A COMPARISON OF THE FORAGING ECOLOGY AND BIOENERGETICS OF THE EARLY LIFE-STAGES OF TWO SYMPATRIC HAMMERHEAD SHARKS

Dana M Bethea, John K Carlson, Lisa D Hollensead, Yannis P Papastamatiou, and Brittany S Graham

ABSTRACT

Juvenile scalloped hammerhead sharks, *Sphyrna lewini* (Griffith and Smith, 1834), were collected in northwest Florida to examine foraging ecology, bioenergetics, and trophic level [30–60 cm fork length (FL); mean FL = 41.5 cm; n = 196]. Diet analysis was performed using single and compound measures of prey quantity, as well as seven broad diet categories. Diet composition and estimated daily ration were compared to previously published information on bonnethead sharks, *Sphyrna tiburo* (Linnaeus, 1758). Diet overlap was low between species. Juvenile *S. lewini* feed on relatively small (85% of prey items < 5% shark length) teleosts (mostly bothids and sciadids) and shrimps, whereas juvenile *S. tiburo* has been documented to feed mostly on crustaceans and plant material. Plant material contributed little to the diet of *S. lewini*. Estimated daily ration was significantly lower for *S. lewini* than for *S. tiburo*, regardless of whether plant material was included in the model. Trophic level was calculated at 4.0 for *S. lewini* and 2.6 for *S. tiburo*. Stable isotope analysis showed *S. lewini* had significantly higher δ¹⁵N values and significantly lower δ¹³C values than *S. tiburo*, consistent with the difference observed in calculated trophic level. These results provide evidence that juvenile hammerhead species coexist in coastal northwest Florida by feeding at separate trophic levels.

Many species of shark are documented top predators and, as such, could play an important role in structuring marine communities (Cortés 1999, Stevens et al. 2000). Within coastal communities, juvenile sharks have been reported to feed on several commercially important species of teleosts and invertebrates of varying trophic levels (Cortés et al. 2008). Therefore, quantitatively describing the diet, habitat use, and predator-prey interactions of coastal juvenile sharks is a key step in an ecosystem approach to fisheries management (e.g., Carlson 2007). Recently, juvenile shark foraging ecology and bioenergetics studies have documented the bays and inlets of northwest Florida (USA) to be potential nursery habitat for several species; however, few of these studies have focused on intra-guild interactions (Bethea et al. 2004). There is evidence that elasmobranchs alleviate interspecies competition by resource partitioning through dietary, spatial, or temporal means (Cartamil et al. 2003, Bethea et al. 2004, Papastamatiou et al. 2006). Understanding resource partitioning among predators within potential nurseries is paramount to providing a clearer view of essential habitat for coastal juvenile sharks.

Scalloped hammerhead, *Sphyrna lewini* (Griffith and Smith, 1834), and bonnethead, *Sphyrna tiburo* (Linnaeus, 1758), sharks are common hammerhead sharks found throughout coastal waters of northwest Florida, some of which are proposed nursery areas (Carlson and Brusher 1999; DM Bethea and JK Carlson, unpubl data). In late spring, mature female *S. lewini* move into the coastal areas of northwest...
Florida to give birth (DM Bethea and JK Carlson, unpubl data). Similarly, young *S. tiburo* recruit to the same coastal waters beginning in April (Carlson and Brusher 1999) and juveniles [45–60 cm fork length (FL)] of both species are present in these areas until they emigrate offshore in the fall (Carlson and Brusher 1999). Both species are benthic foragers and could compete for food and habitat resources. This sympatry provides a unique opportunity to explore the foraging ecology and resource partitioning of early life stage hammerhead shark.

In the present study, we quantified the diet and foraging ecology of juvenile *S. lewini* in northwest Florida and modeled consumption rates using a bioenergetics approach. In an attempt to understand resource partitioning, we compared our findings to previously published diet and bioenergetics data for juvenile *S. tiburo* from the same area (Bethea et al. 2007). Trophic level was quantified for both species using stomach contents data and stable isotope analysis.

