Cercopagis pengoi as a New Prey Item for Alewife (Alosa pseudoharengus) and Rainbow Smelt (Osmerus mordax) in Lake Ontario

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ABSTRACT. Diets of alewife (Alosa pseudoharengus) and rainbow smelt (Osmerus mordax) were examined before (1997) and after (1998 and 1999) the establishment of the predatory cladoceran Cercopagis pengoi in Lake Ontario. Cercopagis pengoi was absent in both fish stomachs and zooplankton samples in 1997, but by August 1998, its distribution was lake-wide and spines of this organism were present in stomachs of both fish species. Incidence of C. pengoi spines was highest in adult alewives. Spines occurred in 72, 100, and 90% of stomachs in August 1998, August 1999, and October 1999, respectively. Spines were found in 15 and 53% of YOY alewife stomachs in August 1998 and October 1999, respectively. Cercopagis pengoi spines were least common in rainbow smelt stomachs (12% in August 1998 and 6% in October 1999). Low frequency of occurrence in rainbow smelt likely resulted from limited spatial overlap with C. pengoi. No C. pengoi spines were found in alewives < 66 mm total length (TL) which suggests that consumption of C. pengoi by YOY alewife is limited by the long caudal spine. Low consumption of C. pengoi by YOY alewife may explain the remarkably rapid population increase of C. pengoi in Lake Ontario in 1998 in the presence of a strong alewife year class. These results indicate that C. pengoi is a competitor of YOY alewives for zooplankton during the summer but also a potential prey item for larger fish throughout the year and for YOY alewife in the fall.

INDEX WORDS: Cercopagis pengoi, alewife, rainbow smelt, Lake Ontario.

INTRODUCTION

Cercopagis pengoi is a predatory cladoceran endemic to the Ponto-Caspian basin (MacIsaac et al. 1999). It is among the most widely distributed species of the genus Cercopagis and has recently been introduced to the Baltic Sea and the Laurentian Great Lakes of North America (Ojaveer and Lumberg 1995, MacIsaac et al. 1999, Gorokhova et al. 2000). Genetic similarity between the Baltic Sea and Great Lakes populations suggests that colonization of North America was the result of transoceanic shipping from the Baltic Sea (Cristescu et al. 2001). Cercopagis pengoi is euryhaline (Mordukhai-Boltovskoi and Rivier 1971) and consequently individuals or diapausing eggs of this organism may survive in ballast tanks even if they are flushed with salt water. Cercopagis pengoi was first observed in Lake Ontario in July 1998 (MacIsaac et al. 1999). By 1999, C. pengoi was also documented in Lake Michigan, Cross Lake (New York), and five of New York State’s Finger Lakes (Charlebois et al. 2001, Makarewicz et al. 2001). Cercopagis pengoi became a major component of the Lake Ontario zooplankton community the same year that it was first observed (Ojaveer et al. 2001, Makarewicz et al. 2001).

The extent to which planktivorous fish species, such as alewife (Alosa pseudoharengus) and rainbow smelt (Osmerus mordax), use C. pengoi as prey has important ecological implications and may vary between size classes and species. Because of its consistent presence and, at times, high abundance, C. pengoi may decrease food availability for planktivorous fish if it substantially decreases the density of other zooplankton through predation and does not serve as a suitable alternate prey. Smaller fish may be deterred from consuming C. pengoi by its up to 10-mm-long caudal appendage that is more than five times longer than its body length. Barn-
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hisel and Harvey (1995) found that lake herring (Coregonus artedi) < 70 mm total length (TL) did not consume Bythotrephes longimanus (previously cederstroemi), a similar cladoceran that also has a long caudal spine.

