Det här verket är upphovrättskyddat enligt *Lagen (1960:729) om upphovsrätt till litterära och konstnärliga verk*. Det har digitaliserats med stöd av Kap. 1, 16 § första stycket p 1, för forskningsändamål, och får inte spridas vidare till allmänheten utan upphovsrättsinehavarens medgivande.

Alla tryckta texter är OCR-tolkade till maskinläsbar text. Det betyder att du kan söka och kopiera texten från dokumentet. Vissa äldre dokument med dåligt tryck kan vara svåra att OCR-tolka korrekt vilket medför att den OCR-tolkade texten kan innehålla fel och därför bör man visuellt jämföra med verkets bilder för att avgöra vad som är riktigt.

This work is protected by Swedish Copyright Law (*Lagen (1960:729) om upphovsrätt till litterära och konstnärliga verk)*. It has been digitized with support of Kap. 1, 16 § första stycket p 1, for scientific purpose, and may no be disseminated to the public without consent of the copyright holder.

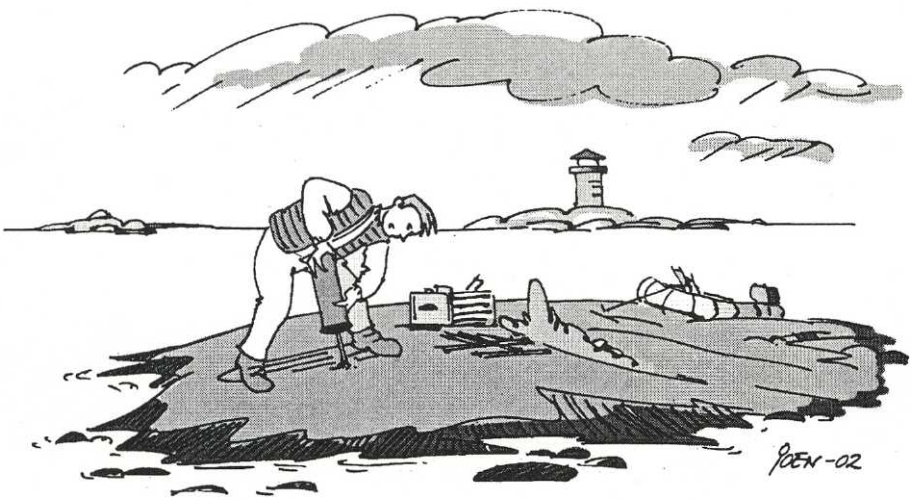
All printed texts have been OCR-processed and converted to machine readable text. This means that you can search and copy text from the document. Some early printed books are hard to OCR-process correctly and the text may contain errors, so one should always visually compare it with the images to determine what is correct.

GÖTEBORGS UNIVERSITET

GÖTEBORGS UNIVERSITETSBIBLIOTEK
1001073092

Interactions between grazers and algal canopies, an experimental approach

Gunnar Cervin



ss 02.995

GÖTEBORGS·UNIVERSITETS·BIBLIOTEK
Biblioteket för
botanik och miljö
Uf. 082

Göteborg University
Faculty of Science

Dissertation

Interactions between grazers and algal canopies, an experimental approach

Gunnar Cervin

Department of Marine Ecology, Marine Botany
Göteborg University
P. O. Box 461
SE 405 30 Göteborg
Sweden

Avhandling för filosofie doktorsexamen i Marin Botanik vid Göteborgs Universitet (examinator: Prof. Inger Wallentinus) som enligt beslut av naturvetenskapliga fakulteten kommer att försvaras offentligt fredagen 12 april 2002 kl 10.00 i föreläsningssalen på Botaniska Institutionen, Carl Skottsbergs Gata 22B, Göteborg.

Fakultetsopponent: Assoc. Prof. Julio Arrontes, Laboratoria de Ecologia, Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, Oviedo, Spain

Cervin, Gunnar 2002. Interactions between grazers and algal canopies, an experimental approach.
Department of Marine Ecology, Marine Botany, Göteborg University, P.O. Box 461, SE 405 30 Göteborg, Sweden

Abstract: Interactions between macroalgae and grazers were investigated in manipulative field experiments on intertidal sheltered rocky shores on the Swedish west coast and on the Isle of Man. One grazer exclosure experiment was also made on semi-exposed shores on the Swedish west coast.

On sheltered shores in Sweden, exclusion of periwinkles *Littorina* spp. did not affect the survival of germlings of the brown alga *Ascophyllum nodosum* in presence of adult canopy. Other grazers such as isopods and amphipods were suggested to be important. However, increased encaged numbers of *L. littorea* caused lower survival. In another experiment the germling survival was affected by complex interactions between *Littorina* spp., adult canopy and germling density. Survival was low in absence of canopy and presence of *Littorina* spp., but higher in absence of *Littorina* spp. Later the survival was lower in presence of *Littorina* spp., irrespective of canopy treatment. Survival of germlings in high densities was lower in presence of canopy than in areas cleared of canopy, but only in presence of ephemeral green algae.

A four-year experiment explored the effect of canopy removal and grazer exclosure on recruitment of *A. nodosum* juveniles and the community structure. Canopy removal transformed the assemblage for at least 31 months. Removal of both canopy and periwinkles increased ephemeral green algae after 3 months. After 18 months a canopy of *Fucus* spp. had developed in plots initially cleared of canopy, but *A. nodosum* juveniles were not affected. A similar experiment on the Isle of Man, manipulating also the red algal turf, canopy removal in interaction with intact turf, resulted in higher abundances of juvenile *A. nodosum*. Removal of both canopy and the limpet *Patella vulgata* resulted in much higher *A. nodosum* recruitment. Canopy removal in interaction with either turf or limpet removal gave a dense cover of ephemeral green algae after 5 months, and later a dense cover of *Fucus* spp.

On semi-exposed rocky shores in Sweden, exclosure of *Littorina* spp. gave no recruitment of fucoids, the reason might be that the exclosure was only effective during the first months.

The results emphasized that complex interactions control these communities.

Key words: Adult canopy; *Ascophyllum nodosum*; Ephemeral green algae; *Fucus serratus*; *Fucus vesiculosus*; Germling survival; Grazer exclusion; Grazing; Interaction; Juvenile survival; *Littorina littorea*; *Littorea saxatilis*; Spatial variation

Inst. för Marin Ekologi, Göteborgs Universitet
Göteborg 2002
ISBN 91-89677-02-1
Printed in Sweden
Kompendiet, Göteborg

BOTANIK- OCH
MILJÖBIBLIOTEKET

To Anna & 'Knyttet'

List of papers

This thesis is based on the following papers, referred to by their Roman numbers:

I. Cervin, G., Åberg, P. (1997). Do littorinids affect the survival of *Ascophyllum nodosum* germlings? Journal of Experimental Marine Biology and Ecology 218:35-47

II. Viejo RM, Åberg P, Cervin G, Lindegarth M (1999). The interactive effects of adult canopy, germling density and grazing on germling survival of the rockweed *Ascophyllum nodosum*. Marine Ecology Progress Series 187:113-120

III. Cervin G, Lindegarth M, Viejo R, Åberg P (MS). Effects of small-scale disturbances of canopy and grazing on intertidal assemblages on the Swedish west coast

IV. Cervin G, Jenkins SR, Åberg P (MS). Processes promoting recruitment in a long-lived plant

V. Lindegarth M, Åberg P, Cervin G, Nilsson P (2001). Effects of grazing on the structure of mid-shore, intertidal assemblages on moderately exposed rocky shores of the Swedish west coast. Marine Ecology Progress Series 212:29-38

Paper I is reprinted with permission from Elsevier Science.
Papers II and V are reprinted with permission from Inter-Research Science Publisher.

A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarizes the accompanying papers. They have already been published or are manuscripts at various stages (in press, submitted or in manuscript).

Contents

1. Introduction 7
   1.1. Background 7
   1.2. The intertidal of rocky shores 8
      1.2.1. Isle of Man 8
      1.2.2. West coast of Sweden, sheltered shores 9
      1.2.3. West coast of Sweden, semi-exposed shores 10
   1.3. Study organisms 10
      1.3.1. *Ascophyllum nodosum* 10
      1.3.2. Red algal turf 12
      1.3.3. *Patella vulgata* 12
      1.3.4. Periwinkles 12
   1.4. Study areas 13
   1.5. Specific aims of the experiments 15
2. Methodological considerations 16
   2.1. Manipulative field experiments 16
   2.2. How to control grazers 17
   2.3. Canopy and turf removal 17
3. The experiments of the present thesis 19
   3.1. Germling survival of *Ascophyllum nodosum* 19
   3.2. The role of grazing and canopy, for juvenile recruitment of intertidal fucoids and community composition 20
4. Results and discussion 23
   4.1. Germling survival of *Ascophyllum nodosum* 23
   4.2. The role of grazing and canopy, for juvenile recruitment of intertidal fucoids and community composition 24
   4.3. Conclusions 26
5. Acknowledgements 28
6. References 30

Cover illustration: Fieldwork in the archipelago on the Swedish west coast, drawn by Joen Wetterholm.

1. Introduction

"As the shore between tidemarks is inhabited both by animals and by seaweeds, our knowledge of its inhabitants has come from botanists as well as from zoologists. Sometimes the botanists have ignored the animals, or the zoologists have ignored the plants; but the best results have emerged when, as has happened fairly often, the algae and animals have been considered together" (Stephenson & Stephenson 1972).

