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# Feeding ecology of *Coregonus albula* and *Osmerus eperlanus* in the limnetic waters of Lake Mälaren, Sweden

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A large block of unpublished information from the late 1960s on the interactive ecology of two highly zooplanktivorous fishes — vendace (*Coregonus albula*) and smelt (*Osmerus eperlanus*) — in Lambarfjärden of Lake Mälaren, Sweden, was used to demonstrate quantitatively diel and seasonal changes in their limnetic feeding distribution, to compare their trophic structures, and to examine their selective use of some 20 different zooplanktonic taxa with those pelagically present by species, size, abundance and vertical distribution. Although there were significant differences in gillraker number, as well as spacing and structure between vendace and smelt, these did not seem to be strongly reflected in selection or use of major zooplanktonic prey taxa during the summer–autumn seasons. While small cladocerans dominated the prey choice of both species during June–September, large-sized calanoid copepods dominated in October. Schoener's overlap indices were high for both vertical distribution and prey taxa use by the two species, suggesting the possibility of strong competitive interaction between their planktivorous stages, though alternative explanations are explored. Their joint use of pelagic space and prey, changing seasonally, may offer a partial explanation for the marked year class fluctuations and periodic failures of vendace recruitment known to occur in Lambarfjärden, and other lakes where the two species coexist. In addition, the comparisons support the image of the environmental cul-de-sac position of vendace as an extreme zooplankton specialist, with a very narrow diet spectrum and habitat range, whereas smelt seem to express a more opportunistic ecology.

## Introduction

The ecological interaction of related species pairs has been of special interest to aquatic biologists from at least the 1950s on (e.g. Northcote 1954, Svärdson 1976, Enderlein 1981a, Mittelbach 1984, Werner 1986, Persson 1988, Bergman 1990, Hammar 1998, Degerman *et al*. 2000, Northcote 2000). In the large Swedish lowland Lake Mälaren, we examine some aspects of the feeding ecology of vendace (*Coregonus albula*) and smelt (*Osmerus eperlanus*). Much of the information on the limnetic spatial distribution of these two species in the Lambarfjärden section has been published (Northcote and Rundberg 1970), but that on their feeding interactions has not. In Finland, Viljanen (1986) noted that relatively little attention has been given to vendace food habits, prey selection, and competitive feeding interactions with other fish species. This disparity in the literature is widespread up to the present in Europe, and is just as great for North American cisco and smelt. An early study giving data on food habits of cohabiting vendace and smelt is in a different lake tributary to Lake Mälaren (Hammar 1968), and the study by Vallin (1969) reports only on vendace feeding in the Lambarfjärden part of Lake Mälaren. Vendace are highly zooplanktivorous throughout their life (Enderlein 1981a), as are smelt in their first year or more (Nellbring 1989), but larger and older stages of smelt may switch in part to feeding on larger crustaceans and fish, including cannibalism.

In addition, the data for our study on feeding ecology of vendace and smelt were obtained in the late 1960s when both vendace and smelt were abundant (Rundberg 1968), and our information may now be of use in the assessment of the various factors leading to the sharp decline in vendace populations and their poor recruitment in central parts of Lake Mälaren, including Lambarfjärden, during the late 1980s and early 1990s (Nyberg *et al*. 2001). The outstanding importance of this lake for fisheries and for the water supply to Stockholm, among other features, has been well described (Degerman *et al*. 2001, Wilander and Persson 2001, Willén 2001a, 2001b).

## Methods

Monofilament nylon gangs of nets, each 30 m long and 10 m deep, and containing equal lengths of 19 and 27 mm (knot to knot) green mesh, were set in Lambarfjärden at approximately two week intervals between late June and early September 1968. Net gangs were suspended from the surface and at 10, 20, 30 and 40 m depths usually for 3-hour fishing intervals near midday (about 10:30 to 13:30) and midnight (about 22:30 to 01:30). All nets were marked by narrow uncoloured portions of the webbing at 2-m depth intervals which facilitated recording the depth distribution of fish in the nets. Fish were removed from nets on the shore less than 30 minutes after lifting and their depth in the net noted. Stomachs of all vendace and smelt were preserved in a 10% formalin solution on removal of the fish from the nets.

Vendace and smelt collections were also made at the Lambarfjärden station by exploding small charges of dynamite (Nitrolit) at 5, 10, 15, 20 and 30 m depths at 09:00 to 12:00 and 14:00 to 16:00 on 30 August 1968 as given in Northcote and Rundberg (1970).

Macro-zooplankton samples were taken with standard Clarke-Bumpus gear (Wetzel and Likens 2000) using a mesh size of 0.132 mm so most rotifers and crustacean nauplii were not quantitatively represented, but a finer mesh would not have permitted reliable volume metering (Lötmarker 1964). Tows were made at a velocity of about 0.8 m $s^{-1}$ covering six depth intervals: 0–4 and 5–9 m at equal time for each intervening metre depth; 10–18, 20–28, 30–38 and 40–48 m at equal time for each two-

**Table 1**. Body size (mm) characteristics of major Lambarfjärden limnetic cladocerans[a] in 1968; females only.

| Species | *n* | Size range | Dates sampled[b] |
|---|---|---|---|
| *Chydorus sphaericus* | 20 | 0.29–0.40 | 2, 4 |
| *Bosmina longispina*[c] | 59 | 0.32–0.86 | 1, 2, 3, 5, 6 |
| *Diaphanosoma brachyurum* | 2 | 0.90–1.10 | 1 |
| *Daphnia cristata sensu lato* | 76 | 0.84–1.29 | 1, 2, 3, 4 |
| *Limnosida frontosa* | 18 | 1.05–1.50 | 1, 2, 3 |
| *Daphnia galeata* | 79 | 0.72–1.65 | 1, 2, 3, 4, 5, 6 |
| *Daphnia cucullata* | 70 | 0.83–1.80 | 1, 2, 3, 4 |

[a] not including the much larger *Bythotrephes longimanus* and *Leptodora kindtii*.
[b] 1 = 9 July, 2 = 25 July, 3 = 3 August, 4 = 20 August, 5 = 4 September, 6 = 22 November.
[c] recorded in the 1970s by the Uppsala limnologists as *Bosmina coregoni* in two size ranges: "small" 0.32–0.49 mm (mean 0.39, *n* = 59) and "large" 0.50–0.86 mm (mean 0.60, *n* = 72).
Today *B. c.* is *Bosmina (Eubosmina) longispina* (adult size > 0.4 mm) but could be replaced by the smaller *B. longirostris* (adult size 0.2–0.3 mm); (E. Bergstrand pers. comm.). Both species therefore may be present in our zooplankton samples.

metre intervening depth interval. All samples were preserved in 4% formaldehyde. Samples were analyzed under the guidance of Dr. Birger Pejler at the University of Uppsala using a 1-ml modified Hensen-Stemple pipette for subsampling and an inverted microscope for counting (Jacobsson and Söderström 1971). Zooplankton body size determinations were made at the Institute of Freshwater Research, Drottningholm, and at the University of British Columbia, Vancouver, with an ocular micrometer in a dissecting microscope (×50 magnification) measuring from the anterior end of the head to the posterior end of the body (excluding cladoceran helmet and mucro spines if present and copepod caudal rami).

Fish stomach samples (lower oesophagus to stomach pyloric sphincter), preserved initially in 10% formaldehyde and washed for a few hours in water before analysis, were examined under a dissecting microscope to remove prey contents. Total volume was measured in a specially constructed tube by liquid displacement, and prey taxa numbers counted individually for small content volumes or estimated by triplicate random subsamples for large volumes. Most different prey taxa were distinguished (ten cladocerans, six copepods, *Monoporeia affinis*, *Mysis relicta*, five insect groups, unidentifiable fish remains).