While the potential for negative impacts exists, C. pengoi may provide an additional food source for larger planktivorous fish in Lake Ontario. After its establishment in Lakes Erie and Ontario, Bythotrephes longimanus became a common prey item of adult planktivorous fish (Mills et al. 1992, Parker et al. 2001). In the Gulf of Riga, Baltic Sea, C. pengoi accounted for the majority (up to 100%) of stomach contents of juvenile and adult Baltic herring (Clupea harengus membras) in 1994 (Ojaveer and Lumberg 1995). These authors suggested that an increase in C. pengoi could contribute to improved feeding conditions and growth of Baltic herring since the cladoceran is a suitable, energetically beneficial, and readily consumed prey.

Whether the presence of C. pengoi increases or decreases availability of prey to planktivorous fish in Lake Ontario will depend both on the impact of C. pengoi on other zooplankton and the extent planktivorous fish utilize C. pengoi. In this paper, the frequency of occurrence of the readily identifiable caudal spine of C. pengoi was investigated in the stomach contents of alewives and rainbow smelt sampled with midwater trawls at various locations and depths across Lake Ontario. Differences in the proportion of the two species that had consumed C. pengoi, differences in C. pengoi consumption between young-of-the-year (YOY) and older alewife, and differences in C. pengoi consumption by YOY in August and October were tested for. Lastly, because fish may be more effective samplers of rare large zooplankton than plankton nets, the diet of fish captured in 1997 was also investigated to determine if C. pengoi was present but not detected in plankton samples in 1997.

**METHODS**

**Fish and Zooplankton Collections**

Fish were collected at night aboard the R/V Seth Green during joint trawl/hydroacoustic surveys of Lake Ontario by the Ontario Ministry of Natural Resources and New York State Department of Environmental Conservation. Trawling was conducted with a 9 m × 7 m mid-water trawl at depths ranging from the surface to 44 m. A depth and temperature sensor was located on the head rope. Each tow lasted 15 min and tow speed was approximately 6.5 km/h (Schaner and Lantry 2000). For each fish, fork length (mm), location, trawl depth, and water temperature at depth of capture were recorded. Fork length measurements were converted to TL using a linear regression equation developed from Lake Ontario alewives and rainbow smelt (D.M. Warner, unpublished data). The digestive tracts of all alewives and rainbow smelt were removed and preserved in formaldehyde in the field.

Zooplankton were collected concurrent with fish samples in August 1997 to 1999 and October 1999 with a conical 50-cm-diameter, 153-µm-mesh nylon net equipped with a flow meter at offshore sites (top 40 m of the water column). Also included were C. pengoi samples collected aboard the USEPA Lake Guardian in August 1999. These data were previously reported by Makarewicz et al. (2001), but they were included because when combined with the August 1999 samples collected aboard the R/V Seth Green, lake-wide density could be estimated from a larger spatial area. Specimens were preserved in the field in 70% ethyl alcohol after they were anesthetized with antacid tablets. Cercopagis pengoi specimens have a tendency to clump, and as a result, they were separated (with other large zooplankton) from smaller zooplankton with a 1.02-mm-mesh sieve. Once separated, C. pengoi specimens were spread homogenously in a gridded Petri dish and at least 100 organisms from a random sub-sample were counted and measured with a microprojector at 20x magnification and a digitizer interfaced with a computer.

**Diet Analysis**

Fish stomachs were examined from fish caught with the same trawl, trawling techniques, and using the same preservation techniques in 1997, 1998, and 1999. Stomachs were examined from fish caught at five sites in western and central Lake Ontario in August 1997, 11 sites throughout the western, central, and eastern portions of the lake in August of 1998, one site in the southeastern portion of the lake in August 1999, and nine sites within the eastern half of the lake in October 1999 (Fig. 1). Stomach contents from each fish were emptied into a Petri dish and examined individually with a stereo dissecting microscope. Because fish were collected throughout the night, and alewives feed primarily during the day, the stomach contents were often highly digested. However, the characteristic chitinous caudal spine of C. pengoi was still recognizable because it is more resistant to digestion than...
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other structures. Therefore, only the presence/absence of C. pengoi spines as frequency of occurrence (including empty stomachs) is presented.

