Beachcombers, landlubbers and able seamen

Effects of marine subsidies on roles of arthropod predators in coastal food webs

by

Kajsa Mellbrand

Plants & Ecology

Plant Ecology 2007/7
Department of Botany
Stockholm University
Beachcombers, landlubbers and able seemen
Effects of marine subsidies on roles of arthropod predators in coastal food webs

Licentiate thesis
by
Kajsa Mellbrand

Supervisor: Peter Hambäck

Plants & Ecology

Plant Ecology 2007/7
Department of Botany
Stockholm University
Abstract

This licentiate thesis is a part of a PhD project aimed at understanding how inflows of marine nutrients affect structure and function of receptor ecosystems in coastal areas of the Baltic Sea. This thesis examines which coastal arthropod predators utilize marine inflows and how inflows affect the roles of predators in the coastal food web. The marine inflows consist of marine algae (mainly green filamentous algae) and emerging phantom midges (Chironomidae) with marine larval stages. The predators included in the thesis are spiders (the most common and abundant predators in the study system) and predatory insects such as nabids, saldids, carabids and Staphylinids. The thesis includes two manuscripts.

To examine to what extent coastal arthropods utilize nutrients of marine origin, analyses of carbon and nitrogen stable isotope ratios ($^{13}$C/$^{12}$C and $^{15}$N/$^{14}$N) were made of arthropods, plants and algae collected on shores. In the first, a bottom-up food web is constructed based on carbon sources of coastal arthropods, in the second the possibility of top-down effects in the coastal food web is examined. The analyses show that spiders utilize nutrients of marine origin to the largest extent. It also seems as if spiders are the only arthropods able to effectively utilize the phantom midge inflow.

To further examine how marine inflow affect coastal food web structure and whether any top-down effects exist, a large scale experiment was made where spiders hunting on the ground (mainly wolf spiders) were removed from small islands (20-2100 m$^2$). Effects of spider removal on other arthropod groups were measured by d-vac sampling using a converted leaf blower. The results indicate that predatory insects are affected negatively by the high abundance of spiders on shores, probably through a combination of increased competition, intraguild predation and behavioural effects on both the insect predators themselves and their terrestrial prey. Treatment had no effect on densities of coastal herbivores or detritivores, which may indicate either an absence of top-down effects on lower levels of the food web, or that any such effects are behaviour mediated rather than a result of direct predation.

The main conclusions of the thesis are that spiders and phantom midges are likely important vectors for transporting nutrients from the Baltic Sea to terrestrial ecosystems in the Baltic Sea area. Spiders are the main beneficiaries from marine inflow among the coastal arthropods, and this affects trophic interactions on the predator level of the coastal ecosystem.
Sammanfattning
Den här licentiatavhandlingen är en del i ett doktorandprojekt som syftar till att förstå hur inflöden av marin näring påverkar struktur och funktion hos strandekosystem. I denna avhandling undersöks vilka rovdjur som utnyttjar sådana näringsflöden på Östersjöstränder i norra Uppland, och hur rovdjurens roller i strandfödoväven påverkas. De näringsflöden som studerats utgörs av marina alger (främst gröna trådalger) och av fjädermyggor (Chironomidae) med larvstadier i havet och vuxenstadier på land. De vanligaste rovdjuren är spindlar (i synnerhet vargspindlar), andra förekommande rovdjur är rovinsekter som rovskinnbaggar, strandskinnbaggar, jordlöpare och kortvingar. Avhandlingen innehåller två manuskript.

För att undersöka hur stor andel av dieten hos strandlevande leddjur som har marint ursprung gjordes analyser av stabila isotoper (\(^{13}\text{C}/^{12}\text{C}\) och \(^{15}\text{N}/^{14}\text{N}\)) hos leddjur, växter och alger. Baserat på resultaten kan en strandfödoväv konstrueras utifrån vilka kolkällor leddjuren i strandekosystemet använder. Den grupp som främst utnyttjar marina näringsflöden är spindlar, och det verkar också som om spindlarna är de enda djur som effektivt utnyttjar inflödet av fjädermyggor.

Förekomsten av eventuella top-downeffekter i strandekosystemet undersöktes i ett storskaligt försök där marklevande spindlar plockades bort från små öar (20-2100 m\(^2\)). Effekten på tätheter av övriga leddjur måttas genom att faunan på öarna ”dammsögs” med en ombyggd lövblås. Resultaten indikerar att rovinsekter missgynnas av de stora mångderna spindlar på stränderna, troligen genom en kombination av intraguild predation, konkurrens, och beteendeeffekter. Inga effekter syntes på tätheter av strandlevande herbivorer eller detrivorer, något som indikerar att eventuella trofiska kaskadeffekter på lägre nivåer i födoväven uppstår som en följd av beteendeförändringar snarare än direkt predation.

Avhandlingens slutsats är att spindlar och fjädermyggor fungerar som viktiga vektorer för att transportera näring från Östersjön till terrestrisk ekosystem. Spindlar är de strandrovdjur som främst utnyttjar marina näringsflöden, vilket påverkar interaktioner på predatornivå i strandekosystemet.
List of papers

The thesis is based on the following manuscripts, referred to by their roman numerals:

I  Utilization of marine nutrients by coastal arthropod predators in the Baltic Sea area: a stable isotope study.

II  Effects of subsidized predators on coastal food webs in the Baltic Sea area.
Introduction

Ecosystem boundaries are important for environmental protection and species conservation, since diversity, productivity and various other ecosystem functions are often higher in these areas compared with ecosystem insides. However, the mechanisms underlying these boundary effects are often poorly understood, although one important component is the flow of matter and organisms across ecosystem boundaries.

In the study of ecosystems, between-system processes have historically often been neglected, although we do know that an ecosystem boundary is highly artificial and that there usually is a considerable amount of movement across the boundary (Polis & Hurd 1996; Polis et al. 1996). These flows of matter and organisms across ecosystem boundaries, hereafter termed subsidies, often compromise an important nutrient and energy source for receptor ecosystems. Subsidies were suggested by Polis & Hurd (1996) to possibly be the dominant factor in shaping the dynamics of both consumers and resources in many ecosystems. One ecosystem boundary where between-system processes may be of great importance (Hodkinson et al. 2001; Polis & Hurd 1996; Polis et al. 1996) is the marine shore-line, a zone in which many organisms are almost exclusively found.

Subsidies from marine to terrestrial systems may consist of marine organic matter drifting ashore (Polis & Hurd 1996; Polis et al. 1997; Bastow et al. 2002), of sea birds feeding on marine nutrients at sea but defecating and breeding on land (Polis et al. 1997, Sanchez-Piñero & Polis 2000; Anderson and Polis 2004), and of animals moving between aquatic and terrestrial habitats as part of their life history pattern (Hodkinson et al. 2001; Murakami & Nakano 2002; Power et al. 2004). This thesis will mainly focus on the last type of inflow: emerging insects moving from aquatic (i.e. the brackish Baltic Sea) to terrestrial ecosystems.
Subsidies from marine to terrestrial systems

Aggregation of predators on shores is a common and widespread occurrence, and one possible explanation is that terrestrial predators are positively affected by aquatic subsidies (Polis et al. 1997; Nakano & Murakami 2000; Murakami & Nakano 2002; Henschel 2004; Power et al. 2004). Of the many predators found to aggregate along coasts, some species occur naturally only close to water, such as for example long-jawed spiders (Tetragnathidae) that build their webs in sedges and reeds (Power et al. 2004). Still, many (if not most) of the shore-line predators are also found far inland, for example many wolf spiders (Lycosidae) as well as other invertebrates and many species of bats and lizards (Polis et al. 1997; Power et al. 2004). On bird-subsidized islands in the Gulf of California, terrestrial predators such as spiders, scorpions, lizards and ants were found to be 10-100 times more abundant than on the mainland (Polis 1994) and spider densities on islands 6 times greater in the supralittoral area than in inland areas (Polis & Hurd 1996).

Apart from the importance of nutrient inflows per se, how subsidies enter receptor ecosystems may be important. Subsidies can enter through different pathways and at different levels of the ecosystem, and the pathway may affect the impact and reach of the subsidy and the relative strength of bottom-up and top-down forces.

In Sweden, the Baltic Sea ecosystems with their mix of marine and freshwater species are unique and during the last decades, eutrophication has become an increasing problem (Swedish Environmental Protection Agency 1997; Karlson et al. 2002). This has led to an increasing focus on nutrient flows at the landscape level, though this far, studies have only concerned nutrient flows from terrestrial to marine and limnic systems, from sewage treatment plants and from agricultural and forest systems via streams and lakes. The general importance of nutrient flows in the opposite direction for ecosystem structure and function in Baltic coastal ecosystems remain largely unknown. On the Baltic Sea shores, marine inflow mainly arrives as marine detritus (mainly algae drifting ashore), as emerging insects with aquatic larval stages (mainly phantom midges, Chironomidae), and locally, as bird faeces. Eutrophication may change amounts, nature and effect of the
subsidies to coastal ecosystems depending on how the subsidizing species (algae, emerging insects) are affected by eutrophication. *Fucus vesiculosus* recruitment is negatively affected by filamentous green algae, a group that has increased in the Baltic Sea lately, and a shift from a *Fucus*-dominated community to one dominated by filamentous green and brown algae means a loss of both algal and faunal biomass in Baltic Sea ecosystems (Råberg & Kautsky 2007). The effects of such a shift for coastal ecosystems are unknown. An increase in filamentous algae may affect the relative importance of algal and phantom midge inflow to shores, through a decrease in inflow of seaweed and an increase in inflow of faster degradable filamentous algae, and through changes in phantom midge production in the Baltic Sea.

An inflow of prey organisms is a common and often important subsidy from aquatic to terrestrial systems, where the emergence of insects with aquatic larval stages subsidizes terrestrial predators (Hodkinson et al. 2001; Murakami & Nakano 2002; Henshel 2004; Power et al. 2004). Flows entering the system through these pathways bypass lower food chain levels, directly subsidizing predators. This allows predators to maintain higher levels than could be supported by local primary production, and possibly to initiate a trophic cascade through depressing local prey (Polis et al. 1997; Henshel 2004). Predators may have a larger effect on prey populations than otherwise possible through mechanisms of apparent competition. Enemy-mediated apparent competition arises when the equilibrium balance of a prey organism is decreased as a result of a numerical response by a shared predator to an increase of alternative prey (Holt & Lawton 1994; Chaneton & Bonsall 2000). In ecosystems with an inflow of alternative prey, higher predation pressure on local prey resulting from aggregation of predators can indirectly decrease the effect of local prey organisms on lower levels of the food chain (Chaneton & Bonsall 2000).

Subsidies consisting of prey entering at higher food chain levels may affect the system differently than a nutrient or detrital subsidy (Polis et al. 1997; Polis et al. 1996). This type of inflow pathway is a common and often very important subsidy from aquatic to terrestrial systems, where the emergence of insects with aquatic larval stages subsidizes
terrestrial predators (Hodkinson et al. 2001; Murakami & Nakano 2002; Henschel 2004; Power et al. 2004). Hodkinson et al. (2001) found a highly significant correlation between Chironomid availability and spider density in an early succession coastal ecosystem of Spitsbergen, Svalbard, and suggest spiders as an important mechanism for trapping and maintaining nutrients within coastal ecosystems.

Whether a prey subsidy actually results in top-down control of the system depends on to what extent subsidized predators affect lower levels of the ecosystem (Polis et al. 1997). The relative importance of bottom-up and top-down forces therefore should be determined by the level of primary production in the receptor ecosystem in relation to flow rates, and to what extent subsidized terrestrial predators utilize marine prey compared to terrestrial prey.