Schoener's (1970) overlap index, $O_{sv}$, was used to quantitatively compare overlap of fish depth distribution and prey type use between smelt (s) and vendace (v); for the latter comparison:

$$O_{sv} = 1 - 0.5\left(\sum_{i=1}^{n}\left|p_{si} - p_{vi}\right|\right) \times 100 \qquad (1)$$

where $p_{si}$ and $p_{vi}$ are proportions (not percentages) of prey type $i$ in any pair of fishes $s$ and $v$, and $p_{si} - p_{vi}$ represents the absolute difference term. The index ranges from zero to 100, zero indicating no common prey type use and 100 indicating identical prey type use. For interpretive use of this index in fish feeding ecology and species interaction *see* Wallace (1981), DeVries and Stein (1992), Davis and Todd (1998), Aku and Tonn (1999) and Hrabik *et al*. (2001).

## Results

### Zooplankton diversity, size and densities

There were 24 species of rotifers recorded in the limnetic zooplankton of Lambarfjärden in summer 1968, but none were found in smelt or vendace stomachs. Information on the main species of cladocerans and copepods present limnetically in Lambarfjärden waters in the summer of 1968 is given in Tables 1 and 2.

**Table 2**. Body size (mm) characteristics of major Lambarfjärden limnetic copepods in 1968.

| Species | Sex | *n* | Size range | Dates sampled[a] |
|---|---|---|---|---|
| *Thermocyclops* | male | 60 | 0.57–0.71 | 1, 2, 3, 4, 5 |
| *ointhonoides* | female | 58 | 0.68–0.90 | as above |
| *Mesocyclops* | male | 50 | 0.66–0.78 | 1, 2, 3, 5 |
| *leuckarti* | female | 46 | 0.81–1.01 | as above |
| *Eudiaptomus* | male | 17 | 1.01–1.19 | 1, 2, 3, 4 |
| *graciloides* | female | 4 | 1.19–1.28 | 3, 4 |
| *Eudiaptomus* | male | 33 | 1.02–1.31 | 1, 2, 3, 4, |
| *gracilis* | female | 68 | 1.17–1.47 | as above |
| *Cyclops* | male | 15 | 1.26–1.49 | 3, 4, 6 |
| *strenuous* | female | 4 | 1.40–1.62 | 7 |
| *Eurytemora* | male | 1 | 1.20 | 1 |
| *lacustris* | female | 2 | 1.50, 1.64 | 1, 2 |
| *Heterocope* | male | 6 | 1.80–2.15 | 1, 3, 4 |
| *appendiculata* | female | 3 | 2.10–2.18 | 1 |
| *Limnocalanus* | male | 70 | 1.92–2.26 | 1, 2, 3, 4 |
| *macrurus* | female | 70 | 1.90–2.43 | as above |

[a] 1 = 9 July, 2 = 25 July, 3 = 3 August, 4 = 20 August, 5 = 4 September, 6 = 22 October, 7 = 22 November.

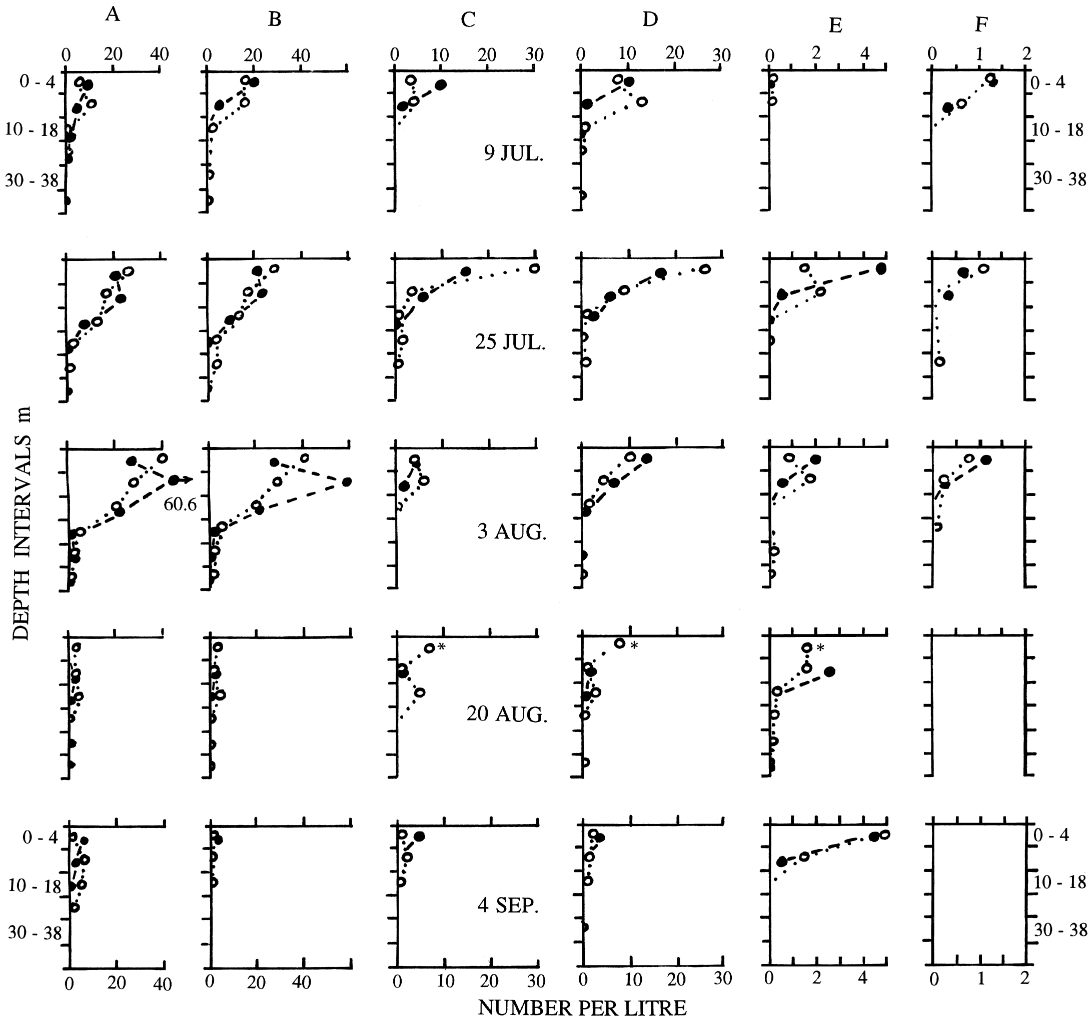


**Fig. 1**. Mean density of major limnetic species of cladocerans in Lambarfjärden from early July to early September 1968; densities for 22 October and 22 November were too low to show. Open circles = midday, solid circles = midnight, * = no data for midnight. **A** = *Bosmina* (*Eubosmina*) *longispina*, **B** = *Daphnia cristata sensu lato*, **C** = *Daphnia cucullata*, **D** = *D. galeata*, **E** = *Diaphanosoma brachyurum*, **F** = *Limnosida frontosa*.

The smallest cladocerans were *Chydorus sphaericus* (body size 0.29 to 0.40 mm) and *Bosmina* (*Eubosmina*) *longispina* (body size 0.32 to 0.86 mm) (Table 1). The next largest were *Diaphanosoma brachyurum* (about 1 mm) and *Limnosida frontosa* (1.05 to 1.50 mm). The three recorded species of *Daphnia* had mean body sizes ranging from about 0.8 to 1.8 mm.

From summer to early autumn highest cladoceran densities in the limnetic waters of Lambarfjärden were always found in the epilimnion above 20 m, and usually in the uppermost 10 m (Fig. 1). In most cases there were not major differences between midday and midnight vertical distribution of the limnetic cladocerans sampled. Highest densities for most species occurred in late July or early August, with sharply reduced numbers by early September for all except *Diaphanosoma brachyurum* (Fig. 1) and very low densities for all species in mid to late autumn (data not shown).

