TESTING THE PENINSULA EFFECT: DOES IT AFFECT FRESHWATER CRUSTACEANS INHABITING EPHEMERAL WETLANDS ON FLORIDA'S RIDGES?

by

DEBRA A. RINNE
B.S. University of Central Florida, 2003

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Arts and Sciences
at the University of Central Florida
Orlando, Florida

Spring Term
2006

ABSTRACT

The peninsula effect is a pattern of diversity wherein species richness decreases along a peninsula from base to tip and is attributed to three mechanisms: historical processes, habitat gradients, and immigration-extinction equilibrium. Numerous studies have reported conflicting results involving the existence, cause, and validity of the peninsula effect in part because they did not account for effects of history or habitat on species richness patterns and because most previous research focused on organisms that actively disperse, which could confound results with behavioral habitat selection. Florida poses an excellent opportunity to study the peninsula effect because of its geological history and its unique ridges have similar histories (e.g. age, elevation, and sediment). Habitat changes down the peninsula, from a warm temperate climate in the north to a subtropical climate in the south. I studied freshwater crustaceans in isolated wetlands because crustaceans are diverse and disperse passively among these discrete habitats. My study design and statistical analyses controlled for two of the three mechanisms (habitat and history) that may generate a peninsula effect to better test for the third hypothesis (immigration-extinction equilbrium) on the Florida peninsula.

Thirty-one wetlands were sampled for crustaceans monthly from November 2004 through April 2005, or until a site dried. Human disturbance was minimized by choosing isolated, ephemeral wetlands located within state reserves, parks, and forests located on four major ridges: Trail, Brooksville, Mount Dora and Lake Wales. I measured several environmental variables to assess habitat variation among sites. Limnological parameters included temperature, pH, dissolved oxygen, conductivity, chlorophyll α, pheophytin, total nitrogen, total phosphorus, and total hardness. Other habitat variables included surface area, distance to nearest water body, fish presence or absence, hydroperiod, total transmitted light and canopy openness. Crustacean species were identified to the lowest practical taxonomic level (typically species) and recorded as present or absent. A total of 53 different crustaceans were identified, including 41 cladocerans, 10 copepods, and 2 ostracods. In a multiple regression, environmental variables and sampling effort accounted for 57% of the variation in species richness. Regression of remaining variation (residuals) against latitude, which measures position along the peninsula, was not statistically significant. The same pattern was obtained when the sequence of regressions was reversed. Therefore, the peninsula effect does affect the species richness of freshwater crustaceans inhabiting ephemeral wetlands on Florida's ridges. Instead, variation in species richness was determined mainly by habitat differences, particularly the complex interaction of phosphorus levels, isolation, fish presence or absence, and hydroperiod. This study may serve as a model for more thorough analyses of mechanisms (history, habitat, and immigration-extinction) of a peninsula effect in other taxa.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Patterns of species diversity have long been a central topic of biogeography, and the peninsula effect is one pattern which is not yet fully understood. Simpson (1964) first observed that species richness on peninsulas was lower than of mainlands, and hypothesized that this was caused by low immigration and high extinction rates. MacArthur and Wilson (1967) found a similar effect for birds on the Florida, Baja California, and Yucatan peninsulas, and used these data to support the Equilibrium Theory of Island Biogeography; in particular,r they attributed reduced immigration rates on peninsulas to the absence of surrounding land.

Numerous studies have examined the peninsula effect over the last forty years (Cook 1969; Taylor and Regal 1978a, 1978b; Seib 1980; Lawlor 1983; Busack & Hedges 1984; Due and Polis 1986; Milne and Forman 1986; Means and Simberloff 1987; Schwartz 1988; Brown 1987, 1990), which can be organized according to three causal hypotheses: historical, habitat, and immigration-extinction. The Historical Hypothesis suggests that past climatic and geological events modified peninsula habitats and eliminated species, leaving the remaining habitats suitable only for some species. This hypothesis requires both sufficient time and opportunity for organisms to disperse plus environmental stability through geologic time. The Habitat Hypothesis predicts that current climatic and habitat gradients determine species richness along a peninsula due to local variation in habitat parameters to which species respond to. However, the habitat variables important in determining species presence or absence are taxon-specific, and the peninsula effect emerges because these habitat variables also exhibit peninsular gradients. The Immigration-Extinction Hypothesis states that species richness patterns result from reduced immigration relative to extinction rates due to peninsular geometry. Immigration cannot offset extinction rates when the peninsula tip is distant from species pools on the mainland. Therefore, long, narrowing extensions from the mainland often have lower species richness than the mainland.

Early studies of the peninsula effect indicated that patterns were caused by immigration-extinction equilibrium (Table 1). However, the idea quickly faded as ecologists found that historical and habitat gradients also played a role. Habitat was considered to be an overriding contributor to peninsular patterns, but the degree to which it contributed has never been determined adequately. Similarly, the immigration-extinction equilibrium remains an unspecified contributor to peninsular patterns and cannot be ignored. My study provides a comprehensive test of the peninsula effect for freshwater crustaceans inhabiting island-like ephemeral wetlands on the Florida peninsula by 1) accounting for habitat and historical differences, and 2) incorporating immigration-extinction equilibrium.

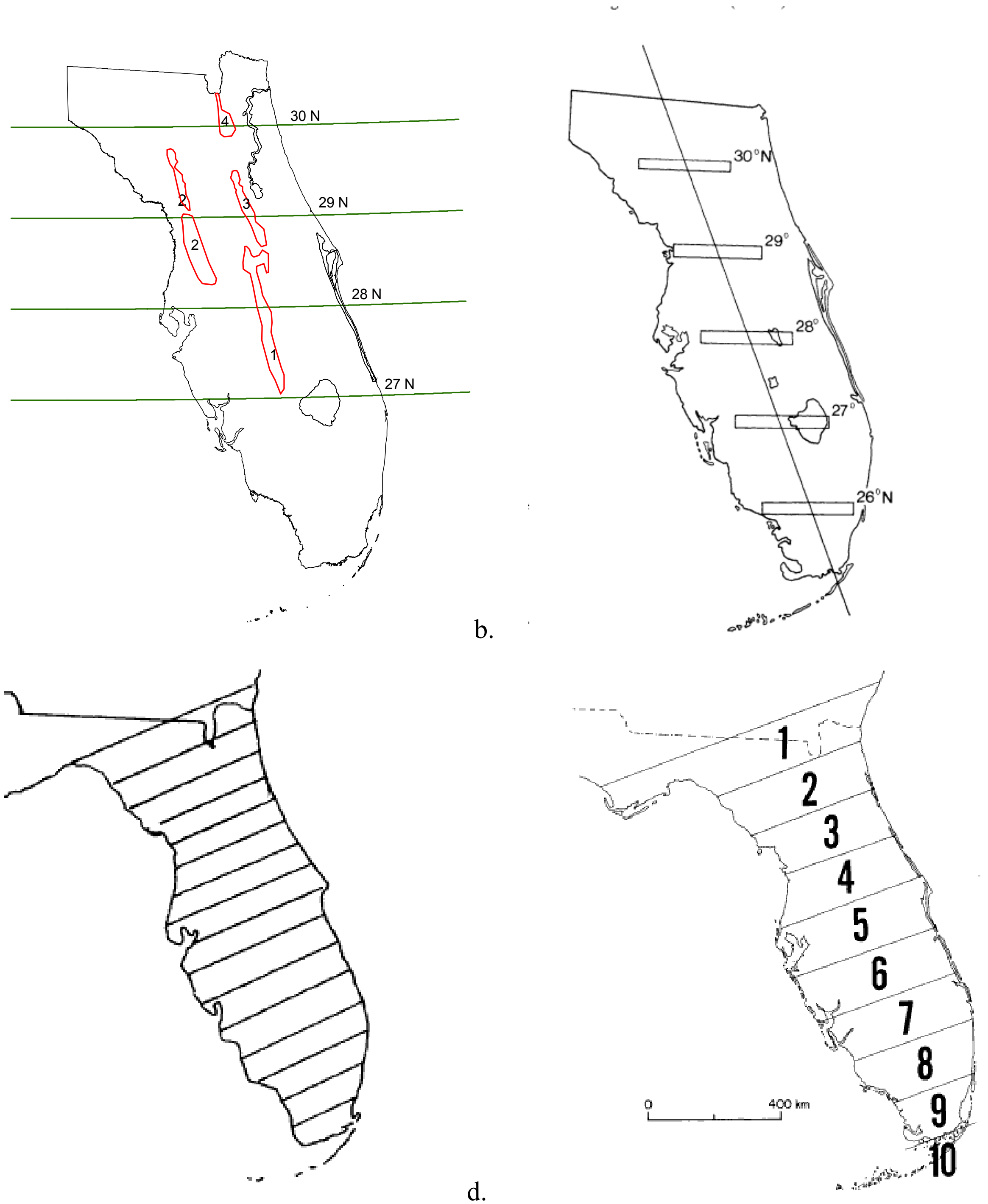
Florida is among the best peninsulas to study because of its ancient ridge landscapes, which essentially have been exposed since their formation during the early Pliocene (Myers & Ewel, 1990). The four major ridges (Figure 1a) were shaped by rising and receding sea levels and have been exposed since the last glaciation approximately 100,000 years ago (Myers & Ewel, 1990). Therefore, these ridges are similar in age, elevation, and sediment. Focusing on Florida's ridges minimizes the effects of differing geological histories among sites, which is the primary component of the Historical Hypothesis. The ridges have been subject to some human modification, but by choosing wetlands within protected areas, I minimized the potential effects of this disturbance. In addition, Florida's peninsula was not previously joined to and did not split from another landmass, unlike Baja California.

Table 1. Summary of previous research on the peninsula effect including the taxa, peninsula of focus, and the presence or absence of a peninsula effect. Some studies that found no peninsula effect uncovered counter-gradients between tropical and temperate species richness. Mechanisms considered important for generating peninsular pattern in each study also are indicated.

Study	Peninsula(s) Studied	Taxa Studied	Peninsular Pattern	History	Habitat	Immigration-Extinction
Simpson 1964	all of North America	Mammals	yes			●
MacArthur & Wilson 1967	Florida	Birds	yes			●
	Baja California		yes			●
	Yucatan		yes			●
Cook 1969	all of North America	Birds	yes	●	●	
Taylor & Regal 1978a,b	Baja California	Heteromyid rodents[1]	yes			●
Seib 1980	Baja California	Reptiles	counter-gradient		●	
Taylor & Pfannmuller 1981	Red Deer Point, Manitoba	Beetles & mammals	no			
Lawlor 1983	Baja California	Mammals	yes[2]		●	
Busack & Hedges 1984	Florida	Lizards	yes	●		
	Baja California		no			
	Yucatan		no			
	Iberia		no			
Due & Polis 1986	Baja California	Scorpions	no			
	Florida		no			
	Italy		yes		●	
Milne & Forman 1986	Maine	Plants	yes		●	
Means & Simberloff 1987	Florida	Herpetofauna	yes		●	
Brown 1987	Baja California	Butterflies	counter-gradient	●	●	●
Schwartz 1988	Florida	Plants	counter-gradient	●	●	
	Aleutian		no			
	Seward		no			
Brown 1990	Florida	Butterflies	counter-gradient		●	●

[1] also considered snakes, birds, lizards, mammals, and bats but did not focus on them

[2] for heteromyid rodents and Artiodactyla only



a. b.

c. d.

Figure 1. Peninsular transects of Florida as defined by various studies: a) this study: 1= Lake Wales Ridge 2= Brooksville Ridge 3= Mount Dora Ridge 4= Trail Ridge; b) Means and Simberloff (1986); c) Schwartz (1987); d) Brown (1990).

