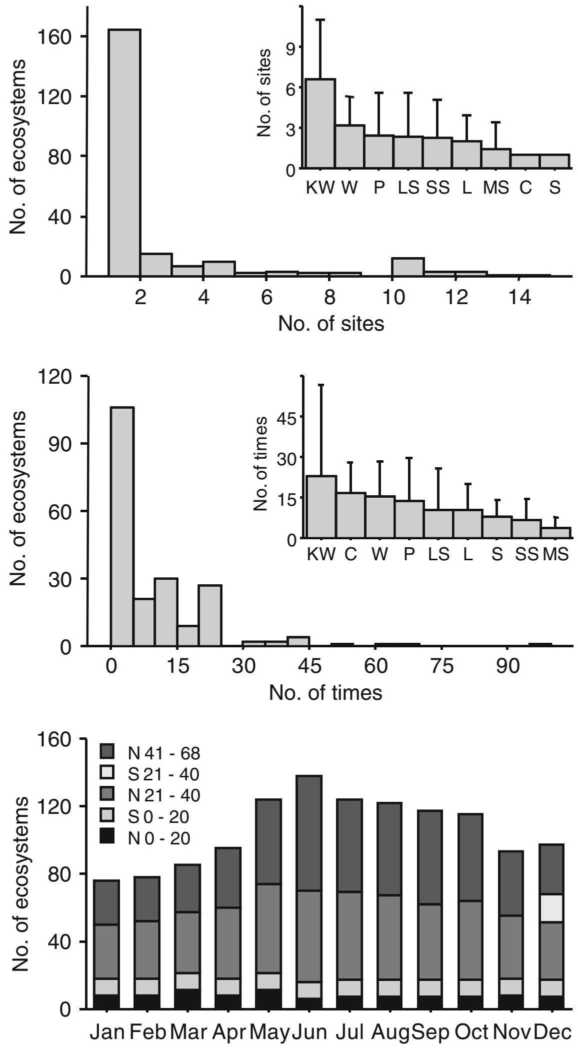

Fig. 2 Sampling protocols across space and time for study-ecosystem combinations ($n = 226$). Five of the 215 ecosystems from the 88 studies were sampled multiple times by different studies. Frequency distributions display the number of sites sampled within an ecosystem (*top*) and the number of times an ecosystem was sampled (*middle*). *Inset bar graphs* aggregate (mean ± SD) the sampling protocols (sites, *top*; times, *middle*) from different ecosystems into nine categories. *KW* Karstic wetland, *LS* large stream, *W* wetland, *P* pond, *SS* small stream, *L* lake, *MS* medium stream, *C* canal, *S* swamp. Most studies sampled at one site, only once. The *bottom panel* presents the monthly distribution of sampling events for each ecosystem by latitude (*N* north of the equator and *S* south of the equator). At lower latitudes sampling occurred during all months, while higher latitudes concentrated sampling efforts during warmer months. See Online Resource 2 for specific details about each study

and ecosystem categories. We found a negative correlation between device size and snail density or standing stock (Fig. 3). Despite this correlation, there was considerable spread in the reported density or standing stock with small sampling devices.

Snail density ranged over four orders of magnitude and standing stock ranged over three orders of magnitude among categories (Fig. 4). Most categories had similar snail densities, but Caribbean karst wetlands were a notable exception. Snail densities in Caribbean karst wetlands were two orders of magnitude lower than large streams, the category with the nearest density estimate. Snail standing stock exhibited a similar pattern, as estimates for Caribbean karst wetlands were an order of magnitude lower than other types of wetlands that ranked second lowest among categories. Small streams, ponds, and lakes had the highest replication among categories, while Caribbean karst wetlands, wetlands, swamps, and canals were categories with lower replication within categories.

Density and standing stock relate through body size. Our calculation of body size revealed that Caribbean karst wetlands contain large snails compared to those from other ecosystem categories (Fig. 4). Canals, ponds, and lakes also had relatively large snails, while wetlands and large streams tended to have relatively small snails.

Discussion

Integrating data from multiple studies to make comparisons among ecosystems offers insight into the processes that determine the distribution and abundance of species. Our review of 88 studies that reported snail density, standing stock, or both for 215 different ecosystems revealed that out of nine categories Caribbean karst wetlands had much lower snail density and standing stock, but on average larger individuals, than any other ecosystem category. We discuss the relative importance of biogeography and ecological (abiotic and biotic) factors that might explain this pattern after considering sampling protocols, sampling gear, and the value of reporting standing stock and body size along with density.