The smallest limnetic copepods were *Thermocyclops ointhonoides* and *Mesocyclops leuckarti*, ranging from about 0.6 to 1.0 mm in body size, with males smaller than females (Table 2). Four other species — *Eudiaptomus graciloides*,

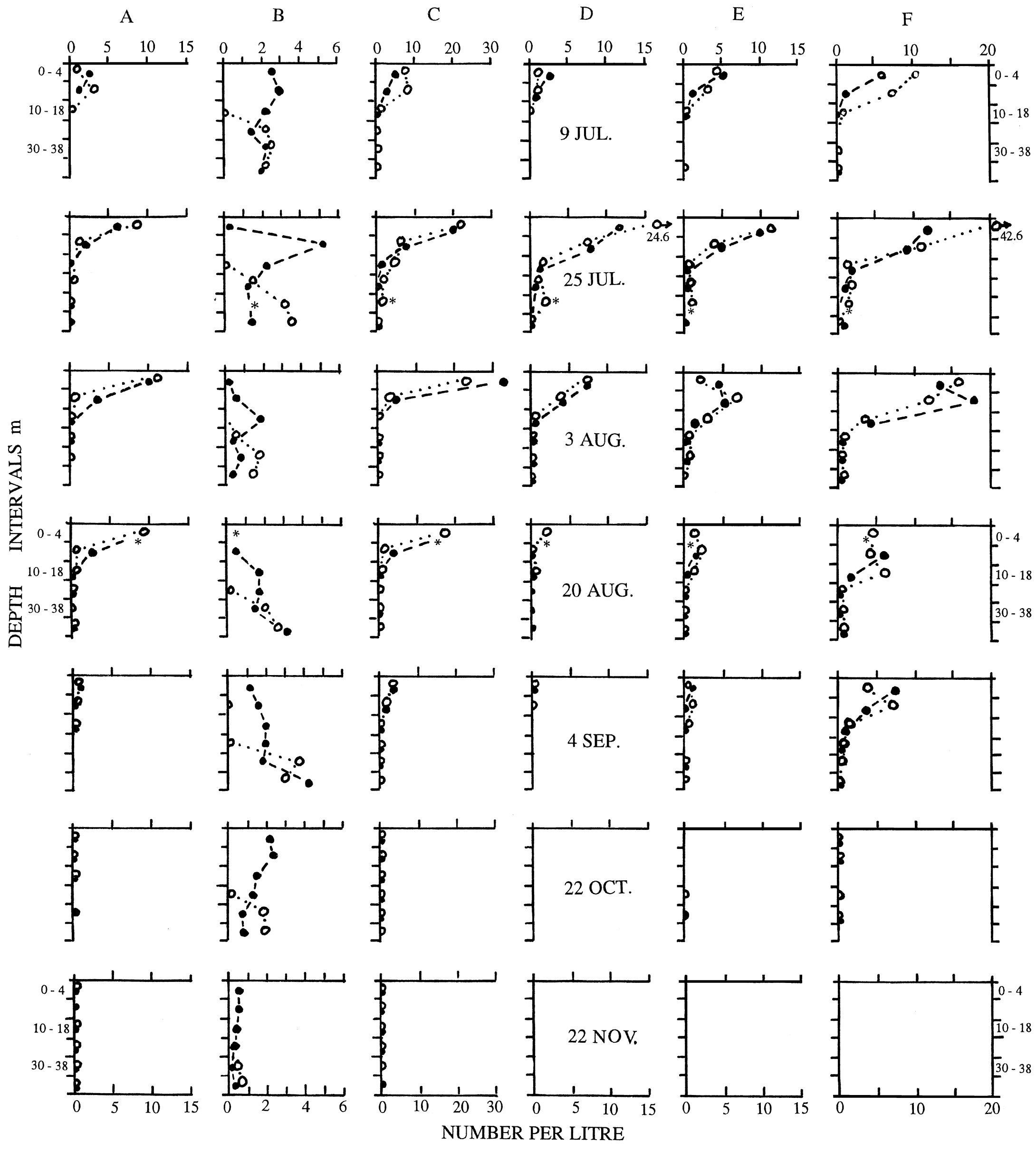


**Fig. 2**. Mean density of major limnetic species of copepods in Lambarfjärden from early July to late November 1968. Open circles = midday, solid circles = midnight, * = no data for midnight. Density values not shown for values < 0.1 zooplankters per litre; **A** = *Eudiaptomus gracilis*, **B** = *Limnocalanus macrurus*, **C** = calanoid copepodids, **D** = *Mesocyclops euckarti*, **E** = *Thermocyclops ointhonoides*, **F** = cyclopoid copepodids.

*E. gracilis*, *Cyclops strenuus* and *Eurytemora lacustris* — formed a mid-sized group (about 1.1 to 1.5 mm). The two largest limnetic copepods, *Heterocope appendiculata* and *Limnocalanus macrurus*, had mean body sizes close to 2 mm, again with males smaller than females.

Moderate densities of calanoid and cyclopoid copepodids, as well as adult *Eudiaptomus gracilis*, *Mesocyclops leuckarti* and *Thermocyclops ointhonoides*, also occurred mainly in the upper 20 m of Lambarfjärden through summer to early autumn (Fig. 2), but in October and November only at very low densities. No major differences between midday and midnight were evident in

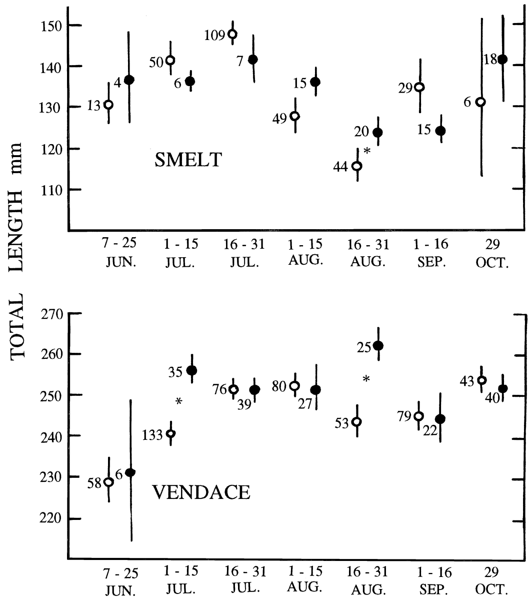


**Fig. 3**. Summer to autumn differences in mean total length of smelt and vendace captured in standard gillnet sets and sampled for feeding analyses, Lambarfjärden 1968. Open circles show means for fish from 0 to 24 m depth, solid circles for those 25–50 m; vertical lines give standard error of means; asterisks show significant differences ($p < 0.05$) between depth range means using non-parametric tests where appropriate; numbers beside means give sample sizes.

vertical distribution or abundance of these forms. In contrast the large calanoid copepod *Limnocalanus macrurus* was virtually absent from the upper 20 m during midday and reached highest densities then in the near-bottom waters of Lambarfjärden (Fig. 2). At night highest densities of this species always occurred in the uppermost 20 m, indicating a marked and extensive diel vertical migration of its adult stage.

## Smelt and vendace size, abundance, and vertical distribution

Smelt obtained by gillnetting and used for seasonal diet comparisons always were smaller in length than vendace (Fig. 3), especially in August. The mean size of smelt was smaller in August, both for those taken above and below 25 m. In contrast, in the latter half of August vendace caught in 25–50 m levels were larger, while those caught in 0–25 m levels were smaller. Except for smelt in the latter half of August, and for vendace in the first half of July and the latter half of August, there were no significant differences in mean size of either species between the upper and lower 25 m depth intervals sampled from June to October.

Limnetic gillnet catches per unit effort (CPUE) of smelt and vendace in Lambarfjärden over the summer and autumn seasons (Table 3) indicated significantly higher values of vendace compared with smelt during both midday and midnight. However gillnets can be species selective, so relative catches of vendace and smelt by this method must be used cautiously to indicate differences in sub-adult to adult density. Our Nitrolit sampling (*see* below) indicates a higher preponderance (nearly 20 times) of sub-adult to adult smelt over vendace at Lambarfjärden in late August 1968, as was indicated in the early 1970s by echo-sounding in Lake Mälaren (O. Enderlein pers. comm.).

**Table 3**. Catch in numbers per hour (catch per unit effort, CPUE) for smelt and vendace in pelagic gillnet sets 0 to 50 m in Lambarfjärden, Lake Mälaren, June to October 1968. Number of sets in parentheses.

| Statistics | Midday sets (10) | | Midnight sets (9) | |
|---|---|---|---|---|
| | A. Smelt | B. Vendace | C. Smelt | D. Vendace |
| Mean CPUE | 1.98 | 15.03 | 5.72 | 10.63 |
| Range | 0–5.00 | 0–29.00 | 2.00–11.00 | 4.83–19.33 |
| Standard error | 0.56 | 3.02 | 1.07 | 2.05 |

Significant differences[a] in CPUE: smelt versus vendace, midday $p = 0.003$, midnight $p = 0.045$; smelt midday versus smelt midnight $p = 0.004$; vendace midday versus vendace midnight not significantly different $p = 0.442$.