**Papers**

The two papers included in this thesis are part of a PhD project aimed at understanding the importance of marine subsidies for coastal ecosystem function and structure, with focus on the roles of coastal predators and on the inland reach of subsidy effects. This thesis examines how marine subsidies, mainly consisting of emerging phantom midges, affect the structure of coastal arthropod communities and the roles of predators in structuring the coastal ecosystem.

**Study area**

The focal ecosystems in this thesis are coastal ecosystems in the northern Uppland archipelago in the Baltic Sea, Sweden. Arthropods, terrestrial plants, and filamentous green and brown algae were collected for isotope analysis (Paper I) on the coast of the Swedish mainland and on the coast of the island of Gräsö (16°45’E, 67°10’N, size about 150 km²) in the northern Uppland archipelago. The spider removal study in Paper II was made on small islands in two areas on the northern and north-eastern coasts of Gräsö.

Most of the study shore-lines, on both mainland shores and islands, are shore meadows separated by rocky beach. The shore meadows are mostly kept open by flooding and
none of the study sites in this thesis are grazed by domestic animals. Water level fluctuations are mainly due to meteorological and hydrological factors (tide is very small in the Baltic Sea) and change both between and over the year (Jerling 1999). Typically, mean water levels in the Baltic Sea are highest in January, lowest in late winter-early spring, and rise again in late-summer-autumn (Jerling 1999). Many of the studied shore meadows are flat, and flooded during large parts of the year. The meadows are generally above water during spring and summer, but occasionally are flooded even then, especially in late summer, depending on wind conditions. The vegetation on shore meadows in the Baltic Sea show a gradient inland, due to factors such as salinity and water content in the soil and duration of flooding (Jerling 1999). Closest to the sea plants such as reeds and sedges often form more or less large stands. Further inland, plants less tolerant of high salinity and water content may establish, and eventually trees replace the meadow vegetation. On the study shores, reeds (*Phragmites australis*) and sedge (*Bolboschoenus maritimus*) often grow closest to water. In rockier areas without reeds, salinity tolerant herbs such as *Triglochin maritima*, *Plantago maritima*, *Aster tripolium* and *Glaux maritima* is often found close to the waterline. Further inland on shore meadows is usually a turf of grasses (often dominated by *Agrostis stolonifera*), interspersed with plants such as *Eleocharis uniglumis*, *Carex nigra*, *Carex disticha*, *Plantago maritima*, *Glaux maritima*, *Spergularia media*, *Blysmus rufus*, *Juncus gerardii*, *Ophioglossum vulgatum*, *Rhinantus serotinus*, *Pedicularis palustris*, *Orchis maculata*, *Filipendula ulmaria* and *Mentha aquatica*. On the rocky beaches vegetation is scarcer and typically consist of species that are also drought tolerant, such as *Lythrum salicaria*, *Sedum acre*, *Sedum telephium*, *Ophioglossum vulgatum*, *Matricaria maritima*, *Viola tricolor*, *Vicia cracca* and *Allium schoenoprasum*. 
Study organisms
The study organisms are phantom midges and marine algae, which subsidize coastal ecosystems in the studied area, and coastal arthropod predators (mainly spiders but also predatory insects).

The two types of marine subsidies included in this thesis are marine algae and phantom midges (Chironomidae). Most of the studied shores and islands in paper I and II are located in shallow bays, and the inflow of algae (especially seaweed) to many of these shores is low. The most common algae in most of the bays are green filamentous algae, which are very fast degradable, providing an ephemeral and thereby less stable habitat for detritivores than algal driftwalls consisting of Fucus algae. In paper II, there is an inflow of Fucus algae only to four of the nineteen islands of the study. Several insect families with aquatic larval stages are common on the study shores, such as for example dragonflies (Odonata), damselflies (Zygoptera), mayflies (Ephemeroptera), caddisflies (Trichoptera) and flies and midges (Diptera), but the by far most abundant are phantom midges (Chironomidae). The phantom midges often appear in large swarms and rest in vegetation close to the waterline when not flying.

The by far most common and abundant arthropod predators on the study shores are spiders, mainly wolf spiders (Lycosidae) of which the most common are Pardosa spiders. Other predators include pirate bugs (Saldidae), damsel bugs (Nabidae), ground beetles (Carabidae, mainly Dyschirius) and rove beetles (Staphylinidae). Common herbivores on the shores are plant hoppers (Homoptera; Cercopidae, Cicadellidae), grass hoppers (Orthoptera), mirids, butterfly larvae and beetles such as weevils (Curculionidae) and chrysomelids. The most common detritivores are springtails (Collembola; mostly Podura aquatica).
**Paper I**

*Aims*

The aims of paper I was to find which coastal arthropods, in particular predators, utilize nutrients of marine origin, and to what degree, and to construct a bottom-up food web based on three carbon sources: marine algae, marine prey (phantom midges, Chironomidae), and terrestrial material (prey, and plants).

*Methods*

Diets of coastal arthropods were examined using stable isotope analysis, a method often used for gaining information about feeding relationships in food webs (Fry 2006). Different stable isotopes of the same element behave somewhat differently in chemical reactions: typically, heavier isotopes cause chemical reactions to be slower. This include the chemical reactions involved in photosynthesis, and cause heavy isotopes of elements such as carbon and nitrogen to have slower incorporation rates in plant tissues than lighter isotopes of the same elements. The result is that stable isotope ratios ($\delta^{13}C/\delta^{12}C$ and $\delta^{15}N/\delta^{14}N$) differ between carbon dioxide and nitrogen in the air, and plant tissue. Also, plants using different modes of photosynthesis, as well as different carbon sources often differ in stable isotope ratios (Fry 2006). For the purposes of Paper I, it is known that marine algae and terrestrial plants differ in stable isotope ratios due to differences in carbon source ($CO_2$ vs $CO_3^-$) and photosynthetic apparatus, terrestrial plants being more $^{12}C$-depleted than marine algae (Fry 2006). This difference can be used to determine whether the main nutrient source of a terrestrial arthropod is of marine or terrestrial origin. Once the isotopes are incorporated in plant tissue, carbon stable isotope ratios tend to be stable between different levels in the food chain, while nitrogen stable isotope ratios tend to be enriched higher in the food chain (Fry 2006). This means that carbon stable isotope ratios can be used to trace primary carbon sources through the trophic chain.

Nitrogen stable isotope ratios also differ between marine and terrestrial environments, but more importantly, $^{15}N$ accumulates up the food chain. Nitrogen isotope ratios thereby provide information about the length of trophic chains, and can be used as an indicator of an organism’s trophic position in the food chain (Post 2002).
Results and conclusions

The results of the isotope analyses show that spiders are the terrestrial predators mainly utilizing nutrients of marine origin in the study system, while most insect predators mainly utilize carbon of terrestrial origin (Fig. 1). Neither plants nor herbivores utilize marine nutrients to any larger extent (Fig. 1), perhaps indicating that marine subsidies in the area are more important when arriving as an inflow of prey rather than as an inflow of marine detritus.

All spiders appear to utilize marine rather than terrestrial nutrients. The mentioned spiders generally have hunting methods well adapted to capture flying prey such as dipterans (Foelix 1996; Barth 2002), and are thereby likely to benefit from an inflow of

Figure 1 Carbon (left) and nitrogen (right) stable isotope ratios (μg) of green filamentous algae, coastal plants, and coastal arthropods (Paper I).
phantom midges. None of the insect predators utilize marine nutrients to a larger extent, though the diet of damsel bugs (Nabidae) has a larger marine component than other insect predators. The predators that benefit most from an inflow of prey are clearly spiders, indicting that eventual effects of marine subsidies for the coastal ecosystems are likely mediated by spiders.

**Paper II**

**Aims**

The aim of paper II was to examine possible top-down effects of spiders in coastal food webs. For this purpose, we performed a large-scale removal experiment where spiders were removed from small islands and the effects of spider removal on densities of other arthropods were estimated.

**Methods**

Spiders (mainly wolf spiders) were removed from small islands (20-2100 m²) during three consecutive years using pitfall traps. Arthropods were sampled using a vacuum sampling device, a Stihl® BG85 Leaf Blower/VAC, at three occasions each summer in 2004-2006. Densities were estimated within a mobile circular enclosure of 0.7 m², and three samples per island were taken at every sampling occasion. Captured animals were returned after counting, with the exception of spiders on treatment islands, which were removed from the islands.

**Results and conclusions**

The results show that spider removal caused insect predator densities to increase, suggesting that insect predators are negatively affected by the high spider densities on shores. Further studies are needed to understand the underlying mechanism for this, but direct mortality from spider predation may have been a decisive factor.

No treatment effects were found on herbivore or detritivore densities (Fig. 2), and we suggest that negative effects of spiders on herbivore and detritivore densities on control islands may be at least partly compensated by increased effect of insect predators.
utilizing mainly terrestrial prey on treatment (removal) islands. This does not exclude the possibility of top-down effects on lower levels of the ecosystem from spiders, but in case they do exist, they are likely behaviour mediated rather than a result of direct spider predation. Behaviours such as cannibalism and intraguild predation are common in spiders and may dampen cascading effects, making it difficult to find top-down effects by spiders (Polis et al. 2000; Finke & Denno 2005). Behavioural effects may include decreased activity and switches in habitat and diet selection (Denno et al. 2003; Cronin et al. 2004; Moran et al. 1996; Schmitz 2004; Beckerman et al. 1997), and such effects can not be found by measuring density effects alone. To find any such effects, all components of the food web, not only arthropods need to be examined. Mainly, further studies should include effects on terrestrial plants to examine whether top-down effects on herbivores through behavioural mechanisms exist. Until such studies have been made, the only conclusion that can be drawn is that spiders tend to affect other arthropod predators negatively, while top-down effects of spiders on lower trophic levels of the food web are either nonexistent or may be compensated by effects of insect predators on treatment islands, resulting in little or no measurable effect of spider removal on herbivores or detritivores. Another possibility is that the spider removal treatment was not effective enough: removal reduced spider density by about 50% on treatment islands, but considering the very high initial spider densities, this may not suffice for treatment effects to be measurable on lower trophic levels. Also, the effects of removal was mainly found between 2005 and 2006 rather than between 2004 and 2005, indicating that the time scale may have been too short for treatment to have had enough effect after only two years.
Figure 2  Arthropod densities 2004-2006 on treatment (○) and control (●) islands (Paper II).
The uniqueness of this study however lies greatly in its scale: these types of experiments are typically made using small (one or a few m$^2$) enclosures in which the food web is manipulated. By using islands as natural enclosures, natural dynamics are incorporated and natural ranges of the studied arthropods are maintained. In a pilot mark-recapture study of wolf spider mobility on Gräsö shores (unpublished data), spiders where found to often move over several square meter areas in the course of 48 hours, and in some cases where recaptured up to 60 meters from the point of release. This indicates that a 1-2 m$^2$ enclosure does not allow for natural movements for at least wolf spiders (but likely for many other arthropods as well). Using enclosures may also affect inflow rates negatively. While the use of islands allows a lesser degree of control of the study system than enclosures do, studies including natural dynamics and movements of organisms are not only an important complement to traditional enclosure studies, but necessary for understanding large scale predator effects.