1.1. Background

In the NE Atlantic, many rocky shores are experiencing tidal range of several metres twice per day. The difference in range is due to the variation in the relative position, distance and speed between earth, sun and moon, but also to geographic position. This tidal range creates the intertidal zone where organisms experience both a marine environment and to some degree a terrestrial environment. It is a special environment in the respect that the plants and animals within it have to be able to cope with saline water, but also to stand draught and large temperature differences within times of hours. This has given these shores a zonation of species (which is recognised by most researchers) as a function of height on the shore, which is especially clear on sheltered shores. The zonation is believed to be caused by physical limitations overruling the physical limits of the species, and competitive abilities by and between the species.

The sheltered rocky shores in the NE Atlantic are covered by a fucoid canopy, which gives more draught sensitive species a chance to grow below as understorey. The most conspicuous of these canopy-forming algae is *Ascophyllum nodosum*, with dense stands in the mid intertidal. Above *A. nodosum* we find a belt of *Fucus spiralis*, which is followed by the uppermost belt consisting of *Pelvetia canaliculata*. Just below *A. nodosum*, *Fucus vesiculosus* and *Fucus serratus* are growing, and that ends the intertidal zone on true tidal shores. Looking closer at the *A. nodosum* belt, we find that it is not totally homogeneous. Small patches of *F. vesiculosus* and *F. serratus* are found within the *A. nodosum* zone, and vertical sides of boulders are often free of *A. nodosum* holdfasts. The main grazers in the *A. nodosum* zone are the limpet *Patella vulgata* and the periwinkle *Littorina littorea*. L. *littorea* is, however, more common in the NW Atlantic, where the abundances can be extremely high compared with the NE Atlantic.

The semi-exposed rocky shores experience more wave action than the sheltered shores. This wave action is of major importance to the species found on these rocks, and it also changes the height of the intertidal zones. The waves and splash from these will give marine organisms the possibility to grow higher up on the rocks, making the intertidal wider on exposed compared to sheltered shores. The species morphologies and composition differs from the sheltered shores, and will be more robust to drag and turbulence caused by the waves. Semi-exposed rocky shores in the NE Atlantic are more or less devoid of canopy algae in the intertidal, instead these are inhabited by

grazing limpets, barnacles and mussels, which increases in abundance with exposure. However, smaller patches of ephemeral macroalgae and bladderless *F. vesiculosus* can be found on these shores. At the lower limit of the intertidal, *F. serratus* and red algal turf constitute the dominating macroalgal cover. The limpet *P. vulgata* has been shown to be a key species on those semi-exposed intertidal shores, preventing establishment of fucoids by grazing (e.g. Southward & Southward 1978; Southward 1979).

The physical conditions on Swedish rocky shores are quite different from those in other parts of the NE Atlantic. The tidal range is very small, and at the same time large differences in water level due to atmospheric pressure occurs, with submergence/ emergence of the intertidal zone for several days/ weeks. Ice-winters are common, but irregular, with ice-scouring disturbing the assemblages. However, the zonation pattern is similar, except that *Pelvetia canaliculata* is missing and most *F. serratus* plants grow in the sublittoral. One major difference in the intertidal is the lack of limpets, why, as in the NW Atlantic, the main gastropod grazers are the periwinkles (e.g. Petraitis 1983; Papers I-III and V).

Differences in interactions within these communities as well as physical disturbances in the intertidal form these communities of the NE Atlantic. How these interactions work and what the effect are of the physical disturbances have attained a lot of interest in many parts of the world. Grazing by limpets has been investigated in e.g. Australia, South Africa and the UK (e.g. Hawkins 1981; Underwood & Jernakoff 1981; Branch *et al.* 1992; Jenkins *et al.* 1999b, a). Periwinkle grazing and ice-scouring have gained a lot of interest in the NW Atlantic (e.g. Lubchenco 1983; Petraitis 1983; McCook & Chapman 1991; Dudgeon & Petraitis 2001). The west coast of Sweden has earned little attention when it comes to experimental studies of plant-animal interactions in the intertidal, and very little is known about these interactions in combination with ice-scouring.

The general purpose of this thesis is to be a part of the work to unravel the effects of plant–animal interactions and physical disturbances in the intertidal of rocky shores. The emphasis is on the Swedish west coast where most of the work have been performed, but as a comparison one experiment was also set up on the Isle of Man in the Irish Sea.

1.2. The intertidal of rocky shores

1.2.1. Isle of Man

Situated in the northern part of the Irish Sea, the rocky shores around the Isle of Man are experiencing a tidal range of 4-8 m twice per day. The water is fully marine in the sense that it is constantly around 33 psu (Lewis 1964a). The water temperature is quite stable, 7-15°C, but the air temperature in the winter can occasionally drop down to about 0°C. The south and southeast shores on the Isle of Man have experienced a lot of attention in

marine biological investigations, as the Port Erin Marine Laboratory (University of Liverpool) is situated there. In this area the *Ascophyllum nodosum* canopy is well developed on sheltered shores. The canopy is especially well developed on only gently sloping shores, where the zone of *A. nodosum* can be more than a hundred metres wide. Looking beneath the canopy cover of *A. nodosum* we find what we call the understorey, which on the Isle of Man mainly consists of either a silty red algal turf or bare rock with the limpet *P. vulgata*. The understorey is experiencing smaller differences in draught and temperature, due to the shading fucoid canopy. This allows the more draught sensitive red algae to grow at this height. They grow as a dense turf, a few centimetres high, trapping loose lying silt and consist predominantly of *Chondrus crispus*, *Gelidium pusillum*, *G. spinosum* (former *G. latifolium*), *Corallina officinalis* as well as *Laurencia* spp., *Rhodothamniella floridula* (former *Audouinella floridula*) and *Lomentaria articulata* (Jenkins *et al.* 1999a). Among this red algal turf, patches of bare rock with a microalgal film can be found, kept free of macroalgae by the grazer *P. vulgata*, which is also found on those vertical ledges that lack the attachments of *A. nodosum*. As one moves into semi-exposed shores, *P. vulgata* increases in abundance and has there an extremely important structuring role by regulating the recruitment of algae into this community (see Hawkins *et al.* 1992 for a review). These semi-exposed shores, have a wider intertidal zone, mainly inhabited by animals such as the barnacle *Semibalanus balanoides*, the blue mussel *Mytilus edulis* and the grazer *P. vulgata*. Several studies have shown *P. vulgata* to be a key species in this community, where removal allows *Fucus vesiculosus* and *F. serratus* to establish in dense stands (e.g. Jones 1948; Southward 1964; Boaventura *et al.* 2002).

1.2.2. West coast of Sweden, sheltered shores

There are large physical differences between the Swedish west coast and the Isle of Man, especially regarding the intertidal zone. To begin with, the tidal range is only around 0.2 m in the Skagerrak (Rodhe 1998), but the sea level may fluctuate up to 2 m in response to changes in atmospheric pressure (Johannesson 1989), which might cause this zone to be kept emerged or submerged for several days to weeks in a row. The salinity is highly variable, typically ranging from 15 to 30 psu. The water is influenced by fully saline water from the North Sea (34 psu) and brackish water from the Baltic Sea (below 10 psu). Water temperature ranges from 0 to 24°C, why ice is not uncommon in winter, especially on sheltered shores. Extreme air temperatures down to -25°C in winter and up to 30°C in summer are not atypical. Ice-winters on the Swedish west coast occurs 25-35% of the years, depending on localities, and with extreme ice-years 7% of the years (Åberg 1992a and references therein). However, no ice-scouring occurred in the experimental plots during the specific experiments. The composition of species is different from the Isle of Man, with a general trend of fewer species on the Swedish west coast. For example *Pelvetia canaliculata* has never been found east of the Norwegian southern tip (Lewis 1964b) and *Patella vulgata* can only be found as a few small populations (Hansson, H.-G. pers. comm.) The common, biggest and most effective epilithic gastropod grazer is the periwinkle *Littorina littorea*. This is similar to

the NW Atlantic, although the densities on the Swedish west coast are much lower. The dominating canopy species are *Fucus vesiculosus* and *Ascophyllum nodosum*, with a few *F. serratus,* which mainly are found in the sublittoral. Which of these species that dominates in the intertidal is spatially very variable, and that can be a result of sharper exposure gradients on smaller scales than normally found in areas with larger tidal ranges. The understorey mainly consists of the crustose red algae *Hildenbrandia rubra*, *Phymatolithon* spp., and sparse individuals of *Cladophora rupestris*, *Chondrus crispus*, *Semibalanus balanoides*, *Mytilus edulis*, and quite a lot of hydroids (e.g. *Obelia* spp. and *Dynamena pumila*).

1.2.3. West coast of Sweden, semi-exposed shores

There is a more pronounced seasonal change in species composition on semi-exposed shores, compared to sheltered shores, as the species are not as long-lived due to physical disturbances. The main animals found on the intertidal shore are *Semibalanus balanoides* and *Mytilus edulis*, and the main algae, depending on time of year, are *Bangia atropurpurea*, *Polysiphonia* spp., *Ceramium* spp., *Hildenbrandia rubra*, *Ulothrix* spp. and *Urospora* spp. *B. atropurpurea* prospers on the semi-exposed intertidal in winter/early spring, covering bare rock as well as benthic animals. The ephemeral green algae *Ulothrix* spp. and *Urospora* spp. are typically found in spring, and the ephemeral red algae *Ceramium* spp. and *Polysiphonia* spp. establish dense stands in spring/early summer. Which one of the animals that will prosper depends largely if there has been an ice-winter or not. After an ice-winter, patches on shores will be scraped clear of algae and benthic animals. The first macro-species to recruit is the barnacle *Semibalanus balanoides*, which a previous study has shown to have a settlement period of about 30 days in March to April (Jenkins *et al.* 2000). These will during spring and early summer become overgrown by filamentous algae. In May/June larvae of *M. edulis* will settle almost anywhere in the intertidal, on bare rock as well as on *S. balanoides* and algae, and will in many places in the autumn totally cover the underlying barnacles. If there is a winter without ice-scouring, smaller patches within the bed of *M. edulis* will open up due to waves, into which the recruitment of *S. balanoides* is restricted. The main grazers found among the algae and benthic animals are *Littorina littorea* and *L. saxatilis*, but there is a large variation in abundance of them among different shores.