**Methods**

**Diet Analysis.**—*Sphyrna lewini* were collected from fishery-independent surveys in two areas in northwest Florida in 1998–2005: Crooked Island Sound and the gulf-side of St. Vincent Island (Fig. 1). Samples were obtained April–October using gillnets (following Carlson and Brusher 1999). For each shark, FL (cm) was measured and sex and life stage were determined (e.g., young-of-the-year and juvenile, following Piercy et al. 2009). For our study, only sharks 30–60 cm FL (i.e., young-of-the-year and juveniles up to age-1.5) were sacrificed for diet analysis. Stomachs were removed and frozen at −20 °C until processing. Stomachs were thawed, opened, and rinsed with water over a 595-µm sieve. Items found in the stomachs were identified to the lowest possible taxon, counted, measured for length (to nearest cm), and weighed (wet weight, to nearest 0.001 g).

The contribution of each prey item to the diet was estimated with three relative measures of prey quantity (number, weight, and frequency of occurrence; Hyslop 1980). The numerical index (%N) was calculated as (the number of individuals of a prey taxon + the total number of individuals among all prey taxa) × 100. The weight index (%W) was calculated as (the wet weight of a prey taxon + the total wet weight of all individuals among all prey taxa) × 100. Herein, the numerical and weight indices were calculated for each individual stomach to provide mean and variability estimates and are presented as %N and %W (Ferry and Cailliet 1996). The percent frequency of occurrence (%FO) was calculated as (the number of stomachs containing a prey taxon + the number of stomachs containing prey) × 100. Diet composition was further described using the index of relative importance [%IRI = (%N + %W) × %FO] and expressed as a percentage (%IRI, Cortés 1997). To generate mean and SE estimate for all prey items, %IRI was also calculated for each stomach.

Non-energetic items found in stomachs (e.g., rocks, hooks, coral, and benthos), parasites (e.g., nematode worms), and unidentifiable digested material were not included in stomach content analysis. To facilitate comparison with *S. tiburo* diet (Bethea et al. 2007), plant material was included. When calculating %N for plant material, one unit equaled one whole component. For example, if three blades of *Thalassia testudinum* were found in one stomach, then n = 3.

To facilitate comparison with *S. tiburo* diet, stomach contents and two other methodologies were applied to mirror methods used in Bethea et al. (2007). First, identifiable items found in the stomachs were grouped into seven broad diet categories (DC): crabs, shrimps, crustaceans other than crabs and shrimps (including unidentified decapods), cephalopods, non-cephalopod molluscs (including unidentified molluscs), plant material, and teleosts. Second, the relative measures of prey quantity on a pooled basis based on the seven broad diet categories (%N DC, %W DC, %FO DC, and %IRI DC) were computed and used in all further bioenergetics and
Figure 1. Map of areas where hammerheads were collected for diet analysis. *Sphyrna lewini* were collected from fishery-independent gillnet surveys in Crooked Island Sound and the gulf-side of St. Vincent Island, 1998–2005. *Sphyrna tiburo* were collected using the same methodology in the same areas, 1998–2000 (Bethea et al. 2007).
trophic level comparison analysis. To compare our results to more recent diet studies, the relative measures of prey quantity on an individual basis (\%N_{DC}, \%W_{DC}, \%IRI_{DC}), as well as corresponding SEs were also computed for the seven broad diet categories.

Cumulative prey curves were examined to determine whether sample sizes and diet variability were adequately described by the analyses. The estimated number of unique prey taxa and 95% confidence intervals were plotted against the cumulative number of non-empty stomachs (Ferry and Cailliet 1996) using the Mao Tao expected richness function in EstimateS (Version 8.2.0, R.K. Colwell, http://purl.oclc.org/estimates). Linear regression of the last five estimated values was used to quantitatively determine if the curve reached an asymptote, signifying an adequate number of samples (Bizzarro et al. 2007). Because comparison to a line with zero slope was considered too restrictive, comparisons were made to a line with 5% slope (JJ Bizzarro, University of Washington, pers comm). Variability of the estimated number of unique prey taxa was visually assessed to evaluate precision of prey curve estimates and dietary diversity. A cumulative prey curve was also constructed and tested in the same way using the estimated number of broad prey categories.

**Predator Size–Prey Size Analysis.**—To estimate changes in prey size with increasing shark size, shark FL vs prey size was plotted for *S. lewini*. All prey sizes used in this analysis were either directly measured crustacean carapace length (mm), teleost total length (mm) from prey found whole in the stomachs, or reconstructed total length using previously published equations (Bethea et al. 2006). Quantile regression techniques (following Scharf et al. 2000) were used to determine how the median (50th quantile), minimum (10th quantile), and maximum (90th quantile) sizes of prey changed with increasing shark size. Patterns in predator-prey size ratios were examined visually to evaluate the ranges of prey sizes consumed. Additionally, a frequency histogram of relative and cumulative prey size–predator size ratios was created to examine the patterns of prey size use.

