Distribution and Stability of Sympatric Populations of *Lucania goodei* and *L. parva* across Florida

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Understanding the distribution patterns of closely related species is critical because the extent to which their ranges overlap determines the opportunity for competition and hybridization. In this study, we used museum records to determine the degree of overlap between two killifish species, *Lucania goodei* and *L. parva*, in Florida. While the broad geographic distributions and habitat characteristics are well-described, the degree of sympatry between the two species, the temporal stability of sympatric populations, and the abiotic and biotic conditions under which sympatric populations occur are unknown. Using the museum records, we identified sites where *L. goodei* and/or *L. parva* had been collected and classified sites as either *L. goodei*–allopatric, *L. parva*–allopatric, or sympatric. For sites that were sampled repeatedly over time, we determined the extent to which their status varied. Approximately 12–19% of sites where *L. goodei* was present were sympatric with *L. parva* at some point in time. However, many sympatric sites were not stable over time. Of the repeatedly sampled sites that were sympatric at some point in time, more than 50% varied between allopatric and sympatric status. Salinity also had large effects on distribution. Approximately two-thirds of sympatric sites were in fresh water, and the remaining one-third were in brackish water. As expected, the fish community varied between *L. goodei, L. parva*, and sympatric sites. The unique contribution of this study is that it provides the first estimate of the degree of overlap between *L. goodei* and *L. parva* and indicates which biotic and abiotic variables may account for this pattern.

UNDERSTANDING the distribution patterns of closely related species is critical for both ecological and evolutionary reasons. In terms of ecology, the degree of overlap between two species indicates how often two species potentially interact and compete (Begon et al., 1996). Also, understanding the habitat characteristics of areas where each species is typically found helps elucidate each species' niche (Chase and Leibold, 2003). In terms of evolutionary biology, understanding the degree of overlap between closely related species is important for two reasons. First, the degree of overlap indicates the extent to which reproductive isolation between two taxa is currently a function of geography because hybridization can only occur in areas of sympatry (Ramsey et al., 2003; Coyne and Orr, 2004). Second, for closely related species, understanding the degree of overlap provides general insight into whether speciation occurred in allopatry or in sympatry (Fitzpatrick and Turelli, 2006). For fishes, the common assumption is that most speciation has occurred in allopatry due to the observation that many sister species do not occur in sympatry (i.e., Jordan's Rule; Jordan, 1905, 1908). However, modern tests of whether speciation has occurred in sympatry or allopatry requires a detailed knowledge of range overlap for multiple species within a clade (Fitzpatrick and Turelli, 2006), and these data are frequently lacking.

The genus *Lucania* contains three species belonging to the family of North American killifish, Fundulidae. *Lucania goodei* is described as a freshwater species and is found primarily in Florida with a few additional populations in Alabama, coastal Georgia, and coastal South Carolina (Gilbert and Burgess, 1980). *Lucania parva* is commonly described as a brackish water species and is found predominantly in coastal populations from Cape Cod around the Florida peninsula and through the Gulf of Mexico coast

(Duggins, 1980; Ross, 2001). The third species, *Lucania interioris*, is endemic to the partially endorheic Bolsón de Cuatro Ciénegas in Mexico and is found in areas of slight to high salinity (Hubbs and Miller, 1965; Miller et al., 2005). Both allozyme and molecular data suggest that *L. goodei* and *L. parva* are closely related and have recently diverged (Duggins et al., 1983; Hrbek, pers. comm.), but there has been no published phylogenetic analysis of the group to date. Despite the fact that *L. goodei* and *L. parva* are common in Florida, good estimates of the extent to which their distributions overlap are lacking. Sympatric populations have been documented in freshwater springs (Hubbs and Allen, 1943; Herald and Strickland, 1949; Burgess et al., 1977). Hubbs et al. (1943) detected hybrids in a population and diagnosed them as such on the basis of intermediate coloration and morphology. Whether these populations represent rare occurrences or are actually a sizable proportion of the distribution of each of these species is unknown.

In this paper, we analyze museum records to address the following four questions: How common are sympatric and allopatric populations of *L. goodei* and *L. parva* in Florida? Are allopatric (or sympatric populations) stable over time? In sympatric sites, what is the relative distribution of the two species? Is one species always common and the other always rare (i.e., a bimodal distribution), or is there a continuous distribution in the relative abundance of each species? How do abiotic (i.e., salinity) and biotic (i.e., other fish taxa) factors affect the distribution of these two species?

MATERIALS AND METHODS

We queried the database at the University of Florida Museum of Natural History for all records of *Lucania goodei* and *L. parva*. Initially, we considered all records provided

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that we could determine the location where the initial collection was made. We then used field numbers (which are assigned to all of the individual species records for a given collection at a particular location and date) to cross list all of the other species recorded in the same collection. Note that a field number refers to an entire sample from a given location whereas catalog numbers identify individual lots (i.e., individual species collected at a given location). From this, we categorized collections as either "*L. goodei*–allopatric" (*L. goodei* was present and *L. parva* was absent in the collection), "*L. parva*–allopatric" (*L. parva* was present and *L. goodei* was absent in the collection), or "sympatric" (both *L. goodei* and *L. parva* were present in the collection). We also calculated the proportion of *L. goodei* and *L. parva* as well as the total number of *Lucania* (number *L. goodei* + number *L. parva*).