1.3. Study organisms

1.3.1. *Ascophyllum nodosum*

The Knotted wrack, *Ascophyllum nodosum*, is often the main canopy forming species found on the mid shore on sheltered rocky shores, where it forms near monospecific cover (Lewis 1964a; Stephenson & Stephenson 1972). In the North Atlantic, the

distribution is from mid Portugal on the eastern side and North Carolina on the western side, and northward up into the Barents Sea (Lüning 1990). On the west coast of Sweden, it is found down to the coast of Kullen in Öresund, where it stops abruptly (von Wachenfeldt 1975). *A. nodosum* is a perennial seaweed with an iteroparous and monophasic life history with dioecious individuals. The plants can become very old, in fact the genet may reach ages of 500-600 years according to demographic model simulations (Åberg 1992b), although undamaged individual fronds are not older than 20 years due to waves, ice and grazing. The plant has a holdfast from which primary fronds grow, and these primary fronds have apical growth with dichotomous and lateral branching. The mean length on the Isle of Man and Tjärnö is 0.96 m and 0.73 m, respectively, with a maximum of 2.5 m on the Isle of Man (Åberg & Pavia 1997). The sex ratio in *A. nodosum* in the two study areas is close to 1:1 (Åberg 1989 and pers. obs.) and adults release their gametes each year. On the Isle of Man the reproductive period is in March and the general trend is that this period is later in the spring or in early summer when going northward in Europe (Printz 1955). On the Swedish west coast, *A. nodosum* reproduces during a short period of one to two weeks, but depending on water temperature and other physical factors like periods of low water in combination with warm air temperature, the onset of the short reproductive period can vary among areas from mid April to late in May (Bacon & Vadas 1991 and P. Åberg pers. comm.). Each year the plants allocate up to 70 % of its annual growth into reproduction by producing a vast amount of gametes (Åberg 1996), with the potential egg rain of 2.5×10^9 eggs m^{-2} (Åberg & Pavia 1997). The eggs are heavy and immobile, typically released when the plants are immerged and can be stuck on the surface of the receptacles for the first hours, and the viability is high for about 15-20 hours. The sinking velocity on the Swedish west coast was estimated to 493 $\mu m * s^{-1}$, and the dispersal 2-20 m depending on water movements (Åberg, in prep.). The mobile spermatozoids are viable for 15-20 hours, and the dispersal is dependent on water movements, and is estimated to be slightly longer than for eggs within the *A. nodosum* zone, but can be much longer if transported outside the zone (Åberg, in prep.). The spermatozoids are at close range attracted to the eggs, by the their release of the pheromone finavarrene (Mueller *et al.* 1982). The zygotes have the same sinking velocity and dispersal as the eggs (Åberg, in prep.), however, studies in the NW Atlantic have shown that the dispersal is very variable and that more than 50% of the zygotes disperse more than 6 m (Dudgeon *et al.* 2001), with an estimated maximum of 30 m (Chapman 1995). The zygotes settle and are the first few weeks found as germlings mainly in small crevices and uneven surfaces like on the calcareous crusts of *Phymatolithon* spp. (pers. obs.). From germlings until juveniles of a few millimetres there is a tremendous loss of individuals (Vadas *et al.* 1982; Chapman 1984; Dean *et al.* 1989; Vadas *et al.* 1990; Lazo *et al.* 1994; Chapman 1995). About 40 juveniles with the size of <10 mm (1.5 years old) are in average found per m^2 in the *A. nodosum* canopy zone on the Isle of Man and Tjärnö, but there is a large variance at the spatial scale of 0.1-1.5 m and 2-30 m (Åberg & Pavia 1997).

The other two main fucoid species found in the sheltered mid intertidal are *Fucus vesiculosus* and *F. serratus* (Jenkins *et al.* 1999a). On the Isle of Man these grow as a dense band just below the *A. nodosum* zone (Lewis 1964a; Stephenson & Stephenson 1972), but these are also found as patches in clearings within the belt of *A. nodosum* (Jenkins *et al.* 1999a and pers. obs.). On the almost atidal sheltered shores of the Swedish west coast, *F. vesiculosus* is found among the *A. nodosum*. Which species that dominates varies, and among these can also be found plants of *F. serratus*, although it is mainly subtidal on the Swedish coast.

1.3.2. Red algal turf

The role of canopy algae in forming the communities of the intertidal have been well recognised in earlier studies (e.g. Chapman 1990; Benedetti-Cecchi & Cinelli 1992; McCook & Chapman 1997). The macroalgal canopy will radically change the physical environment for the understorey species. On sheltered shores on the Isle of Man, dense growth of red algal turf is found under the protective canopy of *Ascophyllum nodosum*. Loss of this canopy in the size of a couple of square metres will cause the turf to ameliorate and die (Jenkins *et al.* 1999a). Apparently the canopy gives physical protection to the red algal species that otherwise are found further down the shore. In the sheltered intertidal, this red algal turf also have the ability to trap loose-lying silt. (See chapter 1.2.1. for description of species.)

1.3.3. *Patella vulgata*

The other major substrate found under the canopy of *Ascophyllum nodosum* on the Isle of Man is patches kept free of macroalgae by grazing *Patella vulgata*. This limpet is the dominant grazer on semi-exposed shores of NW Europe and has a very important community-structuring role regulating the recruitment of algae (see Hawkins *et al.* 1992 for a review). As one moves into sheltered habitats, with dense cover of *A. nodosum*, the number of *P. vulgata* declines (Lewis 1964a). The silty red algal turf, growing under the *A. nodosum* canopy is probably limiting the available space for the grazer (Hawkins *et al.* 1992; Jenkins *et al.* 1999a). *P. vulgata* is a homing animal, that after grazing on the microbial film and recruiting macroalgae returns to its home scar. The shape of the shell is well adapted to drag, plus that the home scar often is lowered into the rock surface. However, silt is believed to be a problem for their ability to stick to the substrate (see Branch 1981; Hawkins *et al.* 1992 for reviews).

1.3.4. Periwinkles

The periwinkle grazers studied in this thesis are *Littorina littorea* and *L. saxatilis*, which are abundant on most Swedish shores. On these shores they are often found together, but *L. littorea* is mainly found on more sheltered shores, while *L. saxatilis* are found on semi-exposed shores or higher up in the intertidal (Paper V), although absent from very

exposed shores unless in sheltered clefts (Lewis 1964b). The distribution of *L. littorea* is from Portugal to the White Sea in the eastern Atlantic, and from Virginia to Labrador in the western Atlantic (see Reid 1996 for a review). *L. littorea* is a versatile opportunist that is able to feed on macroalgae as well as micro-organisms growing on the surface of rock, mud, sand or gravel. As for macroalgae, *L. littorea* prefers ephemeral greens and the ephemeral red *Porphyra* spp. to the various fucoids, which in turn are preferred to perennial reds such as *Mastocarpus stellatus*, *Chondrus crispus* and *Corallina officinalis*. Further, *L. littorea* prefers juvenile plants to adult plants, and has in laboratory experiments been shown to prefer juvenile *Ulva lactuca* to several other species, and to reject juvenile *Ascophyllum nodosum* (see Norton *et al.* 1990 for a review). Several studies in other parts of the world have shown that grazing by *L. littorea* may affect the density and structure of assemblages of plants and animals in sheltered to moderately sheltered areas (Lubchenco 1978; Keser *et al.* 1981; Petraitis 1983; Keser & Larson 1984). Furthermore, Lein (1980, 1984) has shown that *L. littorea* can have an important effect on germling *Enteromorpha* spp. and *Fucus* spp. in the Oslofjord. However, compared to shores on the North West Atlantic, *L. littorea* is much less abundant on European shores (Norton *et al.* 1990) and there has been much less ecological work done on this species in Europe (McQuaid 1996).

Littorina saxatilis is found from North Africa and Virginia, up into the subarctic province and has a wide vertical distribution. It is the periwinkle species with the highest degree of shell variation, and with the widest range of habitats (see Reid 1996 for a review). This species feeds primarily on epiphytic diatoms and other microalgae, cyanobacteria and bacteria, although it is able to feed on macroalgae (Norton *et al.* 1990), and can on wave-swept shores be found in numbers of 1000 to 4000 ind. m^{-2} in the relative shelter of barnacles and clefts in the rock (see Reid 1996 for a review). In sheltered areas it is found higher up in the supralittoral on smooth rocks, but high numbers are also found among shingle and in stony areas lacking *A. nodosum* (Stephenson & Stephenson 1972).

1.4. Study areas

The experiments of this thesis were carried out in two areas, the area around Tjärnö Marine Biological Laboratory (TMBL) (58°53'N, 11°8'E) at the northern part of the Swedish west coast and around the Langness Peninsula (54°5'N, 4°37'W) on the Isle of Man in the northern Irish Sea (Fig. 1).

Beside differences in salinity, temperature and tidal range, there is a difference in type of substrate between these two areas. The bedrock on the Swedish west coast is mainly granite, which is hard and very resistant to weathering and erosion, and thereby gives a good attachment for the algae. Further, the shores of the Swedish studies were steeper, sloping 5-45°. The bedrocks of the gently sloping shores on the Isle of Man, where our study was performed, are instead made of sandstone. This sandstone gives a poorer

attachment for macroalgae such as *Ascophyllum nodosum*, and is probably also the reason why so much silt is trapped among turf algae in the understorey of *A. nodosum*.