Statistical Tests

Alewife were sorted into YOY and adult (age 1 and older) age classes while all rainbow smelt were adults. Statistical comparisons of the proportion of stomachs that contained C. pengoi spines were made using a t-test of arcsine-transformed data, as recommended by Sokal and Rohlf (1969) for testing equality of two proportions. Trawls were considered the sampling unit to decrease the potential for pseudoreplication. Among-year differences in frequency of occurrence of C. pengoi spines in fish stomachs were analyzed using the same methods. Two-tailed tests were used in all cases except when the hypothesis that C. pengoi spines occurred in a smaller proportion of small YOY stomachs (August 1998) than in large YOY (October 1999) was tested. Comparison of frequency of occurrence of spines in stomachs and C. pengoi density among sites was tested with Spearman’s correlation coefficient ($r_s$, Sokal and Rohlf 1995). A Kruskal-Wallis test was used to make comparisons of median C. pengoi density among years. A probability level of $< 0.05$ was considered significant in all statistical tests.

RESULTS

Cercopagis pengoi was absent in zooplankton samples collected in 1997, but it occurred at relatively high densities across Lake Ontario by August 1998, 1 month after it was first observed in eastern Lake Ontario (MacIsaac et al. 1999). Average epilimnetic density at night in August 1998 was 450 per m$^3$ (range 30 to 1,190 per m$^3$, 21 sites). Similar densities were also found in August 1999 (mean $= 448$ per m$^3$, range 35 to 1,370 per m$^3$, 23 sites). There was no difference between median C. pengoi densities in August 1998 and 1999 (Kruskall-Wallis test; $P = 0.68$). Densities in October 1999 were lower (mean $= 136$ per m$^3$, range 0 to 535 per m$^3$, 

FIG. 1. Lake Ontario locations sampled for Cercopagis pengoi, alewives, and rainbow smelt in 1997 to 1999. Numbers adjacent to the symbols correspond to the bottom depth (m) at that location. Open circles represent locations sampled in 1997, while open squares and open triangles represent locations sampled in 1998 and 1999, respectively.
TABLE 1. Average length, percentage of stomachs with *C. pengoi* spines, and sample size for alewives and rainbow smelt collected from Lake Ontario in 1997, 1998, and 1999. Numbers of empty stomachs are shown in parentheses next to the total number of stomachs examined. Alewives are separated into YOY and adult based on total length because consumption of *C. pengoi* differs between these groups. Adult alewife refers to age 1 and older fish (larger than 105 mm).

<table>
<thead>
<tr>
<th>Month/year</th>
<th>Age</th>
<th>Range</th>
<th>Mean</th>
<th>% with spines</th>
<th>Number of stomachs</th>
</tr>
</thead>
<tbody>
<tr>
<td>August 1997</td>
<td>Adult</td>
<td>101–166</td>
<td>139</td>
<td>0.0</td>
<td>21</td>
</tr>
<tr>
<td>August 1998</td>
<td>YOY</td>
<td>35–78</td>
<td>56</td>
<td>15.8</td>
<td>29 (1)</td>
</tr>
<tr>
<td>August 1998</td>
<td>Adult</td>
<td>118–178</td>
<td>152</td>
<td>71.9</td>
<td>54 (2)</td>
</tr>
<tr>
<td>August 1999</td>
<td>Adult</td>
<td>124–182</td>
<td>154</td>
<td>100.0</td>
<td>5</td>
</tr>
<tr>
<td>October 1999</td>
<td>YOY</td>
<td>43–104</td>
<td>72</td>
<td>52.4</td>
<td>31</td>
</tr>
<tr>
<td>October 1999</td>
<td>Adult</td>
<td>112–184</td>
<td>141</td>
<td>90.0</td>
<td>48</td>
</tr>
</tbody>
</table>

Rainbow smelt

<table>
<thead>
<tr>
<th>Month/year</th>
<th>Age</th>
<th>Range</th>
<th>Mean</th>
<th>% with spines</th>
<th>Number of stomachs</th>
</tr>
</thead>
<tbody>
<tr>
<td>August 1998</td>
<td>All</td>
<td>56–190</td>
<td>117</td>
<td>11.9</td>
<td>59</td>
</tr>
<tr>
<td>October 1999</td>
<td>All</td>
<td>78–164</td>
<td>115</td>
<td>5.7</td>
<td>56 (4)</td>
</tr>
</tbody>
</table>

11 sites), but these samples represented a more limited area of the lake.

