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Gastropods Associated with *Laminaria hyperborea* and *Saccorhiza polyschides* in a Norwegian Kelp Forest

Comparison of Sampling and In Situ Imaging Techniques

Hanne Kile Andersen

Marine Coastal Development
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Supervisor: Geir Johnsen, IBI

Norwegian University of Science and Technology
Department of Biology

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Hanne Kile Andersen

Front page: The nudibranch *Limacia clavigera* sitting on a *Laminaria hyperborea* haptera. Photo: Geir Johnsen.

Abstract

The snail fauna (class Gastropoda) associated with the two kelp species *Laminaria hyperborea* and *Saccorhiza polyschides* was sampled during September and December 2009, and March 2011. Over 1000 gastropod individuals comprising 35 identified taxa were found in the 29 kelp individuals sampled in total. The attractiveness for settlement for gastropods of *L. hyperborea* was clearly higher than *S. polyschides*, which also had very little epigrowth compared to *L. hyperborea.* Highest number of gastropod individuals were found on lamina and the highest number of species were found on haptera for both kelp species. High variation in gastropod numbers was found both between kelp individuals and between seasons. Detailed still images were taken of the kelp before sampling, for comparison to the sampled material. 81 % of the gastropod fauna visible in images was identified to either species or family, but only 17 % of the actual number of gastropods (sampled) were visible in images. Visibility of gastropods in images decreases with increasing complexity of the habitat (i.e. kelp part), both structural complexity in the kelp or added complexity by epigrowth. The ratio of gastropods identified from images to gastropods identified from sampled material (image detection success), showed high variation between gastropod taxa, mainly dependent on gastropod size, degree of camouflage or conspicuousness, and what habitat (i.e. kelp part) they live in.

Sammendrag

Faunaen av snegler (klasse Gastropoda) assosiert med de to tareartene *Laminaria hyperborea* og *Saccorhiza polyschides* ble samlet inn i september og desember 2009, og mars 2011. Over 1000 snegleindivider og 35 taxa ble funnet på tilsammen 29 tareindivider. *Laminaria hyperborea* utgjorde tydelig et mer attraktivt substrat for snegler enn *S. polyschides* som også hadde mye mindre påvekst enn *L. hyperborea.* Høyest antall snegleindivider ble funnet på lamina og høyest antall arter ble funnet på hapter for begge tareartene. Høyoppløselige stillbilder ble tatt av tareindividene før innsamling for sammenlikning med det innsamlede materialet. 81 % av sneglene som var synlig på bildene ble identifisert til art eller familie, men kun 17 % av det innsamlede antall snegler var synlig på bildene. Synligheten av snegler på bilder synker med økende kompleksitet av habitatet (i dette tilfellet: teredelen) de lever i, både strukturell kompleksitet i taren i seg selv og kompleksitet tilført av pågroende organismer. Andelen snegler identifisert fra bildene i forhold til gastropoder identifisert fra innsamlingen (bildenes detekterings-suksess), viste høy variasjon mellom snegletaxa, hovedsakelig avhengig av sneglenes størrelse, grad av kamuflasje eller synlighet, og hvilket habitat (dvs. taredel) de lever i.

Contents

1 Introduction

Norway has a total coastline of over 100 000 km (Norwegian Mapping Authority, 2011), including fjords and thousands of islands and skerries, which provides suitable conditions for a high species diversity and areal coverage of marine macroalgae (Jensen, 1999; Steneck et al., 2002). Underwater forests of kelp (laminarian algae) are found from the low tide level and down to as much as 30 meters depth and forms extensive and important ecosystems both in terms of providing habitat for other organisms and primary production (Lüning, 1990). A wide range of organisms is associated with kelp, some living on the kelp itself (epifauna) and some in the adjacent waters or substrates, such as fish (Høisæter & Fosså, 1993; Norderhaug et al., 2005; Lorentsen et al., 2010) and crustaceans (Rinde et al., 1992). The kelp associated fauna also represents an important food source for adjacent food webs (Jørgensen & Christie, 2003). The main canopy algae of the upper sublittoral (from one to a few meters below mean low water) at wave-exposed sites are *Alaria esculanta* and *Laminaria digitata*, while *Saccharina latissima* dominates at more sheltered sites (Lüning, 1990). The midsublittoral zone, where wave action is dampened and the canopy is never exposed to air, *Laminaria hyperborea* dominates (Lüning, 1990; Sjøtun et al., 1995), but several other species contributes at varying quantities, among them *Saccorhiza polyschides*(Lüning, 1990).

The aim of this study is to elucidate the differences, or the lack of these, in gastropod epifauna abundance and gastropod epifauna species composition between the two kelp species *L. hyperborea* and *S. polyschides.* This include differences between kelp individuals as a whole and the separate kelp parts: haptera, stipes and lamina, along with seasonal variations. It also aims to provide a comparison between two techniques: traditional sampling and digital camera images taken *in situ.* The success of images compared to traditional sampling, both their quantitatative detection success and and their success in identifying the gastropod assemblage structure, is discussed, along with a consideration of challenges and advantages of digital camera images as a technique for mapping and monitoring purposes of kelp epifauna.

1.1 *Laminaria hyperborea*

Laminaria hyperborea (Figure 1A) is widely distributed in the north-east Atlantic from Portugal to Russia, including the UK, the Faeroe Islands and Iceland (Kain, 1967; Guiry & Guiry, 2008) and forms extensive kelp forests on exposed and semi-exposed sites (Kain, 1967; Sjøtun et al., 1993). The depth distribution is mainly determined by the light conditions. The lower limit of the kelp forests (considering the boundary of a *Laminaria* forest to be a lamina area index of 1, 1 m^2 of lamina area per 1 m^2 of bottom area, Lüning & Dring, 1979), lies around 2-7 % of the surface irradiance (Lüning & Dring, 1979; Lüning, 1990). Even though the depth distribution of *L. hyperborea* is mainly determined by light, other local factors such as the avilability of hard substrate (Kain, 1962), reasonably flat topography (less than 20 ° to the horizontal; Kain, 1962) and medium to high wave exposure (Kain, 1971) are also important.

Between 5000 (Fosså, 1995) and 10 000 (Indegaard & Jensen, 1991) km^2 of Norwegian shallow subtidal hard-bottom substrate is estimated to be covered of *L. hyperborea.* Sjøtun et al. (2001) reported the density of *L. hyperborea* individuals with stipe longer than 10 cm to vary between 2.8 and 26.7 individuals per m^2 around the north end of Frøya, Sør-Trøndelag, Norway. The highest density was found at the most wave exposed sites. Abdullah and Fredriksen (2004) estimated a primary production of 600-1000 g C m^{-2} yr^{-1} *L. hyperborea* on the coast of Møre og Romsdal county, Norway.

Since the 1970's *L. hyperborea* have been harvested in Norway for the production of alginate (Jensen, 1999). Also, over 2000 km^2 of the kelp forest along the Norwegian coast, mainly from Sør-Trøndelag and northwards, have been heavily grazed by the sea urchin, *Strongylocentrotus droebachiensis* for the past 30 years, leaving wast barren grounds (Sakshaug & Sjøtun, 2002). However, the kelp forest in Sør-Trøndelag have recovered since the 1990's (Rinde et al., 2010).

Because of its abundance, *L. hyperborea* provides important habitats for diverse assemblages of epiflora (Schultze et al., 1990) invertebrates (Schultze et al., 1990; Christie, 1995; Birkett et al., 1998; Christie et al., 2003) and fish (Høisæter & Fosså, 1993; Norderhaug et al., 2005; Lorentsen et al., 2010), and is therefore called a key species (Christie & Rueness, 1998). *Laminaria hyperborea* have an annual lamina, but a perennial haptera and stipe (Christie & Rueness, 1998), which have a common longevity of 10-11 years (Sjøtun et al., 1993) and during this period a variety of epiflora and epifauna establish on the kelp.

1.2 *Saccorhiza polyschides*

The kelp *Saccorhiza polyschides* (Figure 1B) is not as abundant as *L. hyperborea* and little work has been done on this species in Norwegian waters (Rinde et al., 2010). The geographical distribution ranges from the Atlantic coasts of Morocco, Spain, Portugal, and France, all around the British Isles and to approximately 65 °30'N on the west coast of Nor-

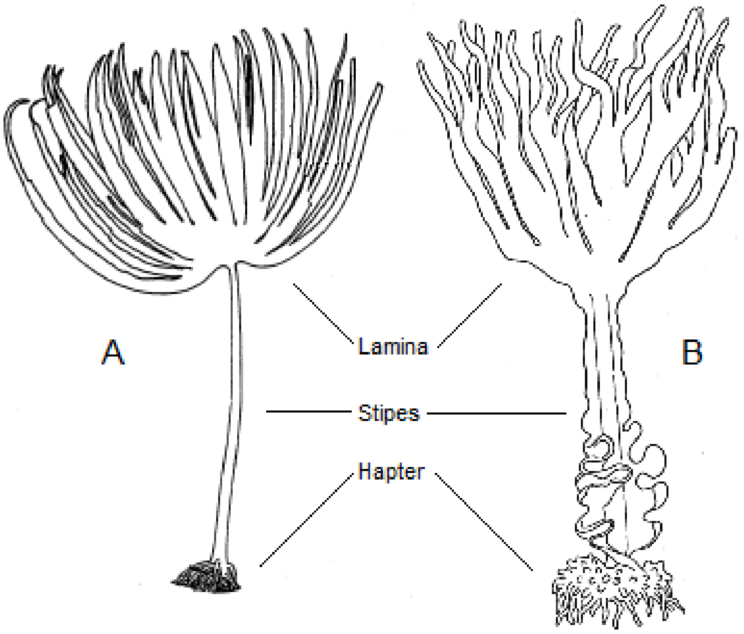


Figure 1: Kelp parts of (A) *Laminaria hyperborea* and (B) *Saccorhiza polyschides.* Figure modified from (A) Kain (1971) and (B) Norton (1970).

way (Norton, 1970). *Saccorhiza polyschides* grow on hard substrate in depth ranges from as shallow as 1 meter (Svendsen, 1962) down to approximately 20 meters depth (Kain, 1960; Norton, 1970). It was first reported in Norwegian waters by Areschoug (1847, cited in Svendsen, 1962) and was in the following decades observed at intervals on the Norwegian coast (Boye, 1896; Tobler, 1908; Norum, 1913 and several more given in Norum, 1913), but no area coverage estimates is known to the author. Norum (1913) gave a thorough description of his findings outside Haugesund, Norway. He found 30 specimens, both alone and in clusters, at 3-20 m depth, in protected bays with some current close to open sea. He also reports a rich growth of epiflora and bryozoans on the haptera in the autumn.

The life cycle of *S. polyschides* is described and studied by several authors (e.g. Printz, 1926; Norton & Burrows, 1969; Norton, 1970; Kain, 1971), and the species is usually regarded as an annual species, but this is not yet fully examined. Spence (1918, cited in Norton, 1970) reported the persistence of large complete individuals into the summer of their second year outside the Orkney Islands. This led him to describe *S. polyschides* as not so much an annual as a monocarpic algae, meaning that death follows reproduction, but does not necessarily follow an annual cycle. Printz (1926) described *S. polyschides* in the Trondheimsfjord to fruitify during July and August after which the thallus gradually decomposes, and same was reported outside Isle of Man by Norton and Burrows (1969), who stated a clear annual cycle with no overlap between the new generation of sporophytes and the decaying haptera of the previous season. The species is considered to be ”fast growing” (Svendsen, 1962). Observations by Printz (1926) suggest that it may attain a length of at least 2 meters within two months, and Rueness (1977) reported it to grow to as much as 4.5 meters during one growth season, both of these are from Norwegian waters.

The morphology and ecology of *S. polyschides* have been described in detail by Norton and Burrows (1969) and Norton (1970) but most of the information comes from UK waters and there might be geographical differences, as shown for other macroalgae (Norton et al., 1981).

1.3 Kelps as habitat for organisms

Generally, kelps consists of three major parts: haptera, stipe and lamina (Figure 1). This structure makes the kelp forest a three dimensional system, in which all parts of the kelp is utilized by both epiflora and epifauna. Kelps provide several resources for exploitation by marine invertebrates, such as surface area, shelter and food (Hayward, 1980). The epifauna on kelp consists mainly of amphipods and other crustaceans, gastropods, bivalves and polychaetes (Adami & Gordillo, 1999; Christie et al., 2003; Tuya et al., 2011), in addition to sessile organisms like bryozoans and hydrozoans (Seed & O’Connor, 1981; Schultze et al., 1990). For many species of bryozoans, crustaceans and polychaetes, kelp is also their primary habitat (Hayward, 1980).

