

Ecosystem effects caused by the wild harvesting of
Ascophyllum nodosum



Auteur: Charlène Linderhof
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Basiseenheid: GELIFES-GREEN
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Abstract

Ascophyllum nodosum is a foundation species that shapes the abiotic and biotic environment. In this study, the effects of *A. nodosum* harvesting on the ecosystem are reviewed. The *A. nodosum* canopy shapes the abiotic environment by decreasing current speed, erosion, desiccation and light irradiance. Furthermore, *A. nodosum* influences the biotic environment by competition for light and space, symbiosis and limiting predation. Harvesting changes the *A. nodosum* canopy by stimulating short bushy growth, causing a decrease in boulder coverage and impacting the ways in which *A. nodosum* shapes the abiotic and biotic environment. These changes in abiotic and biotic environment lead to a loss of habitats for red turf algae, *Chladophora spp.* and invertebrate species. Furthermore, harvesting causes a decrease in amphipod abundance and loss of coverage by sea sponges (*Hymeniacidon spp.*, *Halichondria spp.*), barnacles (*Balanus spp.*) and bryozoans (e.g. *Schizoporella unicornis*). Lastly, harvesting could lead to local extinction of *V. lanosa* and *C. polisiphoniae*. Overall this study shows that mechanical harvesting might have less impact on the ecosystem compared to manual harvesting because the thalli of *A. nodosum* are cut to 50 cm instead of 20 to 25 cm. More research is needed on the effects of wild harvesting of *A. nodosum* on fish abundance, fish species and the differences of the effects of manual and machinal harvesting on the ecosystem.

Inhoud

1. Introduction.....	5
2. Ecosystem functions of <i>A. nodosum</i>	7
2.1 Current speed	8
2.2 Erosion.....	9
2.3 Desiccation	9
2.4 Light intensity and sun exposure.....	10
2.5 Competition.....	10
2.6 Symbiosis.....	11
2.7 Predation.....	11
3. Ecosystem effects of <i>A. nodosum</i> harvesting.....	13
3.1 Physical factors.....	13
3.2 Biological factors	14
4. Discussion and conclusion.....	16
References.....	18

1. Introduction

Seaweeds are marine macroalgae that mostly grow attached on hard substrates. The three major groups found in seaweeds are the *Rhodophyta*, *Chlorophyta* and *Phaeophyta*. The most distinctive characteristic between the major seaweed groups is the pigmentation of the seaweeds. *Rhodophyta* (red seaweeds) contain phycobiliproteins (phycoerythrin and phycocyanin) and chlorophyll a. *Chlorophyta* (green seaweeds) contain chlorophyll a, chlorophyll b, beta-carotene and xanthophylls. *Phaeophyta* (brown seaweeds) contain chlorophyll a and chlorophyll c. The green colour of chlorophyll is masked by fucoxanthin, the pigment that colours the seaweed brown. (Ramus *et al.*, 1976)

The focus of this study will be on the production of the *Phaeophyta* macroalgae *Ascophyllum nodosum* (knotted wrack), because *A. nodosum* serves as a foundation species and ecosystem engineer in many rocky shore communities (Lubchenco, 1980; Bertness & Leonard, 1997; Petraitis & Latham, 1999; Leonard, 2000). *A. nodosum* has major influences on rocky shore communities because of the large biomass production and the long lifespan (Dudgeon & Petraitis, 2005). In some areas the biomass of *A. nodosum* can exceed 3 kg dw m⁻² and the thalli of *A. nodosum* can fully cover rocks (Cousens, 1984; Jenkins *et al.*, 1999). Canopies of *A. nodosum* form the habitat for several species of small fish, other algae and invertebrates.

Seaweeds can be produced for human consumption, for compounds used in the food industry, for the production of organic fertiliser or as animal feed (Lindsey Zemke-White & Ohno, 1999). *A. nodosum* is used as a supplement in animal feed and as a fertiliser and has been used for the production of sodium alginate in the late 1950's (Ugarte & Sharp, 2001a). There are three ways of seaweed production, namely intensive cultivation (controlled cultivation in tanks on land), extensive cultivation and wild harvesting.

Both manual and mechanical harvesting techniques are used to harvest *Ascophyllum nodosum* worldwide. The first mechanical technique that was used is the paddlewheel (Figure 1 A), which was later replaced by the Norwegian suction cutter jet (Figure 1 B). Manual harvesting is mostly done by cutter rake in Canada (Figure 1 C), whilst cutting macroalgae with a sickle is more common in Ireland. (Ugarte & Sharp, 2001b)