Alewife samples from 1998 and 1999 (years when *C. pengoi* was present) included fish ranging from 35 to 180 mm TL (Table 1, Fig. 2). Because age-1 and older alewives generally exceed 100 mm TL during their second summer (O’Gorman et al. 1997), alewife were separated into adults (>104 mm) and YOY (<104 mm) in both years (Table 1). No *C. pengoi* spines were found in stomachs of alewives caught in 1997, but they occurred in a high percentage of adult alewife stomachs from 1998–99 (Table 1). The proportion of adult alewife stomachs that contained *C. pengoi* spines in 1998 and 1999 were not significantly different (test for equality of proportions, t = 1.52, p = 0.14, N = 16 for 1998, 10 for 1999). A higher proportion of adult than YOY alewives had consumed *C. pengoi* in both years (Table 1, Fig. 2; 1998: t = 3.84, p < 0.001, N = 10 for YOY and 16 for adults; 1999: t = 2.54, p = 0.02, N = 7 for YOY and 10 for adults). The occurrence of *C. pengoi* in stomachs of small YOY (August 1998, mean length = 56 mm) was significantly lower than in larger YOY (October 1999, mean length = 70 mm, t = 1.92, p = 0.04, N = 10 in 1998 and 7 in 1999). There was no significant correlation between the frequency of occurrence of *C. pengoi* in adult alewives and *C. pengoi* density in either year (1998, r = −0.26, N = 17, P = 0.28; 1999, r = 0.36, N = 10, P = 0.28).

When the percentages of alewives in each of 16 10-mm size classes that consumed *C. pengoi* in 1998 to 1999 were plotted against alewife length, it appeared that alewife size was a good predictor of *C. pengoi* consumption (Fig. 3). The non-linear regression function was used in SigmaPlot 2000 to develop a model for predicting the percentage of alewives consuming *C. pengoi*. The resulting 3-parameter sigmoidal model was:

\[
y = \frac{81.4}{1 + e^{-\left(\frac{\text{length}_{\text{a}} - 66.3}{4.57}\right)}}
\]

where y = the percentage of alewives at a given length consuming *C. pengoi*. The model was highly significant (F = 50.6, p < 0.0001, r² = 0.89, standard error of the estimate = 13.1).

Rainbow smelt captured in 1998 and 1999 ranged in length from 56 to 190 mm TL (Fig. 4). Only seven of the 111 fish examined contained *C. pengoi*, precluding any meaningful analysis of differences between fish sizes. The smallest rainbow smelt that was found to consume *C. pengoi* was 96 mm TL. No difference in rainbow smelt consumption of *C. pengoi* was detected between years (Table 1; t = 0.67, p = 0.51, N = 11 for both years). *Cercopagis pengoi* spines occurred in rainbow smelt stomachs at lower frequencies than in adult alewife stomachs in both years (Table 1; 1998: t = 4.33, p < 0.001, N = 16 for alewives, N = 11 for rainbow smelt; 1999: t = 10.29, p < 0.001, N = 10 for rainbow smelt).
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Frequency of occurrence of *C. pengoi* spines in YOY alewife and rainbow smelt stomachs did not differ in 1998 (t = 0.25, p = 0.80, N = 10 for alewives and 11 for rainbow smelt), but in 1999 *C. pengoi* spines were significantly more common in YOY alewife diets than in rainbow smelt stomachs (t = 3.30, p < 0.01, N = 7 for alewives and 11 for rainbow smelt). The dominant prey item in rainbow smelt stomachs was *Mysis relicta*.