Throughout this paper, we use the terms allopatric and sympatric. Allopatric refers to the condition where one of the two species is present at a location and the other is absent. Sympatric refers to the condition where both species are present at a location. The term syntopic refers to the condition where both species are present in the same habitat type at a locality and implies a close physical proximity between the two species. Although we consistently find *L. goodei* and *L. parva* in the same habitat in our field sampling (i.e., we collect them in the same seine haul or dipnet), the museum collections do not offer evidence as to habitat preferences for the two species. Therefore, we use the term sympatric for sites where both *L. goodei* and *L. parva* were present and refrain from using the term syntopic.

We discarded museum records with low numbers of total *Lucania* specimens. Museum records with low sample sizes are problematic because it is difficult to designate them as either allopatric or sympatric with any degree of confidence. Collections with low sample sizes may result from several different scenarios. Sites with low recorded numbers of either *L. goodei* or *L. parva* may accurately reflect low abundance at a given site. However, collections with low recorded numbers may also result from instances where collectors kept a single individual of each species or from instances where collectors were sampling non-randomly and keeping few of their non-target species for the collections.

We relied on binomial probabilities to help select which records to consider further. We first analyzed a data set limited to collections with a minimum of ten total *Lucania* (i.e., sum of *L. goodei* and *L. parva*). With a sample size of ten, there was a 90% probability of detecting an individual of each species provided that each species was at least 33% of the combined population of *Lucania*. We later analyzed a data set limited to collections with a minimum of 37 individual *Lucania*. With a sample size of 37, there was a 90% probability of detecting an individual of each species provided that each species was at least 10% of the combined population of *Lucania*. The qualitative results of the two analyses were nearly identical. Here, we report the results from the first analysis where the data set was limited to collections with a minimum of ten *Lucania*.

Designating sites.—Because we wanted to make inferences about populations of *L. goodei* and *L. parva* (as opposed to individual collections), the analysis was conducted on individual sites. The problem with using the data from individual records was that some sites had been sampled repeatedly over time, whereas others had only been sampled once. We identified individual sites based on descriptions of the collection location and on longitude and latitude data. We also determined which sites had been sampled repeatedly.

For sites with multiple records, we determined the average number of *L. goodei*, *L. parva*, and total *Lucania* for each site as well as the average proportion of *L. goodei* and *L. parva* present. Based on these data, we placed sites with multiple records into one of the following five categories: consistently *L. parva*–allopatric, consistently sympatric, consistently *L. goodei*–allopatric, varying sympatric/*L. parva*–allopatric, varying sympatric/*L. goodei*–allopatric. To determine if sampling effort differed across these categories, we used a Kruskal-Wallis test to compare the number of times each site had been sampled, the average number of *Lucania* per site, and the time span between multiple samples among the five categories.

We also examined the relative abundance of *L. goodei* and *L. parva* at sympatric sites to determine whether there was a continuous distribution of relative abundance between the two species or whether one species was always very common and the other very rare, which would result in a bimodal distribution. We used a Kolmogorov-Smirnov test to determine whether the relative frequencies differed from a normal distribution. We analyzed both the raw frequencies and the arcsine transformation of the square root of the relative frequencies, which is an appropriate transformation for proportional data (Sokal and Rohlf, 1995). This analysis included consistently sympatric sites, sites that varied between allopatry and sympatry, and sympatric sites that had only been sampled once.

Salinity.—Most museum records described the salinity as fresh, brackish, or marine. For sites that varied over time in recorded salinity (i.e., fresh, brackish, marine), we categorized the site as the salinity type most frequently recorded. We asked how our five site types ([1] *L. parva*–allopatric, [2] *L. parva*–allopatric/sympatric, [3] sympatric, [4] *L. goodei*–allopatric/sympatric, [5] *L. goodei*–allopatric) were distributed across salinity habitats using a chi-squared test. This analysis combined sites with a single record with sites that had been sampled repeatedly. Sites consistently allopatric for *L. parva* were combined with sites that had been sampled once and found to be allopatric for *L. parva*. Sites consistently allopatric for *L. goodei* were combined with sites that had been sampled once and found to be allopatric for *L. goodei*. Consistently sympatric sites were combined with sites that had been sampled once and found sympatric.

