Food selection and feeding behaviour of Baltic Sea mysid shrimps

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This thesis is based on the following papers, which are referred to by their Roman numerals:


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INTRODUCTION

Mysids – a link between lower trophic levels and fish

Mysid shrimps (Malacostraca, Peracarida, Mysidacea) are common crustaceans which inhabit various aquatic environments, including oceans, estuaries and other brackish water ecosystems as well as freshwater lakes. They are highly adaptive species and therefore also good invaders of new areas (Ketelaars et al. 1999). Most of the species are marine (~95 %), some live in brackish water and a few species occur in freshwater environments. Furthermore, some have become adapted to live in caves and wells and a few live in commensal association with other animals. Some species burrow into the sediment, live just above it or migrate between bottom and surface waters, a few are strictly pelagic species and some live in shallow water in the littoral zone (Mauchline 1980).

In the Baltic Sea, there are currently at least 20 species of mysids, of which over half live only in the area near the entrance to the Baltic Sea, where the salinity is close to oceanic salinity levels (Köhn 1992). Only 7 species occur east or northwards of the Arkona Sea. *Mysis mixta* Lilljeborg and the two sibling species of *M. relicta* Lovén (I and II; Väinölä 1986), are pelagic species. The other four, *Neomysis integer* (Leach), *Praunus flexuosus* (Müller), *P. inermis* (Rathke) and *Hemimysis anomala* G.O. Sars, which is a recent invader from the Pontocaspian region to the northern Baltic (Salemaa & Haitalahti 1993), live more or less in the littoral zone, among macroalgae, in crevices along rocky shores, or on sandy beaches (Fig. 1). The distribution of mysids is mainly regulated by salinity, temperature and the depth of the water column, and they seem to avoid areas where oxygen concentration is low at the bottom (Ackefors 1969, Salemaa et al. 1986).

Mysids utilise a diversity of foods during their life cycle, which spans from a few months to two years (e.g. Lasenby & Langford 1973,
Mauchline 1980, Grossnickle 1982, Rudstam et al. 1989, Toda & Wada 1990, Kjellberg et al. 1991, Hakala et al. 1993, Cartes & Sorbe 1998, Chapman & Thomas 1998, Branstrator et al. 2000). They have species-specific feeding modes (Mauchline 1980) and some species can switch from one feeding mode to another when food availability changes (Viitasalo & Rautio 1998). They feed on small particles such as phytoplankton, rotifers, small cladocerans and detritus, by creating a suspension feeding current, or feed raptorially, i.e. actively capturing selected prey from the environment. By utilising both pelagic and benthic food sources, they provide an energy link between these environments. Together with planktivorous fish, e.g. herring (Clupea harengus) and sprat (Sprattus sprattus), mysids have a strong influence on Baltic zooplankton populations (Hansson et al. 1990a, Rudstam et al. 1992, Thiel 1992, 1996, Johannsson et al. 1994, Aaser et al. 1995, Almond et al. 1996). In the northern Baltic, during autumn, mysids and planktivorous fish have been shown to consume over 50% of the zooplankton production (Hansson et al. 1990a, Rudstam et al. 1992). Furthermore, in autumn they compete for food with fish and may thus have the potential to influence the food gain of other pelagic zooplanktivores (Rudstam & Hansson 1990).

Mysids are prey for many larger predators globally, such as invertebrates, various fish (Thiel 1996, Hostens & Mees 1999), birds and seals (Mauchline 1980), thereby linking primary and secondary production to higher trophic levels. In the Baltic Sea, mysids are eaten, for example, by adult herring (Aneer 1980, Aro et al.
of Finland, while *M. relicta* is dominant in the Bothnian Bay (Salemaa et al. 1986, 1990, Simm & Kotta 1992). In the northern Baltic, both species favour deep (>50 m) and cold water with a high oxygen content. In the southern parts, *M. mixta* is also found in more shallow areas (Salemaa et al. 1990). *M. relicta* is sensitive to sudden temperature changes and therefore stays in deeper, more stable water (Holmquist 1962).

*Mysis*-species are nectobenthic crustaceans which perform diurnal vertical migrations. They remain near the bottom during daytime and rise at dusk towards surface waters to forage. At dawn, the mysids descend to escape visual predation by fish such as herring (Mauchline 1980, Bowers & Vanderploeg 1982, Grabe & Hatch 1982, Rudstam et al. 1986, 1989). Pelagic mysids are adapted to living in a dark environment and their eyes are easily damaged by strong light (Lindström 2000). Thus, the main regulating factor for this vertical migration is light and mysids are shown to avoid light levels exceeding $10^{-4}$ lux (Rudstam et al. 1989).

**Pelagic mysids: Mysis mixta and M. relicta**

The present distribution of the species reflects their biogeographical history. *Mysis relicta* is a glacial relict (Segerstråle 1957, Holmquist 1962), inhabiting both brackish and freshwater environments in the northern hemisphere. The Baltic *M. relicta* have been subdivided, on the basis of electrophoretic findings, into two sibling species, that partly co-occur in the northern Baltic Sea (Väinölä 1986). The *M. relicta* that are found in the study area belong to sibling species II (Väinölä 1986). *M. relicta* is most abundant in the northern Baltic and is not regularly found to the south of 56°N or nor to the west of 18°30´E (Salemaa et al. 1990). *M. mixta* is of Atlantic origin and favours more saline water than *M. relicta*. In the Baltic, *M. mixta* is widely distributed except for in the Bothnian Bay, where low salinity limits its distribution (Köh 1992). It dominates the *Mysis*-populations in the Gulf

**Littoral mysids: Praunus flexuosus**

*Praunus flexuosus* is of north-Atlantic origin and belongs to the marine-euryhaline and eurythermal species. It can tolerate salinities from 3.5 to 37 ‰ (Mclusky 1979) and temperatures from 3 to 22 ºC (Väkipakka 1990). *P. flexuosus* are commonly found from the southern Baltic to the northern parts, with the exception of Bothnian Bay (Köh 1992). In the northern Baltic Sea, they live in salinities from 3 to 7 ‰ and in temperatures between 4 and over 20 ºC. They occur in shallow water, in inshore habitats, mainly among *Fucus vesiculosus* and *Zostera marina* vegetation, where they form small shoals (Hällfors et al. 1975, Väkipakka 1990). *P. flexuosus* migrates horizontally in late summer from shallow (0-1 m) to deeper water (5-15 m), to avoid warm temperatures (>20 ºC). They overwinter in deeper areas and migrate back to inshore habitats in spring after the ice break-up.
Macroalgal vegetation offers *Praunus* spp. a good feeding ground with various phyto- and zooplankton species (Nordström 1997). *P. flexuosus* swim in small swarms and rest in an upright position among algae (Mauchline 1980). They follow algal vegetation zones in their distribution but they are also to be found on bare sand and sandy mud bottoms (Välipakka 1990).

**Northern Baltic plankton community and food availability of mysids**

The plankton community, including both phyto- and zooplankton, changes with the seasons. Most of the phytoplankton species show great year-to-year variations, which cannot be directly associated with changes in the hydrography and nutrient levels (Kononen & Niemi 1984). However, some trends are obvious in the succession of species. In spring, the phytoplankton is composed of large diatoms and dinoflagellates, which form strong spring blooms in the surface waters (Niemi 1975, Kononen & Niemi 1984, Heiskanen 1995). After the bloom, vegetative cells and resting cysts of diatoms and dinoflagellates settle (Heiskanen & Kononen 1994, Kremp & Heiskanen 1999) and constitute a major food source for benthic animals (Kupari et al. 1984), including mysids. During the summer, sedimentation is at its lowest, while autotrophic and heterotrophic pico- and nanoplankton become dominant in the pelagial (Niemi 1975). Thus, summertime is favourable for pelagic feeding of mysids, whereas suspension feeding on detritus at the bottom is more difficult, due to low sedimentation. In late summer, the occurrence of filamentous cyanobacteria increases, of which the most common species are *Aphanizomenon flos-aquae*, *Nodularia spumigena* (Sivonen et al. 1989) and *N. sphaerocarpa* (Lehtimäki et al. 2000). When the weather is calm, water warm and phosphorus available, cyanobacteria may form massive, potentially toxic blooms (Kononen et al. 1996). Cyanobacteria are known to be poor quality food that not all zooplankters can use (Reinikainen et al. 1995, Koski et al. 1999a, Engström et al. 2000). Therefore, the abundance of cyanobacteria in late summer does not improve the food availability for mysids in the Baltic.

In early summer, after the spring bloom, the first zooplankton taxa which increase in numbers are the rotifers (Lignell et al. 1993). Thermal stratification during summer leads to an increase in zooplankton biomass in the pelagic zone. The rotifers are followed by cladocerans and copepods, which are most abundant in warmer waters (Viitasalo et al. 1995, Koski et al. 1999c). For zooplanktivorous mysids the food availability is thus good throughout the summer period, until waters start to cool down in late autumn.