**DISCUSSION**

Although the analysis of alewife and rainbow smelt diets presented here was limited to quantifying the frequency of occurrence of *C. pengoi* spines, several important conclusions can be drawn from these data. First, alewives smaller than 66 mm TL did not consume *C. pengoi*, probably because these small fish have difficulty handling the long caudal spine. Second, although the relative impor-
tance of *C. pengoi* in alewife and rainbow smelt diets remains unknown, it is apparent that consumption of *C. pengoi* by larger alewives is widespread (spines were found in at least 70% of fish larger than 70 mm TL). Consumption of *C. pengoi* by rainbow smelt was less common, probably because of limited spatial overlap between these two species. Third, *Cercopagis pengoi* spines were found in the stomachs of both alewife and rainbow smelt in 1998 and 1999, but not in August 1997. This is consistent with the absence of *C. pengoi* in 1997 zooplankton samples. Thus, *C. pengoi* was either rare or absent in Lake Ontario in 1997 and expanded rapidly through the whole lake in 1998.

Observed densities of *C. pengoi* in August 1998 and August and October 1999 were similar to those previously reported for those years in Lake Ontario (MacIsaac et al. 1999, Makarewicz et al. 2001, Ojaveer et al. 2001, Benoît et al. 2002). August has been identified as the peak month for *C. pengoi* abundance in Lake Ontario (Makarewicz et al. 2001, Benoît et al. 2002). Therefore, much of the data presented here are for the seasonal period when *C. pengoi* is likely most important as predator and prey.

Young-of-year alewives may have difficulty feeding on *C. pengoi*, as the smallest alewife found to consume *C. pengoi* in 1998 and 1999 had total lengths of 72 mm and 66 mm, respectively. None of the stomachs examined from 30 alewives smaller than 66 TL mm contained *C. pengoi* spines (Fig. 3). Other YOY fish species have difficulty feeding on the related cercopagid *B. longimanus*, which also has a long chitinous spine (yellow perch, *Perca flavescens*, Barnhisel 1991, Jarnagin 1998; cisco, *Coregonus artedi*, lake whitefish *C. clupeaformis*, Barnhisel and Harvey 1995). In Lake Ontario, Mills et al. (1992) found lower numbers of YOY alewives containing *B. longimanus* spines relative to adult alewives and Urban and Brandt (1993) did not find any *B. longimanus* in YOY alewife stomachs. In the Baltic Sea, *C. pengoi* has been found to be common in adult but not YOY Baltic herring (*Clupea harengus*) (Ojaveer and Lumberg 1995). Small fish may have problems handling *C. pengoi* because of gape size limitations. The gape height and width of a 65 mm TL alewife are 7.6 and 4.5 mm, respectively (Brooking et al. 1998). Therefore, it is conceivable that the ability of a small alewife to consume a *C. pengoi* with a 7 to 11-mm-long spine is limited by gape size.

*Cercopagis pengoi* spines were found in a larger proportion of both YOY alewives and adult alewives than in rainbow smelt. It is possible that this is due to differences in overlap between *C. pengoi* and these two fish species. Alewives are generally concentrated in the epi and metalimnion at 14 to 24°C (O’Gorman et al. 1997); whereas, rainbow smelt are found at or below the thermocline at 8 to 14°C (Lantry and Stewart 1993). The observations of capture depth and temperature of alewives and rainbow smelt were similar. In August 1998, the average capture depth and temperature for alewife was 16 m (range 3 to 41 m) and 17°C (range 4° to 23°C); whereas, similar values for rainbow smelt were 25 m (range 8 to 41 m) and 12°C (range 4° to 22°C). *Cercopagis pengoi* is primarily found in the epilimnion (Uitto et al. 1999, Ojaveer et al. 2001), often with an abundance peak in the lower epilimnion (Benoît et al. 2002). Of the seven rainbow smelt that did consume *C. pengoi*, six were captured in water 17°C or greater which is generally considered outside the normal temperature range of rainbow smelt (Lantry and Stewart 1993). It is possible that the lower frequency of *C. pengoi* in rainbow smelt stomachs is not because rainbow smelt avoid *C. pengoi* but because these fish do not regularly encounter *C. pengoi*.

