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Effects of depth and overgrowth of ephemeral macroalgae on a remote subtidal NE Atlantic eelgrass (*Zostera marina*) community

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ABSTRACT

We conducted a short-term field sampling complemented with time integrating stable isotope analysis to holistically investigate status and ecological interactions in a remote NE Atlantic *Zostera marina* meadow. We found high nutrient water concentrations, large biomass of fast-growing, ephemeral macroalgae, low abundance, and biodiversity of epifauna and a food web with thornback ray *(Raja clavata)* as intermediate and cod *(Gadus morhua)* as top predator. We observed no variation with increasing depth (3.5–11 m) except for decreasing shoot density and biomass of *Zostera* and macroalgae.

Our results indicate that the Finnøya *Zostera* ecosystem is eutrophicated. During the past three to four decades, nutrients from aquaculture have steadily increased to reach 75% of anthropogenic input while the coastal top predator cod has decreased by 50%. We conclude that bottom-up regulation is a predominant driver of change since top-down regulation is generally weak in low density and exposed *Zostera* ecosystems such as Finnøya.

1. Introduction

In the Anthropocene no area of the ocean is unaffected by human activities and about 40% is strongly affected. Changes of cumulative human impacts are especially fast in coastal areas (Halpern et al., 2008, 2019) where seagrass meadows often are the dominant primary producers. Both areal extent, vertical depth distribution and ecosystem services of seagrasses are in an overall decline (Waycott et al., 2009; Dunic et al., 2021). According to de los Santos et al. (2019) there is still a net loss of global seagrass despite local recoveries. In Scandinavia, historical data (1880–1930) from Danish coastal waters suggest that the dominating seagrass *Zostera marina* (hereafter *Zostera*) at that time grew down to 15–20 m depth (Boström et al., 2003 and references therein). Whereas the recent changes in *Zostera* areal distribution are well documented in the southern part of NE Atlantic, the spatio-temporal status for *Zostera* in the northern NE Atlantic is unknown. While most larger meadows have been mapped recently (Naturbase, 2021) there is little knowledge of the spatio-temporal changes (but see Jørgensen and Bekkby, 2013).

The areal coverage of *Zostera* in the southern part of the NE Atlantic region has suffered significant losses in many regions except in the Baltic and *Zostera* now mainly grows at 2–8 m depth (Balsby et al., 2013; Boström et al., 2003, 2014; Christie et al., 2014; Knutsen et al., 2010; Krause-Jensen and Rasmussen, 2009). In several Nordic areas, *Zostera* has experienced local declines since the 1980s, but mostly in the shallow part of their depth range (Baden et al., 2003; Fredriksen et al., 2004).

In the distribution area in the Northern Hemisphere, *Zostera* meadows serves as foraging, refuge, and reproduction habitat for many species of associated invertebrates and fish (Baden and Pihl, 1984; Boström et al., 2014). *Zostera* typically grows and is monitored in a

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narrow depth range. However, *Zostera* habitat documentations below 10 m depths are rare despite their potentially high conservation value, and we lack estimates of how plant and sediment variables as well as associated faunal structure, diversity and function might respond to changes in depth (Dale et al., 2007; Rueda et al., 2008). Hypothetically, the plant morphology and faunal composition may differ from the shallower parts as the complexity of the seagrass canopy (e.g., shoot density) most often decreases with depth due to light limitation (Dennison and Alberte, 1982; Krause-Jensen et al., 2000; Olesen et al., 2017).

To bridge this knowledge gap, we sampled and analysed a *Zostera* ecosystem on the Norwegian west coast just south of the polar circle spanning from 3.5 to 11 m depth. The aims were to contrast the influence of depth on (1) sediment biogeochemical properties, (2) *Zostera* meadow structure and production, and (3) the associated algal and faunal community food web along a depth gradient and (4) through stable isotope investigations of sampled sediment, primary producers and fauna get a time integrated overview of interactions in this *Zostera* ecosystem, not previously investigated.

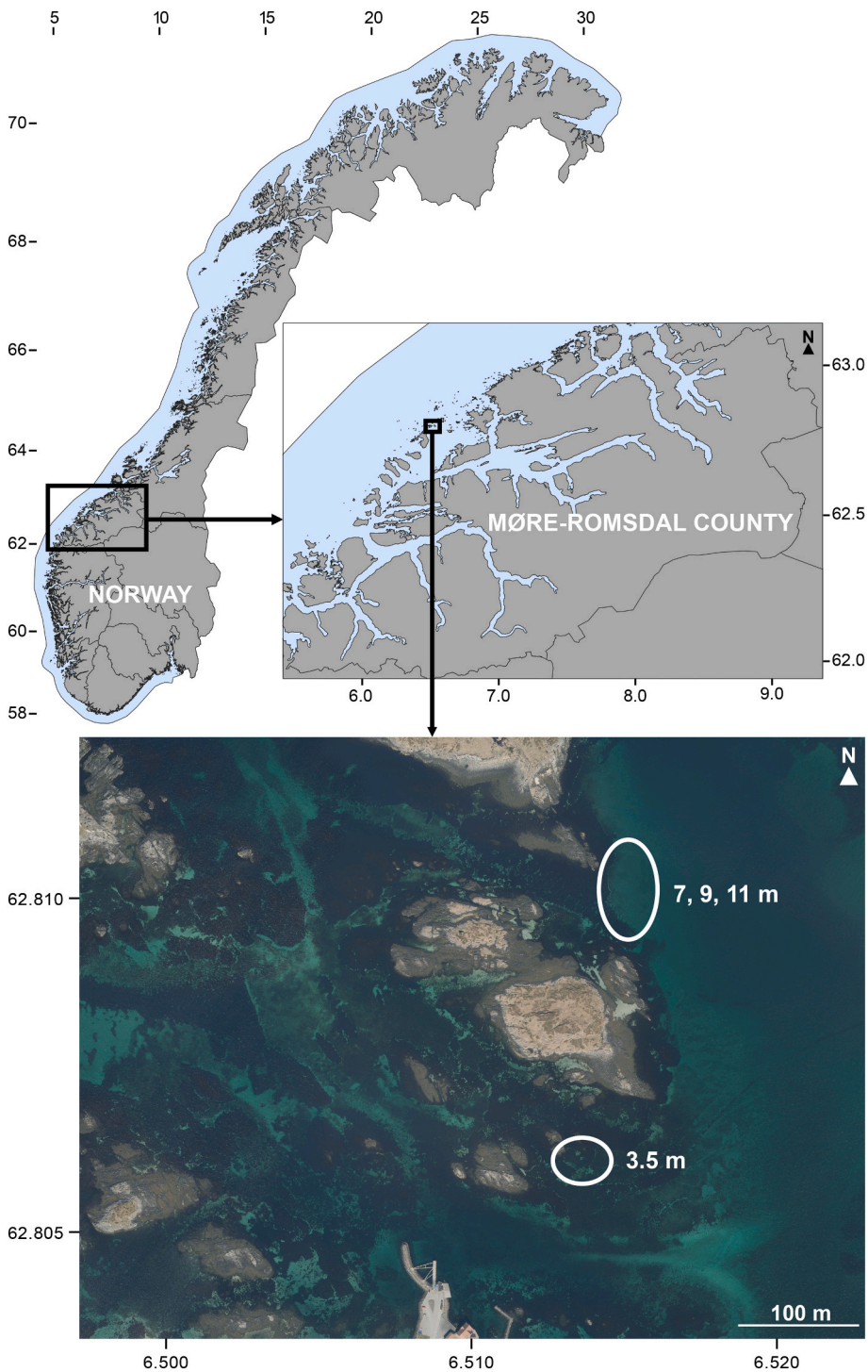

Fig. 1. Map of investigated seagrass beds situated close to Finnøya island on the west coast of Norway (62°48′ N and 6°30′ E). Arial photo by Norwegian Mapping Authority, Omløpsfoto Møre 2018.