The most abundant mesozooplankton species in the northern Baltic are the rotifer *Synchaeta baltica*, the cladoceran *Bosmina longispina maritima* and the copepods *Acartia* spp., *Eurytemora affinis* and *Temora longicornis* (Hernroth & Ackefors 1979, Viitasalo 1992, Viitasalo et al. 1995, Uitto et al. 1997, Koski et al. 1999c). These zooplankters perform vertical migrations within the upper water layer during summertime. In the Gulf of Finland, the migration is mainly regulated by light (Burris 1980). The grazing activity of the dominant cladocerans and copepods also shows variation between day and nighttime. It is most active during night, in the upper water layer, where edible food for zooplankters is abundant (Uitto 2000). The vertical migration of zooplankters affects pelagic mysids that also migrate in search of food.

**Previous studies on the feeding of Baltic mysids**

Most of the studies on mysid feeding have dealt with freshwater *M. relicta* (e.g. Cooper & Goldman 1980, Lasenby & Fürst 1981, Bowers & Vanderploeg 1982, Johannsson et al. 1994, Almond et al. 1996), which have been introduced to many large lakes to increase fish production.
In the Baltic Sea, studies have mostly concentrated on *M. mixta*. The first studies analysed the diet from dissected stomach samples (Rudstam *et al.* 1989, 1992, Hansson *et al.* 1990b) and subsequent ones have mainly dealt with experimental work on functional responses (Mohammadian *et al.* 1997) and on factors affecting feeding rates of *M. mixta* (Gorokhova & Hansson 1997, Hamrén & Hansson 1999). The next phase in the diet studies were investigations with stable isotope analyses and isotope fractionation, which enable reconstruction of the diet from muscle, exuvia and faeces samples (Rolff *et al.* 1993, Hansson *et al.* 1997, Gorokhova & Hansson 1999).


The main conclusion of studies on mysid diets is that they are omnivorous and capable of utilising a wide variety of food sources, depending on food availability. On the other hand, at least *M. mixta* and *P. flexuosus* are predominantly carnivorous and discriminate between cladocerans and copepods. Table 1. shows the previous Baltic feeding studies of the three mysid species: *M. mixta*, *M. relicta* and *P. flexuosus*. My studies add to the previous body of knowledge the aspect of seasonal change in the diet, prey selection and in the effect of environmental factors on feeding success. In addition, the influence of cyanobacteria on the feeding and survival of mysids is studied for the first time.

<table>
<thead>
<tr>
<th>Species</th>
<th>What was studied?</th>
<th>Diet</th>
<th>Prey used</th>
<th>Preferred prey</th>
<th>Selectivity index</th>
<th>Method used</th>
<th>Other findings</th>
<th>Area</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. mixta</em></td>
<td>Stomach contents</td>
<td>Zpl, less detritus and plant mat.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Field animals, stomach anal.</td>
<td>Coastal NBp</td>
<td>1989</td>
<td>Rudstam <em>et al.</em> 1989</td>
</tr>
<tr>
<td><em>M. mixta</em></td>
<td>Stomach contents</td>
<td>Zpl, mostly copepods</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Field animals, stomach anal.</td>
<td>Coastal NBp</td>
<td>1989b</td>
<td>Hansson <em>et al.</em> 1990b</td>
</tr>
<tr>
<td><em>M. mixta</em></td>
<td>Stomach contents</td>
<td>Zpl</td>
<td>-</td>
<td>Cladocerans</td>
<td>Chesson’s electivity index</td>
<td>Field animals, stomach anal.</td>
<td>Coastal NBp</td>
<td>1989</td>
<td>Rudstam <em>et al.</em> 1992</td>
</tr>
<tr>
<td><em>M. mixta</em></td>
<td>Effect of exp. conditions on feeding</td>
<td>-</td>
<td>Artemia, Daphnia</td>
<td>-</td>
<td>-</td>
<td>Lab. exp.</td>
<td>Light, exp. duration, starvation prior exp. affect feeding rates</td>
<td>Coastal NBp</td>
<td>Gorokhova &amp; Hansson 1997</td>
</tr>
<tr>
<td><em>M. mixta</em>, <em>M. relicta</em></td>
<td>Stable nitrogen isotope ratio</td>
<td>Zpl, phytopl</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Field animals, 815N measured</td>
<td>Coastal NBp</td>
<td>1997</td>
<td>Hansson <em>et al.</em> 1997</td>
</tr>
<tr>
<td><em>M. mixta</em></td>
<td>Isotope fractionation</td>
<td>Mesozpl, maybe detritus</td>
<td>Artemia or detritus Eucyclopsoma</td>
<td>-</td>
<td>-</td>
<td>Lab. exp.</td>
<td>Isotope composition in muscle, exuvia, feaces; diet reconstruction</td>
<td>Coastal NBp</td>
<td>Gorokhova &amp; Hansson 1999</td>
</tr>
<tr>
<td><em>M. mixta</em></td>
<td>Effect of herring on mysid feeding</td>
<td>-</td>
<td>Artemia</td>
<td>-</td>
<td>-</td>
<td>Lab. exp.</td>
<td>Herring decreased feeding</td>
<td>NBp</td>
<td>Hamrén &amp; Hansson 1999</td>
</tr>
<tr>
<td><em>P. flexuosus</em></td>
<td>Stomach contents</td>
<td>Zpl, phytopl, detritus, allochthonous mat.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Field animals, stomach anal.</td>
<td>Coastal GF</td>
<td>1997</td>
<td>Nordheim 1997</td>
</tr>
</tbody>
</table>

**Table 1.** Earlier studies on the diet and prey selection of mysids (*Mysis mixta*, *M. relicta* and *Praunus flexuosus*) in the Baltic Sea. Only results concerning feeding of mysids are included in the table, other parts of the papers’ results are excluded. zpl = zooplankton, phytopl = phytoplankton, NBp = Northern Baltic proper, GF = Gulf of Finland.

(Lasenby *et al.* 1986). In the Baltic Sea, the studies have mostly concentrated on *M. mixta*. The first studies analysed the diet from dissected stomach samples (Rudstam *et al.* 1989, 1992, Hansson *et al.* 1990b) and subsequent ones have mainly dealt with experimental work on functional responses (Mohammadian *et al.* 1997) and on factors affecting feeding rates of *M. mixta* (Gorokhova & Hansson 1997, Hamrén & Hansson 1999). The next phase in the diet studies were investigations with stable isotope analyses and isotope fractionation, which enable reconstruction of the diet from muscle, exuvia and faeces samples (Rolff *et al.* 1993, Hansson *et al.* 1997, Gorokhova & Hansson 1999).

Growth of mysids

Crustaceans periodically moult their whole exoskeleton during growth. The moult-cycle has profound effects on many aspects of the function of the animal. In northern regions, such as in the Baltic, low temperatures may inhibit mouling, and hence growth, during late autumn and winter (Mauchline 1980). Juvenile mysids grow by shedding their exoskeleton at intervals which become progressively longer as they approach maturity (Clutter & Theilacker 1971).

Ingested food is partitioned to various components of growth. In freshwater *Mysis relicta*, about 14% of the ingested food goes to somatic growth, 4% to reproduction, 67% to respiration and 15% to mouling and egestion (Mauchline 1980). Partitioning depends upon the ambient temperature as well as on the species and sex of the animal. When the bodyweight of the mysid increases, the energy consumption also increases. The energy consumption is 1.5 times higher for adults than for juveniles (Gorokhova 1998). As the mysid grows, however, the energy losses to metabolism increase faster than consumption, resulting in a smaller proportion of the energy being available for growth (Gorokhova 1998).

In the northern Baltic Sea, pelagic mysids (*Mysis mixta* and *M. relicta*) usually have a one-year life cycle (Rudstam et al. 1986). The young are released in early spring, after the ice breakup. New juveniles grow during summer and autumn and start to breed during late autumn. Ovigerous females carry their brood for 4 to 5 months and begin to release them during early spring. The growth of the juveniles is most rapid during summer, when adults are scarce and food is abundant (Salemaa et al. 1986, Rudstam & Hansson 1990).

In the northern Baltic, the littoral mysid *Prawnus flexuosus* usually produces one summer generation per year. However, several broods are produced, because embryogenesis in littoral mysid marsupium only takes about three weeks. In contrast to the *Mysis* species, littoral mysids do not carry broods during the winter (Salemaa, H., University of Helsinki, personal communication).