The Habitat Hypothesis can be minimized and accounted for through site selection and statistical analyses. Previous studies (Mean & Simberloff 1987, Brown 1990) considered the entire Florida peninsula (Figure 1) and found that habitat caused peninsular patterns there. However, sampling the Everglades and Florida Keys includes ecosystems with drastically different geological histories and habitat, both in topography and vegetation. Extreme habitat differences are minimized by focusing on Florida ridges, and using statistical analysis to quantify the effect of remaining local habitat parameters on species richness patterns.

Finally, the Immigration-Extinction Equilibrium Hypothesis is an island biogeography concept: isolated, ephemeral wetlands are discrete "island" habitats that are not inter-connecting and have reduced immigration rates relative to extinction rates due to distance from a mainland source pool. Immigration-extinction tradeoffs in species richness are most clearly tested with organisms that do not exhibit behavioral site selection among nearby habitats that may confuse dispersal patterns. Previous research (Table 1) on the peninsula effect focused mostly on terrestrial or semi-aquatic vertebrates, and more importantly with active dispersers. Freshwater crustaceans rely on passive dispersal such as wind, rain, and waterfowl to move between discrete habitats (Figuerola et al. 2005, Green and Figuerola 2005) and are presumed to be widely distrubuted (Bohanak and Jenkins 2003). Sampling crustaceans in isolated wetlands allows for evaluation of this presumption, and of the Immigration-Extinction Hypothesis in general.

Crustaceans are also a diverse group and ecologically important in ephemeral wetlands, where they provide a link between primary producers and higher trophic leels. Little is known of the invertebrates living in Florida wetlands, so my study also provides the first species list of crustaceans inhabiting many of these protected areas.

MATERIALS AND METHODS

Site Selection

My study was conducted on four Florida ridges spanning four degrees in latitude: the Trail, Mount Dora, Brooksville, and the Lake Wales Ridges (Figure 2). Study ponds were chosen along each ridge from habitat types based on the National Wetlands Inventory Classification System (Figure 2). A total of thrity-one palustrine wetlands (Table 2) were sampled monthly from November 2004 through April 2005, to encompass succession throughout the entire wet season. All ponds were dry prior to August 1, 2004 and filled simultaneously with Hurricane Charlie, a Category 4 hurricane that made landfall on August 13, 2004. Sites were inaccessible from August through October 2004 due to damage caused by Hurricanes Charlie, Frances (Category 2, landfall on September 4, 2004) and Jeanne (Category 3, landfall on September 21, 2004).

Data Collection

At each site, crustaceans were sampled using 64 micron mesh dipnets swept across all habitat types within a wetland. Samples were collected and preserved with Lugol’s solution (Pennak 1989) for identification in the laboratory. Crustaceans were identified to species (or lowest taxonomic level) using several taxonomic keys (Thorp & Covich 2001, Pennak 1989, Edmondson 1959) and data were recorded as species presence/absence in each wetland.

Wetland area (ha) was calculated using ArcMap (ArcGIS v.9.0, Environmental Systems Research Institute (ESRI)) based on polygons created from digital orthophoto quarterquad (DOQ) aerial photographs. Fish presence or absence was recorded at each site based on observations made during sampling. Geographical Information System (GIS) datalayers

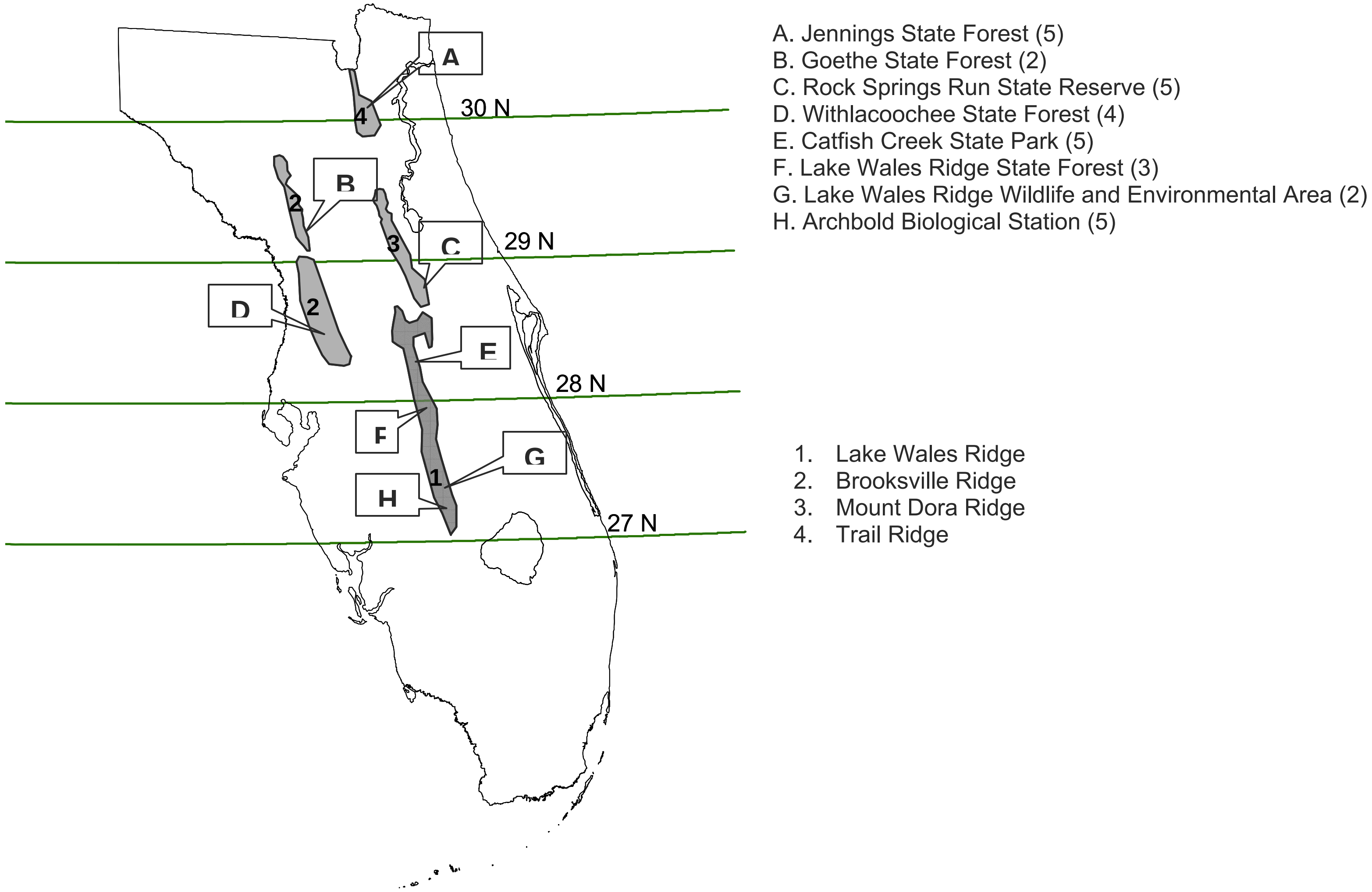


Figure 2. Location of thirty-one wetland sites within conservation areas along Florida's ridges. Numbers in parentheses represent the number of sites sampled within each conservation area.

Table 2. Latitude and sampling frequency of thirty-one wetland sites located on Florida's ridges sampled for crustacean species richness. Ponds were sampled from November 2004 until the site dried or April 2005. One sample was missed from ponds JS2, CROOM7, RS73 and CAT1 due to inaccessibility of sites.

Site[1]	Latitude (degrees N)	November 2004	December 2004	January 2005	February 2005	March 2005	April 2005
JS1	30.15	X	X	X	X	X	X
JS2	30.15		X	X	X	X	X
JS4	30.13	X	X	X	X	X	X
JS5	30.10	X	X	X	X	X	X
JS10	30.10	X	X	X	X	X	X
GF1	29.16	X	X	X	X	X	X
GF11	29.11	X	X	X	dry		
CROOM4	28.8	X	X	X	X	X	X
CROOM5	28.79	X	X	X	X	X	X
CROOM7	28.79		X	X	X	X	dry
CROOM9	28.79	X	X	X	X	X	X
RS2	28.78	X	X	X	X	X	X
RS4	28.61	X	X	X	X	X	X
RS73	28.60	X	X	X	X	X	
RS77	28.58	X	dry				
RS81	28.56	X	dry				
CAT1	27.19	X	X	X		X	X
CAT2	27.18	X	dry				
CAT3	27.18	X	X	X	X	X	X
CAT4	27.18	X	X	X	X	X	X
CAT5	27.18	X	X	X	X	X	X
ARB3	27.67	X	X	X	dry		
ARB5	27.38	X	X	X	dry		
ARB6	27.37	X	dry				
WEA1	27.70	X	dry				
WEA3	27.70	X	dry				
ABS1	27.98	X	X	X	dry		
ABS2	27.98	X	X	X	dry		
ABS3	27.98	X	X	X	dry		
ABS4	27.97	X	X	X	dry		
ABS5	27.97	X	X	X	dry		

---

[1] JS= Jennings State Forest, Clay County, FL
GF= Goethe State Forest, Levy County, FL
CROOM= Withlacoochee State Forest, Croom Tract, Hernando County, FL
RS= Rock Springs Run State Reserve, Orange County, FL
CAT= Allen David Broussard Catfish Creek Preserve State Park, Highland County, FL
ARB= Lake Wales Ridge State Forest, Arbuckle Tract, Highland County, FL
WEA= Lake Wales Ridge Wildlife and Environmental Area, Polk County, FL
ABS= Archbold Biological Station, Polk County, FL

(DOQs, topographic contour lines, and National Wetland Inventory maps) were used to classify ponds as connected or isolated. Field observations and information gathered from park biologists, if available, helped to classify ponds as temporary (hydroperiod <1 year) or permanent (hydroperiod ≥ 1year).

Total precipitation (cm) and monthly mean precipitation (cm) for the entire sampling interval (August 2004 - April 2005) per site were calculated using rainfall data from local water management districts or the Department of Forestry. Data collected monthly from each site were represented as a mean, and minimum and maximum values summarized extreme values. Wetland locations were recorded using a handheld Global Positioning System (GARMIN GPSMAP 76, Olathe, KS), and three digital photographs were taken of site canopies using a Nikon digital camera and 180º fisheye lens. Digital photographs were analyzed with Gap Light Analyzer v2.0 (Simon Frasier University, British Columbia, Canada & Institute of Ecosystem Studies, Millbrook, New York) to estimate mean values of canopy openness (%) and total transmitted light (MJ/m^2/d). Canopy photographs of two sites (Croom7, RS81) were unsuitable for analysis and these sites were assigned a mean value for openness and light based on sites that appeared similar in canopy structure (ABS1-ABS5, WEA1, CAT1, CAT2, CAT5).

Water temperature (°C), dissolved oxygen (mg/L), pH, and conductivity (mS) were recorded at each site with a portable meter (YSI Model #556, Yellow Springs, Ohio) equipped with dissolved oxygen sensor (Model #559) and 2 mil polyethylene membrane cap (Model #5909). A 500 mL water sample was collected at each site by combining four subsamples from varying locations at each pond. Samples were transported on ice to the laboratory, where each sample was analyzed for chlorophyll *a* (mg/L), total nitrogen (mg/L), total phosphorus (mg/L), and water hardness (mg/L). A portion (50-250 mL) of each water sample was filtered through 47 mm glass microfiber filters, which were frozen until analyzed for chlorophyll *a* using methods described elsewhere (American Public Health Association et al. 1989). Total hardness was determined by titration (Lind 1979) using 25 mL of refrigerated samples within three days of collection. The remaining water sample was acidified ($pH \leq 2$) and refrigerated until analyzed using a combined method of total nitrogen and total phosphorus: Total N digestion performed first (Crumpton et al. 1992) followed by the Total P digestion (American Public Health Association et al. 1989).