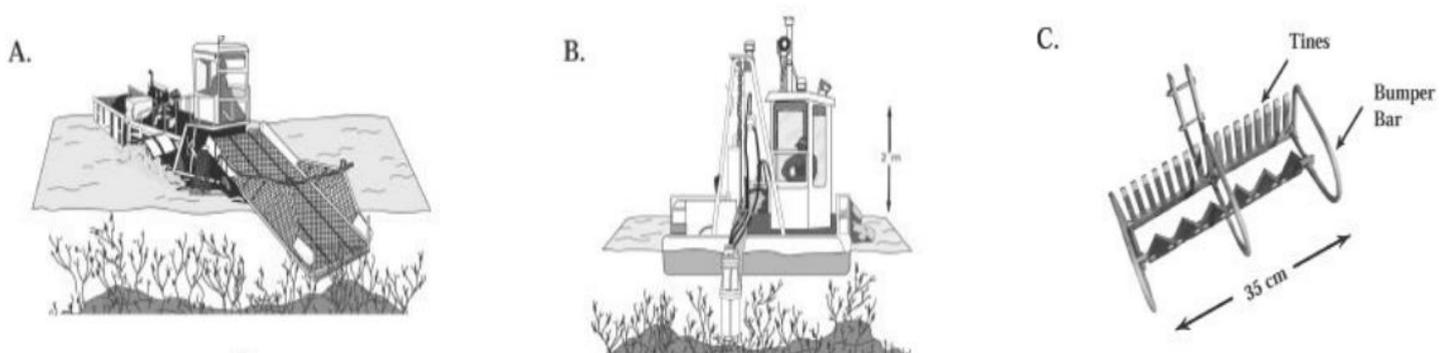


Figure 1: Seaweed harvesting techniques: (A) paddlewheel driven machine, (B) Norwegian suction cutter jet, (C) cutter rake

Since *A. nodosum* is an ecosystem engineer that has a large impact on the ecosystem, wild harvesting has a negative impact on the rocky shore ecosystem. A decrease of one third in average number of species per boulder and a reduction of two thirds of animal cover on the habitable underside of the boulder was found when comparing wild harvested areas with areas that were not harvested (Boaden & Dring, 1980). This could be explained by the impact of harvesting on the ecosystem effects of *Ascophyllum nodosum*. This study is therefore centred around answering the question: "What are the ecosystem effects of the wild harvest of *Ascophyllum nodosum*?"

In this study, the seven ways *A. nodosum* canopies shape the ecosystem and the ways in which seaweed harvesting can affect the ecosystem will be covered. The impacts of *A. nodosum* on the physical environment and the community structure will be discussed. The description of how *A. nodosum* shapes the environment will lead to a conclusion on how wild harvesting negatively impacts the ecosystem and in which areas more research is needed.

2. Ecosystem functions of *A. nodosum*

The perennial brown macroalgae *A. nodosum* from the order *Fucales* mostly grows in canopies on the middle littoral zone between 42° and 65° N latitude (Olsen *et al.*, 2010). *A. nodosum* mainly grows in coastal areas that are sheltered from moderate water waves (Kelly *et al.*, 2001). The thallus of *A. nodosum* can be described as a holdfast from which a composition of shoots and fronds grows (Figure 2) (Reviewed by Kelly *et al.*, 2001). Shoots grow from the apical meristem (Cousens, 1986). One bladder is formed per year, and the internodes (space between bladders) can be used to determine the annual growth of the macroalgae (Cousens, 1986; Kelly *et al.*, 2001). On average, *A. nodosum* grows 8 to 15 cm each year. The lifespan of *A. nodosum* was estimated to be between 50 and 163 years, depending on the environment (Aberg, 1992). *A. nodosum* reproduces both sexually as asexually and has an isomorphic life cycle.

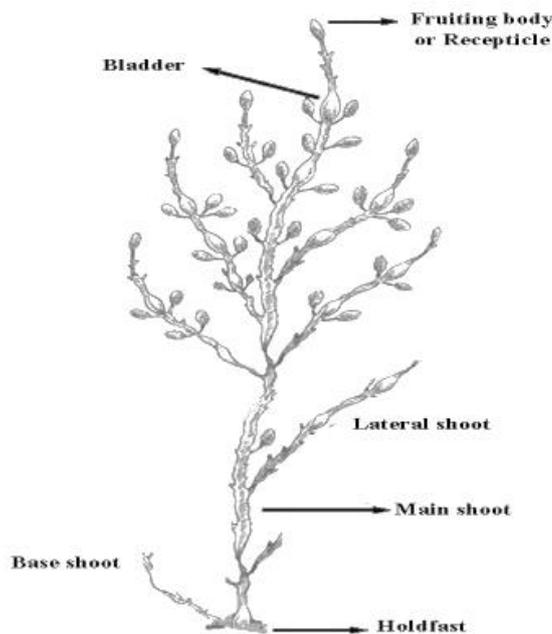


Figure 2: Morphology of *Ascophyllum nodosum* (Kelly *et al.*, 2001)

The macroalgae *A. nodosum* (*Phaeophyta*) functions as an ecosystem engineer and foundation species (Dudgeon & Petraitis, 2005). *A. nodosum* is adapted to desiccation and exposure to high light intensity during low tide. The high abundance and the length of the thallus of *A. nodosum* creates a microclimate for the associated community. This affects four abiotic factors: (1) current speed, (2) erosion, (3) desiccation and (4) light intensity (Figure 3) (Boaden & Dring, 1980). The *A. nodosum* canopy shapes the biotic environment by competition, symbiosis and protection against predators (Figure 3).