Not all species of macroalgae are equally attractive to epifauna, for sessile organisms this is highly due to the choice of substrata by larvae at the time of settlement, as for many bryozoans and hydroids (Seed & O’Connor, 1981). Many factors controls the development and distribution of fauna associated with kelps. In addition to abiotic factors, like wave action (Schultze et al., 1990), the effects of kelp part, algal size and antifouling mechanisms have been studied. Lamina seems generally to support the least number of species of both epiflora and epifauna (Schultze et al., 1990; Adami & Gordillo, 1999; Christie et al., 2003), especially in wave exposed areas (Schultze et al., 1990). This is partly due to the flexibility of the lamina. The flexible bryozoan *Membranipora membranacea* is sometimes the only species covering *Laminaria* lamina to any great extent (Seed & Harris, 1980 cited in Bartsch et al., 2008). Also, lamina is usually annual, preventing accumulation of large numbers of species (Norton, 1971). The haptera usually supports the highest number of individuals and species. This has been explained by the complexity of this kelp part (Hacker & Steneck, 1990; Hauser et al., 2006), but also the stipe, if grown with a substantial amount of epiphytic algae, can provide a complex habitat and thus supporting a high diversity of species and high numbers of epifauna (Christie et al., 2003). The size of the kelp have also shown to have a strong effect on the number of epifauna species, individuals (Christie et al., 2003) and assemblage structure (Christie et al., 1998). Epifauna can be harmful to the kelp, for instance by reducing the lamina strength (Krumhansl et al., 2011), and thus, kelps have a variety of defense mechanisms reducing this (for a review see Bartsch et al., 2008). Defenses include both physical and chemical. For instance, the toughness of the epidermis may reduce the effect of grazing, as shown for grazing by the gastropod *Lacuna vincta* on *Laminaria longicruris* (Johnson & Mann, 1986). Dobretsov and Wahl (2001) found that chemical exudates by *Saccharina latissima* reduced the settlement of blue mussel spat. Fauna in *Laminaria* kelp forests also has different vertical distribution ranges (Norton et al., 1977), suggesting that light, wave exposure, turbulence, competition or predation may all be factors that contribute to the distribution of fauna species.

Epifauna (and flora) of *L. hyperborea* have been extensively studied in Norwegian waters (e.g. Christie et al., 1994; Christie, 1995; Sjøtun et al., 1995; Christie et al., 1998, 2003; Jørgensen & Christie, 2003; Norderhaug et al., 2005, 2007; Eilertsen et al., 2011) and elsewhere in the northeast Atlantic (e.g. Jones, 1971; Moore, 1973; Edwards, 1980; Schultze et al., 1990; Tuya et al., 2011). *Saccorhiza polyschides*, on the other hand, has to my knowledge, no records of studies of the epifauna community from Norwegian waters. The knowledge on this species as a habitat for fauna in the northeast Atlantic is mostly based on studies from the British Isles (e.g. Ebling et al., 1948; Norton, 1971; McKenzie & Moore, 1981).

The epifauna and epiflora of kelps vary throughout the year, with generally higher abundances during August/September and lowest in the winter (November-March) for *L. hyperborea* (Christie et al., 2003). Ríos et al. (2007) reported higher abundances of epifauna on the kelp *Macrocystis pyrifera* in Chile during autumn/winter and lowest during spring/summer, but also reported variation between sites. The seasonal fluctuation may also be different for different epifauna and epiflora species (Norton, 1971) and vary between years (Taylor, 1997). It might be reason to believe that seasonal patterns in epifauna abundances is governed primarily by the food source of epifauna, with taxa responding differently depending on whether their diet consists of seasonally fluctuating food sources, like epiphytic algae or plankton, or more stable food sources such as the living host or detritus derived from the host (Taylor, 1997; Carlsen et al., 2007).

1.4 Optical *in situ* imaging

Mapping of the marine life have usually been dependent on invasive sampling techniques that, in addition to intervening with the underwater life, does not capture valuable information about patterns and ”order” of the community. The development of imaging techniques during the last century have provided researchers with methods of making this kind of information available (Solan et al., 2003). Optical imaging have both advantages and disadvantages over traditional sampling techniques. One of the advantages lies in the non-invasive approach, making researchers able to survey the same area over time and eliminates the confounding effects of trawl and grab sampling when investigating long-term changes in benthic habitats (Kollmann & Stachowitsch, 2001). Photographs can also be stored for practically unlimited time and can be re-analyzed multiple times without losing quality. It also has the potential to be more efficient both in terms of time and costs.

The development of underwater photography started during the 1890s, when Louis Boutan operated along the French Riviera (Vine, 1975). Since then the development have been extensive (Solan et al., 2003). Photographic techniques have been used for a variety of studies, dealing with area coverage or counts of classified features in the picture (Gutt et al., 1996, 1999; Jørgensen & Gulliksen, 2001; Pech et al., 2004), volume and biomass estimations (Abdo et al., 2006; Baguley et al., 2004), population dynamics (Tyler et al., 1993) or megafaunal activity (Smith Jr. et al., 1993), these being merely examples.

Drawbacks of the method mainly discussed in literature (Baguley et al., 2004) is the incomplete qualitative information one get from images, and the uncertainty of species identifications. These issues arise because of factors influencing the images such as spatial resolution, the 3-dimensional structure of habitats (such as kelp forests) and the fact that ocean habitats is usually ever moving and dynamic. These challenges needs consideration and will all be assessed in this thesis.

1.4.1 Digital images

A digital image is actually a long string of 1s and 0s (bits) representing colored light dots, known as pixels, which together makes up the image. When a digital image is created, light is converted into electrical signals by special sensors like Charge-Coupled Device sensors (CCDs) or Complementary Metal Oxide Semiconductor sensors (CMOS) in place of the old film in analog cameras. CCD and CMOS sensors are made up of tiny photo diodes (light sensitive diodes) that becomes electrically charged in accordance with the strength of light that hits it, each photo diode gives information to one pixel in the result image (Inoue, 2011). Both sensors and pixels can be of different sizes, and the number of pixels per image (pixel resolution) may also vary. All of these will affect properties such as the spatial resolution (how small an object can be and still be distinguishable in the image), color depth (number of bits used to represent the color of a single pixel) and light sensitivity of the sensor, again affecting the result image quality.

1.5 Study organisms

Saccorhiza polyschides was chosen because of the limited knowledge of this species in Norwegian waters. For comparison *Laminaria hyperborea* was chosen because it is well known and documented, and also because of its properties like perennial stipe and haptera, and morphology different from *S. polyschides*.

Gastropods were chosen because of their size and high abundance in *L. hyperborea* kelp forests (e.g. Rinde et al., 1992; Norderhaug et al., 2002; Christie et al., 2003; Hauser et al., 2006; Tuya et al., 2011). They include species of a wide range of sizes and forms, and is also relatively easy to collect, preserve and identify. The size also make these organisms a suitable target for a comparison between sampled individuals and *in situ* images from SCUBA operated photography.

1.6 Aims of thesis - study questions

L. hyperborea **and** ***S. polyschides*** **and associated gastropod epifauna**

- Is there a difference in number of gastropod individuals or species between *L. hyperborea* and *S. polyschides*?
- Is there a difference in number of gastropod individuals or species between kelp parts?
- Is there a difference in number of gastropod individuals or species between seasons?

Comparison of ***in situ*** **images to traditional sampling technique**

- Does images capture the same number of gastropod individuals or species as sampled material?
- Does images capture the same gastropod epifauna assemblage structure as sampled material?

2 Methods

2.1 Sampling area

Sampling was done during three cruises with R/V "Gunnerus", 1st of October 2009, 17th of December 2009 and 14th -15th of March 2011 (Table 1), at approximately 10 m depth outside Hitra, Sør-Trøndelag, Norway (63 °39.99'N and 08 °52.26'E, Figure 4 and 5). At this latitude the *Laminaria hyperborea* kelp forest is well developed (Kain, 1967), this particular sampling site has a density of approximately 2-3 individuals per m^2 (Figure 2) and the individuals are medium sized, 0.5-1 meters in September and 1.5-2 meters in March (this study). Figure 3 shows one individual of each species from sampling 1, a lamina of *L. hyperborea* and a hapter of *S. polyschides* from sampling 3.

Figure 2: Kelp forest (*Laminaria hyperborea*) at sampling site, with low density and small kelp individuals. Photo: Geir Johnsen

Table 1: Kelp sampling: Overview of dates and sampled kelp of each sampling.

Sampling no.	Date	***Laminaria hyperborea***			***Saccorhiza polyschides***		
		Haptera	Stipes	Lamina	Haptera	Stipes	Lamina
1	01.10.2009	4	4	4	5	5	5
2	17.12.2009	5	5	5	5	5	5
3	14.-15.03.2011	5	5	5	5	0	0

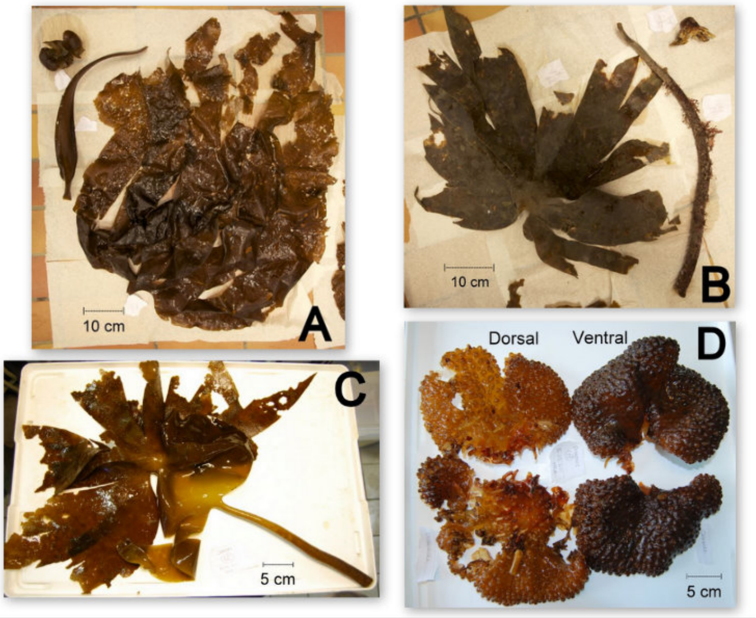


Figure 3: Pictures showing an individual of *Laminaria hyperborea* (A) and an individual of *Saccorhiza polyschides* (B), both from September, a lamina of *L. hyperborea* (C) and a vertically split hapter of *S. polyschides* (D) both from March.