Fish community.—To characterize the fish community, we recorded the presence or absence of other fishes in the collection. For sites with a single record, a given species was either present or absent. For sites with multiple records, we calculated the proportion of collections where each taxon was present. Due to the large numbers of species in the data set, we restricted our analysis to the presence or absence of fish genera with the exception of *Fundulus* and *Lepomis*. We recorded the presence or absence of each species of *Fundulus* due to the fact that *Fundulus* has many freshwater, brackish water, and saltwater species. We recorded the presence or absence of each species of *Lepomis* due to the fact that some species (i.e., *L. gulosus*) are likely predators on adults while other species (i.e., *L. macrochirus, L. punctatus*) most likely

prey only on eggs and possibly juveniles. We excluded any sites that did not document at least one other fish taxon (other than *L. goodei* or *L. parva*). We again used a Kruskal-Wallis test to determine whether the presence of each taxon varied across *L. parva*–allopatric, *L. goodei*–allopatric, and sympatric sites. For this analysis, sites were categorized as sympatric if they had ever been found to be sympatric. All analyses were performed using SAS 9.1 (SAS Institute Inc., Cary, NC) and Systat 11 (Systat Software, Inc., 2004).

Assessing identification error.—To assess the authenticity of the records, we examined 50 lots of *L. parva* (>1900 individuals) and 52 lots of *L. goodei* (>1700 individuals) at the Museum of Natural History at the University of Florida with Dr. Lawrence Page. None of the specimens had been misidentified. The presence of a distinct lateral stripe in *L. goodei* (and its absence in *L. parva*) make these two species easily distinguished.

Additional sampling.—In our original analysis, sites with *L. goodei* were indicated throughout Florida with the exception of the Lower Suwannee River. Similarly, sites with *L. parva* were indicated all along the coasts with the exception of the Lower Suwannee River. To discern whether *Lucania* was really absent at this locale, we collected fish on 18 January 2007 at low tide using dipnets.

Survey sites in Florida.—To determine the extent to which the state of Florida had been thoroughly sampled, we queried the University of Florida Museum of Natural History for all records of the following taxa: *Poecilia, Gambusia, Heterandria, Fundulus, Menidia, Cyprinodon*. There were a total of 9,965 records of which 5,397 had data for latitude and longitude. We refer to these sites as survey sites and have plotted them on a map which is shown in the inset of Figure 1. Our rationale was that an examination of the distribution of the records for the most common fish taxa would provide a general estimate of the degree of sampling across Florida and whether particular areas had been undersampled.

RESULTS

There were a total of 1,394 records of *Lucania* with 609 records of *L. goodei* and 625 records of *L. parva*. There were an additional 80 records of *L. goodei* and *L. parva* from sympatric collections. When the data set was restricted to records with a minimum of ten total *Lucania*, there were 270 allopatric records of *L. goodei* and 313 allopatric records of *L. parva*. There were an additional 62 records of *L. goodei* and *L. parva* from sympatric collections. The remaining results were limited to analyses of the restricted data set.

Sites with multiple records.—Seventy-two sites had been sampled repeatedly over time. The number of repeated samples per site varied from two to 24 (mean = 4.3, SD = 4.6). Thirty-two sites were consistently allopatric for *L. parva*. Twenty-four sites were consistently allopatric for *L. goodei*. Four sites were consistently sympatric for the two species. Twelve sites varied in their allopatry/sympatry status. Ten of these sites varied over time in status between sympatry and *L. parva*–allopatric. At these sites, collections sometimes contained only *L. parva*, but at other times contained both *L. goodei* and *L. parva*. Similarly, two sites varied between sympatry and *L. goodei*–allopatric. There was

no evidence that differential sampling effort accounted for some sites being consistently allopatric or sympatric over time (number of repeated samples, Kruskal-Wallis test statistic = 6.0, P = 0.198, df = 4; average number *Lucania*/sample, Kruskal-Wallis test statistic = 7.5, P = 0.110, df = 4). There was also no evidence that consistent sites had merely been sampled over a shorter window of time (Kruskal-Wallis test statistic = 4.2, P = 0.390, df = 4).

Figure 1 shows the locations of allopatric populations of *L. goodei*, sympatric populations, and allopatric populations of *L. parva* across Florida. The map shows sites with *Lucania* that were sampled repeatedly as well as sites that were sampled once. There was considerable overlap between the two species. If one only considers consistently sympatric sites and sites sampled once and found sympatric, then 15% of sites with *L. goodei* were sympatric with *L. parva*, and 17% of sites with *L. parva* were sympatric with *L. goodei* (Table 1). Including sites that vary between sympatry and allopatry, 19% of sites with *L. goodei* were sympatric with *L. parva*, and 22% of sites with *L. parva* were sympatric with *L. goodei* in Florida. When drainage is the unit of analysis, 12% of sites with *L. goodei* were sympatric with *L. parva*. Analyzing *L. parva* by drainage was more problematic because many populations list the Gulf of Mexico as the drainage.