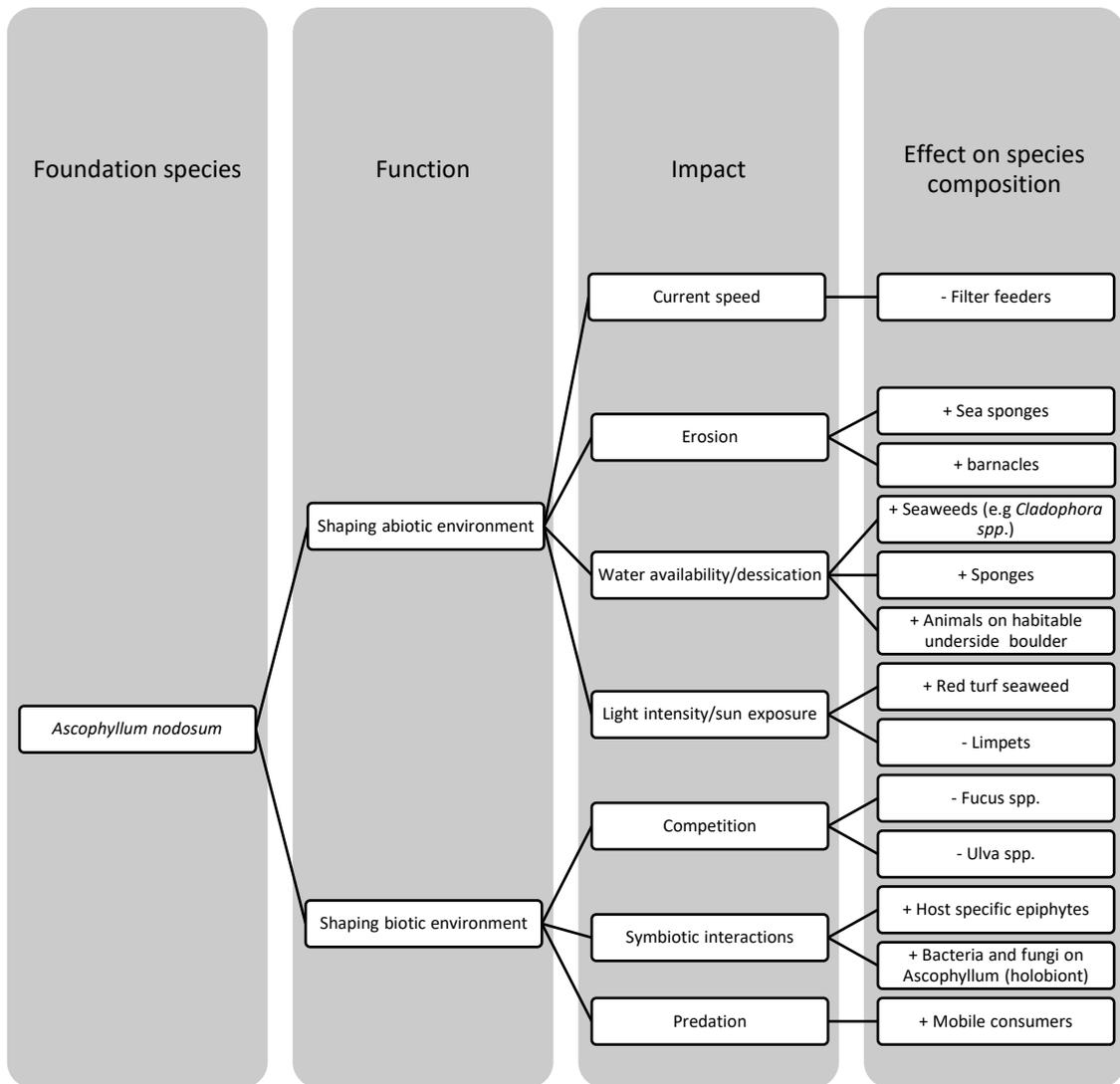


Figure 3: Ecosystem effects of the *Ascophyllum nodosum* canopy that will be described in the following paragraphs.

2.1 Current speed

The decrease of current speed and wave action cause a decrease in mean size of particles that are resuspended in the water column (Boaden & Dring, 1980; Kelly *et al.*, 2001). Filter feeders are dependent on suspended organic matter and food particles. Since *A. nodosum* canopies decrease the amount of suspended food particles in the water column, the abundance of filter feeders in *A. nodosum* canopies is limited.

Wave action is a major cause for the mortality of *A. nodosum* germlings, most likely because the zygotes are maladapted to attachment in an environment with moving water (Vadas *et al.*, 1990). Since the seaweed canopy decreases the current speed, an *A. nodosum* canopy might have a positive feedback mechanism by creating an environment that is more suitable for zygote settlement.