A single study can only capture a portion of the total spatial and temporal variation found in nature. We included any study that reported quantitative data (No./area) on freshwater gastropods to increase the diversity of ecosystems. Some studies collected enough data to parameterize experiments, others examined snail population dynamics for a few years,

Table 1 Different sampling devices used in the 88 studies that reported data from 215 different ecosystems that we placed into nine categories

Device	Area	No. of ecosystems	Typical ecosystem category
Basket trap	0.032	1	Wetland
Box	0.05–0.1	22	Canals, lakes, ponds, small and medium streams, swamp
Bucket	0.05	17	Lakes, ponds, wetlands, swamp
Core	0.002–0.25	15	Canal, small streams, wetlands
Dredge	0.6	8	Lake, pond, small streams
Drop	0.25	1	Lake
Ekman	0.02–0.23	18	Lakes, large streams, ponds
Gerking	0.075	1	Wetland
Hand grab	0.063	1	Large stream
Hess	0.08	1	Small stream
Hester Dendy	0.9	1	Karstic wetland
Hula Hoop	0.48	1	Lake
Mark/recapture	–	2	Lake, medium stream
Net drag	1	1	Wetland
Peterson	–	2	Canal, swamp
Pull trap	4.5	1	Karstic wetland
Quadrat	0.002–1	37	Canals, lakes, ponds, rivers, small, medium, and large streams, wetland
SA cobble	–	16	Lakes, small, medium, and large streams
Scraper net	0.25	4	Lakes
Seine	2.5	1	Karstic wetland
Stove pipe	0.008	1	Pond
Surber	0.06–0.5	27	Ponds, small, medium, and large streams
Sweep	0.25–1.5	8	Karstic wetland, ponds, small streams, wetlands
Throw trap	1	13	Karstic wetlands, lakes, ponds, small and medium streams
Triangular net	0.1	17	Small, medium, and large streams
Unknown	–	16	Lakes, small, and large streams

Several studies used multiple devices for sampling different microhabitats within ecosystems

and still others reported many-year time series. The diversity of goals resulted in considerable variation in the numbers of sites, times, and devices used to sample ecosystems. We assessed the quality of data from ecosystems aggregated into the nine categories by comparing sampling sites, times, and devices among categories. Most studies sampled over time instead of across space. Studies conducted at higher latitudes concentrated efforts in the warmer months presumably, because sampling during the coldest months was not feasible. Quadrats, Surber samplers, and box samplers were common among ecosystems although 45% of devices occurred just once. Regardless of device type, the negative correlations between sampling area and estimated snail density or standing stock suggested that large sampling devices collected fewer snails. Few studies used devices larger than 1 m^2 and those that did reported low values for both measures. However, the considerable variance in estimates from smaller devices (<1 m^2) suggests that researchers chose large sampling devices in ecosystems with low snail density to improve sampling efficiency instead of sampling bias associated with device size. Comparing the number of sites and times sampled revealed a gradient among ecosystem categories. Researchers used numerous devices to sample ecosystems within each category. These conclusions support the notion that estimates for categories are