Many of the sympatric sites occurred in the St. John's River drainage, and the remaining sympatric sites occurred at the confluence of fresh and salt water in coastal areas. Merritt Island was a very interesting area with *L. parva*–allopatric, sympatric, and *L. goodei*–allopatric populations in close proximity to one another. Based on museum records, the mouth of the Suwannee River appeared to be lacking in *L. parva*, but this was due to the fact that none of the collections from this area had either *L. goodei* or *L. parva* in high abundance. There were 12 records of *L. parva* from the lower Suwannee each with 1–3 individuals. We also found a sympatric site in fresh water (0.2 ppt) at the mouth of the Suwannee River with one *L. goodei* and 15 *L. parva* (29°19′N, 83°9′W) on 18 January 2007. This site has been included on our map.

The distribution of relative abundance of *L. goodei* (and inversely *L. parva*) at sympatric sites was continuous and not bimodal (Fig. 2). Although the distribution of the raw data deviated significantly from a normal distribution (Kolmogorov-Smirnov test statistic = 0.132, P = 0.038), the distribution of the arcsin of the square-root transformed data did not differ from a normal distribution (Kolomogorov-Smirnov test statistic = 0.091, P = 0.410). The distribution of the relative abundance did not appear bimodal.

Abiotic and biotic factors.—Salinity has a large role in determining the relative abundance of *L. goodei* and *L. parva*. Table 1 shows the site types across fresh, brackish, and marine habitats (χ^2 = 284.1, df = 8, P < 0.0001). Overall, *L. parva* was found most often in brackish water sites (46%), but was also readily found in freshwater (22%) and marine (32%) sites. *Lucania goodei* was found most often in freshwater sites (92%) with a few populations in brackish water. *Lucania goodei* was recorded in one marine site in 1978. Records indicate that this was a canal population in the city of Delray Beach, Palm Beach Co., FL that was most likely 0.8 km away from the coast. Unfortunately, due to a lack of precise longitude and latitude data (as well as construction and changes in road names), we were unable
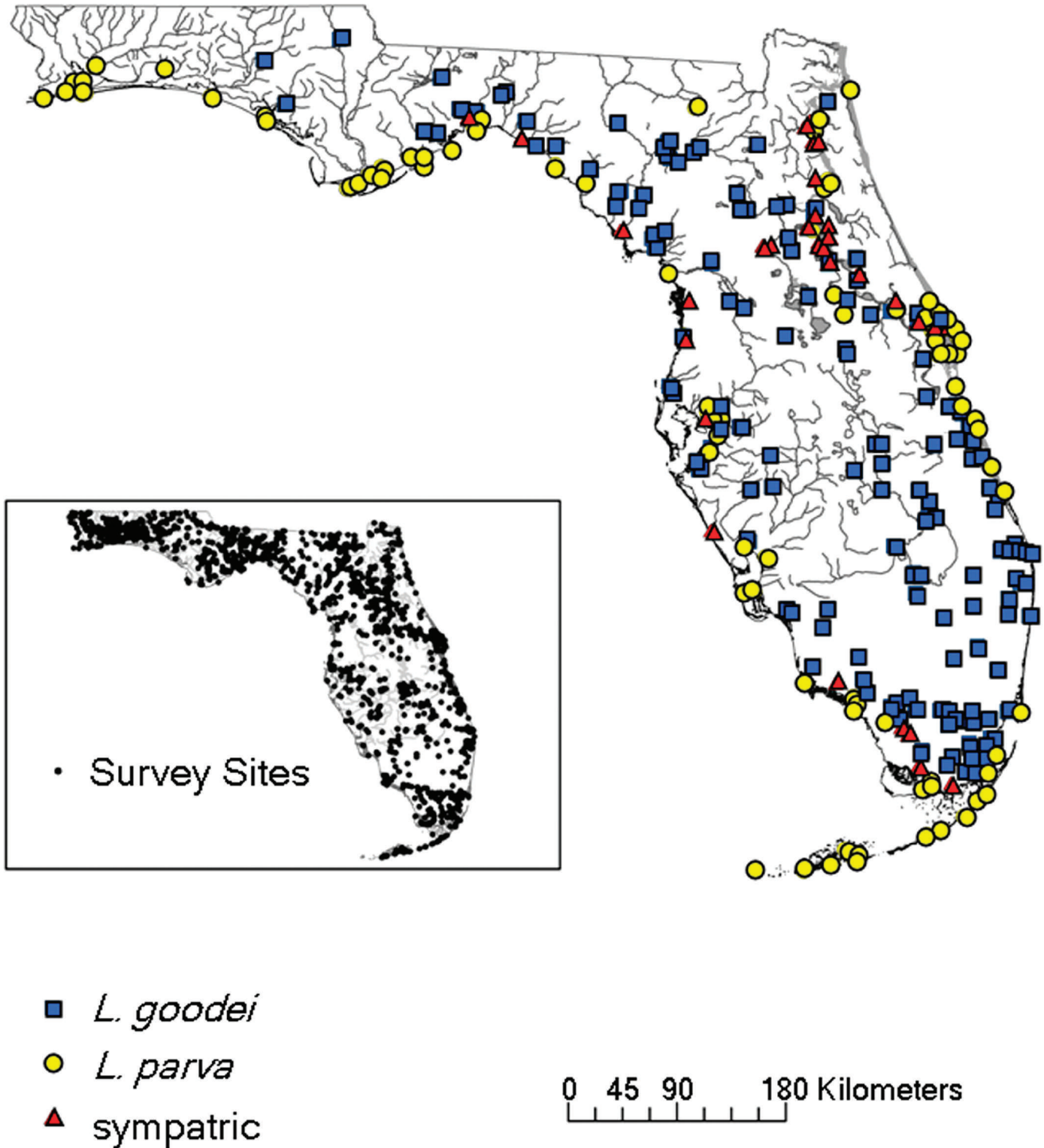
Fig. 1. Location of allopatric sites of *L. goodei*, sympatric sites, and allopatric sites of *L. parva*. Allopatric sites of *L. parva* are indicated in yellow dots. Allopatric sites of *L. goodei* are indicated in blue squares. Sympatric sites are indicated in red triangles. The inset shows the location of survey sites across Florida.