2. Materials and methods

2.1. Study area

The Finnøya island is situated in an archipelago of small islands and narrow sounds on the west coast of Norway (62°48′ N and 6°30′ E) about 450 km south of the polar circle (Fig. 1). The sampled area is intermediate exposed to wave action (Pedersen et al., 2012). The tidal amplitude in this part of the coast is between 1.5 and 2 m. Rocky shores with extensive fucoid vegetation dominate the littoral zone. There are no rivers entering the area and salinity is 30–33. Sea surface temperature has a minimum of 4–5 °C in winter and a maximum of 14–15 °C in summer (Sætre, 1973) but higher summer temperatures may occur in certain years (Moy and Christie, 2012). *Zostera* in this area is found in sheltered locations from 2 to 11 m depth and forms meadows of between 200 m^2 to 65,000 m^2 of areal extension (Naturbase, 2021). The study was performed at four different depths: 3.5, 7, 9 and 11 m from 16 to 23 June 2012 (Fig. 1). The sampling meadow with deep *Zostera* (7, 9 and 11 m, approximate size 15,000 m^2 (1.5 ha)) had no shallow *Zostera* above 4.5 m. A near-by (500 m) shallow *Zostera* site (approximate size 200 m^2, 3.5–5 m) was selected to get a more extended depth profile and for comparing results with other *Zostera* beds in S. Scandinavia where depth extension has decreased (Baden et al., 2003; Boström et al., 2003; Fredriksen et al., 2005; Christie et al., 2009). At the shallowest sampling site *Zostera* was not present above 3.5 m due to the presence of rocky exposed habitats with perennial macroalgae. Sampling at the deep sites (7, 9 and 11 depth) occurred along a fixed transect-rope. The sampling sites were placed about 30 m apart and the replicates at each depth were about 5–15 m from the rope in different directions.

2.2. Water and sediment sampling and analysis

Water column and sediments were sampled at each sampling depth. For determination of dissolved inorganic nitrogen (DIN) and phosphorus (DIP), and $\delta\,^{34}S_{sulfate}$ near-bottom water samples were collected ($n = 3$ at each sampling depth). All water samples were GF/F filtered before freezing within 2 h. The water for analysis of $\delta\,^{34}S_{sulfate}$ concentration was prepared by boiling under acidic conditions followed by precipitation of sulfate with $BaCl_2$ as $BaSO_4$ and measured by elemental analyser combustion continuous flow isotope ratio mass spectroscopy. The stable isotopic signatures were reported in standard delta notation (‰). The international standard for $\delta^{34}S$ is the Canyon Diablo Troilite, a meteorite of FeS, was used as a standard zero point for expression of sulfur isotopes.

The sediment was sampled with cores (l. 20 cm, i.d. 2.5 cm, $n = 3$) and the upper 0–10 cm was fixed with 20% (*w/v*) zinc acetate (1:1 vol) and stored frozen until analysis. Sediment cores (l. 20 cm, i.d. 5.0 cm, n = 3) for sediment characteristics (density, water content, loss of ignition (LOI), particulate organic carbon (POC), particulate organic nitrogen (PON), and molar C:N relationship), sulfide front and pore waters were sliced in the laboratory within one day. Sedimentation rates were measured in vegetated and bare sediments at each depth (at 11 m, only bare) by deploying two sediment traps with five replicate collection tubes (length: 115 mm, diameter: 28 mm). Traps were positioned at the upper canopy level for 2 days. Water column nutrients were determined on a Lachat nutrient analyser.

The rhizosphere sediment preserved in ZnAc was distilled according to the two-step procedure of Fossing and Jørgensen (1989) to obtain the acid volatile (AVS) and chromium reducible sulfur (CRS) fraction. Briefly, an aliquot of 5–10 g of homogenized sediment was transferred to a reaction flask and 10 ml 50% ethanol was added. After degassing with N_2 for 10 min, the sediment was distilled at room temperature with 8 ml 12 M HCl for 30 min to release AVS. CRS was obtained by reduction with 16 ml Cr^{2+} in 0.5 M HCl followed by boiling and distillation for 30 min. The extracted sulfide was precipitated in traps as ZnS and Ag_2S and analysed for sulfide pools (ZnS) according to Cline (1969) and for $\delta^{34}S$ (Ag_2S) as described above.

The sulfide front was determined by deployment of silver sticks in the sediment cores for 6 h. Porewater for determination of sulfides was extracted using Rhizons® positioned in the rhizosphere sediment (1–6 cm) and 1–2 ml of water extracted. Samples were fixed in 20% (*w/v*) zinc acetate solution and later analysed according to Cline (1969). All values were below detection limit (< 1 μM) and data are not shown. Similarly, deployment of silver sticks in the sediments showed limited precipitation of sulfides and the sulfide front was detected at 28 ± 18, 43 ± 13, 19 ± 7 and 27 ± 7 mm from each sampling depth. Sediment characteristics were measured in 1 cm (0–2 cm) and 2 cm intervals down to 10 cm. From the 0–1 cm section a subsample was taken for grain size analysis by a Malvern Mastersizer 3000 particle size analyser and average grain size was calculated according to Folk and Ward (1957). Sediment water content, wet density and porosity were determined from a subsample of 5 ml that was taken using a cut-off 5 ml syringe and weighed before and after drying at 105 °C for 6 h. The dried sediment samples were homogenized in a mortar and divided into two subsamples from which one was used for analysis of sediment loss of ignition (4 h in 520 °C) and carbonate content (acidification of combusted sediment in HCl) and the other for analysis of sediment POC, and PON as well as stable isotopes (SI) $\delta^{13}C$ and $\delta^{15}N$ (see Section 2.4). These samples were acidified for C determination and analysed by EA-MS as described above. From the two uppermost layers also total iron content (TFe) and total phosphorus content (TP) was determined on the combusted sediment and after boiling in 1 M HCl. TFe was measured according to Stookey (1970) and Sørensen (1982) and TP according to (Koroleff, 1983). Sedimentation rates were calculated according to Gacia et al. (1999).

2.3. Plant sampling and analysis

Biomass samples at each sampling depth were obtained by harvesting all above- and belowground *Zostera* biomass and associated macroalgae within five 0.04 m^2 quadrats. In the laboratory we determined the maximum length of all *Zostera* shoots, number of leaves per shoot and shoot density. The shoots were scraped for epiphytes and divided into above- and belowground biomass. The *Zostera* biomass fractions, epiphytic and unattached ephemeral macroalgae from each sample were rinsed in freshwater and dried to constant weight at 60 °C. Macroalgae were identified to species level.