[a] using square root of variate + 0.5 transformed data; unpaired *t*-test for A *vs*. C, B *vs*. D, and C *vs*. D where standard deviations not significantly different; non-parametric test for A *vs*. B where standard deviations were significantly different; CPUE for smelt versus vendace, midday $p = 0.003$.

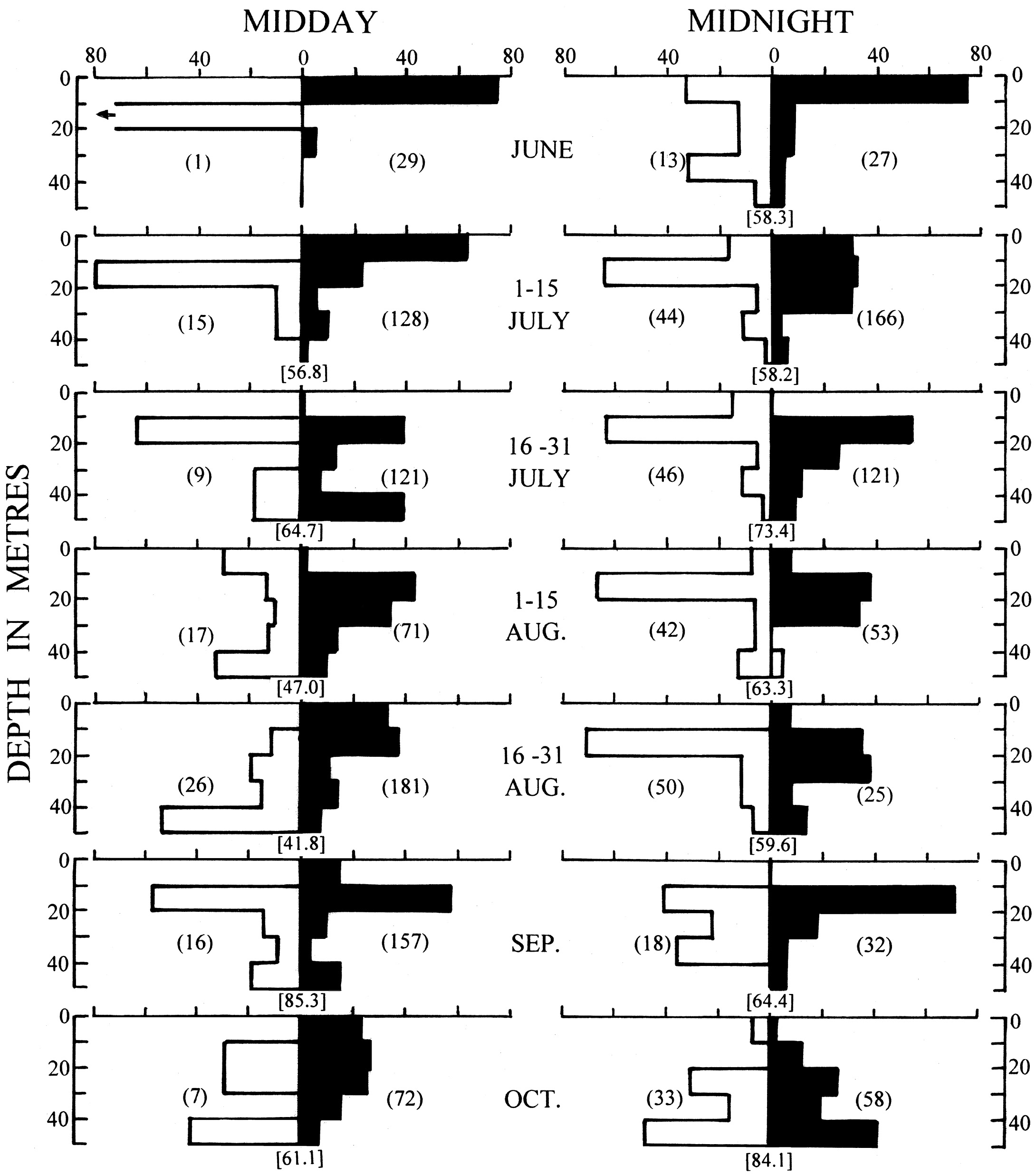


**Fig. 4**. Mean percentage of number per hour for smelt (open bars) and vendace (black bars) gillnetted in 10 m depth intervals (0 to 50 m), at Lambarfjärden June to October 1968. Total numbers caught in 3-hour fishing periods are given in parentheses; the Schoener overlap index for vertical distribution of the two species are given in brackets.

Overlap indices in vertical distribution at 10-m depth intervals from surface to 50 m for the two species were highest at night for all seasonal periods except September (Fig. 4), and ranged from a midday low of 41.8% to a midnight high of 84.1%. If a 60% level is used to indicate ecologically significant overlap (Wallace 1981), then that would occur for three of the seven seasonal periods during midday (lowest level of depth overlap being in August), and for close to all of the seven during midnight.

A special data set for feeding analysis was available from the experimental Nitrolit sampling undertaken in late August (Fig. 5). Overall