2.2 Erosion

The *A. nodosum* canopy protects the coastal line and sessile organisms against scouring and erosion caused by wave action. The decrease in current speed causes a decrease in the mean diameter of resuspended sediment particles, which lower the effect of scour on boulders by wave action (Boaden & Dring, 1980). Scouring and erosion can prevent the settlement of several sessile species. By decreasing erosion and scouring, *A. nodosum* canopies can form an abiotic environment that is suitable for the settlement of sponges (*Hymeniacidon spp.*, *Halichondria spp.*), barnacles (*Balanus spp.*) and bryozoans (*Schizoporella unicornis*) (Boaden & Dring, 1980). Survival of these species is furthermore positively impacted by the *A. nodosum* canopy by the prevention of desiccation and the increase of shading.

2.3 Desiccation

Canopies of *A. nodosum* facilitate several species of red turf algae and *Cladophora spp.* by preventing desiccation during low tide. This is why these seaweed species can grow higher on shore than in situations without *A. nodosum* canopies. The red turf consists primarily of, but is not limited to, *Chondrus crispus*, *Gelidium pusillum*, *G. latifolium*, *Corallina officinalis*, *Osmundea spp.*, *Audouinella floridula* and *Lomentaria articulate* (Cervin & Jenkins, 2005). The red turf algae can dominate up to 90% of the surface under undisturbed *Ascophyllum* canopies (Jenkins *et al.*, 1999; Cervin & Jenkins, 2005). The remaining 10% of surface can be described as bare patches of substrate that are dominated by the limpet *Patella vulgata* (Cervin & Jenkins, 2005).

The *A. nodosum* canopy can indirectly limit the limpet population by facilitating the growth of red turf algae (Jenkins *et al.*, 1999). The growth of red turf algae usually limit the population of limpets by physical swamping of limpets by fast growing algae or pre-emption of space (Underwood & Jernakoff, 1981; Dye, 1993). Larvae of *P. vulgata* are unlikely to settle and survive on red turf algae, therefore limiting recruitment of *P. vulgata* to bare substrate (Lewis & Bowman, 1975; Jenkins *et al.*, 1999). *P. vulgata* rarely grazes on mature macroalgae and mostly feeds on the epilithic microbial film on the boulders (Boaden & Dring, 1980; Hawkins *et al.*, 1989).

Next to red turf algae, the growth of *Cladophora spp.* is facilitated by the retention of water on the boulder surface by *A. nodosum*. *Cladophora spp.* are green filamentous macroalgae that primarily grow on the side of boulders of the rocky shore and are therefore said to grow in belts. *Cladophora spp.* often are heavily covered by epiphytic diatoms (*Synedra spp.*, *Epithemia spp.*, *Licmophora spp.*, *Cocconeis spp.*, *Rhoicosphenia spp.*, *Navicula spp.*) and *Cyanophyta* (Figure 4). On a 24 mm long filament of *Cladophora*, up to 1681 epiphytes can be found. Most epiphytes are found close to the base of the algae in an area that has a dense growth of filament, since this area offers the most protection against herbivores. (Jansson, 1967)

The fauna that is seen in the *Cladophora* belt is mostly herbivorous, eating either *Cladophora* filaments or epiphytic diatoms. Herbivores that consume *Cladophora spp.* are *Idotea baltica* and *Gammarus oceanicus*. The Gastropod *Hydrobia ulvae* and rotifers (primarily *Proales reinhardti*) eat the epiphytes that grow on *Cladophora*. The species *Colurella colurus* and *Taichidius discipes* consume detritus that contains bacteria and faecal pellets of *Gammarus spp.* and *Idotea spp.* (Jansson, 1967)

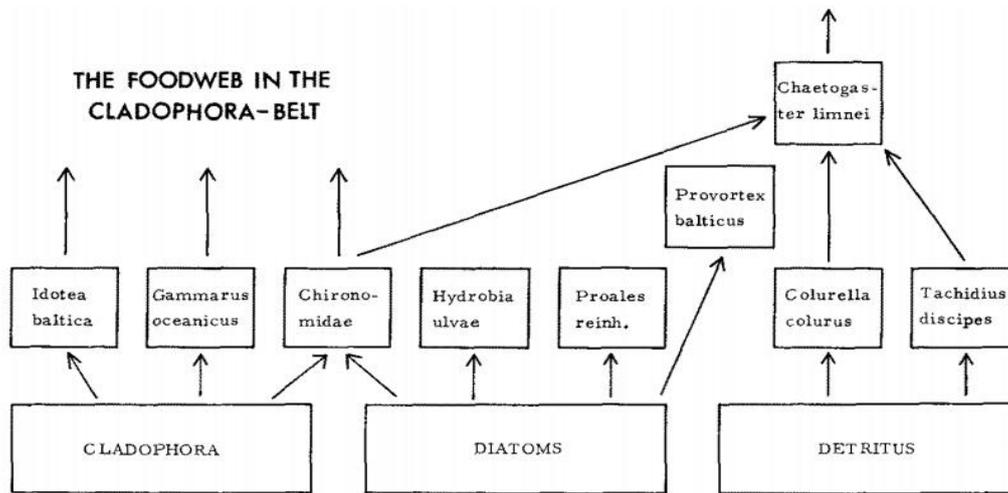


Figure 4: Food-web associated with the Cladophora-belt (Jansson, 1967)

2.4 Light intensity and sun exposure

Red turf seaweeds are not only facilitated by *A. nodosum* by the prevention of desiccation stress, but also by the prevention of excessive light exposure and protection against heating caused by sun exposure. Desiccation, excessive light exposure, high temperatures or a combination of these factors can cause bleaching. The bleaching is caused by the degradation of photosynthetic pigments and leads to the death of red algae. The *A. nodosum* canopy protects the undergrowth and facilitates growth higher on shore than possible without the *A. nodosum* canopy.