For each sampling depth, annual leaf-formation rates were determined using the reconstruction technique (Short and Duarte, 2001). Terminal shoots attached to rhizomes with the largest number of nodes possible were carefully excavated from the sediment. In the laboratory the sequence of internodal lengths (i.e., distance between two successive leaf scars) was measured from the youngest node at the base of the terminal shoot to the oldest node at the distal end of the rhizome. The annual leaf formation rate or plastochrone interval (PI, d $leaf^{-1}$) was derived from annual cycles in rhizome internode lengths on the 5 to 8 oldest shoots harvested. Subsequently, the leaf turnover was calculated as the annual leaf formation divided by the average number of leaves per shoot.

Ten *Zostera* shoots were subsampled to measure nutrient (C, N) and sulfur(S) content as well as stable isotopes $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$. These plants were divided into young leaves, rhizomes, and roots (youngest two leaves, internodes or roots) and rinsed in fresh water before drying. Plant C and N were obtained on grinded leaf material by EA-MS analysis. Plant S and $\delta^{34}S$ were measured in *Zostera* for all plant tissues (leaves, rhizomes, and roots) as described above. Sulfide invasion $F_{sulfide}$ (%) in *Zostera* was calculated from the $\delta^{34}S$ in the plants, from δ^{34} of sulphate in the bottom waters and from $\delta^{34}S$ in sediment sulfide as described by Frederiksen et al. (2006):

$$F_{sulfide} = \left(\delta^{34}S_{tissue} - \delta^{34}S_{sulfate}\right) / \left(\delta^{34}S_{sulfide} - \delta^{34}S_{sulfate}\right)$$

where $\delta^{34}S_{tissue}$ is the value measured in the leaf, rhizome, or root and $\delta^{34}S_{sulfate}$ (of bottom water) and $\delta^{34}S_{sulfide}$ (from AVS pool in sediments, CRS for Sta. N1).

2.4. Faunal sampling and analysis

At each of the four depths three samples for epifauna (defined as mobile and sessile animals associated to the leaf canopy) were taken using a mesh bag (250 μm). The bag was carefully placed over a randomly placed 20 × 20 cm quadrat enclosing all leaves which were cut off at the sediment surface (Fredriksen et al., 2005; Christie et al., 2009). To obtain a qualitative estimate of the fish community, we used Nordic and coastal survey-nets (Nippon Verkko OY, Finland). A Nordic survey net is 30 m long, 1.5 m high and has 12 panels with mesh sizes between 8 and 43 mm. A Coastal survey-net is 45 m long, 1.8 m high and has 9 panels with mesh sizes between 10 and 48 mm. Two Nordic and one coastal survey nets were placed in the *Zostera* 20th of June 2012 between 9 pm and 9 am in the S-SE part of the deeper meadow (5–9 m) (Fig. 1). All fish sampled (n = 22) were identified to species level, euthanized by percussive blow to the head followed by freezing for later stomach and stable isotope analysis. Several thornback rays *(Raja clavata)* were caught in the survey-nets, and they were immediately counted and released except for 3 specimens. Survey-nets were deployed only once since thornback rays were abundant and destroyed the nets.

2.5. Ecological interactions traced by stable isotopes

Stable isotopes (SI) are used as tracers in biological systems, and their ability to track changes and processes over time makes them important to indicate ecological interactions. Stable isotope signatures of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were measured for *Zostera* leaves (see above), dominating macroalgae species, sedimenting detritus, macrofauna, and fish. Macroalgae and detritus collected in the sediment traps (filtered on pre-weighed and combusted 25 mm Whatman GF/F filters) were dried at 60 °C for 24 h to constant weight. Dried plants were grinded and weighed into tin capsules and filters with dried detritus were weighed before analysed for $\delta^{13}C$ and $\delta^{15}N$.

In fish, shrimps, crabs, and large bivalves we used muscle tissue in the analyses since this tissue has been shown to reflect long-term absorption of carbon and nitrogen (Wada et al., 1991). Stomach analysis was carried out on all rays and prey items identified to highest taxonomical level possible. Very small or less abundant invertebrate species sometimes had to be pooled or grouped into family to obtain enough biomass for SI analysis. The faunal material for SI analysis was prepared by drying whole animals or tissue samples (including shells of small molluscs) at 60 °C to constant weight and weighing grinded samples into tin capsules.

2.6. Statistical analysis

The effect of depth on *Zostera* biomass, shoot density and length, macroalgal biomass and epifaunal abundance per g DW *Zostera* leaf biomass and per m^2 bottom area were analysed by one-way ANOVA followed by Tukey's HSD post hoc *test*. Prior to the analysis, normality and homogeneity of variances were tested with the Shapiro-Wilk and Levene's tests, respectively. Data were log-transformed when the demand of variance homogeneity for parametric tests were not met. The statistical analyses were conducted in R-version 3.3.1.

3. Results

3.1. Water and sediment variables

Water column nutrients did not differ across the four stations (Table S1). Only DIP concentration showed an increase at the deepest site from 0.43–0.56 μM at 3.5, 7 and 9 m depth to 2.96 μM at 11 m depth. The NH_4^+ and NOx concentrations were 11.40–13.67 μM and 4.87–7.66 μM, respectively, with no difference between depths. The sedimentation rates in *Zostera* ranged between 6.80 ± 0.69 and 13.44 ± 8.02 g DW m^{-2} d^{-1} (Table S2) and showed no differences among depths and between substrate types (bare vs. *Zostera*). There was no major difference in the trap material in the $\delta^{13}C$ and $\delta^{15}N$ signals across depths and substrate types ($\delta^{13}C$: −12.57 and – 16.87 and $\delta^{15}N$: 5.22–6.04) (Table S2). The $\delta^{13}C$ in the traps suggested a mixed input of the primary producers sampled at the location (Table S6). All sediment parameters showed little variation among stations and with sediment depth (Table S3). Only the C:N ratio tended to increase with sediment depth from 7.29–7.81 in the surface layers to 7.97–8.58 in the deep layers. The sediment density ranged between 1.56 and 1.72 g WW cm^{-3}, water content between 30.5 and 37.3%, LOI between 0.39 and 0.66% DW, POC between 0.13 and 0.73% DW and PON between 0.02 and 0.11% DW (Table S3). Unexpectedly, the average grain size increased with depth from 194 μm at 3.5 m depth to 283 μm at 11 m depth (Table S3), whereas there was limited difference between TP, TFe and carbonate content which ranged between 0.74 ± 0.42 and 1.00 ± 0.44 μmol P g DW^{-1}; 0.89 ± 0.04 and 1.22 ± 0.36 μmol Fe g DW^{-1} and 45.0 ± 3.8 and 56.6 ± 1.6% carbonates, respectively (Table S3). The porewater pools of sulfides were below detection, whereas the CRS pools dominated the particulate sulfides with maximum at the two intermediate depths (Table 1). AVS pools only constituted 1.3–4.1% of the total pool of sulfides in the sediments and the sulfide front was detected between 1.9 and 4.3 cm into the sediments. All the Fe in the sediments was bound in the sulfide pools (TFe 222–304 mmol m^{-2}; Fe in TRS pool). The $\delta^{34}S$ values of the AVS and CRS pools were quite similar, also between depths (ranged between −23.5 to −19.5‰; Table 1). The $\delta^{34}S$ for seawater sulfate was on average 22.0‰ at this location (Table 1).