**Dietary Overlap Analysis.**—Dietary overlap between *S. lewini* and *S. tiburo* was measured using the Pianka overlap index. Our *S. lewini* %IRI_{DC} values were compared to *S. tiburo* %IRI_{DC} values calculated in Bethea et al. (2007). Diet overlap was assessed under the assumption that all resources were equally abundant. Overlap index values range from 0 (no overlap) to 1.0 (complete overlap) where values ≥ 0.6 are considered “biologically significant” (Pianka 1976). Observed dietary overlap was calculated using Ecological Methodology v5.1 software (Krebs 1999).

The observed overlap value was compared to a distribution of expected overlap values based on a null model. The distribution of null model data came from 1000 randomizations of the diet data (R3 randomization algorithm, Winemiller and Pianka 1990). Simulations were performed using EcoSim v7.41 software (Gotelli and Entsminger 2005). The observed value is considered statistically different from the null distribution if it is greater than or less than the simulated indices 95% of the time (P < 0.05, Winemiller and Pianka 1990). An observed value significantly less than the simulation index suggests interspecific competition and diet partitioning between species; an observed value significantly greater than the simulation index suggests a lack of competition or strong competition that has not yet led to resource partitioning.

**Bioenergetic Model.**—To facilitate comparison, a bioenergetic model was constructed for *S. lewini* similar to the model for *S. tiburo* in Bethea et al. (2007). Estimates of consumption were developed following the balanced bioenergetic approach of Winberg (1960) expressed as:

\[ C = (M_r + M_s) + (G_s + G_r) + (W_f + W_u) \]

where \( C \) = consumption; \( M_r \) = routine metabolic rate; \( M_s \) = specific dynamic action due to energetic costs of digestion; \( G_s \) = energy allocated to somatic growth; \( G_r \) = energy allocated to reproduction; and \( W_f \) and \( W_u \) = the energy lost to the production of feces and urine, respectively. All rates were expressed in kilocalories per day.
Daily ration was calculated as: \( DR = \frac{C}{F/W} \), where \( C \) = consumption (kcal d\(^{-1}\)); \( F \) = energy value of the food source (kcal g\(^{-1}\) wet weight); and \( W \) = mass of the shark (g). The mass of an individual was taken from the mean of a distribution of individuals from monthly field survey data April–October (DM Bethea and JK Carlson, unpubl data). Daily ration was then expressed as percent body weight per day (\( DR = \frac{C}{F/W} \times 100 = \%BW \)). Proportions of food for \( S. \) lewini were taken from the calculated \%IRI\(_{dc}\) in Bethea et al. (2007) to facilitate comparison with \( S. \) tiburo. The caloric values of the non-plant diet categories were taken from Bethea et al. (2007) and studies referenced therein.

Information on routine metabolism was taken from the multiple regression model of Lowe (2001): \( \log V_{O_2} = k + a_1(U_{rel}) + a_2(T) \), where \( V_{O_2} \) = oxygen consumption rate (mg O\(_2\) kg h\(^{-1}\)), \( k \) is the intercept, \( a_1 \) and \( a_2 \) are the slopes for tail beat frequency, \( U_{rel} \) is the relative swimming speed, and \( T \) is water temperature (°C). Oxygen consumption rate was converted to calories using the oxycalorific coefficient for fish of 3.25 cal mg O\(_2\)\(^{-1}\) (Brafield and Solomon 1972). A range of relative swimming speeds was taken from \( S. \) lewini telemetry data by Lowe (2002). Temperature was obtained from averages of monthly field survey data when samples were collected for diet analysis (DM Bethea and JK Carlson, unpubl data). Specific dynamic actions were set at 6% based on Sims and Davies (1994). Energetic loss due to feces and urine was set at 27% of consumption based on results of Wetherbee and Gruber (1993). Growth rates (converted to mass) were obtained from published von Bertalanffy growth functions (Piercy et al 2009) and field survey data from \( S. \) lewini captured from April through October (DM Bethea and JK Carlson, unpubl data). The von Bertalanffy predicted growth was estimated as the growth for sharks from birth to age 1.