Data Analysis

A series of linear and multiple regressions was used to examine variation in species richness as a function of environmental variables and latitude (i.e., peninsular location). All variables were examined for normality using Shapiro-Wilk statistics, histograms and normal probability distribution curves and then transformed as appropriate prior to analyses. Species richness, temperature, phosphorus, and maximum pH were normal and remained untransformed. Area, chlorophyll *a*, pheophytin, nitrogen and conductivity were $\log_{10}$ transformed and mean pH, dissolved oxygen, and distance to the nearest water body were square-root transformed. Both measures of light were squared for normality and hardness was normalized by taking the inverse square root. Minimum pH, mean monthly precipitation and total wet season precipitation could not be normalized and were not transformed.

Due to differences in wetland hydroperiod and inaccessibility, sites were sampled 1-6 times (Table 2). Species–sample curves were created to verify that the number of samples sufficiently captured most species present. If cumulative total species richness plotted vs. the number of samples reached a plateau, then species richness was adequately estimated. Analyses were standardized for the number of samples collected by it (herein after referred to as sampling effort) as a variable in the regression model.

Backward stepwise regression was used for the analysis because it reduced the large list of environmental variables to a condensed set that included only major contributors to species richness. Preliminary analyses revealed that much of the data were collinear. Backward elimination regression did not resolve this problem, therefore I examined a Pearson correlation matrix to determine which values were highly correlated in order to reduce the set of variables. Minimum and maximum temperature values were not used because they were highly correlated with mean temperature ($r = 0.944$ and 0.834, respectively). Minimum and maximum pH were significantly correlated with mean pH ($r = 0.912$ and 0.951, respectively), minimum and maximum dissolved oxygen were significantly correlated with mean dissolved oxygen and were removed from the analyses ($r = 0.945$ and 0.902, respectively), and ,inimum and maximum conductivity were highly correlated with the mean conductivity ($r = 0.988$ and 0.986, respectively), so all these minima and maxima were removed. Mean total nitrogen was eliminated because it was correlated strongly with maximum total nitrogen ($r = 0.661$) but not with minimum total nitrogen levels. Therefore, minimum and maximum total nitrogen values were retained in the final analyses. Mean total phosphorus was correlated with minimum and maximum total phosphorus ($r = 0.670$ and 0.771, respectively) so only minimum and maximum total phosphorus values were included in analyses. Minimum chlorophyll *a* was removed because all ponds had levels below detectable limits and maximum chlorophyll values were removed because they were strongly correlated with mean chlorophyll levels ($r = 0.963$). No pheophytin values were considered in analyses because they are used to calculate chlorophyll *a* levels and therefore represent similar data. Minimum and maximum hardness values were removed as they were highly correlated with mean hardness (r = 0.983 and 0.934, respectively). Precipitation was not included in the analyses because rainfall data was unavailable for individual sites. Connected or isolated classification was not considered because only one pond (JS5) connected, and total transmitted light was excluded from analyses because it was highly correlated with canopy openness (r = 0.905). Similarly, ridge and conservation area were excluded because they were strongly correlated with each other (r = -0.862), and with temperature (r = -0.689 and 0.739). Tolerance indices (>0.1) indicated that collinearity had been was not present in the reduced set of variables (Quinn and Keough 2002).

Multiple regression of species richness was performed against all normalized environmental data and sampling effort using SPSS 11.5 (SPSS, Inc., Chicago, Illinois). The remaining unexplained variation (residuals) was then regressed against latitude. This method removed variation due to environment leaving any underlying latitudinal pattern exposed, and was equivalent to entering latitude last into a regression model using Type I (sequential) sums of squares. Next, I reversed the multiple regression series by first accounting for latitudinal variation and then examining the underlying environmental influence to ensure that order of entry did not affect model results. I then repeated these two series of regressions with ridge and conservation area included as variables to determine whether these position variables (related to both environmental and historical effects) affected species richness patterns.

I used one-way ANOVA to test the hypothesis that site selection affected species richness, independent from any peninsular pattern using the eight conservation areas and four ridges as independent variables and species richness as the dependent variable. I also used one-way ANOVA to test whether sampling effort was consistent between ridge and conservation areas, and to test the hypothesis that conservation area or ridge affected habitat variables retained from multiple regression. Significant environmental variables identified by ANOVA were used in canonical discriminant analysis to determine if ridge or conservation area could be predicted as a linear function of habitat variables.

Finally, species co-occurrence analysis was conducted with EcoSim v7.0 (Gotelli and Entsminger 2001) to evaluate the randomness of community structure among all sampled ponds. Species co-occurrence analysis compared a calculated checkerboard score to the distribution of such scores among 5000 randomized species presence/absence matrices (1 row per species, 1column per site). Analyses used fixed rows and area-weighted columns.

RESULTS

Species richness ranged from 2 to 18 microcrustaceans per pond (Appendix A). Overall, 53 different species of crustaceans were identified, including 41 cladocerans, 10 copepods, and 2 ostracods. This mixture of species is not unusual becuase copepods disperse as adults and cladocerans disperse through resting eggs. Rare species included *Strandesia bicuspis*, *Alona costata*, *A. quadranularis*, *Bosmina longirostris*, *Ceriodaphnia quadrangula*, *Cyclocypris sharpei*, *Leydigia leydigi*, and *Moiodaphnia macleayi* while many others were widely distributed (*Acantholeberis curvirostris*, *Chydorus sphaericus*, *Ilyocryptus spinifer*, *Paracyclops fimbriatus*, and *Simocephalus exspinosus).* One taxon, *Polyphemus sp.*, is native to the Great Lakes region of the United States (Pennak 1989), but I collected it at Archbold Biological Station, the southern-most study site along the peninsula.

Although sites were in similar ponds, mean temperature ranged from 12-27º C among sites and their surface areas varied considerably (0.07-6.45 ha). . As expected, the northern-most ponds in Jennings State Forest had the lowest minimum temperatures (7º C) and the southern-most ponds in Archbold Biological Station had the highest maximum temperatures (26º C). All ponds were acidic (pH= 3.92 ± .44SD). Dissolved oxygen and conductivity levels varied among ponds, as did nutrient levels (i.e. total N, total P, chlorophyll *a*, and total hardness). However, ponds were consistently low in nutrients; most ponds were below detection limits for total N, total P, chlorophyll *a,* and total hardness. Total wet season precipitation ranged from 94-127 cm. This was well above normal annual rainfall due to the active 2004 hurricane season. A summary of all environmental data is provided in Appendix B.

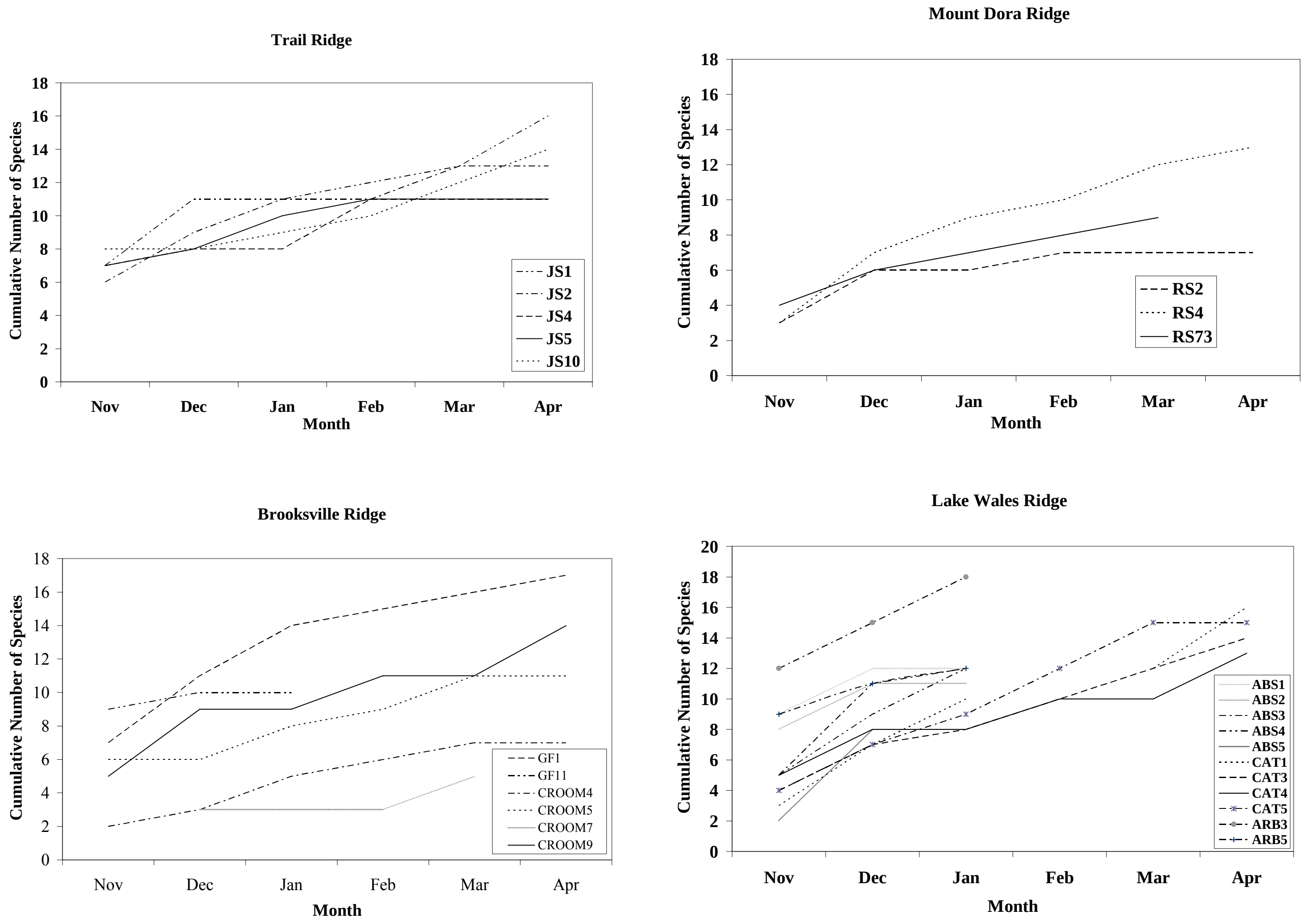


Figure 3. Species-sample curves for all sites that were sampled multiple times. Six sites were sampled once prior to their drying out and are not shown, but all other wetlands were sampled 3-6 times, either until the pond dried or until April, 2005.