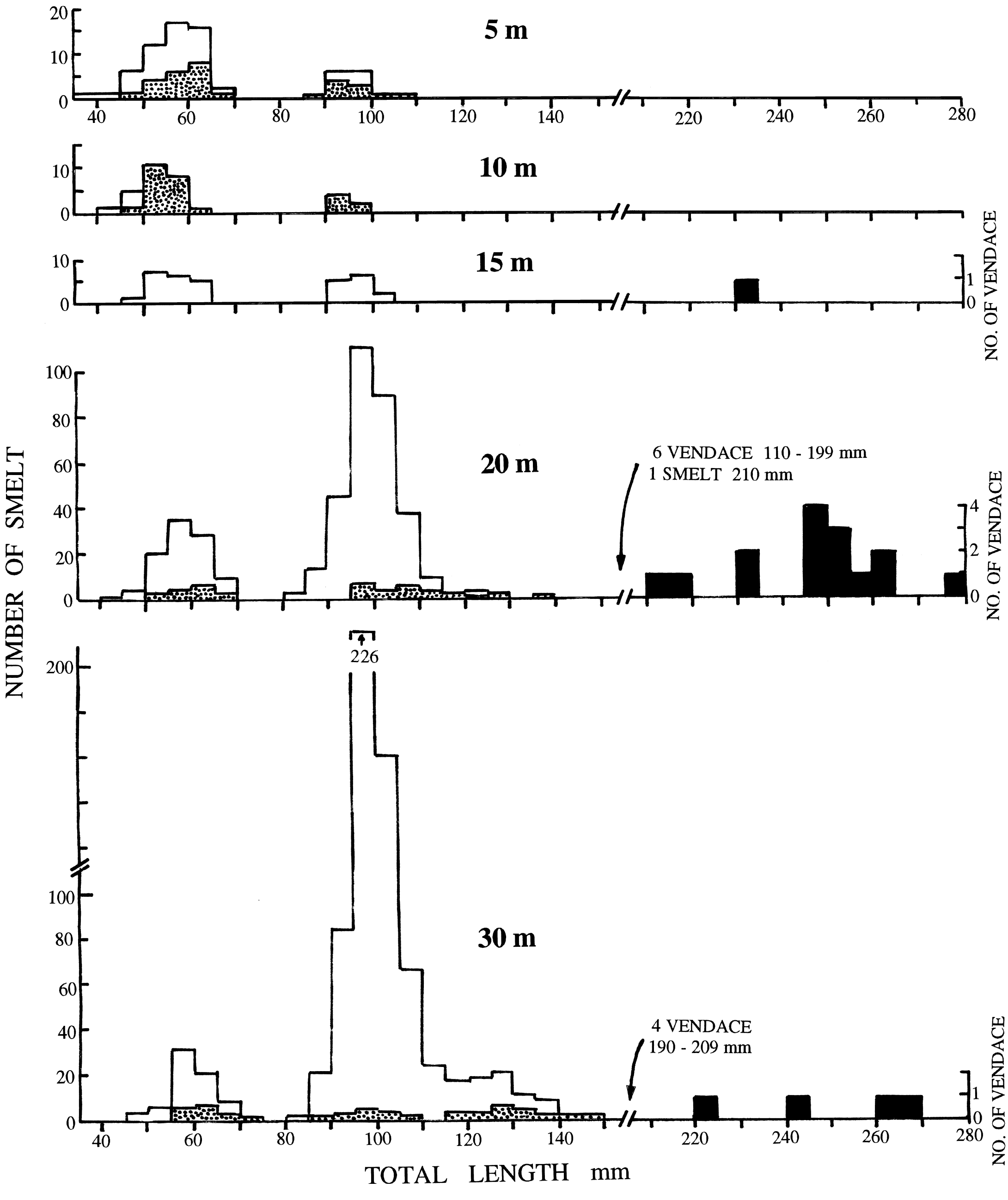


**Fig. 5**. Length–frequency distributions for all smelt captured (blank) and stomach sampled (stippled); also for all vendace captured (solid) and stomach sampled from experimental small (100–400 g) Nitrolit collections at 5, 10, 15, 20 and 30 m depths in Lambarfjärden, 09:10 to 15:00, 30 August 1968. *See* Northcote and Rundberg (1970) for details.

1231 smelt and 32 vendace were taken by this method between 09:10 and 15:00 on 30 August 1968, with a mean catch ratio of smelt to vendace of 19.8:1. In contrast to gillnet sampling, smelt were far more abundant than vendace at all depths sampled by Nitrolit, and occurred in moderate numbers even in the uppermost 10 m where no vendace were taken. Most vendace were captured at 20 m. Smelt taken at this depth were smaller in total length than the vendace, and were composed of two distinct size groupings (Fig. 5), likely representing 0+ and older age groups, respectively. No smelt less than 87 mm was taken by gillnetting in August (or indeed throughout the whole 1968 summer to autumn sampling series), whereas a distinct small size group of smelt of about 45 to 75 mm (likely 0+) were taken at all depths sampled by Nitrolit charges (Fig. 5). During morning to mid afternoon, the Nitrolit collections indicated that the upper 15-m depth zone contained mainly juvenile smelt in the 40–70 mm size range along with smaller numbers in the larger size class, but few vendace. The latter were taken mainly at 20 and 30 m depths along with a few smelt in the smaller size class and many in the larger size class. Stomachs from both modal groups of smelt, and from all vendace, taken in the collections of 30 August were used for diet analyses.

## Smelt and vendace gillraker differences

Although gillraker number in whitefish does not increase appreciably after a fish length of about 10 cm (Lindström 1989, Svärdson 1998), the possibility that there might be significant differences among small and large individuals of smelt and vendace was checked. Gillraker mean numbers were slightly lower in the small size groups, but the differences were not significant ($p$ values always > 0.05). Smelt had fewer gillrakers (mean 34.77, range 32–37) than did vendace (mean 46.95, range 42–52). Comparative details will not be given here, but for individuals of similar size, smelt had shorter gillraker length, wider base spacing between gillrakers, and lacked the small projections on the rear surface of each raker, a characteristic feature of vendace gillrakers.

## Smelt and vendace feeding

### Empty stomachs

For all gillnetted fish over the summer to autumn study period (Table 4), smelt had a lower mean percentage of empty stomachs (17.1) than did vendace (22.9), but the difference was not significant ($p = 0.315$, using arc sin square root transformation of data), nor was that for fish taken only in the upper (< 25 m) water layer. Smelt from deeper waters (25–50 m) did have significantly fewer empty stomachs than vendace ($p = 0.013$, non-parametric Mann-Whitney test with same data transformation). There was no obvious seasonal trend in the percentage of empty stomachs for either species overall, or for the two depth zones considered (Table 4), nor was there between fish taken near midday and midnight (data not shown), though the former was slightly higher than the latter for both smelt (25.5% *versus* 18.7%) and vendace (22.7% *versus* 21.6%).

For Nitrolit-collected smelt in late August (Table 5) those from 5 m had a very high percentage of empty stomachs, well over twice that

**Table 4**. Percentage of empty stomachs in gillnetted smelt and vendace from Lambarfjärden, Lake Mälaren during seven summer to autumn periods in 1968. Number of specimens examined in parentheses.

| Date | Smelt | | | Vendace | | |
|---|---|---|---|---|---|---|
| | Total | < 25 m | 25–50 m | Total | < 25 m | 25–50 m |
| 7–25 June[a] | 29.4 (17) | 38.5 (13) | 0 (4) | 4.7 (64) | 5.2 (58) | 0 (6) |
| 1–15 July | 8.9 (56) | 6.0 (50) | 33.3 (6) | 14.3 (168) | 9.8 (133) | 31.4 (35) |
| 16–31 July | 20.7 (116) | 21.1 (109) | 14.3 (7) | 29.6 (115) | 27.6 (76) | 33.3 (39) |
| 1–15 August | 10.9 (64) | 12.2 (49) | 6.6 (15) | 29.9 (107) | 31.3 (80) | 25.9 (27) |
| 16–31 August | 20.3 (64) | 25.0 (44) | 10.0 (20) | 24.3 (78) | 24.5 (53) | 28.0 (25) |
| 1–16 September | 25.0 (44) | 31.0 (29) | 13.3 (15) | 34.5 (101) | 41.8 (79) | 22.7 (22) |
| 29 October | 4.2 (24) | 0 (6) | 5.6 (18) | 22.9 (83) | 25.6 (43) | 20.0 (40) |
| Overall mean | 17.1 | 19.1 | 11.9 | 22.9 | 23.7 | 23.0 |

[a] two smelt and five vendace from Björkfjärden, Lake Mälaren, 11 June included.

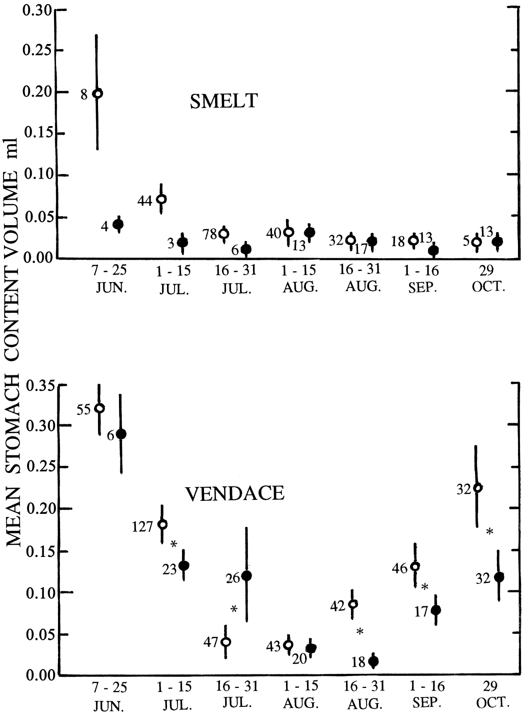


**Fig. 6**. Summer to autumn change in mean stomach content volume of smelt and vendace captured in standard gillnet sets and sampled for feeding analyses, Lambarfjärden 1968. Open circles means for fish from 0 to 24 m depth, solid circles those from 25–50 m; vertical lines give standard error of means; asterisks show significant differences ($p < 0.05$) between depth range means using non-parametric tests where appropriate; numbers beside means give sample size.

for gillnetted samples from about the same time (cf. Table 4). In contrast those from 10, 20 and 30 m had about the same percentage of empty stomachs as did the gillnetted ones, so the difference in collection method would not seem to be a reasonable cause for the high percentage empty at 5 m. High digestion rate at warmer temperatures may be involved.