We used Monte Carlo simulation to assess uncertainty in the model input parameters (Bartell et al. 1986). Probability density functions were developed to describe temperature, relative swimming speed, growth, excretion, specific dynamic action, and diet. Excretion was represented by a triangular distribution with 27% of consumption as the likeliest value using ± 10% as lower and upper bounds. Specific dynamic action was a uniform distribution with 6% and 12% of total consumption as the lower and upper bounds. Annual growth rates obtained from the von Bertalanffy growth equation parameters were assigned lognormal distributions with coefficients of variation of 10% (Bartell et al. 1986). Normal distributions were assigned to swimming speed and environmental temperature. Diet distributions were based on \%IRI\(_{dc}\) values calculated herein and from Bethea et al. (2007).

The simulation process involved randomly selecting a value from the set of input parameters from the probability density functions when calculating daily ration. This process was repeated 2000 times, yielding frequency distributions, means, and confidence intervals for parameter estimates (calculated as the 2.5\(^{th}\) and 97.5\(^{th}\) percentiles). All simulations were run with Microsoft Excel\textsuperscript{©} spreadsheet software equipped with risk analysis software (Crystal Ball\textsuperscript{©} 2000 Academic Edition v5.2.2, Decisioneering, Inc.). An unpaired t-test was used to test for differences in log-transformed daily ration simulations between \( S. \) lewini and \( S. \) tiburo, both including and excluding plant material from \( S. \) tiburo diet.

Foraging Ecology.—Trophic level was calculated for \( S. \) lewini and \( S. \) tiburo using the pooled \%IRI and the seven aforementioned broad diet categories, following the equation in Cortés (1999):

\[
TL_i = 1 + \left( \sum_{j=1}^{n} P_j \times TL_j \right),
\]

where \( TL_j \) = trophic level of species \( k \), \( P_j \) = proportion of diet category \( j \) in the diet of species \( k \), \( n \) = total number of diet categories (herein, 7), and \( TL_j \) = trophic level of diet category \( j \). Trophic levels of diet categories were taken from Cortés (1999).

Tissue samples (muscle posterior to the dorsal fin) of \( S. \) lewini and \( S. \) tiburo were collected in Crooked Island Sound from March through September, 1998–2000, and analyzed for carbon
and nitrogen stable isotope analysis. C:N ratios were low (3.1–3.4), hence lipid extraction was not needed. Samples were dried at 60 °C for at least 48 hrs or until the sample was completely dry, ground into a fine powder, and weighed in tin capsules. Nitrogen and carbon isotope values were determined at the University of Hawaii’s Isotope Biogeochemistry Laboratory using an online CN analyzer (Carlo Erba NC2500) coupled (ThermoFinnigan ConFlo II) to an isotope ratio mass spectrometer (ThermoFinnigan Delta S). Carbon and nitrogen isotope values are reported in standard d-notation relative to V-PDB and atmospheric N₂, respectively. A sample of glycine in which the δ¹³C and δ¹⁵N values were well characterized was measured after every 10 samples to ensure the accuracy of isotope measurements. Several samples were also measured in duplicate and the analytical error associated with all of these measurements was typically ≤ 0.2‰.

RESULTS

DIET.—In total, 196 S. lewini stomachs were examined for dietary analysis (30–60 cm FL; mean FL = 41.5 cm). Of these, 186 (94.9%) contained prey items. Stomach contents included teleosts (representing 12 families), crustaceans (mostly decapod shrimps), molluscs, and plant material (Table 1). The cumulative prey curve calculated for the overall diet (Fig. 2A) indicated that a sufficient number of stomach samples were collected for precise dietary estimates. At lowest possible taxonomic levels, the slope of the observed linear fit (b = 0.077, r² = 0.999) of the last five prey curve endpoints was not significantly different than that of a predicted line of 5% slope (t = −0.474, P = 0.341); however, the number of prey taxa in the diet was highly variable even after 186 non-empty stomachs were analyzed (Fig. 2A). When broad diet categories were used, the resulting cumulative prey curve reached an asymptote once 163 non-empty stomachs were analyzed. Dietary variability was substantial, however, at much smaller sample sizes (Fig. 2B).