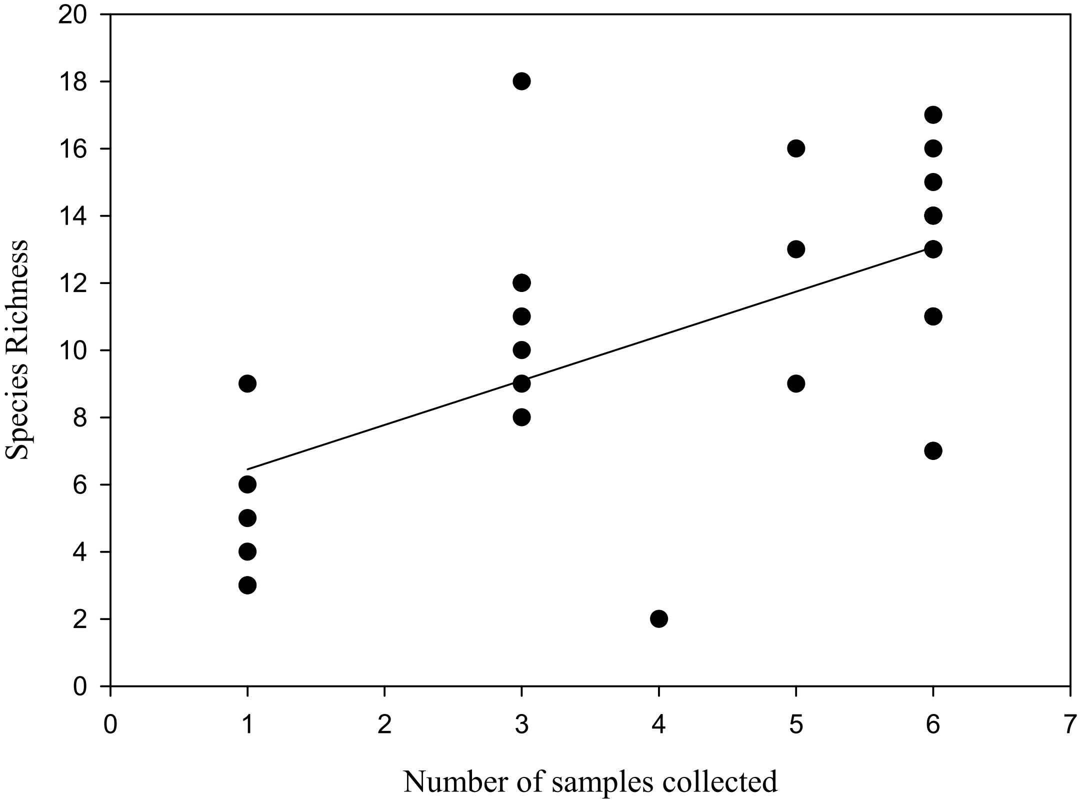


Figure 4. Relationship between species richness values and number of samples collected (F= 16.466, p<0 .001, R^2=0.362).

Species-sample curves (Figure 3) indicated that species richness was not fully inventoried in most wetlands; species richness increased as the number of samples increased (Figure 4). Therefore, I included the number of samples collected (sampling effort) as a regressor.

Multiple regression of species richness versus retained environmental variables and sampling effort accounted for 57% of the variation in species richness, leaving 43% of the variation in species richness unexplained (Table 3; $F_{1,22}$=7.609, p<0.001).

Linear regression of the remaining variation (species richness residuals) against latitude (Figure 5) was not significant ($F_{1,1}$=0.391, p=0.537, R^2=0.013), indicating that latitude was uncorrelated with remaining variation in species richness. Variables retained in the backward elimination regression were mean conductivity, minimum and maximum total P, fish presence or absence, distance to nearest water body, and hydroperiod (temporary or permanent), of which only phosphorus levels significantly affected species richness when analyzed alone (p< 0.01). Reversing the series of regressions did not change these results (Figure 6; F=0.419, p=0.523, R_2=0.014). Regression of residuals vs. environment and sampling effort explained 53% of the variation in species richness (Table 4; $F_{1,22}$=6.621, p<0.001). Thus, latitude (i.e. peninsular location did not account for significant variation in microcrustacean species richness.

In addition, one-way ANOVA of sites versus species richness revealed no significant differences in species richness among ridges (Figure 7a; $F_{1,3}$=1.361, p=0.276) or conservation areas (Figure 7b; $F_{1,7}$=1.733, p=0.151). Sampling effort significantly differed among ridges (p=0.024) and conservation areas (p=0.011), therefore justifying the use of sampling effort as a regressor. Conservation areas differed significantly for mean temperature, mean pH, mean chlorophyll, mean total hardness, fish presence or absence and canopy openness (Table 5).

Table 3. Variables retained by backward stepwise regression of species richness on environmental variables. Standardized beta coefficients and significance values are listed for each source of variation.

Source of variation	standardized β	p
Mean Conductivity (mS/cm)	-0.260	0.058
Minimum Total P (mg/L)	-0.561	**<0.001**
Maximum Total P (mg/L)	0.579	**0.001**
Temporary / Permanent	-0.237	0.091
Distance to Nearest Water body (m)	-0.332	**0.015**
Fish Absence / Presence	0.302	**0.036**

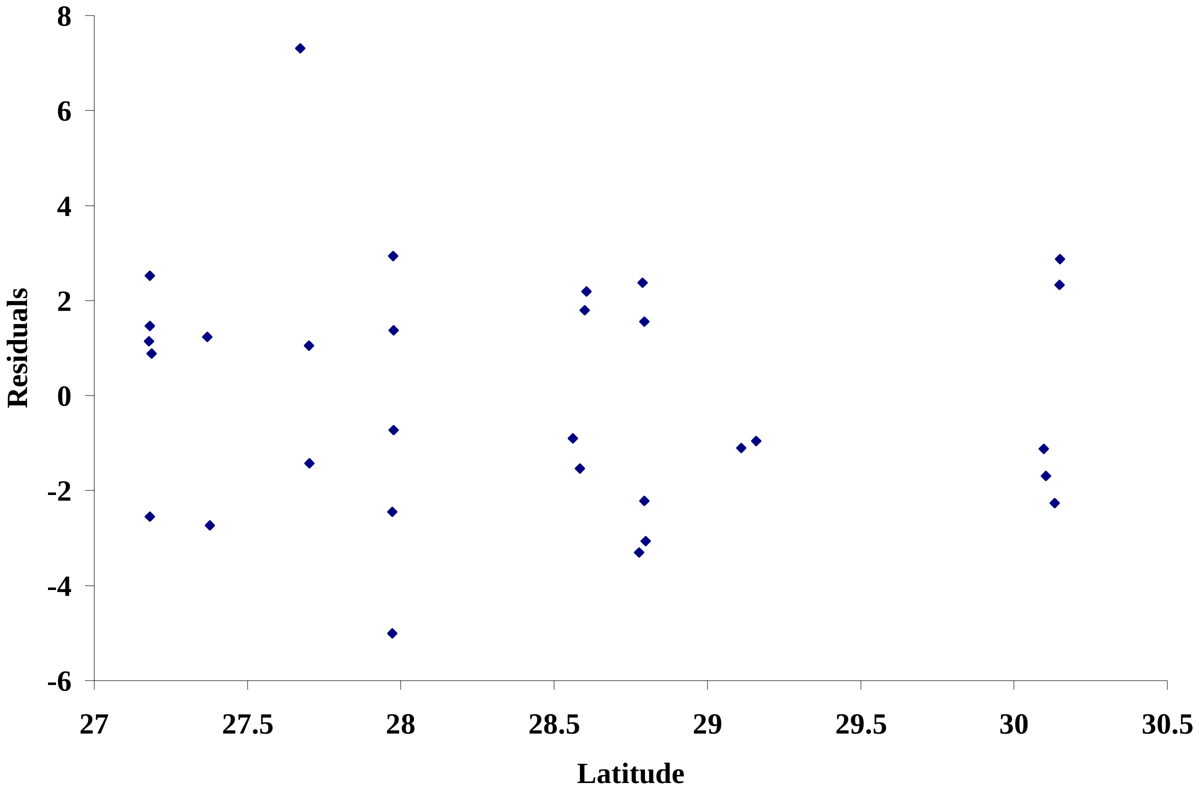


Figure 5. Linear regression of species richness: habitat residuals as a function of latitude ($F_{1,1}$=0.391, p=0.537, R^2=0.013).

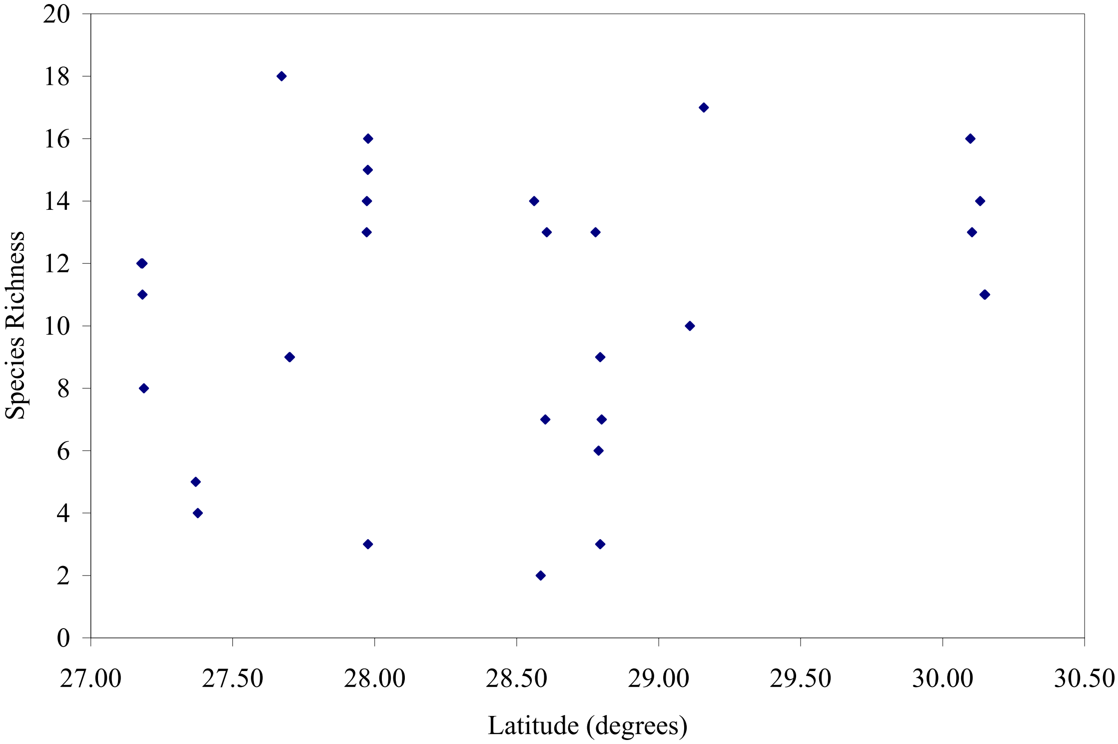


Figure 6. Species richness: latitude relationship for crustaceans inhabiting wetlands located on Florida's ridges (F=0.419, p=0.523, R^2=0.014). Data were not adjusted for habitat (compare to Figure 5).

Table 4. Variables retained by backward stepwise regression of species richness: latitude residuals on environmental variables. Standardized beta coefficients and significance values are listed for each source of variation.