The rapid expansion of the *C. pengoi* population in 1998 in the alewife-dominated environment of Lake Ontario was surprising. Mills et al. (1992) suggested that predation by alewives prevented high abundance of *B. longimanus* in Lake Ontario. A similar control on *C. pengoi* abundance by alewives would be expected, but densities observed in this study exceeded 1,000 per m³ in 1998. Makarewicz et al. (2001) attributed the rapid expansion in 1998 to low numbers of adult alewife in combination with high fecundity, asexual reproduction, and defensive spines of *C. pengoi*. Young-of-year alewives were abundant in 1998 (R. O’Gorman, Oswego Biological Station, Oswego, N.Y., personal communication) but the data in this study suggest that these fish do not consume *C. pengoi* until they reach length of over 66 mm TL and would therefore have little effect on *C. pengoi* abundance until the fall. It is likely that low adult alewife abundance in 1998 contributed to both the strong YOY alewife cohort and the rapid expansion of *C. pengoi* that year.

However, *C. pengoi* densities remained high in 1999, even though the abundance of yearling alewife large enough to consume *C. pengoi* was high that year (R. O’Gorman, personal communication). It is possible, but not likely, that adult alewives only consume a small number of *C. pengoi*. The data presented in this study did not provide a quantitative
assessment of the importance of \textit{C. pengoi} in the diet of alewives, but many of the stomachs examined contained very large numbers of \textit{C. pengoi} spines. It is conceivable that spines are retained for some time in alewife stomachs (as observed for rainbow smelt feeding on \textit{B. longimanus}, Parker \textit{et al.} 2001) and spines may therefore be poor indicators of feeding rates on \textit{C. pengoi}. However, examination of a small number of stomachs from adult alewives collected in August 2001 indicated that \textasciitilde80\% of the organisms found in the stomachs (based on counts of bodies, not spines), were \textit{C. pengoi}. Elsewhere, adult Baltic herring heavily utilized \textit{C. pengoi} (Ojaveer and Lumberg 1995). If predation on \textit{C. pengoi} is high, \textit{C. pengoi} must be able to maintain high rates of population growth. Straille and Hälßich (2000) found that \textit{B. longimanus} exhibited multiple antipredator defenses including high fecundity, diel vertical migration, and spines. \textit{Cercopagis pengoi} is smaller and may have shorter generation time than \textit{B. longimanus}, resulting in faster population growth rates. In addition, the number of \textit{C. pengoi} present in the lake in the beginning of 1999 must have been substantially larger than in the beginning of 1998, potentially allowing the species to increase despite higher predation rates.

The ecological relationship between \textit{C. pengoi} and planktivorous fish in Lake Ontario is dependent on the age and species of fish and the abundance of \textit{C. pengoi}. Benoît \textit{et al.} (2002) have shown that \textit{C. pengoi} probably decreased abundance of small nauplii and copepodes and possibly small cladocerans, as well as caused some of these vulnerable prey to avoid surface waters. Thus, \textit{C. pengoi} may depress the zooplankton prey of small alewife (< 66 mm) without providing an additional food source for these fish. This may result in decreased growth of YOY alewives, possibly leading to lower over-winter survival (O’Gorman \textit{et al.} 1997). The interactions between \textit{C. pengoi} and YOY alewife will depend on the timing of alewife reproduction and the timing and magnitude of the effect of \textit{C. pengoi} on other zooplankton. Effects on adult alewife growth remain unclear but could be positive. \textit{Cercopagis pengoi} is larger and may be a more profitable prey than the smaller zooplankton that may decline due to \textit{C. pengoi} predation. The effect of \textit{C. pengoi} on rainbow smelt is likely minimal.

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