2.5 Competition

In sheltered shores, the *A. nodosum* and *Fucus vesiculosus* compete for light and space and might be alternative stable states in case of disturbances. *F. vesiculosus* has a higher growth speed than *A. nodosum* (Cervin & Jenkins, 2005). Therefore *Fucus spp.* would be expected to dominate coastal communities. However, *A. nodosum* can outcompete *F. vesiculosus* in areas that are sufficiently sheltered. *A. nodosum* can outcompete *F. vesiculosus* in these areas most likely due to the longer lifespan and greater thallus size, which can completely cover boulder surfaces (Carss & Elston, 2003).

Fucus spp. seems to be unable to compete with dense *Ascophyllum* canopies (Cervin & Jenkins, 2005). Patches of *Fucus spp.* occur naturally in *Ascophyllum* canopies that are subjected to disturbances like ice scours (Cervin & Jenkins, 2005). Furthermore, *F. vesiculosus* can outcompete *A. nodosum* in areas with finer sediments (sand, mud, pebbles), to which *A. nodosum* is maladapted. Empirical evidence for this theory was found in the Scottish Loch Etive, where *A. nodosum* dominates the more sheltered littoral coastline with hard substrates (stony shores, rocks or ledges) and *F. vesiculosus* dominated coastlines with sand, pebbles or stones (Carss & Elston, 2003).

2.6 Symbiosis

Vertebrata lanosa (Rhodophyta) is a largely host specific epiphyte with a commensal relation to *A. nodosum*. *V. lanosa* is often found with the host specific alloparasite *Choreocolax polysiphoniae* (Rhodophyta) (reviewed by Garbary & Deckert, 2001). Spores of *V. lanosa* only settle on thalli that have surface irregularities (Scrosati & Longtin, 2010). Grazing causes surface irregularities on *A. nodosum* fonds. *Idotea granulosa*, *Littorina obtustrata* and amphipods graze on *A. nodosum*. The grazing is mostly concentrated on the young apical part of shoots since this tissue has more nutritional value. This causes most epiphytes to grow on young apical shoots of *A. nodosum*.

The surface irregularities promote *V. lanosa* recruitment because the streamlined shape of the *A. nodosum* thallus is interrupted, which improve the hydrodynamic conditions for spore settlement and spore survival (Lobban & Baxter, 1983; Pearson & Evans, 1990; Garbary *et al.*, 1991; Levin & Mathieson, 1991). Furthermore, *A. nodosum* uses periodic skin shedding as an antifouling mechanism and settling in damaged areas and wounds might protect spores of being removed in this manner (Filion-Myklebust & Norton, 1981).

Epiphytes are important for the rocky shore community because they provide food and habitats to several other species. For example, an increase in abundance of macroalgal epiphytes (e.g. *V. lanosa*) on *A. nodosum* causes an increase in the abundance of gammarid amphipods (Pavia *et al.*, 1999; Longtin & Scrosati, 2009). When gammarid amphipods graze on the epiphytic macroalgae, the fitness of the hosting *A. nodosum* individual is increased by the decrease in drag and competition for light and nutrients by the epiphyte (D'Antonio, 1985). The gammarid amphipods that eat the epiphyte can co-consume *A. nodosum* and lower the fitness of *A. nodosum* in this manner (Karez *et al.*, 2000).

2.7 Predation

A. nodosum canopies protect the prey species by forming a three-dimensional structure, which forms a habitat for invertebrates and small fish. In areas that are covered with *A. nodosum*, large populations of mobile consumer species are found and the dynamics of the consumer species populations are most likely linked to the dynamics of the *A. nodosum* population (Jenkins *et al.*, 1999).

The gastropod *Littorina obtusata* mainly grazes on *A. nodosum* and has adapted the shell colour to the colour of *A. nodosum* to camouflage itself in the algal canopy. The shells of *L. obtusata* are shaped as gas bladders of *A. nodosum*, and in canopies with primarily yellow *A. nodosum* fonds the proportion of yellow shelled *L. obtusata* is larger than the proportion of *L. obtusata* with brown shells (Wilbur & Steneck, 1999). This could be caused by natural selection for more camouflaged shells.

The *A. nodosum* canopy limits the effects of large predators on small prey animals. For example, females and ducklings of the species *S. mollissima* feed on invertebrates that are associated with *A. nodosum* canopies in summer (*Littorina spp.*, *Mytilus edulis*, *Gammarus spp.*). The canopy does negatively affect the effectiveness of predation by *S. mollissima* on prey species (Cantin *et al.*, 1974). The decrease of predation pressure by large predators causes an increase in the abundance of invertebrate predators such as *Nucella lapillus*. As a result, the effects of large predators (e.g. *S. mollissima*) on the invertebrate population are smaller than the effects of feeding by small mobile consumers (e.g. *N. lapillus*) (Hamilton & Nudds, 2003).