In the northern Baltic, winter is an unproductive time and the mysid population is at its minimum (Salemaa et al. 1986, Rudstam & Hansson 1990). The maximal growth rate is only 1% of the body weight for *M. mixta* and this decreases continuously during autumn and winter until April, when it is only 0.05% of the body weight for females (Gorokhova 1998).

Mysids can utilise many food sources and food abundance might be a less important factor regulating their growth than food quality. There is no information available on the effects of food quality on the growth of mysids but general trends can be derived from studies on copepods and cladocerans. The effects of food quality upon the growth rates of marine invertebrates can be measured by many different criteria, for example, by the chemical (C:N or C:P ratio) or mineral content of food or by its toxicity (Kiørboe 1989, Jónasdóttir 1994, McKinnon 1996, Sanders et al. 1996, Lindley et al. 1997, Koski et al. 1999b).

Maintenance, growth and reproduction demand different food qualities. Maintenance metabolism requires primarily energy, while growth requires many other essential elements (Sterner & Robinson 1994). Food quality affects the growth of marine crustaceans via mouling and weight (Chen & Folt 1993, McKinnon 1996). Poor quality food is noted as being almost as bad as starving in regard to growth, if no other supplementary food is available (Chen & Folt 1993). Food that is known to be toxic or of poor quality, if offered alone, may however, be a useful supplement in mixed diets. Koski et al. (1999b) found that a toxic prymnesiophyte contained some specific, nutritionally important components which were lacking from other algae and thus copepods produced more eggs on a mixed diet than on any of the algae alone. Similar results are also shown with mixed diets containing cyanobacteria and diatoms (Schmidt & Jónasdóttir 1997). Thus, omnivory may be a
good strategy to optimize nutritional needs for both growth and reproduction.

Conceptual background

The function of an aquatic system depends on a complex web of interactions that includes both numerical and behavioural responses of both predator and prey species. Predation directly influences the next trophic level and its effects may ‘cascade’ to the trophic levels that are further away (Carpenter et al. 1985). In feeding theory, the most important aspect is optimisation; how can animals optimise their feeding towards the maximum energy gain, which can then be allocated to maintenance, growth and reproduction, which all demand different food qualities? The concepts which are relevant to my studies are briefly reviewed below, mainly from the point of view of a predator.

Optimal foraging theory

Most animals have the capability to consume a wider range of prey than they actually choose. According to the optimal foraging theory (MacArthur & Pianka 1966, Hughes 1980), a predator should maximise the overall net energy intake per unit of time. This is a question of whether to invest energy for searching for the most profitable prey or to eat everything ‘in the way’ and spend no energy on searching. The optimal forager balances these two alternatives and, depending on the availability of different prey, selects the best prey (Landry 1981). Large prey may be the best energetically, but they may also be the most difficult to catch, handle and ingest (Pastorok 1981). Nutritional benefit can also be maximised by food selection based on the nutritional quality, which includes digestibility and nutritional value. The optimal forager should discriminate against toxic food, e.g. cyanobacteria, since ingestion would be deleterious even when other food is not available (De-Mott & Moxter 1991). Optimal foraging includes, in addition to the selection of the best prey items, also the choice of the best feeding techniques and foraging locations. To maximise the net energy gain throughout its life cycle, the forager should modify all these choices according to changing conditions (Hughes 1980). Mysids are omnivorous and may therefore select prey items and feed according to the optimal foraging theory.

Functional responses

Changes in prey densities affect predator’s consumption rates and this relationship is known as the predator’s functional response (Solomon 1949). Different responses were classified into three types by Holling (1959). The feeding response adopted by a predator in relation to the abundance of prey is important for the stability of predator-prey relationships. These three types of functional response may have either stabilising or destabilising effects on the population dynamics of prey species. All the functional response types have a phase of increasing ingestion and at a certain prey concentration, the feeding saturates (Fig. 2). Type II functional response occurs if the time spent handling the prey determines the maximum ingestion rate (Chigbu & Sibley 1994). Ingestion rate, therefore, smoothly approaches a plateau, determined by the number of handling times that can be fitted into the total time available. At high prey densities, type II and type III responses are similar. At low densities, the type III curve has an accelerating phase, where an increase in prey density leads to a more than linear increase in ingestion rate. A type III functional response may occur if there is switching between prey species (Gismervik & Andersen 1997) or if the ability of the predator to capture prey increases with the number of encounters with the prey (prey density) (Landry 1981). The optimal forager switches prey when the abundance of the most profitable prey decreases, and switches to another prey, which has
become the more abundant (Abrams 1986). A type IV functional response also exists (Fig. 2, Wootton 1999), which was not included in the original classification by Holling (1959). Type IV response is similar to type II but after the plateau level has been reached, the type IV ingestion curve starts to decrease (Wootton 1999). This could be the type of response, for example, for planktivores feeding on cyanobacteria, when the continual feeding clogs the feeding appendages of animals and thus starts to decrease the feeding efficiency.

I studied the functional responses of *M. mixta* in relation to the changing natural prey assemblages from summer to autumn. Functional responses for the total prey community indicate the overall feeding patterns of the studied predators but the influence on individual prey species cannot be elucidated.

**Predation cycle**

The predation cycle consists of several steps, which combine to produce the outcome of the predation trial (O’Brien 1986). Differences in predation may be due to optimal choice by the predator or differing vulnerabilities of prey or both (Pastorok 1981). The optimal strategies and prey also differ for predators having different feeding strategies (cruising vs. ambush predators; Gerritsen & Strickler 1977, Hughes 1980). The predation cycle begins with the location of the prey item. Visually hunting predators, such as fish, locate prey from a distance, whereas non-visual predators such as mysids, locate their prey by mechanoreception, i.e. from hydromechanical signals that the prey create when moving through the water (Zaret & Kerfoot 1975, Drenner et al. 1978, Gardner 1981). Several physical and behavioural traits influence the location process. Pelagic prey may reduce the possibility of being located by being small (O’Brien et al. 1976, Gardner 1981, Pastorok 1981, Gerritsen 1984, Greene 1986) and transparent (Thetmeyer & Kils 1995), by decreasing ingestion and thus gut pigmentation (Tsuda et al. 1998, Cieri & Stearns 1999) and by moving smoothly and slowly through the water (Gerritsen 1984, Tiselius et al. 1993). Vertical migration to darker water layers also decreases the risk of being detected by predators (e.g. O’Brien 1986, Leibold 1991).

From the predator’s point of view, the encounter rate of prey is important and varies with swimming speed (Evans 1989, Kiørboe & Vissing 1999). Fast swimming prey are encountered more often and therefore they are also detected more frequently (Gerritsen & Strickler 1977, Gerritsen 1984, Tiselius et al. 1993). When a prey has been located, the predator has the choice of either pursuing it or continuing to search for a better prey (Hughes 1980). If the predator decides to try to capture the prey, the pursuit and

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**Fig. 2.** Idealised functional responses (types I, II, III and IV) (Wootton 1999). $N_A$ = Number of prey ingested, $N$ = Density of prey.
attack phase start. After attacking the prey, the escape response of the prey determines the success of the attack. Escape responses of prey differ very much (e.g. Lonsdale et al. 1979, Greene & Landry 1985, Browman et al. 1989, Viitasalo et al. 1998). Cladocerans and rotifers generally have weak escape responses compared to copepods and, therefore, they usually rely more on being undetectable (Greene 1986). Capturing is followed by handling and finally ingestion of the prey item. Prey may make it impossible for the predator to handle and ingest it by, for example, being spiny (Walls & Ketola 1989), excreting a mucus sheet (Kitchell & Carpenter 1986), growing a helmet (Havel 1986), or by producing chemical defences (Scrimshaw & Kerfoot 1986). Chemical factors are also important when the predator suspension feeds on algae and tries to avoid toxic species. Avoidance happens when an algal cell, filament or colony has been captured and the predator discriminates against toxic forms and avoids their ingestion (DeMott & Moxter 1991). This is beneficial for both the predator and the toxic algal population.

Ramcharan et al. (1985) showed that the controlling factor of a mysid’s prey preference is the capture success of different prey. Mysids prefer prey that move slowly and are therefore easy to capture (Nero & Sprules 1986). Three other factors in addition to mechanical capture and handling efficiency are known to affect the prey selection of M. relicta: the vigour of prey escape response, predator-prey encounter frequency and the availability of prey (Cooper & Goldman 1980). In my work, predation efficiency and prey selection of the pelagic M. mixta were studied using natural prey assemblages. Also, the avoidance of toxic algae was studied with toxic and non-toxic cyanobacteria.

**Trade-offs**

Life-history traits are often compromises. Individuals need to decide whether to invest more energy in one trait or another. Trade-offs are benefits for fitness gained from one process at the expense of another (Colinvaux 1986, Stearns 1989, Begon et al. 1990). The most prominent life-history trade-offs involve the cost of reproduction. The trade-off may be intra-individual, between reproductive effort made by a female in one season and the probability that she will survive to the next season to breed again, or it may be intergenerational; between a female’s reproductive effort and the probability that her offspring will survive to the next season (Stearns 1989). My study concentrated on intra-individual trade-offs.