The intrusion of sulfides into *Zostera* was highest in the roots (21–29%) and similar in rhizomes and leaves (12–15%; Table 2). There was no difference between depths with a tendency to higher intrusion at the shallowest site. The TS content varied between 0.26 and 0.37% DW with no trend between depths (Table 2).

3.2. Plant variables

Zostera shoot density and biomass varied markedly among depths showing a more than 10-fold decrease from shallow to deep water (Fig. 2a & c). Hence, shoot density (mean ± SE) decreased from a maximum of 455.0 ± 43.7 shoots m^{-2} at 3.5 m to 45 ± 5.6 shoots m^{-2} at 11 m depth (ANOVA: $F_{3,16} = 31.6$, $p < 0.001$). The average shoot length (i.e. height of leaf canopy) varied significantly with depth and was

Table 1
Sediment sulfide pools found in the acid volatile (AVS) and chromium reducible sulfur pools (CRS) for 0–15 cm in mmol m^{-2} (mean ± SE, n = 3). The total reducible sulfur pool (TRS) is given by the sum of AVS and CRS (mmol m^{-2}). The δ^{34} signal is given for the AVS pool ($\delta^{34}S_{AVS}$, pooled samples, n = 3) and the CRS pool ($\delta^{34}S_{CRS}$, mean ± SE, n = 3). Depths: N = 3.5 m, N1 = 7 m, N2 = 9 m and N3 = 11 m.

	AVS (mmol m^{-2})		CRS (mmol m^{-2})		TRS (mmol m^{-2})	$\delta^{34}S_{AVS}$ (‰)	$\delta^{34}S_{CRS}$ (‰)	
N	29.3 ±	17.1	689.1 ±	171.6	718.4	−20.9	−23.2 ±	1.8
N1	12.2 ±	2.4	893.2 ±	37.9	905.4		−22.0 ±	0.9
N2	22.5 ±	8.8	973.8 ±	45.6	996.3	−21.1	−22.0 ±	0.9
N3	10.8 ±	3.6	719.8 ±	149.6	730.6	−19.3	−22.5 ±	0.9

Table 2
Plant characteristics divided into leaf (LE), roots (RO) and rhizomes (RH). Stable sulfur isotopes (δ^{34}S, ‰), sulfide intrusion ($F_{sulfide}$ %), total sulfur content (TS, %DW), stable carbon (δ^{13}C, ‰) and nitrogen isotope (δ^{15}N, ‰) and carbon (POC, %DW) and nitrogen content (PON, %DW. Mean ± SE (n = 3–5). Depths: N = 3.5 m, N1 = 7 m, N2 = 9 m and N3 = 11 m.

		δ^{34}S (‰)		Fsulfide (%)		TS (%DW)		δ^{13}C (‰)		δ^{15}N (‰)		POC (%DW)		PON (%DW)	
N	LE	15.42±	2.40	15.34±	5.66	0.30±	0.02	−8.04±	0.36	5.39±	0.69	36.08±	0.24	1.89±	0.05
	RO	9.38±	6.47	29.42±	15.09	0.36±	0.10								
	RH	16.18±	1.89	13.57±	4.38	0.26±	0.02								
N1	LE	16.11±	1.52	13.72±	3.53	0.30±	0.02	−8.19±	0.35	5.31±	0.80	36.12±	0.23	1.82±	0.03
	RO	11.56±	3.70	24.34±	8.61	0.33±	0.05								
	RH	16.41±	1.56	13.02±	3.65	0.27±	0.02								
N2	LE	16.83±	1.85	12.06±	4.35	0.30±	0.02	−8.48±	0.10	5.53±	0.95	35.64±	0.83	1.80±	0.05
	RO	12.94±	4.04	21.11±	9.39	0.32±	0.05								
	RH	17.00±	1.90	11.66±	4.41	0.27±	0.02								
N3	LE	16.60 ±	1.75	12.58±	4.09	0.30±	0.02	−8.57±	0.21	5.67±	1.04	34.75±	0.94	1.93±	0.24
	RO	12.16±	2.02	22.92±	8.16	0.37±	0.02								
	RH	16.98±	1.09	11.71±	4.40	0.27±	0.02								

longer at 3.5 and 9 m depth (47.7 ± 1.3 and 53.1 ± 4.1 cm, respectively) than at 11 m depth (33.1 ± 4.0 cm) (ANOVA: $F_{3,16} = 7.8$, $p = 0.002$, Fig. 2b). Leaf width varied between 0.41 ± 0.02 cm and 0.48 ± 0.02 cm and was unaffected by depth (ANOVA: $F_{3,16} = 1.93$, $p = 0.165$). The above-ground biomass (mean ± SE) declined with increasing depth from 225 ± 31.4 g DW m^{-2} at 3.5 m to 15.2 ± 3.3 g DW m^{-2} at 11 m depth and the below-ground biomass (rhizomes + roots) declined from 115.0 ± 16.3 g DW m^{-2} to d 10.1 ± 1.6 g DW m^{-2} at 11 m (ANOVA: $F_{3,16} = 44.8$ and 40.6, respectively, $p < 0.001$, Fig. 2c). The ratio of above- to belowground biomass showed no clear depth related pattern and was highest at 9 m depth (3.6 ± 0.7) and of similar magnitude (1.5 ± 0.2–2.0 ± 0.3) at 3.5, 7, and 11 m as indicated by Tukey-test (ANOVA: $F_{3,16} = 7.2$, $P = 0.003$).

The sampled meadows were associated with abundant ephemeral and epiphytic macroalgae (most on the older leaves (4–6) of the *Zostera* plants). The algae assemblages consisted of 28 different species (Table S4) of which the brown algae *Ectocarpus fasciculatus* and *Punctaria latifolia* and to a lesser extend the green alga *Acrosiphonia arcta* dominated at all depths. The algal biomass declined significantly with depth from a maximum of 320 ± 92.8 g DW m^{-2} at 3.5 m depth to a minimum of 7.6 ± 4.7 g DW m^{-2} at 11 m depth (ANOVA, $F_{3,16} = 22.8$, $p < 0.001$, Figs. 2d, 5a-c). The biomass of macroalgae relative to the aboveground biomass of *Zostera* tended to decrease (ANOVA, $F_{3,16} = 2.8$, $p = 0.070$) slightly from 1.38 ± 0.31 at 3.5 m depth to 0.97 ± 0.25, 0.66 ± 0.32 and 0.42 ± 0.17 at 7, 9 and 11 m depth, respectively.