**Table 5**. Percentage of empty stomachs in Nitrolit collection of smelt and vendace from Lambarfjärden, Lake Mälaren on 30 August 1968 (09:10–15:00).

| Species | Depth (m) | Total length (mm) | Number sampled | Empty (%) |
|---|---|---|---|---|
| Smelt | 5 | < 75 | 20 | 60.0 |
| | 5 | > 75 | 9 | 66.7 |
| | 10 | < 75 | 15 | 6.7 |
| | 10 | > 75 | 6 | 0 |
| | 20 | < 75 | 15 | 13.3 |
| | 20 | > 75 | 24 | 12.5 |
| | 30 | < 75 | 15 | 13.3 |
| | 30 | > 75 | 35 | 8.6 |
| Vendace | 20, 30 | 112–280 | 27 | 40.7 |

## Prey volume

Although the prey volume seemed to decline from late June–early July in smelt collected in shallow waters, there were no significant differences in means of stomach content volume either seasonally or between the two depth levels considered (Fig. 6). On the other hand, for vendace there were large seasonal and some depth level differences evident. Seasonally, a significant decline in mean stomach volumes occurred between June and mid August followed by an increase again in September/October. For the two depth zones there were significantly higher stomach volumes in vendace from > 25 m in the latter half of July, and in those at < 25 m from the latter half of August to October (Fig. 6). For vendace, midday mean volumes were significantly greater than midnight ones for June, the first half of July, the latter half of August, September and October (Table 6). Furthermore for most cases except in August, and for both times of day sampled, vendace mean stomach volumes were greater than those of smelt, likely a result of the larger body size and hence stomach size of vendace.

There were significant differences in smelt mean stomach volume for the daytime Nitrolit collections among the four depths sampled (Table 7). The small size group of smelt taken at 20 and 30 m had about double the mean volume of those from 5 and 10 m, but the larger size group had no significant differences in mean stomach volume among depths. The few vendace taken had small volumes of prey in their stomachs.

## Total prey numbers in vendace and smelt

Over the June to October sampling period, means for total prey numbers taken by vendace and smelt greatly declined (Fig. 7), in smelt from over 250 in June and the first half of July to below 25 in the latter half of August, September and October. Mean number of prey taken by vendace showed a similar seasonal decline from the June peak of nearly 3000 to below 250 from mid-July through August and in October. Mean prey numbers taken by vendace were higher than those of smelt during all sampling periods except 16–31 August and 29 October (Fig. 7).

## Major prey used by vendace and smelt

Throughout the summer and into early autumn, bosminids were the major prey item for vendace, forming from nearly 40%–80% of total prey taken. Except for the latter half of July, when bosminids still contributed close to 50% of their diet, vendace used bosminids more heavily than did smelt, significantly so in four out of the seven time periods (Fig. 8). Daphnids were significantly the more abundant prey taken by vendace in June and the first half of July, were nearly equal contributors in the second half of July, and they again became significantly greater contributors to smelt diet in the first half of August, a pattern continued into late summer. Small diaptomids (mainly *Eudiaptomus gracilis*) were minor prey items until the latter half of August when their contribution increased on into autumn, especially so in the vendace diet. This same pattern was followed for the large calanoids (mainly *Heterocope* and *Limnocalanus*) that became the major prey for both species of

**Table 6**. Mean stomach volume (ml) for vendace and smelt gillnetted near midday and midnight in limnetic waters of Lambarfjärden, Lake Mälaren, 1968. Asterisks indicate significant differences between midday and midnight stomach volumes within each species.

| Species | Time and number | Period | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | June | 1–15 July | 16–31 July | 1–15 Aug. | 16–31 Aug. | Sep. | Oct. |
| Vendace | midday | 0.45 | 0.29 | 0.10 | 0.03 | 0.10 | 0.15 | 0.22 |
| | *n* | 29 | 43 | 35 | 40 | 32 | 47 | 39 |
| | midnight | 0.20 | 0.14 | 0.05 | 0.04 | 0.02 | 0.04 | 0.11 |
| | *n* | 25 | 99 | 24 | 34 | 19 | 16 | 25 |
| | | * | * | | | * | * | * |
| Smelt | midday | 0.09 | 0.06 | 0.02 | 0.04 | 0.01 | 0.02 | 0.02 |
| | *n* | 5 | 4 | 2 | 19 | 11 | 11 | 5 |
| | midnight | 0.19 | 0.05 | 0.02 | 0.03 | 0.02 | 0.01 | 0.02 |
| | *n* | 7 | 44 | 31 | 35 | 39 | 11 | 13 |
| | | | | | | | * | |

**Table 7**. Mean stomach volume (ml) for smelt and vendace taken by Nitrolit sampling at selected depths in Lambarfjärden, Lake Mälaren, 30 August 1968, 09:10–15:00.

| Species | Total length (mm) | Sampling depths (m) | | | |
|---|---|---|---|---|---|
| | | 5 | 10 | 20 | 30 |
| Smelt | < 75[a] | 0.014 | 0.017 | 0.035 | 0.028 |
| | *n* | 9 | 14 | 13 | 13 |
| | > 75[b] | 0.015 | 0.032 | 0.014 | 0.022 |
| | *n* | 3 | 6 | 20 | 31 |
| Vendace | 112–280 | – | – | 0.011 | 0.004 |
| | *n* | 0 | 0 | 8 | 8 |

[a] ANOVA among depths $p = 0.0001$; [b] ANOVA among depths $p = 0.0993$.

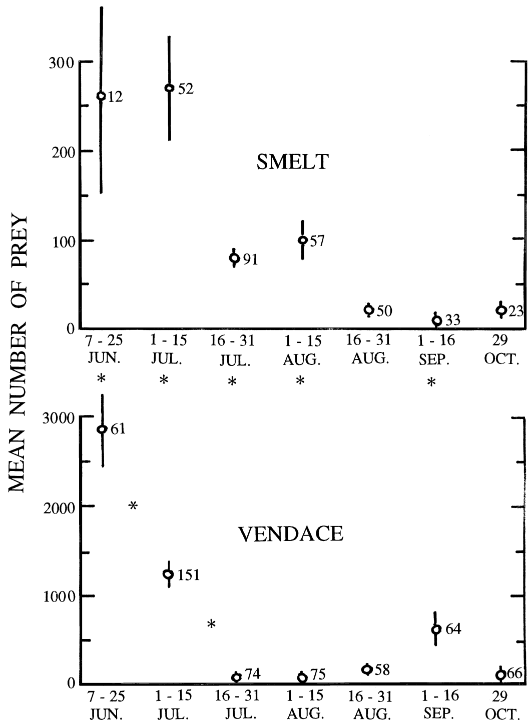


**Fig. 7**. Seasonal change in mean number of total prey taken by gillnet captured smelt and vendace, Lambarfjärden 1968. Vertical lines give standard error of means; asterisks between means for species and those between smelt and vendace below upper date periods show significant differences ($p < 0.05$); numbers beside means give sample size.

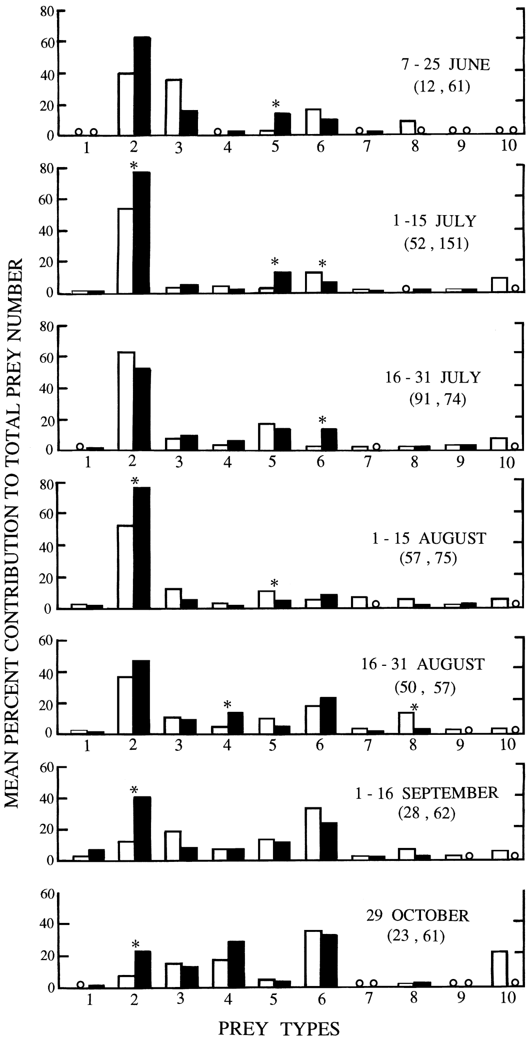


**Fig. 8**. Mean contribution (%) of ten prey types — arranged roughly in an increasing size order; 1 = chydorids, 2 = bosminids, 3 = cyclopoids, 4 = diaptomids, 5 = daphnids, 6 = large calanoids, 7 = large cladocerans, 8 = *Monoporeia affinis*, *Mysis relicta*, 9 = insects, 10 = fish — to total prey numbers taken by smelt (blank) and vendace (solid) during summer to autumn 1968 in Lambarfjärden. * = significant difference ($p < 0.05$) between smelt and vendace using arcsin data transformation; numbers in parentheses beneath dates give sample sizes for smelt and vendace respectively; o = not present.