Many fish species eat *Littorina spp.*, amphipods, harpacticoid copepods or *Carcinus maenas*, which are present in high abundances in *A. nodosum* canopies (Steele, 1963; Sherman & Perkins, 1971; Tyler, 1971; Levin, 1991). The *A. nodosum* canopies form an important nursery habitat for several fish species (Rangeley, 1994). The fish species composition is affected by whether *A. nodosum* or *F. vesiculosus* is dominating the littoral zone. Fish is present in higher abundance in *A. nodosum* canopies than *F. vesiculosus* canopies (Figure 5) (Carss & Elston, 2003). *Symphodus melops* and *Gobyusculus flavescens* are species that are only found in *A. nodosum* canopies.

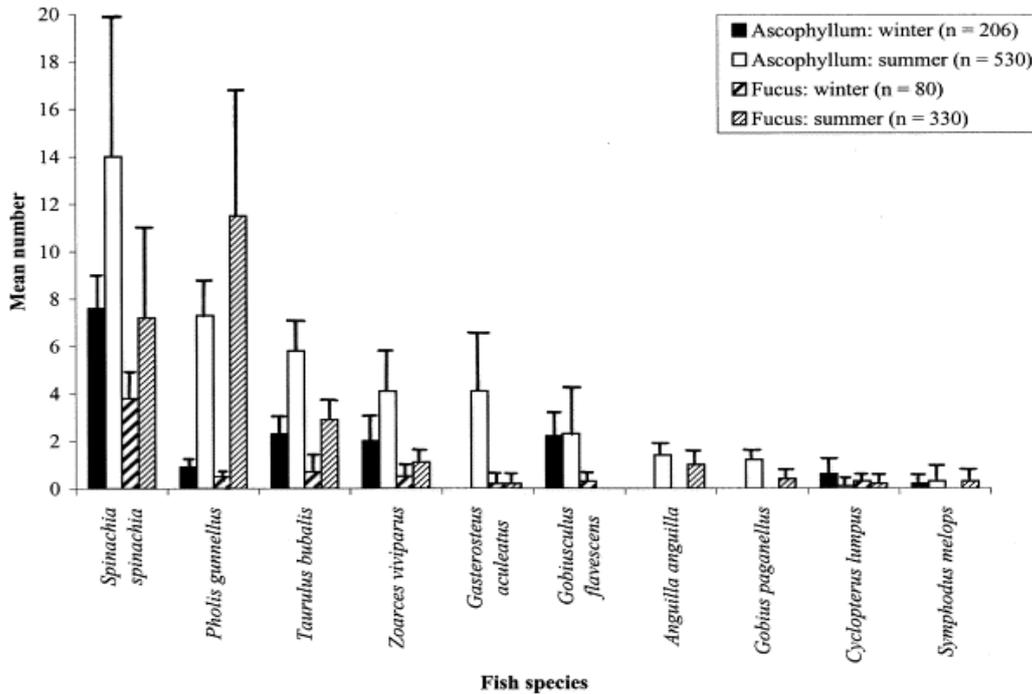


Figure 5: Comparison of fish abundance in *A. nodosum* canopies and *F. vesiculosus* canopies in summer and winter (Carss & Elston, 2003)

3. Ecosystem effects of *A. nodosum* harvesting

Harvesting influences the morphology of *A. nodosum* by stimulating dormant shoots, which increases the growth speed of *A. nodosum* and causes bushy growth with increased branching (Ugarte *et al.*, 2006). However, the overall length of the thalli of *A. nodosum* is decreased. This is why harvesting can decrease the shore cover by *A. nodosum* by 20% (Boaden & Dring, 1980). The changes in morphology and the decrease in boulder coverage impact the ecosystem effects and ecosystem functions of *A. nodosum* by increasing current speed, erosion, desiccation and light irradiance. Harvesting also effects competition, symbiotic relationships and decreases the protection against predators. Boarden & Dring (1980) found a decrease of one third in average number of species per boulder and a reduction of two thirds of animal cover on the habitable underside of the boulder when comparing wild harvested areas with areas that were not harvested.

The effects of harvesting on the shore cover by *A. nodosum* and consequently the ecosystem can vary based on several factors, namely the technique used to harvest, the intensity of harvesting and the history of the site. Mechanical harvesting might be less harmful to the ecosystem than manual harvesting. In a study that was executed in Clew Bay (Ireland), the effects of hand harvesting with a sickle was compared with the effects of mechanical harvesting with the Norwegian suction cutter jet. The study found that the effectiveness of mechanical *A. nodosum* harvesting can be lower than hand harvesting depending on the physical environment. Hand harvesting 50 m of shore took 4 to 5 hours whilst harvesting 50 m of shore mechanically took 4 to 10 hours (Kelly *et al.*, 2001). Furthermore, hand harvesting cut *A. nodosum* thalli to a length of 20 cm while the mechanical harvester left thalli of a length around 50 cm, meaning less *A. nodosum* biomass was removed from the environment by harvesting mechanically (Kelly *et al.*, 2001). As a result, boulder coverage by *A. nodosum* was higher in areas that were mechanically harvested compared to the areas that were hand harvested.