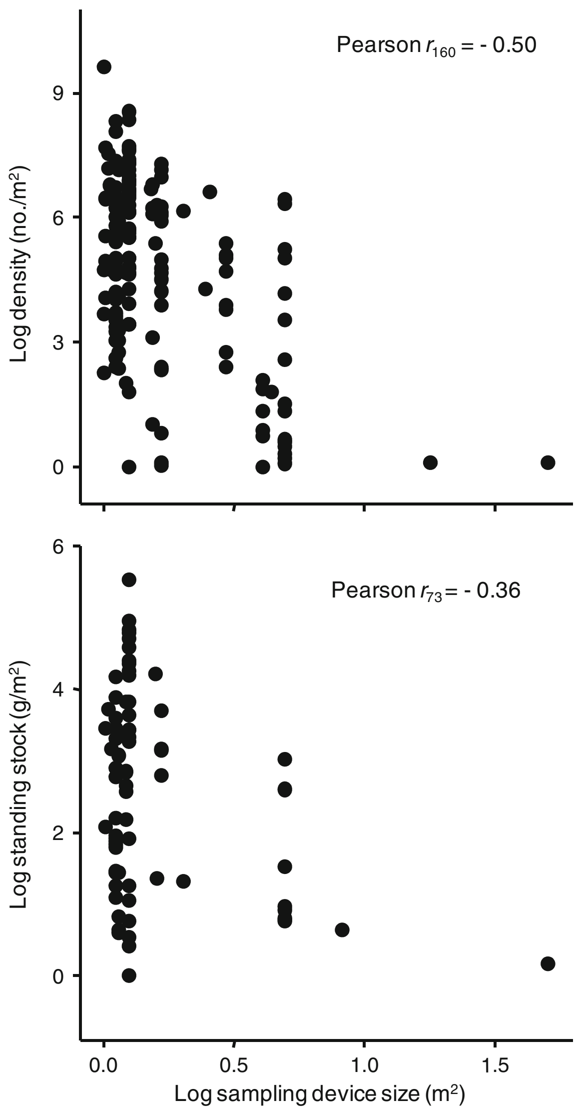

Fig. 3 Effect of sampling device size on estimates of snail density (no./m^2, *top*) and standing stock (g/m^2, *bottom*) for studies that provided information on sampling size for ecosystems. Few researchers used devices larger than 1 m^2 to sample snails. Two studies used very large devices and reported low densities or standing stocks, while studies using smaller devices reported a wide range of densities and standing stocks

comparable because the ecosystems within categories exhibited a similar range of protocols and devices for sampling snail density and standing stock.

Density, standing stock, and body size are all indicators of the influence taxa have on the community or ecosystem they inhabit. Standing stock is a better measure of the ecological significance of any particular group because it is more closely related to metabolism than density and contains information on body size (Osenberg et al., 1994; Cohen et al., 2003; Saint-Germain et al., 2007). Body size reveals general information on life history characteristics like age at maturity and growth rate (Peters, 1983; Brown et al., 2004). Recent studies advocate the importance of reporting both body size and density (White et al., 2007) or body size and standing stock (Cohen et al., 2003). The majority of studies we found reported snail density; however, the incidence of reporting both increased steadily during the last decade signifying the growing emphasis on reporting multiple measures to understand the influence of snails on community structure and ecosystem function.

The most striking result from the review was that Caribbean karst wetlands had much lower snail density and standing stock, but larger individuals, compared to the other eight categories. Karst ecosystems in this study represent a subset of all karst-associated freshwater ecosystems throughout the world. We may have categorized other karst ecosystems into the remaining eight categories because authors generally did not report the geology of ecosystems studied. Therefore, our conclusions are limited to the Caribbean karst wetlands for which we have data.

Apple snails (Ampullariidae) explain the large average body size in Caribbean karst wetlands. Ampullariids are large (>30 mm adult shell length) caenogastropods that occur in many ecosystems throughout the tropics and sub-tropics (Cowie, 2002), but body size data on ampullariids was not available for other categories. Therefore, large body size is likely a characteristic of ecosystems containing ampullariids in the tropics and sub-tropics instead of a unique characteristic of Caribbean karst wetlands. This conclusion suggests that latitude affects snail body size distributions. Bergmann's rule states that body size increases with increasing latitude or decreasing temperature (Mayr, 1956; Blackburn et al., 1999). There is mixed support for the rule in ectotherms (Blackburn et al., 1999); some studies support the rule (e.g., Lindsey, 1966), and others show the reverse trend (Mousseau, 1997; Belk & Houston, 2002; Adams & Church, 2008). The data we present for snails does not support Bergmann's rule, but a single ecosystem

