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Antipredator behaviour of Baltic planktivores

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- III Lindén, E. 2006: The more the merrier: Swarming as an anti-predator strategy in the mysid *Neomysis integer*. – Aquatic Ecology (in press).
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Predation is an important source of mortality for most aquatic animals. Thus, the ability to avoid being eaten brings substantial fitness benefits to individuals. Detecting predators and modifying behaviour accordingly are of prime importance in escaping predation. Here I contribute to the study of predator-prey interactions by investigating the different behavioural responses of Baltic planktivores to predation risk. Predator detection abilities and antipredator behaviour were examined in various planktivores, *i.e.* the littoral mysids *Neomysis integer* and *Praunus flexuosus*, three-spined stickleback *Gasterosteus aculeatus* larvae, pelagic mysids *Mysis mixta* and *M. relicta*, and the predatory cladoceran *Cercopagis pengoi*, with cues from their respective predators European perch *Perca fluviatilis* and Baltic herring *Clupea harengus membras*. The use of different aquatic macrophytes as predation refuges by the littoral planktivores was also examined.

All pelagic planktivores and stickleback larvae were able to detect the presence of their predator by chemical cues alone. Even the nonindigenous *C. pengoi*, which invaded the Baltic only 14 years ago, responded to chemical cues from herring, suggesting a general avoidance of any fish species. In contrast, the littoral mysids *N. integer* and *P. flexuosus* responded only when chemical and visual predator cues were combined. Vision is important for littoral mysids in their well-lit shallow-water habitat, whereas pelagic mysids, performing diel vertical migration, spend most of their time in near darkness, and hence the ability to detect predators by chemical cues alone is essential for their survival. The better predator detection abilities of stickleback larvae compared with littoral mysids reflect the more highly developed sensory systems of vertebrates. In addition, the responses of stickleback larvae were stronger to the combined cues than the chemical cue alone, indicating threat-sensitive behaviour.

A common antipredator behaviour in all of the planktivores studied was decreased ingestion rate in response to predator cues. In addition, *N. integer* and stickleback larvae also decreased their swimming activity, which reduces encounters with predators and the probability of being detected by predators. Pelagic mysids and *C. pengoi* also altered their prey selectivity patterns in response to predator cues. Modifications in feeding behaviour may reflect the increased vigilance of individuals under predation threat.

The effects of predator cues on the swarming behaviour of *N. integer* were examined. Swarming has many advantages, including antipredator defences. Swarming also brings clear antipredator advantages to *N. integer*, since when they feed in a swarm, they do not significantly decrease their feeding rate. This can be attributed to collective vigilance in the swarm. However, the swarming behaviour of *N. integer* was not affected by predation risk, but was instead a fixed strategy. Despite the presence or absence of predator cues, *N. integer* individuals attempted to associate with a swarm and preferred larger to smaller swarms.

In studies with aquatic macrophytes, stickleback larvae and *P. flexuosus* utilized vegetation as a predation refuge, spending more time within vegetation when under predation threat. There were significant differences between macrophyte species in their suitability to littoral planktivores as a refuge. The two macroalgal species studied, bladderwrack *Fucus vesiculosus* and stonewort *Chara tomentosa*, were preferred by *P. flexuosus*, whereas Eurasian watermilfoil *Myriophyllum spicatum* was strongly avoided by *N. integer* and stickleback larvae. In fact, when in dense patches in aquaria, *M. spicatum* caused acute and high mortality (> 70%) in littoral mysids, but not in sticklebacks, whereas *C. tomentosa* and northern watermilfoil *M. sibiricum* did not. The mortality is probably due to polyphenols excreted by *M. spicatum*. In contrast, only 2-4% mortality in *N. integer* was observed with intact and broken stems of *M. spicatum* in field experiments.

The distribution of littoral mysids in different vegetations, however, suggests that *N. integer* avoids areas vegetated by *M. spicatum*.

Each of the Baltic planktivore species studied manifests a unique set of antipredator traits that work in combination to decrease its predation risk. The differences between the pelagic and littoral habitats are reflected in the antipredator behaviours exhibited by the planktivores. Furthermore, past and ongoing changes in the Baltic Sea, e.g. eutrophication-induced changes in the composition of the macrophyte communities to the dominance of unfavourable species, probably play a role in the predator-prey interactions between planktivores and their predators. Behaviour needs to be taken into account in food web studies, since many antipredator behaviours, such as reduced feeding, result in effects on the lower trophic levels similar to those caused by direct predation on the planktivores.

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1. INTRODUCTION

1.1 Predation

Predation, in which an animal consumes another animal, is a major process shaping aquatic ecosystems, and affects individuals, populations and communities (Aneer 1980, Kerfoot & Sih 1987, Rudstam *et al.* 1992, Thiel 1996, Abrahams & Kattenfeld 1997). Virtually every animal is potential prey for others, at least during certain life stages, and predation is an important source of mortality (Bailey & Houde 1989, Sih *et al.* 1992, Brönmark & Hansson 2000, Scharf *et al.* 2003). Predators are able to control prey populations by altering the relative and absolute abundances (Carpenter *et al.* 1985, Uitto *et al.* 1995, Diehl & Kornijów 1997), species composition and population structure of their prey (Wooldridge & Webb 1988, Hansson *et al.* 1990, Benoit *et al.* 2002, Laxson *et al.* 2003), and can even drive their prey into extinction (Murdoch & Bence 1987, Dorn & Mittelbach 1999).

A predation event can be divided into separate succeeding stages, forming a cycle: location, pursuit, attack, capture, handling and ingestion (Gerritsen & Strickler 1977, O'Brien 1987, Ohman 1988, Carson & Merchant 2005, Clarke *et al.* 2005). However, various predators may have different skills at each stage, and prey may likewise differ in their vulnerability at each stage (Gerritsen & Strickler 1977, O'Brien 1987). Furthermore, many environmental variables and individual properties affect the success of the predator at each stage; *e.g.* location probability can be affected by light level, prey density, and the relative sizes and speeds of the predator and prey (Gerritsen & Strickler 1977, O'Brien 1987, Stemberger & Gilbert 1987, Bailey & Houde 1989). Pursuit probability can be

affected by the inner state of the predator, *e.g.* hunger (Wootton 1984), density of the prey, and the profitability of the prey, *e.g.* size (Gerritsen & Strickler 1977, O'Brien 1987, Bailey & Houde 1989, Hirvonen & Ranta 1996). Attack probability is affected by the skills and strategy of the predator, the evasion ability of the prey, density of the prey, and the simultaneous presence of more than one prey animal in the encounter field of the predator (Gerritsen & Strickler 1977, O'Brien 1987, Stemberger & Gilbert 1987, Bailey & Houde 1989, Hirvonen & Ranta 1996). Ingestion probability can be affected by the chemical and morphological properties of the prey (Wootton 1984, Scrimshaw & Kerfoot 1987, Stemberger & Gilbert 1987). Thus, the process of predation is by no means straightforward and not necessarily always completed, since the prey always attempt to stop the cycle at the earliest possible stage.

In addition to direct mortality, predators have important indirect effects on their prey, such as changes in morphology (Dill 1987, Larsson & Dodson 1993, Stabell & Lwin 1997, Merilaita 2001, Schoeppner & Relyea 2005), life history (Reznick *et al.* 1990, Flinkman *et al.* 1994, Slusarczyk 1999, Chivers *et al.* 2001a, Sakwinska & Dawidowicz 2005) and behaviour (Sih 1987, Ohman 1988, Lima 1998a, Brown & Cowan 2000, Hölker & Stief 2005). Some of these changes are permanent and fixed, *i.e.* not dependent on ambient predation pressure, and some are flexible and inducible (Dill 1987, Havel 1987, Brown & Smith 1998, Sakwinska & Dawidowicz 2005, Cohen & Forward 2005). Fixed antipredator traits are common in prey that are not likely to survive their first encounter with a predator and thus cannot afford to gather information on local predation risk to make adaptive changes in their traits (Dill 1987,

Sih 1987, 1992a). Flexible traits are possible when the costs of gathering information are lower (Havel 1987). Environmental variability also plays a role: fixed antipredator traits are favoured in stable environments, whereas flexible traits are beneficial under variable conditions (Dill 1987, Havel 1987, Sih 1987, Brönmark & Pettersson 1994).

Morphological antipredator adaptations include changes in body size or shape, such as spines that make the prey more difficult to handle and ingest, *e.g.* in fishes (Wootton 1984, Brönmark & Pettersson 1994, Stabell & Lwin 1997), amphibians (Relyea 2001, Schoeppner & Relyea 2005) and cladocerans (Walls & Ketola 1989, Boeing *et al.* 2005). Spines and other projections of the body may also increase the apparent size of the prey and thus discourage predators with a limited gape size from attacking (Wootton 1984, O'Brien 1987, Stemberger & Gilbert 1987, Makarewicz *et al.* 2001, Scharf *et al.* 2003). Lateral compression can reduce the vulnerability of zooplankton to gill raker retention by planktivorous fish (O'Brien 1987). Morphological antipredator structures can also be obtained through behavioural processes in caddisfly larvae (Boyero *et al.* 2006). Prey may also deter predators by being distasteful or producing toxic substances (Scrimshaw & Kerfoot 1987).

Life history adaptations include a high birth rate that offsets the death rate (Stemberger & Gilbert 1987, Reznick *et al.* 1990), synchronized reproduction and emergence of the young (Mordukhai-Boltovskoi & Rivier 1971, Sih 1987, Bailey & Houde 1989, Johnston & Ritz 2001), small maturation size (Reznick *et al.* 1990, Burks & Lodge 2002, Sakwinska 2002, Sakwinska & Dawidowicz 2005), production of digestion-resistant eggs (Flinkman *et al.* 1994), diapause (Hairston 1987, Slusarczyk 1999), and timing of reproduction (Bailey & Houde

1989, Crowl & Covich 1990) and hatching (Chivers *et al.* 2001a, Kusch & Chivers 2004). Each of these can be either fixed or flexible traits, depending on the species in question.

An individual may temporarily go hungry, or fail to find a mate with which to reproduce within a given time, but these shortcomings may have only minimal influence on the individual's lifetime fitness, *i.e.* lifetime production of offspring. Clearly, being eaten reduces fitness dramatically and irrevocably; hence, the need to avoid predation is often put ahead of all other needs. Often the same behavioural traits that make an animal efficient in foraging simultaneously increase its own risk of being eaten (Sih 1992b, Lima 1998a). Even where resources are abundant, the organism may not be able to utilize them due to the conflicting need to avoid predators. There are trade-offs involved in all antipredator traits (Dill 1987, Lima & Dill 1990, Loose & Dawidowicz 1994, van Duren & Videler 1996, Lima 1998a,b, Chivers *et al.* 2001b, Viherluoto & Viitasalo 2001b, Boyero *et al.* 2006). Prey with defences often have lower metabolic, feeding, growth, developmental and/or reproductive rates than prey without defences, *e.g.* those living in permanently predator-free environments (Stemberger & Gilbert 1987, Walls & Ketola 1989, Loose & Dawidowicz 1994, Jachner 1997, Tsuda *et al.* 1998, van Buskirk 2000).

The benefit of flexible defences is that they only need to be produced or manifested when the risk of predation is real. The time required to prepare a certain defence is dependent on its nature: behavioural defences can be manifested immediately and affect the fitness of the individual, but morphological and life history defences operate on an intergenerational time scale and thus affect the fitness of the population.

The intensity of these defences can change, depending on the hunger level, mating opportunities and patterns in current versus future reproductive success and potential of the prey individual (van Duren & Videler 1996, Lima 1998b, Brown & Cowan 2000, Hartman & Abrahams 2000, Skajaa *et al.* 2004). In certain situations individuals are more willing to take the risk of being eaten than in others. An individual must balance the immediate benefits and long-term costs of antipredator defences (Lima 1998a,b).

Predation may also influence other ecological interactions of their prey, such as inter- or intraspecific competition for resources (Coen *et al.* 1981, Dill 1987, Wiederholm 1987, Lima 1998a, Schofield 2003). Through direct lethal effects, predators can reduce the density of their prey and thus decrease the intensity of competition. Predators can also induce changes in prey niches via nonlethal effects and thus either increase or decrease the intensity of competition, depending on whether the prey use the same or different antipredator strategies (Coen *et al.* 1981, Dill 1987, Mittelbach & Chesson 1987, Lima 1998a,b, Schofield 2003). Competition increases if predation pressure forces prey to share limited refuges, but decreases if prey have similar niches in the absence of predators and different when predators are present. The outcome of competition can also change as an indirect effect of predation (Leibold 1991, Lima 1998a,b, Relyea 2000). In addition, there may be “apparent competition” between prey species that do not directly compete for resources but nonetheless have negative effects on each other through their common predator (Holt 1977, Abrams 1987, Dill 1987, Sih 1987).

Alternatively, the predation rates on a prey species may decline when another prey species becomes available to the predator, depending on the abundance and predation

vulnerability of the alternative prey, and on the possibility of the predator to respond numerically to increased prey availability (Cooper & Goldman 1980, Abrams 1987, Bailey & Houde 1989). Predation may facilitate invasions by exotic species if the native species is a more vulnerable or preferred prey than the invader (Dorn & Mittelbach 1999). On the other hand, multiple predators preying on a single species may lead to either enhancement or reduction in its predation risk through nonindependent predator effects (Diehl & Kornijów 1997, Warfe & Barmuta 2004, Vance-Chalcraft & Soluk 2005, Van de Meutter *et al.* 2005b, Griffen & Byers 2006). Omnivory, *i.e.* consumption of prey from more than one trophic level, further complicates the trophic relationships, because the intraguild predators show both competitive and consumer-resource interactions (Johannsson *et al.* 1994, Diehl & Kornijów 1997, Warfe & Barmuta 2004, Winkler & Greve 2004, Griffen & Byers 2006).

Predation on one trophic level may induce effects on levels lower down, *i.e.* on levels that the predators do not directly consume. These are referred to as trophic cascades or “leapfrog” effects (Carpenter *et al.* 1985, Dill 1987, Kerfoot 1987, Romare & Hansson 2003, Reisewitz *et al.* 2006). Predators may decrease the abundance of the prey population and thus release the prey population of their prey from predation pressure (Uitto *et al.* 1995, Diehl & Kornijów 1997, Laxson *et al.* 2003, Griffen & Byers 2006). Changes in biotic habitats resulting from trophic cascades may influence species utilizing these habitats (Reisewitz *et al.* 2006). The effects can also be mediated through behavioural changes in the prey population, changing the way they feed, *i.e.* what, where and when (Bowers & Grossnickle 1978, Jeppesen *et al.* 1997,

Lima 1998a,b, Romare & Hansson 2003, Reichwaldt & Stibor 2005). In addition to top-down effects, trophic cascades can also operate from bottom-up: an increase in abundance of a prey population may lead to increased foraging activity of its predator, with a consequent increase in its vulnerability to the top predator (Dill 1987). In most cases, direct lethal and indirect behavioural effects interact to produce the outcome of trophic cascades (Lima 1998a,b).