Lastly, manual harvesting might be more harmful for the ecosystem because 6% of the *A. nodosum* thalli that have been harvested with cutter rakes contain the holdfast of the macroalgae (Ugarte, 2011). Sexual reproduction is most likely not be the main reproductive mechanism. Asexual reproduction by constant shoot production from the base is probably more important for the maintenance of the *A. nodosum* populations (Stengel & Dring, 1997). When the holdfast of a macroalgae is removed, the individual cannot grow back. The lower density of *A. nodosum* is expected to negatively impact boulder coverage. Since *A. nodosum* has a long life span and a low recruitment rate, there might be an additive effect when harvesting multiple times in the same area within a short time span (Aberg, 1992; Jenkins *et al.*, 1999).

3.1 Physical factors

The increase of sediment size and the improved oxygenation of the sediment causes an increase in crustacean meiofauna. The highest increase in crustacean meiofauna was found in *Harpacticoida spp.* (Boaden & Dring, 1980). The increase in current speed can also negatively impact the recruitment of *A. nodosum*. Wave action is a major cause for the mortality of *A. nodosum* germlings, most likely because the zygotes are maladapted to attachment in an environment with moving water (Vadas *et al.*, 1990).

In case of patchy canopies with clearings, mussel beds and macroalgae canopies can be alternative stable community states for situations with high current speeds and low current speeds (Bertness *et al.*, 2002). If an alternative stable state will develop is dependent on the microhabitat and clearing size (Dudgeon & Petraitis, 2005). In large clearings, the mortality of *A. nodosum* by sweeping by fronds and grazing is increased. Recovery from mussel beds to *A. nodosum* has only been found when consumers of *A. nodosum* are absent (Bertness *et al.*, 2002).

Harvesting of *A. nodosum* increases erosion and scour by the increase of impact of wave action on boulders (Boaden & Dring, 1980). After harvesting, a decrease in sponges (*Hymeniacidon spp.*, *Halichondria spp.*), barnacles (*Balanus spp.*) and bryozoans (*Schizoporella unicornis*) was found (Boaden & Dring, 1980).

Desiccation, excessive light exposure, high temperatures or a combination of these factors can cause bleaching. The bleaching is caused by the degradation of photosynthetic pigments and leads to the death of red algae. Several studies have found a decrease in cover by red turf algae caused by *A. nodosum* harvesting (Boaden & Dring, 1980; Jenkins *et al.*, 1999, 2004; Cervin & Jenkins, 2005).

When the bleaching of red turf algae increase the area of bare substrate, the limpet population increases whilst the average size of the limpets decreases (Jenkins *et al.*, 2004; Boaden & Dring, 1980). The decrease of red turf algae and the resulting increase of limpets can still be visible 12 years after the *A. nodosum* was harvested (Jenkins *et al.*, 2004). The increase of the limpet population, the decrease of boulder coverage by red turf algae and the removal of the canopy can negatively influence the recruitment rate of *A. nodosum*.

The increase of grazing by limpets limits the recruitment of *A. nodosum* and survival of *A. nodosum* recruits that have settled on red turf algae is low. In southwestern Nova Scotia for example, 99,9% of settled zygotes is eaten by grazers after one year (Lazo *et al.*, 1994). The highest recruitment rate of *Ascophyllum* has been found in areas in which the limpets were removed but the canopy was left in place. In areas that were dominated by red turf algae, the removal of the canopy increased *A. nodosum* recruitment. This shows that harvesting will most likely lower recruitment, because the area on which *A. nodosum* can settle and survive are decreased. Canopy removal on a small scale can lead to long term changes in both the canopy as the undergrowth community structure. (Cervin & Jenkins, 2005)

Kelly *et al.* (2001) did not find a difference in red turf cover. The impact of *A. nodosum* harvesting on the undergrowing red algae might be location specific, depending on the percentage of the biomass harvested or a combination of these factors. Kelly *et al.* (2001) have left 50 cm long standing *A. nodosum* crop after cutting where other studies have cut the *A. nodosum* to a length of 10 to 25 cm. This difference could explain why no effects on red turf algae coverage were found.

Next to the loss of red turf algae, a decrease in coverage by *Chladophora spp.* has been reported as an effect of harvesting (Black & Miller, 1991). A decrease in *Gammarus spp.*, amphipods, nemerteans and *Littorina obtusata* is also observed, since these species graze on *Chladophora spp.* or the diatoms that grow on *Chladophora spp.*

3.2 Biological factors

The removal of the *Ascophyllum* canopy causes an increase of space and light, leading to an increase of *Fucus spp.* and ephemeral macroalgae like *Ulva spp.* (Boaden & Dring, 1980). Ephemeral macroalgae are competitively dominant directly after the disturbance because of the high growth speed. This competitive dominance is most likely broken by the grazing pressure of periwinkle snails (*Littorina spp.*), after which succession to furoid algae (*Fucus spp.* or *A. nodosum*) takes place. The increase of grazing by periwinkle snails may disturb the germling settlement of *A. nodosum* (Dudgeon & Petraitis, 2005). The high increase of the ephemeral macroalgae might temporarily increase littoral herbivory levels (Kelly *et al.*, 2001).