to determine the exact location of this site and verify the salinity.

Sympatric populations were most common in fresh water (66%) and brackish water (34%). Sixty-three percent of freshwater sites with *L. parva* were sympatric with *L. goodei*. Seventy-two percent of brackish water sites with *L. goodei* were sympatric with *L. parva*.

The fish community varied greatly among *L. goodei*–allopatric, sympatric, and *L. parva*–allopatric sites (Tables 2–4). For this analysis, we pooled sympatric sites with sites that varied between sympatry and allopatry. A handful of taxa did not vary across *L. goodei*–allopatric, sympatric, and *L. parva*–allopatric sites (*Membras, Harengula, Clarias, Lophogobius, Paralichthys, Centropomus, Orthopristis, Dormitator, Eu-*
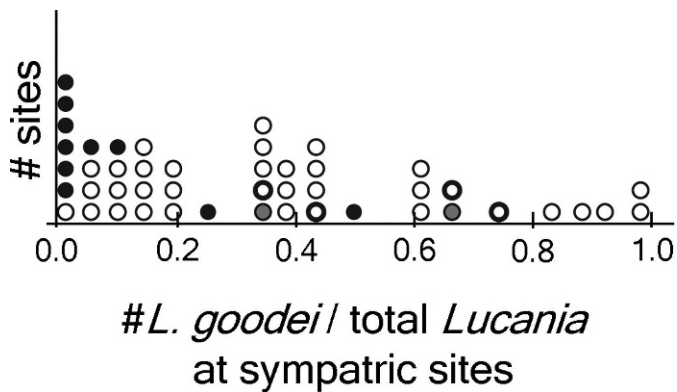
Fig. 2. Frequency distribution of the proportion of *L. goodei* (relative to total number of *Lucania*) across sympatric sites. Black dots show sites that varied between allopatry and sympatry for *L. parva*. Gray dots show sites that varied between allopatry and sympatry for *L. goodei*. White dots in bold outline show sites that were consistently sympatric. All other dots are sites that were sampled once. For sites sampled repeatedly, we calculated the average proportion of *L. goodei*. This graph shows that the distribution of the abundance of *L. goodei* relative to *L. parva* is not bimodal.

gerres, Oreochromis, Tilapia, Opsopoeodus, Anguilla, Pteronotropis, Percina) mainly due to low statistical power as a result of low occurrence across all sites. Twenty-four taxa were most abundant in allopatric sites of *L. goodei* (Table 2), and 36 taxa were most abundant in allopatric sites of *L. parva* (Table 3). Only nine taxa were most abundant in sympatric sites (Table 4). The taxa most common in sympatric sites were *Poecilia* (55%), *Gambusia* (50%), and *Lepomis punctatus* (48%), although all three were more abundant in allopatric populations of *L. goodei* (Table 2). Three taxa (*Trinectes, F. seminolis,* and *F. confluentus*) gave a strong signature of significantly greater abundance in sympatric sites when compared to allopatric sites of either *L. goodei* or *L. parva* (Table 4). These data demonstrate that the biotic conditions vary between *L. goodei*–allopatric, sympatric, and *L. parva*–allopatric populations. These species may be potential competitors and/or predators. While many of the taxa listed in Tables 2–4 are too small to prey upon adult *Lucania*, many could prey on eggs and fry.

Finally, it is worth noting that the overall coverage of survey sites across Florida was good. The bottom inset of Figure 1 shows the location of survey sites in Florida as reflected by records for *Gambusia, Poecilia, Heterandria, Fundulus, Menidia,* and *Cyprinodon*. While there are a few inland and coastal areas that lack records, there does not appear to be any large, systematic bias in the collections.

DISCUSSION

The unique finding of this study is the considerable overlap in the distribution of *L. goodei* and *L. parva* in Florida.