1.2 Predator detection

The ability to detect the presence of a predator gives a prey animal a chance to adjust its behaviour to reduce the probability of completion of the predation cycle, *i.e.* being detected, attacked, caught and ingested (Rademacher & Kils 1996, Hartman & Abrahams 2000, Gilbert & Buskey 2005, Hemmi & Zeil 2005, Hölker & Stief 2005). The prey can evaluate predation risk by detection of different cues from predators. Many prey animals have remarkably sophisticated mechanisms to distinguish predators from similar nonpredators (Mathis & Vincent 2000), different predator species (Relyea 2001), actively foraging predators from inactive (Phillips 1978), predators that have fed on different diets (Brönmark & Pettersson 1994, Stirling 1995, Brown & Cowan 2000, Vilhunen & Hirvonen 2003, Schoeppner & Relyea 2005), predators with different foraging strategies (Ritz *et al.* 1997, Boyero *et al.* 2006), predators of different sizes (Chivers *et al.* 2001b, Engström-Öst & Lehtiniemi 2004, Kusch *et al.* 2004, Carson & Merchant 2005) and hungry predators from satiated (Walls & Ketola 1989, Jachner 1997, Ejdung 1998, Schoeppner & Relyea 2005). However, many prey animals

likely face a deficit of accurate information, and thus the behaviour of prey is not only influenced by the actual risk of predation, but also by the subjectively perceived risk (Sih 1992a, Lima 1998b, Hemmi & Zeil 2005, Wong *et al.* 2005). Individuals can also perceive predation threat by monitoring the behaviour of their conspecifics (Ryer & Olla 1991, Vilhunen *et al.* 2005, Wong *et al.* 2005), or if predators have regular foraging patterns, cues related to season or time of day can be used (Havel 1987). The reaction distance is often of central importance in escape success (Viitasalo *et al.* 1998, Visser 2001, Scharf *et al.* 2003, Clarke *et al.* 2005, Gilbert & Buskey 2005).

In aquatic environments, predators can be detected by the visual, chemical and/or hydromechanical cues that they emit (Blaxter & Batty 1985, Kiørboe & Visser 1999, Mathis & Vincent 2000, Cohen & Ritz 2003, Lehtiniemi 2005). Visual cues include the size, shape, colour and movement of the predator (Batty 1989, Gregory 1993, Mathis & Vincent 2000, Hemmi & Zeil 2005, Lehtiniemi 2005). However, the underwater visual environment is highly variable compared with most terrestrial environments: illumination and turbidity levels can change dramatically due to both natural and anthropogenic factors, and this has important consequences, *e.g.* for predation (Johnsen 2005). Thus, under certain circumstances, such as darkness, turbidity or in the case of sit-and-wait predators, vision is of little or no use, and hence other cues play a major role (Jachner 1997, Ejdung 1998, Brown & Cowan 2000, Hartman & Abrahams 2000, Mathis & Vincent 2000).

Chemical predator cues include those cues emitted from the predator *per se* (*i.e.* kairomones), from the remains of prey in the faeces of the predator and cues released by injured or partly consumed prey in the

vicinity of an active predator (*i.e.* alarm cues) (Loose *et al.* 1993, Hamrén & Hansson 1999, Quirt & Lasenby 2002, Vilhunen & Hirvonen 2003, Cohen & Forward 2005, Schoeppner & Relya 2005, Boyero *et al.* 2006). The ability of an animal to intercept and interpret these chemical cues may depend on both large-scale environmental flows and on small-scale movements and currents generated by the animal itself (Phillips 1978, Moore & Grimaldi 2004, Mead 2005). A predator may also be able to suppress the release of kairomones to conceal its presence when attacking (Cohen & Ritz 2003).

All organisms moving in an aquatic environment create hydromechanical cues that can be distinguished, since they can vary significantly among species (Blaxter & Batty 1985, Viitasalo *et al.* 1998, Kiørboe & Visser 1999, Gilbert & Buskey 2005, Mogdans 2005). Detection of a disturbance in the water is dependent on the strength of the disturbance, the distance between the disturbance and the animal, the sensitivity of the animal's receptors and the relative level of noise, such as turbulence (Gerritsen & Strickler 1977). Hydromechanical cues may carry the information later than chemical or visual cues, when the predator is already attacking, and may thus give sufficient warning only for flight responses (O'Brien 1987, Viitasalo *et al.* 1998, Clarke *et al.* 2005, Gilbert & Buskey 2005).

To detect predators, fishes utilize visual (Batty 1989, Bishop & Brown 1992, Gregory 1993, Mikheev *et al.* 2002, Lehtiniemi 2005) and chemical (Jachner 1997, Brown & Cowan 2000, Vilhunen & Hirvonen 2003, Kusch *et al.* 2004, Lehtiniemi 2005) sensory modes together with their lateral-line system (Blaxter & Batty 1985, Mogdans 2005). Crustaceans also utilize visual (Rademacher & Kils 1996, Cohen & Ritz

2003, Browman 2005, Hemmi & Zeil 2005) and chemical cues (Stirling 1995, van Duren & Videler 1996, Ejdung 1998, Cohen & Ritz 2003, Åsbjörnsson *et al.* 2004) in predator detection and they also have hydromechanical sensors on their antennae and body (Haury *et al.* 1980, Visser 2001, Clarke *et al.* 2005, Fields & Weissburg 2005, Gilbert & Buskey 2005).

1.3 Antipredator behaviour

Prey can alter their behaviour both before and after their encounter with a predator, *i.e.* when the predator detects and recognizes its prey (Sih 1987, Ohman 1988, Brodie *et al.* 1991, Scharf *et al.* 2003, Carson & Merchant 2005). Avoidance behaviours act to reduce the probability of encounters (Brown & Smith 1998, Ejdung 1998, Mathis & Vincent 2000, Quirt & Lasenby 2002, Scharf *et al.* 2003). Escape behaviours act to increase the probability of surviving the encounter (Rademacher & Kils 1996, Viitasalo *et al.* 1998, Scharf *et al.* 2003, Clarke *et al.* 2005, Gilbert & Buskey 2005). Often these behaviours are intermixed and one type of behaviour serves both causes. Antipredator behaviour can be fixed or flexible, *i.e.* a lifestyle or induced by predator detection, respectively (Sih 1987, 1992a). However, fixed vs. flexible behaviours are only endpoints along a continuum, and a behaviour that is basically flexible may appear fixed due to a long time lag in response to a changing environment (Sih 1987, 1992a, van Duren & Videler 1996, Laurel *et al.* 2004).

If behaviour is flexible, the prey are not only able to express the behaviour when needed, but also to vary the intensity of the response according to factors that affect the predation risk, such as abundance

of predators (Loose & Dawidowicz 1994, Hölker & Stief 2005), size of the predator (Bishop & Brown 1992, Chivers *et al.* 2001b, Engström-Öst & Lehtiniemi 2004, Carson & Merchant 2005), distance to the predator (Hemmi & Zeil 2005) or distance to the refuge (Hartman & Abrahams 2000, Lehtiniemi 2005). In addition, prey that are more susceptible to predation, such as a size class that is preferred by predators or insect larvae that have undergone autotomy, show stronger antipredator responses (Sih 1982, Abrahams & Cartar 2000, Mathis & Vincent 2000, Chivers *et al.* 2001b, Quirt & Lasenby 2002, Gyssels & Stoks 2006). Adjusting behaviour according to the perceived predation risk is termed threat-sensitivity (Helfman 1989, Bishop & Brown 1992, Mathis & Vincent 2000, Chivers *et al.* 2001b, Hölker & Stief 2005). Usually the behavioural response to increased predation risk occurs rapidly, but the response to decreased predation risk occurs much more slowly (Lima & Dill 1990, Loose 1993, Jachner 1997, Burks & Lodge 2002, Dalesman *et al.* 2006). The recovery is also slower with higher predation risk (Sih 1987, 1992a, Lima & Dill 1990, Lima 1998b, Wong *et al.* 2005). Behavioural defences, being flexible and reversible, are useful if the individual has only incomplete information on predation risk, in contrast to costly morphological defences (Schoepfner & Relyea 2005).

However, even strong antipredator responses can fail to prevent mortality (Sih 1992b, Lima 1998a,b). Antipredator behaviour may be ineffective due to phylogenetic and developmental constraints or conflicting demands (Sih 1992b). The responses of prey to a particular predator can make the prey more susceptible to attacks from other predators. Escaping from one predator can make the prey more conspicuous to other

predators; a change in habitat use or activity to avoid one type of predator may increase vulnerability to some other type (Sih 1987, Vance-Chalcraft & Soluk 2005, Van de Meutter *et al.* 2005b, Laurel & Brown 2006).

1.3.1 Decreased activity

Decreased activity reduces the encounter frequency with predators, as well as the probability of being detected and recognized as prey (Gerritsen & Strickler 1977, Sih 1987, Lima & Dill 1990, Lima 1998ab, Weissburg *et al.* 2002). These activities include swimming and other types of movement, as well as feeding (Stein & Magnuson 1976, Ejdung 1998, Mathis & Vincent 2000, Hölker & Stief 2005, Lehtiniemi 2005). However, the prey swimming speed that best avoids encounters with predators is dependent on the predominant type of predator present, *i.e.* cruising or ambush predators (Gerritsen & Strickler 1977, Ohman 1988).

In extreme cases, when the predation risk is perceived as being so high that an escape appears impossible or the prey lack effective escape responses, prey may escape passively (*e.g.* dead-man response in cladocerans) to reduce the ability of the predator to relocate the prey (Sih 1987, Stemberger & Gilbert 1987, Ohman 1988). In addition to reducing their swimming speed, animals can change the way they swim to remain undetected (Ohman 1988, Bailey & Houde 1989, van Duren & Videler 1996). The trade-offs of decreased activity include lost opportunities to feed or mate, resulting in lower growth and/or fecundity (Tiselius *et al.* 1993, van Duren & Videler 1996, Tsuda *et al.* 1998, Hölker & Stief 2005, Lehtiniemi 2005).

1.3.2 Swarming

Swarming has several antipredator benefits (reviewed in Alexander 1974, Ohman 1988, Lima & Dill 1990, Magurran 1990, Ritz 1994). First, it reduces the encounter frequency with predators (Brock & Riffenburgh 1960, Clutter 1969). Second, the predator is often capable of consuming only a fraction of available prey, which is called the dilution effect (Clutter 1969, Major 1978, Foster & Treherne 1981, Byholm 1998, Foster *et al.* 2001). In combination these two factors effectively reduce individual predation risk (Turner & Pitcher 1986). The predator may become confused in trying to choose a single prey individual for attack (Major 1978, Heller & Milinski 1979, Magurran 1990, Jakobsen *et al.* 1994, Ritz 1994). The confusion may be easier to overcome if the predator can focus on individuals that differ from the others in appearance (Wolf 1985, Landeau & Terborgh 1986, Lima & Dill 1990, Rees & Saulnier 1997, Byholm 1998), which may lead to size-assortive aggregations (O'Brien 1988, Carleton & Hamner 1989, Ranta & Lindström 1990, Ribes *et al.* 1996, Peuhkuri 1997). Coordinated group avoidance and escape manoeuvres can also be utilized (Mullin & Roman 1986, Magurran & Pitcher 1987, O'Brien & Ritz 1988, Magurran 1990, Ritz 1994).

Swarming behaviour can be triggered by predator cues (Pijanowska & Kowalczewski 1997, Brown & Smith 1998, Brown & Cowan 2000) or changes in light intensity (O'Brien 1988, Modlin 1990, Milne *et al.* 2005), the latter reflecting avoidance of predators that use vision to locate their prey, and also the fact that vision is important to maintain contact within the aggregation (Steven 1961, Partridge & Pitcher 1980, Ritz 1994, Buskey 2000, Timmermann *et*

al. 2004). In addition, organic compounds may serve as pheromones that aid in maintaining zooplankton swarms (Burks & Lodge 2002). Mechanoreception may also play a role (Clutter 1969, Mauchline 1971c, Zelickman 1974, Buskey 2000), including the lateral line in fishes (Partridge & Pitcher 1980, Timmermann *et al.* 2004).

Trade-offs of swarming behaviour include increased visibility and chemical detectability of large aggregations (Brock & Riffenburgh 1960, Ohman 1988, Magurran 1990, Weissburg *et al.* 2002, Botham *et al.* 2005), competition for resources between group members (Alexander 1974, Eggers 1976, Magurran 1990, Ranta *et al.* 1993, Ritz 1994), and spreading of diseases and parasites (Alexander 1974, Hamner 1984). Swarming may be highly disadvantageous when predators are many orders of magnitude larger than their swarming prey, such as in the case of euphasiids and baleen whales (Reid *et al.* 2000, Gill 2002).

1.3.3 Hiding

Hiding decreases the possibility of being detected and recognized by predators (Ohman 1988, Lima & Dill 1990, Diehl & Kornijów 1997, Jeppesen *et al.* 1997, Brönmark & Hansson 2000). Prey can utilize physical refuges such as aquatic vegetation (Gotceitas & Colgan 1987, Lauridsen *et al.* 1997, Romare & Hansson 2003, Lehtiniemi 2005, Van de Meutter *et al.* 2005b), benthic habitats (Stein & Magnuson 1976, Eklöv & Persson 1996, Ejdung 1998, Hossain *et al.* 2002, Hölker & Stief 2005) and phytoplankton blooms (Engström-Öst *et al.* 2006). Predators may also have difficulties in capturing prey in the refugia (Vince *et al.* 1976, Stoner 1982, Winfield 1986, Diehl 1988, Warfe &

Barmuta 2004) and prey may have a better ability to assess the actual risk of predation, once they are near their refuge (Hemmi & Zeil 2005, Wong *et al.* 2005). However, the behaviour and size of the predator and prey in question determine the effectiveness of the refuge (Coen *et al.* 1981, Savino & Stein 1982, 1989, Ryer 1988, Laurel & Brown 2006).