Source of variation	standardized β	p
Mean Conductivity (mS/cm)	-0.251	0.079
Minimum Total P (mg/L)	-0.533	**0.001**
Maximum Total P (mg/L)	0.564	**0.001**
Temporary / Permanent	-0.272	0.065
Distance to Nearest Water body (m)	-0.337	**0.018**
Fish Absence / Presence	0.303	**0.044**

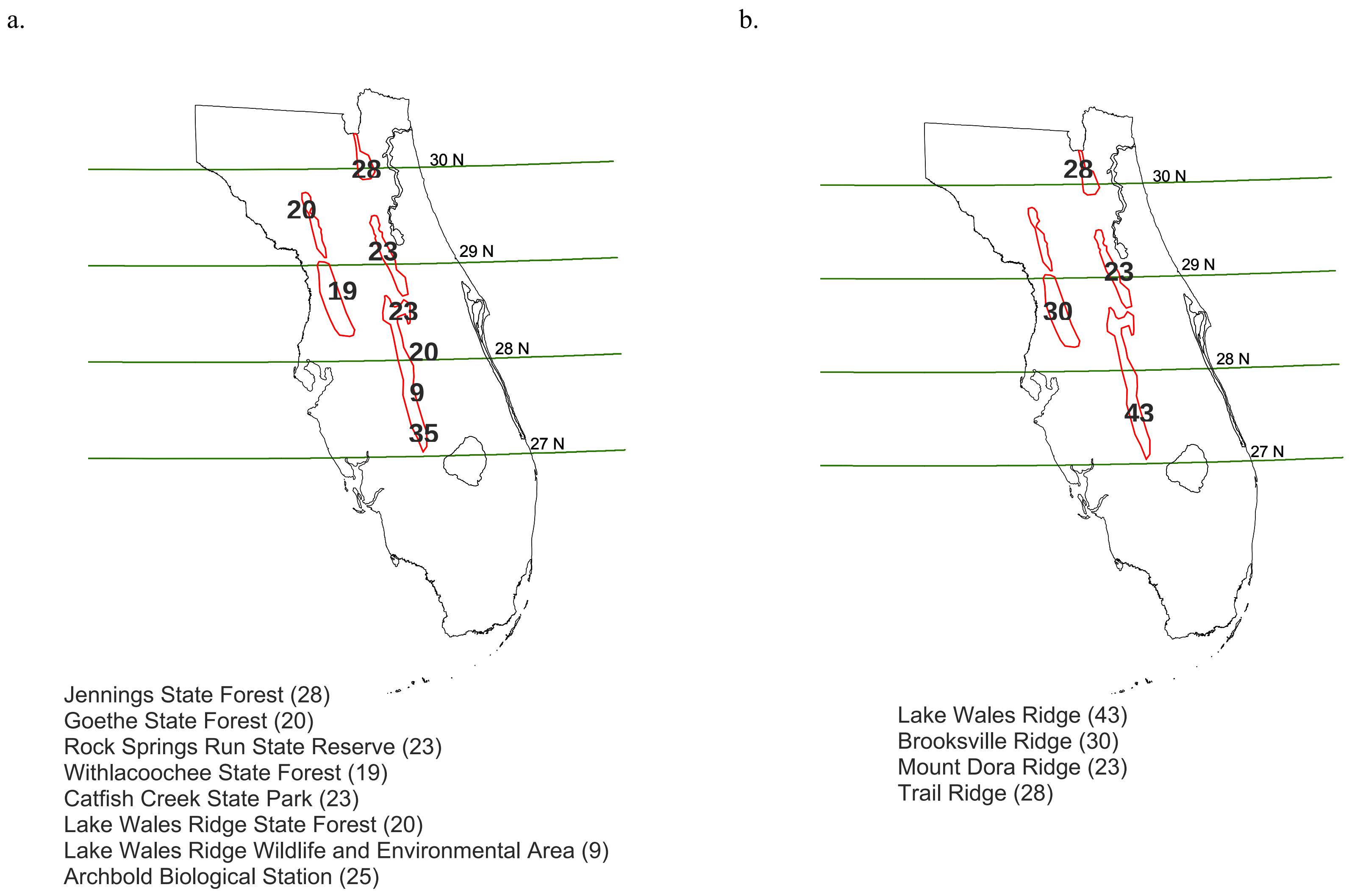


Figure 7. Species richness (in parentheses) and location of each conservation area (a) and ridge (b) along the Florida peninsula.

Table 5. Results of one-way analysis of variance for each environmental variable using both ridge and conservation area as the independent variables.

	Ridge				Conservation Area			
	Sum of Squares	Mean Square	$F_{1,3}$	p	Sum of Squares	Mean Square	$F_{1,7}$	p
Area (ha)	16.397	5.466	2.789	0.060	16.549	2.364	1.031	0.437
Mean Temperature (°C)	259.007	86.336	10.989	**<0.001**	16.549	48.016	8.179	**<0.001**
Mean pH	2.969	0.990	9.705	**<0.001**	3.643	0.520	5.758	**0.001**
Mean Dissolved Oxygen (%)	2966.834	988.945	1.702	0.190	6526.171	932.310	1.768	0.143
Mean Cond. (mS/cm)	0.005	0.002	1.791	0.173	0.009	0.001	1.419	0.245
Minimum Total N (mg/L)	0.003	0.001	.401	0.753	0.016	0.002	0.861	0.551
Maximum Total N (mg/L)	0.110	0.037	1.348	0.280	0.268	0.038	1.526	0.208
Minimum Total P (mg/L)	0.007	0.002	2.021	0.135	0.012	0.002	1.594	0.187
Maximum Total P (mg/L)	0.010	0.003	2.124	0.120	0.022	0.003	2.218	0.071
Mean Chlorophyll A	0.075	0.025	1.165	0.341	0.449	0.064	7.284	**<0.001**
Mean Hardness (mg/L)	12.102	4.034	.189	0.903	376.096	53.728	5.789	**0.001**
Temporary / Permanent	2.586	0.862	8.214	**<0.001**	2.669	0.381	3.189	**0.016**
Distance to Nearest Water body (m)	50938.602	16979.534	1.846	0.163	108391.935	15484.562	1.865	0.123
Fish Absence / Presence	2.044	0.681	3.266	**0.037**	6.127	0.875	12.989	**<0.001**
% Canopy Openness	4755.634	1585.211	25.467	**<0.001**	5083.550	726.221	12.348	**<0.001**

Ridges differed significantly in mean temperature, mean pH, temporary or permanent water body, and canopy openness (Table 5). Of these, only fish presence or absence and temporary or permanent water body were also retained by the backward elimination regression of species richness on environment variables (Tables 3 and 4).

The first two significant canonical discriminant functions of environmental variables ($p<0.001$) accounted for 76% of the total variation among conservation areas (Table 6a) and these functions included as variables only fish presence or absence and canopy openness. Canonical discriminant analysis correctly predicted 67.7% of the conservation areas that sites were located within according to environmental variables (Table 6b). The first significant function of stepwise canonical discriminant analysis for ridges explained 74.5% of the variation between ridges using only canopy openness as the predictor variable (Table 7a). Canonical discriminant analysis correctly predicted the ridge based on environmental variables for 80.6% of all sites (Table 7b).

Species co-occurrence analysis (EcoSim v7.0) revealed that species presence or absence was not significant with latitude ($p=0.628$) and that species were randomly distributed.

In summary, crustacean species richness within ephemeral wetlands on the ridges of the Florida peninsula was determined by local environmental variables, not location along the peninsula or on ridges or conservation areas. Significant variables (distance to nearest water body, fish presence or absence, and minimum and maximum phosphorus levels) retained from the backward elimination regression were not strong predictors of species richness individually in univariate regressions (Figure 8). Also, wetlands on different ridges and in different conservation areas differed in environmental variables that were not retained in peninsula-wide analyses, and thus did not confound peninsula-effect analyses.

Table 6. (a) Results of stepwise canonical discriminant function analysis of environmental parameters, including eigenvalues and % variance explained for the first four functions. (b) Classification of sites into one of the eight conservation areas based on environmental parameters is provided both in count (top) and % accuracy (bottom) results.

a.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	7.980	58.0	58.0	0.943
2	2.486	18.1	76.0	0.844
3	1.799	13.1	89.1	0.802
4	1.501	10.9	100.0	0.775

b.

		Predicted Group Membership								
	Conservation Area	1	2	3	4	5	6	7	8	Total
Original Count	1	3	0	2	0	0	0	0	0	5
	2	0	2	0	0	0	0	0	0	2
	3	0	0	4	1	0	0	0	0	5
	4	0	0	1	1	0	0	1	1	4
	5	0	0	0	0	3	0	2	0	5
	6	0	0	0	0	0	2	1	0	3
	7	0	0	0	0	0	0	2	0	2
	8	0	0	0	1	0	0	0	4	5
Accuracy (%)	1	**60.0**	.0	40.0	.0	.0	.0	.0	.0	100.0
	2	.0	**100.0**	.0	.0	.0	.0	.0	.0	100.0
	3	.0	.0	**80.0**	20.0	.0	.0	.0	.0	100.0
	4	.0	.0	25.0	**25.0**	.0	.0	25.0	25.0	100.0
	5	.0	.0	.0	.0	**60.0**	.0	40.0	.0	100.0
	6	.0	.0	.0	.0	.0	**66.7**	33.3	.0	100.0
	7	.0	.0	.0	.0	.0	.0	**100.0**	.0	100.0
	8	.0	.0	.0	20.0	.0	.0	.0	**80.0**	100.0

Table 7. (a) Results of stepwise canonical discriminant analysis of environmental parameters including the eigenvalues and % variance explained for the first two functions. (b) Classification of sites into one of the four ridges based on environmental parameters is provided both in count (top) and % accuracy (bottom) results.

a.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	3.670	74.5	74.5	0.886
2	1.217	24.7	99.2	0.741

b.

		Predicted Group Membership				
	Ridge	1	2	3	4	Total
Original Count	1	14	1	0	0	15
	2	0	5	0	0	5
	3	1	1	3	1	6
	4	0	1	1	3	5
Accuracy (%)	1	**93.3**	6.7	.0	.0	100.0
	2	.0	**100.0**	.0	.0	100.0
	3	16.7	16.7	**50.0**	16.7	100.0
	4	.0	20.0	20.0	**60.0**	100.0

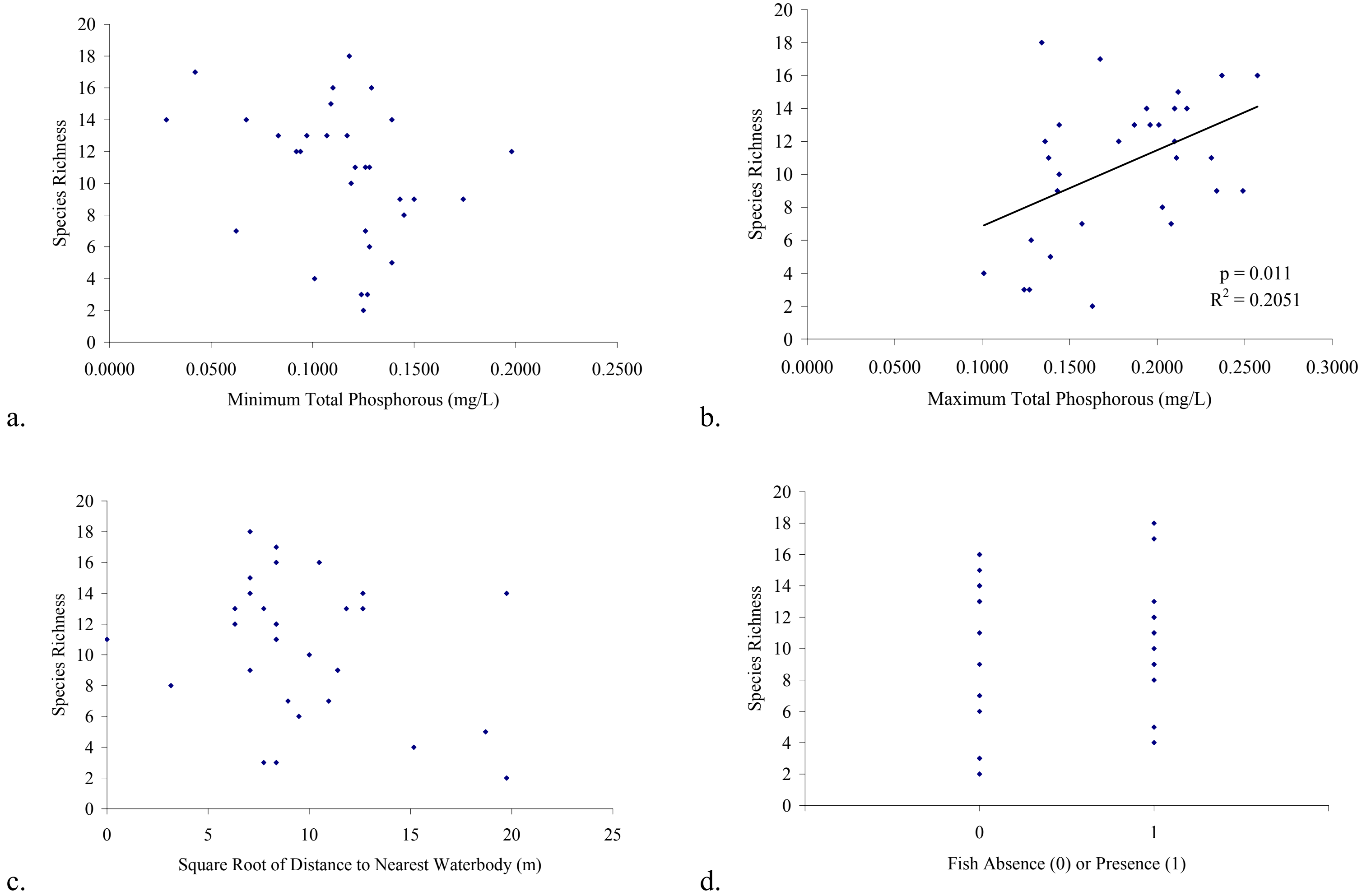


Figure 8. Species richness of freshwater crustaceans as a function of individual habitat variables: a) minimum total phosphorus (mg/L), b) maximum total phosphorus (mg/L), c) distance to nearest water body (√m) and d) fish presence.