Further and more detailed descriptions can be found in each Paper.

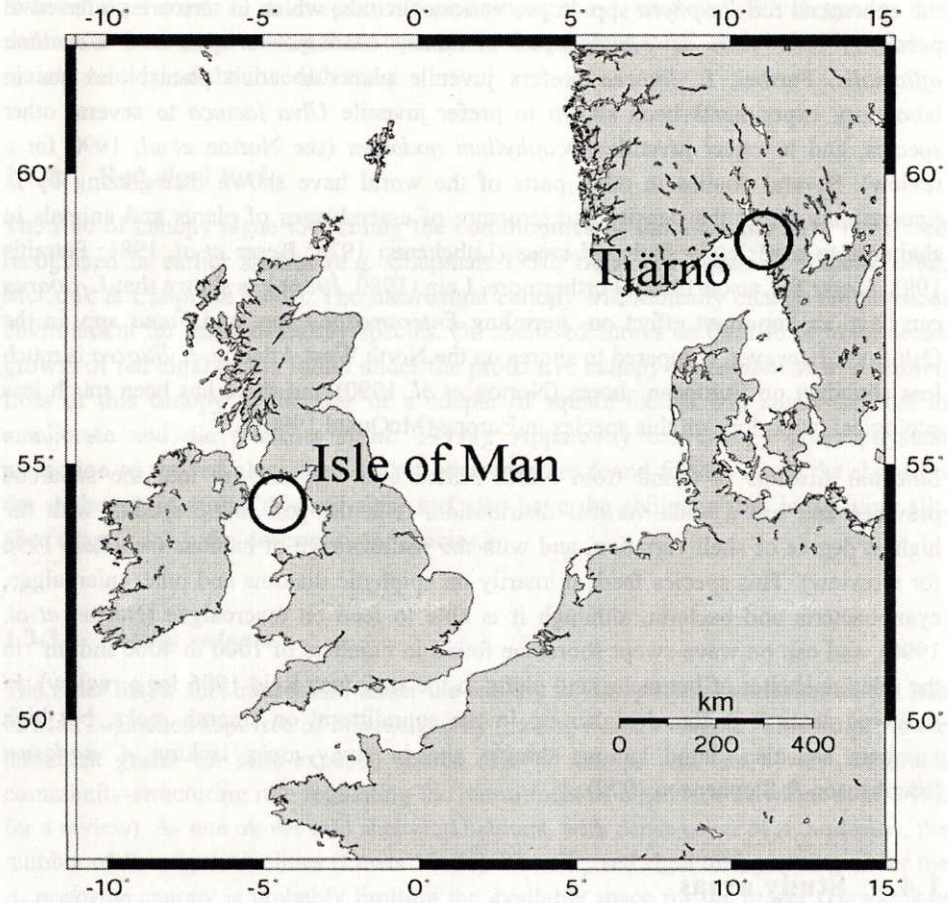


Fig. 1. The areas of the studies.

1.5. Specific aims of the experiments

The Swedish intertidal rocky shores are spatially heterogeneous, and close by shores quite often differ in biological composition. Interactions within and physical disturbances on the intertidal form these communities. How these interactions work and what the effect are of the physical disturbances have attained a lot of interest in other parts of the world. Grazing by limpets have been investigated in for example Australia, South Africa and UK. The EU Mast III project Eurorock investigated the interactive effects of limpet grazing on a European scale, and most of the work in this thesis is part of Eurorock (Papers II-V) (Chelazzi *et al.* in prep.). Periwinkle grazing and ice-scouring have gained a lot of interest in the NW Atlantic. However, the west coast of Sweden has earned little attention when it comes to plant-animal interactions in the intertidal, and very little is known about these interactions in combination with ice-scouring. More specifically the aims of the experiments on which this thesis is based were:

- to investigate the short time effects of mesoherbivores (Paper I) and periwinkles (Papers I and II) on germling survival of the canopy alga *Ascophyllum nodosum* on the Swedish west coast
- to investigate how periwinkles, adult canopy and germling density, alone or in combination, affect germling survival of *A. nodosum* on the Swedish west coast (Paper II)
- to investigate how small scale losses of adult canopy and gastropod grazers, alone or in combination, affect recruitment of juvenile *A. nodosum*, in a typical tidal area versus an almost atidal area (Papers III and IV)
- to investigate how periwinkles affect the macroalgal composition in canopy free areas on the Swedish west coast (Papers III and V)

2. Methodological considerations

2.1. Manipulative field experiments

All papers presented in this thesis are based on manipulative field experiments, and I dare say that these intertidal studies are quite exceptional for the Swedish west coast. They have, on the Swedish west coast, been performed on both sheltered and semi-exposed shores, during summer as well as winter seasons, in the almost atidal intertidal of these often steep rocks. Especially Paper V has demanded a lot of effort, with quite a few minor accidents (some potentially major). The problems of working on semi-exposed and exposed shores on the Swedish west coast are probably the cause why so few experiments have been made there, especially including winter seasons. Hopefully more studies in this line will be performed in the future. There is a lot to do!

Then, why use manipulative field experiments if it is so time consuming and effort demanding? Well-designed field observations are necessary to establish patterns and relationships between different variables. Such observations are often the first step in a research programme and can be used to generate testable hypotheses (Underwood 1997). To unravel the mechanisms generating a pattern, likely factors can be manipulated and their effect on a response variable can be studied in a controlled experiment in the laboratory. If several factors are manipulated in the same experiment, and replicated in an orthogonal way, the interactive effect of the factors can also be studied. However, to be able to work out the importance of these mechanisms for a given community, you have to perform these experiments in that community. If a manipulative factor has an effect in an environment where other factors vary naturally, I believe that this is a stronger support for a real importance of the factor in natural communities. The drawback is that more replicates are needed to be able to show significant effects, due to the natural variability. The ultimate experiment is to be able to control the factors of interest, and keep everything else natural. This is of course not possible to do for all factors, why laboratory experiments also are important to point out mechanisms. For example has the feeding preference of *Littorina littorea* for germlings of different macroalgal species been tested with laboratory studies (Watson & Norton 1985). There is also a spatial variation in nature, and to be able to specify general, but also specific trends, this variation has to be known or included in the experiments. In Papers I and V, the spatial variation was included as a factor, where the variation could be separated for different spatial scales. In Papers II-IV, due to the time consuming methods, the spatial variation was included in the residual variation by using random plots over the whole area, not making it possible to separate the variation at different scales, but still taking it into consideration.

2.2. How to control grazers

One tricky question is how to manipulate grazers. Limpets are quite easy as they do not climb over fences, but periwinkles are something else, and amphipods and isopods are even worse. Limpets are also restricted to patches of bare rock on those sheltered shores we studied in Paper IV, why we only had to remove all the limpets in such a patch surrounding the plot of interest, with no need of fences. Cages have been used quite often to manipulate periwinkles (e.g. Lubchenco & Menge 1978; Lein 1984; Underwood & Jernakoff 1984; Parker *et al.* 1993), and we used these in Paper I to manipulate periwinkles and larger amphipods. They are useful in short time experiments, but they easily clog and will thereby change the physical properties too much over longer periods. In Papers II, III and V, we used fences to try to keep periwinkles out of plots in Sweden, in both sheltered and semi-exposed areas. The fences we used were quite alike those so successfully used with limpets (Jenkins *et al.* 1999b), but as an extra precaution the upper part of the fence was bent down outwards to make it more difficult for periwinkles to climb past it. However, these fences were not completely successful in excluding the periwinkles, why we in Paper II removed the invading periwinkles by hand during the whole experiment, and in Paper III during the first three months. In Paper V invading periwinkles were removed at each time of monitoring. Toxic paint has also been used to manipulate sluggish grazers, but the toxicity can have side effects on the algae and recruitment of these, why we chose not to use this method. Isopods and amphipods are small and fast, and more or less hopeless to manipulate in the field. In Paper I we used cages of different mesh size to manipulate the number of larger amphipods by size, but we were not able to manipulate the smaller ones, as that would have demanded more or less solid walls and roof. I believe that experiments with isopods and amphipods demand laboratory studies, which on the other hand changes all other environmental conditions.

2.3. Canopy and turf removal

In Paper II-IV the role of adult *Ascophyllum nodosum* canopy was investigated for the survival of its germlings and recruitment of its juveniles. The role of *A. nodosum* canopy was also investigated for the recruitment of other canopy forming fucoids and composition of the understorey. In Paper IV from the Isle of Man, the red algal turf that is found as the major substrate under the *A. nodosum* canopy was removed to investigate its role for recruitment of fucoid canopy species (see Paper IV for details). The area of canopy removal has been different in different experiments (Jenkins *et al.* 1999a; Dudgeon & Petraitis 2001; Papers II and IV). The reason for this is the different aims of the experiments. For example Dudgeon and Petraitis (2001) showed how different sizes (1-8 m in diameter) of open patches influenced the recruitment of *A. nodosum*, mimicking severe ice-scouring that occasionally occurs on those shores. In the study by Jenkins *et al.* (1999a), the areas with canopy removal were several square metres, and probably chosen to be sure to show relevant mechanisms. However, in Papers II-IV the manipulations were made to mimic small-scale losses, which we

believe are typical for the areas. Whole plants of *A. nodosum* have been removed from the plots, cutting off the holdfast as close as possible to the rock surface. On the shores of the Swedish west coast, such a removal is not uncommon, due to ice-scouring. On the Isle of Man, the bedrock made of sandstone, which disrupts quite easily, causes these occasional losses of adult plants. To minimise effects of sweeping and shading from surrounding plants, those were cropped so that their fronds did not reach into the plots, doing as little damage as possible to those plants. The plants and animals growing under the adult canopy have not been manipulated, unless they were one of the experimental factors.