Teleosts were the most important dietary category (48.70 %N DC, 44.32 %W DC, 40.51 %FO DC, and 53.71 %IRI DC; Table 2A). Identifiable teleosts included mostly bothids (Citharichthys sp.) and sciaenids (Stellifer lanceolatus, Bairdiella chrysoura, Micropogonias undulatus, Leiostomus xanthurus, and Cynoscion spp.; see Table 1). Shrimp-like crustaceans were the second most important diet category (24.87 %N DC, 30.17 %W DC, 23.42 %FO DC, and 26.35 %IRI DC; Table 2A). This diet category was dominated by penaeid shrimp (Farfantepenaeus spp., Xiphopeneaus kroyeri, and Litopeneaeus setiferus; Table 1). Crustaceans other than shrimp and crab (mostly unidentified to species) were the third most important diet category (16.29 %N DC, 18.01 %W DC, 19.30 %FO DC, and 15.57 %IRI DC; Table 2A). Cephalopods and plant material (mostly Loliuncula brevis and Halodule wrightii; Table 1) were found in the diet infrequently and in small amounts, contributing little to the diet by category (1.24 and 1.99 %IRI DC, respectively; Table 2A). Crabs (portunid) and molluscs other than cephalopods (bivalves) made up the smallest percentage of the diet by category (1.08 and 0.07 %IRI DC, Table 2A).

PREDATOR SIZE–PREY SIZE.—Examination of predator-prey size scatter plots revealed that minimum sizes of prey consumed by S. lewini remained constant over all body sizes while maximum sizes increased significantly (50th quantile: P = 0.02, 90th quantile: P = 0.03, 10th quantile: P = 0.15; Fig. 3). This indicates that as juvenile S. lewini increase in size, they continue to include small prey in their diet. Examination of the frequency histogram of relative and cumulative prey size–predator size ratios
Table 1. Stomach contents of young-of-the-year *Sphyrna lewini* (30–60 cm FL; mean FL = 41.5 cm; n = 186) in Crooked Island Sound by mean percent number (%N), mean percent weight (%W), percent frequency of occurrence (%FO), and the mean index of relative importance on a percent basis (%IRI). The seven major diet categories are in bold. – indicates item was < 0.01%. SE = standard error.

<table>
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<th>Prey taxon</th>
<th>%N</th>
<th>SE</th>
<th>%W</th>
<th>SE</th>
<th>%FO</th>
<th>%IRI</th>
<th>SE</th>
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<td>0.20</td>
<td>0.44</td>
<td>0.30</td>
<td>1.08</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>Palaemonidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Palaemonetes</em> spp.</td>
<td>0.57</td>
<td>0.38</td>
<td>0.80</td>
<td>0.53</td>
<td>1.08</td>
<td>0.37</td>
<td>0.33</td>
</tr>
<tr>
<td>Penaeidae</td>
<td>0.27</td>
<td>0.25</td>
<td>0.44</td>
<td>0.42</td>
<td>0.54</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td><em>Farfantepenaeus duorarum</em> (Burukovsky, 1997)</td>
<td>0.60</td>
<td>0.51</td>
<td>0.90</td>
<td>0.61</td>
<td>1.08</td>
<td>0.55</td>
<td>0.51</td>
</tr>
<tr>
<td><em>Farfantepenaeus</em> spp.</td>
<td>1.87</td>
<td>0.68</td>
<td>1.85</td>
<td>0.74</td>
<td>4.84</td>
<td>0.85</td>
<td>0.52</td>
</tr>
<tr>
<td><em>Litopenaeus setiferus</em> (Linnaeus, 1767)</td>
<td>0.67</td>
<td>0.32</td>
<td>1.12</td>
<td>0.58</td>
<td>2.15</td>
<td>0.39</td>
<td>0.29</td>
</tr>
<tr>
<td><em>Trachypenaeus constrictus</em> (S. I. Smith, 1885)</td>
<td>0.25</td>
<td>0.18</td>
<td>0.07</td>
<td>0.05</td>
<td>1.08</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td><em>Xiphopenaeus kroyeri</em> (Heller, 1862)</td>
<td>2.87</td>
<td>0.93</td>
<td>3.55</td>
<td>1.16</td>
<td>5.38</td>
<td>1.67</td>
<td>0.74</td>
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<td>Sicyoniidae</td>
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</tr>
<tr>
<td><em>Sicyonia</em> spp.</td>
<td>0.18</td>
<td>0.17</td>
<td>0.11</td>
<td>0.11</td>
<td>0.54</td>
<td>0.06</td>
<td>0.06</td>
</tr>
<tr>
<td>Isopoda</td>
<td>0.17</td>
<td>0.12</td>
<td>0.02</td>
<td>0.02</td>
<td>1.08</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Stomatopoda</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Squillidae</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Squilla empusa</em> (Say, 1818)</td>
<td>0.45</td>
<td>0.30</td>
<td>0.37</td>
<td>0.26</td>
<td>1.08</td>
<td>0.37</td>
<td>0.25</td>
</tr>
<tr>
<td>Shrimps (unidentified)</td>
<td>16.74</td>
<td>2.25</td>
<td>23.32</td>
<td>2.58</td>
<td>26.88</td>
<td>18.86</td>
<td>2.40</td>
</tr>
</tbody>
</table>
showed that *S. lewini* consumed prey that were small fractions of their length; 98.1% of all items measured from stomachs were < 20% of FL and 84.9% of all items were < 5% of FL (Fig. 4).