Discussion

Assembling the coastal food web

In this thesis, the results of paper I provide a framework for closer examinations of feeding relationships in the coastal food web while in paper II the possibility of top-down effects in the food chain is explored. The results of paper I allow the drawing of a coastal food web from the bottom-up, based on three available carbon sources in the area (Fig. 3), though the picture remains obscure in some aspects. The finding that spiders are the main beneficiaries of marine subsidies may be a reason for caution: How important is the function of spiders that almost exclusively utilize nutrients of marine origin in the terrestrial arthropod food web? The results show that terrestrial plants and herbivores mainly utilize nutrients of terrestrial origin (Fig. 1); hence the inflow of phantom midges could possibly be of greater relative importance than inflow of algal detritus in the study system. Theoretically, a high inflow of alternative prey bypassing lower levels of the food chain and subsidizing predators directly could enhance top-down effects in the ecosystem (Polis et al. 1997; Henschel 2004).
In this thesis no direct evidence of top-down effects on levels below predator levels of the ecosystem could be found (Paper II). Still, both web building spiders and spiders that hunt actively utilize marine material as a nutrient source to a very high degree (Paper I). This is not surprising since hunting behaviours of all spiders in the two studies are well adapted to capture flying prey such as dipterans: The orb webs of araneid and thetragnathid spiders are designed specifically to catch flying prey (Foelix 1996), and webs placed close to the water are very likely to catch emerging insects. Most of the sheet web weavers included in paper I and II are however building webs very close to the ground and while these webs can still catch flying insects, they are well designed to catch prey dwelling on the ground or in vegetation as well (Foelix 1996). Linyphiid spiders may thereby catch a larger proportion of terrestrial prey than orb web weavers, and since
the carbon isotope ratio of springtails (Collembola), like that of phantom midges, is consistent with that of marine algae we cannot separate between these prey types. It is possible, maybe even likely, that small spiders that hunt close to the ground (e.g. linyphiids) includes detritivores such as springtails in their diet.

Wolf spiders are cursorial hunters and prey capture is triggered by movement, probably through both visionary and vibratory cues (Foelix 1996; Barth 2002). Wolf spiders have good vision (for arthropods) and the buzzing of insects such as flies and midges are easily distinguished from background vibrations through its frequency (Foelix 1996). This makes fast moving, buzzing prey attractive to wolf spiders as prey, and being fast, active hunters, wolf spiders are well adapted to catch such prey. The stable isotope analyses confirm that wolf spiders utilize nutrients of marine origin to a large degree (Paper I), and since they are also the by far most common and abundant predators on shores, they could have large effects on the ecosystem even when feeding almost exclusively on marine prey.

Paper II show that insect predator densities are negatively affected by high spider densities on shores. Nearly all common and abundant spiders on shores utilize mainly nutrients of marine origin (Paper I), which may appear somewhat contradictive of the top-down effect, however weak, found in paper II. Still, in a scenario where spider densities are very high, spiders may need to feed on terrestrial prey only rarely to have a top-down effect on densities of the less abundant insect predators. The stable isotope analyses also show that insect predators, even those typically found close to the waterline such as Dyschirius beetles (Lindroth 1961) and shore bugs (Saldidae) (Schuh & Slater 1995) utilize mainly nutrients of terrestrial origin (paper I), indicating that these predators are unable to effectively utilize marine prey. Competition from spiders for terrestrial prey may thereby further reinforce the negative effect of spider intraguild predation on insect predator densities.

Considering the high spider densities on shores, spiders may also affect insect predator densities through behavioural mechanisms. The mere presence of spiders has been shown
to increase antipredatory behaviours such as a decreased activity, increased hiding and changes in habitat choice in herbivores (Denno et al. 2003; Cronin et al. 2004; Moran et al. 1996; Schmitz 2003; Beckerman et al. 1997). If high spider densities cause an increase in antipredatory behaviours in insect predators or in their prey, prey capture would be made more difficult for the insect predators even if spiders did not hunt for terrestrial prey at all.

Though no certain evidence of top-down effects is found, the results still indicate that spiders may have an important role in the terrestrial food web. The negative effect of high spider density on insect predator densities is likely best explained as a combination of behavioural effects, competition and intraguild predation, and further studies would be needed to separate these effects. Another field which calls for further investigation is whether top-down effects of spiders on lower levels of the food web exist, and if so, are behaviour mediated. Since only effects on arthropod densities were measured, this does not exclude the possibility of such effects. One conclusion from the spider removal study (Paper II) was that the effects of spiders on herbivore and detritivore populations on shores may be compensated by the effects of increases in more specialized insect predator densities on removal islands. If this is the case, removal of all arthropod predators would be necessary to discover top-down effects on herbivore and detritivore levels of the food web. Since effects may also be behaviour mediated, and have been shown to be so in several studies concerning spiders (Denno et al. 2003; Cronin et al. 2004; Moran et al. 1996; Schmitz 2003; Beckerman et al. 1997), it is however also possible that top-down effects exist that cannot be found by measuring arthropod densities alone. If the top-down effects are behaviour mediated, they may show at the plant level of the food web even in the absence of density effects on the herbivore level. A next step would be to measure effects of herbivores on plants as well as effects of predators on herbivores.
Conclusions and future aims

The conclusions when regarding the combined results of paper I and II is foremost that the coastal food web is highly complex and measurements of densities and stable isotope analyses are in themselves far too blunt tools to unravel this web. In combination they however make it possible to sketch a crude picture of the coastal food web and to separate the different roles of the coastal predators to some extent. Here I would like to reconnect to my title (beachcombers, landlubbers and able seamen) since the theme of this thesis after all is the roles of different actors in the coastal food web. For those who do not know: an able seaman makes his living from the sea. A beachcomber largely makes his living of what can be found on the beach, washed ashore by the sea, while a landlubber wants nothing to do with anything marine at all. These definitions fit well with the three main nutrient sources this thesis is concerned with: marine prey, marine detritus (material washed ashore by the sea), and terrestrial material (prey, plants, detritus).

The main finding in this thesis is that spiders by far benefit the most from marine subsidies, and I can conclude that most spiders on shores are indeed able seamen, largely utilizing marine prey. Most coastal insects are landlubbers, with the exception of the springtails who could be described as beachcombers. With risk of generalizing too far, we can regard the coastal food web as three somewhat separate food chains: a landlubber-chain based on primary production of terrestrial plants and the terrestrial detritivore food chain, a beachcomber-chain based on detritus of marine origin drifting ashore, and a seaman-chain based on marine primary production (Fig. 4). In the coastal ecosystem, spiders and phantom midges likely function as the main vectors in transporting nutrients from the Baltic Sea into terrestrial food webs on shores. In addition, spiders may provide another connection between marine and terrestrial ecosystems through top-down effects on parts of the coastal food web.
This thesis of course leaves a number of questions unanswered. The roles of beachcombers in the coastal food web needs to be investigated further, and it would be interesting to be able to better separate effects of the two main inflow pathways (phantom midges and marine algae) both in the food web as a whole and in the spider community. Another question still unanswered is whether top-down effects on lower level of the food web exist. These are all questions I would like to examine further and since this licentiate thesis is part of a larger PhD project, I hope I will manage to find at least some more answers in time (in addition to a number of other questions not addressed in this thesis...).
Acknowledgements

I would like to thank a lot of people, but some of the most important are:

– My supervisor Peter Hambäck, for always being willing to share your experience, knowledge and time, all of which I have been in great need of lately...
– Lena Kautsky, my assistant supervisor, for giving useful comments on my manuscripts from a marine point of view.
– All the people in the plant ecology department for creating such a nice working environment.
– All the people who have helped doing field work during my three field seasons at Gräsö, in order of appearance: Örjan Östman (a big thank you to both you and Anna for all your hospitality and nice dinners and tea parties in Öregrund), Gundula Kolb, Maria Enskog, Petra Mellbrand, Anna Engström (Knävlar i det!) and Johan Jacobsson. Thank you all, not only for doing field work, but also for being good company on Gräsö.
– Torbjörn Kronestedt (Swedish Museum of Natural History) for help and advice on wolf spider species determination and spider literature.
– My family in Skåne who supports me from a distance, in spite of my decision to emigrate to Sweden (nej pappa, här finns fortfarande inga renar på gatorna, bara på Skansen). Thank you mamma for reading the manuscripts. Thank you Elin for expert advice on the front page of this thesis. And thank you Petra for all the skype discussions about qualitative vs. quantitative methods and other interesting topics in late evenings.
– Solna Brass and Sjövärnskårens Musikkar (and all the nice people in them) who forces me to remember that the world is not only made up of food webs, spiders and statistics but of beautiful music as well, and that rubber boots are not suitable for all occasions after all (such as grand concerts or tattoos).
References


Följande publikationer ingår i utgivningen:

1978:1 **Liljelund, Lars-Erik**: Kompendium i matematik för ekologer.
1978:2 **Carlsson, Lars**: Vegetationen på Littejåkkadeltat vid Sitasjaure, Lule Lappmark.
1978:3 **Tapper, Per-Göran**: Den maritima lövskogen i Stockholms skärgård.
1978:4 **Forsse, Erik**: Vegetationskartans användbarhet vid detaljplanering av fritidsbebyggelse.
1979:1 **Engström, Peter**: Tillväxt, sulfatupptag och omsättning av cellmaterial hos pelagiska saltvattensbakterier.
1979:2 **Eriksson, Sonja**: Vegetationsutvecklingen i Husby-Långhundra de senaste tvåhundra åren.
1979:3 **Bråvander, Lars-Gunnar**: Vegetation och flora i övre Teusadalen och vid Auta- och Sitasjaure; Norra Lule Lappmark. En översiktlig inventering med anledning av områdets exploatering för vattenkraftsändamål i Ritsemprojektet.
1979:5 **Reinhard, Ylva**: Avloppsinfiltration - ett försök till konsekvensbeskrivning.
1980:2 **Hilding, Tuija**: Populationsstudier på *Spergularia marina* och *Spergularia media*.

II Resursallokering och mortalitet.
1980:3 **Eriksson, Ove**: Reproduktion och vegetativ spridning hos *Potentilla anserina* L.
1981:1 **Eriksson, Torsten**: Aspekter på färgvariation hos *Dactylorhiza sambucina*.
1983:1 **Blom, Göran**: Undersökningar av lertäkter i Färentuna, Ekerö kommun.
1986:1 **Svanberg, Kerstin**: En studie av grusbräckans (*Saxifraga tridactylites*) demografi.
1987:1 **Edenholm, Kristo**: Undersökningar av vegetationspåverkan av vildsvinsbök i Tullgarnsområdet.
1987:2 **Nilsson, Thomas**: Variation i fröstorlek och tillväxthastighet inom släktet *Veronica*.

1988:2 **Dinnétz, Patrik**: Local variation in degree of gynodioecy and protogyny in *Plantago maritima*.

1988:3 **Blom, Göran och Wincent, Helena**: Effekter av kalkning på ångsvegetation.

1989:1 **Eriksson, Pia**: Täthetsreglering i Littoralvegetation.

1989:2 **Kalvas, Arja**: Jämförande studier av *Fucus*-populationer från Östersjön och västkusten.

1990:1 **Kiviniemi, Katariina**: Groddplantsetablering och spridning hos smultron, *Fragaria vesca*.

1990:2 **Idestam-Almquist, Jerker**: Transplantationsförsök med Borstnate.

1992:1 **Malm, Torleif**: Allokemisk påverkan från *mucus* hos åtta bruna makroalger på epifytiska alger.

1992:2 **Pontis, Cristina**: Om groddknoppar och tandrötter. Funderingar kring en klonal växt: *Dentaria bulbifera*.

1992:3 **Agartz, Susanne**: Optimal utkorsning hos *Primula farinosa*.

1992:4 **Berglund, Anita**: Ekologiska effekter av en parasitsvamp - *Uromyces lineolatus* på *Glaux maritima* (Strandkrypa).