3. The experiments of the present thesis

3.1. Germling survival of *Ascophyllum nodosum*

Despite the vast amount of eggs produced each year, only about 40 juveniles less than 1.5 years old are in average found per m^2 in the *A. nodosum* canopy zone on the Isle of Man and around TMBL on the Swedish west coast (Åberg & Pavia 1997). Although we do not know the success of fertilisation of these eggs, other studies of fucoids have shown that fertilisation is high (>90%) (e.g. Brawley 1992; Serrão *et al.* 1996; Serrão *et al.* 1999) so there is probably a tremendous loss between the zygote stage and juvenile recruits of this fucoid species. As these juvenile *A. nodosum* are very patchily distributed (Åberg & Pavia 1997), despite reports of zygote dispersal over more than 12 metres (Dudgeon *et al.* 2001), the mortality must be spatially heterogeneous. In general, early post-settlement mortality is considerable in seaweeds (see Vadas *et al.* 1992 for a review), and several factors, both physical and biological, affect the mortality. For example, settlement in unsuitable habitats, shading, desiccation, waves, ice-scouring, sweeping algae, animal movements and grazing have been shown to be of importance (Dayton 1971; Velimirov & Griffiths 1979; Mathieson *et al.* 1982; Hawkins & Hartnoll 1983; Reed & Foster 1984; Vadas *et al.* 1992; Dudgeon & Petraitis 2001; Boaventura *et al.* 2002). Shading and/or sweeping of adult canopy generally limits the survival of macroalgal recruits (Reed & Foster 1984; Dean *et al.* 1989; Kendrick 1994), however, in the intertidal zone the positive effects of adult canopies on reducing heat and desiccation stress may outweigh the negative effects (Brawley & Johnson 1991; Paper II). There are also the intra-specific densities of recruiting zygotes, which may have both positive and negative effects for survival (Paper II). The contrasting effects may be generated by differences in physical properties of the habitats of the species. For seaweeds growing in the intertidal, crowding of recruits can provide protection against physical stress, which increases collective survival and reinforces the patchiness in their spatial distribution (Hruby & Norton 1979; Ang & Wreede 1992; Paper II). Moreover, high germling recruitment can be a means of escaping grazing. Saturating the habitat with high numbers of propagules facilitates the survival of some of these individuals (Underwood & Jernakoff 1981; Vadas *et al.* 1992). Studies of the survival of *A. nodosum* include the influence of grazing on the mortality of two months to one year old juvenile plants (e.g. Lazo *et al.* 1994) and estimates of the effect of waves on newly settled zygotes (Vadas *et al.* 1990). Even though the grazing *Littorina littorea* does not prefer a diet of germling *A. nodosum* (Norton *et al.* 1990), they might still cause removal of germlings by passively dislodging those from the substrate as they move around (Watson & Norton 1985; Paper I).

The survival of germling *A. nodosum* was investigated in Paper I and II. In both these investigations the germlings were grown in the laboratory onto moulded discs, to ensure a certain density and firm attachment. As newly settled germlings of *A. nodosum* have been shown to be very sensitive to waves (Vadas *et al.* 1990), this method ensured that no such losses would occur. After a defined time interval (see the Papers for details) the

discs were transported to specific shores. After their specific treatments in the field, these discs were transported back to the laboratory for monitoring of survival.

In Paper I we investigated the survival of these germlings under an intact adult *A. nodosum* canopy. We tested how the survival was affected by grazing periwinkles (mainly *L. littorea*), by comparing the survival of germlings in plots containing a natural composition of periwinkles with plots cleared of periwinkles. As this was a short-time experiment, periwinkles were removed daily by handpicking. As the densities of *L. littorea* on our sheltered intertidal shores are very low compared to reports from the NW Atlantic (Norton *et al.* 1990), inclusion of *L. littorea* to raise the density was tested, using cages. We also tested whether other potential grazers, such as amphipods and isopods, might affect the survival of the germlings. By using cages of different mesh-sizes, effects of access by size were tested. As there is a spatial variation in density of juvenile *A. nodosum* (Åberg & Pavia 1997) at both a smaller scale of 0.1-1.5 m and between 2-30 m, spatial replication covering these scales was included.

In Paper II, we investigated the interactive effects of several factors for the survival of these germlings, using a multifactorial experiment. Grazing, adult canopy and germling density were tested, separately and interactively, as all these factors have been shown to have effects on germling survival in other systems (e.g. Hruby & Norton 1979; Reed & Foster 1984; Dean *et al.* 1989; Brawley & Johnson 1991; Ang & Wreede 1992; Vadas *et al.* 1992; Kendrick 1994; Lazo *et al.* 1994; Creed *et al.* 1996). We were also interested in whether the effects of these factors would change over time, why the survival was monitored at two different times (after 5 and 23 days). Grazing periwinkles were excluded with stainless fences. The efficiency of these was not the best, why invading snails were removed every second day during the experimental period. Canopy was removed as described in chapter 2.3. As the methods used in this experiment was quite time consuming, we chose not to replicate the treatments at different spatial scales, instead spreading the plots over a larger area. With that design we would not be able to separate the variation between islands from the overall variation, but the variation was still included.

3.2. The role of grazing and canopy, for juvenile recruitment of intertidal fucoids and community composition

Grazing gastropods have in other parts of the world been shown to have a major influence on the structure and composition of assemblages of plants and animals on rocky shores (e.g. Hawkins 1981; Underwood & Jernakoff 1981; Lubchenco 1983). Manipulations with limpets have a long history on the Isle of Man, with studies made on both sheltered and semi-exposed shores (e.g. Jones 1948; Southward 1964). These classic works showed that limpets prevented *Fucus vesiculosus* from extending into

semi-exposed shores. Confirmation of these theories occurred with the severe oil spill accident with the tanker "Torrey Canyon" in 1967, which caused 14 000 tons of crude oil to strand along 150 km of the coast of West Cornwall in England (Southward & Southward 1978; Southward 1979). To clean the rocks 10 000 tons of detergents were used, which killed most marine life on these shores (Southward & Southward 1978; Southward 1979). Ephemeral green algae were the first to recolonise these rocks, and after these a dense cover of *Fucus vesiculosus* and *F. serratus* settled on both sheltered and semi-exposed shores. It took the limpets about two years to recolonise the rocks, and after ten years there was some degree of normality (Southward & Southward 1978). Compared with the limpet *Patella vulgata*, the periwinkle *Littorina littorea* is of minor importance in the *A. nodosum* zone on the Isle of Man. *L. littorea* has instead earned a lot of interest in the NW Atlantic, where it had a rapid spread along the shores in the early 19th century, and has since then made a significant impact on the intertidal flora. However, there is still a debate whether this is an introduced species or not (see Reid 1996 for a review). *L. littorea* does not often exceed 200 ind. m^{-2} in Europe, but numbers exceeding 800 ind. m^{-2} are common in New England (e.g. Norton *et al.* 1990).

The effect of grazing gastropods on fucoid recruitment, and on the other benthic species found in these assemblages, was investigated on sheltered shores on the Isle of Man (Paper IV), and on both sheltered and semi-exposed shores on the Swedish west coast (Paper III and V, respectively).

In Paper III, the effects of small-scale disturbances on the adult *A. nodosum* canopy and the epilithic grazing snail *L. littorea*, were studied in a four-year experiment on intertidal sheltered shores on the Swedish west coast. Canopy disturbances mimicking ice-scouring, and exclosure of grazers using fences, were performed on small islands and islets in the area around TMBL. The effect of canopy removal and grazer exclosure, separately and in interaction, was studied with special emphasis on recruitment of juvenile *A. nodosum*. However, the effect of other species in this assemblage was also monitored. Fences were used to exclude *L. littorea*, but these snails were observed inside and climbing over the fences. Therefore, handpicking every 2 d the first four weeks, and weekly for another two months was used in the grazer exclusion treatment. Because of this, we can only be sure that we managed to keep the grazers under control the first three months.

In Paper IV, the effects of small-scale disturbances on the adult *A. nodosum* canopy, the red algal turf in the understorey, and the epilithic grazing limpet *P. vulgata*, were studied with a two-year experiment on intertidal sheltered shores of the Isle of Man. Previous studies have suggested interactive effects of these factors, using larger patches (Jenkins *et al.* 1999a). In Paper IV we tested these suggestions, using what we believe are more relevant sizes of canopy-losses. This study was separated into two different experiments, since limpets are not present in the red algal turf. Canopy and turf removal was made as described in chapter 2.3., and limpets were removed as described in chapter 2.2.

The limpet *P. vulgata* has been shown to regulate growth of *Fucus serratus* and *F. vesiculosus* in the intertidal of semi-exposed rocky shores on the British Isles (see Hawkins *et al.* 1992 for a review). In Paper V, we wanted to investigate whether periwinkles on semi-exposed shores on the Swedish west coast might have the same effect. Plots of the size of 50 by 50 cm were placed in the middle of the intertidal, and fences were used to exclude periwinkles. Two different semi-exposed areas around TMBL were used, and within these areas different shores with replication of plots were used. Time was included in the design, with one winter start, and one summer start of the experiments. The cover and development of different species were measured using 100 points in each plot. Fences used to exclude periwinkles were not very successful, and the plots were cleared of invading periwinkles at each time of monitoring.