Predators can influence prey communities through selective predation, affecting the behavioural patterns of prey and forcing them to avoid predation by hiding or escaping more vigorously or by changing their habitats (Sih 1986). Predation avoidance is costly for prey (Power 1986) and thus less energy is left for other functions, such as growth, which in turn affects feeding through body size. In aquatic systems some prey species perform diel vertical migration (DVM) to avoid predation (e.g. Zaret & Suffern 1976, Ghan et al. 1998), which is energetically costly (Lampert 1989, Dodson 1990, Fiksen & Carlotti 1998). The costs of DVM are reduced growth and fecundity (Pastorok 1981, Lampert 1989). However, DVM may also benefit migratory animals. It has been suggested that DVM provides a metabolic or demographic advantage and also that, by migration from the food rich surface waters, predators give the phytoplankton community an opportunity to grow and recover from intensive foraging (Lampert 1989, review).

Pelagic mysids migrate vertically through the water column to minimise the risk of being eaten by visually hunting fish and to maximise food intake (Mauchline 1980, Bowers & Vanderploeg 1982, Rudstam et al. 1986, 1989). In my thesis the effect of light on the feeding rates of both pelagic and littoral mysids was studied and the probable trade-off between the minimisation of predation risk and the maximisation of feeding was discussed.
OBJECTIVES OF THE STUDY

Mysids are an important part of the Baltic food web and the zooplankton community. Their feeding and ecology are studied mainly because of their importance as a food source for various fish species (Aneer 1980, Bowers & Vanderploeg 1982, Aro et al. 1986, Rudstam et al. 1986, 1989, Rudstam & Hansson 1990, Arrhenius & Hansson 1993, Aarnio et al. 1996). Previous studies have investigated their feeding and also their effect on the zooplankton community, upon which they feed. This thesis contributes to our knowledge of mysids by taking into account the seasonal aspect, which greatly affects feeding through the growth of the mysids and through the seasonal succession of plankton communities. Therefore, I have concentrated my studies on the three seasons which cover the most efficient growth period for both pelagic and littoral mysids: spring, summer and autumn (Salemaa et al. 1986, Rudstam & Hansson 1990, Aaser et al. 1995).

I studied the diet, prey selection and growth of pelagic mysids, and also the effects of some environmental factors (light and cyanobacteria) on mysid feeding rates by collecting samples from the field and by conducting experiments in the laboratory. The first two studies are based on field data. Paper I is about the diet change of the pelagic mysids, M. mixta and M. relicta during their growth from spring to autumn. This was undertaken in order to gain knowledge of the food items actually consumed in natural conditions and how the diet changes. Stomach analyses have been done previously from Baltic M. mixta (Rudstam et al. 1989, Hansson et al. 1990b, Rudstam et al. 1992) but not from M. relicta. In study II, the influence of food quality (phyto- vs. zooplankton and benthic vs. pelagic food) on the growth rate of M. mixta was studied. It is important to take food quality into consideration when studying growth, because it also has a major influence on growth at the population level. The other three manuscripts are based on laboratory experiments on animals collected from the field. Study III deals with prey selection and functional responses in natural prey assemblages during summer and autumn. I wanted to know how the change in natural prey composition affects the predation rates and responses of mysids during their growth period.

Light is an important environmental factor, which clearly influences mysid behaviour by increasing the risk of predation by visual predators. In the fourth study (IV), the aim was to determine the effects of light on both pelagic and littoral mysids’ feeding rates. I wanted to know if the response of mysids to increasing light and predation risk would be different in different habitats.

In the fifth study (V) the effects of both non-toxic (Aphanizomenon flos-aquae and Nodularia sphaerocarpa) and toxic strains (Nodularia spumigena) of Baltic cyanobacteria on mysid feeding and survival were studied. This has not been previously undertaken, and because cyanobacteria blooms are a common phenomenon in late summer and seem to be increasing (Kahru et al. 1994), it is important to investigate their effects on common planktivores, including mysids. A feeding experiment with better quality food (green flagellate Brachionus submara-rina) was also conducted, to see if the mysids feed more actively on high quality food, than on cyanobacteria. The approaches and experimental set-ups are summarised in Table 2.
MATERIAL AND METHODS

Study area

The Baltic Sea is one of the largest brackish water areas in the world. It is a semi-enclosed and shallow (mean depth 55 m) sea, surrounded by a large catchment area. It is characterised by strong seasonality and vertical thermal and salinity stratification, partial ice-cover during winter and lack of tidal movements. Salinity is regulated by river discharge and saline water pulses from the North Sea (Ackefors 1969, Segerstråle 1969). Saline water pulses occur irregularly and quite rarely, depending upon meteorological conditions in the Danish Straits (Hänninen et al. 2000). The large salinity gradient between the Bothnian Bay in the north and the Danish Straits in the south results in the establishment of different species compositions. Species inhabiting the Baltic Sea are mainly either of marine or fresh water origin, even though true brackish water species are also to be found. In the brackish water, most of the species live at

<table>
<thead>
<tr>
<th>Mysid species</th>
<th>Time</th>
<th>What was studied</th>
<th>No. of exp./sampling</th>
<th>Time of the exp.</th>
<th>Zpl / Phytopl. µg C l⁻¹</th>
<th>No. of replicates</th>
<th>Study</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. mixta</td>
<td>June (\text{to September} ) 1997</td>
<td>Diet</td>
<td>7</td>
<td>-</td>
<td>-</td>
<td>10</td>
<td>I</td>
</tr>
<tr>
<td>M. mixta</td>
<td>June (\text{to September} ) 1997</td>
<td>Food quality and growth</td>
<td>7</td>
<td>-</td>
<td>-</td>
<td>10</td>
<td>II</td>
</tr>
<tr>
<td>M. mixta</td>
<td>June to October 1998</td>
<td>Prey selection and functional responses</td>
<td>5</td>
<td>12 h</td>
<td>Varying concentrations</td>
<td>3 - 6</td>
<td>III</td>
</tr>
<tr>
<td>M. mixta</td>
<td>July to October 1999</td>
<td>Effect of light</td>
<td>3</td>
<td>2 - 6 h</td>
<td>Acartia 90 µg C l⁻¹</td>
<td>3 - 5</td>
<td>IV</td>
</tr>
<tr>
<td>P. flexuosus</td>
<td>June and August 1999</td>
<td>Effect of cyanobacteria on feeding</td>
<td>3</td>
<td>3 h</td>
<td>Different cyanobacteria 50-350 µg C l⁻¹ Acartia 60-209 µg C l⁻¹</td>
<td>5</td>
<td>V</td>
</tr>
<tr>
<td>M. mixta</td>
<td>September to October 1999</td>
<td>Effect of cyanobacteria on survival</td>
<td>1</td>
<td>7 weeks</td>
<td>-</td>
<td>6</td>
<td>V</td>
</tr>
</tbody>
</table>

Table 2. Experimental designs and study purposes of the field and laboratory studies presented in the thesis. Exp. = experiment, Zpl = zooplankton, Phytopl. = phytoplankton.
the limits of their distribution and often suffer from osmotic stress (Aniansson 1990). Therefore, there are only a few species of both algae and animals that live permanently in the Baltic and thus food webs are often shorter and less complex than in the oceans.

Studies for this thesis were undertaken at the entrance to the Gulf of Finland, in the northern Baltic Sea (Fig. 3). The coastal area is characterised by thousands of islands and a very complex shore and bottom topography (Pitkänen 1999). In the study area, there is no permanent halocline, the average salinity of the water is 6‰ (Kuparinen et al. 1984), and a thermocline is formed during the summers. In the sampling area, hydrographical variations are regulated by meteorological conditions and mesozooplankton community dynamics are regulated by changes in water temperature and salinity (Viitasalo et al. 1995).

Pelagic mysids living in deeper water, mainly below the thermocline (Rudstam et al. 1989), were sampled from open exposed sea areas from the Ajax deep (59°43N, 23°13E) (depth 80 m) and Längden (depth 60 m), situated to the south of the Tvärminne Zoological Station (TZS), on the Hanko Peninsula (Fig. 3). The bottom is mainly soft, with a high organic content in the surface sediment. Littoral mysids were collected from a shallow, more sheltered area (mean depth 1-2 m), a rocky shore near the Zoological Station. The shoreline is rocky and the hard bottom mainly covered with Fucus vesiculosus vegetation.

Fig. 3. Map of the study area showing the mysid sampling stations at Längden and Ajax and the zooplankton sampling station at Storfjärden, in the Gulf of Finland, northern Baltic Sea. TZS = Tvärminne Zoological Station.