Epiphytes primarily grow on apical shoots since these areas of *A. nodosum* are most commonly damaged by herbivores. Because epiphytes like *V. lanosa* grow on the young apical shoot area, harvesting will remove a large proportion of the epiphytes. The decrease in abundance of *V. lanosa* will lead to a decrease in the host specific allopasite *C. polysiphoniae* (Garbary, 2017). Since *C. polysiphoniae* is dependent on a species that is largely removed from the ecosystem, local extinction may occur in some areas.

Harvesting of *A. nodosum* leads to an increase in predation and a decrease in animal abundance. Black & Miller (1991) found a decrease in animal abundance of 66% and the strongest decrease was found in *L. obtusata*, amphipods and nemertean. The mean shell size of *L. obtusata* is decreased in cut areas and the abundance of yellow shell colour morphs is increased in harvested areas (Boaden & Dring, 1980).

4. Discussion and conclusion

Harvesting of *A. nodosum* impacts the abiotic environment by influencing current speed, erosion, desiccation and light exposure. The biotic environment is impacted by harvesting because the removal of *A. nodosum* biomass influences competition between macro algae species, symbiotic relations and predation. These changes in abiotic and biotic environment lead to a loss of habitats for red turf algae, *Chladophora spp.* and invertebrate species. Furthermore, harvesting causes a loss of coverage by sea sponges (*Hymeniacidon spp.*, *Halichondria spp.*), barnacles (*Balanus spp.*) and bryozoans (*Schizoporella unicornis*). Lastly, harvesting can lead to local extinction of *V. lanosa* and *C. polisiphoniae*.

An increased current speed causes an increase in the mean size of particles that are resuspended (Kelly *et al.*, 2001; Boaden & Dring, 1980). The increase in resuspended particle size is most likely due to the loss of dampening effects of *A. nodosum* fronds on wave action (Kelly *et al.*, 2001). The increase of current speed could cause an increase in resuspended food particles as well, therefore an increase in the abundance of filter feeders is expected.

The expected increase in ephemeral algae might be impacted by the decrease in competition for the nutrients that are dissolved in the water since harvesting causes a sharp decrease in *A. nodosum* biomass. Whether the competition for nutrients also impacts the ephemeral algae population and how large the impact of nutrient competition is on the ephemeral algae is still unclear.

N. lapillus benefits from dense *A. nodosum* canopies (Hamilton & Nudds, 2003). Therefore, harvesting will most likely cause a decrease in the abundance of *N. lapillus*. Rockweed harvesting decreases the effectiveness of *S. mollissima* predation in summer, because this is the period in which ducklings and females feed on the invertebrates that live in *A. nodosum* canopies (Hamilton & Nudds, 2003). When the canopy is removed, increased effects of predation by *S. mollissima* on invertebrate prey species *Littorina spp.*, *Mytilus edulis* and *Gammarus spp.* are expected.

Because *A. nodosum* canopies form a habitat for several prey species of fish and form an important nursery habitat for several fish species, harvesting is expected to negatively impact fish composition and fish abundance (Rangeley, 1994). The largest impact of harvesting would be expected in species that are found specifically in *A. nodosum* canopies (e.g. *S. melops* and *G. flavescense*). In case of a change from a *A. nodosum* to a *F. vesiculosus* canopy, the fish species composition might change. Effects of harvesting on fish abundance might be location specific. Whilst fish species composition in undisturbed *A. nodosum* canopies was studied, no studies that focussed on the effects of harvesting on fish species composition and abundance were found.

Most literature used in this review has focussed on the effect of manual seaweed harvesting, which is the most used technique. The effects of hand harvesting and mechanical harvesting are most likely different because of the difference in length on which *A. nodosum* is cut. The effects of harvesting on current speed, erosion, desiccation, light intensity, competition and predation rate seem to be limited when *A. nodosum* fronds are cut to a length of at least 50 cm instead of 20 to 25 cm (Kelly *et al.*, 2001). Since epiphytes grow mostly on the young apical shoots of *A. nodosum*, cutting fronds to a length of 50 cm will still impact the abundance of epiphyte *V. lanosa*.

Whether the impact of harvesting *A. nodosum* to a length of 50 cm instead of 20 to 25 cm could limit the ecosystem effects in all harvest areas is unclear. The effectiveness of this precaution in protecting the rocky shore ecosystem is likely influenced by the density of *A. nodosum* on boulder surfaces. Possible long term ecosystem effects of harvesting to a length of 50 cm on the environment are still unclear. The study on which this conclusion was based only focussed on short term effects of harvesting and there were no other studies found that compared the effects of manual and mechanical harvesting. More research is needed on the effects of wild harvest on fish abundance, fish species and the differences of the effects of manual and machinal harvesting on the ecosystem before a definitive conclusion can be made.

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