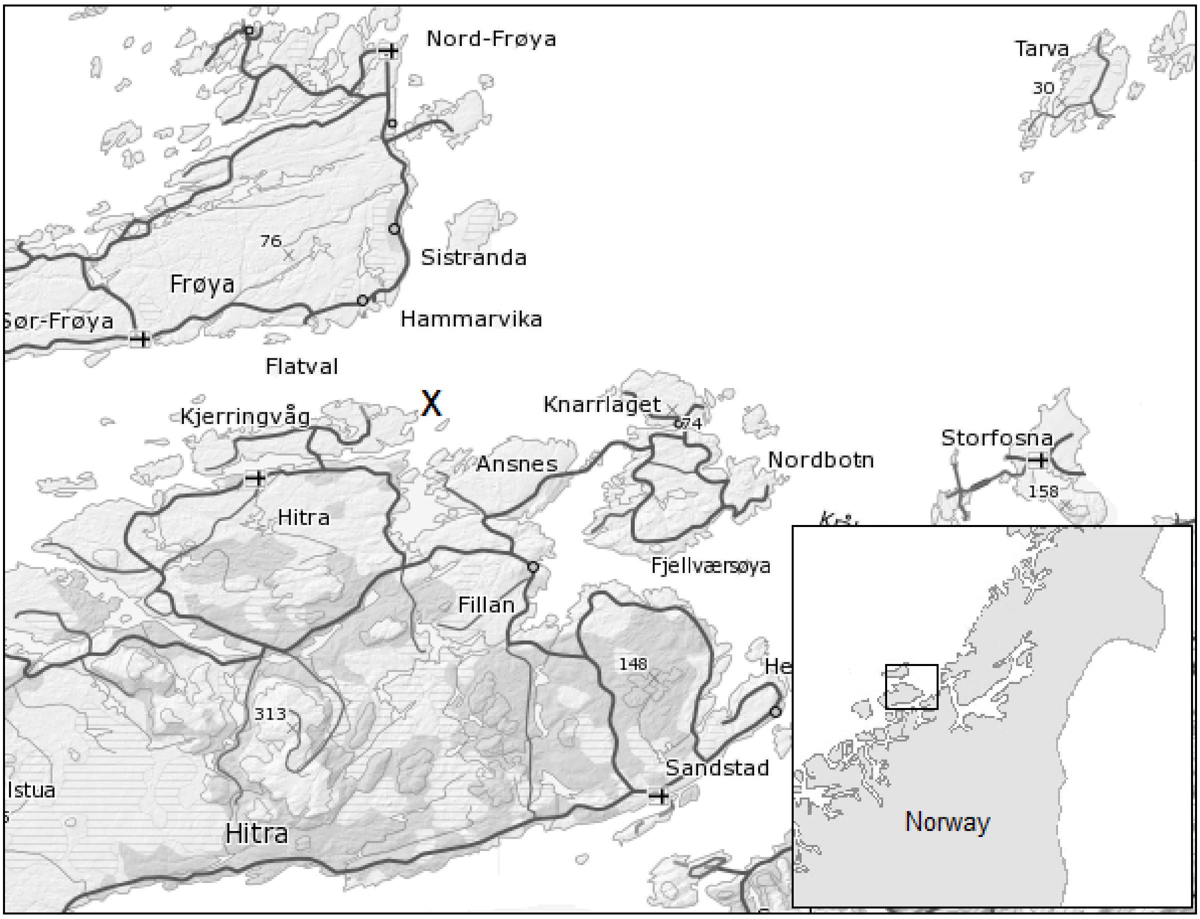
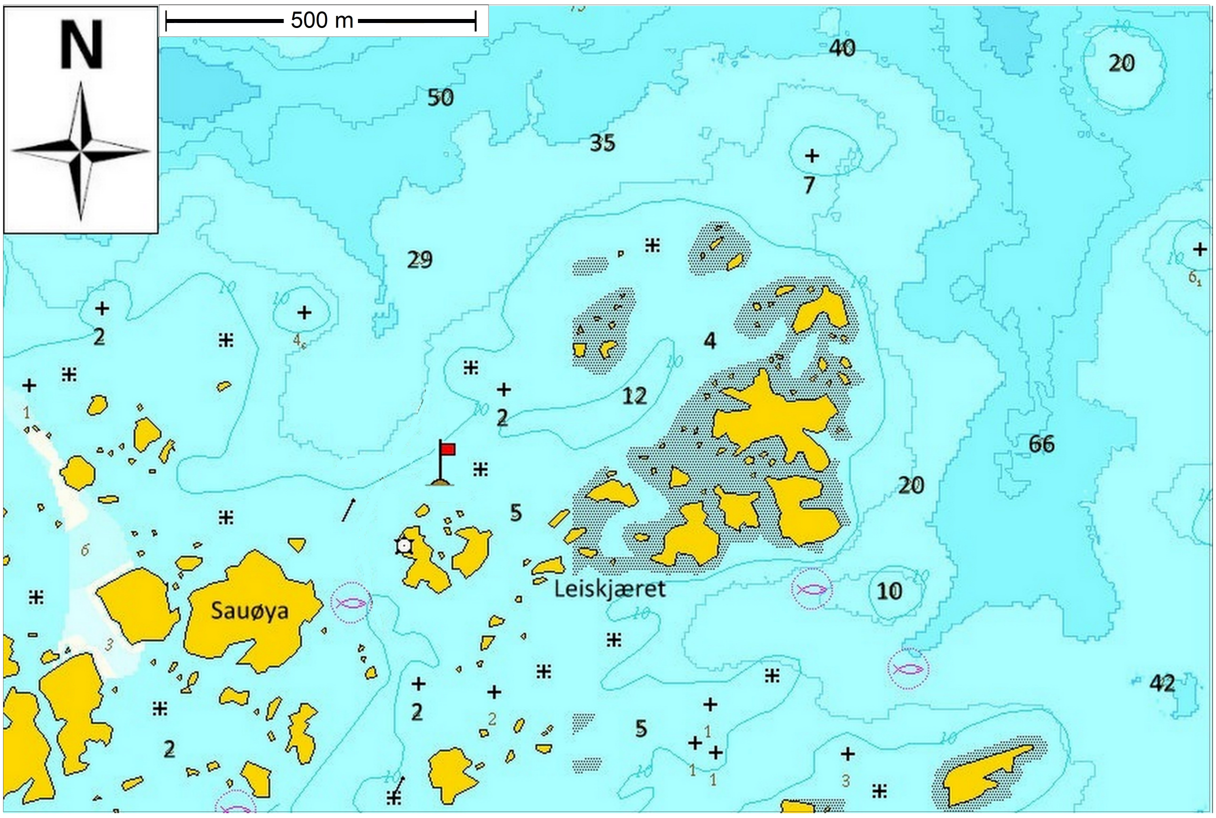
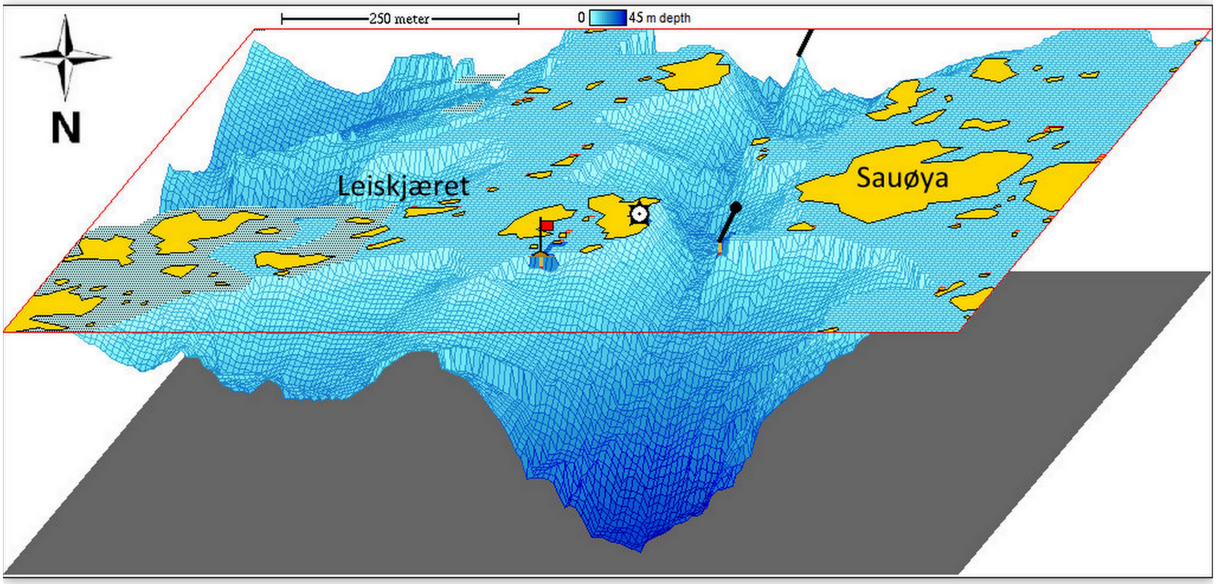


Figure 4: Map of sampling area on the north side of Hitra, Sør-Trøndelag, Norway. Sampling site indicated with an X (Map source: Norwegian Mapping Authority).



(a) Overview of sampling site with depths



(b) Bottom topography

Figure 5: Overview map (a) and bottom topography (b) at sampling site. The kelp was sampled in the area of 10 meters depth within 50 meters of the flag. Note that north is towards you in (b). Maps made in Olex.

2.2 Sampling method

Sampling was carried out by SCUBA diving. Each kelp part (haptera, stipe and lamina) of five haphazardly selected individuals of each algae species (*Laminaria hyperborea* and *Saccorhiza polyschides*) where collected using collection bags (home made, polyester, pore size < 0.5 mm) to avoid loss of epifauna. First a bag was closed around the lamina, leaving the epifauna as undisturbed as possible. The lamina was then separated from the stipe with a knife, and the bag was sealed. The stipe and haptera were sampled in the same way. Bags with kelp where kept in constantly exchanged sea water on board R/V ”Gunnerus” before examined. All gastropod epifauna from each kelp part was picked by hand and preserved at 96 % ethanol before quantified and identified to lowest taxonomic level possible. All kelp parts where photographed (Figure 3) for documentation. The sample size, 5 individuals of each kelp species at each sampling was chosen from practical reasons, like maximum diving time (approx 1 hour) and boat time available (larger sample sizes would require several dives and thus more days using the boat). The planned design could not be followed precisely. During the first sampling, one individual of *L. hyperborea* was lost, so the final number of sampled individuals from this sampling was four. In March, during the last sampling, all stipes and lamina of *S. polyschides* had decayed, so only haptera where sampeled. An overview of the sampled material is given in Table 1.

2.3 *In situ* underwater imaging

All kelp individuals where photographed *in situ* before sampled. At least two photos of each kelp part was photographed before the kelp individual was sampled. Most images was taken using ambient light with a Subtronic flash illuminating the kelp details. Specifications of the photographing for each sampling is given in Table 2. After sampling the images where analyzed and all visible gastropods where quantified and identified to the lowest taxonomic level possible.

2.4 Taxonomic identification

Identification of gastropods was done mainly following Sneli (1975), Bondesen and Winther (1975) and Høisæter (2009), for Rissoidae also Fretter and Graham (1978) was used. The systematics and taxon names follows the World Register of Marine Species (Appeltans et al., 2011). Sizes of gastropods given are the length in the longest direction (usually height of the shell or length of animals without shell), and are based on the material from this study.

Table 2: Specifications for photographing for each sampling

Sampling	**1**	**2**	**3**
Camera	Canon 5D EOS Mark II (system camera)	Canon EOS 5D Mark II (system camera)	Canon PowerShot G11 (compact camera)
Lens	Canon EF 14-70 mm	Canon Macro EF 50 mm	Not interchangeable
House	Subal Underwater house 5D MII	Subal Underwater house 5D MII	Ikelite Compact Digital Housing for Canon Powershot G11
Dome	Wide angle	Flat macro	Ikelite WD-4 Wide Angle Conversion Dome
Max aperture	f:4.0	f:2.5	f:8[1]
Sensor type	CMOS	CMOS	CCD
Sensor size	35 mm = 36 x 24 mm	35 mm = 36 x 24 mm	1/1.7”
Pixel resolution	21 megapixel	21 megapixel	10 megapixel
File size	25.8 MB	25.8 MB	9.7 - 12.8 MB
Total no. of pictures	86	176	66
Average no. of pictures per kelp individual	9	18	7

[1] Not comparable to the system camera apertures

2.5 Statistical and numerical methods

To determine any statistically significant ($P < 0.05$) differences between means of two or more samples, statistical tests was applied whenever the sample sizes was equal to or larger than 14. At this threshold the power of the test was regarded high enough, considering the trade-off between statistical power and practical issues mentioned above (section 2.2). All means of numbers of gastropod individuals are given followed by a Coefficient of Variation (CV), as a measure of dispersion of the data from the mean (i.e. a measure of variation). The CV is the standard deviation (SD) of the mean represented as a percent of the mean. All statistical analysis was done in S-PLUS (TIBCO Software Inc., 2010), except power analyses that where done in R (R Development Core Team, 2011).

2.5.1 Sampled material

Differences in mean number of gastropod individuals and species per kelp individual between the two kelp species where statistically analyzed using a Welch's t-test (unequal variances t-test). To meet the assumption of normality of the test, the data where ranked before the test was executed. This test was selected over the more conventional Student's *t*-test because the former is shown to perform much better when the variances are unequal (Ruxton, 2006), which they were. The same was done to test the difference in mean number of gastropod individuals and species between the haptera of the two species. Differences in mean number of gastropod individuals and species between kelp parts in *L. hyperborea* was tested using one-way ANOVA followed by Tukey-Kramer post-hoc (unplanned) comparisons. A one-way ANOVA is used to test whether there is a significant difference between two or more samples, it reveals if there is a significant difference between two or several of the groups, but not which groups. The Tukey-Kramer comparisons is therefore used after a significant difference is detected by the one-way ANOVA to determine which of the groups differ, this is done by considering the confidence interval of the difference between the means (mean of group A minus mean of group B), if the confidence interval exclude 0 then there is a significant difference. To meet the assumption of normality, the data were transformed (log(y+1)) before the test was executed.

2.5.2 *In situ* images

The gastropod detection success of images, meaning their ability to quantify gastropods compared to the actual number of gastropods present (sampled), was evaluated both for the different kelp parts and for different gastropod taxa. For kelp parts this was calculated as the percentage of the total number of gastropods sampled in one kelp part, that were visible in images of the same kelp part. For different gastropod taxa it was calculated as the a ratio of numbers of individuals identified by images to the number identified by samples. Assemblage identification success of the images, i.e. their ability to identify the gastropod assemblage structure, was evaluated by comparing the relative abundance of gastropods on genus level (percentage for each genus of the total number of individuals found) in the images to the sampled material.

2.6 Terms used

There are some differences in the meaning of some terms used in the literature: the word epiphyte seem to be referring both to flora and fauna, but with no universal definition. Therefore, this term will not be used. Following are definitions of the terms used in this thesis.

Epiflora Macroalgae growing on the kelp.

Epifauna Fauna living on the kelp.

Epigrowth Refers to sessile organisms of both epiflora (like red algae) and epifauna (like bryozoans and hydrozoans).

Macrofauna Fauna between 0.5 mm to 5 cm, unless otherwise stated. Epifauna usually refers to macro-epifauna in this thesis.

3 Results

3.1 Sampled material

3.1.1 Seasonal variation in kelp morphology and general epigrowth

Saccorhiza polyschides had generally very little epigrowth, and little epigrowth variation between individuals (Table 3). In September and December, stipe and lamina of *S. polyschides* were still intact. Even in December they did not show any sign of decay. In March, however, the stipe and lamina was fully decayed, leaving only the haptera, which were large and complex. Some haptera also started to show signs of decay.

Table 3: Representative images of each kelp part of *S. polyschides* from each sampling. In March all lamina and stipes were decayed, leaving only haptera.

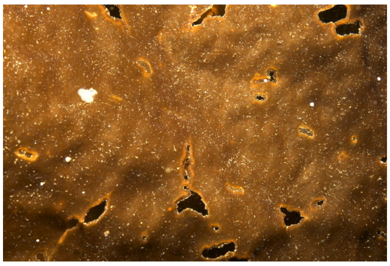
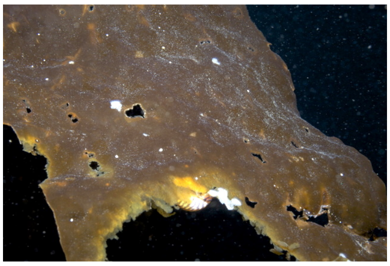
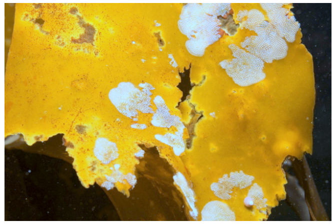
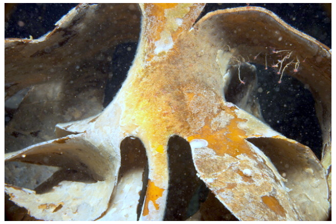
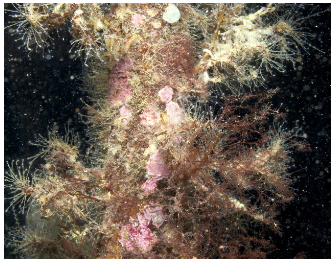
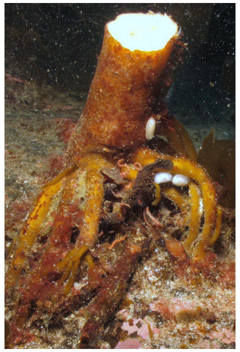
	September	December	March
Lamina			
Stipe			
Haptera			

Table 4: Representative images of each kelp part of *L. hyperborea* from each sampling

	September		December		March
Lamina					
Stipe					
Haptera					

The haptera in September and December were quite similar to each other, being small and less complex. *Laminaria hyperborea* had more epigrowth compared to *S. polyschides* and showed a large variation in epigrowth between individuals within each season for September and December. In March there was generally less epigrowth, and also less variation between individuals. Table 4 shows representative images from each sampling. For the samplings from September and December, two images of each kelp part is given, one with little epigrowth and one heavily overgrown, to show the span in variation. Since the individuals in March had less variation, only one representative image is provided.