fish in October (Fig. 8). For the most part large crustacean prey, especially *Monoporeia affinis* and *Mysis relicta*, were major contributors to smelt diet, and rarely were taken by vendace in small numbers. Fish only appeared in the diet of large smelt, but could not be identified to species.

The smallest limnetic cladoceran in the zooplankton community of Lambarfjärden, *Chydorus sphaericus* (Table 1) and also the least abundant one, was never used as a major prey item by smelt or vendace (Fig. 8). But the next smallest cladoceran, *Bosmina longispina*, moderately abundant throughout the July to September sampling period (Fig. 1), was the major prey item for both species from early June through August and well into September for vendace (Fig. 8), and was in most cases taken in greater abundance by vendace (significantly so in four out of seven sampling periods). Large calanoid copepods, especially *Limnocalanus macrurus*, moderately abundant at all sampling depths from July to October (Fig. 2) were important prey for both vendace and smelt throughout the study period, and especially so from mid August to late October (Fig. 8), a pattern also followed by intermediate sized diaptomid copepods. Cyclopoid copepods (D, E in Fig. 2), of intermediate size 0.66 to 1.01 mm and moderately abundant until early August, were taken by vendace and smelt on all sampling dates, in greater numbers by smelt in five out of seven of them (Fig. 8), even when they were taken in very low abundance or absent in the zooplankton samples from September to November (Fig. 2).

### Diet overlap

The Schoener overlap index was used to compare relative contributions to smelt and vendace of five major taxa of zooplankton prey — bosminids, cyclopoid copepods, small diaptomids, daphnids, and large calanoid copepods (Table 8). The other taxa could not be included because their infrequency of occurrence especially in vendace, and irregularity of occurrence in smelt could not be accommodated in the calculations. Zooplankton diet overlap between smelt and vendace was lowest in June, but even then over 66%, and rose to virtually 80% or more for five of the six other summer and autumn time periods.

## Discussion

Four obligate zooplanktivorous fishes occur in the limnetic waters of Lambarfjärden — smelt, vendace, bleak *(Alburnus alburnus*), and three-spine stickleback (*Gasterosteus aculeatus*) — and three partial zooplanktivores as juvenile fish or as periodic visitors — perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*), and roach (*Rutilus rutilus*). In late August 1960, our Nitrolit sampling in the limnetic waters of Lambarfjärden, probably much less species- and size-selective than gillnetting, indicated that smelt were the most abundant zooplanktivore then, followed by vendace. Of 2085 fish caught by trawling at Lambarfjärden in October/November of 1989/1990 99.23% were smelt and only 0.24% vendace, the remainder being a few ruffe (*Gymnocephalus cernuus*), pikeperch and bream (*Abramis brama*) (Pettersson 1991). By the late 1980s and early 1990s the abundance of vendace in central parts of Lake Mälaren including Lambarfjärden was greatly reduced as a result of low recruitment (trawl catches: Pettersson 1991; echo-sounding: Nyberg *et al*. 2001), with smelt still in high abundance. In Ivösjön, southern Sweden, vendace also appeared to be far more abundant than smelt as indicated by gillnet catches, but these greatly underestimated smelt abundance as shown by explosive collections (Hamrin 1986).

There were differences in vertical distribution between sub-adult/adult smelt and vendace in the limnetic waters of Lambarfjärden, especially near midday when smelt were more concentrated in deeper water layers than were vendace. Rarely were maximum gillnet catch rates of the two species recorded within the same 10-m depth interval during midday, and their overlap indices averaged less than 60%. On the other hand, in the hours near midnight, through vertical migration towards surface waters, both species broadened their distribution range so maximum catch rates occurred within the same depth interval for at least six of the seven seasonal comparisons, and their spatial overlap indices rose to an average of over 67%, indicative of a significant degree of overlap (Davis and Todd 1998). But overall our intensive vertical gillnet catch data, when combined with information on vertical distribution from echo sounding and Nitrolit collections, suggest that these two limnetic zooplanktivorous

**Table 8**. Diet overlap indices[a] for subadult/adult smelt and vendace use of zooplanktonic taxa[b] in the limnetic waters of Lambarfjärden, Lake Mälaren, from June to October 1968.

| Monthly period | Number examined | | Diet overlap index[a] |
|---|---|---|---|
| | Smelt | Vendace | |
| June | 12 | 61 | 67.7 |
| 1–15 July | 52 | 151 | 79.7 |
| 16–31 July | 91 | 74 | 84.2 |
| 1–15 August | 57 | 68 | 80.0 |
| 16–31 August | 50 | 57 | 84.7 |
| September | 28 | 62 | 74.8 |
| October | 23 | 61 | 83.5 |

[a](Schoener 1970); [b](bosminids, cyclopoid copepods, small diaptomids, daphnids, large calanoid copepods); *see* text for details.

fishes showed no sharp spatial segregation in open waters of Lambarfjärden over the summer to autumn seasons of 1968, either by day or night. Autumn 1989 and 1990 trawl catches of 0+ to 4+ and older smelt in Lambarfjärden (Pettersson 1991) were small in the uppermost 0–10 and 10–20 m layers, and peaked at 22–25 m, with vendace being taken in low numbers only between 17–25 m. In general the available data indicate considerable overlap of the two species in pelagic waters of Lake Mälaren.

In the several Scandinavian lakes where spatial distribution of cohabiting vendace and smelt have been studied in limnetic waters there is considerable overlap of these two species from late spring to autumn, but generally with smelt being more abundant in deeper layers and vendace mainly in the upper 20 m (Almer and Larson 1974, Nilsson 1979, Filipsson 1983, Hamrin 1986, Sandlund 1992). In Polish lakes, vendace and smelt schools were usually at 20 to 30 m during the day but dispersed at night to cover much of the water column (Dembinski 1971).

Sub-adult to adult vendace in Lake Mälaren had at least ten more gillrakers than the smelt, and other features of their raker morphology that might promote better prey retention (smaller base spacing, posterior projections). Vendace therefore may be a more effective zooplanktivore (Nilsson and Pejler 1973, Svärdson 1976, Nilsson 1978) and select a different species or size range of prey, thereby reducing competitive interactions with smelt. Laboratory observations show 0+ vendace to be a cruising predator whereas smelt act as an ambush or intermediate predator (Karjalainen *et al.* 1997b). Many studies have noted that smelt feed on *Mysis relicta* whereas vendace and planktivorous whitefish do not (Huitfeldt-Kaas 1917, Hammar 1988, Sterligova *et al.* 1995). More experimental studies of feeding behaviour and gillraker function are needed to better understand this particular aspect of smelt and vendace feeding and its possible interactive significance.