Sampling

Sampling of the pelagic mysids, M. mixta and M. relicta, was done at nighttime, during darkness, to prevent possible eye damage (Lindström 2000). Pelagic mysids were collected with a large plankton net, with a mesh size of 0.5 mm, diameter of 0.8 m and length 3 m, which was lowered near the bottom and then lifted slowly to the surface. In studies IV and V, mysids were also collected using an epibenthic sled, which was drawn along the bottom for 10 minutes and then slowly lifted up. Littoral mysids were collected with an arm net, which was pulled through F. vesiculosus algae in the littoral zone (depth 1-2 m) (IV).

The samples for the diet analyses (I and II) were preserved in 4 % buffered formaldehyde (final conc.) immediately after sampling. Mysids for the experiments (III, IV and V) were placed into insulated containers with cold seawater from below the thermocline. Within an hour, the
mysids were transported to a temperature-controlled room (13 °C), maintained in darkness from 22.00 to 06.00. The mysids were gently transferred to 0.2 μm filtered seawater with a sieve and a pipette. The mysid species were identified and kept in aerated filtered seawater without food, for 24 h before the experiments.

Zooplankton for the studies was collected using a 100 or 200 μm mesh zooplankton net from the same place as the mysids (III) or from Storfjärden (I, IV and V), a 35 m deep archipelago area (Fig. 3). A larger mesh-size net was used for the last studies (IV and V), because only copepods were needed in the experiments.

Field studies

Field data was used in studies I and II for the stomach and growth analyses. First, all mysids were measured from the tip of the rostrum to the end of the telson and their stage of sexual maturity was recorded. Second, to identify the food particles in the stomachs, the mysids were carefully dissected, the stomachs and their contents transferred onto a glass slide (Nordström 1997), and observed with an inverted microscope (100× to 400× magnification). 50 individual food items were identified from each stomach. *Mysis mixta* was abundant in every sample and 10 stomachs were examined for each size class from June to September. In contrast, *M. relicta* was rare throughout the summer and therefore, all of the *M. relicta* stomachs were studied. Altogether 180 *M. mixta* and 74 *M. relicta* were analysed.

Laboratory experiments

Experiments were conducted in the laboratory to reveal the prey selection patterns and the effects of light and cyanobacteria on the feeding rates of mysids. Experiments were performed in 1.18 l glass bottles in a slowly rotating (0.5 RPM), plankton wheel, to maintain random distribution of the food particles throughout the duration of the experiments (III, IV and V). Mortality experiments with toxic cyanobacteria (*Nodularia spumigena*) were conducted in 2.2 l aquaria (V). The experiments were performed in a temperature controlled room at 12-13 °C, with a 16:8 h light:dark cycle. The average light level in the experimental bottles (IV) was 12 μE (1 μE = 6.02 × 10¹⁷ qu/m²/s), which corresponds to the level near the thermocline in our study area during summertime (Lindström, M., Tvariinne Zoological Station, personal communication). In the experimental bottles and aquaria, there was always one mysid per bottle and a counted/measured amount of zooplankton or algae (Table 2).

Statistical analyses and equations

Parametric tests were used when the assumptions of normal distribution, homogeneity of variances and independency of observations were fulfilled or when the data could be transformed and thus meet these assumptions (Zar 1999). These tests include two factor analysis of variance (ANOVA) on log (x+1) transformed data (IV), 1-way and 2-way ANOVA and regression analysis (V). When parametric tests could not be used, the analyses were done using non-parametric tests: Mann-Whitney U-test (I, V), Wilcoxon signed ranks test (I, II, V), Fisher’s exact test (III), Spearman correlation test (III) and the Scheirer-Ray-Hare test (V).

In study II, the length distributions of mysid populations were separately studied for every sampling day, to elucidate their different growth lines. The best-fit distributions were counted for the mysid population using the MIX programme (an interactive program for fitting mixtures of distributions; Macdonald & Green 1988). The program analyses histograms as mixtures of statistical distributions, that is, by finding a set of overlapping component distributions that gives the best fit to the histogram.
The equations, which were used in this thesis, are the following:

The percentage overlap of diets \((P_{jk})\) of the mysid species (I) was counted with the Schoener overlap index (Schoener 1970):

\[
P_{jk} = \left[ \sum (\text{minimum } P_{ij}, P_{ik}) \right] \times 100
\]  

(1)

where \(P_{ij}\) and \(P_{ik}\) are proportions of resource \(i\) (i.e. a certain food item/particle) of the total resources used by (mysid) species \(j\) and species \(k\) or size classes, and \(n\) is the total number of resource states (i.e. all food particles).

Probable nitrogen limitation of mysids (II) was calculated according to Urabe & Watanabe (1992) who showed how to estimate a theoretical maximum for food C:N ratio, above which the consumer is nitrogen limited. The equation is as follows:

\[
Q^*_{c-e} = \frac{Q_{z-e}}{K_c}
\]  

(2)

where \(Q^*_{c-e}\) is the maximum elemental ratio of food (here C:N), \(Q_{z-e}\) is the elemental ratio of the consumer (C:N) and \(K_c\) is the gross growth efficiency of the consumer in carbon. We used a \(K_c\) of 0.22, derived from annual production and consumption estimates (g C m\(^{-2}\) yr\(^{-1}\)) for Mysis mixta in the northern Baltic proper (Rudstam et al. 1986).

The chi-squared based selectivity index \(C\) by Yate’s correction for continuity (Pearre 1982) (III) was calculated for every prey group in the natural zooplankton assemblage, to find out the selection intensity for different prey:

\[
C = \pm \left( \chi^2 / n \right)^{1/2} \text{ or } C = \pm \left[ \left( \sum_{a,b,d,e} (a \cdot b - e)^2 / abde \right) - n/2 \right]^{1/2}
\]  

(3)

where

<table>
<thead>
<tr>
<th></th>
<th>Species</th>
<th></th>
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<tbody>
<tr>
<td></td>
<td>A</td>
<td>Others</td>
<td>Total</td>
<td></td>
</tr>
<tr>
<td>Diet</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>a(_d)</td>
<td>b(_d)</td>
<td>a(_d) + b(_d) = d</td>
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<tr>
<td>Environment</td>
<td>a(_e)</td>
<td>b(_e)</td>
<td>a(_e) + b(_e) = e</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>a(_d) + a(_e) = a</td>
<td>b(_d) + b(_e) = b</td>
<td>a(_d) + a(_e) + b(_d) + b(_e) = n</td>
<td></td>
</tr>
</tbody>
</table>

The selectivity index was calculated for each prey group, to determine the selection intensity for different prey, using the average abundance percentages derived from the carbon contents of prey in the diet and in the environment.

RESULTS AND DISCUSSION

Food utilisation during growth

Generally, mysids feed omnivorously on phyto- and zooplankton and also on benthic material (I) when staying near the bottom during daylight hours. Pelagic mysids (Mysis mixta and M. relicta) grow rapidly from being a few millimeters in length in spring, to two centimeters in autumn and their nutrition changes along with growth (I, II and III). Diet change may be due to two important reasons. First, the availability of different plankton groups in the Baltic Sea changes during the course of the year (Niemi 1975, Viitasalo et al. 1995, Uitto et al. 1997, Koski et al. 1999c). Second, small mysids are less able to capture evasive zooplankton species than larger individuals (e.g. Cooper & Goldman 1980). Therefore the small size of the mysids, together with the early summer’s plankton community, forces the diet to differ compared to that of large sized mysids’ with late summer/autumn plankton availability. During the first months of the life of a mysid, the food available mainly consists of diatoms, dinoflagellates and rotifers.

The seasonal stomach content analyses showed clear changes in the utilised food. In June, the 4 to 7 mm long M. mixta foraged almost exclusively on phytoplankton, mainly settled diatoms and other benthic phytoplankton particles (I). This is consistent with the stomach analyses of M. relicta in Stony Lake (Lasenby & Langford 1973), which showed that small individuals eat only algae and detritus. Generally, phytoplankton biomass is at its minimum in July (Niemi 1976), whereas the abundance of cladoceran and copepod species is close to their maxima (Viitasalo et al. 1995). Therefore,
zooplankton availability is high for the mysids that are capable of capturing them. Notably, the share of copepods in the diet increased strongly in August, simultaneously with their increased abundance in the water. Also, the utilisation of pelagic food increased steadily from early summer to autumn. This was probably due to the change in food availability, the growth of mysids and the change in light conditions during the seasons. In early summer, the water column is more illuminated and settled diatoms offer a good food supply for small mysids. Towards autumn, the light level decreases, which further reduces the predation risk and the pelagic plankton community is feasible for large mysids.