As in other antipredator mechanisms, there are trade-offs involved in hiding behaviour. While hiding reduces encounter rates with predators, it also tends to reduce the encounter rates between prey and their own resources (Sih 1987, Lima & Dill 1990, Diehl & Kornijów 1997, Ejdung 1998). Often the habitats that are energetically most profitable are also the most dangerous, since the distribution of predators tends to match their prey's resource distribution (Lima 1998a,b). The refugia may be poorly adaptable for feeding and other essential activities, such as reproduction (Lima & Dill 1990, Diehl & Kornijów 1997, Jeppesen *et al.* 1997, Warfe & Barmuta 2004, Hölker & Stief 2005). Predation pressure may be relatively high also inside the refugia, by different predator species or size-classes than outside it (Jeppesen *et al.* 1997, Burks & Lodge 2002, Wojtal *et al.* 2003, Åsbjörnsson *et al.* 2004, Van de Meutter *et al.* 2005b). Competition for resources may be intensified within the limited dimensions of the refuge (Lima 1998a, Laurel *et al.* 2004).

1.3.4 Migration

Light level has a crucial effect on the ability of visual predators to locate their prey (O'Brien 1987). A free-swimming individual can indirectly control its ambient light level by migration. In pelagic environments with sufficient depth, many

organisms undergo diel vertical migration (DVM). Zooplankton and other smaller organisms avoid visual predators, mainly fish, by descending at dawn to greater depths and rising at dusk to surface waters to feed (McLaren 1974, Bollens & Frost 1989, Loose 1993, Stirling 1995, Cohen & Forward 2005, Leising *et al.* 2005). Some zooplankton species also use modified DVM to avoid contact with invertebrate predators that themselves migrate to avoid fish (Burris 1980, Bowers & Vanderploeg 1982, Stemberger & Gilbert 1987, Ohman 1988, Lampert 1989). In addition to antipredator benefits, DVM gives the phytoplankton community a chance to recover during day from grazing during night, possibly resulting in higher feeding rates (Lampert 1989, Reichwaldt & Stibor 2005). However, deeper waters usually have colder temperatures and less food, and energy must be spent swimming up and down the water column, all of which are costly to the migrating individuals in terms of decreased growth rates and fecundity (Lampert 1989, Dodson 1990, Dawidowicz & Loose 1992, Loose & Dawidowicz 1994, Sakwinska & Dawidowicz 2005).

In shallow habitats horizontal migration is more common. Many zooplankton species perform diel horizontal migration especially in lakes, spending the daylight hours under cover of the littoral macrophyte vegetation and migrating to the open pelagic to feed at night (Lauridsen & Lodge 1996, Lauridsen *et al.* 1997, Wojtal *et al.* 2003). Many macrophytes are repellent to zooplankton, so again there is a trade-off involved (Lauridsen & Lodge 1996, Lauridsen *et al.* 1997, Burks & Lodge 2002). In predator-free environments, such as fish-free lakes, horizontal migration does not occur and the zooplankton reside in the open water (Lauridsen *et al.* 1997).

The proximate cue for migrations (both vertical and horizontal) is light, which also regulates their amplitude, but cues of predator presence and food availability may modify the pattern (Bohl 1980, Rudstam *et al.* 1989, Loose & Dawidowicz 1994, Lauridsen *et al.* 1997, Gal *et al.* 1999). In the case of DVM, common crustacean species in temperate areas follow an isolume, moving vertically to maintain the same subjective level of light intensity (Johnsen 2005). Diel and seasonal changes in the buoyancy of copepods can also influence their vertical migrations (Thorisson 2006). Migration behaviour is generally more pronounced in the more conspicuous individuals, *i.e.* large, pigmented or carrying eggs (Lampert 1989, Lima 1998b).

1.3.5 Flight

Escape responses are the final option to reduce the chance of being captured when the predator is attacking its prey (O'Brien & Ritz 1988, Ohman 1988, Neil & Ansell 1995, Brönmark & Hansson 2000). These responses include high-speed "leaps" and swimming bursts, often aided by protean, *i.e.* unpredictable, movement patterns that aim to confuse the predator so that it cannot relocate the prey after an attack (Rademacher & Kils 1996, Viitasalo *et al.* 1998, Cohen & Ritz 2003, Vilhunen & Hirvonen 2003, Gilbert & Buskey 2005). These require abundant energy, and thus cannot be maintained for longer periods of time (Larsson & Dodson 1993, Fields & Weissburg 2005, Gilbert & Buskey 2005). Flight is most effectively triggered by mechanosensory (Blaxter & Batty 1985, Viitasalo *et al.* 1998, Green *et al.* 2003, Gilbert & Buskey 2005) or visual cues (Batty 1989, Bishop & Brown 1992), but chemical stimuli may also be effective

(Cohen & Ritz 2003, Vilhunen & Hirvonen 2003).

The success of a flight response is dependent on its timing, velocity and orientation (reviewed in Neil & Ansell 1995). Flight success is enhanced by the proximity of refuges, so that after a rapid escape response the prey can utilize concealment (Sih 1987, Lima & Dill 1990). The strength of the flight response increases with size and/or developmental stage (Blaxter & Batty 1985, Ohman 1988, Bailey & Houde 1989, Batty 1989, Fuiman 1993).

2. STUDY AREA

2.1 Baltic Sea

The Baltic Sea is the largest brackish water sea in the world, with an area of 415 266 km² and stretching between 54°N and 66°N, but shallow, with a mean depth of only 55 m. It is characterized by a year-round stable salinity gradient, declining from > 20 psu in its opening area towards the North Sea to about 2 psu in the Bothnian Bay (Kullenberg 1981). The organisms are of both marine and freshwater origin in addition to true brackish water species, their distribution being largely determined by the salinity gradient (Haage 1975, Hällfors *et al.* 1981, Snoeijs 1999). The Baltic has relatively low species diversity, in part because of its young age – it has been in its present form for only about 7 500 years. In addition, its low salinity and temperature and strong seasonality with an annual ice cover result in physiological stress to organisms, many of which live near their tolerance limits. The Baltic has been and is constantly invaded by nonindigenous species that colonize available niches (Ojaveer *et al.* 1999, Leppäkoski *et al.* 2002a, 2002b).

The Baltic has a large drainage basin, 1 729 000 km², with a population of about 85 million people living in 14 countries, and the impact of human activities is profound. Eutrophication is perhaps the most serious and widespread problem, causing community changes and turbidity (Larsson *et al.* 1985, Bonsdorff *et al.* 1997, Karjalainen 1999, Laamanen *et al.* 2004, Weckström 2005). The Baltic, except for the Bothnian Bay, is strongly stratified, with a seasonal thermocline and a permanent halocline, below which the water is irregularly subjected to periods of hypoxia or anoxia and presence of H₂S (Larsson *et al.* 1985, Matthäus 1995, Snoeijs 1999).

2.2 Ekenäs Archipelago

The Ekenäs Archipelago is located in southwest Finland, at the entrance to the Gulf of Finland, where the average salinity is about 6 psu. The Archipelago can be divided into outer, middle and inner zones that have different characteristics in exposition and occurrence of hard and soft bottoms. The land is constantly rising about 3–4 mm yr⁻¹ as a result of recovery from the last Ice Age. As a consequence, small semienclosed bays (flads) along the coastline are becoming increasingly cut off from the sea. These bays undergo a succession of changes in their geology, physical conditions and community structure, especially macrovegetation (Munsterhjelm 1997, 2005, Wallström *et al.* 2000). In spring after the ice break-up, the shallow bays warm up quickly to temperatures higher than in the open sea (Munsterhjelm 1997) and act as important nursery areas for many fish species (Urho 2002).

The Ekenäs Archipelago is widely used for recreation, such as boating activities,

and many summer houses are located there. The anthropogenic impact can be seen as local eutrophication, but nutrient loading from the open sea of the Gulf of Finland also affects the area (Kangas *et al.* 1982, Wallström *et al.* 2000). There is practically no tide in the Baltic Sea, which has special implications for littoral ecosystems. The hydrolittoral zone of the Baltic is defined as the zone that extends above the annual minimum water level to the mean summertime level, and the sublittoral is the part that is permanently submerged (Snoeijs 1999). The annual wind-induced water level changes can be substantial, up to 2 m in the Bothnian Bay.

3. STUDY OBJECTS

3.1 Littoral mysids

Neomysis integer (Leach 1814) (Mysidacea, Crustacea) is the most common and widespread mysid species in the Baltic Sea, occurring in all areas except for the Bothnian Bay (Köhn 1992, Kotta & Kotta 1999, Kotta *et al.* 2004). It also occurs in brackish lakes in Europe (Irvine *et al.* 1993, Aaser *et al.* 1995, Søndergaard *et al.* 2000) and estuaries of the North Sea and northwestern Atlantic between 36°N and 63°N (Apel 1992, Moffat & Jones 1992, Mees *et al.* 1994, Hostens & Mees 1999, Fockedey 2005). It is a genuine brackish water species, with a salinity tolerance of 1–38 psu and temperature tolerance of 0–33 °C (Arndt & Jansen 1986, Köhn 1992, Kotta & Kotta 2001, Fockedey 2005). However, sexual maturation is only possible within a range of 5–15 psu and 15–25 °C, and the size-at-maturity increases with increasing salinity and decreasing temperature (Fockedey 2005). *Neomysis*

integer occurs in large swarms (Mauchline 1971c, Arndt & Jansen 1986, Debus *et al.* 1992, Köhn 1992, Byholm 1998), especially in early summer, and these swarms are often assorted according to size (Köhn 1992, Välipakka 1992, Kauppila 1994, Fockedey 2005). In the northern Baltic Sea, *N. integer* breeds from May to September and usually produces two generations per year (Rudstam *et al.* 1986, Köhn 1992, Kauppila 1994).

Praunus flexuosus (Müller 1776) (Mysidacea, Crustacea) is a marine euryhaline species that is common throughout the Baltic Sea, except in the Bothnian Bay (Köhn 1992). It also occurs in estuaries and along the coast of the northern Atlantic (Mauchline 1971b, Winkler & Greve 2004). Its salinity tolerance ranges from 3.5 to 37 psu (McLusky 1979). *Praunus flexuosus* is a phytophilous species: its distribution pattern is positively influenced by the density of aquatic vegetation and its entire life cycle occurs in the phytobenthic zone (Kotta & Kotta 1999). Its most important habitat in the Baltic is the bladderwrack *Fucus vesiculosus* L. belt (Kauppila 1994). It breeds from June to September, usually producing one but sometimes two generations per year (Köhn 1992, Kauppila 1994). *Praunus flexuosus* is mainly solitary but may occur in loose shoals (Mauchline 1971c).

In the Baltic, *N. integer* and *P. flexuosus* occupy mainly shallow coastal waters (Arndt & Jansen 1986, Välipakka 1992, Väinölä & Vainio 1998, Kotta & Kotta 1999, 2001), but perform seasonal horizontal migration, leaving the uppermost littoral in winter, as well as in summer when the water temperature reaches about 20 °C (Arndt & Jansen 1986, Välipakka 1992, Kauppila 1994, Nordström 1997, Kotta & Kotta 1999). *Neomysis integer* also undergoes diel horizontal and vertical migra-

tions (Hansson *et al.* 1990, Debus *et al.* 1992, Irvine *et al.* 1993, Speirs *et al.* 2002, Fockedey 2005). Littoral mysids are omnivorous, feeding on bottom detritus, organic material in suspension in the water, various phyto- and zooplankton and meiofauna (Mauchline 1971a,b, Nordström 1997, Fockedey 2005, Koho 2005, Gorokhova in press). The relative importance of each group changes with season, habitat and size of the mysid (Arndt & Jansen 1986, Nordström 1997, Fockedey 2005). These two mysid species may compete for food, although *P. flexuosus* utilizes more zooplankton and is more specialized for consuming certain food items than *N. integer*, whose diet is broad and contains more detritus (Nordström 1997, Winkler & Greve 2004). *Neomysis integer* also preys on the eggs and larvae of the Baltic herring *Clupea harengus membras* L. 1761 (Lehtiniemi *et al.* unpubl.), whereas *P. flexuosus* may prey on the smaller-sized *N. integer* (Winkler & Greve 2004). In many areas, including the southern Baltic, *N. integer* is able to control zooplankton abundance and composition, but this is unlikely in the northern Baltic, where *Mysis* spp. and young-of-the-year clupeids are the dominant planktivores (reviewed in Fockedey 2005).

Littoral mysids are important prey for a number of fish species, including European perch *Perca fluviatilis* L. 1758, roach *Rutilus rutilus* L. 1758, three-spined stickleback *Gasterosteus aculeatus* L. 1758 and Baltic herring (Thiel 1996, Aarnio & Bonsdorff 1993, Hostens & Mees 1999, Granqvist & Mattila 2004, Gorokhova *et al.* 2004, Fockedey 2005). *Neomysis integer* may also compete with larval herring for zooplankton food (Fockedey 2005, Koho 2005). In addition to fish, macrocrustaceans and wading birds are important predators of *N. integer* (reviewed in Fockedey 2005).

3.2 Pelagic mysids

The pelagic mysid species that has conventionally been referred to as *Mysis relicta sensu lato* (Mysidacea, Crustacea) actually consists of four sibling species with different distributions, zoogeographical histories and ecological characteristics (Väinölä 1986, Väinölä *et al.* 1994, Väinölä & Vainio 1998, Audzijonyte & Väinölä 2005). Of these four species, *M. relicta s. str.* (Lovén 1862) and *M. salemaai* (Audzijonyte and Väinölä 2005) occur in the Baltic Sea (Väinölä 1986, Väinölä *et al.* 1994, Audzijonyte & Väinölä 2005). Both species are primarily marine taxa, but separated from their common marine ancestor at different times. *Mysis relicta* has a considerably longer (> 1 Myr) freshwater history, whereas *M. salemaai* colonized the continental waters more recently (Audzijonyte 2006). During the last glacial maximum (20 kyr ago) the main refugia of *M. relicta* were along the eastern margins of the ice sheet, from where it colonized the Baltic Sea and Northern European lakes (Väinölä *et al.* 1994). The main refugium of *M. salemaai* appears to have been in the North Sea area, and the species colonized the Baltic Sea via the Yoldia Sea connection (Audzijonyte & Väinölä unpubl. data).