4. Results and discussion

4.1. Germling survival of *Ascophyllum nodosum*

The results from Papers I and II, showed that under an intact canopy of adult *Ascophyllum nodosum*, and during the short time of one week after outplanting, natural densities of periwinkles (mainly *Littorina littorea*) had no effect on the survival of germlings of *A. nodosum*. The density of periwinkles on the shores of these studies was only 10 ind. m^{-2}, which might have been the cause for lack of effect within one week. However, a complementary study with inclusion of *L. littorea* in cages for two days, raising the density ten times, resulted in lower survival of the germlings (Paper I). In Paper II we also found a trend for a negative effect of *L. littorea* on germling survival after 23 d, independent of adult canopy, and despite the low natural density of periwinkles. That is, given longer time, periwinkles can at low densities have an effect on the survival of *A. nodosum* germlings under an intact adult canopy. However, there was an effect of periwinkles within one week, when the canopy was removed (Paper II). Removal of both periwinkles and canopy, allowed ephemeral green algae to grow in these plots. Among the ephemeral green algae, germlings with a higher density had higher survival compared to those with lower density. The opposite result of germling density was found under intact canopy of *A. nodosum*.

The interesting results from these studies are the interactive effects. Removal of periwinkles was shown to have an effect in interaction with canopy removal, allowing ephemeral green algae to develop. This cover of ephemeral algae probably protected the germlings from desiccation, and it might also have hidden the germlings from other grazers such as isopods and amphipods. These small and fast moving crustaceans might have an important role as grazers, and might explain the overall low survival of germlings (5-6%) during the first week which was independent of exclosure of periwinkles (Paper I). High density of germlings gave higher survival than low density of germlings, in interaction with canopy removal, but only when periwinkles were excluded which means there was a protective cover of ephemeral green algae. The physical conditions in cleared plots, with no protective ephemeral green algae, were probably too difficult for the germlings, as during this period the water level was extremely low for several days. The survival in the two different densities of germlings was the opposite under intact canopy of adult *A. nodosum*. Higher density caused lower survival, probably because there was no problem with desiccation, but rather an intra-specific competition for light and nutrients between the germlings, and between the germlings and the adults. Lower density also profited the possibility for the germlings to develop a good attachment to the substrate. The lower survival of germling *A. nodosum* due to periwinkles, found within one week for raised abundances of periwinkles, and

after 23 d independent of adult canopy, might as well be caused by passive dislodgement as by grazing (Watson & Norton 1985). Previous laboratory studies have shown that *L. littorea* prefers to graze on ephemeral green algae and other algae compared to germling *A. nodosum* (Watson & Norton 1985). However, several student projects have shown that *L. littorea* can consume considerable amounts of fucoids (H. Pavia pers. comm.).

Besides interactive effects, there was a spatial variation within these shores. Previous studies have shown that there is a spatial variation in numbers of juvenile *A. nodosum* at two different spatial scales, 0.1-1.5 m and 2-30 m, and have suggested that there is a substantial variation on a smaller scale of <0.15 m (Åberg & Pavia 1997). This is supported by the results in Paper I, where no difference in survival of germlings was found between different shores, but that there was a difference in survival within shores at the spatial scale of 2-30 m. This spatial variation in survival of germlings might be caused of spatially variable densities of periwinkles or other grazers, in interaction with spatially variable disturbances on the canopy. In Paper II, where the plots were spread out in a larger area, the design was such that the spatial variation was included in the residual variation, why the variation could not be separated into different spatial scales.

4.2. The role of grazing and canopy, for juvenile recruitment of intertidal fucoids and community composition

The results from Paper III, showed that small-scale disturbances in the adult *Ascophyllum nodosum* canopy or removal of the epilithic grazer *Littorina littorea*, separately or in interaction, did not affect the natural recruitment of juvenile *A. nodosum* on the Swedish west coast. A similar study on the Isle of Man in Paper IV showed quite different results, where all the factors (adult canopy, turf and the major grazer *Patella vulgata*) were important for the recruitment of *A. nodosum*. In Paper V, no effect of periwinkles could be seen on recruitment of macroalgae, and removal of these grazers did not allow fucoids to recruit. This is in opposite to other Eurorock experiments with a similar design but where grazing limpets were removed (Chelazzi *et al.* in prep.). These studies showed a major difference in efficiency between the different grazers with their local abundances. However, the exclusion of periwinkles in Papers III and V was of limited efficiency, using fences for four and two years, respectively. Still, the grazing pressure was lowered for several months and that could have initiated processes that could have been seen after several years. However, the results were clear and did not indicate this. The studies in Papers III and IV were different from those in Papers I and II, in that the juvenile *A. nodosum* were so big that they could be seen by the naked eye, and that these had settled and grown naturally in the field. They were therefore older and had been through a much longer time of biological interactions and physical disturbances.

In Paper III, there were both short- and long-time effects by small-scale disturbances of the *A. nodosum* canopy. Grazer exclusion was successful during the first three months, due to complementary handpicking. Canopy disturbances in interaction with grazer exclusion thus gave a positive short-time effect on ephemeral green algae. There was also an interesting trend, with a positive relation between this cover of ephemeral green algae and recruitment of *Fucus* spp. As was suggested in Paper II, the ephemeral green algae might protect fucoid germlings from physical stress and maybe also from grazing by other grazers than periwinkles, thus, grazing periwinkles might indirectly retard growth of *Fucus* spp. by eliminating the protective ephemeral green algae. In the *A. nodosum* zone on the Isle of Man, similar short-time effects were the results of canopy removal in interaction with both turf removal and grazer removal, respectively. Dense cover of mainly *Enteromorpha* spp. grew in these plots, but a thin cover was also found in plots with canopy removal in interaction with intact turf. Associated with the ephemeral green algae in the turf removal was a thick layer of silt, probably originating from the surrounding silty turf. This silty layer was present through the whole period of *A. nodosum* zygote settlement, which might have been of major importance for the recruitment of *A. nodosum* in the turf experiment during spring 1998. In the interaction of removal of both canopy and limpets, only a thin layer of silt was associated with the ephemeral green algae. These plots did also have more *A. nodosum* juveniles in November 1998, which might mean that the ephemeral green algae, just as in Paper II, did instead have a protective role for the recruiting *A. nodosum* germlings, in absence of silt. Other short-time effects on sheltered shores of the Swedish west coast, was a declining cover of the red alga *Hildenbrandia rubra* and increasing cover of the barnacle *Semibalanus balanoides*, due to canopy removal. These effects disappeared with development of a new fucioid canopy (see below).

Long-time effects (2-4 years) were the recruitment of *Fucus* spp. in the two studies (Paper III and IV). *Fucus* spp. was positively affected by canopy removal, turf removal and grazer removal on the Isle of Man, and also positively affected by canopy removal on the Swedish west coast. As it is difficult to distinguish the *Fucus* species at young stages, these were treated as a group. Removal of turf and removal of limpets, both gave higher numbers of juvenile *Fucus* spp. on the Isle of Man in November 1998, and the silty load in plots with turf removal did not affect the settlement, as the numbers of *Fucus* spp. were not significantly different from those in plots with limpet removal. The effect was the same one year later, although the numbers were lower. Owing to differences in growth rates of *Fucus* spp. beneath intact canopy and in canopy removal plots, the percentage cover of *Fucus* spp. in November 1999 was higher in plots with canopy removal. Canopy removal also caused a positive recruitment of *Fucus* spp. on the Swedish west coast. In both these Papers (III and IV), growing *Fucus* spp. developed into a new fucoid canopy, restoring the physical conditions in the understorey. Another long-time effect on the Isle of Man was regrowth of turf under intact canopy, and degradation of intact turf with canopy removal, which is fully in accordance with previous studies (Jenkins *et al.* 1999a).

Paper V is different from the others, in that it deals with more exposed rocky shores. The fences used to exclude *Littorina littorea* and *L. saxatilis* were not totally effective, thus we did not manage to keep these periwinkles excluded from these plots. Therefore, we cannot say whether periwinkles were responsible for the lack of *Fucus* spp. on these shores, as *P. vulgata* has been reported to be in the British Isles (e.g. Southward & Southward 1978; Southward 1979; Hawkins & Hartnoll 1983). However, despite the natural access of periwinkles to these plots, dense cover of red ephemeral algae managed to recruit in early summer. Therefore, we believe that *L. littorea* and *L. saxatilis* have a low impact on the recruitment of macroalgae on semi-exposed rocky shores on the Swedish west coast. However, it is possible that the composition of these assemblages would have been different if these periwinkles had not been present. It might be possible that these periwinkles do not prefer red algae, such as *Ceramium* spp. and *Polysiphonia* spp., and instead graze on ephemeral green algae that were not found in any abundance, and maybe also on *Fucus* spp. Periwinkles have previously been shown to affect the cover of ephemeral green algae (e.g. Lein 1980; Lubchenco 1983 and Papers II and III). Observations in Paper V show that these semi-exposed shores are very variable in assemblages of species, and I believe that the specific shores probably have a more or less fixed succession of species due to physical properties, such as elevation of the shore and access of sunlight, and due to disturbances, such as waves and ice-scouring, but that has to be formally tested. The experiment was started after a winter of severe ice-scouring, with the shores more or less cleared of larger sessile biota. What was left was bleached calcareous crusts. These shores were totally covered by *Semibalanus balanoides* by a short settlement period in March (Jenkins *et al.* 2000), which grew in size, developing into a pillow-like micro landscape with shafted *S. balanoides*. Parallel studies showed that *S. balanoides* grew far bigger on the Swedish west coast, compared with populations in Ireland and the Isle of Man (Jenkins *et al.* 2001). The difference in growth might very well be caused by the difference in tidal range, with barnacles on the Swedish west coast experiencing submergence due to waves more or less 24 h per day and hence have more time for food intake. Subsequent recruitment of ephemeral red algae and *Mytilus edulis* occurred on some of the shores.