DISCUSSION

A peninsula effect did not account for significant variation in the species richness of freshwater crustaceans inhabiting Florida isolated wetlands. Instead, six habitat variables accounted for over one-half of the variation in species richness. Reversing the order of analysis, accounting for latitude first and habitat second, did not change these results. The same six variables were retained in the regression model: mean conductivity, minimum and maximum total phosphorus, distance to nearest water body, pond permanence, and fish presence or absence. These six factors commonly control richness of many taxa in wetland ecosystems (Mitsch & Gosselink 2000, Wetzel 2001). Individually, however, each environmental variable was not a significant predictor of microcrustacean species richness.

In addition, no relationship was found between species richness and area as expected from Island Biogeography Theory (MacArthur & Wilson 1967) perhaps because crustacean species richness is better predicted by hydroperiod of ephemeral wetlands (Frisch et al. 2006, Eitam et al. 2004, Jenkins et al. 2003, Rundle et al. 2002, Spencer et al 1999, Schneider & Frost 1996). Furthermore, the wetlands I sampled may be more analogous to a stepping-stone model (MacArthur & Wilson 1967) due to their isolation by distance and location on the peninsula.

One of the habitat factors, conductivity, quantifies the ability of a solution to carry electrical current (Wetzel 2001) and is an indicator of ionic concentrations (e.g., dissolved minerals and nutrients). Major ions measured by conductivity include calcium, magnesium, sodium, potassium, and chloride. Calcium is crucial to crustaceans because it is used to build their exterior carapace (Neufeld & Cameron 1993, Alstad et al. 1999, Waervagen et al. 2002), and higher conductivities could increase crustacean species richness. Conductivity alone was not a significant predictor of microcrustacean species richness, but my results suggest it contributes to species richness patterns when examined with other habitat variables. In addition, all ponds I sampled had low conductivities, so there was little variation in total ionic concentration.

Phosphorus is a limiting nutrient in many freshwater wetlands (Mitsch & Gosselink 2000), and total phosphorus is widely used to indicate the trophic status of freshwater (Mitsch & Gosselink 2000, Wetzel 2001). Crustacean species richness increased with maximum total phosphorus in my study ponds. Total phosphorus levels were generally low, so even slight increases had a large effect on species richness. It is also reasonable to predict that species richness would peak at intermediate phosphorus levels and then decrease as nutrient loads increase toward eutrophic conditions, consistent with the Intermediate Disturbance Hypothesis (Connell 1978). Therefore, the relatively low phosphorus levels observed in my study contributed monotonically to crustacean species richness.

Distance to the nearest water body was an index of the degree of isolation for each wetland. Sites closer to other water bodies were slightly higher in species richness, perhaps because dispersal distances were shorter, leading to increased immigration opportunities. This interpretation is a local version of the immigration-extinction hypothesis (MacArthur and Wilson 1967). Isolated ponds have a minimal chance of connecting to other water bodies during extreme flood events (e.g. three consecutive hurricanes: Charlie, Frances and Jeanne) and are often temporary wetlands. Although temporary or permanent classification of a site (i.e. hydroperiod) was retained in the backward elimination regression model, it was not significant as a sole predictor of species. However, interconnectivity between temporary ponds creates larger water bodies, which can support a greater number of species (Dodson 1992), and enhances dispersal probability (Frisch et al. 2006). Larger ponds also tend to have longer hydroperiods (Schneider & Frost 1996) so fish and other invertebrate predators are able to colonize, ultimately limiting crustacean species richness due to competition and predation. Larger ponds in this study had longer hydroperiods and contained fish or other predators, but, fish presence/absence was not a significant predictor of species richness when analyzed alone.

Fish presence may have been a result of short-term hurricane flooding, which caused sheet flow between otherwise isolated ponds. Fish presence/absence may have to be considered long term (over many wet seasons) to assess their effects. It is also possible that the presence of fish in larger, more permanent ponds may reduce the number of species and nullify a species-area or peninsula effect given that a species-area effect was found for fishless ponds in this study. Despite its lack of effect on species richness when considered alone, fish presence/absence was retained in the regression (although not significant). Species richness appeared to be slightly higher in the presence of fish, which would suggest top-down control (Shurin & Allen 2001).

Previous investigations did not provide clear evidence of a peninsula effect (Taylor & Pfannmuller 1981), presented contradictory results subject to interpretation (Milne & Forman 1986, Seib 1980) or did not address all three hypotheses (Taylor & Regal 1978a, Due & Polis 1986, Busack & Hedges 1984). In contrast, my study accounted for two of the three hypotheses through study design and statistical analyses to isolate and test for the effects of immigration-extinction. Historical differences were minimized by focusing on Florida ridges, which are similar in age, sediment, and topography (Myers & Ewel 1990). While ridges differed significantly in mean temperature, mean pH, hydroperiod and canopy openness, both ridge and conservation area were eliminated during stepwise regression analysis as contributing to species richness. Therefore, site location was of minor importance compared to local habitat parameters; the latter were the major source of variation in microcrustacean species richness. Past geologic and climatic events also influence the immigration-extinction equilibrium hypothesis because dispersal of mainland species along the peninsula is limited by time since peninsular formation, the extent of the peninsula, and the taxon's dispersal abilities. Therefore, it is reasonable to consider how long crustaceans have dispersed down the Florida peninsula. In studies on zooplankton dispersal, colonization of new habitats (≤1 year) did not occur as readily as expected (Jenkins 1995, Jenkins & Underwood, 1998) despite the widespread belief that zooplankton move easily between habitats by wind, rain, floods, and waterfowl. Stemberger (1995) further noted that many copepod species had not extended their postglacial distribution (~10,000 years), while others were widely distributed. Lack of a peninsula effect in my study implies that zooplankton species have dispersed fully along the Florida peninsula since its formation ~100,000 years ago (Myers & Ewel 1990). Species co-occurrence analysis (EcoSim v7.0) revealed that species presence or absence was random along the peninsula and that species were not limited in distribution. Based on my results and those of Stemberger (1995), zooplankton apparently colonized wetlands of the Florida ridges over the past ~10-100,000 years. In addition, the optimal time to observe a peninsular pattern is at the end of an interglacial stage when differential dispersal is fully expressed, not at present (Myers & Ewel 1990).

Other studies (Brown 1987 & 1990, Seib 1980, Schwartz 1988) that found no peninsula effect suggested that counter-gradients were the cause: i.e. that mainland species decline base to tip, while in Florida, tropical or Caribbean species decrease tip to base. The presence of counter-gradients, or a dual-effect, could confound an underlying peninsular pattern (Brown 1987 & 1990). However, no exotics or species of Caribbean origin were collected throughout my study and a dual effect was dismissed for these organisms.

Wetlands are complicated ecosystems affected by various local and regional processes that interact to determine overall species richness. The most important processes in determining microcrustacean species richness are still undetermined in many wetlands, but appear to be process- and habitat-dependent (Kiflawi et al. 2003). Local conditions (e.g., habitat permanence and resource availability) can regulate zooplankton species richness and colonization can limit accumulation of species in hydrologically-isolated systems (Holland & Jenkins 1998, Rundle et al. 2002). Given sufficient time, colonization should have occurred in all habitats sampled in this study, leaving local conditions as the sole determinant of community structure (the quorum effect; Jenkins & Buikema 1998).

Crustaceans are a model organism for studying the peninsula effect because they rely on passive dispersal, which limit habitat selection as a process determining species presence or absence. Some may argue that crustaceans exhibit seasonal succession and some species may have been missed in one-month sampling intervals. However, I sampled ponds across >3° of latitude under the same protocol, so comparisons between ponds are viable. In addition, differences in the number of samples per site were standardized by including the number of samples collected as a variable in all multiple regressions.

In conclusion, crustacean species richness in wetlands along Florida's ridges is largely determined by habitat. Position on the peninsula did not contribute significantly to species richness; the peninsula effect does not exist for freshwater crustaceans in ephemeral wetlands of

Florida. The methods outlined in this study may serve as a model for future analyses of the peninsula effect. Previous research should be re-examined to address the three current hypotheses (habitat, history and immigration-extinction hypotheses), as a more comprehensive test of this long-debated topic in ecology (Simpson 1964, MacArthur & Wilson 1967, Means & Simberloff 1987).

APPENDIX A:

PRESENCE AND ABSENCE OF SPECIES

Genus	Species	JF1	JF2	JF4	JF5	JF10	RS2	RS4	RS73	RS77	RS81	GF1	GF11	Croom4	Croom5	Croom7	Croom9	CAT1	CAT2	CAT3	CAT4	CAT5	ARB3	ARB5	ARB6	WEA1	WEA3	ABS1	ABS2	ABS3	ABS4	ABS5	TOTAL
Acanthocyclops	*vernalis*	X	X	X		X		X						X	X	X				X	X	X											11
Acantholeberis	*curvirostris*	X	X	X	X	X						X	X					X				X	X	X				X	X	X	X	X	16
Alona	*affinis*		X			X		X				X											X					X	X	X			8
Alona	*circumfimbriata*																	X		X	X	X											4
Alona	*costata*		X																														1
Alona	*guttata*	X			X	X						X	X		X						X		X							X			9
Alona	*monocantha*	X	X									X		X	X		X	X		X	X	X	X	X							X	X	14
Alona	*quadrangularis*					X																						X	X				3
Alona	*rustica*																														X		1
Alona	*setulosa*	X			X	X						X									X	X	X								X		8
Biapertura	*karua*	X		X	X			X							X		X	X		X		X		X	X				X	X			13
Bosmina	*longirostris*																						X										1
Bryocamptus	*sp.*											X																					1
Camptocercus	*sp. 1*	X	X	X		X						X											X										6
Ceriodaphnia	*quadrangula*																											X					1
Ceriodaphnia	*reticulata*	X												X	X	X	X	X		X	X	X											9
Chydorous	*sphaericus*	X	X	X	X	X		X				X					X	X		X	X	X	X		X			X	X	X	X	X	19
Cyclocypris	*sharpei*						X	X																									2
Cyclops	*thomasi*								X																								1
Cypridopsis	*okeechobi*								X																								1
Daphnia	*laevis*						X					X					X																3
Diaphanosoma	*birgei*											X					X						X					X					4
Diaphanosoma	*brachyurum*	X	X					X						X	X		X	X		X		X	X			X		X					12
Diaptmous	*dorsalis*					X								X	X		X																4
Diaptomus	*floridanus*						X	X				X	X																				4
Ephemeroporus	*acanthodes*							X				X	X					X					X	X	X				X			X	9
Eucyclops	*agilis*								X																								1
Eucyclops	*prionophorus*																	X		X													2
Graptoleberis	*testudinaria*												X									X	X				X						4
Halicyclops	*sp.*																												X				1
Ilyocryptus	*agilis*			X						X													X										3
Ilyocryptus	*sordidus*																										X						1
Ilyocryptus	*spinifer*	X	X		X	X		X	X		X		X		X		X	X	X	X	X	X						X	X	X	X	X	20
Kurzia	*latissima*	X		X				X										X		X							X	X			X	X	9
Latonopsis	*occidentalis*		X									X																X	X				4
Leydigia	*leydigi*											X																					1
Macrocylcops	*ater*					X							X	X			X							X	X								6
Macrothrix	*rosea*	X						X				X	X		X						X	X	X	X	X								10
Microcylcops	*varicans*		X	X			X		X		X							X		X	X							X	X	X		X	12
Moinodaphnia	*macleayi*																									X							1
Notodromus	*sp*																									X							1
Orthocyclops	*modestus*									X																							1
Paracyclops	*fimbriatus*				X	X	X		X			X	X		X			X		X	X	X	X	X	X						X	X	16
Polyphemus	*sp.*																													X	X		2
Pseudosida	*bidentata*		X	X	X	X		X	X														X	X	X		X		X	X	X		13
Scapholebris	*mucronata*	X		X	X			X	X														X		X					X	X		9
Simocephalus	*exspinosus*		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X			X		26
Simocephalus	*serrulatus*	X		X							X																			X			4
Simocephalus	*vetulus*													X			X													X			3
Strandesia	*bicuspis*						X										X																2
Streblocerus	*pygmaeus*	X	X		X	X					X				X		X			X	X	X											10
Streblocerus	*serricaudatus*										X							X															2
Tropocyclops	*prasinus*	X													X			X		X	X	X											6
Unknown	***cyclopoida***																		X														1
Unknown	***harpacticoida***														X																		1
Unknown	***calanoida***																									X							1
		16	13	11	11	14	7	13	9	3	6	17	10	7	13	2	14	16	3	14	13	15	18	9	9	5	4	12	11	12	12	8	