3.1.2 Number of gastopod individuals

Difference between kelp species

In total, 1129 gastropod specimens were found, 941 on 14 individuals of *L. hyperborea* and 188 on 15 individuals of *S. polyschides*. Number of gastropod individuals per kelp individual varied greatly, especially for *L. hyperborea* (Figure 6). Mean number of gastropod individuals (Table 5) in *L. hyperborea* was 67.2 (CV 74.0 %) gastropods per kelp individual for all samplings together, this was significantly larger than for *S. polyschides* with an average of 12.5 (CV 73.6 %) gastropods per kelp individual (for all samplings together, Welch's t-test, $t_{(2)27} = 7.06$, $P < 0.001$). However, there was no statistically significant difference detected in gastropod numbers between the haptera of *L. hyperborea* and *S. polyschides* (Welch's t-test, $t_{(2)26.7} = 1.87$, $P = 0.07$), but the test had low power ($\beta \approx 0.55$) due to large variation between individuals and small sample sizes, so a difference may be there even though the test was not able to detect it. The same was not possible to test for stipe and lamina, due to small sample sizes.

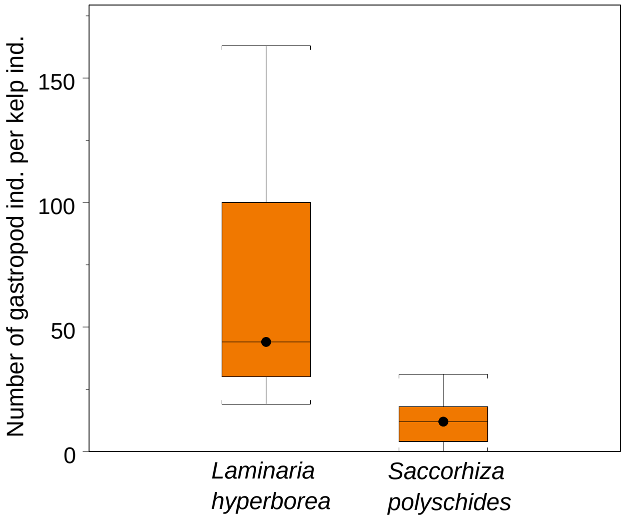


Figure 6: Box plot of the total number of gastropods on whole individuals (hapteron, stipe and lamina) of *L. hyperborea* (N=14) and *S. polyschides* (N=15), the boxes showing the interquartile range, whiskers showing the smallest and largest values, and the circle and line showing the median gastropod numbers.

Difference between kelp parts

For both kelp species about 50 % of the total number of gastropod individuals were found on the lamina, and the least number of gastropods were found on the stipe (Table 5; Figure 7). A one-way ANOVA showed a significant difference in number of gastropods between kelp parts ($F_{2,39} = 4.5$, $P = 0.02$) for *L. hyperborea*. Tukey-Kramer post-hoc (unplanned) comparisons showed that the mean of 32.9 (CV 117.9 %) gastropods per lamina was significantly different from the stipe mean (14.8, CV 195.9 %), but not significantly different from the haptera mean (14.8, CV 95.1 %), neither was there any significant difference between haptera and the stipe. Some difference in kelp parts is also suggested by the data for *S. polyschides* with a mean of only 0.5 (CV 200 %) gastropods per stipe, against 4.1 (CV 107.3 %) and 5.5 (CV 80.5 %) gastropods per haptera and lamina, respectively (not possible to test statistically).

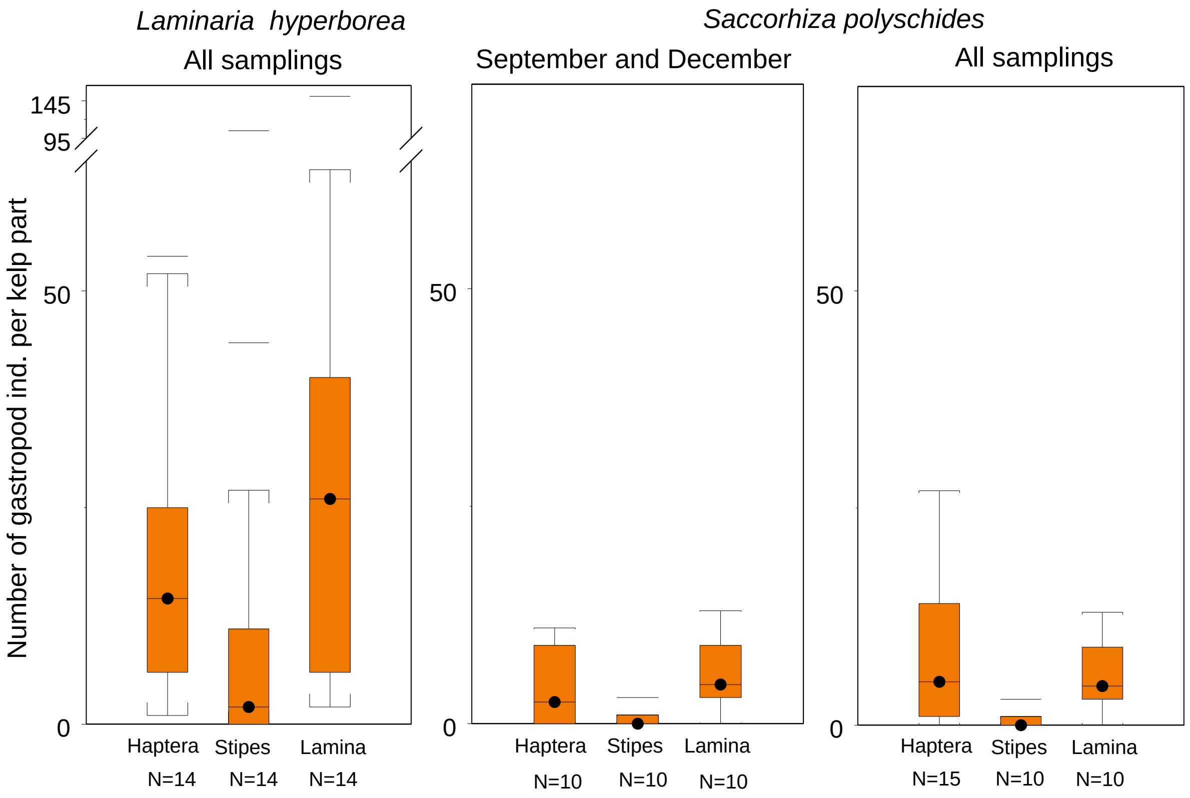


Figure 7: Box plot of the number of gastropod individuals on each kelp part for all samplings for *L. hyperborea* and *S. polyschides*. Total for the samplings in Septemer and December only is included for *S. polyschides*, to show the distribution of gastropods on whole kelp individuals (in March *S. polyschides* consisted only of haptera). The boxes show the interquartile range, whiskers show the smallest and largest values, circle and line show the median gastropod numbers, and independent lines show outliers[1].

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[1] An outlier is here defined as a data point lying 1.5 times the interquartile range or more above or below the upper or lower quartile, respectively.

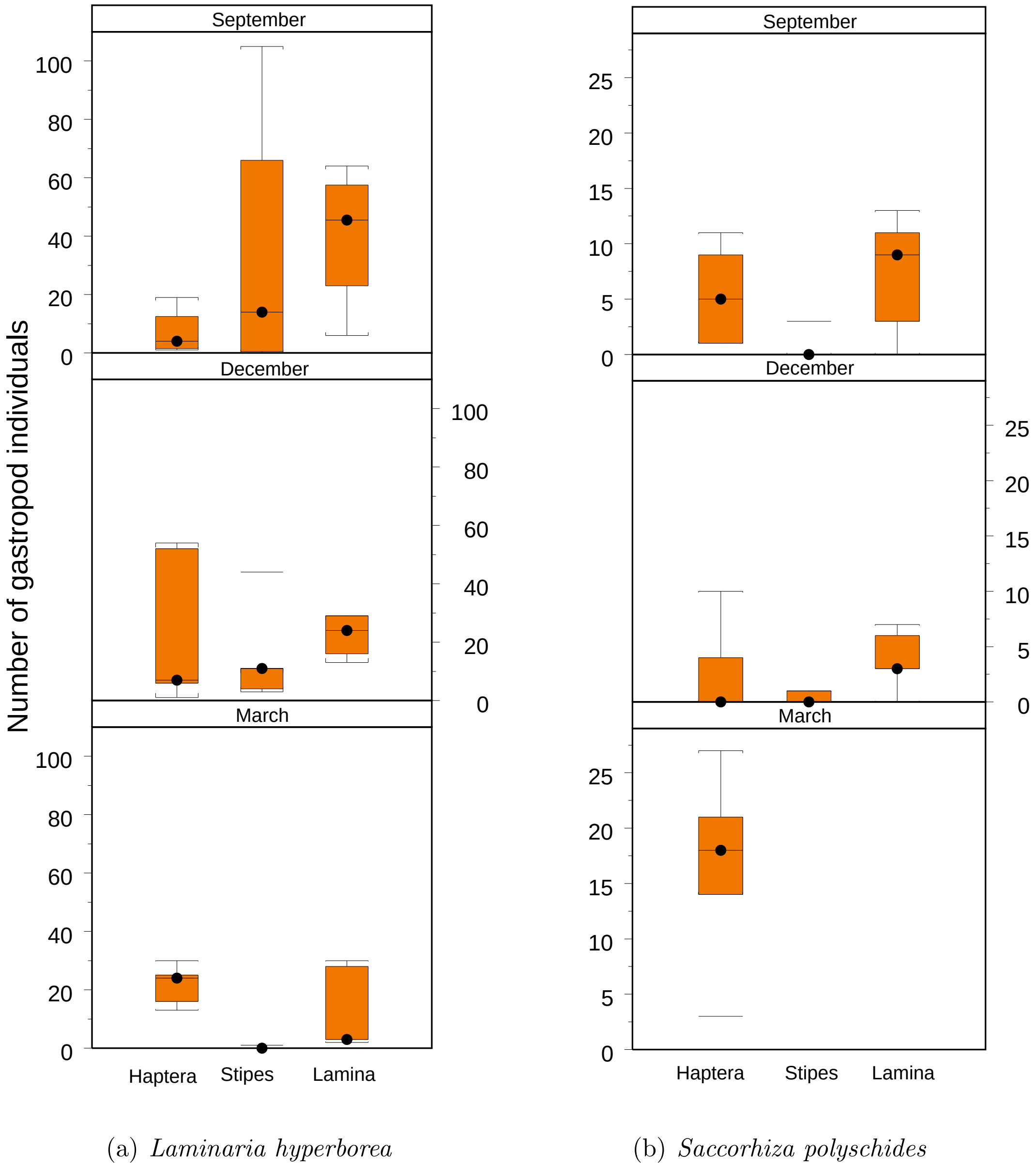
Table 5: Descriptive statistics summarizing the number of gastropod individuals and species on each whole kelp individual (in bold) and each kelp part of *L. hyperborea* and *S. polyschides* for each sampling, in the sampled material. For *S. polyschides* only haptera was found in March, so numbers for September and December is used instead of all samplings together, for a better comparison of number of gastropods in different kelp parts (numbers from all saplings are given in brackets).

	Sample size	Total number of gastropods	Percent of total no. of gastr.	Mean number of gastr.	SD	CV (%)	Total number of species	Mean number of species
Laminaria hyperborea								
All samplings	**14**	**941**	**100**	**67.2**	**49.7**	**74.0**	**34**	**9.7**
- haptera	14	274	29.1	18.3	17.4	95.1	22	4.9
- stipe	14	207	22	14.8	29.0	195.9	17	2.7
- lamina	14	460	48.9	32.9	38.8	117.9	11	3.8
September	**4**	**322**	**100**	**80.5**	**54.9**	**68.2**	**10**	**5.8**
- haptera	4	28	8.7	7.0	8.3	118.6	4	2.0
- stipe	4	133	41.3	33.3	49.4	148.3	8	2.8
- lamina	4	161	50.0	40.3	24.9	61.8	6	3.3
December	**5**	**435**	**100**	**87.0**	**61.0**	**70.1**	**27**	**15.0**
- haptera	5	129	29.7	24.0	26.6	110.8	15	5.2
- stipe	5	73	16.8	14.6	16.9	115.8	17	5.2
- lamina	5	233	53.6	46.6	58.7	126.0	8	5.0
March	**5**	**184**	**100**	**36.8**	**14.8**	**40.2**	**23**	**10.6**
- haptera	5	117	63.6	21.6	7.0	32.4	18	6.8
- stipe	5	1	0.5	0.2	0.4	200	1	0.2
- lamina	5	66	35.9	13.2	14.4	109.1	8	3.0
Saccorhiza polyschides								
Sept. and Dec.	**10**	**101**	**100**	**10.1**	**8.2**	**81.2**	**14**	**3.7**
(all samplings)	(15)	(188)		(12.5)	(9.2)	(73.6)	(21)	(4.4)
- haptera	10	41	40.6[1]	4.1	4.4	107.3	13	2.2
	(15)	(128)		(8.3)	(8.5)	(102.4)	(20)	(3.4)
- stipe	10	5	5	0.5	1.0	200.0	4	0.5
- lamina	10	55	54.5	5.5	4.4	80.0	4	1.5
September	**5**	**66**	**100**	**13.2**	**10.0**	**74.9**	**12**	**4.4**
- haptera	5	27	41.0	5.4	4.6	85.2	11	2.8
- stipe	5	3	4.5	0.6	1.3	216.7	3	0.6
- lamina	5	36	54.5	7.2	5.5	73.3	4	1.8
December	**5**	**35**	**100**	**7.0**	**5.4**	**76.9**	**10**	**3.0**
- haptera	5	14	40.0	2.8	4.4	157.1	7	1.6
- stipe	5	2	6.3	0.4	0.5	125.0	2	0.4
- lamina	5	19	54.3	3.8	2.8	73.7	3	1.2
March	**5**	**87**	**100**	**17.4**	**10.2**	**58.7**	**15**	**5.8**
- haptera	5	87	100	16.6	9.0	54.2	15	5.8
- stipe	0	0	0	0	0	0	0	0
- lamina	0	0	0	0	0	0	0	0

[1] Percent for all samplings not included because of different sample sizes for different kelp parts.