3.3. Eelgrass production and leaf nutrients

Rhizome internode lengths demonstrated a distinct annual cycle and indicated that the harvested rhizomes were more than 2 years old (Fig. 3). The longest internodes (mean length ± SE) produced varied from 18.5 ± 5.1 mm at 9 m to 25.2 ± 1.8 mm at 11 m depth and were 4.4 to 6.1 times longer than the shortest internode produced during winter. The number of rhizome internodes between two consecutive winter minima indicated that shoots from the four depths produced on average 14.0 to 16.2 leaves $shoot^{-1}$ yr^{-1}. The annual leaf formation at the shallow depth was slightly lower than at 7 m but similar to rates at 9 and 11 m depth (ANOVA, $p = 0.0186$, Tukey test). The annual leaf turnover rates, varied from 3.2 at 3.5 m depth to 2.6 at 9 at 11 m depth. Leaf tissue carbon (C) and nitrogen (N) content (± SE) was similar among depths and ranged from 34.75 ± 0.94 to 36.08 ± 0.06% DW for carbon and from 1.80 ± 0.06 to 1.93 ± 0.25% DW for nitrogen.

3.4. Epifauna and fish

The macrofaunal assemblage was composed of 29 taxa and dominated by amphipod crustaceans and gastropod snails (Table S5a & b). Expressed as individuals per gram *Zostera* (DW) the snail *Lacuna* sp. and the amphipod *Dexamine spinosa* contributed on average 35% and 22%, respectively, to the total abundance (Fig. 4a). *Mytilus edulis*, and *Idotea* sp. 4% and the amphipod genera such as *Ischyrocerus anguipes* and *Aoridae* sp. contributed by 6% and 3%, respectively. Total abundance (±SE) per gram *Zostera* (DW) was lowest at the shallow (3.5 m) station (6.2 ± 3.2) and highest (48.3 ± 23.9) at the 11 m station, while the abundance at intermediate depths ranged from 18 to 40 ind g^{-1} *Zostera* (ANOVA: $F_{3,8} = 6.7$, $p < 0.05$, Fig. 4b, Table S5a). Expressed as number of individuals per m^2 seafloor, the epifaunal community contained more individuals at 7 m compared to 3.5 and 9 m, respectively (ANOVA: $F_{3,8} = 7.3$, $p < 0.05$, Fig. 4c, Table S5b). The average abundance ranged from 327 (3.5 m) to 4398 (7 m) ind·m^{-2}.

The fish community sampled at 6–12 m depth was dominated by thornback ray *(Raja clavata, n* = 9, 67–71 cm, Fig. 5b) cod *(Gadus morhua, n* = 7, 38–56 cm) and juvenile pollock (*Pollachius pollachius*, n = 9, 7–10 cm), and a few specimens of flatfish *(Platichtus flesus,* 35 cm, *Scopthalmus maximus*, 74 cm), and shorthorn sculpins (*Myxocephalus scorpius*, 15 cm). Stomach analysis of the thornback rays (the only fish species with stomach content) showed dominance of crustaceans: hermit crabs *Pagurus bernhardus* (5–15 mm), *Idotea baltica* (2–3 cm), mysids (1.2–1.5 cm) and amphipods *Dexamine spinosa* (3–6 mm). Further, Nereid polychaetes (4–6 cm), sand goby (*Pomatochistus minutus*) and green algae fragments *(Ulva* sp.) made up 20% of the stomach content.

3.5. The seagrass food web

The stable isotope biplot (Fig. 6, Table S6) displays 3–4-year-old cod and a large turbot as top predators with δ^{15}N signatures above 13.5‰, which is 1.5 units higher than the dominant intermediate predator thornback ray (Fig. 6). Between the intermediate predators and the herbivores with low δ^{15}N around 6‰ (amphipods, isopods, gastropods, and small polychaetes) are four decapods and nemerteans with δ^{15}N of 8–9‰ as well as the clam *Arctica islandica* showing an unexpected high δ^{15}N signal of about 9‰. The δ^{13}C of *Zostera* is −9.7‰, brown algae (−13 to −22‰), green algae (−18 to −21‰) and with red algae having the lowest δ^{13}C of −19 to −35‰.

4. Discussion

This holistic sampling of a presumably pristine *Zostera* ecosystem in NW Norway revealed some unexpected findings. Firstly, relatively high nutrient concentrations of NOx and NH_4 in the water and high biomass of epiphytes revealed an eutrophicated ecosystem. Secondly, the eelgrass vegetation supported a surprisingly low abundance of macrofaunal assemblage and finally the dominant intermediate predator was thornback rays *(Raja clavate)* of large size.

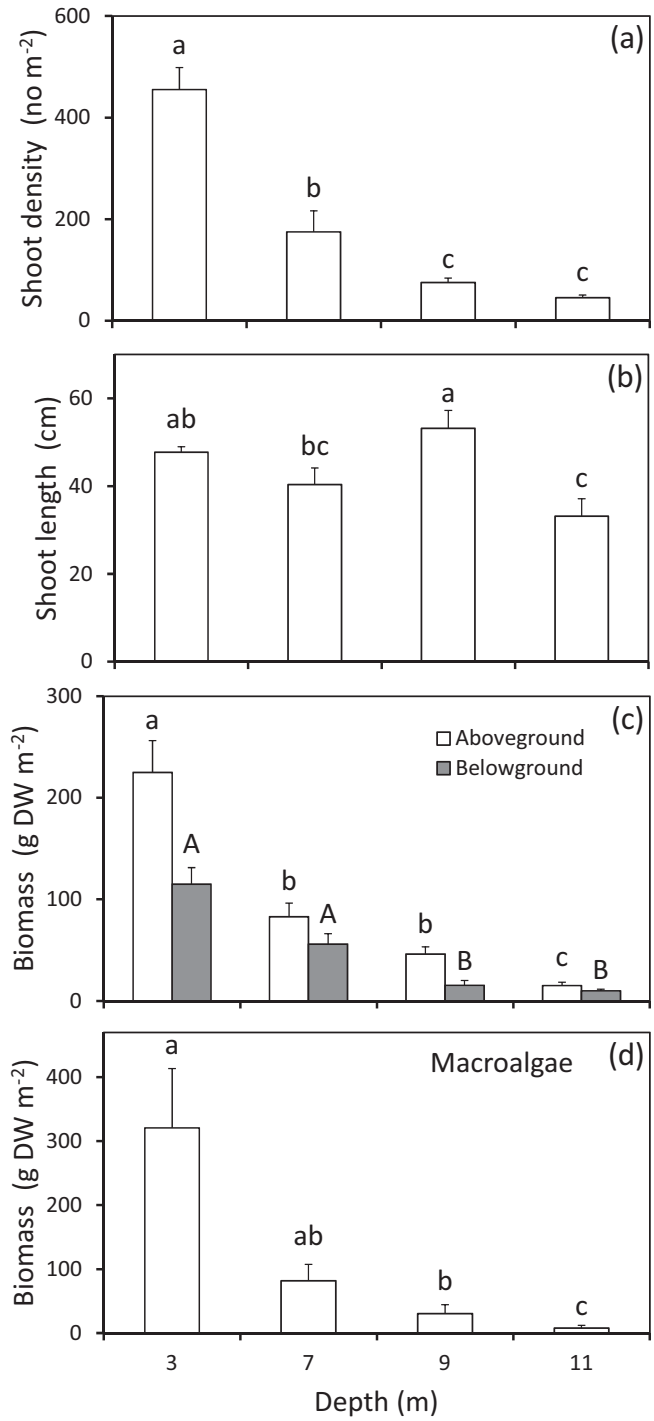

Fig. 2. Finnøya *Zostera marina* (a) shoot density, (b) shoot length (c) standing biomass and (d) associated epiphytic and ephemeral macroalgae at different depth (3.5, 7, 9, 11 m). Different letters indicate statistical differences between depths given by the ANOVA ($p < 0.05$) (mean ± SE, $n = 5$).