1992:5 **Ehn, Maria**: Distribution och tetrasporophytes i populationer av *Chondrus crispus* Stackhouse (Gigartinaceae, Rhodophyta) på den west coast of Sweden.


1994:1 **Fröborg, Heléne**: Pollination and seed set in *Vaccinium* and *Andromeda*.

1994:2 **Eriksson, Åsa**: Makrofossilanalys av förekomst och populationsdynamik hos *Najas flexilis* i Sörmland.

1994:3 **Klee, Irene**: Effekter av kvävetillförsel på 6 vanliga arter i gran- och tallskog.

1995:1 **Holm, Martin**: Beståndshistorik - vad 492 träd på Fagerön i Uppland kan berätta.


1995:3 **Norberg, Ylva**: Morphological variation in the reduced, free floating *Fucus vesiculosus*, in the Baltic Proper.


1996:1 **Eriksson, Åsa**: Plant species composition and diversity in semi-natural grasslands - with special emphasis on effects of mycorrhiza.

1996:2 **Kalvas, Arja**: Morphological variation and reproduction in *Fucus vesiculosus L.* populations.

1996:3 **Andersson, Regina**: Fågelspridda frukter kemiska och morfologiska egenskaper i relation till fåglarnas val av frukter.
<table>
<thead>
<tr>
<th>Year</th>
<th>Author</th>
<th>Title</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996:4</td>
<td>Lindgren, Åsa</td>
<td>Restpopulationer, nykolonisation och diversitet hos växter i naturbetesmarker i sörmländsk skogsbygd.</td>
</tr>
<tr>
<td>1996:5</td>
<td>Kiviniemi, Katariina</td>
<td>The ecological and evolutionary significance of the early life cycle stages in plants, with special emphasis on seed dispersal.</td>
</tr>
<tr>
<td>1996:7</td>
<td>Franzén, Daniel</td>
<td>Fältskiktsförändringar i ädellövskog på Fagerön, Uppland, beroende på igenväxning av gran och skogsavverkning.</td>
</tr>
<tr>
<td>1997:1</td>
<td>Wicksell, Maria</td>
<td>Flowering synchronization in the Ericaceae and the Empetraceae.</td>
</tr>
<tr>
<td>1997:3</td>
<td>Kiviniemi, Katariina</td>
<td>A study of seed dispersal and recruitment of plants in a fragmented habitat.</td>
</tr>
<tr>
<td>1997:5</td>
<td>Löfgren, Per</td>
<td>Population dynamics and the influence of disturbance in the Carline Thistle, Carlina vulgaris.</td>
</tr>
<tr>
<td>1998:1</td>
<td>Mattsson, Birgitta</td>
<td>The stress concept, exemplified by low salinity and other stress factors in aquatic systems.</td>
</tr>
<tr>
<td>1998:2</td>
<td>Forsslund, Annika &amp; Koffman, Anna</td>
<td>Species diversity of lichens on decaying wood - A comparison between old-growth and managed forest.</td>
</tr>
<tr>
<td>1998:4</td>
<td>Fröborg, Heléne</td>
<td>Biotic interactions in the recruitment phase of forest field layer plants.</td>
</tr>
<tr>
<td>1999:1</td>
<td>Mattsson, Birgitta</td>
<td>Salinity effects on different life cycle stages in Baltic and North Sea Fucus vesiculosus L.</td>
</tr>
<tr>
<td>1999:2</td>
<td>Johannotessen, Åse</td>
<td>Factors influencing vascular epiphyte composition in a lower montane rain forest in Ecuador. An inventory with aspects of altitudinal distribution, moisture, dispersal and pollination.</td>
</tr>
<tr>
<td>1999:3</td>
<td>Fröborg, Heléne</td>
<td>Seedling recruitment in forest field layer plants: seed production, herbivory and local species dynamics.</td>
</tr>
<tr>
<td>1999:4</td>
<td>Franzén, Daniel</td>
<td>Processes determining plant species richness at different scales - exemplified by grassland studies.</td>
</tr>
<tr>
<td>1999:6</td>
<td>Iversen, Therese</td>
<td>Flowering dynamics of the tropical tree Jacquinia nervosa.</td>
</tr>
<tr>
<td>1999:7</td>
<td>Isæus, Martin</td>
<td>Structuring factors for Fucus vesiculosus L. in Stockholm south archipelago - a GIS application.</td>
</tr>
<tr>
<td>1999:8</td>
<td>Lannek, Joakim</td>
<td>Förändringar i vegetation och flora på öar i Norrtälje skärgård.</td>
</tr>
</tbody>
</table>
2000:1 Jakobsson, Anna: Explaining differences in geographic range size, with focus on dispersal and speciation.
2000:2 Jakobsson, Anna: Comparative studies of colonisation ability and abundance in semi-natural grassland and deciduous forest.
2000:4 Öster, Mathias: The effects of habitat fragmentation on reproduction and population structure in Ranunculus bulbosus.
2001:1 Lindborg, Regina: Projecting extinction risks in plants in a conservation context.
2001:2 Lindgren, Åsa: Herbivory effects at different levels of plant organisation; the individual and the community.
2001:3 Lindborg, Regina: Forecasting the fate of plant species exposed to land use change.
2001:4 Bertilsson, Maria: Effects of habitat fragmentation on fitness components.
2001:5 Ryberg, Britta: Sustainability aspects on Oleoresin extraction from Dipterocarpus alatus.
2001:6 Dahlgren, Stefan: Undersökning av fem havsvikar i Bergkvara skärgård, östra egentliga Östersjön.
2001:7 Moen, Jon; Angerbjörn, Anders; Dinnetz, Patrik & Eriksson Ove: Biodiversitet i fjällen ovan trädgränsen: Bakgrund och kunskapsläge.
2001:8 Vanhoenacker, Didrik: To be short or long. Floral and inflorescence traits of Bird’s eye primrose Primula farinose, and interactions with pollinators and a seed predator.
2001:9 Wikström, Sofia: Plant invasions: are they possible to predict?
2001:11 Forsén, Britt: Survival of Hordelymus europaeus and Bromus benekenii in a deciduous forest under influence of forest management.
2001:12 Hedlin, Elisabeth: Bedömningsgrunder för restaurering av lövängsrester i Norrtälje kommun.
2002:1 Dahlgren, Stefan & Kautsky, Lena: Distribution and recent changes in benthic macrovegetation in the Baltic Sea basins. – A literature review.
2002:2 Wikström, Sofia: Invasion history of Fucus evanescens C. Ag. in the Baltic Sea region and effects on the native biota.
2002:3 Janson, Emma: The effect of fragment size and isolation on the abundance of Viola tricolor in semi-natural grasslands.
2002:5 Hedman, Irja: Hävdhistorik och artrikedom av kärlväxter i ängs- och hagmarker på Singö, Fogdö och norra Väddö.
2002:7 Isæus, Martin: Factors affecting the large and small scale distribution of fucoids in the Baltic Sea.
2003:3 Isæus, Martin: Wave impact on macroalgal communities.
2003:5 Sundblad, Göran: Using GIS to simulate and examine effects of wave exposure on submerged macrophyte vegetation.
2004:1 Strindell, Magnus: Abundansförändringar hos kärlväxter i ädellövskog – en jämförelse av skötselåtgärder.
2004:2 Dahlgren, Johan P: Are metapopulation dynamics important for aquatic plants?
2004:3 Wahlstrand, Anna: Predicting the occurrence of Zostera marina in bays in the Stockholm archipelago,northern Baltic proper.
2004:4 Råberg, Sonja: Competition from filamentous algae on Fucus vesiculosus – negative effects and the implications on biodiversity of associated flora and fauna.
2004:8 Niklasson, Camilla: Effects of nutrient content and polybrominated phenols on the reproduction of Idotea baltica and Gammarus ssp.
2004:9 Lönnberg, Karin: Flowering phenology and distribution in fleshy fruited plants.
2005:2 Vanhonenacker, Didrik: The evolutionary pollination ecology of Primula farinosa.
2005:5 Öster, Mathias: Landscape effects on plant species diversity – a case study of Antennaria dioica
2005:6 Boalt, Elin: Ecosystem effects of large grazing herbivores: the role of
nitrogen.


2005:8 Schmalholz, Martin: Patterns of variation in abundance and fecundity in the endangered grassland annual Euphrasia rostkovia ssp. Fennica.

2005:9 Knutsson, Linda: Do ants select for larger seeds in Melampyrum nemorosum?

2006:1 Forslund, Helena: A comparison of resistance to herbivory between one exotic and one native population of the brown alga Fucus evanesens


2006:3 Lönnberg, Karin: Recruitment patterns, community assembly, and the evolution of seed size

2006:4 Mellbrand, Kajsa: Food webs across the waterline - Effects of marine subsidies on coastal predators and ecosystems

2006:5 Enskog, Maria: Effects of eutrophication and marine subsidies on terrestrial invertebrates and plants

2006:6 Dahlgren, Johan: Responses of forest herbs to the environment

2006:7 Aggemyr, Elsa: The influence of landscape, field size and shape on plant species diversity in grazed former arable fields

2006:8 Hedlund, Kristina: Flodkräftor (Astacus astacus) i Bornsjön, en omnivors påverkan på växter och snäckor

2007:1 Eriksson, Ove: Naturbetesmarkernas växter- ekologi, artrikedom och bevarandebiologi

2007:2 Schmalholz, Martin: The occurrence and ecological role of refugia at different spatial scales in a dynamic world

2007:3 Vikström, Lina: Effects of local and regional variables on the flora in the former semi-natural grasslands on Wäsbys Golf club’s course

2007:4 Hansen, Joakim: The role of submersed angiosperms and charophytes for aquatic fauna communities

2007:5 Johansson, Lena: Population dynamics of Gentianella campestris, effects of grassland management, soil conditions and the history of the landscape

2007:6 von Euler, Tove: Sex related colour polymorphism in Antennaria dioica

Utilization of marine nutrients by coastal arthropod predators in the Baltic Sea area: a stable isotope study

Kajsa Mellbrand and Peter Hambäck

Department of Botany, Stockholm University, SE-106 91 Stockholm, Sweden

Abstract

The aims of this paper are to find which coastal arthropods, in particular predators, utilize nutrients of marine origin, and to what degree. Diets of coastal arthropods were examined using carbon and nitrogen stable isotope analysis to determine whether the main nutrient sources of terrestrial arthropods are of marine or terrestrial origin. The results suggest that spiders are the terrestrial predators mainly utilizing nutrients of marine origin in the area, while insect predators on shores largely utilize terrestrial nutrients, possibly due to differences in hunting behaviour. Neither plants nor herbivores utilize marine nutrients to any larger extent, perhaps indicating that marine subsidies in the area are more important when arriving as an inflow of prey rather than as an inflow of marine detritus. Springtails, the most common detritivore group, however had a carbon isotope ratio largely consistent with that of marine algae. That spiders are the predators that benefit the most from the marine inflow may indicate that eventual effects of marine subsidies for the coastal ecosystem as a whole are likely mediated by spiders.
Introduction

Many predators are known to aggregate in large numbers in coastal areas around the world (Polis et al. 1997; Nakano & Murakami 2001; Murakami & Nakano 2002; Henschel in Polis 2004; Power et al. in Polis 2004). One theory explaining these aggregations is that inflow of marine nutrients and matter to coastal areas increase prey abundance and thereby subsidizes predator growth rates. Several studies have also shown a close linkage between aquatic and terrestrial food webs (Polis & Hurd 1996; Polis et al. 1997; Nakano & Murakami 2001; Murakami & Nakano 2002), but various types of nutrient inflows may not affect different organisms of the receptor ecosystem the same. Basal nutrient inflows, such as the flow of marine detritus to shorelines, tend to increase coastal plant production (Polis et al. 1997), whereas the effects of subsidies to higher trophic levels of the ecosystem are more difficult to predict and may vary depending on properties of the receptor ecosystem, the subsidy, and the receptor organism. In studies of islands in the Baja California, Polis et al. (1997) found the aggregation of predators such as arachnids and lizards on beaches to be caused mainly by an inflow of marine detritus and a subsequent increase in detritivore population densities. They also found that islands housing colonies of fish-eating birds, acting as vectors for marine nutrients, supported higher densities of invertebrates than islands without such colonies. The same aggregation of predators on shores have been observed in running waters, where emerging insects have been shown to be of great importance as a food source for terrestrial predators (Nakano & Murakami 2001; Akamatsu et al. 2004).