The species referred to as *M. relicta* (II) most likely includes both *M. relicta* and *M. salemaai*. These two species occur sympatrically in the Bothnian Bay, but only *M. salemaai* is found in the Bothnian Sea (Väinölä *et al.* 1994, Väinölä & Vainio 1998, Audzijonyte & Väinölä 2005). In other areas of the northern Baltic Sea, *M. relicta* occurs mostly near the coast and is replaced by *M. salemaai* in deeper offshore waters (Väinölä 1986, Väinölä *et al.* 1994, Väinölä & Vainio 1998, Audzijonyte & Väinölä 2005). Thus the animals collected

as *M. relicta* from the Bothnian Sea (II, Table 1) are most likely *M. salemaai*, while those collected from the Bothnian Bay (II, Table 1) most likely include both species. Hybridization between the two species has been reported from the Bothnian Bay but this is a rare phenomenon (Väinölä & Vainio 1998). The ecological differences found so far between *M. relicta* and *M. salemaai* relate to the timing of breeding (Väinölä 1986, Väinölä & Vainio 1998) and to the spectral sensitivity of their eyes (Lindström 2000, Audzijonyte *et al.* 2005), neither of which are likely to be of major importance in the present study. Moreover, separation of these two species in live animals is impossible, since it requires dissection followed by the use of genetic (Väinölä 1986, Väinölä *et al.* 1994, Väinölä & Vainio 1998, Audzijonyte & Väinölä 2005) and microscopy (Väinölä *et al.* 2002, Audzijonyte & Väinölä 2005) techniques. Hence they are treated as one species and referred to as *M. relicta* in II and the following discussion.

Mysis mixta (Lilljeborg 1852) (Mysidacea, Crustacea) is of North Atlantic origin and has adapted to the brackish water of the Baltic Sea (Salemaa *et al.* 1986). It dominates mysid communities in the Gulf of Finland, the northern Baltic proper and the Gulf of Riga (Rudstam *et al.* 1986, Salemaa *et al.* 1986, Kotta & Kotta 2001). *Mysis mixta* and *M. relicta* co-occur in the Bothnian Sea, but *M. relicta* dominates the mysid communities in the Bothnian Bay (Salemaa *et al.* 1986, 1990, Väinölä & Vainio 1998). The northern distribution limit of *M. mixta* lies in the Quark area between the Bothnian Sea and Bothnian Bay, whereas the southern distribution limit of *M. relicta* lies at 56° N and western at 18°30' E (Köhn & Gosselck 1989, Salemaa *et al.* 1990). *Mysis* spp. are the most frequently occurring mysids in Baltic open sea areas (Köhn

1992). Most *Mysis* populations in the northern Baltic breed in autumn and carry the embryos in a marsupium over winter (Rudstam *et al.* 1986, Salemaa *et al.* 1986, Väinölä & Vainio 1998). The juveniles are released in spring, *M. relicta* earlier than *M. mixta* (Salemaa *et al.* 1986, Rudstam & Hansson 1990). However, *M. salemaai* breeds throughout the year in the Gulf of Finland (Väinölä & Vainio 1998). *Mysis* individuals may breed as one- or two-year-olds, but only one generation is produced annually (Salemaa *et al.* 1986, Väinölä & Vainio 1998).

Mysis spp. undergo DVM (Salemaa *et al.* 1986, Rudstam *et al.* 1989, Hansson *et al.* 1990, Rudstam & Hansson 1990). The migration is regulated by light intensity: the mysids rise from their daytime near-bottom habitat up the water column to feed at dusk and descend at dawn, avoiding light levels above 10^{-4} lux (Salemaa *et al.* 1986, Rudstam *et al.* 1989, Rudstam & Hansson 1990). *Mysis mixta* rises higher than *M. relicta*, but rarely through the thermocline (Salemaa *et al.* 1986). Part of the *M. mixta* population does not migrate, but also remains near the bottom during night (Rudstam *et al.* 1989, Rudstam & Hansson 1990).

Pelagic mysids are of widespread ecological importance in the open sea areas of the Baltic, because they effectively link primary and secondary production to higher trophic levels as well as benthic to pelagic ecosystems (Grossnickle 1982, Viherluoto *et al.* 2000, Viherluoto 2001). Both *Mysis* species are opportunistic omnivores, feeding on phytoplankton, detritus, copepods, cladocerans, rotifers, ciliates and protists (Rudstam *et al.* 1989, Rudstam & Hansson 1990, Viherluoto 2001, Albertsson 2004, Koho 2005). Their feeding habits are dependent on life stage, season and DVM. Herbivory is important for the newly re-

leased juveniles at the time of the spring phytoplankton bloom and early summer (Bowers & Vanderploeg 1982, Rudstam & Hansson 1990, Viherluoto *et al.* 2000, Lindén & Kuosa 2004). In June, zooplanktivory is limited due to the high light levels that inhibit DVM (Rudstam & Hansson 1990), poor availability of zooplankton, and the small size and poor capture ability of the mysids (Cooper & Goldman 1980, Viherluoto *et al.* 2000). Later in the season, as mysids grow larger and zooplankton more abundant, zooplankton predominate in the diet (Bowers & Vanderploeg 1982, Viherluoto *et al.* 2000, Lehtiniemi *et al.* 2002, Koho 2005). *Mysis mixta* ingests more detritus and other benthic material during the day when near the bottom, whereas they ingest more zooplankton and also phytoplankton during the night when they have ascended (Rudstam *et al.* 1989). *Mysis mixta* is more zooplanktivorous than *M. relicta* (Viherluoto *et al.* 2000) and may be able to regulate zooplankton abundance and species composition in the northern Baltic proper (Rudstam *et al.* 1986, 1992, Hansson *et al.* 1990, Rudstam & Hansson 1990). Pelagic mysids are important prey for adult Baltic herring (Aneer 1980) and European smelt *Osmerus eperlanus* L. 1758 (Horpila *et al.* 2003, Ojaveer *et al.* 2004), but at the same time they compete for the same zooplankton prey (Hansson *et al.* 1990, Rudstam & Hansson 1990, Johannsson *et al.* 1994).

3.3 Predatory cladoceran

Cercopagis pengoi

Cercopagis pengoi (Ostroumov 1884) (Cladocera, Crustacea) is native to the Ponto-Caspian Basin, occurring in the Caspian Sea, Sea of Azov, Aral Sea,

estuaries of the Black Sea, several rivers and freshwater reservoirs (Mordukhai-Boltovskoi & Rivier 1971). It was first described in the Baltic in 1992 in Pärnu Bay and the Gulf of Riga (Ojaveer & Lumberg 1995), and an observation of the species was also made in the same year in the Gulf of Finland (S. Saesmaa, Finnish Institute of Marine Research, pers. comm.). In addition to these areas, it today occurs in the Åland Sea, Archipelago Sea, Bothnian Sea, northern Baltic proper, Curonian and Vistula lagoons, and the Gulf of Gdansk (MacIsaac *et al.* 1999, Bielecka *et al.* 2000, Gorokhova *et al.* 2000, Leppäkoski *et al.* 2002a, Finnish Institute of Marine Research unpubl. data). In some years the distribution of *C. pengoi* reaches even the Bothnian Bay in the northernmost Baltic (Finnish Institute of Marine Research unpubl. data). It has also invaded North American lakes: it was identified from Lake Ontario in 1998 (MacIsaac *et al.* 1999), from Lake Michigan (Charlebois *et al.* 2001) and the Finger Lakes a year later (Makarewicz *et al.* 2001), and from Lake Erie and Muskegon Lake in 2001 (Therriault *et al.* 2002).

Cercopagis pengoi is a euryhaline species, tolerating salinities from < 1–17 psu as well as freshwater (Mordukhai-Boltovskoi & Rivier 1971, Bielecka *et al.* 2000, Gorokhova *et al.* 2000). It is also a thermophilous species (Mordukhai-Boltovskoi & Rivier 1971) and its abundance varies yearly according to temperature (Antsulevich & Välipakka 2000, Leppäkoski *et al.* 2002a, but see Ojaveer *et al.* 2004), reaching a maximum in late summer/early autumn (Ojaveer & Lumberg 1995, Krylov & Panov 1998, Krylov *et al.* 1999, Antsulevich & Välipakka 2000, Gorokhova *et al.* 2000).

Cercopagis pengoi has two modes of reproduction: parthenogenesis and sexu-

al reproduction, *i.e.* gamogenesis (Mordukhai-Boltovskoi & Rivier 1971). The change from asexual to sexual reproduction in cladocerans is induced by chemical signals from conspecifics and possibly also from predators (reviewed in Larsson & Dodson 1993). In the Baltic, parthenogenesis is prevalent for most of the summer and gamogenic females and males are rare (Grigorovich *et al.* 2000, Gorokhova *et al.* 2000, Uitto *et al.* 1999, Simm & Ojaveer 2006). The major production of gamogenic resting eggs begins in late summer (Krylov & Panov 1998, Antsulevich & Välipakka 2000, Gorokhova *et al.* 2004, Simm & Ojaveer 2006). The eggs hatch in May and the first generation is morphologically distinct from the following parthenogenic generations (Simm & Ojaveer 2006). In the Caspian Sea, cercopagids undergo DVM (Mordukhai-Boltovskoi & Rivier 1971), but this behaviour has not been reported from the Baltic Sea (Krylov *et al.* 1999) or Lake Ontario (Benoit *et al.* 2002, Laxson *et al.* 2003). The body length of the female is 1.2–2.3 mm and that of the male 1.1–2.1 mm (Ojaveer & Lumberg 1995, MacIsaac *et al.* 1999, Bielecka *et al.* 2000, Grigorovich *et al.* 2000, Makarewicz *et al.* 2001). The caudal appendage of *C. pengoi* can be as much as 8–10 times body length, terminating in a distinctive loop (Mordukhai-Boltovskoi & Rivier 1971, MacIsaac *et al.* 1999, Grigorovich *et al.* 2000, Makarewicz *et al.* 2001, Simm & Ojaveer 2006), and probably serves as an antipredator defense (Makarewicz *et al.* 2001, Laxson *et al.* 2003).

Cercopagis pengoi is a predatory cladoceran: it has raptatory thoracopods with no filtering exopods (Mordukhai-Boltovskoi & Rivier 1971, MacIsaac *et al.* 1999). It feeds on zooplankton (Laxson *et al.* 2003, Gorokhova *et al.* 2005) and may control

zooplankton abundances during occurrence at high densities (Uitto *et al.* 1999, Benoit *et al.* 2002, Laxson *et al.* 2003, Kotta *et al.* 2004, Ojaveer *et al.* 2004, Lehtiniemi & Gorokhova unpubl. data). Since its invasion of the Baltic, *C. pengoi* has become important prey for Baltic herring, European sprat *Sprattus sprattus* L. 1758, sticklebacks and smelt (Ojaveer & Lumberg 1995, Antsulevich & Välipakka 2000, Gorokhova *et al.* 2004, 2005, Ojaveer *et al.* 2004, Peltonen *et al.* 2004), while pelagic mysids (Gorokhova & Lehtiniemi unpubl. data) and *Neomysis integer* (Gorokhova in press) also prey on *C. pengoi*. However, *C. pengoi* may be a strong competitor for zooplankton food with planktivorous fish (Benoit *et al.* 2002, Laxson *et al.* 2003, Ojaveer *et al.* 2004, Peltonen *et al.* 2004, Gorokhova *et al.* 2005) and possibly also with mysid shrimps (Kotta *et al.* 2004). Due to its caudal appendage, *C. pengoi* individuals easily become entangled, forming dense aggregations, e.g. on fishing gear, which may cause economic losses to fishermen in the Baltic (Ojaveer & Lumberg 1995, Antsulevich & Välipakka 2000, Bielecka *et al.* 2000).

3.4 Three-spined stickleback *Gasterosteus aculeatus* L.

The three-spined stickleback is a small, euryhaline fish (adult size 35–80 mm) that is found in fresh, marine and brackish waters throughout the Northern Hemisphere (Wootton 1984). It is the most common fish species in the littoral zones of the northern Baltic Sea (Lemmetyinen & Mankki 1975, Sundell 1994, Rajasilta *et al.* 1999). Adult stickleback migrate from the open sea in early spring to spawn in coastal waters, and the larvae and juveniles are very abundant in shallow bays during July and August (Lemmetyinen & Mankki 1975, Rajasilta

et al. 1999). During the breeding season, stickleback are territorial: the males select and defend territories in which they build nests and to which the females are attracted to lay eggs (Keenleyside 1955, Wootton 1984).

Although the three-spined stickleback is of no commercial importance, it is a central link in the trophic web of the Baltic Sea (Lemmetyinen & Mankki 1975). It is a visual predator (Wootton 1984) and feeds on zooplankton, littoral mysids, benthic invertebrates, and fish eggs and larvae (Lemmetyinen & Mankki 1975, Hangelin & Vuorinen 1988, Thiel 1996, Ojaveer *et al.* 2004, Peltonen *et al.* 2004). Three-spined stickleback constitute an important part of the diet of several waterfowl species and fish (Lemmetyinen & Mankki 1975, Wootton 1984, Reimchen 1994).

3.5 Predators

The European perch is a freshwater species that is widely distributed throughout Europe, and it is also the most common freshwater species in shallow areas of the Ekenäs Archipelago (Sundell 1994, Lappalainen *et al.* 2001). It is the main target of the recreational fishery in Finnish sea areas (Finnish Game and Fisheries Research Institute 2004). The perch is a food generalist that undergoes a series of ontogenetic niche shifts, whereby its diet changes (Sandström 1999). In the study area, mysids, together with amphipods and fish are the main food items for smaller perch (12–20 cm total length), whereas larger perch (> 20 cm TL) feed mainly on fish, including gobies, herring and three-spined stickleback (Lappalainen *et al.* 2001). The perch is a visual predator that needs sufficient light levels for foraging (Diehl 1988, Diehl & Kornijów 1997, Sandström 1999).

The Baltic herring is a pelagic schooling species, although it spawns in coastal areas (Laine 2003). It is a visual predator that consumes mainly zooplankton and mysids (Aneer 1980, Hansson *et al.* 1990, Rudstam *et al.* 1992, Arrhenius & Hansson 1993, Koho 2005), competing for zooplankton food with sprat (Rönkkönen *et al.* 2004, Koho 2005). The Baltic herring is the most important commercial fish species in Finnish sea areas (Finnish Game and Fisheries Research Institute 2005). In recent decades the weight-at-age of Baltic herring has decreased significantly, presumably caused by a salinity-induced change in zooplankton species composition (Flinkman *et al.* 1998, Cardinale & Arrhenius 2000, Rönkkönen *et al.* 2004), and food competition with sprat (Casini *et al.* 2006). The mysid populations in the Baltic also have declined, possibly due to poor oxygen conditions on the bottom, and these energetically profitable food items occur in the stomachs of large herring less often than before (Arrhenius & Hansson 1993, Koho 2005). In addition, the nonindigenous cladoceran *Cercopagis pengoi* has altered the pelagic food web structure, and although several studies indicate that it is a preferred food item for herring (Ojaveer & Lumberg 1995, Ojaveer *et al.* 1999, 2004, Antsulevich & Välipakka 2000, Gorokhova *et al.* 2004), the full effects of this invasion on the predator-prey and competitive interactions between Baltic planktivores remain to be resolved.