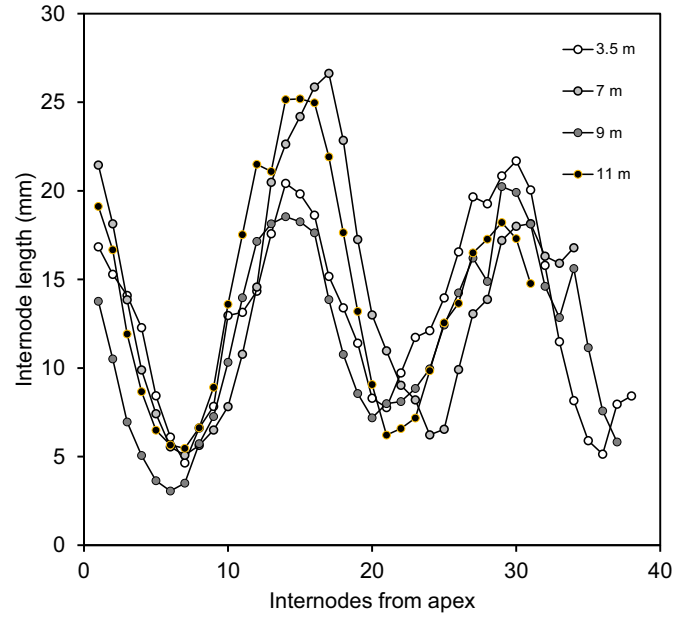

Fig. 3. Seasonal pattern in internode lengths (mean ± SE) along *Zostera marina* rhizomes from the youngest internode close to apex at time of sampling (June) to the oldest rhizome portions retrieved. Values are means of 5 to 8 replicate rhizome pieces.

4.1. Water and sediment biogeochemistry

The DIN (NOx and NH_4) concentrations around Finnøya are in the higher level of coastal waters around the world (Valiela et al., 2018) and compared to monitoring measurements in Norway (Helland and Bergslien, 2011). Despite being during the productive season (June) the summed water column NOx and NH_4, concentrations of 15–20 μM at Finnøya (Table S1) are relatively high and comparable to the highest winter concentration found in eutrophicated coastal waters around Fyn, Denmark, (Rask et al., 1999). These concentrations correspond to the water type levels classified as "very bad" for NOx and "bad" for NH_4 about 400 km south of Finnøya (Helland and Bergslien, 2011). According to Abdullah and Fredriksen (2014) the near bottom NO_3 concentrations around Finnøya at about 5 m depth in June 1996 and 1997 were 0.5 to 1.2 μM. In June 2012 the NOx concentrations (NO_3 by far dominating NOx) were 4.87 to 7.66 μM, (Table S1). Thus, NO_3 concentrations were several times higher after 15 years.

The physico-chemical parameters of the Finnøya *Zostera* sediment showed very little variation with depth which could be due to relatively strong wave exposure reaching equally down to 11 m depth. Hence, the sediment organic content was low (~0.5%DW), and the density and grain size were high, reflecting an exposed seagrass sediment similarly to other exposed Scandinavian *Zostera* meadows (Baden et al., 2010; Röhr et al., 2016, 2018). The low C:N of the sediment (8–9) and $\delta^{13}C$ close to the phytoplankton signal of both the sediment (−16 to −19‰) and trap material (−13 to −17‰) suggests that phytoplankton is the most important organic matter source in the sediments, whereas seagrass detritus is exported (Röhr et al., 2016, 2018). The sediment particulate sulfide pools and the iron contents were low in these relatively carbonate-rich sediments (~50% DW). Low pools of dissolved sulfides in the sediment pore water also indicates an exposed site with low sulfide exposure of *Zostera* (Holmer and Hasler-Sheetal, 2014). This is consistent with the observed low sulfide intrusion in *Zostera* roots, rhizomes and leaves independent of water depth similarly to *Zostera* in low organic sediments in the Baltic Sea (Holmer et al., 2009; Holmer and Hasler-Sheetal, 2014).

4.2. Zostera and macroalgae

The pattern of decreasing shoot density and biomass with increasing depth is commonly reported in seagrasses and is controlled by light attenuation in the water column (Dennison, 1987; Krause-Jensen et al., 2000; Olesen et al., 2017). These changes suggest a considerable reduction in the structural complexity from a relatively dense vegetation (450 shoots m^{-2}) at the shallow site to sparse vegetation (45 shoots m^{-2}) at the deepest edge (Fig. 5 a-c). Reductions in shoot density and leaf biomass with depth reduce the degree of leaf self-shading, thereby

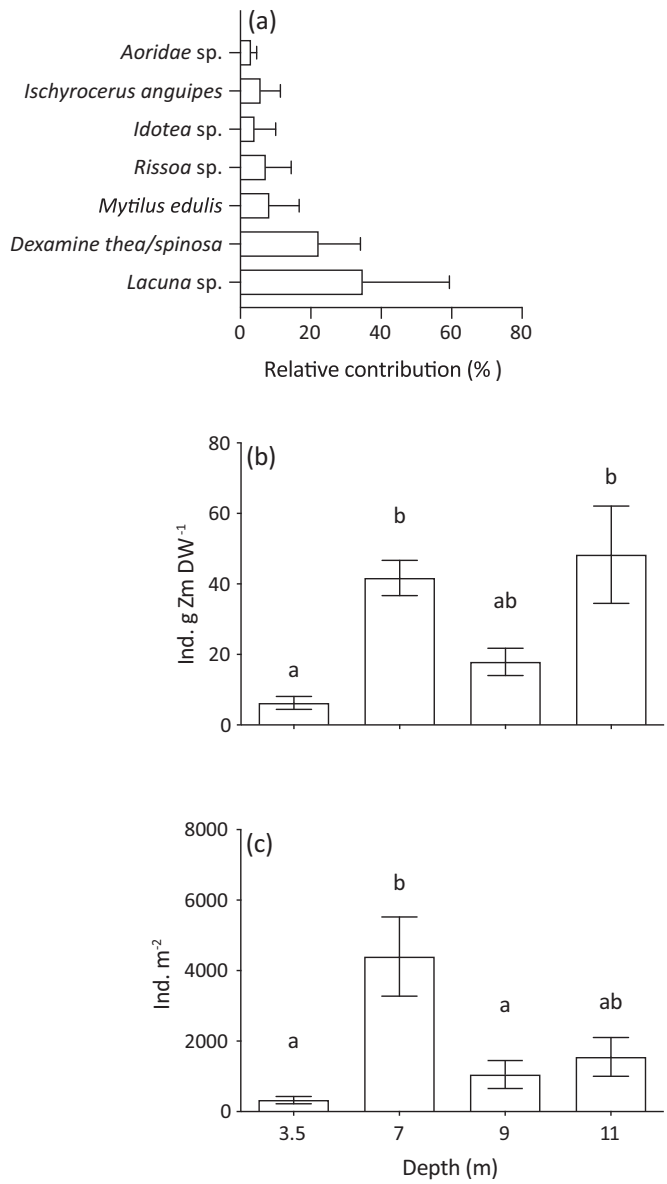

Fig. 4. Finnøya *Zostera marina* epifauna. (a) Relative contribution (mean + SE, $n = 12$) of different species or group of species. (b) abundance of epifauna per g *Zostera* leaves (DW) at different depth (3.5, 7, 9, 11 m), (mean ± SE, $n = 3$), and (c) abundance of epifauna per m^{-2} bottom at different depths (3.5, 7, 9, 11 m) (mean ± SE, n = 3).