Difference between seasons

Mean gastropod number per *L. hyperborea* individual for September, December and March was 80.5 (CV 68.2 %), 87.7 (CV 70.1 %) and 36.8 (CV 40.2 %) gastropods, respectively. These data do indicate a difference in mean gastropod abundance in different kelp parts between samplings for *L. hyperborea* (Figure 8a), especially for the stipes. *Saccorhiza polyschides* (Figure 8b) had a higher mean number of gastropods per kelp individual in March (17.4, CV 58.7 %) than in September (13.2, CV 74.9 %) and December (7, CV 76.9 %), even though the individuals in March consisted only of haptera.



(a) *Laminaria hyperborea* (b) *Saccorhiza polyschides*

Figure 8: Box plot of the total number of gastropods on each kelp part of (a) *L. hyperborea* and (b) *S. polyschides* for each sampling. Note the different scales on y-axis. The boxes show the interquartile range, whiskers show the smallest and largest values, circle and line show the median gastropod numbers, and independent lines show outliers (outlier at 151 gastropods in one lamina of *L. hyperborea* in December is not included to make the scales more reasonable).

3.1.3 Gastropod species

Difference between kelp species

In total 35 taxa were recorded, 34 on *L. hyperborea* and 21 on *S. polyschides*. There was a statistically significant difference between the mean number of species on each individual of *L. hyperborea* (9.7 gastropod species per kelp individual) and *S. polyschides* (4.4 gastropod species per kelp individual, Welch's t-test, $t_{(2)27} = 4.4$, $P < 0.001$). However, no statistically significant difference in number of gastropod species were detected between the haptera *L. hyperborea* and *S. polyschides* (Welch's t-test, $t_{(2)27} = 1.3$, $P = 0.2$), but the test had low power ($\beta \approx 0.3$) due to large variation between individuals and small sample sizes, so a difference may be there even though the test was not able to detect it. The three most abundant gastropod species on *L. hyperborea* was *Lacuna vincta* (on average 30.2 specimens per kelp individual), *Rissoa parva* (on average 9.5 specimens per kelp individual) and *Gibbula cineraria* (on average 5.7 specimens per kelp individual), in total for all seasons. On *S. polyschides Nassarius incrassatus* was the most abundant species (on average 4.1 specimens per kelp individual) followed by *Gibbula cineraria* (on average 2.9 specimens per kelp individual) and *Lacuna vincta* (on average 1 specimen per kelp individual). The full species list and counts are listed in Appendix 1, showing the precision of identification (species, family, etc.), the parts of the kelp and samplings at which they were found. A total of 11 gastropod species were found only on *L. hyperborea* and 2 were only found on *S. polyschides*, but these were at low abundances (4 individuals or less), making any conclusion about species-specificity difficult. However, some gastropod species, though not restricted to one kelp species, were found in much higher abundances on one than the other, such as *Lacuna vincta*, *Rissoa parva*, *Onchidoris muricata* and *Patella pellucida* that were much more abundant on *L. hyperborea*, and *Nassarius incrassatus* that were more abundant on *S. polyschides* (Appendix 1).

Difference between kelp parts and seasons

On both kelp species the haptera was found to support the highest number of species (Table 5). A one-way ANOVA showed a significant difference in number of gastropod species between kelp parts ($F_{2,39} = 3.91$, $P = 0.02$) for *L. hyperborea*. Tukey-Kramer post-hoc (unplanned) comparisons showed that the mean number of gastropod species per haptera was significantly different from the stipe mean, but not significantly different from the lamina mean, neither was there any significant difference between lamina and the stipe. The haptera of *S. polyschides* sampled in March (lamina and stipes were decayed) supported a higher mean number of species (5.8) than haptera from the other seasons (2.8 in September and 1.6 in December). Different species dominated the different kelp parts for both kelp species (Table 6). In *S. polyschides Nassarius incrassatus* dominated the haptera in total for all seasons together, but the most dominating species showed some variation between seasons. *Gibbula cineraria* dominated the lamina for both seasons were lamina was present. No species dominated the stipe in any season but were equally present in low numbers. In *L. hyperborea Rissoa parva* was the most dominant species in haptera in all seasons. In September the stipes were dominated by *Lacuna vincta*, and by *R. parva* and *L. vincta* in December, no species dominated this kelp part in March. The lamina of *L. hyperborea* was in September and December highly dominated by *Lacuna vincta*, but this species was totally replaced by *Patella pellucida*, *Onchidoris muricata* and *Gibbula cineraria* in March (only 2 individuals of *L. vincta* present on lamina in March).

Table 6: List of dominating species (in descending order) in each kelp part for the different seasons in *L. hyperborea* and *S. polyschides*, with percentage of total number of individuals within that kelp part and season (a "dominating" species is here defined as a species representing 10 % or more of the total assemblage, except for species with only one individual present, then it is not considered dominating even though the percentage may be more than 10). Lamina and stipes of *S. polyschides* were not present in March.

Season	Haptera		Stipes		Lamina	
L. hyperborea						
Sept.	*Rissoa parva* *Margarites helicinus* *Lacuna vincta*	43 % 39 % 14 %	*Lacuna vincta*	84 %	*Lacuna vincta* *Gibbula cineraria*	81 % 13 %
Dec.	*Rissoa parva*	56 %	*Rissoa parva* *Lacuna vincta*	30 % 23 %	*Lacuna vincta* *Gibbula cineraria*	66 % 14 %
Mar.	*Rissoa parva* *Onoba semicostata* *Alvania punctura*	20 % 17 % 15 %	No dominating species		*Patella pellucida* *Onchidoris muricata* *Gibbula cineraria*	33 % 32 % 24 %
S. polyschides						
Sept.	*Nassarius pygmea* *Onchidoris muricata* *Nassarius incrassatus* *Margarites helicinus*	19 % 19 % 14 % 11 %	No dominating species		*Gibbula cineraria* *Lacuna vincta*	56 % 28 %
Dec.	*Nassarius incrassatus* *Nassarius pygmea*	36 % 28 %	No dominating species		*Gibbula cineraria*	89 %
Mar.	*Nassarius incrassatus* *Onoba semicostata* *Rissoa parva*	49 % 10 % 10 %				

3.2 *In situ* underwater images

In total, 329 images were analyzed and 189 gastropods specimens were found, of which 110 could be identified to genus level and 44 to species level, the rest was not possible to identify to any lower taxonomic level than class Gastropoda. This means that 24 % of the gastropod fauna visible in images was possible to identify to species level and 81 % to genus level. However, only 17 % of the 1129 gastropod individuals sampled were visible in images (Figure 9). Mean gastropod abundance per kelp from *in situ* images was 3.8 (CV 117.1 %) for *L. hyperborea* and 0.3 (CV 169.5 %) *S. polyschides*. There were found a total of 71, 75 and 43 gastropod individuals in images from September, December and March, respectively.

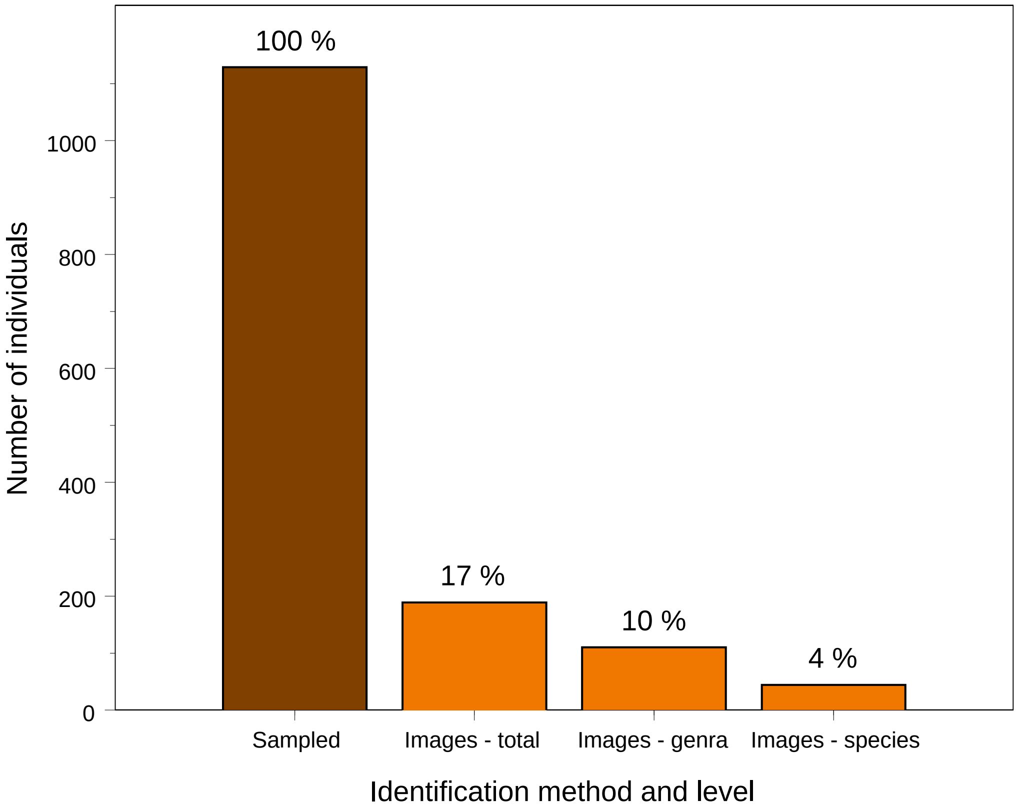


Figure 9: Total number of gastropod individuals found in sampled material and images (regardless of host kelp species) and to what taxa level they were identified with percentages of total sampled for each identification method and level.

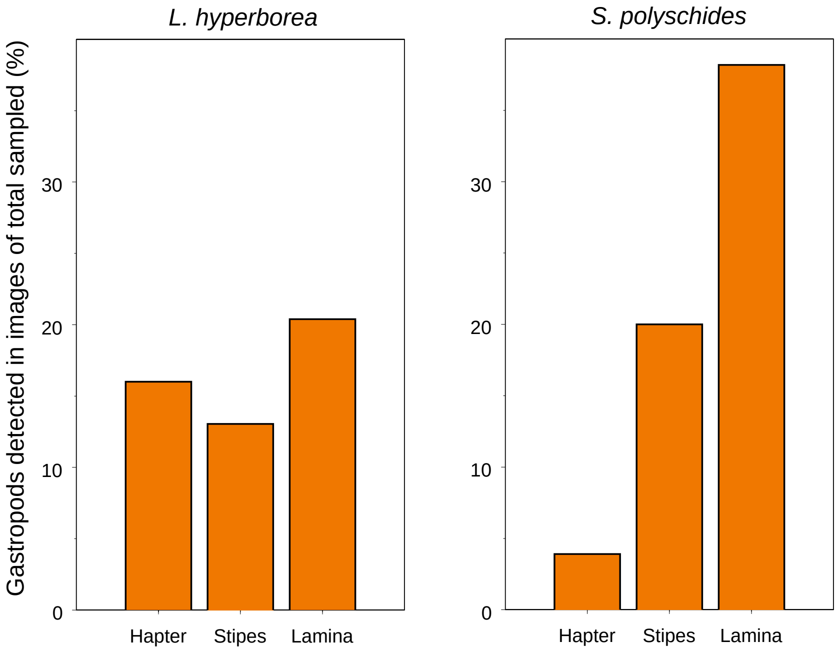


Figure 10: Gastropods detected in images of each kelp part of *L. hyperborea* and *S. polyschides*, as percentage of the total number found on the same kelp part in sampled material.

Gastropod detection success

The percentage of total sampled material that were found in *in situ* images varied between kelp parts (Figure 10). For both kelp species, the images of lamina had greatest detection success, but the difference between kelp parts were less evident in *L. hyperborea*. In *S. polyschides* the images from haptera had a success of 4 %, from stipes 20 % and lamina 38 %. The detection success increased with the number of images taken. The number of images was 86 (detection success = 22 %), 176 (det. success = 37 %) and 66 (det.success = 24 %) for the samplings in September, December and March, respectively. The detection success of *in situ* images for different gastropod taxa (ratio of numbers of individuals identified by images to the number identified by samples) varied greatly, from 0 (several species) to 2.40 (*Polycera quadrilineata*). Full species list with level of precision and counts is given in Table 7 along with the detection success of the images for each taxa identified from images.