4.3. Conclusions

The epilithic periwinkle grazers on the shores of the Swedish west coast have a negative effect on ephemeral green algae, with a trend for a secondary negative effect on juvenile fucoids. No effect has, however, been seen for red algae. As opposed to studies in other areas (e.g. Lubchenco 1983), the ephemeral green algae can protect juvenile fucoids from desiccation, as the intertidal on these shores can be emerged for several days to weeks, with extreme physical conditions. There is also the possibility of protection from grazers, if germling fucoids manage to settle within these ephemeral algae. The abundances of these periwinkles are spatially very variable, and they might therefore have a spatially variable impact. But the normal impact on fucoid recruitment is very low compared to the impact of limpets on the Isle of Man. *L. littorea* does, however,

have a negative impact on germling *A. nodosum* at higher abundances and with longer time.

Small-scale disturbances in the *A. nodosum* canopy will cause both short- and long-time effects, allowing other species to coexist. Disturbance of canopy, in interaction with disturbance of the main grazer, will on sheltered shores on both the Swedish west coast and the Isle of Man, allow ephemeral green algae to recruit and prosper for a short time. This interaction gave also very clear effects on fucoid recruitment on the Isle of Man, where small-scale disturbance of the *A. nodosum* canopy also affected the red algal turf negatively. However, a larger disturbance of the canopy than 40 cm in diameter is needed to really affect the red algal turf. Small-scale loss of red algal turf allowed *Fucus* spp. to recruit in great numbers, however, removal of both turf and canopy was needed to allow the *Fucus* plants to grow into a dense fucoid cover. A dense *Fucus* spp. cover was also achieved by removal of both limpets and canopy. However, recruitment of juvenile *A. nodosum* was not improved by loss of turf, as was suggested by Jenkins *et al.* (1999a), probably as a cause by the small clearings that guaranteed access of silt from the close by red algal turf. Fast recruitment and growth of *Fucus* spp. within one and a half year, restored the understorey conditions. These dense stands of juvenile *Fucus* spp. might also ameliorate the conditions for recruiting *A. nodosum* germlings, although this has to be formally tested. These effects on recruitment of juvenile *A. nodosum* were not found on the Swedish west coast.

Interactions between animals and plants, between plant species, between different stages of the same species, and direct as well as indirect effects, are for sure very important for the specific assemblages in nature. These studies have shown some of these interactions, and tried to explain the pattern of the investigated shores. The manipulative studies in the field have been very time consuming and physically demanding, which probably is the cause why so little has been done previously in our almost atidal conditions. Observations made during the studies, urge me to ask for more effort into this line of research on the Swedish west coast.

5. Acknowledgements

I thank Per Åberg and Inger Wallentinus for reading the text and providing constructive criticism. You have been a great support these last months.

I owe a lot to my supervisor Per Åberg, for his academic support. Besides introducing me to the life of European rocky shores by bringing me into the project Eurorock, you also introduced me to the lovely little island Isle of Man and it's culture of beer. I have lost count of the pints we have taken together at the Falcon's Nest. My dear co-authors, Per Åberg, Stuart Jenkins, Mats Lindegarth, Per Nilsson, Rosa Viejo, and my colleagues at Marine Botany and at the dept of Botany, you have been a great support through the years. A special thanks to the inner circle of my project group, Per Åberg, Annelie Lindgren, Henrik Pavia and Gunilla Toth, who have been quite patient with all my sidetracks. Henrik Pavia, all those discussions and ideas we have had in our office, of which you have managed to realise a big part. I miss them! The staff at Tjärnö Marine Biological Laboratory, with whom I have spent a great deal of my time, you have been a great help through your warm atmosphere and technical solutions. Port Erin Marine Laboratory, whose friendly staff made the study on the Isle of Man possible. I am grateful for the help in field by Maria Dahlin, Maria Granberg, Mats Lindegarth, Örjan Karlsson, Suzanne Kay, Emma LaCroix, Per Nilsson, Göran Nylund, Susanne Svensson, Anette Ungfors and the joyful assistance by my four-legged friend Sassa. Without you a lot more accidents would have happened, or I would have given up!

I want to give a special thanks to Susan and Stuart, who have welcomed me into their home in Port St. Mary on the Isle of Man. Your friendship and all your friends made these fieldtrips into great social happenings. I will never forget the 'ompa-pompa' beer singing in the State Hall, or the Halloween at the Station. You and your friends are great!

Without my friends in Göteborg and especially the student orchestra Tongångarne, all my years as a student would have been unbearable. So much fun we have had during this time. That such a small instrument as the flute can be to so much joy!

I also want to mention my family, and especially my parents who introduced me to the sea and all the fun therein, and at the same time forming me into the person I am. Mother, you are my hero, I am just beginning to understand the extent of work carrying and raising five kids!

Last and most of all I want to thank my wife Anna for her love, patience and trust. You have had a rough time with 'Knyttet', and have still been able to support and encourage me.

Financial support: A doctoral student position was provided by the Faculty of Science at Göteborg University. Additional financial support was provided by the EU Mast III project Eurorock (MAS3-CT95-0012), by the Royal Swedish Academy of Sciences (Hierta-Retzius foundation), by the foundations of Wilhelm & Martina Lundgren, Kapten Karl Stenholm, Adlerbertska, Kungliga och Hvitfeldtska Stiftelsen (Överskottsfonden), Stiftelsen Ahrenberg, Helge Ax:son Johnson, Per Adolf Larsson, and by the Swedish Natural Science Research Council through the contract B-BU 9949-302 to P. Åberg. Financial support was also given by STINT (The Swedish Foundation for International Cooperation in Research and Higher Education) to broaden my PhD-studies and build a network within the field of chemical interactions.

6. References

Åberg P. (1989) Distinguishing between genetic individuals in *Ascophyllum nodosum* populations on the Swedish west coast. *British Phycological Journal*, 24, 183-190

Åberg P. (1992a) A demographic study of two populations of the seaweed *Ascophyllum nodosum*. *Ecology*, 73, 1473-1487

Åberg P. (1992b) Size-based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. *Ecology*, 73, 1488-1501

Åberg P. (1996) Patterns of reproductive effort in the brown alga *Ascophyllum nodosum*. *Marine Ecology Progress Series*, 138, 199-207

Åberg P. & Pavia H. (1997) Temporal and multiple scale spatial variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*. *Marine Ecology Progress Series*, 158, 111-119

Ang P.O. & Wreede R.E.D. (1992) Density-dependence in a population of *Fucus distichus*. *Marine Ecology Progress Series*, 90, 169-181

Bacon L.C. & Vadas R.L. (1991) A model for gamete release in *Ascophyllum nodosum* (Phaeophyta). *Journal of Phycology*, 27, 166-173

Benedetti-Cecchi L. & Cinelli F. (1992) Effects of canopy cover, herbivores and substratum type on patterns of *Cystoseira* spp. settlement and recruitment in littoral rockpools. *Marine Ecology Progress Series*, 90, 183-191

Boaventura D., Alexander M., Della Santina P., Smith N.D., Ré P., Cancela da Fonseca L. & Hawkins S.J. (2002) The effects of grazing on the distribution and composition of low-shore algal communities on the central coast of Portugal and the southern coast of Britain. *Journal of Experimental Marine Biology and Ecology*, 267, 185-206

Branch G.M. (1981) The biology of limpets: physical factors, energy flow, and ecological interactions. *Oceanography and Marine Biology: an Annual Review*, 19, 235-380

Branch G.M., Harris J.M., Parkins C., Bustamante R.H. & Eekhout S. (1992) Algal 'gardening' by grazers: a comparison of the ecological effects of territorial fish and limpets. In: *Plant-animal interactions in the marine benthos* (eds. John DM, Hawkins SJ & Price JH), pp. 405-423. Clarendon Press, Oxford

Brawley S.H. (1992) Fertilization in natural populations of the dioecious brown alga *Fucus ceranoides* and the importance of the polyspermy block. *Marine Biology*, 113, 145-157

Brawley S.H. & Johnson L.E. (1991) Survival of fucoid embryos in the intertidal zone depends upon developmental stage and microhabitat. *Journal of Phycology*, 27, 179-186

Chapman A.R.O. (1984) Reproduction, recruitment and mortality in two species of *Laminaria* in southwest Nova Scotia. *Journal of Experimental Marine Biology and Ecology*, 78, 99-109

Chapman A.R.O. (1990) Effects of grazing, canopy cover and substratum type on the abundances of common species of seaweeds inhabiting littoral fringe tide pools. *Botanica Marina*, 33, 319-326

Chapman A.R.O. (1995) Functional ecology of fucoid algae: twenty-three years of progress. *Phycologia*, 34, 1-32

Chelazzi G., Benedetti-Cecchi L., Åberg P., Arrontes J., Hartnoll R.G., Hawkins S.J., Hughes R.N., Myers A.A. & Paula J. (in prep.) Eurorock: An integrated study on interactions of physical and biological factors in the surf and swash zone of European rocky shores.