APPENDIX B:

SUMMARY OF ALL ENVIRONMENTAL DATA

Latitude	Site	Area (m^2)	Species Richness	Min. Temp (°C)	Max. Temp (°C)	Mean Temp (°C)	Min. pH	Max. pH	Mean pH	Min. D.O$_2$ (%)
N30°05.829' W81°55.366'	JS1	0.72	16	7.36	19.90	13.90	3.55	3.90	3.71	42.80
N30°06.217' W81°55.541'	JS2	1.58	13	7.30	17.50	12.18	3.63	4.05	3.85	29.30
N30°08.969' W81°53.577'	JS4	0.15	11	7.78	19.00	13.79	3.56	4.05	3.82	29.00
N30°08.866' W81°53.854'	JS5	6.45	11	9.42	18.40	14.41	3.38	3.87	3.69	28.90
N30°07.930' W81°53.627'	JS10	1.55	14	9.16	18.50	14.79	3.84	4.83	4.06	9.10
N29°09.537' W82°35.947'	GF1	0.38	17	9.29	20.92	15.64	3.50	4.38	3.91	45.40
N29°06.597' W82°34.685'	GF11	0.14	10	7.22	17.80	14.23	3.97	4.32	4.15	23.70
N28°36.022' W82°15.387'	Croom4	0.57	7	11.90	22.25	17.93	3.50	4.55	4.08	18.70
N28°36.355' W82°17.217'	Croom5	1.18	13	12.38	22.23	18.19	4.42	4.88	4.61	38.50
N28°35.066' W82°16.325'	Croom7	6.45	2	11.14	20.18	16.39	4.35	5.30	4.83	23.40
N28°33.672' W82°16.946'	Croom9	1.35	14	11.67	20.55	16.72	3.84	5.03	4.45	21.70
N28°47.950' W81°27.057'	RS2	0.45	7	10.28	25.40	19.17	4.41	5.38	4.98	35.00
N28°46.672' W81°27.287'	RS4	0.73	13	12.95	26.05	19.20	3.96	4.54	4.23	30.60
N28°447.674' W81°27.438'	RS73	1.03	9	11.71	22.30	17.83	3.86	4.28	4.07	17.20
N28°47.663' W81°27.235'	RS77	0.07	3	20.60	20.60	20.60	3.78	3.78	3.78	55.20
N28°47.298' W81°27.590'	RS81	0.19	6	24.78	24.78	24.78	3.80	3.80	3.80	111.80
N27°10.703' W81°21.540'	ABS1	0.26	12	13.40	26.20	20.23	3.33	3.52	3.45	35.30
N27°10.902' W81°21.438'	ABS2	1.20	11	14.99	23.70	19.88	3.30	3.54	3.42	47.00
N27°10.904' W81°21.323'	ABS3	0.68	12	14.17	25.07	20.05	3.47	3.70	3.57	26.20
N27°10.918' W81°21.362'	ABS4	0.13	12	13.73	25.40	20.03	3.45	3.59	3.52	32.90
N27°11.208' W81°21.438'	ABS5	0.13	8	17.48	26.30	21.85	3.50	3.78	3.61	35.60
N27°22.173' W81°19.705'	WEA1	0.15	5	28.70	28.70	28.70	4.90	4.90	4.90	64.00
N27°22.628' W81°20.790'	WEA3	0.69	4	26.20	26.20	26.20	3.62	3.62	3.62	71.00
N27°40.337' W81°24.785'	ARB3	0.77	18	15.89	20.04	18.59	3.44	3.74	3.57	58.00
N27°42.003' W81°26.210'	ARB5	0.29	9	18.78	20.58	19.52	3.34	3.42	3.37	60.50
N27°42.084' W81°26.335'	ARB6	1.09	9	21.82	21.82	21.82	3.55	3.55	3.55	76.10
N27°58.630' W81°29.543'	CAT1	0.23	16	19.68	20.64	20.15	3.61	3.97	3.73	27.30
N27°58.550' W81°29.578'	CAT2	0.27	3	26.96	26.96	26.96	3.58	3.58	3.58	152.40
N27°58.367' W81°29.602'	CAT3	0.50	14	17.45	20.93	19.10	3.56	4.16	3.83	16.40
N27°58.311' W81°29.518'	CAT4	0.58	13	17.68	24.69	21.38	3.37	4.17	3.79	66.20
N27°58.537' W81°29.728'	CAT5	0.85	15	19.35	26.06	22.45	4.01	4.32	4.12	67.10

Max. D.O$_2$ (%)	Mean D.O2 (%)	Min. Cond. (mS/cm)	Max. Cond. (mS/cm)	Mean Cond. (mS/cm)	Min. Tot. N (mg/L)	Max. Tot. N (mg/L)	Mean Tot. N (mg/L)	Min. Tot. P (mg/L)	Max. Tot. P (mg/L)	Mean Tot. P(mg/L)
69.00	52.15	0.026	0.047	0.03	0.0963	0.2080	0.17	0.1290	0.2370	0.19
67.30	52.06	0.033	0.039	0.04	0.1074	0.2120	0.16	0.0831	0.1960	0.14
66.00	46.12	0.041	0.059	0.05	0.1089	0.2180	0.16	0.1210	0.2310	0.17
69.50	53.22	0.053	0.067	0.06	0.0880	0.1632	0.12	0.1260	0.2110	0.16
66.30	46.40	0.030	0.036	0.03	0.0979	0.2030	0.13	0.0674	0.2100	0.15
71.30	58.48	0.037	0.055	0.04	0.0096	0.9247	0.23	0.0421	0.1674	0.12
71.40	42.80	0.025	0.039	0.03	0.0790	0.1450	0.10	0.1190	0.1440	0.14
64.00	29.58	0.020	0.024	0.02	0.1340	0.2310	0.17	0.1260	0.2080	0.16
74.40	51.48	0.022	0.027	0.03	0.0841	0.1930	0.12	0.1070	0.2010	0.13
51.70	37.50	0.047	0.062	0.06	0.0550	0.1960	0.14	0.1250	0.1630	0.14
55.00	35.37	0.019	0.024	0.02	0.0690	0.2310	0.15	0.0280	0.1940	0.12
90.00	56.58	0.037	0.042	0.04	0.0178	0.7640	0.23	0.0623	0.1570	0.12
55.40	44.88	0.061	0.078	0.07	0.1285	0.2800	0.19	0.0971	0.1440	0.13
43.00	26.62	0.100	0.115	0.11	0.0752	0.2270	0.16	0.1500	0.2340	0.18
55.20	55.20	0.115	0.115	0.12	0.0796	0.0796	0.08	0.1270	0.1270	0.13
111.80	111.80	0.038	0.038	0.04	0.1885	0.1885	0.19	0.1280	0.1280	0.13
39.00	36.60	0.051	0.051	0.05	0.0921	0.2120	0.15	0.0920	0.1360	0.12
72.20	55.70	0.054	0.063	0.06	0.0930	0.1740	0.13	0.1280	0.1380	0.13
55.10	37.77	0.053	0.060	0.06	0.0870	0.1723	0.12	0.1980	0.2100	0.21
62.50	51.07	0.054	0.057	0.06	0.0450	0.1751	0.11	0.0940	0.1780	0.14
77.30	62.27	0.058	0.067	0.06	0.0630	0.1280	0.11	0.1450	0.2030	0.17
64.00	64.00	0.016	0.016	0.02	0.2010	0.2010	0.20	0.1390	0.1390	0.14
71.00	71.00	0.170	0.170	0.17	0.1430	0.1430	0.14	0.1010	0.1010	0.10
65.70	62.20	0.046	0.053	0.05	0.0398	0.1890	0.11	0.1180	0.1340	0.13
79.30	69.90	0.042	0.092	0.07	0.0068	0.2010	0.12	0.1742	0.2490	0.20
76.10	76.10	0.065	0.065	0.07	0.1957	0.1957	0.20	0.1430	0.1430	0.14
93.50	60.50	0.058	0.073	0.06	0.1023	0.2010	0.14	0.1100	0.2573	0.14
152.40	152.40	0.084	0.084	0.08	0.2023	0.2023	0.20	0.1240	0.1240	0.12
79.30	44.42	0.046	0.059	0.05	0.0870	0.2020	0.13	0.1390	0.2170	0.18
92.00	80.80	0.033	0.043	0.04	0.0879	0.2180	0.17	0.1170	0.1870	0.15
100.40	89.13	0.029	0.039	0.04	0.0723	0.1946	0.12	0.1090	0.2120	0.15