Assemblage identification success

The assemblage structure of gastropods at genus level did look different between sampled material and images for both kelp species. Table 8 show the structure of the gastropod assemblages from sampled material and from images, for each kelp species, listing the 5 dominating genera in descending order. For *L. hyperborea* images managed to identify *Lacuna* sp., as the most abundant genus. However, for *S. polyschides*, the most abundant genus in sampled material, *Nassarius* sp., was not found in images at all, instead *Gibbula* sp. dominated greatly (70 %) compared to sampled material (23 %).

Table 7: List of gastropod taxa and counts identified from *in situ* images of *L. hyperborea* and *S. polyschides*, compared to counts found in sampled material, with ratio of number of gastropod individuals identified by images to number of individuals identified by samples for each taxa. Gastropod taxa not found in images is not included (- = does not apply).

	No. of ind. in images	No. of ind. in samples	Ratio of no. identified in images/identified in samples
Lacuna sp.	61	446	0.14
Trivia arctica	1	1	1[1]
Tectura virginea	1	2	0.50
Patella pellucida	7	47	0.15
Gibbula cineraria	2	124	0.02
Gibbula sp.	47	126[2]	0.39
Onchidoris muricata	12	53	0.23
Limacia clavigera	10	12	0.83
Polycera quadrilineata	12	5	2.40
Aplysia punctata	1	2	0.50
Gastropoda indet	35	-	-
Total	189	1129	1.06[3]

[1] Not the same individual, in images found on *L. hyperborea* and in samples found on *S. polyschides*.

[2] All from genus *Gibbula* found in sampled material

[3] Mean ratio for the species actually found in images.

Table 8: Ranking list of the 5 most abundant genera (in descending order) in *L. hyperborea* and *S. polyschides* found in sampled material and images with percentage of total. "Others" refers to all other specimens, both identified and not-identified, except in images for *S. polyschides* where no other taxa were identified than the five listed.

L. hyperborea			
Sampled material		*In situ* images	
Lacuna sp.	46 %	*Lacuna* sp.	36 %
Rissoa sp.	16 %	*Gibbula* sp.	19 %
Gibbula sp.	9 %	*Onchidoris* sp.	7 %
Onchidoris sp.	6 %	*Polycera* sp.	7 %
Patella sp.	5 %	*Limacia* sp.	6 %
Others	17 %	Others	26 %
S. polyschides			
Sampled material		*In situ* images	
Nassarius sp.	33 %	*Gibbula* sp.	70 %
Gibbula sp.	23 %	*Lacuna* sp.	11 %
Margarites sp.	9 %	*Limacia* sp.	4 %
Lacuna sp.	8 %	*Polycera* sp.	4 %
Rissoa sp./*Onoba* sp.	5 %	*Tectura* sp.	4 %
Others	25 %	Others (not id.)	7 %

4 Discussion

4.1 *L. hyperborea* and *S. polyschides* as habitat for gastropods

The effect of kelp species

The attractiveness for settlement for gastropods of *L. hyperborea* is clearly higher than that of *S. polyschides*, both in terms of numbers of gastropod individuals and species (Figure 6, Table 5). One explanation might be that *L. hyperborea* provides a larger area and more complex habitat because of more epigrowth, as have shown to increase the number of epifauna individuals and species (Jarvis & Seed, 1996; Norderhaug et al., 2002; Hauser et al., 2006; Norderhaug et al., 2007).

Saccorhiza polyschides had very little epigrowth compared to *L. hyperborea* which may be because it is an annual species, so less epiflora and epifauna have time to settle. Older kelp individuals have shown to carry a higher percentage cover, abundance and number of epiphytic algal species (Christie et al., 1994). But the difference in gastropod quantities may also be explained by chemical (Walters et al., 1996) or physical (Walters & Wethey, 1991) characteristics of the kelp. However, the patterns of colonization of both epiflora and epifauna or possible defensive mechanisms in the kelps has not been a focus of prior research, and needs to be examined closer in the future (Bartsch et al., 2008).

Another explanation for the differences in gastropod abundances between *L. hyperborea* and *S. polyschides* might be the feeding behavior of the gastropods. Norton (1971) reported observations of several gastropod species feeding on the lamina of *S. polyschides*, including *Lacuna vincta* which also feed on *L. hyperborea* (Johnson & Mann, 1986). This species were not so much abundant on *S. polyschides* as on *L. hyperborea* in my samples, which may also indicate a preference of *L. hyperborea* as host species over *S. polyschides* if they both provide a potential food source.

The overall assemblage did not differ that much between *Laminaria hyperborea* and *S. polyschides*, even though the abundances were different. Both *Lacuna vincta* and *Gibbula cineraria* were among the three most abundant gastropods in each kelp species. The study by Tuya et al. (2011) also indicated a lack of difference in haptera epifauna assemblage structure (for all epifauna groups) between *S. polyschides* and *L. hyperborea.* They concluded that the provision by kelp haptera of food and living space for the entire epifauna assemblage does not depend on the shape of the kelp haptera. However, they used large taxonomic groups (families, order or phyla) and their result could have been different if using species as the targeted taxonomic level, as implied by Anderson et al. (2005).

Also Norton (1971) found a composition to other laminarian algae (*L. hyperborea, L.*

digitata and *Saccharina latissima*). Although the composition of species was similar, he found some species to be more abundant in *S. polyschides*, including the gastropods *Lacuna vincta* and *Gibbula cineraria*, and the bryozoa *Membranipora membranacea. Patella pellucida* have also been reported abundant on *S. polyschides* Ebling et al. (1948), but this species was not very abundant on *S. polyschides* in this study. These contradictions to my study indicates that other factors may also influence the distribution of gastropod species.

The effect of kelp part

About 50 % of the gastropods were found on the lamina for both *L. hyperborea* and *S. polyschides* (Table 5, Figure 7). Schultze et al. (1990) studied macro-epifauna (> 0.5 mm) on *L. hyperborea* and *L. digitata* around Helgoland, and found a higher fraction of the general epifauna associated with haptera, especially at more exposed sites, a pattern also evident for the gastropods. The same pattern is also found by Norton (1971) for all fauna groups associated with *S. polyschides.* This suggests that the exposure or wave action might be a factor influencing the distriution of gastropods on the kelp thallus, and may indicate that the area sampled in this study is fairly sheltered, because of the high numbers of gastropod on the lamina of both kelp species. Also complexity influences the distrubution of gastropods between the kelp parts. Christie et al. (2003) found the highest number of gastopods associated with the stipe (71 % of total) of *L. hyperborea*, but also reported a corresponding high volume of epiflora growth on the stipes. Also in my samples, the stipes from September and December, that had more epigrowht than in March, supported a higher number of gastropod individuals and species.

When examining the gastropod assemblages on each kelp part for *L. hyperborea* and *S. polyschides* there is a clearer difference, not only between kelp parts, but also between kelp species, than when looking at the kelp individuals as a whole. In *L. hyperborea* species like *Lacuna vincta*, *Gibbula cineraria* and *Patella pellucida* dominates the lamina, while haptera is dominated mostly by *Rissoa parva.* The stipes seem like a transition habitat influenced both by the haptera and lamina assemblage, dominated mostly by *L. vincta* and *R. parva.* The lamina of *S. polyschides* is also dominated by *Gibbula cineraria* and in september also by *Lacuna vincta*, while the haptera was mostly dominated by different species than the haptera of *L. hyperborea*, like *Nassarius incrassatus*, *N. pygmea* and *Onchidoris muricata.*

If the gastropods choose their habitat based on host species only, it might be reasonable to believe that once the lamina and stipe of *S. polyschides* decays, the fauna simply move to the haptera, but this is not evident when comparing the assemblage of the haptera from the March sampling to the other kelp parts from the other seasons (Figure 6), indicating that the gastropods have a stronger preference for kelp part than for kelp species in the choice of habitat.

Comparison of abundances with other studies

On average 67 gastropod individuals were found per individual of *L. hyperborea*, ranging from 19 to 163 gastropods on one kelp. These abundances is low compared to other epifauna studies of *L. hyperborea* in Norwegian waters, e.g. Christie (1995) (between 151 and 781 gastropods per kelp hapteron), Norderhaug et al. (2002) (more than 30 000 gastropod individuals on 12 haptera and stipes) and Christie et al. (2003) (more than 2000 gastropod individuals on average per kelp individual), but not that different to those found by Schultze et al. (1990) around Helgoland. The big difference compared to some of the studies may be due to several factors. The kelp forest in the area of this study is of medium density (1-3 ind. per m^2) and the individuals are of small to medium size (height $\approx$ 0.5-1.5 m), which might influence the gastropod abundance. Age of the forest have shown to have an impact on the fauna abundance and diversity (Christie et al., 1998), but the kelp forest in this area have, to my knowledge, not been extensively disturbed during the recent years. Sampling error might have affected on the gastropod enumeration, especially for the more complex parts of the kelp, such as the haptera. Small gastropod individuals (often less than 1 mm) may be hard to see and find if the kelp is not studied carefully. Lack of experience with this may have led to errors, especially for the first sampling. However, the method used for sampling of the kelp: putting the bags over one kelp part before separating it from the others; and keeping the kelp parts separate, is considered the best way to do it, as opposed to for instance separating the whole kelp from the substrate and then putting it in a bag, not keeping the parts separate. Perhaps the most likely factor influencing the number of gastropod individuals and species is depth. All the studies mentioned above (Christie, 1995; Christie et al., 2003; Norderhaug et al., 2002) sampled their kelp at 4-5 meters depth, while the samples in this study were taken at 10 meters. Many other researchers than the ones already mentioned have investigated the macro-epifauna associated with *L. hyperborea*, but some have studied only other species groups like amphipods (Hacker & Steneck, 1990; Norderhaug, 2004; Eilertsen et al., 2011), or the general epifauna, with no records of numbers of gastropods provided (Tuya et al., 2011). Others reported only epifaunal assemblage structure (Tuya et al., 2011) or species richness (Blight & Thompson, 2008) making comparisons of gastropod numbers found in this study difficult.

Saccorhiza polyschides had generally very little epigrowth and epifauna, which seems less than reported in previous studies of this kelp in UK waters (Ebling et al., 1948; McKenzie

& Moore, 1981; Norton, 1971). It also less than Norum (1913) reported from Norway, but he did not report any kind or enumeration, making any conclusions impossible. In addition, because some reported only specific taxa or only species lists without any enumeration, comparisons of the gastropod abundances found in this study is difficult. There was, in this study, found an average of 12 gastropods per individual, ranging from 0 to 31, which does seem similar to what reported by McKenzie and Moore (1981).

Seasonal differences

There was a higher number of both gastropod individuals and species on *S. polyschides* haptera in March (Figure 8, Table 5), compared to the other seasons. This might be explained by an increase in both size (as shown for both *S. polyschides* and *L. hyperborea*: Norderhaug et al., 2007; Tuya et al., 2011), and complexity of the haptera (shown for artificial kelp: Norderhaug et al., 2002; Hauser et al., 2006; Section 3.1.1).

Laminaria hyperborea showed an opposite pattern, with less gastropod individuals and species in March, which was expected (Christie et al., 2003). This was largely due to a large drop in number of gastropod individuals and species on the stipe (Figure 8), which also correlated with a drop in general epigrowth (Section 3.1.1), and on the lamina. The pattern were not the same for the haptera, indicating that the provision of habitat of the *L. hyperborea* haptera does not depend on epigrowth. There was also some differences in the gastropod assemblage between seasons, the most striking difference being the almost total replacement of *Lacuna vincta* by *Patella pellucida* and *Onchidoris muricata* on *L. hyperborea* lamina in March compared to the other seasons. The overall epigrowth on lamina was not so different between the sampling in March and the other sesons, which might indicate influence of other factors. Norton (1971) recorded large fluctuations in the epifauna abundances of *S. polyschides* throughout the year, with no apparent pattern. The fluctuation were also different for different epifauna species and he reported some species (e.g. *Membranipora membranacea*, Bryozoa) to seemingly have a seasonal pattern of their own.

In this study it might seem that the overall most important factor controlling the distribution of number of gastropod epifauna individuals and species between kelp parts, is the size and complexity of the kelp part for both species, although other factors, like season related factors or the availability of food, can not be ruled out. The distribution of the individual gastropod species seem to be highly influenced by complexity of the substrate for some species, while other seem to be influenced by other factors.

4.2 Evaluation of imaging method

4.2.1 The success of *in situ* images compared to sampled material

As much as 81 % of the gastropod epifauna in the pictures was possible to identify to either species or family. But then again, only 17 % of the actual gastropod epifauna was visible in images (Figure 10). This shows that quantification of organisms by imaging is a difficult task, at least in complex environments like kelp forests. The possible reasons for this is summarized and further discussed in section 4.2.2.

Gastropod detection success for different kelp parts

The percent of sampled gastropods that were visible in the images differed between kelp parts both within and between the two kelp species (Figure 10). Generally the total trend was more visible gastropods in less complex kelp parts, both regarding structural complexity of the species itself or added complexity by epigrowth. For *S. polyschides* the difference between kelp parts were quite clear, with a much higher percentage of gastropods visible on lamina than haptera. The low percentage in haptera is probably due to the structure; because it is hollow and (especially in young individuals) less complex on the outside, it is reason to believe that most of the gastropods live on the inside (also supported by McKenzie & Moore, 1981), which images is not able to capture. The sampling method used did not have any secure way of recording this, but during examination of the sampled kelp, most of the haptera gastropods were observed on the inside.