Approximately 12–19% of *L. goodei* sites were sympatric with *L. parva.* These data indicate that there is appreciable overlap between *L. goodei* and *L. parva* in Florida. The critical assumption of this analysis is that the collection records represent a random sample of populations. It is highly doubtful that these sites were chosen in a truly random manner across Florida. Many of the sites are close to the University of Florida (Gainesville), Florida State University (Tallahassee), around NASA's Cape Canaveral launch site, Merritt Island, and in south Florida south of the Tamiami trail. In addition, many of the collections have been made at man-made structures such as bridges and boat ramps with easy access to water. Another census study focused on fish communities in the inland areas of the Everglades and found no sympatric sites (Ruetz et al., 2005). However, this study focused on freshwater inland sites where *L. goodei* tends to be allopatric. The critical question is whether the nature of the museum records predisposes the collections to be made disproportionately in either allopatric or sympatric sites. We addressed this question by considering the distribution of records for some of the most common fish taxa across Florida (*Gambusia, Poecilia, Heterandria, Cyprinodon, Fundulus, Menidia*). The overall coverage of survey sites in Florida is good (Fig. 1). We believe that our estimate of 12–19% overlap of *L. goodei* with *L. parva* is reasonable.

The second novel finding of this study is that some sites are consistently sympatric whereas others vary between sympatry and allopatry. Most of the sites that varied in status did so between being allopatric for *L. parva* and sympatric. An examination of Figure 2 shows that these sites had a high relative abundance of *L. parva*. Hence, the inconsistency of these sites may be a reflection of sampling and detection problems rather than true variation in site type. There were two sites where *L. goodei* was less than 1% and an additional three sites where *L. goodei* was less than 5% of the total *Lucania.* To be 90% assured of detecting *L. goodei* when it is less than 1%, one would need a sample size of 387. However, if we only consider sites where the relative abundance of *L. goodei* is more than 10% but less than 90% (Fig. 2), we still find that approximately 50% of the sympatric sites with repeated measures varied in status between sympatric and allopatric. This supports the idea that areas of sympatry may be unstable over time, at least in some areas. The consistently sympatric populations were all found in springs that have fresh water with high mineral content. Populations that varied between sympatry and allopatry were found at the confluence between fresh and salt water. This suggests that sympatric populations found in springs are stable over time, whereas sympatric populations that emerge at the confluence of fresh and salt water are more variable possibly due to fluctuations in water flow between different wet and dry seasons, seasonal variation in

Table 1. Frequency of Five Site Types (*L. parva*–Allopatric, *L. parva*–Allopatric/Sympatric, Sympatric, *L. goodei*–Allopatric/Sympatric, *L. goodei*–Allopatric) across Salinity.

	L. parva–allopatric	*L. parva*–allopatric/sympatric	sympatric	*L. goodei*–allopatric/sympatric	*L. goodei*–allopatric
fresh	18	4	25	2	189
brackish	78	6	10	0	6
marine	65	0	0	0	1

Table 2. Taxa Most Common in Allopatric Sites of *L. goodei.* Means and standard errors of the probability of occurring in each site type are shown. Sample sizes are as follows: *L. goodei* = 190, sympatric = 43, *L. parva* = 144. Sample sizes differ from Table 1 because some collections only recorded *L. goodei* and/ or *L. parva* but no other fish taxa.

Taxa	*L. goodei*	sympatric	*L. parva*
Gambusia	0.79 (0.03)	0.50 (0.07)	0.28 (0.04)
Heterandria	0.74 (0.03)	0.34 (0.07)	0.06 (0.02)
Poecilia	0.61 (0.03)	0.55 (0.07)	0.42 (0.04)
L. punctatus	0.55 (0.04)	0.48 (0.07)	0.04 (0.02)
L. gulosus	0.48 (0.04)	0.33 (0.07)	0.01 (0.01)
Micropterus	0.46 (0.04)	0.36 (0.07)	0.08 (0.02)
F. chrysotus	0.43 (0.04)	0.16 (0.06)	0.02 (0.01)
Jordanella	0.38 (0.03)	0.26 (0.07)	0.02 (0.01)
Labidesthes	0.34 (0.03)	0.22 (0.06)	0.02 (0.01)
Notemigonus	0.31 (0.03)	0.17 (0.05)	0.02 (0.01)
Etheostoma	0.31 (0.03)	0.14 (0.05)	0.01 (0.01)
Elassoma	0.29 (0.03)	0.13 (0.05)	0.01 (0.01)
Enneacanthus	0.28 (0.03)	0.12 (0.04)	0.01 (0.01)
Ameiurus	0.22 (0.03)	0.21 (0.06)	0.03 (0.01)
Noturus	0.22 (0.03)	0.13 (0.05)	0.01 (0.01)
Erimyzon	0.22 (0.03)	0.05 (0.03)	0.01 (0.01)
Lepisosteus	0.15 (0.03)	0.08 (0.04)	0.02 (0.01)
Aphredoderus	0.14 (0.02)	0.03 (0.03)	0.01 (0.01)
Esox	0.07 (0.02)	0.02 (0.01)	0.01 (0.01)
Cichlasoma	0.07 (0.02)	0.00 (0.00)	0.01 (0.01)
Amia	0.04 (0.01)	0.00 (0.00)	0.00 (0.00)
Pomoxis	0.05 (0.02)	0.05 (0.03)	0.00 (0.00)
Dorosoma	0.04 (0.01)	0.04 (0.03)	0.00 (0.00)
F. lineolatus	0.04 (0.01)	0.00 (0.00)	0.00 (0.00)

aquatic vegetation, and possibly due to storm water surges from hurricanes.