Min. Chlor. A	Max. Chlor. A	Mean Chlor. A	Min. Pheo. A	Max. Pheo. A	Mean Pheo. A	Min. Hardness (mg/L)	Max. Hardness (mg/L)
BDL	0.2890	0.07	BDL	0.0568	0.01	BDL	8.14
BDL	0.0376	0.01	BDL	0.2788	0.07	BDL	3.05
BDL	0.4263	0.07	BDL	0.0690	0.02	BDL	4.07
BDL	0.5827	0.13	BDL	0.0120	BDL	1.02	4.07
BDL	0.2577	0.04	BDL	0.1043	0.02	BDL	3.05
0.0053	1.2354	0.34	BDL	BDL	BDL	BDL	4.07
BDL	1.9647	0.65	BDL	0.2417	0.08	2.03	2.03
BDL	0.3704	0.07	BDL	0.0619	0.01	1.02	3.05
BDL	1.1204	0.20	BDL	0.2058	0.04	0.61	8.14
BDL	0.0894	0.04	BDL	0.2669	0.07	0.61	4.07
BDL	1.3873	0.27	BDL	0.0906	0.02	1.02	3.05
BDL	0.0120	BDL	BDL	0.0759	0.02	2.03	6.10
BDL	0.2980	0.05	BDL	0.3235	0.06	0.61	8.14
BDL	0.1948	0.05	BDL	0.0869	0.02	2.03	8.14
BDL	BDL	BDL	0.0078	0.0078	0.01	5.09	5.09
0.0107	0.0107	0.01	BDL	0.0000	BDL	4.07	4.07
BDL	0.0109	BDL	BDL	0.0214	0.01	BDL	3.05
BDL	0.0053	BDL	BDL	0.0152	0.01	BDL	2.03
0.0032	0.0208	0.01	BDL	0.0187	0.01	BDL	1.02
0.0025	0.0088	0.01	BDL	0.0150	0.01	BDL	2.03
BDL	0.0336	0.02	BDL	0.0160	0.01	BDL	3.05
BDL	BDL	BDL	BDL	BDL	BDL	18.31	18.31
BDL	BDL	BDL	BDL	BDL	BDL	20.35	20.35
0.0021	0.0336	0.02	BDL	0.0417	0.01	BDL	5.09
BDL	0.0753	0.03	BDL	0.0155	0.01	BDL	0.20
BDL	BDL	BDL	0.0044	0.0044	BDL	2.03	2.03
BDL	1.3472	0.41	BDL	0.0040	BDL	2.03	4.07
BDL	BDL	BDL	0.1289	0.1289	0.13	2.03	2.03
BDL	0.5423	0.13	BDL	0.0023	BDL	BDL	4.07
BDL	0.5935	0.10	BDL	0.7101	0.13	BDL	3.05
BDL	0.4969	0.15	BDL	0.2942	0.05	0.61	4.07

Mean Hardness (mg/L)	Monthly Mean Precipitation (cm)	Total Wet Season Precipitation (cm)	Temporary (0)/ Permanent (1)	Connected (0)/ Isolated (1)	Distance to Nearest Waterbody (m)	Fish Absence(0)/Presence (1)	% Canopy Openess	Total Transmitted Light (MJ/m^2/d)
1.73	10.58	95.20	0.00	1	110	0	59.98	23.32
1.78	10.58	95.20	1.00	1	160	0	62.99	23.83
2.37	10.58	95.20	0.00	1	70	0	31.39	11.84
2.65	10.58	95.20	1.00	0	0	1	37.58	16.19
2.03	10.58	95.20	0.00	1	160	0	51.10	20.86
2.03	12.63	113.67	0.00	1	70	1	61.13	24.78
2.03	12.63	113.67	0.00	1	100	1	47.08	21.49
2.03	13.86	124.76	1.00	1	80	0	70.28	27.23
3.66	13.86	124.76	1.00	1	40	0	59.65	24.46
2.70	13.86	124.76	0.00	1	390	0	65.00	25.00
1.87	13.86	124.76	1.00	1	390	0	54.68	19.53
3.82	10.51	94.59	1.00	1	120	0	71.36	26.80
3.38	10.51	94.59	0.00	1	140	1	65.91	23.02
3.56	10.51	94.59	1.00	1	50	0	62.60	23.45
5.09	10.51	94.59	0.00	1	60	0	66.11	24.93
4.07	10.51	94.59	0.00	1	90	0	82.00	27.00
1.02	12.90	116.10	0.00	1	40	1	80.17	23.45
0.68	12.90	116.10	0.00	1	70	1	81.25	23.26
0.41	12.90	116.10	0.00	1	70	1	85.02	28.82
0.68	12.90	116.10	0.00	1	70	1	82.72	26.35
1.02	12.90	116.10	0.00	1	10	1	88.85	28.97
18.31	10.92	98.27	0.00	1	350	1	79.11	27.79
20.35	10.92	98.27	0.00	1	230	1	80.68	28.29
1.90	9.74	87.63	0.00	1	50	1	81.20	28.32
0.07	9.74	87.63	0.00	1	130	1	81.78	28.22
2.03	9.74	87.63	0.00	1	130	1	81.39	28.46
2.65	14.16	127.46	0.00	1	70	0	80.13	28.38
2.03	14.16	127.46	0.00	1	70	0	79.17	26.97
1.70	14.16	127.46	0.00	1	50	0	82.36	28.40
1.63	14.16	127.46	0.00	1	60	0	79.63	28.09
2.65	14.16	127.46	0.00	1	50	0	83.77	28.32

REFERENCES

Alstad, N.E.W., Skardal, L. and Hessen, D.O. 1999. The effect of calcium concentration on the calcification of *Daphnia magna*. *Limnology and Oceanography* **44**: 2011-2017.

American Public Health Association, American Water Works Association & Water Pollution Control Facilities. 1989. Standard Methods for the Examination of Water and Wastewater, 17th edition. Washington, DC, USA: APHA, AWWA & WPCF.

Bohonak, A.J. and D.G. Jenkins. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters* **6**:783-796.

Brown, J.H. and Lomolino, M.V. 1998. Biogeography. Sunderland: Sinauer Associates.

Brown, J.W. 1987. The peninsula effect in Baja California: an entomological assessment. *Journal of Biogeography* **14**: 359-365.

Brown. J.W. and Opler, P.A. 1990. Patterns of butterfly species diversity in peninsular Florida. *Journal of Biogeography* **17**: 615-622.

Busack, S.D. and Hedges, S.B. 1984. Is the peninsula effect a red herring? *American Naturalist* **123**: 266-275.

Cook, R.E. 1969. Variation in species density of North American birds. *Systematic Zoology* **18**: 63-84.

Crumpton, W.G., Isenhart, T.M. and Mitchell, P.D. 1992. Nitrate and organic N analyses with second-derivative spectroscopy. *Limnology and Oceanography* **37**: 907-913.

Dodson, S. 1992. Predicting crustacean zooplankton species richness. *Limnology and Oceanography* **37**: 848-856.

Due, A.D. and Polis, G.A. 1986. Trends in scorpion diversity along the Baja California peninsula. *American Naturalist* **128**: 460-468.

Edmondson, W.T. editor.1959. Freshwater biology. 2nd ed. New York: John Wiley & Sons.

Eitam, A., Blaustein, L., Van Damme, K., Dumont, H.J. and Martens, K. 2004. Crustacean species richness in temporary pools: relationships with habitat traits. *Hydrobiologia* **525**: 125-130.

Figuerola, J., Green, A.J. and Michot, T.C. 2005. Invertebrate eggs can fly: evidence of waterfowl-mediated gene flow in aquatic invertebrates. *American Naturalist* **165**: 274-280.

Frisch, D., Moreno-Ostos, E. and Green, A.J. 2006. Species richness and distribution of copepods and cladocerans and their relation to hydroperiod and other environmental variables in Doñana, south-west Spain. *Hydrobiologia* **556**: 327-340.

Gilpin, M.E. 1981. Peninsular diversity patterns. *American Naturalist* **118**: 291-296.

Gotelli, N.J. and Entsminger, G.L. 2001. EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey Bear. http://homepages.together.net/~gentsmin/ecosim.htm

Green, A.J. and Figuerola, J. 2005. Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. *Diversity and Distributions* **11**: 14-156.

Holland, T.A. and Jenkins, D.G. 1998. Comparison of processes regulating zooplankton assemblages in new freshwater pools. *Hydrobiologia* **387/388**: 207-214.

Jenkins, D.G. 1995. Dispersal-limited zooplankton distribution and community composition in new ponds. *Hydrobiologia* **313/314**: 15-20.

Jenkins, D.G. and Buikema, A.L. 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecological Monographs* **68**: 421-443.

Jenkins, D.G., Grissom, S. and Miller, K. 2003. Consequences of prairie wetland drainage for crustacean biodiversity and metapopulations. *Conservation Biology* **17**: 158-167.

Jenkins, D.G. and Underwood, M.O. 1998. Zooplankton may not disperse readily in wind, rain, or waterfowl. *Hydrobiologia* **387/388**: 15-21.

Kiflawi, M., Eitam, A. and Blaustein, L. 2003. The relative impact of local and regional processes on macro-invertebrate species richness in temporary pools. *Journal of Animal Ecology* **72**: 447-452.

Lawlor, T.E. 1983. The peninsular effect on mammalian species diversity in Baja California. *American Naturalist* **121**: 432-439.

Lind, O.T. 1979. Handbook of common methods in limnology. St. Louis: Mosby.

MacArthur, R.H. and Wilson, E.O. 1967. The theory of island biogeography. Princeton: Princeton University Press.

Means, D.B. and Simberloff, D. 1987. The peninsula effect: habitat-correlated species decline in Florida's herpetofauna. *Journal of Biogeography* **14**: 551-568.

Milne, B.T. and Forman, R.T. 1986. Peninsulas in Maine: woody plant diversity, distance, and environmental patterns. *Ecology* **67**: 967-974.

Mitsch, W.J. and Gosselink, J.G. 2000. Wetlands. New York: John Wiley & Sons.

Myers, R.L. and Ewel, J.J. 1990. Ecosystems of Florida. Orlando: UCF Press.

Neufeld, D.S. and Cameron, J.N 1993. Transepithelial movement of calcium in crustaceans. *Journal of Experimental Biology* **184**: 1-16.

Orr, R.T. 1960. An analysis of recent land mammals. *Systematic Zoology* **9**: 171-178.

Pennak, R.W. 1989. Freshwater invertebrates of the United States: protozoa to mollusca. New York: John Wiley & Sons.

Quinn, G.P. and Keough, M.J. 2002. Experimental design and data analysis for biologists. Cambridge: Cambridge University Press.

Rundle, S.D., Foggo, A., Choiseul, V. and Bilton, D.T. 2002. Are distribution patterns linked to dispersal mechanism? An investigation using pond invertebrate assemblages. *Freshwater Biology* **47**: 1571-1581.

Schneider, D.W. and Frost, T.M. 1996. Habitat duration and community structure in temporary ponds. *Journal of North American Benthological Society* **15**: 64-86

Schwartz, M.W. 1988. Species diversity patterns in woody flora on three North American peninsulas. *Journal of Biogeography* **15**: 759-774.

Seib, R.L. 1980. Baja California: a peninsula for rodents but not for reptiles. *American Naturalist* **115**: 613-620.

Shurin, J.B. and Allen, E.G. 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. *American Naturalist* **158**: 624-637.

Simpson, G.G. 1964. Species density of North American recent mammals. *Systematic Zoology* **13**: 57-73.

Spencer, M., Blaustein, L., Schwartz, S.S. and Cohen, J.E. 1999. Species richness and the proportion of predatory animal species in temporary freshwater pools: relationships with habitat size and permanence. *Ecology Letters* **2**: 157-166.

Stemberger, R.S. 1995. Pleistocene refuge areas and postglacial dispersal of copepods of the northeastern United States. *Canadian Journal of Fisheries and Aquatic Sciences* ***52:***

2197-2210.

Taylor, R.J. and Pfannmuller, L.A. 1981. A test of the peninsula effect on species diversity. *Canadian Field Naturalist* **95**: 144-148.

Taylor, R.J. and Regal, P.J. 1978a. The peninsular effect on species diversity and the biogeography of Baja California. *American Naturalist* **112**: 583-593.

— 1978b. Erratum: the peninsular effect on species diversity and the biogeography of Baja California. *American Naturalist* **112**: 658.

— 1980. Reply to Seib. *American Naturalist* **115**: 621-622.

Thorp, J.H. and Covich, A.P Ecology and classification of North American freshwater invertebrates. San Diego: Academic Press.

Wærvågen, S.B., Rukke, A.N. & Hessen, D.O. 2002. Calcium content of crustacean zooplankton and its potential role in species distribution. *Freshwater Biology* **47**: 1866-1878.

Watts, W.A. 1971. Postglacial and glacial vegetation history of Southern Georgia and Central Florida. *Ecology* **51**: 17-33.

Wetzel, R.G. 2001. *Limnology: lake and river systems*. San Diego: Academic Press.