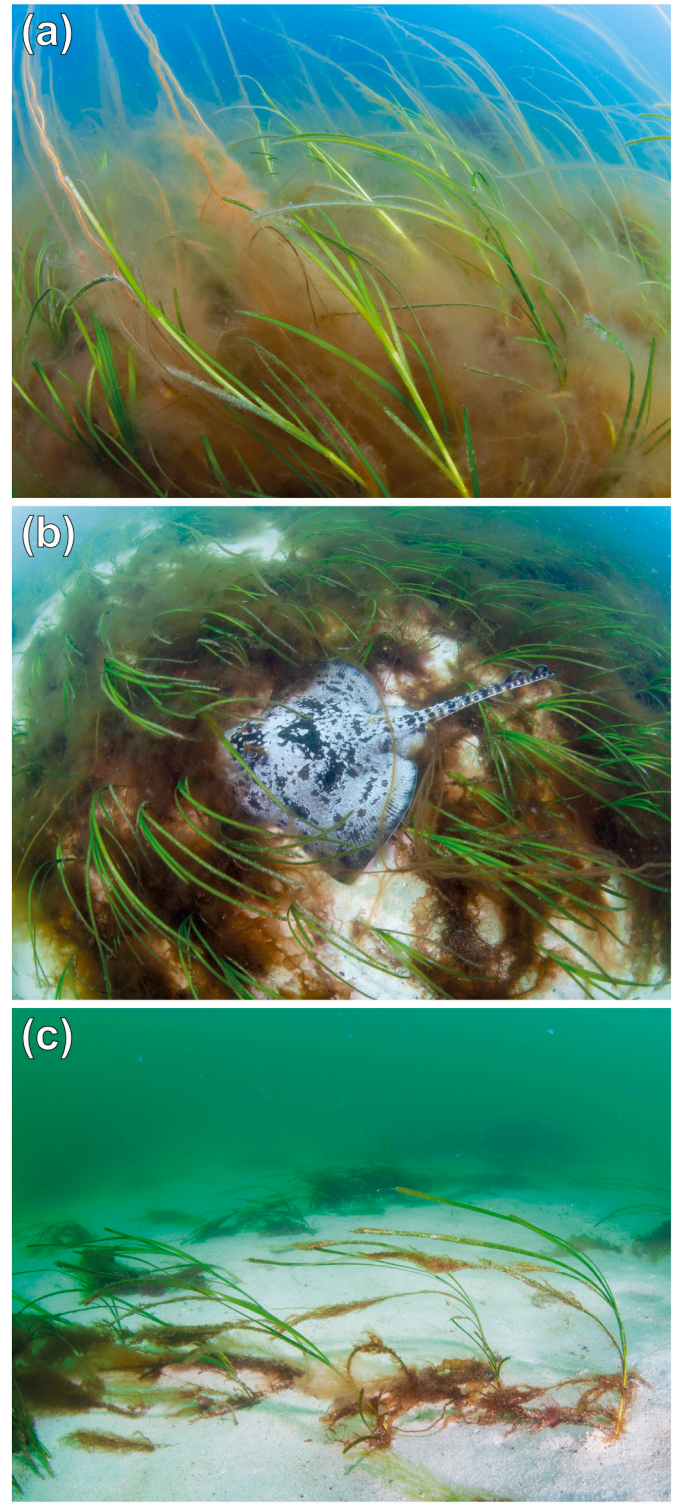

Fig. 5. UW pictures of Finnøya *Zostera marina* and ephemeral macroalgae at a) 4.7 m b) 9 m with a thornback ray (*Raja clavata*) and c) 11.7 m.

compensating for the lower light availability above the canopy at the lower region of the meadow (Ralph et al., 2007). This may explain the comparable shoot production (annual leaf formation per shoot) across depths observed in this and other studies of seagrass meadows. (Olesen et al., 2017). Likewise, the annual leaf turnover rates were nearly constant among depths, indicating that leaf tissue available for colonization by algae and fauna were of similar age among depths.

The maximum leaf biomass at the shallowest depth (225 g DW m^{-2}) was comparable to the overall average of maximum summer biomass (245–246 g DW m^{-2}) of shallow *Zostera* meadows across the distribution range (Olesen and Sand-Jensen, 1994; Clausen et al., 2014). However, the present investigation was carried out in mid-June and biomass is expected to increase until the seasonal biomass peak is reached, which typically occurs in August at this northern latitude (Clausen et al., 2014). The annual leaf formation per shoot (14–16 leaves $year^{-1}$) was within the low range observed in more southern regions (Olesen et al., 2015; Beca-Carretero et al., 2019) and is probably controlled by a combination of long dark winters and low temperatures, although the dense aggregations of macroalgae may also affect leaf formation negatively. Hence, faster annual leaf formation rates (23.5–24.2) have been recorded in upper sub-tidal *Zostera* population at Hopavågen Lagoon, 63°N by Duarte et al. (2002). Leaf tissue concentrations of nitrogen (1.8–1.9% DW) were like the median value (1.8% DW) recorded for seagrasses in a global comparison, which has been used to predict potential nutrient limitation (Gerloff and Krombholz, 1966; Duarte, 1990). However,