While predator aggregations along shore-lines are well-known, it is not evident that all predators benefit from the marine inflow. First, species vary in their ability to utilize this inflow as a consequence of differences in prey capture ability. When inflow occurs as emerging insects, this is mostly used by predators hunting in vegetation rather than on ground level. We could particularly expect these inflows to benefit generalist predators capable of catching flying and fast moving prey. For a generalist predator utilizing allochtonous prey, the ability to switch to local prey during periods when inflow rates are low enables predators to maintain higher population sizes and also allows them to suppress local prey more effectively (Polis et al. 1997; Chaneton & Bonsall 2000; Anderson & Polis 2004). On the other hand, other predator groups may benefit from inflows that mainly increase detritivore densities, such as detrital inflows.
In order to understand variations among species in their ability to utilize marine derived nutrients, a first step would be to trace nutrients up the food web and, based on this information, construct a bottom-up food web. This is possible using the fact that basal resources in marine and terrestrial environments show large differences in carbon isotope composition. Due to differences in carbon source (CO$_2$ vs CO$_3^-$) and photosynthetic apparatus, terrestrial plants are typically much more $^{13}$C-depleted than marine (Fry 2006), even though brown algae (seaweed) and green algae also differ in carbon isotope composition (Fredrikssen 2003). These differences are sufficiently large to enable tracing of primary carbon sources up the food chain. Even though minor fractionation of carbon isotopes may occur for each trophic step (typically <0.1 %), this is much smaller than the known difference in carbon isotope ratios between the primary carbon sources (typically >0.8%) (Fry 2006; McCutchan et al. 2003). Nitrogen isotope ratios similarly show different signals in marine and terrestrial environments, but more importantly, $^{15}$N accumulates up the food chain. As a consequence isotope ratios provide information on the length of trophic chains (Post 2002).

Using this general methodology, the purpose of our study was to construct bottom-up food webs for shore-lines in the Baltic Sea area, where inflow of marine nutrients consist mainly of marine algal detritus, emerging aquatic insects (e.g. phantom midges, Chironomidae), and locally as bird faeces, and to identify if predators vary in their use of marine versus terrestrial food items. In the area, the most common and abundant predators are wolf spiders. In wandering spiders such as wolf spiders, hunting behaviour is triggered by movement (Foelix 1996; Barth 2002), making flying and fast moving arthropods attractive prey. Phantom midges are small enough to be preyed on by spiders of all sizes, as are smaller terrestrial arthropods. For larger spiders in particular, prey however also include smaller conspecifics (Foelix 1996; Denno et al. 2004) and body size may thereby affect diet (Woodward & Hildrew 2002). Since active hunters like wolf spiders often hunt for the most common prey available, smaller conspecifics may be an important part of the diet for larger spiders, especially during periods when inflow rates are low.

Web building spiders are also present in large numbers on Baltic Sea shores and the most common and abundant web builders can be roughly separated into sheet web weavers (Linyphiidae), random web weavers (Dictynidae and Theridiidae) and orb web weavers (Araneidae and Tetragnathidae). The orb webs, as well as some sheet webs and many random webs, are designed to catch mainly flying prey (Foelix 1996), and these spiders are therefore
also likely to benefit from an inflow of phantom midges. Akamatsu et al. (2004) found that orb-weaving riparian spiders utilized nutrients of both aquatic and terrestrial origin (e.g. emerging insects from the studied river as well as terrestrial insects). Since web building spiders are rather stationary, they are less likely to interact with conspecifics than active hunters are, and their diet may thereby more accurately reflect inflow levels.

Other coastal predators are insect predators, mainly beetles (Carabidae, Staphylinidae) and predatory Heteropterans (Nabidae, Saldidae). These are all active hunters, but they are mostly slower than wolf spiders and therefore less likely to be very efficient hunters of flying insects such as midges. Many rove beetles (Staphylinidae) are predators, but smaller species may be detritivores or fungivores (Sandhall & Lindroth 1976). The most common ground beetles (Carabidae) on the study shores are *Dyschirius* beetles which dig tunnels on sandy shores (Lindroth 1961; Sandhall & Lindroth 1976). Shore bugs (Saldidae) are only found very close to the waterline on the ground (Chinery 1988; Schuh & Slater 1995), while damsel bugs (Nabidae) are the only of these insect predators hunting in the vegetation rather than on the ground (Chinery 1988; Douwes et al. 1997). Damsel bugs are typically generalist predators, feeding on small arthropods (Schuh & Slater 1995).

Their differences in natural history suggest that spiders may be more able to utilize emerging insect adults, such as phantom midges (Chironomidae) as prey, and therefore be expected to have a carbon isotope composition that resembles marine algae, whereas many insect predators may be more likely to utilize detritivores and terrestrial herbivores. Depending on the relative importance of these food items, we could thus expect differences in isotope composition of spiders and terrestrial predators.

**Material and methods**

**Study system**

The study was conducted in coastal areas along the Baltic Sea, in central Sweden. Arthropods, terrestrial plants, and filamentous green algae were collected on both mainland coasts and on a larger island. The study shores are rocky with patches of vegetation ranging from damp (marsh vegetation) to very dry. The inflow of marine nutrients consists mainly of marine macroalgae (mostly green and brown filamentous algae) and emerging phantom midges (Chironomidae). The most common herbivores are planthoppers (Homoptera; Cercopidae, Cicadellidae). Other common herbivores include mirids, grasshoppers, and butterfly larvae.
The most common detritivores are springtails (Collembola, mainly *Podura aquatica*). The most common and abundant predators on the shores are spiders. Among spiders, the most common and abundant group is wolf spiders of genera *Pardosa*, in total 7 species of which the most common is *Pardosa amentata*. Apart from *Pardosa*, 5 other wolf spider genera can be found on the shores: *Trochosa* (3 species), *Arctosa* (1 species, *A. leopardus*), *Alopecosa* (2 species), *Xerolycosa* (2 species) and *Pirata* (1 species, *P. piraticus*). Other spiders on the islands belong to families Gnaphosidae, Clubionidae, Salticidae, Pisauridae, Philodromidae, Thomisidae, Araneidae, Tetragnathidae, Theridiidae, Dictynidae and Linyphiidae. Common insect predators include predatory heteropterans (Nabidae, Saldidae) and coleopterans (Carabidae, Staphylinidae). Not all rove beetles are predatory, and in this study we have not separated rove beetle species. Common rove beetles on the study shores are however *Paederus* sp., that are predatory (Chinery 1988).

**Methods**

Arthropod, plant and macroalgal samples were collected for stable isotope analysis during June and July 2002-2006. Arthropods were captured using pitfall traps (plastic jars, 8 cm diameter and 6 cm height), sweep netting and d-vac sampling using a vacuum sampling device, a Stihl® BG85 Leaf Blower/VAC. Terrestrial plant samples were collected on shores (two species, *Filipendula ulmari* and *Lysimachia vulgaris*), and filamentous green algae at the water’s edge in year 2002.

Plant material and macroalgal material was air-dried, arthropods were freeze-dried, and all specimens were ground to a powder prior to analysis. Stable isotope ratios (δC=13C/12C and δN=15N/14N) were measured by UC Davis Stable Isotope facility, California, USA, and analysed using an Isotope Ratio Mass Spectrometer type *Europa integra*. Stable isotope ratios was measured for each individual animal when possible, but composite samples were used for Chironomidae and Collembola since individual sizes were too small (<0.7 mg dry weight) for stable isotope estimates. When possible, legs only were used for analysis of spider tissue, since turnover rates may be lower than in soft body tissue. For some groups/individuals of spiders and for most insects, larger body parts or whole individuals had to be used to achieve sufficient weight. For 20 *Pardosa* spiders, we examined the variability among body parts by analyzing legs, cephalothorax and abdomen separately. Finally, to examine trophic shifts among wolf spiders of different size, we examined the correlation between the N-isotope ratio and body weight for the two major genera (*Pardosa* and *Trochosa*). Differences
in stable C and N isotope ratios between predator families, spider families, spider species, and spider bodyparts were analyzed with MANOVAs, using Pillai-Bartlett statistic to test for differences between groups. Response variables (carbon and nitrogen isotope ratios) were also analysed separately with ANOVAs. Nitrogen isotope ratios of wolf spiders of different size were analyzed with ANCOVA. All statistical analyses were performed using R 2.5.0.

Results

There was a significant difference between stable isotope ratios of different body parts in *Pardosa* spiders (MANOVA $F=3.0$; $p=0.02$). This was due to a significant difference in nitrogen isotope ratio (ANOVA $F=5.0$; $p=0.01$) between leg tissue and abdomen and cephalothorax tissue (Fig.1), while we found no significant difference in carbon isotope ratios (ANOVA $F=0.78$; $p=0.47$) (Fig.1).

![Figure 1](image_url) Carbon (top) and nitrogen (bottom) stable isotope ratios ($\mu g$) of *Pardosa* wolf spider body parts. $\delta C$-values on y-axis of the top figure are inverted.
We also found a significant difference between nitrogen stable isotope ratios of wolf spiders of different size. Larger spiders (e.g. adult *Trochosa* spiders) have significantly higher nitrogen stable isotope ratio compared to smaller spiders (e.g. *Pardosa* spiders) (ANOVA F=19.0; p=7.1*10^{-05}).

![Graph showing nitrogen stable isotope ratios vs. log weight for different species of spiders.]

*Figure 2*  Nitrogen stable isotope ratios (μg) of wolf spiders of different size.

There was a significant difference in both N and C stable isotope ratios between different arthropod groups (MANOVA F=10.8; p=2.2*10^{-16}). The terrestrial plants and marine macroalgae differ in carbon stable isotope ratio. The only detritivores in the analysis, collembolans, have a carbon isotope ratio corresponding to that of macroalgae rather than terrestrial plants (Fig.3). The carbon isotope analyses show that the coastal predators utilizing marine nutrients to the largest extent are spiders (Fig. 3). Of the analyzed spiders, those with a carbon isotope ratio most consistent with that of marine algae and marine prey (e.g. phantom midges) is the web weaver families Dictynidae and Araneidae, and the active hunters *Thanatus striatus* (Philodromidae) and *Clubiona phragmites* (Clubionidae) (Fig.3). Most spiders however have a carbon isotope signal suggesting a predominance of marine rather than terrestrial food items in the diet. The insect predators generally have a more terrestrial diet, and also, with the exception of damsel bugs (Nabidae), tend to have lower nitrogen stable isotope ratios than nearly all the analyzed spiders. Damsel bugs are also the insect
predators that utilize marine nutrients to the largest extent, though they still have a more terrestrial diet than most spider groups. Rove beetles (Staphylinidae) have lower nitrogen stable isotope ratio than any other analyzed predator.