3.6 Aquatic macrophytes

Aquatic macrophytes were included in the study as possible predation refuges for littoral planktivores. The bladderwrack *Fucus vesiculosus* (Phaeophyceae) is a perennial marine brown alga and the

dominant (the only one in the study area) canopy-forming macroalga in the Baltic Sea (Jansson *et al.* 1982, Kautsky *et al.* 1992, Snoeijs 1999). Its northern distribution limit is at the Bothnian Sea/Bothnian Bay boundary where the salinity is about 4 psu (Jansson *et al.* 1982, Kautsky *et al.* 1992, Snoeijs 1999). *Fucus vesiculosus* forms belts between 0.3 and 12 m in depth, depending on the water clarity (Haage 1975, Jansson *et al.* 1982, Kautsky *et al.* 1992, Snoeijs 1999). It requires clean, hard substrates to attach its thallus (Kangas *et al.* 1982, Eriksson & Johansson 2003) and is therefore found on rocky shores (Snoeijs 1999). It is often covered with epiphytic algae (Kautsky *et al.* 1992, Snoeijs 1999) and supports a diverse community of fish and invertebrates (Haage 1975, Kangas 1978, Jansson *et al.* 1982, Kautsky *et al.* 1992, Hemmi 2003).

The stonewort *Chara tomentosa* L. (Characeae, Chlorophyta) is a macroalga of freshwater origin, but is also found in brackish waters (Snoeijs 1999). In the Baltic Sea it is restricted to sheltered coastal bays (Schubert & Yousef 2001). It requires clear water and soft bottoms, where it is anchored by rhizoids (Kautsky 1988, Munsterhjelm 1997, 2005, Snoeijs 1999). *Chara tomentosa* is very sensitive to anthropogenic changes in the environment, such as eutrophication (Koistinen & Munsterhjelm 2001, Munsterhjelm 2005).

The Eurasian watermilfoil *Myriophyllum spicatum* L. (Haloragaceae) is a freshwater vascular plant species that is also adapted to living in brackish water (Aiken *et al.* 1979, Snoeijs 1999). *Myriophyllum spicatum* is very abundant in the Ekenäs Archipelago (Munsterhjelm 1997, Wallström *et al.* 2000) as well as in other coastal areas in the Baltic Sea, growing at 1–5-m depths (Smith & Barko 1990). It benefits

from eutrophication and has increased in recent decades (Munsterhjelm 1997, Eriksson *et al.* 2004, Roos *et al.* 2004). It is a strong competitor (Grace & Wetzel 1978, Kautsky 1988, Smith & Barko 1990, Madsen *et al.* 1991) and was introduced into North America by the 1880s, where it has become a nuisance plant, replacing many native species (Aiken *et al.* 1979, Nichols & Shaw 1986, Smith & Barko 1990, Madsen *et al.* 1991).

The northern watermilfoil *Myriophyllum sibiricum* Kom. is a circumpolar freshwater plant species occurring in Eurasia, Greenland and North America (Aiken 1981, Ceska & Ceska 1986). In North America, it was first described as *M. exalbescens* Fernald, which is now considered a synonym for *M. sibiricum* (Ceska & Ceska 1986). The species is very similar in appearance to *M. spicatum*, but since it requires a more sheltered habitat than *M. spicatum*, it is not as widely spread in the study area.

4. OBJECTIVES OF THE STUDY

There were two main goals in the studies of this thesis, of which the first was to reveal how Baltic planktivores, inhabiting both littoral and pelagic environments, detect their predators. The objective was to determine the importance of chemical and visual predator cues in predator detection (I, II, IV). The second main goal was to reveal how planktivores modify their behaviour to avoid predation, once they have detected the presence of a predator. All the planktivores studied are important prey for a number of predators, including perch and Baltic herring. The main objective was to examine the different antipredator strategies and the flexibility in behaviour of the various planktivore species (I–IV).

The experiments with pelagic planktivores, *i.e.* *Mysis mixta*, *M. relicta*, and *Cerropagis pengoi*, focused on feeding behaviour (II). The objective was to examine how they change their feeding activity and prey selectivity in response to chemical predator cues from herring (II). Other aspects of antipredator behaviour, *i.e.* swimming activity (I, IV), hiding (I, IV) and swarming (III), were also studied in experiments with the littoral planktivores *Neomysis integer*, *Praunus flexuosus* and stickleback larvae. The objectives were to determine how littoral planktivores change their swimming activity, refuge use and feeding activity in response to predator cues from perch (I, IV) and to examine how the swarming behaviour of *N. integer* is used as an antipredator strategy (III).

In addition to the antipredator behaviour as such, one of the main factors affecting the predation vulnerability of planktivores in the littoral zone was also examined: aquatic macrophyte vegetation. The relative abundance of the different macrophyte species changes along with environmental changes, especially eutrophication. The objectives were to determine the differences between littoral planktivore species in their refuge use, as well as the differences between the macrophyte species (I, IV).

Manipulative experiments were carried out in the laboratory (I–IV). In addition, previously unpublished field data are included in the thesis to obtain additional information on the effects of macrophytes on the survival and distribution of littoral mysids. Field mortality experiments were conducted with *N. integer* and both intact and broken stems of *Myriophyllum spicatum* to determine the lethality of this macrophyte in a natural setting. In the distribution study, mysids were sampled in four

shallow bays with different macrophyte communities to investigate the effects of macrophyte species composition on the occurrence and distribution of mysids.

5. MATERIALS AND METHODS

All studies were conducted at the Tvärminne Zoological Station (TZS) (University of Helsinki) and its nearby sea areas, located in the Ekenäs Archipelago, or aboard the R/V Aranda (Finnish Institute of Marine Research).

5.1 Laboratory experiments

5.1.1 Sampling

5.1.1.1 Littoral planktivores. All sampling was performed during the day near TZS in the littoral zone (depth 0–2 m). *Neomysis integer* (I, III, IV) (mean length 16.0–18.2 mm) were caught with a hand net equipped with a long handle, or with a beach seine. *Praunus flexuosus* (I, IV) (mean length 23.6–24.1 mm) were caught with a hand net that was pulled through *Fucus vesiculosus* vegetation. Three-spined stickleback larvae (IV) (mean TL 9.1 mm) were caught with a hand net from a shallow lagoon. The animals were transported to the laboratory in ambient seawater.

5.1.1.2 Pelagic planktivores. Pelagic mysids and *Cercopagis pengoi* (II) were collected aboard the R/V Aranda. *Mysis mixta* (mean length 12.8 mm) were collected from stations in the Bothnian Sea, and *M. relicta* (mean length 15.9 mm) from stations in the Bothnian Sea and the Bothnian Bay. The mysids were caught at night using a plankton net (mesh size 0.5 mm, diameter 0.8 m and length 3 m) with a cod end, which was lowered near

the bottom and then lifted slowly to the surface. *Cercopagis pengoi* (mean length 2.4 mm) were collected during day at a station in the Gulf of Finland, from 50 m to the surface with a WP-2 plankton net (200 µm) equipped with a cod end.

5.1.1.3 Predators. Perch (I, III, IV) were caught in a fish trap from a shallow bay near TZS. The trap was set up in the evening and emptied the following morning. The fish were transported to the laboratory in ambient seawater. Baltic herring (II) were caught in Helsinki with hook and line. The chemical predator cue from perch (I, III, IV) was prepared by keeping the fish for about 6 h before the experiments in a 30–80 l container, where they were fed littoral mysids or stickleback larvae, according to the experiment in which the chemical cue was used. The visual predator cue from perch (I, III, IV) was accomplished by placing a perch in an aquarium next to the experimental aquarium. Since herring were not available during the experiments aboard the R/V Aranda, the chemical predator cue from herring (II) was prepared beforehand by keeping the fish in a 10 l container for about 30 min immediately after catching. The water containing the herring cue was frozen, melted just before the experiments and sieved through a 100 µm net to remove impurities.

5.1.1.4 Aquatic macrophytes. All macrophytes studied as predation refuges for littoral planktivores were collected near TZS with a rake. *Chara tomentosa* (I, IV), *Myriophyllum spicatum* and *M. sibiricum* (IV) were collected from shallow bays and *Fucus vesiculosus* (I) from rocky littoral. The artificial vegetation, used as a control, consisted of green plastic strings attached to metal plates.

5.1.1.5 Zooplankton and brine shrimp. Zooplankton, which were used as prey in the experiments in paper II, were collected from various stations around the northern Baltic Sea while aboard the R/V Aranda, from 30 m to the surface with a WP-2 plankton net (100 μ m). For the experiments in papers III and IV, zooplankton were collected with a plankton net (100 μ m) from about 20 m to the surface in an open sea area near TZS (Storfjärden, 59°57'30" N, 23°16' E, depth 33 m). Brine shrimp (*Artemia* sp.), which were used as prey in experiments in papers I and III, were hatched from commercially available eggs at 26 °C in 20-psu water with strong aeration.

5.1.2 Feeding experiments

Feeding experiments were conducted with the littoral mysids *Neomysis integer* (I, III) and *Praunus flexuosus* (I), with the pelagic mysids *Mysis mixta* and *M. relicta* (II) and the cladoceran *Cercopagis pengoi* (II). In addition, the feeding rate of the stickleback larvae was determined in the video filming experiments (IV).

The ingestion rate experiments (I) were performed to test the effects of visual and chemical predator cues from perch on littoral mysid (*N. integer* and *P. flexuosus*) feeding rates on brine shrimp. The experiments were conducted at TZS and performed in 2 l aquaria at ambient water temperature (9–16 °C) under normal indoor lighting conditions. Each set of experiments lasted about 3 h.

The two-prey experiments (II) were conducted aboard the R/V Aranda and performed at 13 °C in 1 l clear glass bottles with two prey types, evasive and nonevasive, offered together to the planktivore, *i.e.* *M. mixta*, *M. relicta* and *C. pengoi*. Experiments with mysids were conducted in the dark and those with *C. pengoi* in light, be-

cause the eyes of *Mysis* spp. are not used to light. To study the effect of predator presence on prey selection, we used a chemical predator cue from herring. The incubations were terminated after 2 h (with mysids) or 12 h (with *C. pengoi*).

In the natural prey experiments (II), ingestion rates and prey selection of mysids (*M. mixta* and *M. relicta*) in natural zooplankton assemblages was studied with and without a chemical predator cue from herring. The experiments were performed aboard the R/V Aranda, and the experimental procedures were the same as those in the two-prey experiments. After 2 h of incubation, the mysids were preserved in buffered 4% formalin. The stomach contents of preserved mysids were examined, compared with the zooplankton assemblage offered, and prey selection was estimated by calculating selection indices.

The swarming experiments (III) were conducted at TZS to compare the effects of chemical and visual predator cues from perch on feeding rates of *N. integer* on brine shrimp when feeding alone or in a group of 20 individuals. The experiments with single mysids were performed in cubic 1 l aquaria (width 10 cm \times depth 10 cm \times height 10 cm) and the experiments with 20 mysids in rectangular 20 l aquaria (26 cm \times 37 cm \times 20 cm) at ambient water temperature (9–12 °C) in normal indoor lighting conditions. The experiments lasted about 1 h.

All feeding rates were calculated as prey per predator per hour.

5.1.3 Video filming

The antipredator behaviour of the littoral mysids *Neomysis integer* and *Praunus flexuosus* (I, IV) and stickleback larvae (IV) was studied by video filming at TZS. The effects of chemical and visual perch cues

and different aquatic macrophyte refuges (*Chara tomentosa*, *Fucus vesiculosus*, *Myriophyllum spicatum* and artificial vegetation) were studied. The experiments were conducted under conditions similar to those in the ingestion rate experiments described above, except for the *M. spicatum* experiments with mysids (IV) that were conducted in a larger cubic aquarium (20 cm × 20 cm × 20 cm). The behaviour of the mysids was studied for 15 min and the behaviour of sticklebacks for 20 min by video filming. The time spent swimming and hiding within the vegetation were determined from the films, as well as the attack rate of sticklebacks on zooplankton.

5.1.4 Swarming experiments

The swarming experiments (III) were undertaken to determine how predator cues from perch influence the swarming behaviour of *Neomysis integer*. The experiments were conducted at TZS and performed in a 150 l rectangular tank (width 100 cm × depth 50 cm × height 30 cm) with 100 l of water at ambient water temperature (8–9 °C) under normal indoor lighting conditions. The tank was divided into three compartments: the middle part (width 40 cm × depth 50 cm × height 30 cm) was the experimental arena, which was separated from both end compartments (each 30 cm × 50 cm × 30 cm) by a transparent 200 µm net (cf. Fig. 1 in III). The end compartments contained the stimuli (predator or mysid swarms). The focal mysid was observed for 15 min and the total time spent within 6 cm of either net wall was recorded.

5.1.5 Mortality experiments

In addition to studying how the littoral planktivores use aquatic macrophytes as

predation refuges, their survival in different types of macrophyte vegetation was investigated in the mortality experiments (IV). They were conducted at TZS in rectangular 2.2 l aquaria (width 15.1 cm × depth 7.2 cm × height 20 cm) with *Myriophyllum spicatum* (*N. integer*, *P. flexuosus*, *G. aculeatus*), *M. sibiricum* (*N. integer*, *P. flexuosus*), *Chara tomentosa* (*N. integer*), or without macrophytes (*N. integer*, *P. flexuosus*, *G. aculeatus*), at 16 °C under normal indoor lighting conditions. The experiments lasted for 3 h, after which the survival of the animals was determined.

5.2 Field studies

5.2.1 Field mortality experiments

The field mortality experiments (unpublished) were undertaken to determine if *Myriophyllum spicatum* vegetation kills *Neomysis integer* individuals under natural conditions, as it did in the laboratory experiments (IV, see below). The experiments were conducted in September 2004 in a shallow bay (Jovskärsfladan) near TZS. The mysids were collected with a hand net from the littoral zone in the evening preceding each experiment and transported immediately to the laboratory, where they were kept in 20 l containers in ambient seawater with aeration. The mysids were not fed before the experiments.