The third novel finding of this study is the roughly continuous distribution of relative abundance between *L. goodei* and *L. parva* in sympatric sites (Fig. 2). This is in contrast to Loftus and Kushlan (1987) who found that sympatric sites typically involved one species being quite common and the other quite rare. The difference between their findings and this study may be due to the fact that many of their sites were ponds and boat ramps in the Everglades. Open systems, such as spring fed rivers, may allow for the zone of sympatry to move over time as conditions change.

Our results also emphasize the importance of salinity in structuring the abundance and location of *L. goodei* and *L. parva*. Salinity has long been known to influence the distribution of these two species (Duggins, 1980; Gilbert and Burgess, 1980; Dunson and Travis, 1991). In this study, *L. goodei* was found primarily in freshwater habitats, whereas *L. parva* was euryhaline and readily found in freshwater, brackish, and marine habitats. This is not the first study to indicate that *L. parva* is euryhaline (Tremain and Adams, 1995; Serafy et al., 1997; Jordan, 2002). The intriguing result is that *L. parva* was found in fresh water so frequently (22% of sites) where it was likely to be sympatric with *L. goodei*. If adaptation to salinity has been critical in the divergence of these taxa, then one might expect a smaller range of overlap between the two species and a lower abundance of *L. parva* in fresh water. However, *L. parva* can clearly survive and reproduce in fresh water. Fuller et al. (2007) and Fuller (2008) have found that *L. parva* can survive from egg to adulthood in fresh water. Furthermore, Fuller et al. (2007)

documented the continued presence of *L. parva* at two freshwater sites at multiple censuses over a two-year period. We have found *L. parva* at a range of sizes and stages (juvenile fish, gravid, adult females, mature males; Fuller, unpubl. data). Taken together, this evidence suggests that *L. parva* have stable, reproducing populations in fresh water.

The validity of the salinity analysis depends on the accuracy of the collectors in diagnosing fresh, brackish, and marine water. Some studies took direct measurements of the salinity (Kilby, 1955), but this probably did not occur in all of the collections. It is easy to imagine that one might diagnose the water based on the fish species being caught. For example, one would diagnose a site as freshwater if one were collecting fish species predominantly associated with fresh water. *Lucania parva* is often described as a marine or brackish water species (Page and Burr, 1991). If collectors tend to classify sites with *L. parva* as brackish, then the fact that 22% of sites with *L. parva* were diagnosed as freshwater is a conservative result.

The fourth contribution of this study is its ability to identify taxa that are common (or, conversely rare) in sympatric sites (Tables 2–4). The observation that fish communities vary between allopatric populations of *L. goodei* (i.e., freshwater habitats), allopatric populations of *L. parva* (i.e., euryhaline habitats), and sympatric populations (i.e., freshwater and brackish habitats) is not novel. However, these data allow for a much more subtle consideration of possible biotic interactions. For example, taxa such as *F. confluentus* are most common in sympatric sites (Table 4) leading to the hypothesis that they occur in niches that favor sympatry between *L. goodei* and *L. parva*. Taxa such as *Erimyzon* occur in appreciable frequencies in

Table 3. Taxa Most Common in Allopatric Sites of *L. parva*. Numbers and sample sizes follow those in Table 2.