When comparing only spiders, there are significant differences between stable isotope ratios of both spider families (MANOVA F=2.2; p=0.003) and spider species (MANOVA F=2.0; p=0.00015). Of the different wolf spider species included in the analysis, the spiders utilizing nutrients of marine origin to the largest extent are three species of *Pardosa* spiders: *P. amentata*, *P. monticola* and *P. agricola* (Fig.4). *Trochosa* juveniles also utilize marine nutrients to a large extent, more so than adult *Trochosa*. The wolf spiders utilizing marine nutrients the least are *Pirata piraticus* (but consider the very high variation), *Arctosa leopardus* and *Alopecosa* spiders.

![Figure 3](image-url)  
*Figure 3* Carbon(left) and nitrogen (right) stable isotope ratios (μg) of green filamentous algae, coastal plants, and coastal arthropods.*
Figure 4  Carbon and nitrogen stable isotope ratios ($\mu$g) of coastal wolf spiders (Point 5 and 6 are overlapping).

Discussion
In this study, we show that spiders utilize nutrients of marine origin to a larger extent than most insect predators. The carbon isotope composition of most spiders closely matched that of the main group of emerging insects, phantom midges (Chironomidae), and that of chironomid food (green algae) (Fig. 3). This suggests a fairly straight food chain from green algae to spiders, with little inclusion of terrestrial food items (Fig. 5). Most insect predators, on the other hand, have a carbon isotope composition that more closely match that of terrestrial herbivores (Homoptera, Heteroptera, Coleoptera) and plants. Thus, it seems that spiders, but not insect predators, are the main beneficiaries of marine inflow (Fig.5).

The difference between spider and insect predators in their ability to utilize emerging flying insects may be due to that spiders in the area have hunting methods more efficient in
capturing flying prey. This conclusion is further supported by the fact that many spiders that utilize marine nutrients to a large extent are web spiders, which are highly specialized on flying prey. Springtails, the most common detritivores, like phantom midges have a carbon isotope ratio matching that of marine algae. It is thereby not possible for us to fully exclude the possibility that spiders feed on springtails rather than phantom midges, though the latter is more likely considering the hunting methods of the spiders in this study. For spiders hunting on the ground, springtails may be encountered and eaten, but are not likely the main prey for most adult spiders.

![Diagram of suggested coastal food web of Baltic Sea shores.](image)

**Figure 5** *Suggested coastal food web of Baltic Sea shores.*

The spider family Dictynidae had the strongest marine signal of the predators included in the analysis. Dictynids have small body size and build aerial, random webs well suited to capture small flying insects such as phantom midges. Dictynidae is however only represented with one individual in our analyses; hence the only conclusion that may be drawn from this result
is that further dietary studies of coastal predators in the Baltic Sea area should include this family. Most of the web-building spiders in this study are orb-weavers (Araneidae, Tetragnathidae) and sheet-web weavers (Linyphiidae). Both orb-webs and sheet-webs are designed to be efficient in capturing flying prey (Foelix 1996), which would make web building spiders on shores likely to benefit much from a marine subsidy consisting of dipterans such as phantom midges. This is supported by our results, showing that web building spiders on shores have a strong marine signal in their carbon stable isotope ratios. This is in particular true for orb web weavers, which is not surprising considering that the common orb web weavers on the study shores generally build their webs at greater height (0.3-2 m above ground) than the sheet web weavers. Most studied sheet web weavers build their webs in very low vegetation or between rocks, and are thereby likely to capture more of prey organisms living in the vegetation or on the ground, in addition to dipterans, than the orb web weavers. The most common orb web weavers on the studied shores, Larinioides cornutus and Tetragnatha extensa, typically live close to water and often build their webs in reeds and sedges. They are thereby as likely to have their webs suspended over water as over land, something that should increase the proportion of marine prey captured in webs.

Of the large number of spiders hunting on the ground, wolf spiders are the by far most common and abundant in the area. Our results show that wolf spiders on shores do utilize nutrients of marine origin to a very large extent, and this is likely the reason for their high abundance on the study shores. The carbon isotope ratio of wolf spiders is also largely consistent with that of phantom midges (Chironomidae). Wolf spiders are fast running, active hunters, and prey capture is likely triggered by movement, through both visual and vibratory cues (Foelix 1996; Barth 2002). This makes them well suited for hunting fast moving prey, such as midges and flies (but also other wolf spiders). The three wolf spiders utilizing marine prey to the largest extent are Pardosa wolf spiders, and these three species (P. amentata, P. agricola and P. monticola) are all very common and abundant on the studied shores. However, there also seem to be small but significant differences among taxa that may be related to differences in hunting strategy.

In our study, we found no difference in carbon stable isotope ratios between body part tissues of Pardosa spiders, showing that spiders in coastal areas are consistently feeding on marine prey. The difference in nitrogen stable isotope ratios between leg and body tissue however indicate that the food chain position occupied by adult wolf spiders vary somewhat over time.
This is not surprising since wolf spiders are well-known generalists, and behaviours such as cannibalism and intraguild predation are common. Several studies have shown that it is common for wolf spiders to prey on smaller conspecifics, and that cannibalism in wolf spiders increases with difference in body size (Balfour et al. 2003; Rickers & Scheu 2005; Borre et al. 2006). Another wolf spider group utilizing marine nutrients to a large extent is juvenile Trochosa spiders, that utilize marine nutrients to a larger extent than adults of either of the two species included in the analyses (T. ruricola and T. terricola). One possible explanation is a niche shift in prey size between juvenile/subadult and adult Trochosa spiders. Adult Trochosa are large wolf spiders, and phantom midges are likely a somewhat small prey for adults, though not for juveniles. This interpretation is supported by the finding that adult Trochosa spiders have higher nitrogen isotope ratios than smaller spiders, indicating a higher position in the food chain.

The beetles are hunters better adapted to catch prey that are slower than dipterans. The most common ground beetle near the water’s edge (Dyschirius) hunts below ground, mostly for rove beetles (mainly Bledius) (Lindroth 1961; Sandhall & Lindroth 1976). Being rove beetle specialists as well as living underground, Dyschirius beetles are unlikely to utilize flying prey such as midges. Their main prey, Bledius rove beetles, feed on unicellular algae (Sandhall & Lindroth 1976). The most common rove beetles on shores are generally small, and the stable isotope analyses indicate not only that they mainly utilize terrestrial nutrients, but the nitrogen isotope ratio suggests that they are not on a very high level of the food chain. It is possible that at least some of the studied rove beetle species are detritivores or fungivores rather than predators, and in any case likely to be preyed upon by larger predators.

The predatory Heteropterans in our study are shore bugs (Saldidae) and damsel bugs (Nabidae). Shore bugs are typically found in damp areas close to the waterline (Schuh & Slater 1995), yet our results indicate that they utilize nutrients of terrestrial origin to a larger extent than any of the other predators. Schuh & Slater (1995) describe shore bugs as extremely agile, being able to both jump and fly. That they still do not feed on marine prey may reflect habitat choice: Though being close to the waterline, shore bugs are capable of hunting both on the ground surface and below it, and this may cause them to encounter less phantom midges and more detritivores when hunting. Damsel bugs also had a mainly terrestrial diet, which is not surprising since they are likely too slow to be very efficient predators on midges and flies, but they still utilize marine material to a larger extent than the other studied insect predators. This
may be due to habitat choice: hunting in vegetation rather than on the ground, they are likely to encounter more marine prey such as phantom midges than insect predators hunting in detritus do. The Nitrogen stable isotope analysis also places them higher in the food chain than any other analyzed insect, as high as many of the spiders.

**Consequences for coastal ecosystems**

The carbon stable isotope ratios of coastal insects, regardless of food chain level, indicate that marine inflow to shores is of little importance for insects as a nutrient source with the exception of springtails. If so, spiders are the only predator group and one of the few arthropod groups on the shores capable of utilizing nutrients of marine origin. This could potentially disconnect spiders from the terrestrial food web, seemingly making them part of the marine rather than the coastal ecosystem. Still, being generalist predators, even if spiders rarely feed on terrestrial prey, they may however affect coastal ecosystem structure and function simply as a consequence of their high densities on shores (Beckerman et al. 1997; Denno et al. 2003; Schmitz 2003; Cronin et al. 2004). Even if most spiders only occasionally feed on terrestrial prey, spider densities on shores may be high enough for spider predation to still affect prey populations negatively. For instance, several studies have shown that spiders affect local prey populations through behavioural effects as well as through direct predation. Spiders affect behaviours such as feeding, activity and movement patterns in herbivores, and these behavioural effects can affect ecosystem function even in the absence of direct density effects (1996; Beckerman et al. 1997; Denno et al. 2003; Schmitz 2003; Cronin et al. 2004). Since intraguild predation is common in spiders (Foelix 1996), behavioural effects may appear not only in typical prey organisms, such as herbivores and detritivores, but also in other coastal predators. This may affect not only predatory interactions within the food web, but also competitive interactions between coastal predators. In conclusion, the large numbers of spiders on Baltic shores may have profound consequences for ecosystem function notwithstanding that terrestrial prey constitutes only a low proportion of spider diets. Further and more detailed studies would be needed for closer examination of the feeding relationships and the roles of spider predators in coastal food webs.
Acknowledgements

We want to thank all field workers who helped collect data for this study: Maria Enskog, Charlotte Gabrielsson and Petra Mellbrand. We also want to thank Torbjörn Kronestedt at the Swedish Museum of Natural History for advice on wolf spider species determination. This study was financially supported by grants from Vetenskapsrådet (The Swedish Research Council) and FORMAS (The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning) to Peter Hambäck.

References


Vanden Borre, J., Bonte, D. & Maelfait, J-P. (2006) Interdemic variation of cannibalism in a wolf spider (Pardosa monticola) inhabiting different habitat types. – Ecological Entomology 31(2) 99-105(7)
Effects of subsidized predators on coastal food webs in the Baltic Sea area

Kajsa Mellbrand, Örjan Östman* and Peter Hambäck

Department of Botany, Stockholm University, SE-106 91 Stockholm, Sweden
*Department of Ecology and Evolution, Uppsala University, SE-752 36 Uppsala, Sweden

Abstract

The aim of this study is to examine possible top-down effects of spiders in subsidized coastal food webs. This was done through a large-scale removal experiment, where spiders were removed from small islands using pitfall traps, and the effects of spider removal on densities of other arthropods were estimated. Arthropods were sampled using a vacuum sampling device at three occasions each summer in 2004-2006. The results suggest that the high spider densities on shores have negative effects on insect predator densities, probably through a combination of increased competition and increased intraguild predation from spiders. No treatment effects were found on herbivore or detritivore densities, and we suggest that the negative effect of spiders on herbivore and detritivore densities on control islands may be at least partly balanced by an increased effect of insect predators utilizing mainly terrestrial prey on treatment (removal) islands. Our study does not exclude the possibility of top-down effects in the system from spiders, but in case they do exist, they are likely behaviour mediated rather than a result of direct spider predation. The uniqueness of this study however lies greatly in its scale: these types of experiments are typically made using small (one or a few m²) enclosures in which the food web is manipulated. By using islands as natural enclosures, natural dynamics are incorporated and natural ranges of the studied arthropods are maintained. Though the use of islands allows a lesser degree of control of the study system than enclosures, large-scale studies such as this one are not only an important complement to traditional enclosure studies, but necessary for understanding large-scale predator effects.
**Introduction**

Both vertebrate and invertebrate predators are known to aggregate in large numbers in coastal areas around the world (Polis et al. 1997; Henschel 2004; Power et al. 2004), and these aggregations are typically explained by a high inflow of marine nutrients and matter, subsidizing terrestrial organisms. These movements of nutrients and matter across ecosystem boundaries, and the resulting high predator densities, may have a profound influence on the receptor ecosystem structure and dynamics (Polis et al. 1997; Polis & Hurd 1996; Nakano & Murakami 2001; Murakami & Nakano 2002, Knight et al. 2005), and several vectors have been identified for nutrient transport between aquatic and terrestrial systems (Polis et al. 2004; Polis et al. 1997; Polis & Hurd 1996, Bastow et al. 2002). The effects of marine subsidies are in part related to the type of inflow. Inflow at the detrital level of the food web (such as dead organic matter washed ashore) will mainly promote bottom-up control of the food chain, while the effect of inflow on higher levels of the food chain, such as emerging insects with aquatic larval stages, is harder to predict, but has the potential to promote trophic cascades (Polis et al. 1997; Knight et al. 2005). Whether this truly happens seems to be highly dependent on the nature and dynamics of the terrestrial food web, with behavioural responses of organisms in the receptor ecosystem being of great importance.