Surprisingly, prey absence in the stomach rarely seems to be considered as a piece in the puzzle of sorting out potential competitive interactions in cohabiting fishes. However, information first is needed on stomach evacuation rate for prey in relation to time intervening between prey capture, fish capture, temperature, and stomach preservation. For our Lambarfjärden samples, time between fish capture and stomach preservation was at most three hours and often two hours or less. Vendace can have high evacuation rates (Enderlein 1981b), with only 25% to 35% of most zooplankton prey remaining in the stomach following a 2–3 hour interval after consumption. Sterligova *et al.* (1995) suggested earlier hours of feeding peaks for smelt than for vendace after recording remains of prey only in the posterior part of the intestine of smelt caught with a trawl at 11:00, whereas in vendace food was still found in the stomach. Specimens captured by Nitrolit charges should have most of the prey remaining in the stomach on preservation as the interval between capture and preservation was only a few minutes. If similar stomach evacuation rates prevailed for smelt and vendace, then the gillnet catches in the upper 25 m indicated similar percentages of empty stomachs for the two species — 19.1 and 22.9, respectively. For catches in the 25–50 m zone the percentage of empty stomachs was nearly double that for vendace compared with smelt. The Nitrolit collections showed over a three times higher percentage of empty stomachs in vendace as compared with that in smelt in the 20–30 m zone, suggesting that smelt may be more active deepwater zooplanktivores than vendace.

Although being the second smallest among the recorded cladocerans, *Bosmina longispina* was the most abundant prey found in sub-adult to adult vendace and smelt throughout the summer season, and for vendace also in September–October. Obviously both species of fish showed a preference for *Bosmina* even when its numbers became greatly reduced towards late summer and autumn. The significance of *Bosmina* as prey for small-sized coregonids has been pointed out in many other studies (ref. in Hammar 1988). Towards the end of the summer season both smelt and vendace shifted gradually over to a diet of large and intermediate sized calanoids, likely reflecting the increasing dominance of these copepods among the available zooplankton. The five largest species of cladocerans ranging from 0.8 to 1.8 mm, several of them moderately abundant, were of only minor use as prey by vendace and smelt.

Throughout July and August the planktivorous stages of Lambarfjärden smelt and vendace had a diet overlap index ranging from 80%–85% for zooplanktonic prey taxa, declining slightly in autumn months but still above the 60% level considered to indicate strong interaction (Wallace 1981). The same index exceeded 70% for a similar spectrum of prey taxa used by the smelt and vendace in Lake Vänern (using data from Nilsson 1979).

High diet overlap in terms of indicating severity of competitive interaction is open to widely varying interpretation. One view is that high overlap values simply indicate use of a superabundant food resource with little competitive interaction (Degerman *et al*. 2000, Hammar 2000). Another is that high overlap values represent strong exploitation competition as a negative influence, the view adopted for cisco feeding on zooplankton with lake whitefish (Davis and Todd 1998), for rainbow smelt feeding interactions with yellow perch (Hrabik *et al*. 2001), and possibly applicable to those of Lambarfjärden limnetic smelt and vendace feeding. The prerequisite for these interactive indications may be a restricted food supply. However in the mesocosm field experiments of Davis and Todd (1998), zooplankton prey was not considered to be in short supply, and yet the negatively affected cisco consumed less and grew less when in the presence of lake whitefish where the mean prey overlap index was 89%. The Schoener overlap index in fish diet also has been used to evaluate competitive potential between bluegill and gizzard shad (De Vries and Stein 1992), and to determine if dietary patterns of cisco reflected temporal variation in their vertical distribution (Aku and Tonn 1999). Field mesocosm and laboratory behavioural experimentation are needed to resolve the question of whether or not competitive feeding interaction occurs between smelt and vendace in Lake Mälaren and elsewhere.

Small cladocerans, especially *Bosmina*, were major summer prey components for both smelt and vendace in Lambarfjärden, but usually more so for vendace. Copepods, notably the large calanoids (*Heterocope*, *Limnocalanus*) were major autumn prey for both smelt and vendace. Large profundal crustaceans (*Monoporeia affinis*, *Mysis relicta*) were frequently used by smelt but rarely by vendace in Lambarfjärden. In Lilla Ullevifjärden, a tributary system to Mälaren, copepods (*Cyclops* and *Limnocalanus*) were the dominant prey for both smelt and vendace (Hammar 1968), followed by cladocerans (*Bosmina*, *Daphnia*) for late spring and summer months. In Lake Vänern (Nilsson 1974, 1979), the late summer to autumn prey of smelt and vendace showed minor differences in relative use of the cladoceran and copepod prey components — smelt feeding to a lesser extent on small cladocerans and more on larger copepods. In the large Norwegian Lake Mjøsa, smelt diet included bosminids, daphnids, the copepods *Limnocalanus macrurus* and *Cyclops*, *Mysis relicta*, and fish, with that of vendace by the same cladocerans and copepods but no mysids and fish (Huitfeldt-Kaas 1917, Sandlund *et al*. 1987). Young smelt in the pelagic zone of three Finnish lakes (Karjalainen *et al*. 1997a) preyed mainly on copepods whereas juvenile vendace preferentially selected cladocerans (largely *Daphnia* and *Bosmina*). Also in Oulujärvi, a lake in Finland, the diet overlap of small-sized smelt and vendace caught by trawling in September was 51%, with pelagic *Daphnia longispina*, *Bythotrephes longimanus*, *Bosmina kessleri* and *Leptodora kindtii*, being their joint major prey, and the differences explained by the discrepancy in depths during their peak foraging hours (Sterligova *et al*. 1995). In the Norrbotten part of the Gulf of Bothnia, Sweden (Enderlein 1981b), *Eurytemora* spp. and *Limnocalanus grimaldi* were important prey throughout summer and autumn for both smelt and vendace, along with *Bosmina (E.) longispina*, though in August it was more abundant (> 70%) in vendace than in smelt (< 20%). Large prey there such as mysids and fish were only found in smelt.

In general, information on limnetic prey use by sub-adult to adult North American smelt *Osmerus mordax* (given without reference to that of cisco/lake herring *Coregonus artedii* if cohabiting) — Schneberger (1937), Gordon (1961), Burbridge (1969), Foltz and Norden (1977), Selgeby *et al*. (1978), Stedman and Argyle (1985), Evans and Loftus (1987), Lantry and Stewart (1993) — was similar to that outlined above for European smelt. So too was that of sub-adult/adult stages of the North American counterpart to vendace, *C. artedii* (Engel 1976, Barnhisel and Harvey 1995, Johnson and Kitchell 1996, Link 1996, Aku and Tonn 1999).

In conclusion a few final comments can be made on the feeding ecology of this cohabiting species pair. First one should note that evidence of predation by older smelt on 0+ vendace may be underestimated or missed by rapid stomach digestion and evacuation at the higher temperatures of summer. Even in our stomach sampling and quick preservation which was done within two to three hours after fish capture, fish remains in stomachs usually could not be identified later to species or size.

In Lake Mälaren smelt and vendace both have gillraker numbers and characteristics of zooplanktivores, and are strong zooplanktivores over much of their life span (all of it for vendace). Furthermore smelt can reach very high population densities there, greatly outnumbering vendace. These features alone would suggest that competitive interactions between this limnetic species pair may be severe unless one or both exploit means of mitigation such as spatial, temporal, or prey type/size segregation (Nilsson 1967, 1978, Enderlein 1981a). Results of our study indicate that all of these mitigatory means are at best only partial. Although vendace have a higher number of gillrakers than smelt with narrower spacing as well as other morphological features that might help in small prey capture, the smelt do not seem to have difficulty preying on most of the same small zooplankters that are taken by vendace. With regards to spatial segregation in Lambarfjärden limnetic waters where both species occur closely together horizontally, one might have expected to find strong vertical stratification. Such was not the case. Nor did there seem to be much evidence of temporal segregation between the two species in the pelagic zone, except for smelt during the day being slightly lower than vendace. Explanations for the long-term co-existence of these two highly zooplanktivorous species awaits more experimental field work such as that by Davis and Todd (1998), and more laboratory research such as that by Karjalainen *et al*. (1997a, 1997b) on their interactive behaviour. The significance of mysid predation on zooplankton, and its interactive impact on zooplanktivorous fish (Hammar 1988), along with its role as a regulator of the balance between smelt and vendace (Svärdson *et al*. 1988) should also contribute to the understanding of the interactive ecology of smelt and vendace.

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