Comparison of the diets of pelagic *Mysis*-species revealed a distinct difference (I). *M. relicta* utilised more phytoplankton and benthic food than *M. mixta* (Fig. 4). The difference was evident throughout the study period, but it was largest in the middle of the summer, in July and August, when *M. relicta* fed on average 90% on benthic material. The reason for *M. mixta*'s more carnivorous diet could be its larger size in the study area and the reason for its more pelagic feeding habits, its vertical migration to upper waters compared to the vertical migration of *M. relicta* (Salemäa et al. 1986).

**Fig. 4.** The monthly averages of (A) zooplankton:phytoplankton ratio and (B) pelagic:benthic ratio in the diet of *Mysis mixta* and *M. relicta*. Symbols denote the means and vertical lines denote standard deviations.

The growth rate of *M. mixta* varied during the study period (II). In June, the juvenile population had a unimodal size distribution but, in the middle of July, a part of the juvenile population started to grow faster (Fig. 5). These two different parts of the population had different diets; the smaller cohort fed on average 50% on zooplankton and 6% on pelagic material, and the larger ones 75% and 27%, respectively. Thus, the difference is clear in both diet components.
At the beginning of July, when the two cohorts started to grow at different rates, both cohorts changed their diets to a more zooplanktivorous composition. However, the larger and more zooplanktivorous cohort grew more rapidly than the smaller, less zooplanktivorous cohort. The larger cohort kept its growth rate steady until September, after which their growth slowed down. The growth of mysids seems to be associated with the amount of zooplankton in their diet. Animal food may nutritionally be of better quality for mysids than phytoplankton or detritus, as has been suggested for copepods (e.g. Conover & Corner 1968, Corner et al. 1976, Heinle et al. 1977, Stoecker & Capuzzo 1990). For instance, it is known that green algae (Dunstan et al. 1992) and cyanobacteria (Reinikainen et al. 1995, Koski et al. 1999a) are not high quality foods compared to zooplankton or dinoflagellates. Also decomposing benthic material, for example, detritus and diatoms, can be low quality food compared to fresh pelagic material (e.g. Stoecker & Capuzzo 1990, Dittel et al. 1997, Lehtonen 1997). Therefore, it is suggested that the mysids that fed on pelagic food and zooplankton grew more rapidly than the benthic feeders and phytoplankton grazers.

I suggest that, at the beginning of July, mysids at the larger end of the size distribution started to be large enough to capture zooplankters, and thus gain more protein and amino acid rich animal food (Stoecker & Capuzzo 1990, a review). In contrast, the rest of the population continued to feed mainly on phytoplankton (decomposing diatoms, cyanobacteria and green algae) and their growth rate remained lower than that of individuals already feeding raptorially, which may provide more energy per unit time than phytoplankton grazing. This may be because of differences in migration behaviour. Some mysids have spent more time near the bottom, whereas other mysids have migrated to the upper water column, where zooplankters are available. After gaining this growth advantage, the larger mysids have continually better chances to capture larger prey than smaller mysids have (Cooper & Goldman 1980), which further separates their size distributions and, hence, their diets. In August, the mysids of the smaller cohort also reached the threshold size for zooplankton feeding (freshwater, *Mysis relicta* > 7 mm, Grossnickle 1982), their growth rate consequently increased and in mid-September the two cohorts again united. Thus, at the beginning of September, the size frequency distribution was again unimodal (Fig. 5). There was a fairly close relationship between the pelagic feeding habits on zooplankton and mysid size. Since the pelagic particles in late summer and autumn were mostly zooplankton, we suggest that *M. mixta* needed to attain a threshold size in order to start effective feeding on zooplankton.

This diversified feeding may be beneficial for the mysids, because it is likely to reduce intraspecific competition for food (Hughes 1980) and thus increase survival during the growth period. Omnivorous feeding habits of mysids may also benefit the plankton community since, as many different species are fed upon, it is unlikely that any of the prey species is foraged too intensively for a long time. If certain prey become scarce, mysids probably switch to other more abundant prey.

**C:N ratio**

Generally, a low C:N ratio of food indicates good food quality (Kiorboe 1989, McKinnon 1996, Lindley et al. 1997). However, while some studies show a strong effect of both mineral and chemical composition of food on reproductive success (Kiorboe 1989, Jonasdottir 1994, Kleppel et al. 1998, Koski et al. 1998) or growth (Sterner 1997, Schulz & Sterner 1999) of zooplankton, in other studies such an effect has not been observed (e.g. Sanders et al. 1996).

A few studies have investigated nitrogen and carbon content of mysids. Donnelly et al. (1993) measured the C:N ratio of three mysid species (*Eucopia sculpticauda, E. unguiculata, Gnath-
ophausia ingens) in the Gulf of Mexico. Compared to these values (5.9 to 7.3), my values for Baltic *M. mixta* are very low (3.3 to 4.0) but similar to Gorokhova’s (1999) results for juvenile *M. mixta* (3.8) in the northern Baltic proper. I also attempted to estimate the nitrogen limitation of *M. mixta*. According to Urabe and Watanabe (1992), it is possible to estimate a theoretical maximum for the food C:N ratio, above which the consumer is nitrogen limited. My results indicate that mysids are not limited by nitrogen in the northern Baltic and that the C:N ratio of food does not explain the different growth rates of the two cohorts of pelagic mysids during summer (II). Food quality, and thus growth, may also depend upon other essential components, such as unsaturated fatty acids (Tang & Dam 1999, Anderson & Pond 2000). Knowledge of the role of essential fatty acids for mysids is lacking and therefore conclusions about their influence on mysid growth cannot be drawn. However, omnivory, which confers a higher probability of obtaining all the required nutrients, probably provides a better quality diet for mysids than phytoplankton or detritus alone, as several studies have shown with other marine invertebrates (e.g. Conover & Corner 1968, Heinle et al. 1977, Gifford & Dagg 1988, Stoecker & Capuzzo 1990, review).

The main conclusions of the studies I and II, are that both food availability and mysid growth probably affect the diet composition of *Mysis* species in the northern Baltic Sea. The mysids that feed on pelagic food and zooplankton grow more rapidly than the benthic feeders and phytoplankton grazers, which is consistent with earlier findings concerning copepods (e.g. Heinle et al. 1977, Stoecker & Capuzzo 1990, review). Both of the pelagic mysid species are omnivorous and the same diet shift from phytoplankton and benthic material to zooplankton and pelagic material occurs during mysid growth. However, there is a clear difference between the diets of these species. *M. mixta* utilises more zooplankton and pelagic food than *M. relicta*. This may reduce competition between mysids living in the same deep-water areas in the northern Baltic Sea.

**Selective feeding**

By selective predation, invertebrate predators can influence zooplankton communities by controlling population sizes and relative abundances of prey (e.g. Dodson 1974, Murtaugh 1981, Branstator 1995, Spencer et al. 1999). In the Baltic Sea, mysid predation is considered to be an important factor affecting zooplankton communities (Rudstam & Hansson 1990, Rudstam et al. 1992, Thiel 1996). Mysids are omnivorous and their diet usually reflects the availability of different food items (I), but consistent patterns of prey preference have also been detected (III, Rudstam et al. 1992). *M. mixta* selected different prey taxa during their growth period (III). Small mysids do not have the capability of capturing the most evasive prey and therefore their ‘preference’ is probably based on apparent selectivity, i.e. the escape ability of prey regulates their foraging (Greene 1986). Furthermore, capture of large prey requires faster swimming speed, which requires more energy (Buskey 1998), therefore it is not beneficial for small mysids to try to capture large prey if the probability of success is low. Small mysids fed mainly on rotifers during early summer (III), which is probably due to the undeveloped predatory abilities of these mysids (Lasenby & Langford 1973) and could also be a consequence of rotifers being the most abundant taxa in the water. Rotifers do not perform strong escape jumps and are probably captured by filter feeding current (Viitasalo & Rautio 1998). Although the diverse phytoplankton mainly forms the diet of small juveniles (I), providing essential nutrients and fatty acids (Tang & Dam 1999, Anderson & Pond 2000), rotifers are an important additional food (III) in regard to energy, when intensive growth of the juveniles starts (II).

During summer and autumn, the main component of the diet was copepods (I, III). Cope-
pods were abundant and after mysids had attained the threshold size of ~7 mm (Grossnickle 1982), also constituted feasible prey. Thus, mysids feed on larger prey as they grow and their physical capabilities develop, which is in accordance with the optimal foraging theory which states that, most of the time in nature, the net energy gain is of central importance (Hughes 1980). Mysids may also change their diet when a certain prey population becomes too scarce and find some other, more abundant prey instead (Fulton 1982), thus optimising their energy intake. In lakes Tahoe and Michigan, *M. relicta* changes its prey preference depending on the relative abundance of prey species available (Bowers & Vanderploeg 1982, Folt *et al.* 1982).