In the Baltic area, a major flow from the marine to the terrestrial environment consists of emerging phantom midges (Chironomidae), with aquatic larval and terrestrial adult stages. When entering the terrestrial food web, the midges directly subsidize coastal predators, bypassing lower levels of the food chain, and isotope data suggest that the main beneficiaries of this inflow are spiders (Paper I). Not surprisingly, the most common and abundant predators in the coastal systems are spiders, and mainly several species of wolf spiders (Lycosidae) (Mellbrand, unpubl. data). Because many spiders are generalists (Foelix 1996), the very high densities in coastal areas may strongly affect other parts of the coastal food web both directly and indirectly through trophic cascades (Anderson & Polis 2004; Beckerman et al. 1997; Cronin et al. 2004; Denno et al. 2003; Moran et al. 1996; Polis et al. 1997; Schmitz 2004; Schmitz et al. 2000). The actual impact on the density of other arthropods could however be weakened by intra-guild
predation between spiders (inter- and intraspecifically, Denno et al. 2004), that has also been documented among wolf spiders in the study area (Paper I). Moreover, the strong marine inflow may also cause spiders to concentrate on marine food items and thereby cause spiders to functionally be part of the marine rather than terrestrial sub-web. Hence, the high spider density in coastal areas cannot be sufficient evidence that spiders are important structuring factors on the coastal food web.

The traditional approach for studying effects of arthropod predators on lower trophic levels is through small-scale enclosure studies (e.g., Schmitz 2003; Beckerman et al. 1997), or by selectively removing predators on focal plant individuals (e.g., Marquis & Whelan 1994). These studies are excellent for examining underlying mechanisms but may be less informative about large scale effects. The reason is that small scale studies may impede natural movements and exclude population level feed backs (Inouye et al. 2005). In our area, we know that *Pardosa* wolf spiders may move up to 60 m in a 48 h time period (Mellbrand & Hambäck, unpubl. data) but no predator enclosure or exclosure studies with invertebrate predators have yet been performed at a spatial scale allowing for such large-scale movement behaviours. One alternative is to use areas defined by natural boundaries while still small enough to be manipulated, such as islands (e.g., Hambäck et al. 2004). Small islands are comparatively simple and undisturbed ecosystems, characteristics that make them suitable as mesocosms for studying terrestrial food web interactions. The waterline is a well-defined natural barrier that most organisms still are able to disperse across (to a varying degree). This makes it possible to manipulate the whole system without loosing natural dynamics, apart from treatment effects. For the purpose of this study, subsidies have also been shown to have a larger relative impact on smaller islands (Polis & Hurd 1996).

In this study, we examined the effect of removing the main spider group, wolf spiders (Lycosidae), on densities of other arthropods in coastal ecosystems. For this purpose, we have removed spiders from small islands (20-2100 m²) using pit-fall trapping during three consecutive years. Because of the openness of the system, we were unable to completely eliminate spiders but comparisons with control islands suggest that wolf
spider densities nevertheless were reduced by 50-60%. We then observed if this reduction in spider densities affected densities of both other predators on the islands and herbivores.

**Material and methods**

*Field sites*

Field experiments were conducted during the summers 2004-2006 on 19 islands outside the coast of Gräsö. Gräsö (16º45’E, 67º10’N) is one of the larger Swedish islands, about \(\sim 150 \text{ km}^2\), and located in the Uppland archipelago in the Baltic Sea outside the coast of Northern Uppland, Sweden. The study islands are located in two areas outside the Gräsö coast: 10 islands in Örskärssund on the northern coast of Gräsö, and 9 islands north of Skoga hamn, Långaröd on the north-eastern coast of Gräsö. Three treatment and two control islands, at Skoga hamn, were not included in the experiment in 2004, but were added in 2005. The islands range from 20 to 2100 \(\text{m}^2\) in size and are located in shallow bays very close to the Gräsö coast (Table 1). The islands generally vary in size both between and over the year due to changes in water level of the Baltic Sea, causing lower parts of the islands to be flooded during large parts of the year, but the estimated sizes are for an average summer period. This has the consequence that some island may have narrow bridges with the mainland during periods of extremely low water, but also that smaller islands may be completely flooded during periods of extremely high water. Water level fluctuations are mainly due to meteorological and hydrological factors, and typically mean water levels in the Baltic Sea are highest in January, lowest in late winter-early spring, and rise again in late-summer-autumn (Jerling 1999).

*Study system*

The study islands are rocky with patches of vegetation ranging from wet shore meadow to very dry in rockier parts. About 40% of the island area is covered in vegetation, though this varies both between islands and with water level. Larger islands are generally higher and therefore rockier, while low areas of all islands usually are vegetated but also easily flooded. The vegetation mainly consists of low grasses, reeds, sedges and herbs, although the largest islands have occasional small trees and bushes. Both landscape structure and vegetation types on islands are generally similar to that of the near Gräsö shores, and so
is the associated fauna. The distance across open water to the nearest larger island (usually Gräsö) is not more than 20-30 m for any of the islands. Due to the small distances across open water, lack of a species that is present on the nearest larger island is likely due to small island size (few habitats) or larger wind and wave exposure, rather than to dispersal limitation.

The most common and abundant predators on the islands are spiders, and the most common and abundant spiders are wolf spiders (Lycosidae) of the genus *Pardosa*, in total 7 species, of which the most common are *P. amentata* and *P. prativaga*. Apart from *Pardosa*, 5 other wolf spider genera can be found on the islands: *Trochosa* (3 species), *Arctosa* (1 species), *Alopecosa* (2 species), *Xerolycosa* (2 species) and *Pirata* (1 species). Of these, *Trochosa ruricola*, *T. terricola* and *Arctosa leopardus* are common and abundant while remaining genera are found in smaller numbers on few of the islands. Other spiders on the islands belong to the families Araneidae, Tetragnathidae, Philodromidae, Gnaphosidae, Clubionidae, Salticidae, Theridiidae, Pisauridae, Thomisidae, Dictynidae and Linyphiidae. Most of these spiders are caught only occasionally and in smaller numbers, with the exceptions of *Pachygnatha clercki* (Tetragnathidae), *Thanatus striatus* (Philodromidae) and small Linyphiidae (money spiders). Our removal method (pitfall trapping, see below) does not work for the families Salticidae, Therididae, Thomisidae and Clubionidae which are able to climb out of traps. Neither does it work for web builders (Araneidae, *Tetragnatha*, Theridiidae, Dictynidae, Linyphiidae), though it may have some small effect on small linyphiids making webs at ground level.

Insect predators include beetles (Carabidae, Staphylinidae), predatory Heteropterans (Nabidae, Saldidae) and Neuroptera larvae. The most common herbivores on the islands are plant hoppers (Homoptera: Cercopidae, Cicadellidae), and to a lesser extent, mirids, grasshoppers, and butterfly larvae. The most common detritivores are springtails (Collembola), mainly *Podura aquatica* close the shore-line, and sow bugs (Isopoda).
Methods

Spiders were removed from five islands in Örskärssund and five islands in Skoga; remaining islands (five in Örskärssund and four in Skoga) were used as controls. Among these, 5 islands (3 removal and 2 control) in the Skoga area were added in 2005 (Table 1), causing changes in the sample size among years. In 2004, spider removals were unsuccessful, due to insufficient removal intensity during the latter part of the season. For this reason, we use density data from this year as an additional control of treatment effects. Spiders (mainly wolf spiders) were removed using pitfall traps, and also caught by hand when encountered. In 2006, we also removed larger web spiders (Araneidae, *Tetragnatha*) by hand, but these spiders are very few compared to the abundant wolf spiders. Hence, the removal treatment is mainly a wolf spider removal treatment. Plastic jars (8 cm diameter and 6 cm height) were used as pitfall traps and emptied once every day or every two days from mid-May to mid-July on treatment islands. Caught spiders were removed from the island; other invertebrates were released on the island. The number of traps varied between islands due to island size, and between years (and at occasions within years) due to varying water levels. In total, we removed 3854 spiders in 2005 and adult spiders in 2006, and the number varied strongly with island size (Table 1).

In order to estimate food web responses, arthropods were sampled using a vacuum sampling device, a Stihl® BG85 Leaf Blower/VAC, at three occasions each summer in 2004-2006. Sampling was made in mid-June, mid-July and mid-August. Densities were estimated within a mobile circular enclosure of 0.7 m², and three samples per island were taken at every sampling occasion. Captured animals were returned after counting, except for spiders. Sampled arthropods were sorted into groups. For each island, the mean number of individuals per island and sampling occasion were calculated.

Because of differences in the number of islands for 2004 versus 2005-06, we separated the analysis into two time periods, 2004-05 and 2005-06. The initial tests for each time period was to examine effects on the arthropod community, as divided into 8 broad groups (Table 2), using a MANOVA. In the MANOVA, group densities for year 2 (05 or 06) in each time period were dependent variables while group densities in year 1 (04 or
05), treatment and island size were independent variables. In cases when the MANOVA indicated a significant effect of year-by-treatment or year-by-size-by-treatment interactions, we performed a separate ANOVA for each group. In addition, we also performed analyses of total herbivore and predator densities (excluding wolf spiders) for the two time periods, using the same independent variables. This analysis provides some complementary information to the MANOVA as small correlated changes in several predator, or herbivore, groups may be hidden by the large variability in the MANOVA. Prior to analyses all densities and island sizes were loge-transformed. All statistical analyses were performed using R 2.5.0.

**Results**

The removal of wolf spiders was fairly successful, and control islands had about 50% lower wolf spider density than removal islands in 2005 and 2006 (Fig. 1). The main effect of removal occurred between years 2004 and 2005, while in 2006 removal mainly maintained low spider densities on treatment islands (Fig. 1). The exception was one island during 2006, where the removal treatment seemed to have failed. We therefore decided to exclude this island from further analyses of the changes in other arthropod densities due to spider removals. In the pitfall traps, mainly wolf spiders where caught (70-95 %), but they also caught smaller number of *Pachygnatha clercki* and small linyphiids.
Figure 1  Spider densities in treatment (■) and control (♦) islands between years 2004 and 2005.

Table 1. Spider removal. Data includes adult and subadult spiders; small juveniles in traps (often spiderlings carried by female wolf spiders) were removed from islands but not counted.