**Dietary Overlap.**—Observed dietary overlap was not “biologically significant” (0.047). Null model analysis mirrored the observed dietary overlap value; the expected simulated mean overlap value was “biologically” low (0.278), but not significantly lower than expected (p = 0.212).

**Bioenergetics.**—Daily ration was estimated at 4.6 %BW d\(^{-1}\) for juvenile *S. lewini*. Confidence limits expressed as 2.5 and 97.5 percentiles were 3.4% and 5.9%, respectively. Plant material was retained in the *S. lewini* bioenergetic model regardless of its relative unimportance in the diet (0.7 %IRI\(_{dc}\)). Bethea et al. (2007) calculated daily ration estimates for young-of-the-year *S. tiburo* in northwest Florida as 5.4% BW d\(^{-1}\) (CI: 1.4%–15.0%). Daily ration estimates differed significantly between hammerhead species regardless if plant material was included in *S. tiburo* diet (t-test: t = 1.96, P = 0.02 including plant material, P < 0.00001 excluding plant material). Sensitivity analysis (measured by contribution to total variance) revealed that uncertainty in growth of an individual (43.3%) and temperature (26.2%) contributed the most uncertainty in the model. Other input variables of significance included mass of an individual (18.6%), excretion (8.6%), and diet (3.2%).

**Foraging Ecology.**—A total of 25 *S. lewini* (46.7 cm mean FL) and 24 *S. tiburo* (45.1 cm mean FL) muscle tissue samples were collected for stable isotope analysis from Crooked Island Sound. There was no difference in length between the two shark species (Student’s t-test: df = 38, t = −0.56, P = 0.577). *Sphyra lewini* had significantly higher δ\(^{15}\)N values and significantly lower δ\(^{13}\)C values when compared to *S. tiburo* [δ\(^{15}\)N = 14.0‰ ± 0.8 and 11.7‰ ± 0.9, respectively (df = 43, t = −10.6, P <
Figure 2. Cumulative prey curves for *Sphyrna lewini* (*n* = 186). Species richness per stomach sample was plotted for (A) lowest possible taxon (*n* = 48) and (B) broad diet categories (*n* = 7). Dashed lines represent 95% confidence intervals.

Using the broad diet categories and their associated trophic levels outlined in Cortés (1999), we calculated trophic level at 4.0 for *S. lewini* and 2.6 for *S. tiburo*. Our calculated trophic level for *S. lewini* is comparable to that estimated by Cortés (1999, 4.1). Our calculated trophic level for *S. tiburo* is lower than Cortés (1999, 3.2); however, Cortés (1999) calculated trophic level (TL) across all life-stages.

δ^{13}C = −15.1‰ ± 0.4 and −14.8‰ ± 0.5, respectively (df = 43, *t* = 2.7, *P* = 0.009). δ^{15}N values of *S. lewini* were 2.3‰ higher than *S. tiburo* (Fig. 5).
Discussion

Based on both stomach contents and stable isotope analysis, early life stages of *S. lewini* feed at a higher trophic level than those of *S. tiburo* in northwest Florida. The driving factor behind the difference in calculated trophic level is that juvenile *S. lewini* feed mostly on teleosts whereas juvenile *S. tiburo* feed almost exclusively on crustaceans (Bethea et al. 2007). In addition, plant material often occurs in the stomachs of juvenile *S. tiburo* (62.1% IRI, Bethea et al. 2007). Although stomach content analysis captures diet only during a “snap-shot period,” stable isotope values provide a time-integrated view of what an animal assimilates. Higher δ¹⁵N values suggest that *S. lewini* juveniles feed at a higher trophic level than do *S. tiburo* juveniles. For a marine predator that consumes a high-quality, high-protein diet (like teleost fish), a trophic enrichment factor of ~2.4 could be expected (Vanderklift and Ponsard 2003, Graham et al. 2007). As a result, the difference in the δ¹⁵N values between *S. lewini* and *S. tiburo* suggests that there is up to one trophic level difference between these two species. This estimate is comparable to that calculated using stomach content data separated into broad dietary categories (i.e., trophic level difference of 1.4). The δ¹³C values of consumers is an indication of the source of primary producers at the base of the food chain from which the predator feeds, with animals that forage on
pelagic prey having lower δ¹³C values than those feeding on more benthic-associated prey (France 1995). Although the isotopic difference is small (~0.3‰), the lower δ¹³C values in *S. lewini* may suggest this species forages on more pelagic prey. Alternatively, these results could also be an artifact of measurement variability as the isotopic difference is almost the same as the sample replication (0.2).