For *L. hyperborea* the difference was smaller between kelp parts. The different trends in the two kelp species may be due to the difference in epigrowth. When there is much epigrowth, as in *L. hyperborea* there is more added complexity. In *S. polyschides* there is no added complexity by epigrowth so the effect of difference in structural complexity between kelp parts on the visibility of gastropods in images is more evident.

Detection success of images for different gastropod taxa

The high variability in the detection success of the images between gastropod taxa may be explained by differences in size and degree of conspicuousness between the different gastropod taxa. Taxa with a high detection success, like nudibranchs (e.g. *Polycera quadrilineata*, det. success = 2.4) or *Gibbula* (det. success = 0.39), is generally bigger than 1 cm and have conspicuous colors or patterns which makes them easy to detect in images. Also the photographers attention may be drawn to such species, if the camera is operated by a person (as in this study). Images does in fact seem to be a better method for mapping or recording of nudibranchs, compared to traditional sampling methods. Other taxa, with a detection success of 0, like the genera *Rissoa* (that were present in very high abundances in sampled material), is usually very small (< 5 mm) and with less conspicuous colors.

Another factor influencing the different detection success for different gastropod taxa is their choice of habitat. Like *Rissoa* that, in addition to being very small, mostly live in kelp parts with high complexity, like haptera or overgrown stipes. Also *Nassaridae*, even though they are somewhat bigger than *Rissoa* (7-10 mm), were not detected in images. These were also mostly present in complex kelp parts, and especially in the hollow haptera of *S. polyschides*. In contrast, *Lacuna*, despite the small size (around 7 mm or smaller), had a detection success of 0.14. These species live on the less complex lamina of both kelp species, which makes it easier to capture in images.

Assemblage identification success

The relative abundance of gastropod species in images was not very similar to the one revealed in the sampled material for any of the kelp species. These results suggests that images, the way they are used in this study, is not reliable neither in terms of quantification of gastropods, nor in identification of the composition of the gastropod community, supported by the fact that only 9 of 35 species found in sampled material was identified in the images.

4.2.2 Factors influencing imaging

This study shows that images gives limited information compared to traditional sampling methods. There are three main reasons for this: images does not capture everything; the quality of images is not always good enough; and identification of species from images is difficult. The factors affecting these three challenges are addressed in this section.

Factors affecting the area captured by images

Dimensionality of kelp forests: Both the kelp individuals alone and the kelp forest as a whole is a three dimensional (3D) system, and since images is a two dimensional medium it is impossible to cover all sides of kelp in a kelp forest by images. Thus a great amount of information will be lost (Figure 10). Increasing the amount of images might give more information (Section 3.2), but still gastropods and other epifauna will not be detected in complex or hollow structures like haptera.

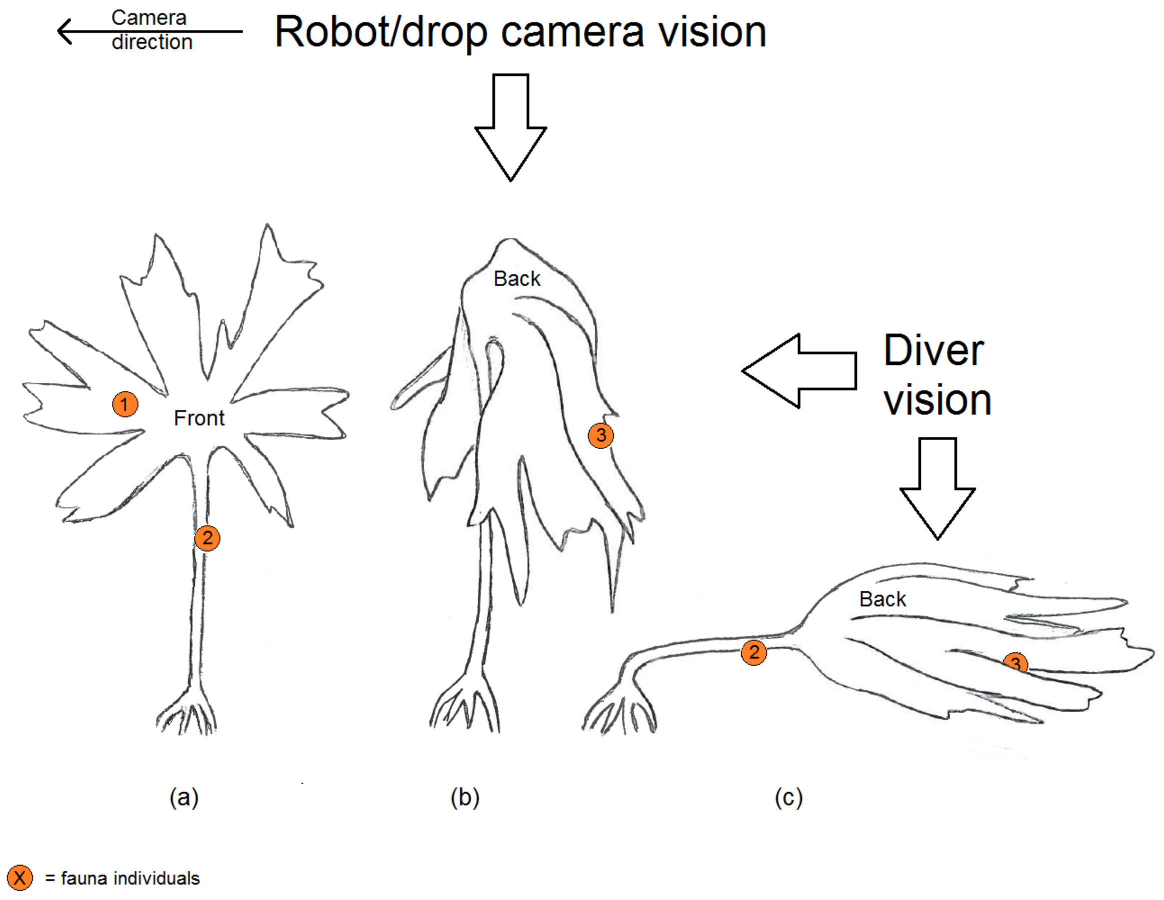


Figure 11: Different positions for a given kelp bed is determined by wave action and tidal currents. This affects what fauna (indicated by numbered dots) is visible. The same fauna is not visible in the different kelp positions, affecting what a camera is able to capture of present fauna. Also different methods for imaging (here represented as a diver and a camera mounted on a robot or a drop camera) will affect this. Likewise, wave action in combination with tidal currents may induce high differences in a given kelp bed regarding mapping of area, morphology and areal coverage.

Water motion: One of the most challenging factors is the fact that kelp forests are dynamic, ever moving environments. Figure 11 shows schematically three possible positions of kelp, with different visible gastropods on each. The positions are affected by the degree of water motion, current speed and direction. These abiotic factors may also affect the morphology of the kelp species. In areas with very high exposure, some kelp species have a flexible stipe, while the stipe of the same species is rigid and erect in more sheltered areas (Denny et al., 1997; Gaylord & Denny, 1997). This is because a rigid stipe would break in highly exposed areas, but in sheltered areas it will increase the amount of light hitting the lamina. In addition, the morphological response to water motion varies greatly among kelp species (Norton et al., 1981). All of this will affect the kelp forest apparence, making it highly dynamic, both between sites and time of year. This makes comparison of images from different sites and different times, and estimates of areal coverage, challenging. It is important to mention that kelps would never be positioned like the one in Figure 11a, at least not for very long, even though it might be easy to think that they do.

Method: Whether the camera is operated by a SCUBA diver or mounted on a platform, like an AUV (Autonomous Underwater Vehicle), ROV (Remotely Operated Vehicle) or a drop camera from a boat, will affect what images capture. The vision of a camera mounted on a platform will usually be top-down and with horizontal movement. This means that in a kelp bed with kelps in positions like in Figure 11b, less epifauna may be visible than if the kelp is positioned like in Figure 11c. A SCUBA diver will be able to decide the angle of imaging to capture as much of the kelp as possible, or an area as representative as possible.

Practical issues: SCUBA dive time affects how much one is able to capture by images, and is again determined by the amount of air available to the diver. Usually only 1 hour of diving is possible and this limits the amount of images the diver is able to take. Current procedures regarding scientific SCUBA diving requires 2-3 divers with diving gear, security equipment, and a diving boat with crew and communication, making such surveys expensive and time consuming.

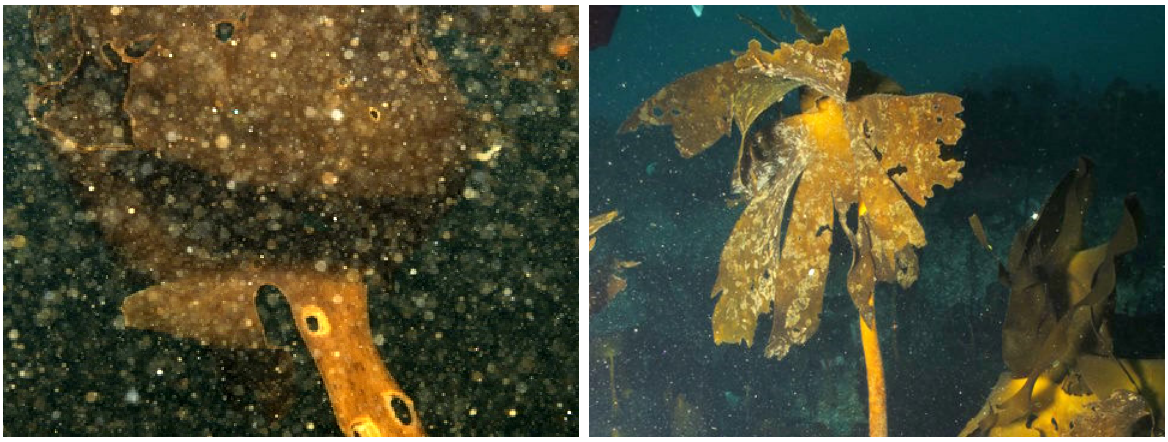
Factors affecting the quality of the images

The term spatial resolution in biological imaging surveys usually refers to the size of organisms that can be distinguished in an image, but not necessarily species determined. Low spatial resolution makes identification of organisms or species difficult and is closely related to the water transparency, distance from camera lens to the object of interest (OOI), light exposure and the camera used. All of these will be further discussed below.

Water transparency: The spectral attenuation (total diffuse attenuation coefficient, K_d) of seawater is influenced by all optically active components, comprising the water itself (K_w), plankton and other particulate organic matter(K_{POM}), colored dissolved organic matter (K_{cDOM}) and particulate inorganic matter (K_{PIM}; Johnsen et al., 2009). They do all contribute to reducing image quality (sharpness, contrast, colors) by affecting the water transparency. Water also attenuate wavelengths especially in the blue (450-480 nm) and red (620-750 nm) part of the visible spectrum (400-700 nm) affecting the colors in the image (Johnsen et al., 2009).

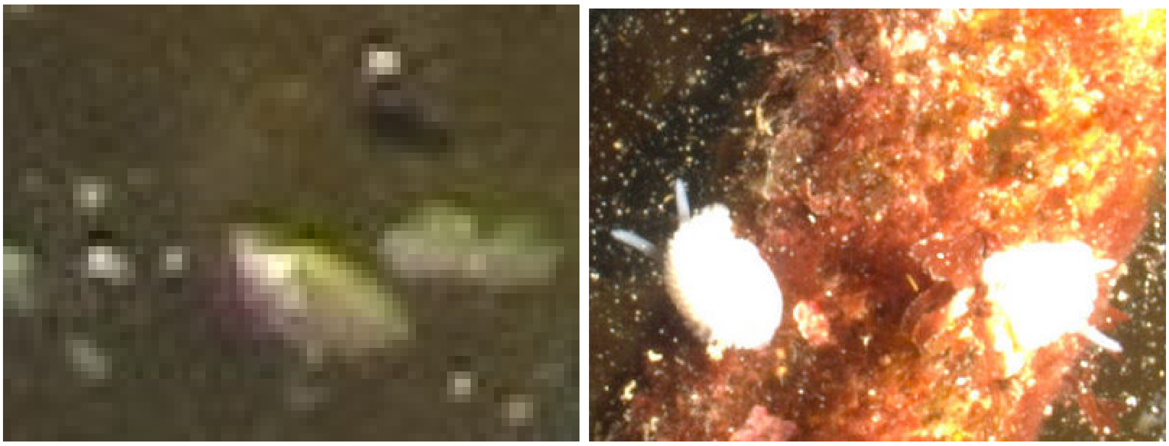
Distance: The spectral attenuation (K_d) increases with the optical pathlength, i.e. distance from the camera to OOI, and lowers the quality of the image and the spectral resolution (less colors). In Figure 12b it is clear that the spectral resolution is lower for the kelps farthest away from the camera, even for the kelp closest to the camera identification of epifauna species would be a challenge if the overall spatial resolution of the image is not high. Distance will also increase the reflection from particles in the water, because more particles is between the kelp and the camera, this will induce further noise in the image. Usually the closer to OOI the better.

Light exposure: Both light quality (spectral distribution of light from flash, lamp or natural light) and quantity (amounts of photons reaching the sensor, inducing different signal to noise ratio) (Figure 12d) will affect the sensor (CCD/CMOS) sensitivity (ISO) needed. The ISO should be kept as low as possible to avoid "grainy" images. Both under- and overexposure affects the image quality and the ease of species identification. The angle of illumination to camera is important to avoid scattered and backscatter light. A set up of light 90 degrees to camera will reduce some of the backscattered light.