Taxa	*L. goodei*	sympatric	*L. parva*
Menidia	0.07 (0.02)	0.31 (0.07)	0.57 (0.04)
Cyprinodon	0.05 (0.02)	0.27 (0.07)	0.51 (0.04)
Syngnathus	0.02 (0.01)	0.11 (0.04)	0.39 (0.04)
Eucinostomus	0.02 (0.01)	0.12 (0.05)	0.35 (0.04)
F. grandis	0.00 (0.00)	0.13 (0.05)	0.33 (0.04)
Gobiosoma	0.01 (0.01)	0.22 (0.06)	0.32 (0.04)
Floridichthys	0.00 (0.00)	0.02 (0.02)	0.30 (0.04)
Microgobius	0.01 (0.01)	0.29 (0.07)	0.30 (0.04)
Mugil	0.03 (0.01)	0.10 (0.04)	0.27 (0.04)
F. similis	0.01 (0.01)	0.01 (0.01)	0.21 (0.03)
Strongylura	0.00 (0.00)	0.18 (0.05)	0.20 (0.03)
Lagodon	0.01 (0.01)	0.10 (0.04)	0.20 (0.03)
Anchoa	0.00 (0.00)	0.05 (0.03)	0.19 (0.03)
Cynoscion	0.00 (0.00)	0.01 (0.01)	0.14 (0.03)
Adinia	0.00 (0.00)	0.05 (0.03)	0.13 (0.03)
Leiostomus	0.01 (0.01)	0.03 (0.02)	0.12 (0.03)
Bairdiella	0.01 (0.01)	0.02 (0.01)	0.12 (0.03)
Oligoplites	0.00 (0.00)	0.01 (0.01)	0.11 (0.03)
Opsanus	0.00 (0.00)	0.01 (0.01)	0.10 (0.02)
Achirus	0.01 (0.01)	0.00 (0.00)	0.09 (0.02)
Diapterus	0.01 (0.01)	0.02 (0.01)	0.07 (0.02)
Chasmodes	0.00 (0.00)	0.00 (0.00)	0.08 (0.02)
Archosargus	0.01 (0.01)	0.01 (0.01)	0.06 (0.02)
Sciaenops	0.00 (0.00)	0.01 (0.01)	0.06 (0.02)
Lutjanus	0.00 (0.00)	0.04 (0.03)	0.06 (0.02)
Arius	0.01 (0.01)	0.05 (0.03)	0.05 (0.02)
Synodus	0.01 (0.01)	0.00 (0.00)	0.04 (0.02)
Hippocampus	0.00 (0.00)	0.00 (0.00)	0.04 (0.02)
Sphoeroides	0.00 (0.00)	0.00 (0.00)	0.04 (0.02)
Micropogonias	0.00 (0.00)	0.02 (0.01)	0.03 (0.01)
Atherinomorus	0.00 (0.00)	0.00 (0.00)	0.03 (0.02)
Brevoortia	0.00 (0.00)	0.00 (0.00)	0.03 (0.01)
Symphurus	0.00 (0.00)	0.00 (0.00)	0.03 (0.01)
Bathygobius	0.00 (0.00)	0.00 (0.00)	0.03 (0.01)
Pogonias	0.00 (0.00)	0.00 (0.00)	0.03 (0.01)
Chilomycterus	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)

allopatric populations of *L. goodei* but are rare in both sympatric populations and allopatric populations of *L. parva*. One possibility is that *Erimyzon* cannot occur in the same habitats as sympatric and *L. parva* populations. Another possibility is that *Erimyzon* has negative effects on *L. parva* either through competition or through predation on eggs. Obviously, Tables 2–4 cannot be used to test these

hypotheses, but they provide the general pattern for the formation of subsequent hypotheses. These patterns are not necessarily apparent from a general consideration of freshwater, brackish, and marine communities.

Finally, it is worth noting that the interaction between abiotic and biotic factors may be critical in determining the relative distribution of these two species. Dunson and Travis

Table 4. Taxa Most Common in Sympatric Sites. Numbers and sample sizes follow those in Table 2.

Taxa	*L. goodei*	sympatric	*L. parva*
L. macrochirus	0.39 (0.04)	0.43 (0.07)	0.05 (0.02)
L. microlophus	0.30 (0.03)	0.40 (0.07)	0.09 (0.02)
F. seminolis	0.22 (0.03)	0.39 (0.07)	0.03 (0.01)
Notropis	0.36 (0.03)	0.38 (0.07)	0.01 (0.01)
F. confluentus	0.13 (0.02)	0.32 (0.07)	0.15 (0.03)
Trinectes	0.10 (0.02)	0.29 (0.06)	0.06 (0.02)
L. auritus	0.15 (0.03)	0.16 (0.05)	0.01 (0.01)
Elops	0.01 (0.01)	0.07 (0.04)	0.03 (0.01)
Gobionellus	0.00 (0.00)	0.07 (0.04)	0.04 (0.02)

(1991) have shown that salinity (0 vs. 15 ppt) can alter competition coefficients between *L. goodei* and *L. parva* (but see Rowe and Dunson [1995] for data on competition between *L. parva* and other marine species). Differential energy allocation to osmoregulation may alter the amount of energy animals have to spend on competition (Dunson and Travis, 1991, 1994; Evans et al., 2005). Tables 2–4 also demonstrate that there is a host of other fish that differ between *L. goodei*, *L. parva,* and sympatric sites. One possibility is that *L. goodei* and *L. parva* are differentially adapted to compete or avoid predation with different fish independent of salinity. Another possibility is that the magnitude of the biotic interactions varies critically with salinity (Dunson et al., 1998).

In conclusion, we found that there is appreciable overlap in the distribution of *L. goodei* and *L. parva*. Approximately 12–19% of the sites where *L. goodei* was present were sympatric with *L. parva*. Two-thirds of sympatric sites were found in fresh water, and the remaining one-third were found in brackish water. The relative abundance of *L. goodei* (and *L. parva*) was continuous among sympatric sites which contradicts previous assertions that sympatric populations occur when one species is quite common and the other quite rare. Finally, as previously reported, *L. goodei* was found primarily in fresh water whereas *L. parva* was euryhaline and readily found in fresh, brackish, and marine water which differ dramatically in fish community.

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