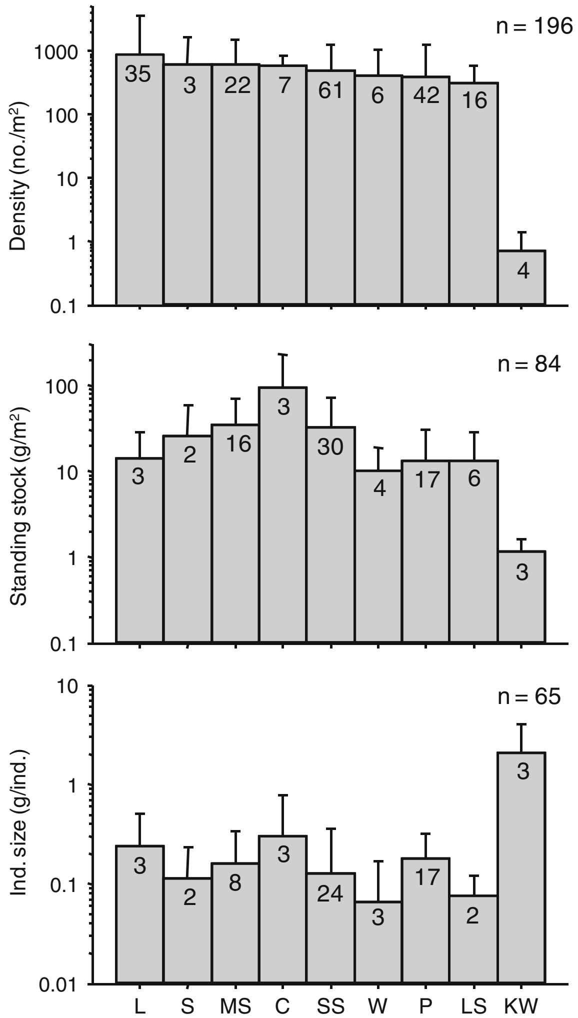

Fig. 4 Patterns (mean ± SD) of snail density (no./m^2, *top*), standing stock (g/m^2, *middle*), and individual size (g/ind., *bottom*) for different categories. *Bars* are ranked in decreasing order according to density for each graph to illustrate differences among measures. The number of ecosystems used for calculating estimates is within bars. Density estimates were from 81 studies that reported data from 196 ecosystems; standing stock estimates were from 30 studies that reported data on 84 ecosystems; individual size estimates were from 23 studies that reported data from 65 ecosystems. We calculated body size for each category from the studies that reported density and standing stock or provided data on body size that allowed us to calculate standing stock. Note the very low snail density and standing stock values but the large body size for snails in Caribbean karst wetlands. The *y*-axis is log-scale on all three graphs. *L* lake, *S* swamp, *MS* medium stream, *C* canal, *SS* small stream, *W* wetland, *P* pond, *LS* large stream, *KW* karstic wetland. See Online Resource 2 for further details on ecosystems and categories

type and a single taxon heavily influence our data. A rigorous test of Bergmann's rule in gastropods will require additional data on snail body size along latitudinal or temperature gradients.

The unusually low snail density and standing stock values in Caribbean karst wetlands suggests that abiotic factors, biotic factors, or both strongly limit snails. Surface-water calcium concentration in the Florida Everglades is sufficient for snail shell growth as it is well above 5 mg/l (Price, 2001; Harvey & McCormick, 2009) suggested by Lodge et al. (1987) as a lower limit required by most snails. Belizean, Mexican, and Venezuelan karst wetlands likely have similar water chemistry because they have similar geology (Eisenberg, 1979; Wicks et al., 1995; Schmitter-Soto et al., 2002; Singurindy & Berkowitz, 2004). Other factors that may limit snails in Caribbean karst wetlands include predation, disturbance, and resource quality.

Predators consume large numbers of snails with cascading effects on primary production and community structure in most freshwater ecosystems (Crowl & Covich, 1990; Brönmark & Weisner, 1996; Chase, 1999; Lewis, 2001; Turner & Chislock, 2007). Predation might explain why there are so few snails in Caribbean karst wetlands if their effect was much larger in these ecosystems compared to other categories. Food-web theory predicts that molluscivore density should be high if snails were a major energy source (Hairston et al., 1960; Brönmark et al., 1992). *Rostrhamus sociabilis* (Vieillot, 1817) (snail kites) and *Aramus guarauna* (Linnaeus, 1766) (limpkins) primarily consume apple snails. These birds and other avian predators are limited by seasonal changes in habitat complexity associated with water depth (Snyder & Snyder, 1969; Reed & Janzen, 1999; Bennetts et al., 2006) suggesting they have limited effect on overall snail standing stock and density. Focusing on the aquatic food-web reveals that standing stocks of decapods, fishes, and other invertebrates, many of which are molluscivores, are comparatively low in the Everglades (Turner et al., 1999). Similar to avian predators, the influence of large predatory fishes, including molluscivorous fishes, is diminished by seasonal changes in water depth (Chick et al., 2004; Dorn et al., 2006; Chick et al., 2008). Therefore, predation likely affects local snail populations in

Caribbean karst wetlands at times, but does not explain the pattern among ecosystem categories because molluscivores are more numerous in other freshwater ecosystems that maintained much higher snail density and standing stock.

Disturbance, defined as the removal of biomass (Grime, 1977), has profound effects on population size and stability within communities and ecosystems (Sousa, 1984; Grimm & Fisher, 1989). Seasonal drying is a prominent disturbance affecting many freshwater aquatic communities, including wetlands (Wellborn et al., 1996). Seasonal drying might explain the low numbers of snails in Caribbean karst wetlands if drying differentially affected the snail species in these ecosystems compared to other ecosystems by way of founder effects. However, studies report that both ramshorn snails (Boss, 1974; Heeg, 1977; Fretter & Peake, 1979) and apple snails aestivate (Cowie, 2002) indicating they are resistant to seasonal drying. Further, representative species from these families were the most numerous in the Caribbean karst wetlands (Kushlan, 1975; Darby et al., 1999; Bennetts et al., 2006; Karunaratne et al., 2006; King & Richardson, 2007). Therefore, the life history of species that occur in Caribbean karst wetlands appears to buffer them from the negative effects of seasonal drying.