The bioenergetic model predicted higher daily ration estimates for *S. lewini* in northwest Florida than previously determined for this species. Using a gastric evacuation model, Bush and Holland (2002) estimated daily ration as 2.7–3.5 %BW d⁻¹ for similar sized juvenile *S. lewini* in Kaneʻohe Bay (Hawaii). Lowe (2002) estimated maintenance ration in situ as 3.7 %BW d⁻¹ for *S. lewini* in the same bay, but developed estimates using a bioenergetic model. While statistical comparison of the model outputs could not be performed, the higher estimates of daily ration for sharks in northwest Florida are likely due to these individuals being exposed to warm water temperatures throughout the summer months. Kaneʻohe Bay water temperatures were recorded at 22–28 °C (Lowe 2002), whereas water temperature in northwest Florida averaged 26–29 °C during sampling months (DM Bethea and JK Carlson, unpubl data). Exposure to consistently higher water temperatures would elevate metabolic demands, resulting in higher daily ration estimates. This has also been shown for *S. tiburo* along a latitudinal gradient in the western Gulf of Mexico: young-of-the-year *S. tiburo* in Florida Bay (southern Gulf of Mexico) have an elevated metabolism relative to young-of-the-year in northwest Florida (Bethea et al. 2007). Additionally, it is thought that *S. lewini* in Kaneʻohe Bay are food limited and ultimately starve (Bush and Holland 2002). It may be that immature *S. lewini* and *S. tiburo* in northwest Florida are likely due to these individuals being exposed to warm water temperatures throughout the summer months.
Florida have adequate access to their particular prey items which would allow them to co-exist and have a higher daily ration.

Partitioning of available resources (i.e., prey, micro-habitat, time of foraging activity) could allow these mostly benthic-foraging hammerhead sharks to co-exist within specific areas in northwest Florida in high numbers (DM Bethea and JK Carlson, unpubl data). In Crooked Island Sound, *S. lewini* were collected in somewhat deeper waters over mud bottoms and more often at night (DM Bethea and JK Carlson, unpubl data). Early life stages of *S. lewini* in Kane‘ohe Bay, O‘ahu (Hawaii), also prefer deeper waters with mud and silt bottoms (Duncan and Holland 2006) and exhibit greater foraging activity at night (Bush 2003). In contrast, *S. tiburo* in Crooked Island Sound are often associated with sandy bottoms, mud flats, and seagrass beds along the shallower fringe of the sound (DM Bethea and JK Carlson, unpubl data). This suggests some level of micro-habitat and temporal partitioning between *S. lewini* and *S. tiburo* in this small sound.

Early life stages of *S. lewini* in Kane‘ohe Bay (Hawaii) have been shown to feed primarily on crustaceans (62.1%, mostly alpheid shrimp; Bush 2003) and teleosts (32.5%, mostly gobiids; Lowe 2002). The differences in diet between early life stages of *S. lewini* in Florida and Hawaii are likely due to the differences in abundance of potential prey species associated within regional habitat. Bush (2003) used several techniques to estimate potential prey abundance and found the most abundant species available were the same species that were most important in the diet. Similarly, other species collected in lower abundance in the environment seldom showed up in the diet. Bethea et al. (2006) used gillnets and otter trawl to enumerate potential prey items in Crooked Island Sound and found benthic teleosts [*Opisthonema oglinum* (Lesueur, 1818) and *Lagadon rhomboides* (Linnaeus, 1766)] associated with seagrass beds followed by *Brevoortia patronus* to be the most abundant teleost species. The lack of the most abundant teleost species in the diet of *S. tiburo* could be