The experiments were conducted in rectangular cages (height 100 × width 30 × depth 30 cm). The walls of the cages were plankton nets (mesh size 500 µm) fitted around a metal frame. The floors and the roofs of the cages were of cotton fabric equipped with opening and closing devices. There were two *M. spicatum* treatments in the field experiments, the first of which was

conducted with intact vegetation, because the stems of *M. spicatum* had to be cut to fit the aquaria in the mortality experiments conducted in the laboratory (IV). With the aid of a self-contained underwater breathing apparatus (SCUBA) diver, the cages were placed in dense *M. spicatum* patches about 2 m apart and secured in an upright position with the help of weights. Each cage was carefully placed around approx. eight intact stems and the floor was closed tightly around them to prevent mysids and predators from exiting and entering the cages. The second *M. spicatum* treatment was conducted with naturally broken stems, which could be abundantly found from the shoreline of TZS. The cages, with their floors closed, were placed on bare sediment as described above. Eight broken stems were added to each cage. In both treatments, 10 mysids were added to each cage through the roof, which was then closed tightly. There were five replicates in each treatment.

The incubation lasted about 20 h (intact vegetation 20.02 ± 0.07 , broken stems 20.44 ± 0.12), after which the cages were lifted up. The mysids were immediately counted and determined as dead or alive. The water temperature in the bay ranged from 12.6 to 14.3 °C and oxygen levels from 8.2 to 10.2 ppm during the experiments. The water level always reached the upper half of the cages, but at no time were the cages completely submerged.

5.2.2 Distribution study

In the distribution study (unpublished), the occurrence and distribution of mysids were examined in relation to aquatic macrophyte species composition. The mysids were sampled with a beach seine from four different shallow bays in the Ekenäs Archipelago: Solbacksfladan, Älgöfladan, Danskogsfladan, and Åkernäsfladan (Table 1) three times (May, June and July) during

Table 1. Characteristics of the flads. There are no data on the area of Danskogsfladan, but it is approximately the same as in Åkernäsfladan. The dominant vegetation is listed according to Munsterhjelm (1997) and Wallström et al. (2000).

	Solbacksfladan	Älgöfladan	Danskogsfladan	Åkernäsfladan
Location	N 59°54'01'' E 23°21'25''	N 59°52'20'' E 23°22'15''	N 59°53'87'' E 23°23'25''	N 59°53'39'' E 23°28'36''
Mean depth (m)	0.8	1.5	App. 1.5	0.6
Max. depth (m)	2.2	> 4.3	2.6	4.0
Area (km²)	0.13	0.6	–	0.16
Dominant vegetation	<i>Chara tomentosa</i> , <i>C. baltica</i> , <i>Najas marina</i>	<i>Myriophyllum spicatum</i> , <i>Potamogeton</i> spp.	<i>Myriophyllum spicatum</i> , <i>Potamogeton pectinatus</i> <i>Vaucheria</i>	<i>Chara tomentosa</i> , <i>Potamogeton pectinatus</i>
Sampling dates	May 8 th June 11 th July 9 th	May 8 th June 12 th July 11 th	May 8 th June 11 th July 9 th	May 8 th June 12 th July 11 th

the summer of 2001. Five seine samples were taken at each bay at each date. All the mysids in the samples were identified to species and counted. The water temperature was recorded and the salinity measured with a salinometer at each location (Fig. 1a-b). The macrophyte species composition at each sample site was taken from the literature (Munsterhjelm 1997, Wallström *et al.* 2000).

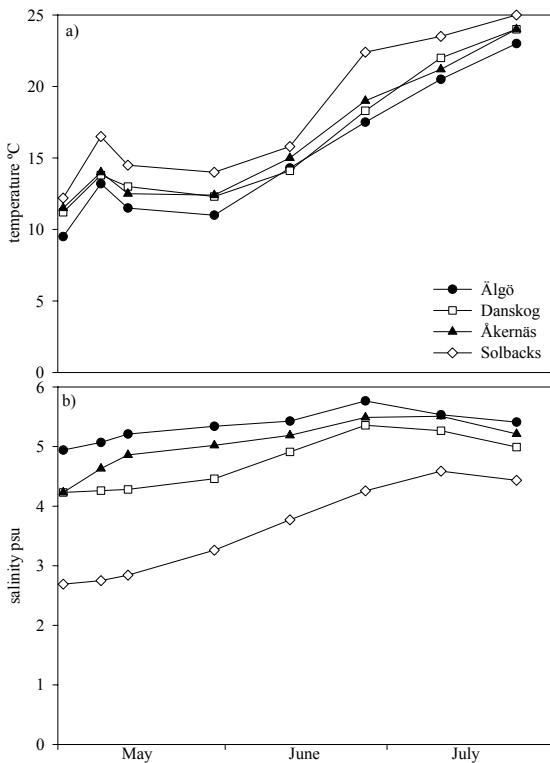


Figure 1. Water temperature (°C) and salinity (psu) in each bay during the field sampling period.

5.3 Statistical analyses and equations

The data were tested for statistical significance with parametric tests, if the appropriate assumptions were fulfilled, *i.e.* the normal distribution of the data and homogeneity of variances. In some cases transformations ($\log(x+1)$ or \arcsin) were used to fulfil these assumptions. The parametric tests used were the t-test (I–III), one-way (III) and two-way (I, III, IV) analysis of variance (ANOVA), and three-way analysis of covariance (ANCOVA) (II). Otherwise nonparametric tests were used, *i.e.* the Mann-Whitney U-test (II–IV), Wilcoxon signed ranks test (III), Kruskal-Wallis one-way ANOVA (IV) and Fisher's exact test (II, IV, field mortality experiments). Tukey HSD multiple comparisons was used as the posthoc test (IV).

The chi-squared-based selectivity index C (II) was calculated using Yates' correction for continuity (Pearre 1982). The C index was chosen because it is zero-valued for no selection, is symmetrical (ranging between -1 and $+1$), is not sensitive to rare prey species and is statistically testable (Pearre 1982).

$$C = \pm (\chi^2_y/n)^{1/2} \text{ or}$$

$$C = \pm [(|a_d b_e - b_d a_e| - n/2)^2 / abde]^{1/2} \quad (1)$$

where

	Species		
	A	Others	Total
Diet	a_d	b_d	$a_d + b_d = d$
Environment	a_e	b_e	$a_e + b_e = e$
Total	$a_d + a_e = a$	$b_d + b_e = b$	$a_d + a_e + b_d + b_e = n$

6. RESULTS AND DISCUSSION

6.1 Predator detection

All the planktivores studied detected predators by the emitted cues. Changes in feeding rate were used as a measure of predator detection (Magurran 1990, Jachner 1997, Ejdung 1998). Hamrén & Hansson (1999) found that *Mysis mixta* decreases its feeding rate in response to the odour of Baltic herring, indicating that the mysid can detect its predator by chemical cues. The experiments reported in this thesis confirmed this finding for *M. mixta* (II), and it also held for *M. relicta* (II), the cladoceran *Cercopagis pengoi* (II), and three-spined stickleback larvae (IV). In contrast, the littoral mysids *Neomysis integer* and *Praunus flexuosus* did not respond to either chemical or visual predator cues alone, but when combined these predator cues resulted in a reduction in their feeding rate (I).

The differences in predator detection abilities of pelagic and littoral mysids may be explained by the different habitats they live in. Mysids have well-developed compound eyes and are known to use vision in various situations (Fulton 1982, Lindström 2000). However, pelagic mysids live in near darkness, remaining near the bottom during day and rising up only at night (Salemaa *et al.* 1986, Rudstam *et al.* 1989, Hansson *et al.* 1990, Rudstam & Hansson 1990), and probably have little use for vision. Littoral mysids, in contrast, can utilize vision in the well-lit shallow water they inhabit (Lindström 1992). Both *N. integer* and *P. flexuosus* are well adapted to the light regime in aquatic vegetation, where the chlorophyll of macroalgae and vascular plants absorbs longer wavelengths (Lindström 2000). Thus, the differences in habitats apparently affect the way in which mysids detect pred-

ators: chemical cues are relatively more important for pelagic than littoral mysids, and the ability of pelagic mysids to detect predators by chemical cues alone is important for their survival.

Although the sticklebacks used in these experiments were immature, their predator detection abilities (IV) were more precise than that of adult littoral mysids (I), which occupy the same habitat. This difference is derived most likely from the better-developed sensory system of vertebrates compared with invertebrates. The sensory systems of larval fish are not all functional throughout posthatching development (Bailey & Houde 1989), and larger larvae are better able to judge the magnitude of threats (Fuiman 1993). Thus, the predator detection abilities of stickleback larvae continue to develop as they grow and interindividual variation in this development plays a major role in their survival. Growth rate alone does not explain the differences in early life mortality, but it is coupled with the development of sensory and locomotory performance (Fuiman *et al.* 2005). There may be significant differences in fish larvae of the same species and size in their predator recognition and avoidance abilities (Vilhunen & Hirvonen 2003, Fuiman *et al.* 2005).

The response of stickleback larvae was also stronger to combined chemical and visual cues than to the chemical cue alone (IV). Similar results were obtained previously with both stickleback and northern pike *Esox lucius* L. 1758 larvae (Lehtiniemi 2005, Lehtiniemi *et al.* 2005). Stickleback larvae are clearly capable of threat-sensitive behaviour (Bishop & Brown 1992), *i.e.* they interpret two simultaneous predator cues as a more convincing threat of predation. For larval newts *Notophthalmus viridescens* (Rafinesque 1820), visual predator cues alone carry only general information

on danger, and chemical cues are needed to fully evaluate the threat (Mathis & Vincent 2000). For fishes, the situation is reversed and visual cues are more important than chemical (Hartman & Abrahams 2000, Chivers *et al.* 2001b). Vision is also the predominant sensory modality of sticklebacks and they have good colour and form vision (Wootton 1984). Thus, visual predator cues combined with chemical cues result in stronger antipredator behaviour (IV).

Cercopagis pengoi invaded the Baltic Sea only 14 years ago (Ojaveer & Lumberg 1995); before that time it was not exposed to Baltic herring. Therefore, its ability to detect herring by chemical cues is quite remarkable and most probably a general strategy to avoid any fish predator, because *C. pengoi* is prey for many fish species in the Baltic and elsewhere (Antsulevich & Väli-pakka 2000, Charlebois *et al.* 2001, Bushnoe *et al.* 2003, Gorokhova *et al.* 2004, Ojaveer *et al.* 2004, Peltonen *et al.* 2004).

Cercopagis pengoi has a large compound eye (Grigorovich *et al.* 2000), but its visual capabilities, *e.g.* for image forming, are unknown. It is likely that chemical and hydromechanical cues are the most important for *C. pengoi* in detection of both prey and predators. A general fish avoidance strategy as well as acquiring species-specific predator detection would both favour the invasion and establishing of viable populations to new areas and thus be a major advantage for *C. pengoi*.

6.2. Decreased activity

The responses of the planktivores studied to predator cues were numerous and variable (Table 2). However, a feature common to all of the species was that they decreased their feeding rate in response to predation threat (I–IV), *i.e.* exhibited an inducible antipredator defence (Sih 1987). Decreased

Table 2. Antipredator behaviours of Baltic planktivores (I–IV).

Study object		<i>Neomysis integer</i>	<i>Praunus flexuosus</i>	<i>Mysis mixta</i>	<i>Mysis relicta</i>	<i>Cercopagis pengoi</i>	<i>Gasterosteus aculeatus</i>
Cues needed for predator detection		Chemical + visual (I, IV)	Chemical + visual (I, IV)	Chemical (II)	Chemical (II)	Chemical (II)	Chemical, visual (IV)
Responses to predator cues	Feeding rate	Decreased (I, III)	Decreased (I)	Decreased (II)	Decreased (II)	Decreased (II)	Decreased (IV)
	Prey selection	–	–	Decreased (II)	Decreased (II)	Increased (II)	–
	Swimming activity	Decreased (I, IV)	No change (I, IV)	–	–	–	Decreased (IV)
	Swarming	No change (III)	–	–	–	–	–
	Hiding	No change (I, IV)	Increased (I, IV)	–	–	–	Increased (IV)

feeding activity may reflect the increased vigilance of the individuals, which remain alert for possible attacks by the predator detected, and hence focusing less on locating and capturing food items. Reduced feeding as an antipredator behaviour involves a clear trade-off, *i.e.* reduced energy intake, which can have a fundamental impact on individual fitness (Tiselius *et al.* 1993, van Duren & Videler 1996, Tsuda *et al.* 1998, Hölker & Stief 2005, Lehtiniemi 2005). Continuous, efficient feeding is especially important to larval fish, which need to grow rapidly to be able to survive the following winter and to outgrow predators (Adams & DeAngelis 1987, Bailey & Houde 1989, Pedersen 1997).

Neomysis integer (I, IV) and stickleback larvae (IV) also decreased their swimming activity in response to predation threat, whereas *Praunus flexuosus* did not (I, IV). *Praunus flexuosus* is closely associated with aquatic vegetation and relies primarily on hiding in its predator avoidance behaviour (I, IV). Hiding may decrease the need for the prey to reduce its activity in the presence of predators, because hiding decreases the abilities of predators to detect prey (Diehl & Kornijów 1997). On the other hand, reduction in activity may in some cases result from the increased use of a refuge (Lima & Dill 1990, Lima 1998a,b, Laurel & Brown 2006), which may have been the case for stickleback larvae (IV). Decreased swimming may be, as an alternative to hiding, a way to avoid being detected by the approaching predator (Lima 1998b), especially when the predator locates prey primarily through vision or the lateral line. Decreased activity is especially useful in environments without physical structure, where movement is easily perceived visually (O'Brien 1987, Tiselius *et al.* 1993, Kiørboe & Visser 1999, Kiørboe *et al.*

1999, but see Torgersen 2003). Prey may also limit their activity to places or times at which predators are inactive, *i.e.* use spatial or temporal refuges (Lima 1998b, Tsuda *et al.* 1998, Torgersen 2003, Takahashi *et al.* 2004). For example, planktonic animals with full guts are visually more conspicuous, and hence they may limit their feeding activity to nighttime (Ohman 1988, Cieri & Stearns 1999).

In addition to antipredator benefits, swarming may increase feeding (Foster 1985, Clark & Mangel 1986, Ryer & Olla 1992, Ritz 1994, Milne *et al.* 2005) and mating efficiency (Clutter 1969, O'Brien 1988, Ritz 1994, Ribes *et al.* 1996) and bring advantages in energy use (Hough & Naylor 1992, Ritz 2000). When *N. integer* were feeding in a swarm, their feeding rate was not significantly decreased in the presence of a predator, as when the mysids were feeding alone (III). This may be attributed to collective vigilance, *i.e.* the individual that has detected the predator informs the others in the group, which enables individuals to spend less time being alert for predators and allocate more time to feeding (Clutter 1969, Clark & Mangel 1986, Lima & Dill 1990, Magurran 1990, Ritz 1994). Group size, position of the individual within the group and group composition are important factors in vigilance (Lima & Dill 1990, Peuhkuri 1997, Lima 1998b).