*M. mixta* feeding was not solely based on the availability of prey items (III). Selection was evident during the summer, but in September and October there was not much difference between the preferences for different prey species (Fig. 5 in III). During autumn, large mysids are apparently capable of capturing almost anything in the water and this may explain the low degree of selection observed. The copepod, *Temora longicornis*, was selected from natural zooplankton assemblage even when it was relatively inabundant. Reasons for this selection could be the large size of this copepod, which makes it interesting as a food item and also creates stronger hydrodynamic signals that non-visual predators can detect (Drenner *et al.* 1978). The other positively selected copepod was *Eurytemora affinis*, although it performs strong escape jumps and is considered a difficult prey to capture (Viitasalo *et al.* 1998). The preference of *M. mixta* for *E. affinis* shows true selection (Greene 1986), despite the expectation of rejection due to its good escape ability. The third most common copepod, *Acartia* sp., was mostly rejected, which may also indicate true selection, i.e. the decision not to pursue. *Acartia* sp. are quite fast escapers, which might be the reason for their rejection (Viitasalo & Rautio 1998). *E. affinis* swims more abruptly, creating larger hydro-mechanical signals compared to *Acartia* (personal observation) and is therefore more easily detected by the mysid.

Cladocerans were neither very abundant nor selected, with the only exception being the species *Evadne nordmanni*, which is large compared to the other cladocerans available (*Bosmina longispina maritima*, *Pleopsis polyphemoides*). Our results indicate that, firstly, the predation success mostly depends on prey escape capabilities and mysids’ ability to capture and handle prey but also that true selection exists for certain prey species. Secondly, that different prey species and groups are important during different phases of the mysids’ growth period.

Changes in prey densities also affect the consumption rates of predators, as described by Solomon (1949) and Holling (1959). Some studies on the functional responses of mysids have been performed in freshwater lakes (e.g. Folt *et al.* 1982, Chigbu & Sibley 1994) and in the Baltic Sea (Mohammadian *et al.* 1997, Viitasalo & Rautio 1998), mostly concentrating on a few prey species at a time. We studied the functional responses and ingestion rate of *M. mixta* with a natural zooplankton assemblage (III). The variation in ingestion rates was best explained by the sigmoidal functional response (type III, Holling 1959) curve, with explanatory levels of 86 to 97%. The sigmoid functional response may occur if the ability of the predator to capture prey increases with the number of encounters with the prey (prey density, Landry 1981). The month of June was the only exception, when the saturation levelled out already at a food concentration of 50 µg C l⁻¹ and the functional response did not fit properly to any of the types of functional response curves. In June, the mysids were small (average 5 mm) and their natural diet mainly consisted of phytoplankton (I). This was not offered in these experiments and therefore the ingestion rate stayed at a very low level despite the increased zooplankton concentration.

The ingestion rate increased with increasing zooplankton concentration, until the saturation level was reached. This level occurred at between 400 and 500 µg C l⁻¹, depending upon the month.
If we compare the ingestion rate of *M. mixta* and the average zooplankton density in the Baltic (~40 μg C l⁻¹, Mohammadian *et al.* 1997), we can conclude that mysids cannot saturate their feeding, unless they are able to detect and forage in denser zooplankton patches. In dense patches, however the saturation is possible, since zooplankton densities as high as 850 ind. l⁻¹ have been observed in the southern Baltic (Kils 1992).

**Effects of environmental factors on feeding success**

**Abiotic factors: the effect of light**

Many physical factors, such as salinity, temperature (DeGraeve & Reynolds 1975, McLusky 1979, Mauchline 1980) and oxygen concentration (Ackefors 1969, Salemaa *et al.* 1986), have a strong influence on the survival, distribution and behaviour of mysids. Environmental factors also affect predation rates and prey-capture ability. Increased temperature is shown to increase the movement and feeding rate of mysids up to a certain limit, after which their mortality starts to increase (DeGraeve & Reynolds 1975, Chipps 1998). However, the most important physical environmental factor which governs the behaviour and distribution of mysids, is light (Mauchline 1980). In general, mysids are attracted to weak sources of light but avoid bright light. Bright light often inhibits the swimming activity (Mauchline 1980) and swarming behaviour (Steven 1961), and may damage their large, sensitive eyes (Lindström 2000). Light is an important factor controlling the vertical migration of pelagic mysids (e.g. Rudstam *et al.* 1989). It is usually assumed that mysids do not require light to capture prey but rather use mechano-reception to locate moving plankton (Cooper & Goldman 1980, Murtough 1981, Viitasalo *et al.* 1998). If mysids benefit from hunting in the more illuminated, upper water column, there should be a trade-off between the maximising of feeding rate in the upper water column and the minimising of the risk of predation (e.g. Zaret & Suffern 1976, Loose & Dawidowicz 1994). In contrast, littoral mysids are used to a very broad light spectrum in shallow water and are therefore well adapted to the light level (Lindström 2000).

The difference between mysids living in the pelagial and in the littoral was clear from their feeding rates in light and in darkness (IV). Littoral mysids fed at the same rate despite the prevailing light conditions and, in addition, the feeding was not affected by changes in the natural light conditions during the course of the seasons. The treatments did not thus have any influence on the feeding rates of *P. flexuosus*, whereas the body mass of mysids affected their feeding efficiency. Littoral mysids do not perform vertical migrations to avoid bright light but escape visually hunting fishes by hiding among the macroalgal vegetation. Predation avoidance does not necessarily, therefore, interfere with the feeding of these mysids, because they can continue capturing prey and suspension feeding among the algae.

In contrast, pelagic mysids were clearly affected by light during the experiments. They suppressed their feeding rate in light and fed at a higher rate in total darkness. *M. mixta* is shown to be able to detect a chemical substance released by herring and then decrease its feeding (Hammén & Hansson 1999). In our study, this could not be the reason for suppressed feeding, because no predators were kept in the experimental water. The reason for this suppressed feeding could be an endogenous reaction to avoid moving in well-lit water, even when predators are not present.

The ingestion rate of *M. mixta* differed significantly between the three experimental periods, being lowest during early summer and highest in the autumn. However, the differences in feeding rates of pelagic mysids between experimental periods were small when the ingestion rates were calculated per dry weight of mysids. This shows that pelagic mysids feed at the same rate relative to their body mass throughout their growth period, despite the change in natural light.
conditions with one exception. In July, the ingestion rate of *M. mixta* in light differed considerably from other feeding rates, because no feeding occurred in this experiment.

At the Baltic latitudes, light conditions change from the beginning of summer to late autumn and so mysids are adapted to a decrease in light as the season changes. The duration of the vertical migration changes through the course of the seasons. Pelagic mysids ascend later and descend earlier relative to sunrise and sunset during early summer than in the autumn (Teraguchi et al. 1975, Rudstam et al. 1989). This was expected to be seen in the results of the pelagic mysids, as an increase in the difference of feeding rates in dark and in light towards the autumn. However, no such a trend was observed.

In short, pelagic mysids are more vulnerable to changes in light conditions than littoral mysids and neither of the mysid species benefited from increased light. This suggests that pelagic and littoral mysids rely on mechano-reception for locating and capturing their prey, regardless of the habitat and its natural light conditions.

**Biotic factors: the effect of cyanobacteria**

Pelagic mysids that migrate to the upper water column (Rudstam et al. 1989) frequently encounter cyanobacterial blooms which are common phenomena in the Baltic during late summer (Kahru et al. 1994, Kononen et al. 1996). As omnivorous animals, they probably ingest, either actively or passively, cyanobacteria filaments, in addition to other algae and zooplankton. Cyanobacteria blooms are often toxic (Sivonen et al. 1989) and therefore feeding on these strains may have significant effects on the mysid populations. Generally, mysids are shown to be very sensitive to toxins such as dredge spoil, industrial waste (Nimmo & Hamaker 1982) and pesticides (Robinson 1999) and therefore cyanobacterial toxins may also reduce their survival.