Creed J.C., Norton T.A. & Kain J.M. (1996) Are neighbours harmful or helpful in *Fucus vesiculosus* populations? *Marine Ecology Progress Series*, 133, 191-201

Dayton P.K. (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*, 41, 351-389

Dean T.A., Thies K. & Lagos S.L. (1989) Survival of juvenile giant kelp: the effects of demographic factors, competitors, and grazers. *Ecology*, 70, 483-495

Dudgeon S. & Petraitis P.S. (2001) Scale-dependent recruitment and divergence of intertidal communities. *Ecology*, 82, 991-1006

Dudgeon S., Kubler J.E., Wright W.A., Vadas R.L. & Petraitis P.S. (2001) Natural variability in zygote dispersal of *Ascophyllum nodosum* at small spatial scales. *Functional Ecology*, 15, 595-604

Hawkins S.J. (1981) The influence of season and barnacles on the algal colonization of *Patella vulgata* exclusion areas. *Journal of the Marine Biological Association of the UK*, 61, 1-15

Hawkins S.J. & Hartnoll R.G. (1983) Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology: an Annual Review*, 21, 195-282

Hawkins S.J., Hartnoll R.G., Kain J.M. & Norton T.A. (1992) Plant-animal interactions on hard substrata in the north-east Atlantic. In: *Plant-animal interactions in the marine benthos* (eds. John DM, Hawkins SJ & Price JH), pp. 1-32. Clarendon Press, Oxford

Hruby T. & Norton T.A. (1979) Algal colonization on rocky shores in the Firth of Clyde. *Journal of Ecology*, 67, 65-77

Jenkins S.R., Åberg P., Cervin G., Coleman R.A., Delany J., Della Santina P., Hawkins S.J., LaCroix E., Myers A.A., Lindegarth M., Power A.-M., Roberts M.F. & Hartnoll R.G. (2000) Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *Journal of Experimental Marine Biology and Ecology*, 243, 209-225

Jenkins S.R., Åberg P., Cervin G., Coleman R.A., Delany J., Hawkins S.J., Hyder K., Myers A.A., Paula J., Power A.-M., Range P. & Hartnoll R.G. (2001) Population dynamics of the intertidal barnacle *Semibalanus balanoides* at three European locations: spatial scales of variability. *Marine Ecology Progress Series*, 217, 207-217

Jenkins S.R., Hawkins S.J. & Norton T.A. (1999a) Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Marine Ecology Progress Series*, 188, 81-92

Jenkins S.R., Hawkins S.J. & Norton T.A. (1999b) Interaction between a fucoid canopy and limpet grazing in structuring a low shore intertidal community. *Journal of Experimental Marine Biology and Ecology*, 233, 41-63

Johannesson K. (1989) The bare zone of Swedish rocky shores: why is it there? *Oikos*, 54, 77-86

Jones N.S. (1948) Observations and experiments on the biology of *Patella vulgata* at Port St. Mary. *Proceedings and Transactions of the Liverpool Biological Society*, 56, 60-77

Kendrick G.A. (1994) Effects of propagule settlement density and adult canopy on survival of recruits of *Sargassum* spp. (Sargassaceae: Phaeophyta). *Marine Ecology Progress Series*, 103, 139-140

Keser M. & Larson B.R. (1984) Colonization and growth of *Ascophyllum nodosum* (Phaeophyta) in Maine. *Journal of Phycology*, 20, 83-87

Keser M., Vadas R.L. & Larson B.R. (1981) Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under various harvesting regimes in Maine, U.S.A. *Botanica Marina*, 24, 29-38

Lazo L., Markham J.H. & Chapman A.R.O. (1994) Herbivory and harvesting: effects on sexual recruitment and vegetative modules of *Ascophyllum nodosum*. *Ophelia*, 40, 95-113

Lein T.E. (1980) The effects of *Littorina littorea* L. (Gastropoda) grazing on littoral green algae in the inner Oslofjord, Norway. *Sarsia*, 65, 87-92

Lein T.E. (1984) A method for the experimental exclusion of *Littorina littorea* L. (Gastropoda) and the establishment of fucoid germlings in the field. *Sarsia*, 69, 75-137

Lewis J.R. (1964a) *The ecology of rocky shores.* The English Universities Press Ltd., London

Lewis J.R. (1964b) The littoral fringe on rocky coasts of southern Norway and western Sweden. In: *Proceedings of the Fifth Marine Biological Symposium* (ed. Levring T), pp. 129-143. Botanica Gothoburgensia 5, Göteborg, Sweden

Lubchenco J. (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *The American Naturalist*, 112, 23-39

Lubchenco J. (1983) *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology*, 64, 1116-1123

Lubchenco J. & Menge B.A. (1978) Community develoment and persistence in a low rocky intertidal zone. *Ecological Monographs*, 48, 67-94

Lüning K. (1990) *Seaweeds. Their environment, biogeography, and ecophysiology.* John Wiley & Sons, Inc., New York.

Mathieson A.C., Penniman C.A., Busse P.K. & Tveter-Gallagher E. (1982) Effects of ice on *Ascophyllum nodosum* within the Great Bay estuary system of New Hampshire-Maine. *Journal of Phycology*, 18, 331-336

McCook L.J. & Chapman A.R.O. (1991) Community succession following massive ice-scour on an exposed rocky shore: effects of *Fucus* canopy algae and of mussels during late succession. *Journal of Experimental Marine Biology and Ecology*, 154, 137-169

McCook L.J. & Chapman A.R.O. (1997) Patterns and variations in natural succession following massive ice-scour of a rocky intertidal seashore. *Journal of Experimental Marine Biology an Ecology*, 214, 121-147

McQuaid C.D. (1996) Biology of the gastropod family *Littorinidae*. II. Role in the ecology of intertidal and shallow marine ecosystems. *Oceanography and Marine Biology: an Annual Review*, 34, 263-302

Mueller D.G., Gassmann G., Marner F.J., Boland W. & Jaenicke L. (1982) The sperm attractant of the marine brown alga *Ascophyllum nodosum* Phaeophyceae. *Science*, 218, 1119-1120

Norton T.A., Hawkins S.J., Manley N.L., Williams G.A. & Watson D.C. (1990) Scraping a living: A review of littorinid grazing. *Hydrobiologia*, 193, 117-138

Parker T., Johnson C. & Chapman A.R.O. (1993) Gammarid amphipods and littorinid snails have significant but different effects on algal succession in littoral fringe tidepools. *Ophelia*, 38, 69-88

Petraitis P.S. (1983) Grazing patterns of the periwinkle and their effect on sessile intertidal organisms. *Ecology*, 64, 522-533

Printz H. (1955) Phenology of *Ascophyllum nodosum*. In: *Second international Symposium* (eds. Braarud T & Sørensen NA), pp. 198-202. Pergamon Press Ltd., Trondheim

Reed D.C. & Foster M.S. (1984) The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology*, 65, 937-948

Reid D.G. (1996) *Systematics and evolution of Littorina*. The Ray Society, London.

Rodhe J. (1998) The Baltic and North Seas: a process-oriented review of the physical oceanography. In: *The Sea* (eds. Robinson AR & Brink KH), pp. 699-732. John Wiley & Sons, Inc., New York

Serrão E.A., Brawley S.H., Hedman J., Kautsky L. & Samuelsson G. (1999) Reproductive success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. *Journal of Phycology*, 35, 254-269

Serrão E.A., Pearson G., Kautsky L. & Brawley S.H. (1996) Successful external fertilization in turbulent environments. *Proceedings of the National Academy of Sciences of the USA*, 93, 5286-5290

Southward A.J. (1964) Limpet grazing and the control of vegetation on rocky shores. In: *Grazing in Terrestrial and Marine Environments.* (ed. Crisp DJ), pp. 265-273, Blackwell, Oxford

Southward A.J. (1979) Cyclic fluctuations in population density during eleven years recolonisation of rocky shores in West Cornwall following the "Torrey Canyon" oil-spill in 1967. In: *Cyclic phenomena in marine plants and animals* (eds. Naylor E & Hartnoll RG), pp. 85-92. Pergamon Press, Oxford

Southward A.J. & Southward E.C. (1978) Recolonisation of rocky shores in Cornwall after use of toxic dispersants to clean up the *Torrey Canyon* spill. *Journal of the Fisheries Research Board of Canada*, 35, 682-706

Stephenson T.A. & Stephenson A. (1972) *Life between tidemarks on rocky shores*. W. H. Freeman and company, San Fransisco.

Underwood A.J. (1997) *Experiments in ecology. Their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge.

Underwood A.J. & Jernakoff P. (1981) Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia*, 48, 221-233

Underwood A.J. & Jernakoff P. (1984) The effects of tidal height, wave-exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in New South Wales. *Journal of Experimental Marine Biology and Ecology*, 75, 71-96

Vadas R.L., Johnson S. & Norton T.A. (1992) Recruitment and mortality of early post-settlement stages of benthic algae. *British Phycological Journal*, 27, 331-351

Vadas R.L., Miller S.L., Bolis C.M., Bacon L. & Wright W. (1982) Population dynamics of *Ascophyllum nodosum*: factors influencing recruitment and germlings. In: *First International Phycological Congress.*, p. a51, St. John's, Newfoundland, Canada

Vadas R.L., Wright W.A. & Miller S.L. (1990) Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. *Marine Ecology Progress Series*, 61, 263-272

Velimirov B. & Griffiths C.L. (1979) Wave-induced kelp movement and its importance for community structure. *Botanica Marina*, 22, 169-172

von Wachenfeldt T. (1975) Marine benthic algae and the environment in the Öresund. I-II. *Ph.D thesis*, Department of Systematic Botany, Lund University, Lund, 328 pp.

Watson D.C. & Norton T.A. (1985) Dietary preferences of the common periwinkle, *Littorina littorea* (L.). *Journal of Experimental Marine Biology and Ecology*, 88, 193-211

På grund av upphovsrättsliga skäl kan vissa ingående delarbeten ej publiceras här.
För en fullständig lista av ingående delarbeten, se avhandlingens början.

Due to copyright law limitations, certain papers may not be published here.
For a complete list of papers, see the beginning of the dissertation.

GÖTEBORGS UNIVERSITET