<table>
<thead>
<tr>
<th>Island</th>
<th>Island size (m²)</th>
<th>Removed spiders 2005</th>
<th>Removed spiders 2006</th>
</tr>
</thead>
<tbody>
<tr>
<td>2T</td>
<td>1136</td>
<td>708</td>
<td>295</td>
</tr>
<tr>
<td>6T</td>
<td>382</td>
<td>345</td>
<td>153</td>
</tr>
<tr>
<td>8T</td>
<td>79</td>
<td>194</td>
<td>48</td>
</tr>
<tr>
<td>10T</td>
<td>277</td>
<td>100</td>
<td>150</td>
</tr>
<tr>
<td>13T</td>
<td>1834</td>
<td>804</td>
<td>350</td>
</tr>
<tr>
<td>20T</td>
<td>312</td>
<td>253</td>
<td>372</td>
</tr>
<tr>
<td>22T</td>
<td>26</td>
<td>52</td>
<td>206</td>
</tr>
<tr>
<td>24T</td>
<td>1170</td>
<td>552</td>
<td>916</td>
</tr>
<tr>
<td>27</td>
<td>177</td>
<td>93</td>
<td>528</td>
</tr>
<tr>
<td>28T</td>
<td>1067</td>
<td>753</td>
<td>933</td>
</tr>
</tbody>
</table>
When comparing densities between years 2004 and 2005, we found that the MANOVA suggested no changes due to treatment and we therefore did not perform any analyses on the separate groups. We did however find a significant effect of treatment on densities of pooled predators (ANOVA Sum of squares=1.02; p<0.05) (Fig. 2), while no such effect was found for pooled herbivore densities (ANOVA Sum of squares=0.54; N.S.).

\[ \text{Island size} \]

\[ \ln(\text{Density 2006}) - \ln(\text{Density 2005}) \quad \ln(\text{Density 2005}) - \ln(\text{Density 2004}) \]

**Herbivores**

**Predators**

*Figure 2* Changes in pooled herbivore density and pooled predator density on treatment (○) and control (●) islands, related to island size.

In the comparison of densities between 2005 and 2006, we found a significant effect in the MANOVA of treatment-by-year on the arthropod community (MANOVA F=2.58;
p<0.05). From the following variance analyses of arthropod groups (Table 3), it is evident that this significant effect in the MANOVA was due to density responses in four groups: ground spiders, predatory heteropterans and ground beetles (Carabidae). First, we found a significant effect of treatment for ground spiders, where densities are significantly lower on treatment than on control islands. For carabids, densities are positively affected by treatment (Table 3; Fig. 3), and increased significantly between years 2005 and 2006 (Table 3; Fig. 3). We also found a significant relation between treatment and island size: The increase is larger on smaller islands (Table 3; Fig. 4). For predatory heteropteran densities, densities seem to be positively affected by treatment, though this trend is not significant (Table 3; Fig. 3). We also found a significant relationship between treatment and island size: On small islands, the increase in density is smaller on control than on treatment islands, while on large islands the increase is larger on control islands (Table 3; Fig. 4). When performing ANOVAs on pooled predator densities for years 2005 and 2006, we found no significant effects related to treatment for either herbivores or predators (Fig. 2).

Table 3 ANCOVA, density 2006 tested against density 2005, island size and treatment (Sum of squares; p-value).

<table>
<thead>
<tr>
<th>Group, density 2006</th>
<th>Density 2005</th>
<th>InSize</th>
<th>Treatment</th>
<th>Treatment* InSize</th>
</tr>
</thead>
<tbody>
<tr>
<td>ground spiders</td>
<td>0.15; N.S.</td>
<td>0.86; N.S.</td>
<td>1.55; &lt;0.01</td>
<td>1.98; N.S.</td>
</tr>
<tr>
<td>web spiders</td>
<td>0.71; N.S.</td>
<td>0.04; N.S.</td>
<td>0.09; N.S.</td>
<td>0.003; N.S.</td>
</tr>
<tr>
<td>carabids</td>
<td>1.22; &lt;0.05</td>
<td>1.30; &lt;0.05</td>
<td>1.36; &lt;0.05</td>
<td>3.46; &lt;0.01</td>
</tr>
<tr>
<td>staphylinids</td>
<td>0.08; N.S.</td>
<td>0.10; N.S.</td>
<td>1.27; N.S.</td>
<td>0.17; N.S.</td>
</tr>
<tr>
<td>parasitoid hymenoptera</td>
<td>0.30; N.S.</td>
<td>0.51; N.S.</td>
<td>0.11; N.S.</td>
<td>0.68; N.S.</td>
</tr>
<tr>
<td>predatory heteroptera</td>
<td>0.20; N.S.</td>
<td>0.17; N.S.</td>
<td>4.67; N.S.</td>
<td>11.31; &lt;0.05</td>
</tr>
<tr>
<td>herbivorous heteroptera</td>
<td>0.26; N.S.</td>
<td>0.85; N.S.</td>
<td>0.46; N.S.</td>
<td>0.002; N.S.</td>
</tr>
<tr>
<td>Homoptera</td>
<td>2.88; N.S.</td>
<td>2.03; N.S.</td>
<td>0.07; N.S.</td>
<td>0.41; N.S.</td>
</tr>
</tbody>
</table>
Figure 3 Arthropod densities years 2004-2006 on treatment (○) and control (●) islands.
Figure 4 Changes in arthropod density on treatment (○) and control (●) islands, related to island size.
Discussion

Spiders are by far the most common and abundant arthropod predators in the studied coastal areas. Isotope analyses (Paper I) also show that many spiders in these coastal ecosystems utilize nutrients of marine origin to a high degree, while many insect predators on shores feed almost exclusively on nutrients of terrestrial origin. Since most spiders are generalists (Foelix 1996), subsidized spider populations are also capable of suppressing local prey more effectively (Chaneton & Bonsall 2000; Polis et al. 1997). Hence, we should expect several groups of arthropods to increase in density on wolf spider removal islands. Still, our results show no effect of spider removal on either herbivore or detritivore densities, but indicate that spiders do suppress densities of other terrestrial predators.

While the lack of effect on herbivore and detritivore densities may be partly due to the fact that spider densities were only reduced by 50% on treatment islands, it is also possible that the predation by other predators compensated for the reduction in mortality from spider predation. Predatory insects increased when spider densities decreased, and all of these predator groups are likely to have increased their prey capture. The underlying mechanism for increases in other predators cannot be deduced from this study, but the fairly immediate response suggests that direct mortality from spider predation may have been a decisive factor. All of these predator groups are also typically much smaller in size than the average wolf spider in the area, and predators such as nabids, small carabids and smaller spiders are probably easy prey for fast running lycosid spiders. Understanding the exact mechanism underlying the observed changes requires detailed studies in more tightly controlled experiments, we do however believe that larger scale studies like this one, including natural dynamics and processes, are an important complement to traditional enclosure experiments.

The top-down effect of spiders, even though quite weak, contrasts somewhat with the impression from the isotope studies (Paper I). These studies suggested that wolf spider diets were heavily dominated by marine food items, probably mostly adult midges. It is however important to remember that food webs derived from isotope data only show the
bottom-up flow of carbon and nitrogen. Rare prey items are not likely to affect the isotope composition of the predator, but predation by a highly abundant predator on these prey items may nevertheless have a strong top-down effect. In our case, the inflow of marine prey seems to have a strong positive effect on predators, such as spiders, able to effectively utilize such prey. Predators less able to do so are however negatively affected by the resulting high spider densities, and we suggest that this is mainly a consequence of interactions within the coastal ecosystem. The difference in insect predator densities between treatment and control islands can be explained by a combination of high spider densities on control islands and spider behaviour, further reinforced by a landscape effect of small island size.

Small islands generally have a high temporal variation in terrestrial primary production, but also have a high coast-inland ratio that make them more heavily subsidized than larger islands (Anderson & Polis 2004). Anderson & Polis (2004) found web building spiders on small islands to maintain more stable populations, which was explained by a larger inflow of marine nutrients relative to island size, providing a higher resource baseline for predators able to utilize that inflow, and decoupling them from terrestrial productivity. Most spiders are typically generalist predators (Foelix 1996), including wolf spiders that are also by far the most common and abundant predators on the studied islands, and subsidized generalist predators are known from literature to suppress local prey more effectively (Chaneton & Bonsall 2000; Polis et al. 1997). Predators less able to utilize marine subsidies will thereby not only be more dependent on terrestrial productivity, but also exposed to higher levels of competition as well as intraguild predation from subsidized generalist predators released from such dependency. On treatment islands, predatory insects tend to increase, likely as a response to less competition and intraguild predation by spiders.

The high prevalence of behaviours such as intraguild predation and cannibalism in spiders (Foelix 1996) make finding evidence for top-down effects in terrestrial arthropod systems difficult (Moran et al. 1996; Polis et al. 2000; Finke & Denno 2005). In a classic top-down controlled system, we should expect to find effects of the spider removal
treatment on herbivores and detritivores as well. We did not however find any evidence for such effects, which may be due to the increase in insect predators as spider densities decreases: On treatment islands, the effect of decreased predation by spiders may be compensated by increased predation by predatory insects on terrestrial prey. The lack of a treatment effect may however also be a result of the potential time delay in treatment effects, mentioned above.

Top-down effects have been shown to often be behaviour mediated. Predator presence can induce changes in behaviour in prey populations, such as decreased activity and switches in habitat and diet selection (Denno et al. 2003; Cronin et al. 2004; Moran et al. 1996; Schmitz 2003; Beckerman et al. 1997). Spider presence alone, apart from predation, may cause herbivores to become less active (Denno et al. 2003), migrate (Cronin et al. 2004; Moran et al. 1996), or cause adaptive shifts in herbivore diet and habitat selection (Schmitz 2003; Beckerman et al. 1997). Beckerman et al. (1997) showed that in plots containing spiders, herbivores fed more on leafy herbs and less on grasses than in patches without spiders, thereby affecting vegetation structure in plots. In this study, only arthropod densities were measured, and numerical responses give little or no information regarding behavioural effects. We therefore cannot draw conclusions about the presence/absence of top-down effects on lower levels of the ecosystem based on the results of this study alone. Still, a discussion of top-down effects assumes that coastal spiders feed on both marine and terrestrial prey. If the spiders however utilize nutrients of marine origin to a degree where they actually are almost completely decoupled from the terrestrial food web, eventual top-down effects on other terrestrial arthropods should be solely behaviour mediated and not a result of direct predation by spiders.

The inflow may also affect intraguild interactions, with possible indirect effects as a result, and thereby determine how terrestrial predators less able to utilize marine prey will be affected by marine subsidies. Behavioural responses in herbivores may interact with spider behaviour to strengthen the effect of spiders on insect predators. If the high predator densities on control islands increase defensive behaviours such as hiding or switching habitat in terrestrial prey organisms, hunting may become more difficult for the
insect predators dependent on this type of prey. If predatory insects are forced to spend more time hunting, it would also increase their exposure to intraguild predation from spiders. Alternatively, the insect predators themselves may exhibit predator avoidance behaviours as a response to high spider densities, further decreasing their effect on terrestrial prey.

Conclusions
In this study we could not completely unravel the coastal food web, mainly due to the lack of evidence for or against top-down effects on lower levels of the food web. The increases in other predators suggest that to further improve our understanding of these interactions, it is necessary to exclude wider groups of arthropod predators. We can however conclude that marine subsidies do affect the structure and dynamics of coastal ecosystems in the Baltic Sea area, and suggest that one of the main effects of the subsidies are changes in interactions on predator levels of the food web. Our near future plans involve measurements of plant responses to spider removal on the studied Baltic Sea islands, in order to find eventual behaviour mediated effects of predators on herbivores and detritivores, and effects of herbivores on coastal plants.

Acknowledgements
We want to thank all field workers who helped collect data for this study: Marcus Brage, Hanna Barck, Maria Enskog and Petra Mellbrand. We also want to thank the landowners in Skoga and Örskärssund on the island of Gräsö for allowing us to work on their islands. This study was financially supported by grants from Vetenskapsrådet (The Swedish Research Council) and FORMAS (The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning) to Peter Hambäck.
References