![Figure 4. Relative frequency distributions of prey size-predator size ratios for *Sphyrna lewini* in Crooked Island Sound, Florida. Bars = relative frequencies at 1% intervals of prey size–predator size ratios. Filled circles = cumulative frequencies at 1% intervals.](image-url)
due to sampling methods not adequately capturing the biodiversity of the sound. The gillnets used when sampling ranged from 2.5 to 14 cm stretch mesh and prey items found in stomachs were often < 2 cm. It could also be that *S. tiburo* is out-competed for the most abundant prey as the sound is also used by larger sub-adult and adult sharks (*Carcharhinus brevipinna* (J.P. Müller and Henle, 1839), *Carcharhinus isodon* (J.P. Müller and Henle, 1839), *Carcharhinus limbatus* (J.P. Müller and Henle, 1839), *Carcharhinus leucas* (J.P. Müller and Henle, 1839), *Rhizoprionodon terraenovae* (J. Richardson, 1836), and *Sphyrna mokarran* (Rüppell, 1837)) as well as marine mammals, *Tursiops truncatus* (DM Bethea and JK Carlson, unpubl data and pers obs). No conclusions can be drawn regarding the availability of crustaceans in the area as prey for *S. tiburo* because Bethea et al. (2006) did not provide data on invertebrates due to their infrequent occurrence in catches and poor condition from the trawl.

The morphology of the mouth and teeth differ between the two hammerhead shark species. *Sphyrna tiburo* have plate-like, non-serrated teeth used to grab and crush invertebrates (Wilga and Motta 2000) whereas *S. lewini* have more pointed and triangular-shaped teeth, more like those of *S. mokarran*—teeth that are used to pierce and tear teleosts (Motta and Wilga 2001). Regardless of prey capture methodology (and thus prey type), distributions of relative teleost prey size for young-of-the-year *S. lewini* are comparable to relative crustacean prey size for juvenile *S. tiburo* in northwest Florida (Bethea et al. 2007); the majority of the prey items for both species are < 10% of shark length. *Raja* spp. and spiny, *Squalus acanthis* (Linnaeus, 1758), and smooth dogfish, *Mustelus canis* (Mitchill, 1815), from the northeast US continental shelf have also been shown to consume relatively small-sized prey (Scharf et al. 2000). Although prey size–predator size ratios were not calculated, Bush (2003) found that early life stages of *S. lewini* in Kane‘ohe Bay (Hawaii) fed exclusively on small-sized prey such as gobies and alpheid shrimp. Like young-of-the-year *S. tiburo*

![Figure 5. Bi-plot of stable isotope values Sphyrna lewini (n = 25) and Sphyrna tiburo (n = 24) from Crooked Island Sound, Florida.](image-url)
(Bethea et al. 2007) and, to an extent, young-of-the-year Atlantic sharpnose shark (*R. terraenovae*) in northwest Florida (Bethea et al. 2006). *S. lewini* continue to include small-sized prey in their diet as they grow through their first 1.5 yrs of life. The size of prey captured may be based more on the size (thus, swimming speed and gape) and experience of the predator than capture methodology.

One of the main differences between the foraging ecology and daily ration of the early life stages of these sympatric hammerhead sharks is the inclusion of plant material in the diet of *S. tiburo* as compared to *S. lewini*. Trophic level differences are less pronounced when plant material is excluded from the analysis (trophic level difference of 0.5) and bioenergetic differences are more pronounced. The agreement between the relatively lower trophic level of *S. tiburo* compared to *S. lewini* is validated by stomach content analysis, showing *S. lewini* as primarily piscivorous and *S. tiburo* feeding on crustaceans (when plant material is excluded). The occurrence of omnivory in coastal benthic sharks could impact food web stability and potentially mitigate the top-down effects of commercial fishing of shark populations (Bascompte et al. 2005). Presently, it is assumed that plant material is incidentally consumed while *S. tiburo* forages on benthic prey and that this species is unable to digest or assimilate this plant material. However, we still cannot support or refute this assumption. The digestive capabilities of sharks and their ability to assimilate plant material may have been underestimated previously. Herbivorous fish do not produce cellulase enzymes in the stomach and instead rely on mechanical breakdown of cells, or lysis, of plant cells by the secretion of strong acids (e.g., Zemke-White et al. 1999). Sharks are capable of secreting even stronger acidic fluids than herbivorous fish, and may therefore be able to lyse plant cell walls (Papastamatiou and Lowe 2004). More research (e.g., captive feeding studies using gastric pH loggers) is needed to clarify whether these hammerhead species can assimilate seagrass.

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**Literature Cited**


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