We studied the feeding on both toxic (*Nodularia spumigena*) and non-toxic cyanobacteria (*N. sphaerocarpa* and *Aphanizomenon flos-aquae*) and the effects of aggregate-forming cyanobacteria on the raptorial feeding success and survival of pelagic mysids. Our studies show that *M. mixta* feed on both toxic and non-toxic cyanobacteria. The different strains of cyanobacteria were morphologically similar, all occurring as single filaments since they were grown in culture. Thus, it seems that mysids can recognise the toxins, since the feeding rate on toxic cyanobacteria was always lower than that on non-toxic ones (V). Reduction of feeding rate when alternative food is not available seems to be an adaptive behaviour, which is also found in copepods (Engström et al. 2000). Copepods are known to select less strongly against low quality food when nothing else is available, i.e. high quality food is scarce or absent (DeMott 1995), which may also explain the behaviour of the mysids. Only rarely, is only a single food species available in nature. Even though cyanobacteria is often the dominant species during intensive blooms, there is always something else to feed upon. Only few filaments of cyanobacteria were found in the stomachs of mysids in 1997 (I), when cyanobacterial blooms were especially intense. This shows that mysids can select between toxic cyanobacteria and other food and concentrate on foraging for high quality food. Nevertheless, the feeding rate on better quality food (the green flagellate, *Brachiomonas submarina*) was not different from that on the cyanobacteria in the feeding experiment with *M. mixta*. The small *B. submarina* cells may also be suboptimal food for mysids, as they have been observed to utilise larger algae, e.g. filamentous diatoms in natural conditions (Bowers & Grossnickle 1978, Mauchline 1980).

The avoidance of toxic food was also supported by the mortality experiment, in which the toxic cyanobacteria, *N. spumigena* did not increase the mortality of adult mysids (V). The mortality of mysids fed with daphnids in filtered seawater was not different from the mortality in the water with a bloom concentration of toxic cyanobacteria. This supports the idea that mysids can ac-
tively avoid cyanobacteria filaments in the water when better food is available. Another possibility is that they are resistant to the toxin, which has been demonstrated for the cladocerans *Bosmina longirostris* and *Moina macrocopa*, as well as the rotifer *Brachionus calyciflorus* (Starkweather & Kellar 1983, Hanazato & Yasuno 1987, Fulton 1988). Tolerance to toxins in Baltic mysids could be an evolutionary adaptation in areas where toxic blooms are frequent and animals cannot totally avoid waters with high densities of cyanobacteria filaments. In order to prove this hypothesis, we would need a comparison of mortality rates of animals in toxic cyanobacteria water from an area where cyanobacteria blooms are common (e.g. the Baltic Sea) and from an area where toxic blooms do not occur (e.g. the Atlantic).

Cyanobacteria also have other negative effects. We observed that *M. mixta* fed on *Acartia* sp. at a lower rate in the presence of aggregate-forming *N. sphaerocarpa* than in clear filtered seawater. The reason for this decreased feeding on copepods in the presence of cyanobacteria could be that the mysids also fed on algae. However, this is unlikely because mysids tend to shift their diet to a more carnivorous one when they are large enough to capture, e.g. copepods (I, II). Therefore, the studied mysids (~14 mm long) concentrate their feeding on copepods instead of cyanobacteria. Cyanobacteria filaments have a tendency to form aggregates in the water. These clumps may clog the feeding appendages of mysids and thus hamper their feeding. We observed cyanobacteria filaments in the feeding appendages of every mysid which had been kept in the cyanobacteria water, which shows that aggregates probably interfere with both filter feeding and raptorial feeding during intensive blooms.

Thus, it seems that mysids utilise both toxic and non-toxic cyanobacteria but also avoid the intake of toxin by decreasing ingestion when only toxic cyanobacteria are available. Survival of mysids in the presence of toxic cyanobacteria was high, which further supports the idea that they avoid toxic food when other food is available but it may also be because of tolerance against cyanobacterial toxins. Mysids can reduce their intake of toxins in nature by switching, selective feeding and by avoiding algal bloom areas. Future studies should focus on toxin resistance in combination with feeding selectivity and the potential effect of cyanobacteria on the reproduction of mysids.

**CONCLUSIONS**

The most important findings of my thesis are linked to the seasonal change in both food composition and mysid growth. The pelagic mysids, *M. mixta* and *M. relicta*, fed actively on both phyto- and zooplankton and their diet changed remarkably from small juveniles to mature adults, though being omnivorous at all stages of their life cycle (I). The same shift in the diet also took place when the predatory behaviour of *M. mixta* was studied. Prey selection changed, concentrating at first on rotifers and, after the mysids had attained the threshold size for effective zooplankton capturing, copepods became the most selected prey (III). The growth of *M. mixta* was clearly associated with the proportion of zooplankton food (I, II, III). Increased feeding on copepods in particular increased the growth rate. Two other important findings were firstly, that the response to light differed between pelagic and littoral mysids, probably due to their different ways of predation avoidance, and secondly, that *M. mixta* discriminated between common non-toxic and toxic cyanobacteria and thus, reduced toxin intake. However, cyanobacteria aggregates clogged the feeding appendages of mysids and therefore lowered their feeding efficiency.

Although the pelagic mysid *M. mixta* is omnivorous, it shows some prey preference. The prey selection may be strongest when many different zooplankton groups are available and selection between them is possible. Otherwise, mysids probably feed on other plankters, includ-
ing phytoplankton and do not suffer from severe food shortage (Adare & Lasenby 1994). The influence of mysid predation on the zooplankton community is strongest during summer and autumn, when zooplankton is most abundant, and minimal in spring, when the zooplankton abundance is lower and mysids are small. When the abundance of mysids is sufficiently high, they may stabilise the seasonal fluctuations of zooplankton population sizes in the northern Baltic Sea. The regulating influence on zooplankton populations is especially large when the effect of all planktivores (including planktivorous fish, e.g. herring and sprat) is taken into account (Hansson et al. 1990a, Rudstam et al. 1992).

Mysids utilise several trophic levels during their life cycle, including primary producers, herbivorous and carnivorous secondary producers and decomposers from the sediments. In addition, they have an influence on fish populations both in pelagial and in bottom habitats (Aneer 1980, Rudstam & Hansson 1990, Thiel 1996). Thus, they have a major influence on other trophic levels by acting as both top-down and bottom-up regulators (Fig. 6).

The changing state of the Baltic Sea, including lowered salinity (Hänninen et al. 2000) and increased eutrophication with cyanobacteria blooms (e.g. Kahru et al. 1994, Bianchi et al. 2000), has a strong influence on the plankton communities. For mysids, the most crucial change would be a large change in salinity both in the surface (littoral mysids) and deep waters (pelagic mysids), because species distribution is strongly limited by salinity (Mauchline 1980, Köhn 1992). Changes in hydrographical conditions would also have an influence on the food availability and quality, through changes in plankton communities. Decreasing salinity in the northern Baltic would favour species such as the copepod, *E. affinis*, and some cladoceran and rotifer species (Viitasalo et al. 1995). This would also favour mysids, which feed on rotifers as juveniles and select for *E. affinis* (III, Hansson et al. 1990a) and cladocerans (Rudstam et al. 1992) as adults. The changes in the state of the Baltic Sea also have effects on higher predators, such as fish, which further influence mysid populations through top-down regulation.

Increased nutrient loading (Karjalainen 1999) may have severe effects on both phyto and zooplankton communities. Mysids are also affected by eutrophication of the Baltic. Increasing primary production increases the amount of settling material and thus oxygen consumption near the bottom. In addition, the occurrence of filamentous algae increases, which leads to oxygen depletion in the littoral zone. Mysids are nektobenthic animals and lowered oxygen concentrations near the bottom may force them to change their habitats for better oxygenated areas, since

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**Fig. 6.** The role of pelagic mysids in the food web of the northern Baltic Sea. Light grey arrows in the background indicate energy flows from lower trophic levels, through mysids to fish. Dark grey arrows indicate environmental factors studied in this thesis, which affect the feeding efficiency of mysids.
they avoid anoxic bottoms (Salemaa et al. 1986). Decreasing oxygen near the bottom forces pelagic mysids to feed more in the pelagial and less on benthic material. Furthermore, increasing time spent in the upper water column and decreased possibility to migrate to deeper and darker waters, exposes them even more to fish predation.

In addition, eutrophication decreases light penetration through the water due to increased phytoplankton abundance. This may harm littoral mysids, because decreased light reduces the growth of Fucus vesiculosus (Ruuskanen 2000), which provides important shelter for mysids avoiding predators. Decreased light in the water may benefit pelagic mysids by reducing predation risk, as well as increasing intensity of vertical migration and thus better access to the food supply.

The increased phytoplankton production is another consequence of increased nutrient loading. Nitrogen-fixing cyanobacteria in particular are favoured by increased phosphorous loading (Kononen et al. 1996). Cyanobacteria blooms affect many trophic levels. The effect ranges from increased competition with other algae to potential toxic effects on top predators such as birds (Bianchi et al. 2000), as well as effects upon the mysids themselves. They may feed on cyanobacterial filaments (I, V) primarily, if nothing else is available, or incidentally, while filter feeding on other algae. The discrimination between toxic and non-toxic strains is an important way to increase survival during intensive blooms (V). Cyanobacteria, especially Nodularia spp., which form aggregates, may hamper feeding efficiency of all mysids by clogging their feeding appendages and therefore reducing feeding success.

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