6.3 Prey selection

Reduced feeding activity can involve prey selection: the prey switches its own diet towards food items that are easier to detect, catch and ingest, which reduces the effort required in swimming activity and enables alertness (Lima & Dill 1990, Lima 1998b, Mikheev *et al.* 2002, Torgersen 2003), or

towards food items that, once ingested, do not make them more detectable by predators (Dill 1987). In addition to decreased feeding rate, the pelagic mysids *Mysis mixta* and *M. relicta* as well as the cladoceran *Cercopagis pengoi* altered their prey selection patterns in response to predation risk (II).

In the absence of predator cues, *C. pengoi* did not select for either prey type, evasive or nonevasive, and consumed them at similar rates, whereas when predator cues were present, it consumed more nonevasive than evasive prey, significantly selecting for the nonevasive prey items (II). The evasive prey, *i.e.* copepod nauplii, are energetically more profitable than the nonevasive prey, *i.e.* rotifers (Flinkman *et al.* 1998, Koski *et al.* 1999, Viherluoto & Viitasalo 2001a, Pertola *et al.* 2002). Thus *C. pengoi* switched to prey items that were easier to catch when under predation risk, although it would have gained more energy from the evasive prey. This gives the planktivore an opportunity to continue feeding and still maintain vigilance for predators, while remaining relatively inconspicuous (Lima & Dill 1990, Lima 1998b, Mikheev *et al.* 2002, Torgersen 2003), but includes a trade-off in terms of energy gain.

The behaviour of the mysids differed somewhat between the two types of experiment (II). In the experiments in which the mysids were offered two types of prey, evasive and nonevasive, *M. mixta* selected the nonevasive prey regardless of predator presence or absence (II). This is somewhat surprising, since the nonevasive prey, the rotifers, contain much less energy than the evasive prey, *Eurytemora affinis* Poppe (1880) copepodites (Flinkman *et al.* 1998, Koski *et al.* 1999, Viherluoto & Viitasalo 2001a, Pertola *et al.* 2002). Thus, in the absence of predator cues, *M. mixta* would have been expected to select the prey that

contains more energy. However, the strong flight reaction of copepodites (Browman *et al.* 1989, Viitasalo & Rautio 1998, Viitasalo *et al.* 1998) may explain why *M. mixta* selected the nonevasive prey. In the two-prey experiments, *M. relicta* did not exhibit significant prey selection in either predator treatment, although it consumed the more evasive prey, copepodites, in the absence of predator cues (II).

In contrast, both mysid species selected cladocerans in the absence of predator cues when they fed on a natural zooplankton assemblage, but exhibited no significant selection in their presence (II). Despite the ability of mysids to switch between raptorial and suspension feeding modes in response to prey availability (Viitasalo & Rautio 1998), *M. mixta* and *M. relicta* exhibited no switching behaviour in response to predation risk. However, they abandoned their selective feeding when predator cues were present, indicating that they were being more vigilant towards predators and focusing less on feeding, as was *C. pengoi*. Both increases, as in *C. pengoi*, and decreases, as in *Mysis* spp., in food selectivity in response to predation risk have been reported in vertebrates (Lima & Dill 1990, Lima 1998b).

In addition to the abundance of different prey items and predation pressure, the diet of an organism in the field is partly determined by its ability to detect an item from a distance (Gerritsen & Strickler 1977, Viherluoto & Viitasalo 2001a, Weissburg *et al.* 2002). Mysids utilize mainly mechanoreception to locate their prey (Cooper & Goldman 1980, Viitasalo *et al.* 1998, Viherluoto & Viitasalo 2001b), whereas the prey detection modes of *C. pengoi* are unknown. Another predatory cladoceran, *Leptodora kindti* (Focke 1884) (Haplopoda), initiates an attack only upon direct contact with po-

tential prey (Browman *et al.* 1989). More knowledge of the basic biology of *C. pen-goi* is needed to further examine its feeding behaviour.

6.4 Swarming

The aggregative behaviour of mysids has been studied extensively throughout the world (*e.g.* Steven 1961, Clutter 1969, Mauchline 1971c, Zelickman 1974, Dadswell 1975, O'Brien 1988, Carleton & Hamner 1989, Modlin 1990, Ohtsuka *et al.* 1995, Buskey 2000). However, studies from the Baltic Sea and of *Neomysis integer* are lacking (but see Byholm 1998). In the current study (III), *N. integer* individuals actively tried to join swarms. Swarming tendency was strong both in the presence and absence of a predator (III), indicating that it is a fixed strategy (Sih 1987) and not an inducible defence. Fixed defences are favourable when acquiring information on local predation risk is dangerous, or when local predation risk is consistently high (Sih 1987). This holds for *N. integer*, which inhabits shallow littoral zones together with a wide array of predators (Aarnio & Bonsdorff 1993, Thiel 1996, Hostens & Mees 1999, Granqvist & Mattila 2004).

Similarly, *N. integer* individuals preferred the larger swarm regardless of predator presence (III). The predation risk of an individual declines as the group size increases (Major 1978, Turner & Pitcher 1986, Ritz 1994, Byholm 1998, Foster *et al.* 2001). Coordinated avoidance or escape responses are easier to perform when the swarm is large (O'Brien & Ritz 1988). The predator often aims to break up the cohesive prey aggregation (Zelickman 1974, Major 1978, Magurran & Pitcher 1987, Parrish 1989, Foster *et al.* 2001), and as

the initial size of the aggregation increases, relatively fewer individuals will become separated from the main group. The avoidance of perch by *N. integer* individuals was stronger when the swarm was present (III), which indicates that stragglers, *i.e.* individuals separated from a swarm, are at greatest risk of being preyed upon (Parrish 1989, Lima & Dill 1990, Magurran 1990, Ritz 1994, Byholm 1998). Solitary *N. integer* individuals utilize decreased activity (I) and flight (Rademacher & Kils 1996) to avoid predation.

In addition to protection from predators, swarming also brings energetic (Hough & Naylor 1992, Ritz 2000) and feeding benefits (I) to *N. integer*. The ingestion rates were consistently higher, despite predator presence or absence, when the mysids were feeding in a swarm of 20 individuals than when alone (I). This can result from more efficient location of patchily distributed food or social facilitation (Clark & Mangel 1986, Ryer & Olla 1992, Ranta *et al.* 1993, Ritz 1994). As group size increases, however, interference and competition between group members become more intense (Clark & Mangel 1986, Lima & Dill 1990, Ranta *et al.* 1993, Ritz 1994). Thus, the feeding advantage observed in this study with a relatively small swarm may not be relevant in natural surroundings, where the densities of *N. integer* may reach 600 individuals per m² in the Baltic (Debus *et al.* 1992, Thiel 1992) or even higher in brackish lakes (Aaser *et al.* 1995, Søndergaard *et al.* 2000) and estuaries (Fockedeey 2005).

The fixed swarming behaviour of *N. integer* resembles that of other mysid species (Clutter 1969, Mauchline 1971c, Zelickman 1974, O'Brien 1988, Buskey 2000). Some other small aquatic animals exhibit more flexible swarming behaviour: grass shrimps *Palaemonetes pugio* Holthuis 1949 and *P.*

vulgaris (Say 1818) increase grouping behaviour as well as the number of individuals in a group under predation risk (Carson & Merchant 2005), and juvenile Atlantic cod *Gadus morhua* L. 1758 switch from an avoidance and hiding strategy to a schooling strategy, depending on habitat, predator type and population density (Laurel *et al.* 2004, Laurel & Brown 2006). However, *N. integer* individuals are clearly capable of observing their social situation, *i.e.* solitary occurrence vs. swarming, as well as ambient predation risk, and adapting their behaviour accordingly (III).

6.5 Hiding

Hiding decreases the possibility of being detected and recognized by predators (Ohman 1988, Lima & Dill 1990, Jeppesen *et al.* 1997). *Praunus flexuosus* (I, IV) and stickleback larvae (IV) increased their use of the vegetation refuge in response to the presence of predator cues, but *Neomysis integer* did not (I, IV). Instead, *N. integer* utilizes other antipredator behaviours, *e.g.* swarming (Mauchline 1971c, Byholm 1998, Fockedey 2005, III), decreased swimming (I, IV) and feeding (I, III) activity, and flight (Rademacher & Kils 1996). *Praunus flexuosus* spends its entire life in contact with aquatic vegetation (Kotta & Kotta 1999); thus hiding seems a natural antipredator strategy for this species, although not a fixed strategy (Sih 1987), since it is induced by predator cues.

Three-spined sticklebacks occupy a wide range of different habitats (Wootton 1984) and exhibit a similarly wide selection of antipredator defences. They have morphological defences, *e.g.* lateral plates, dorsal spines and cryptic coloration (Wootton 1984, Reimchen 1994). They

also exhibit variable behavioural defences: in addition to hiding (IV), they utilize reduced swimming and feeding activity (Wootton 1984, Bishop & Brown 1992, Godin & Crossman 1994, Lehtiniemi 2005, IV), schooling, both as young and adults (Keenleyside 1955, Wootton 1984, van Havre & FitzGerald 1988, Peuhkuri 1997), predator inspection (Wootton 1984, Bishop & Brown 1992, Godin & Crossman 1994) and flight (Wootton 1984, Bishop & Brown 1992). Different defences militate best against different predators, *e.g.* the perch is a superior forager in dense littoral vegetation compared with roach and bream *Abramis brama* L. 1758 (Diehl 1988). Stickleback larvae probably balance their antipredator behaviours according to the predator in question, available habitat, and developmental stage, *i.e.* capabilities of each individual, in an adaptive manner. For example, stickleback schools do not hide in vegetation as an antipredator response, as stickleback do when alone (Keenleyside 1955). Swarming is a less efficient strategy in habitats with aquatic vegetation (Savino & Stein 1982, Flynn & Ritz 1999, Laurel & Brown 2006), under conditions of poor visibility, *e.g.* night or turbidity (Brock & Riffenburgh 1960, Zelickman 1974, Twinning *et al.* 2000) and against predators that utilize ambush tactics (Flynn & Ritz 1999, Laurel & Brown 2006), schooling (Major 1978, Ritz 1994, Foster *et al.* 2001) or sensory modalities other than vision to locate their prey (Magurran 1990, Ritz 1994, Sørnes & Aksnes 2004).

There are also qualitative differences between refugia: aquatic vegetation may be structurally and chemically very different, depending on the macrophyte species that form the community (Coen *et al.* 1981, Ryer 1988, Lauridsen & Lodge 1996, Warfe & Barmuta 2004, Lehtiniemi 2005)

and the density of vegetation also plays a significant role (Vince *et al.* 1976, Savino & Stein 1982, Gotceitas & Colgan 1987, Stansfield *et al.* 1997, Snickars *et al.* 2004, but see Warfe & Barmuta 2004). The macrophyte species were utilized as a refuge differently, depending on the planktivore in question (I, IV) (Table 3). *Praunus flexuosus* preferred *Fucus vesiculosus* vegetation (I), and also sought refuge in *Chara tomentosa* (I) as well as in *Myriophyllum spicatum* vegetation (IV). In contrast, stickleback larvae strongly avoided *M. spicatum* in the absence of predator cues and, in the presence of predator cues, utilized it as a refuge less than artificial vegetation (IV). *Neomysis integer* spent significantly less time within *M. spicatum* vegetation than in artificial vegetation (IV). In addition to the planktivores studied, *M. spicatum* is repellent to cladocerans (Pennak 1973, Lauridsen & Lodge 1996).

The presence of *M. spicatum* also decreased the feeding rate of stickleback larvae (IV). Almost no attacks occurred within *M. spicatum* vegetation. The complex morphology of *M. spicatum* may lower the feeding efficiency of fish (Coull & Wells 1983), but since the feeding of stickleback larvae is unaffected by similarly structured *C. tomentosa* (Lehtiniemi 2005), the chemical properties of *M. spicatum* are likely to be more important (see below).

In pelagic environments where hiding within physical structures is impossible, other hiding mechanisms must be used. Crypsis, including mimicry of immobile objects and camouflage coloration, is often combined with decreased activity (Wootton 1984, Sih 1987, Sandström 1999, Merilaita 2001). Many planktonic organisms, *e.g.* crustaceans and larval fish, utilize transparency (Stemberger & Gilbert 1987, Bailey & Houde 1989, Langsdale 1993, Thet-

Table 3. Effects of aquatic macrophytes on Baltic littoral planktivores (I, IV, field mortality experiments, and distribution study).

A. Lethality		<i>Fucus vesiculosus</i>	<i>Chara tomentosa</i>	<i>Myriophyllum spicatum</i>	<i>Myriophyllum sibiricum</i>
<i>Neomysis integer</i>	Laboratory	–	0% (IV)	89% (IV)	0%
	Field	–	–	2–4%	–
<i>Praunus flexuosus</i>	Laboratory	–	–	73% (IV)	0% (IV)
<i>Gasterosteus aculeatus</i>	Laboratory	–	–	0% (IV)	–
B. Repellence					
<i>Neomysis integer</i>	Laboratory	No (I)	No (I)	Yes (IV)	–
	Field	–	No	Yes	–
<i>Praunus flexuosus</i>	Laboratory	No (I)	No (I)	No (IV)	–
<i>Gasterosteus aculeatus</i>	Laboratory	–	–	Yes (IV)	–

meyer & Kils 1995, Tsuda *et al.* 1998) and small size (O'Brien 1987, Tiselius *et al.* 1993, Tsuda *et al.* 1998, Kjørboe & Visser 1999, Sakwinska 2002) to avoid detection by predators. DVM, performed by pelagic mysids (Salemaa *et al.* 1986, Rudstam *et al.* 1989, Hansson *et al.* 1990, Rudstam & Hansson 1990), can be seen as use of a temporal refuge.

6.6 Effects of aquatic vegetation

6.6.1 Mortality

Myriophyllum spicatum was acutely lethal to littoral mysids in the laboratory in dense patches (IV). The mortality of *Neomysis integer* was 89% and that of *Praunus flexuosus* 73%. This is the first time a larger aquatic invertebrate was shown to be killed by submerged macrophytes, although the negative effects of *M. spicatum* on the growth and survival of mosquito and midge larvae were reported (Dhillon *et al.* 1982, Johnson & Mulla 1983). The surviving mysids were also in weak condition, turning from transparent to opaque (IV). In the control (filtered seawater), *M. sibiricum* and *Chara tomentosa* treatments no mortality of mysids was observed (IV). Three-spined stickleback larvae also experienced no mortality in the experiments (IV).