Comparing the rank distribution of snail density or standing stock among categories offers additional evidence that seasonal drying does not explain the paucity of snails in Caribbean karst wetlands. An inverse relationship between drying frequency and snail density or standing stock among categories would suggest that seasonal drying strongly limited snails within ecosystems. There was weak evidence for this trend in lentic and no evidence in lotic ecosystems. For example, density in lotic ecosystems varied widely with small streams, typically thought to dry frequently, ranking above large streams. Among lentic ecosystems, Caribbean karst wetlands ranked lowest and lakes ranked highest in density; however, other wetlands and ponds had similar density. A clear distinction between wetlands, which dry more frequently, and ponds would be compelling evidence indicating that seasonal drying limits snails in Caribbean karst wetlands.

Resource quality between Caribbean karst wetlands and other categories could account for discrepancies in snail density and standing stock. Resource quality affects the rate of resource acquisition and determines the number and types of animals an ecosystem support (Power, 1992). Periphyton is an important food resource for grazers in freshwater ecosystems. Generally, lower carbon-to-phosphorous ratios indicate higher periphyton quality as measured by consumer growth (Elser et al., 2000; Frost et al., 2002; Frost et al., 2005; Tibbets et al., 2010). In addition, periphyton often exhibits mechanical and chemical defenses that also reduces their quality (Huntly, 1991; Steinman, 1996). The Everglades, and other Caribbean karst wetlands, have much higher periphyton standing crops than all other freshwater ecosystems reviewed (Vymazal, 1995; Goldsborough & Robinson, 1996; Turner et al., 1999). These extensive periphyton mats contain little phosphorous per gram of periphyton (Gaiser et al., 2006; King & Richardson, 2007) resulting in comparatively high carbon-to-phosphorous ratios. Periphyton mats in Caribbean karst wetlands are composed of green algae, coccoid, and filamentous blue green algae, diatoms, and fungi that are held together by a calcareous matrix of mucopolysaccharides secreted by cyanobacteria (Browder et al., 1994; Rejmankova et al., 2004; Gaiser et al., 2006). The complex mat structure and secretion of calcium carbonate serves to mechanically defend periphyton from grazers (Geddes & Trexler, 2003; Chick et al., 2008). High carbon-to-phosphorous ratios and mechanical defense combines to yield low quality resources for grazers in Caribbean karst wetlands. We propose that poor quality resources are the primary factor that limits snails in Caribbean karst wetlands compared to other categories.

Few snails and other grazers combined with the extensive periphyton mats suggests energy transfers to upper trophic levels occur through alternative pathways in Caribbean karst wetlands. A microbial loop may process the majority of periphyton-captured energy in these ecosystems. Primary production is recycled and gradually decomposed by bacterial activity within a microbial loop and energy is transferred to upper trophic levels through small detritivores that are then consumed by predators (Azam et al., 1983; Hairston & Hairston, 1993; Hall & Meyer, 1998). Studies in karst wetlands should test for evidence of a microbial loop as an important component of the food web that functions to process periphyton and recycle nutrients.

In this review, we compare snail density, standing stock, and body size among freshwater ecosystems.

Sampling regimes and devices for collecting snails varied widely. Future studies should strive to standardize methods and sample with a frequently used collection device like quadrats. Few studies reported standing stock or body size data for snails despite the importance of these data for understanding the ecological and evolutionary significance of snails within communities, ecosystems, and regions. The dearth of snails in Caribbean karst wetlands was the most striking result from the review. Resource quality is likely the key factor that limits snails in these ecosystems. Phosphorous additions from agricultural field run-off may improve resource quality and result in larger consumer population sizes that could alter ecosystem structure or function. Future research should consider the role of phosphorous as a limiting factor for snails in Caribbean karst wetlands. We demonstrate that comparisons of density, standing stock, and body size among ecosystems can be profitable for generating hypotheses about the major abiotic and biotic factors that determine the distribution and abundance of species in nature.

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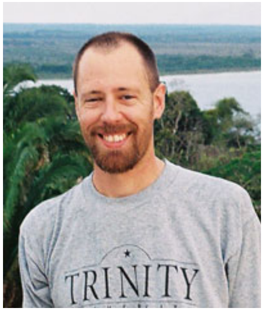

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