(a) Low water transparency due to particles

(b) Large distance to OOI



(c) Large pixel size (and low density)

(d) Over-exposure to light

Figure 12: The factors influencing the quality of images is mainly (a) water transparency, (b) distance from object of interest (OOI), (c) camera specification such as large pixel size and density, and (d) light exposure (both over- and under-exposure), which all makes it hard to detect and identify organisms. Photos: (a) Geir Johnsen; (b),(c) and (d) Torjus Haukvik.

Camera specifications: As mentioned, the type and quality of the camera and optics is of importance for the quality of images, like the sensor type (CCD/CMOS), sensor size, pixel density and pixel size (Figure 12c). But also file formats should be considered. Using non-compressed image formats, such as RAW format, enables higher plasticity of editing image quality, compared to compressed formats such as JPG.

Factors affecting the identification of species

This is related to the image quality, but can be distinguished as problems that arises despite high quality of images.

Size of organisms: This study shows that the sizes of gastropods one is able to identify in an image, is limited. This is of course highly dependent on the quality of the image and the spatial resolution, but generally individuals less than 0.5 mm is very hard to spot and identify, especially if they don't have very conspicuous colors or patterns.

Dimensionality of organisms: Figure 13 shows an example of how hard it can be to spot and identify gastropods from a picture with high spatial resolution (21 megapixel). The small images shows magnified parts of the big picture at the top. Even in a clear image like this the gastropods (apart from the nudibranch) was not possible to identify to family or species, because key characteristics were not visible.

Determining spatial scale: If no scale is included close to the OOI (for example by two parallel laser points with known distance between them) it may be impossible to determine sizes with high accuracy.

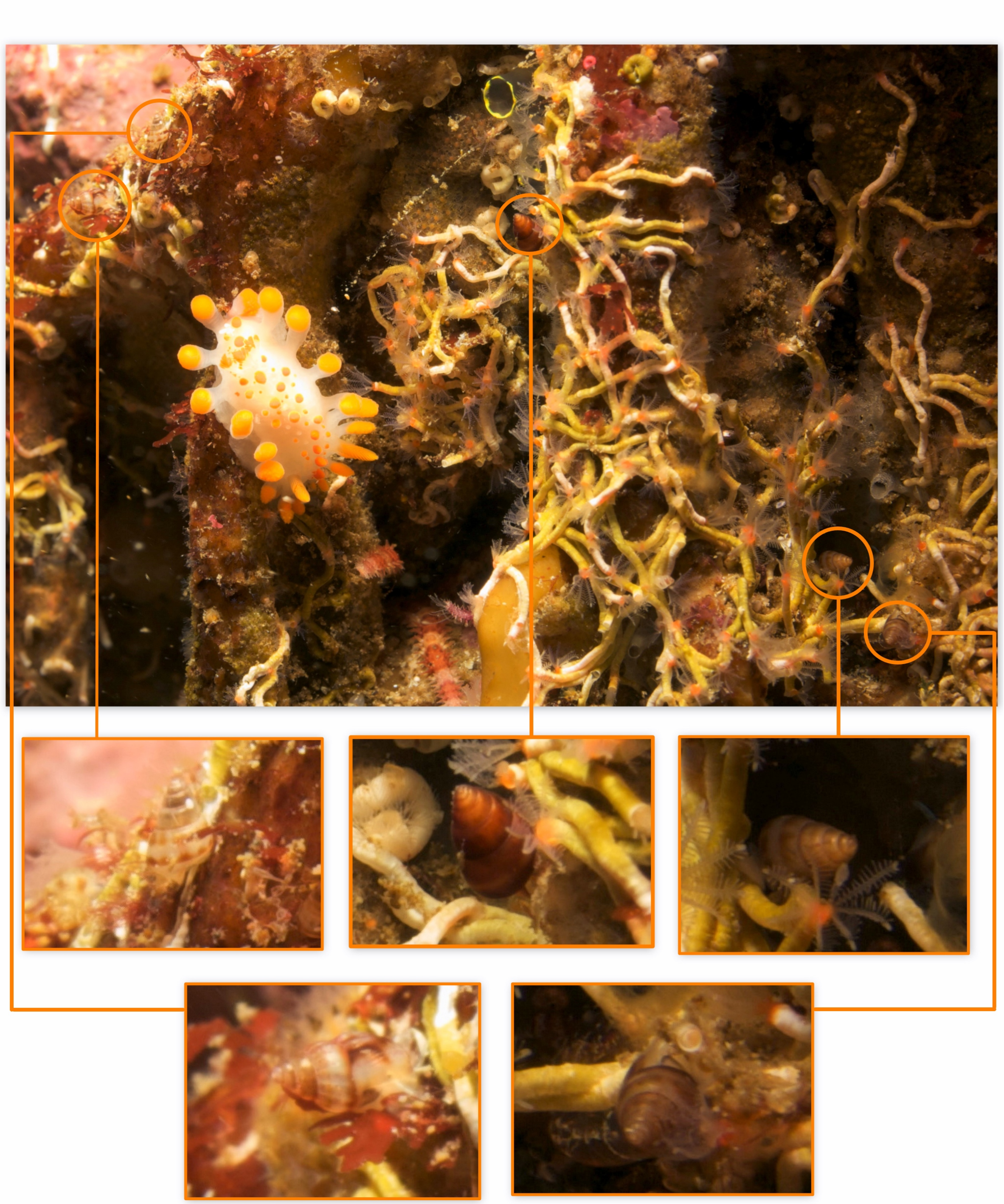


Figure 13: Haptera of *L. hyperborea in situ* with visible gastropod fauna. The nudibranch *Limacia clavigera* is seen in the upper image, and the small images is other gastropod fauna magnified from the big image, non of these were identified to a lower level than class Gastropoda, because key characteristics is not visible. High spectral resolution and sufficient illumination is essential to even see the gastropods. Also specimens may hide in the 3D structure of the hapter. Photo: Geir Johnsen.

4.3 Conclusions and future perspectives

4.3.1 *L. hyperborea* and *S. polyschides* as habitat for organisms

Both *L. hyperborea* and *S. polyschides* provide an extensive habitat for gastropod fauna, and in particular the haptera of the two species provide habitats for different gastropod species. Yet the knowledge about distribution patterns and controlling factors for specific species is limited.

Laminaria hyperborea is the main constituent in Norwegian kelp forest, for that reason, and because it has been subject to heavy grazing by sea urchins, the knowledge about this species is extensive. The same cannot be said about *S. polyschides*. *Saccorhiza polyschides* remains almost the single species with this limited knowledge in Norwegian waters. Both its biology and its role in the kelp forest ecosystem, needs further research.

4.3.2 *In situ* images as sampling method

Currently, mapping and trend monitoring of benthic habitats using still images is done by a detailed photo of a given area (usually less than 1 m^2) to get the "overall distribution of species". Norwegian Standards (2008) requires 1 photo ($>$ 1.7 megapixels) per 30 meters, less than 3 meters above the sea floor. The present study shows that this approach gives limited information compared to traditional sampling. Even though using SCUBA divers, targeting the kelp epifauna and capturing more than 11 images per kelp closer than 1 meter, with 10-21 megapixel images, only 17 % of the actual gastropod fauna present is captured. If using a robot or a camera towed from a boat, this percentage would be much lower. Table 9 sums up the main suggested criteria for *in situ* imaging found in this study. More similar studies would be able to tell if the image success found in this study is universal, and if *in situ* images may be used as a proxy or substitute for traditional sampling if the objective of the study allows it. Images does have the potential to be more time and money efficient, but considering the requirements needed to reduce the loss of information about the overall abundance and distribution of species, this may not be true.

Table 9: Suggested criteria for imaging as sampling method, based on this study of gastropods in kelp forests. Only factors one is able to control is included.

Factor	Criteria or actions
Number of images	When using 18 images per kelp individual 37 % of the gastropod epifauna was detected in images. The level of success required will depend on the objective of the study.
Water transparency	Impossible to control, but should be adjusted for by shorter distance to OOI or using a 90 degree angle of light source to camera lens to minimize backscatter. It can also be avoided by planning, considering the weather and season.
Distance	Depending on the spatial resolution, light available and the identification requirements of the study the minimum distance may vary, but generally the distance from camera lens to OOI should be less than 0.5 meters to be able to identify organisms less than 1 cm.
Spatial resolution	The size of the smallest organism that can be detected or identified to species would vary with the objective of the study. However, this study have shown that to be able to identify the real assemblage structure of gastropods, the size of organisms that can be identified to species or genera have to be at least 1 mm, but this would still be difficult for reasons discussed in Section 4.2.2.
Light exposure	Dependant on the natural light available, distance to OOI and the water transparency. But the quantity of light should be high enough to keep the sensor (CCD/CMOS) light sensitivity low, e.i. ISO between 100-400 (ISO > 400 will induce "grainy" images with lower spatial resolution).
Pixel resolution	This would largely depend on the size of OOI, and distance from camera to OOI. For identifying gastropods at a size of 0.5-1 mm a pixel resolution of more than 10 megapixles is needed.

4.3.3 List of most important results and conclusions

L. hyperborea and *S. polyschides* and associated gastropod epifauna

- General epigrowth was much less in *S. polyschides* than *L. hyperborea.*
- There was a significantly higher mean number of both gastropod individuals and species per kelp individual of *L. hyperborea* than *S. polyschides.*
- For both *L. hyperborea* and *S. polyschides* the highest number of gastropod individuals were found on lamina, and the least on stipes.
- For both *L. hyperborea* and *S. polyschides* the highest number of gastropod species were found on haptera, and the least on stipes.
- *Laminaria hyperborea* supported the highest number of both gastropod individuals and species in September and December, wich correlated with more epigrowth in this seasons.
- *Saccorhiza polyschides* had a highest mean number of both gastropod individuals and species per kelp individual in March, even though the individuals in March

consisted only of haptera, which correlated with both larger and more complex haptera.

- Different species dominated the different kelp parts for both *L. hyperborea* and *S. polyschides* and the dominating species showed some variation between the studied seasons.

Comparison of *in situ* images to traditional sampling technique

- 17 % of the 1129 sampled gastropod individuals was visible in the *in situ* images. 24 % of these could be identified to species (4 % of total sampled) and 84 % could be identified to genus (10 % of total sampled).
- Detection success of gastropods in images decreases with increasing complexity of the habitat (i.e. kelp part), both structural complexity in the kelp or added complexity by epigrowth.
- The gastropods detection success of images varies greatly between gastropod taxa and depends mostly on size and degree of camouflage or conspicuousness of the gastropods, and what habitat (i.e. kelp part) they live in.
- The success of images in identifying the true (sampled) assemblage structure was low, mainly because images does not capture everything, the quality of images is not always good enough and species identification in images is difficult.

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Appendix 1: List of species/taxa

Number of gastropod specimens on kelp parts within each kelp species and recorded at sampling (1-3)

Kelp species		*Laminaria hyperborea*			*Saccorhiza polyschides*			Sampling
Kelp part		Haptera	Stipe	Lamina	Haptera	Stipe	Lamina	no.
(no. of samples)		(N=14)	(N=14)	(N=14)	(N=15)	(N=10)	(N=10)	
Family	Species							
SUBCLASS CAENOGASTROPODA								
Cerithiopsidae	*Cerithiopsis* sp.	3						2,3
Littorinidae	*Lacuna vincta*	9	129	285	3	1	11	1,2,3
	Lacuna sp.			8				2
Rissoidae	*Onoba semicostata*	30			9			2,3
	Alvania punctura	19			2			2,3
	Alvania beani	1						3
	Pusillina sarsii	2						2
	Cingula trifasciata	11	1		1			2,3
	Cingula cf. *trifasciata*	4						3
	Cingula semistriata	15			3			2,3
	Cingula turgida	2						2,3
	Cingula sp.	1						2
	Rissoa parva	107	24	2	9			1,2,3
	Rissoa lilacina		1					2
	Rissoa cf. *membranacea*	3						3
	Rissoidae indet.	1						2
	Rissoidae juv.	11	7					1,2
Triviidae	*Trivia arctica*				1			3
Buccinidae	*Buccinum undatum*	1			3			1,2,3
Nassariidae	*Nassarius incrassatus*	15	5		52			1,2,3
	Nassarius pygmea		1		10			1,2,3
	Nassarius cf. *pygmea*		2					1
Raphitomidae	*Raphitoma linearis*	1						2
SUBCLASS PATELLOGASTROPODA								
Lottiidae	*Tectura virginea*	1	4		2			2,3
	Testudinalia testudinalis	1	1					2,3
Patellidae	*Patella pellucida*		1	46		1	5	1,2,3
SUBCLASS VETIGASTROPODA								
Turbinidae	*Margarites helicinus*	18	4	4	10	1	2	1,2,3
	Margarites striatus				4			3
Trochidae	*Gibbula cineraria*	5	6	69	5	2	37	1,2,3
	Gibbula cf. *tumida*	2						3
SUBCLASS HETEROBRANCHIA								
Pyramidellidae	*Odostomia striolata*	2						2,3
Onchidorididae	*Adalaria loveni*			1				2
	Onchidoris muricata		15	38	6			1,2,3
Polyceridae	*Limacia clavigera*	7	1	3	1			1,2,3
	Polycera quadrilineata			2	3			1,3
Eubranchidae	*Eubranchus pallidus*		1		1			1,2
Tergipedidae	*Cuthona foliata*	1						3
Flabellinidae	*Flabellina verrucosa*		1					2
Facelinidae	*Facelina auriculata*		1	1	2			1,2,3
Aplysiidae	*Aplysia punctata*		2		1			2
Velutinidae	*Lamellaria* sp.			1				3
Gastropoda juv.				1				3
Total number per kelp part		275	207	461	128	5	55	
Total number per kelp species			941			188		