I suggest that the mortality may have been caused by polyphenols excreted by *M. spicatum* (Planas *et al.* 1981, Gross & Sütfeld 1994, Gross *et al.* 1996, Nakai *et al.* 2000, Gross 2003). Possible mechanisms behind the toxicity and repellence of polyphenols to both invertebrates and vertebrates are numerous, such as membrane-damaging activity or interference with catecholamine metabolism and other neural control mechanisms (reviewed by

Singleton & Kratzer 1969). However, *M. sibiricum*, albeit belonging to the same genus as *M. spicatum* and having a high phenolic acid content (Spencer & Ksander 1999), induced no mortality in mysids (IV). Therefore the mechanism that caused the high mortality in mysids remains unknown. *Myriophyllum spicatum* is also known to produce alkaloids (Ostrofsky & Zettler 1986) and fatty acids (Nakai *et al.* 2005) that may play a role.

Myriophyllum spicatum releases several polyphenols into the surrounding water (Gross & Sütfeld 1994), but tissue damage may facilitate the production and excretion of chemicals from aquatic macrophytes (Levin 1971, Cronin & Hay 1996). In the mortality experiments conducted in the laboratory (IV), the stems of *M. spicatum* had to be cut to fit the aquaria, which probably accelerated the release of chemicals. However, autofragmentation of *M. spicatum* plants typically occurs after flowering periods, as does damage by waves and human activities such as mechanical weed harvesting and boating traffic (Grace & Wetzel 1978, Aiken *et al.* 1979, Nichols & Shaw 1986, Smith & Barko 1990). Damaged *M. spicatum* stems commonly occur under natural conditions; therefore we conducted field mortality experiments with both intact and cut stems of *M. spicatum*.

The mortality of mysids was much lower in the field than in the laboratory, both in treatments with intact and with broken stems. One out of 50 mysids (2%) was found dead in the intact vegetation treatment and two (4%) in the broken stem treatment. The difference in mortality rates between the two treatments was not statistically significant (Fisher's exact test: $p = 0.5080$). A total of five mysids were not found after the experiments; these were probably lost in the recovery process.

The difference in the results of the laboratory and field mortality experiments may be explained by different dilution volumes present in the aquaria and in the bay. Although the bay where the field experiment was conducted is shallow, small, sheltered and has a low water exchange rate, the concentration of toxins released from *M. spicatum* vegetation is still unlikely to rise as high as in the aquaria where the laboratory experiments were conducted. Thus, *M. spicatum* vegetation may not cause mortality in mysids in the field as in the laboratory, or the mortality may be much lower, as observed in the field experiments. However, taking into account the life span of *N. integer*, mortality of even 2% per day can accumulate to significant mortality on the population level.

6.6.2 Distribution

Under natural conditions mysids are able to migrate away from toxic or otherwise unfavourable vegetation. In laboratory experiments (IV), *Neomysis integer* avoided *Myriophyllum spicatum* compared with artificial vegetation. The distribution of mysids in areas with different vegetation can give insight into the repellent effects of *M. spicatum* under natural conditions, although the varying physical conditions in different locations naturally also play a role. The hypothesis was that fewer mysids would be found at sites where *M. spicatum* dominates the macrophyte community.

The vegetation in Solbacksfldan is dominated by *Chara tomentosa* (Wallström *et al.* 2000). No mysids were found in Solbacksfldan at any sampling time. During the entire sampling period, the water in Solbacksfldan was warmer and less saline than in the other bays (Fig. 1a-b), which

may represent unfavourable physical conditions for mysids (Köhn 1992, Fockedeý 2005).

Älgöfladan is a relatively open bay and the vegetation is quite variable (Munsterhjelm 1997, Wallström *et al.* 2000). Several macrophyte species are found at the site where the mysids were sampled: *M. spicatum*, *M. sibiricum*, rigid hornwort *Ceratophyllum demersum* L., fennel pondweed *Potamogeton pectinatus* L. and fan-leaved water-crowfoot *Ranunculus circinatus* Sibth. (Wallström *et al.* 2000). *Neomysis integer* individuals were found in Älgöfladan only in May (Fig. 2). Macrophytes are not yet fully developed by that time and the later absence of mysids in the bay may be a sign of avoidance of the predominating *M. spicatum* vegetation. Älgöfladan had the lowest temperature and highest salinity of the bays studied throughout the study period (Fig. 1a-b), and hence these factors should not limit the occurrence of mysids. In addition to *N. integer*, one *Praunus flexuosus* individual was found in Älgöfladan in May and one in June.

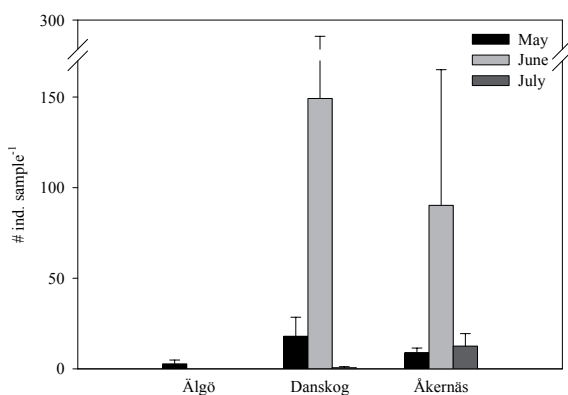


Figure 2. Number of *Neomysis integer* individuals (mean + SE) in field samples in each bay.

Most mysids were found in Danskogfladan and Åkernäsfladan, especially in June (Fig. 2). Most of Danskogfladan is covered by *Vaucheria* cf. *dichotoma* (L.) Martius and *M. spicatum* occurs only in the opening and immediately inside it (Munsterhjelm 1997). Mysids were sampled at two locations; one dominated by *C. demersum* and one by beaked tasselweed *Ruppia maritima* L. and *P. pectinatus* L. (Munsterhjelm 1997). Some common reed *Phragmites australis* (Cav.)

Trin. ex Steud. occurs at both sites (Munsterhjelm 1997). In June, when the highest abundance of mysids was recorded, most mysids occurred at the *Ruppia*-*Potamogeton* site (Fig. 3a), which could indicate avoidance of *C. demersum*. Three-spined stickleback larvae avoid *C. demersum* vegetation compared with *C. tomentosa*, even in the presence of cues from a predator (Lehtiniemi 2005). This repellence is probably chemically induced: *C. demersum* is repellent to a freshwater snail (Sterry *et al.* 1983) and it has an inhibitory effect on several phytoplankton species (Nakai *et al.* 1999, Körner & Nicklisch 2002, Gross 2003, Gross *et al.* 2003) and garden cress *Lepidium sativum* L. (Kleiven & Szczepanska 1988). It also produces alkaloids (Ostrofsky & Zettler 1986) that may serve as chemical deterrents, possibly also to mysids or their food.

In Åkernäsfladan mysids were sampled at three locations: one dominated by *C. tomentosa*, one by *C. demersum* and one by *M. spicatum*; *P. pectinatus* also occurs at each site (Wallström *et al.* 2000). Again the highest abundance of mysids was recorded in June, and most mysids occurred at the *Chara*-dominated site (Fig. 3b). These results lend support to the hypothesis that mysids do indeed avoid *M. spicatum* and *C. demersum* and prefer *C. tomentosa* vegetation as a habitat, as found in the laboratory experiments (I, IV) as well as with stickleback larvae (IV, Lehtiniemi 2005). Thus, even if the direct mortality of mysids caused by *M. spicatum* is quite low in the field, macrophyte species composition can have a strong effect on the distribution of mysids, and most likely on other organisms, such as fish larvae, as well (Keast 1984, Carpenter & Lodge 1986).

Very high (> 9) and stable pH values have been found in *M. spicatum* vegetation both in the laboratory and in the field

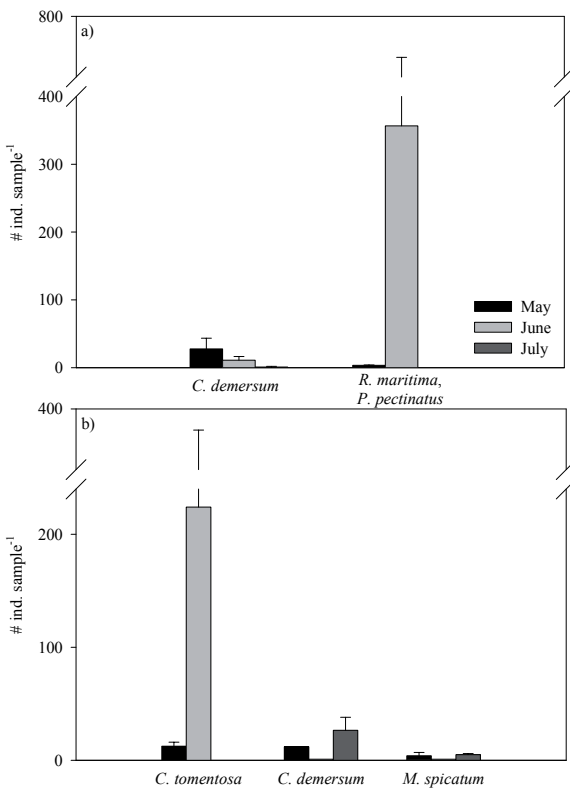


Figure 3. Number of *Neomysis integer* individuals (mean + SE) in a) Danskogfladan at two sampling locations, dominated by *Ceratophyllum demersum* and *Ruppia maritima*/*Potamogeton pectinatus*, and b) Åkernäsfladan at three sampling locations, dominated by *Chara tomentosa*, *Ceratophyllum demersum* and *Myriophyllum spicatum*.

(Eicher 1946, Halstead & Tash 1982). This probably gives *M. spicatum* a competitive advantage for carbon over phytoplankton, since it is able to utilize HCO_3^- ions at elevated pH (Grace & Wetzel 1978), but it also has a major impact on aquatic animals, since few species, especially very few fish species, have adapted to tolerate high levels of pH (Trama 1954, McCarragher 1971, Daye & Garside 1975, Witschi & Ziebell 1979, Wootton 1984). Unfortunately there are no data available on the pH of the bays studied, but pH may have a significant impact on the distribution of both mysids and larval fish in vegetated areas.

7. CONCLUSIONS

The ability to detect predation risk and to modify behaviour accordingly to avoid being consumed is critically important to small aquatic animals. The main findings of my thesis were the variable and flexible behavioural responses of the planktivores to predator cues (Table 2), which indicate that they have adapted to different predator regimes and thus employ different antipredator strategies. The differences between the pelagic and littoral habitats are profound and are reflected in the predator detection modes and antipredator behaviours exhibited by the planktivores.

Littoral mysids live in well-lit shallow waters and are thus able to use visual cues in predator detection, whereas pelagic mysids, which rarely have much ambient light, must rely on chemical cues of predation risk. In the littoral, *Praunus flexuosus* and three-spined stickleback larvae utilize aquatic macrophyte vegetation as a predation refuge, whereas pelagic mysids, which lack a structural refuge, utilize a temporal one by undergoing DVM. In addition to

behavioural traits, mysids and *Cercopagis pengoi* hide from predators by being transparent, and stickleback larvae by their cryptic coloration. Sticklebacks and *C. pengoi* also gain protection by their morphology, and *Neomysis integer* by their swarming behaviour. Regardless of habitat, however, for all of the planktivores studied, reduced feeding activity was a common antipredator defence. The pelagic planktivores furthermore altered their prey selectivity patterns in response to predation risk. Each of the Baltic planktivore species studied thus manifests a unique set of antipredator traits that operate in combination to decrease its predation risk. The actual benefit of these traits, measured as reduced predation mortality, should be studied further.

The Baltic Sea is under heavy anthropogenic influence. This can have major influence on the species composition of the aquatic macrophyte communities (Jeppesen *et al.* 1997). *Chara tomentosa* suffers from increased turbidity caused by boating activities (Eriksson *et al.* 2004), eutrophication (Dahlgren & Kautsky 2004) and dredging and is currently declining in many areas (Munsterhjelm 1997, 2005, Koistinen & Munsterhjelm 2001, Schubert & Yousef 2001). *Fucus vesiculosus*, the most important habitat for *P. flexuosus*, is also declining in many areas due to eutrophication (Kangas *et al.* 1982, Kautsky *et al.* 1986, 1992, Vogt & Schramm 1991, Hemmi 2003, Berger *et al.* 2004, Roos *et al.* 2004). However, it may benefit from ferryboat traffic due to the mechanical disturbance of the propellers, which cleans the substrate necessary for successful recruitment (Eriksson & Johansson 2003, Eriksson *et al.* 2004, Roos *et al.* 2004). On the other hand, *Myriophyllum spicatum* and *Ceratophyllum demersum*, species that are unfavourable habitats for littoral mysids and larval fish (IV, Lehti-

niemi 2005), benefit from the turbid conditions caused by eutrophication, dredging and traffic (Nichols & Shaw 1986, Smith & Barko 1990, Munsterhjelm 1997, Dahlgren & Kautsky 2004, Eriksson *et al.* 2004, Roos *et al.* 2004). These two species are also less susceptible to mechanical damage by waves and boats than *Potamogeton* spp. (Eriksson *et al.* 2004, Schutten *et al.* 2004). The increased dominance of macrophyte species that are unsuitable predation refuges may substantially increase the predation-related mortality of littoral planktivores and thus have important consequences for the entire littoral food web.

Turbidity as such has major effects on the predation vulnerability (Miner & Stein 1996, Utne-Palm 2002, De Robertis *et al.* 2003, Granqvist & Mattila 2004, Johnsen 2005) and antipredator behaviour (Hartman & Abrahams 2000, Snickars *et al.* 2004, Johnsen 2005, Lehtiniemi *et al.* 2005, Van de Meutter *et al.* 2005a) of aquatic organisms and may therefore alter trophic interactions directly. Under turbid conditions, the use of vision by both predators and prey is hampered, and thus chemically and hydromechanically mediated predator-prey interactions become more prevalent.

The indirect effects of predators on planktivores are crucial to the study of trophic interactions and implications of environmental change. The predation effects mediated by antipredator behaviour can alter consumption rates, prey selectivity and distribution of planktivores. Predators, even without causing increased mortality in their prey populations, can induce cascading effects on lower trophic levels through decreased feeding rates of their prey. The flexibility and variability of antipredator behaviour highlighted in this thesis pose a challenge to forecasting and making generalizations about trophic dynamics.

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