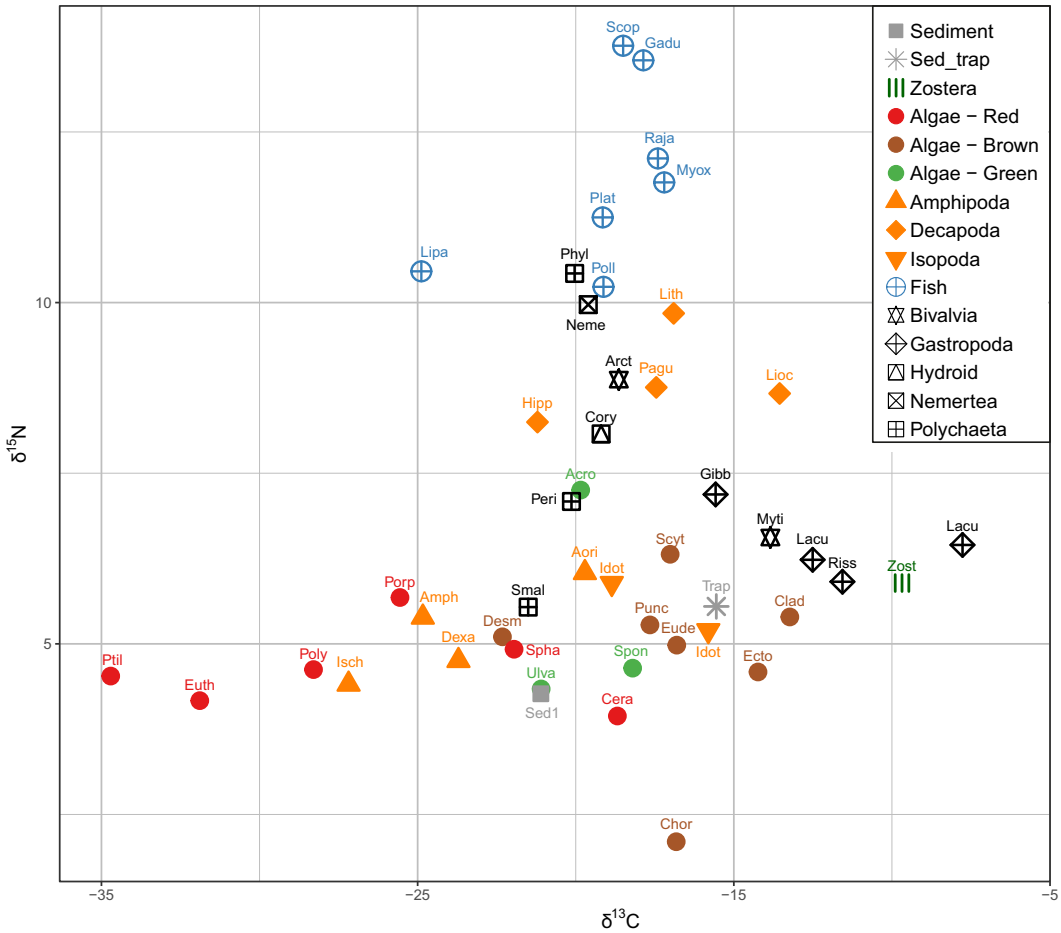

Fig. 6. Stable isotope bi-plot ($\delta^{13}C$, $\delta^{15}N$) of *Zostera marina* ecosystem. Abbreviations in the bi-plot refer to species and the full name is given in table S6.

determination of nitrogen dynamics in a Danish *Zostera* meadow showed negligible growth response to enrichment during summer months, although leaf nitrogen content was as low as 1% DW (Pedersen and Borum, 1993), suggesting that nutrients were not a major growth controlling factor in this study.

Stable C and N isotope values of *Zostera marina* were in the range found in the Northern hemisphere (Röhr et al., 2018). The $\delta^{15}N$ was lower than the global average indicating lower influence of land-derived antropogenic N probably due to the Finnøy location being closer to the open ocean with low $\delta^{15}N$ compared to the more coastal locations as also found in Röhr et al. (2018). Unexpectedly, the eelgrass community contained a high biomass of epiphytic and ephemeral algae (320 g DW m^{-2} at 3.5 m depth) reaching the same or higher biomass than the *Zostera*. In fact, this is the double biomass of macroalgae compared to sheltered and eutrophied Danish fjords (Rasmussen et al., 2013; Thormar et al., 2016) and approaching the biomasses recorded in eutrophicated Baltic Sea eelgrass meadows, i.e. 430 g DW m^{-2}; (Gustafsson and Boström, 2014). The high macrophyte biomass could be the result of high to moderate inorganic nitrogen concentrations observed in the water around the Finnøya island (See 4.1). Dense, long-term aggregations of epiphytes and ephemeral algae have often been linked to eutrophication-related effects such as reduced growth and increased mortality of seagrass shoots (Hauxwell et al., 2001; Holmer and Nielsen, 2007). The cover of ephemeral algae "per se" can be highly variable in time and space (Rasmussen et al., 2013). It is therefore difficult to evaluate the implications of these blooms which may drift away after rough weather. However, we obviously sampled during a calm period since the biomass of the ephemeral algae was high. As found by Olsen et al. (2011) in a moderately eutrophied location of Waqouit Bay at Cape Cod (USA) the ratio between the DW of macroalgae and *Zostera* may give an integrated status over a longer period. We found a ratio of 1.38 ± 0.31 at 3.5 m depth which in the Waquoit Bay *Zostera* indicated a high nitrogen load of 35 kg N ha^{-1} yr^{-1}.

The accumulation of algae does not, however, seem to negatively affect the biogeochemical conditions in the sediment having a very low organic content likely due to hydrodynamic exposure. Furthermore, the intrusion of sulfides was low indicating limited pressure from sediment derived sulfides on *Z. marina*. Thus, the seasonal dynamics of algae productivity and cover in the studied meadow as well as the export of organic matter (eelgrass leaves, attached epiphytes and macroalgae), which must be considerable, deserves further study.

4.3. Epifauna and fish

Dale et al. (2007) is one of the few studies that have explored the variation in *Zostera* associated fauna along a depth gradient to 10 m. They found no significant differences in infaunal community structure with depth. In this study, the epifauna was most abundant at intermediate depths (7 m) and was dominated by crustaceans (mainly *Dexamine spinosa*) at shallower depths and by molluscs (mainly *Lacuna* sp.) deeper down (Table S5a). These results are consistent with previous observations of epifauna from *Zostera* meadows along the SE coast of Norway (Skagerrak) and the Norwegian west coast (Fredriksen et al., 2010; Christie et al., 2014). However, Fredriksen et al. (2005) found higher number of species and other species of amphipods and gastropods most characteristic for *Zostera* at the Norwegian Skagerrak coast, while the dominating fauna species from this study resemble more dominant species found in kelp forests in the study area (Christie et al., 2003). In

contrast, Fredriksen et al. (2005) and Christie et al. (2009) found distinct fauna species composition in *Zostera* beds compared to different macroalgal beds. While *Zostera* beds and perennial macroalgal beds housed similar diversity and density of macrofauna further south (Fredriksen et al., 2005; Christie et al., 2009), the Finnøya *Zostera* bed housed much lower diversity and density than the nearby kelp forest. In general, the Norwegian epifauna tends to consist of larger individuals and more abundant and diverse amphipod and isopod communities compared to the depauperate epifaunal communities in *Zostera* in the Swedish Skagerrak (Jephson et al., 2008; Baden et al., 2012). However, in this study the total faunal abundance was 100 times lower than reported in Christie et al. (2009, 2014) where densities between 50,000 and 200,000 individuals m^{-2} were common. This could be due to seasonal effects since the sampling at Finnøya was carried out in mid-June, which is still early summer at this latitude, whereas the sampling in Christie et al. (2009, 2014) was conducted some months later. Such a seasonal effect, which mainly derives from the difference between pre- and post-recruitment, was found by Baden (1990) in Swedish west coast *Zostera* fauna.

The abundance of epifauna in Scandinavian *Zostera* meadows is found to be independent of plant biomass (Baden, 1990; Christie et al., 2014; Riera et al., 2020) above a low threshold biomass as described in the Baltic Sea (Möller et al., 2014). In this study, when standardizing the epifaunal abundance to plant biomass, the highest values were found at intermediate (7 m) and lower depths (11 m) (Fig. 4b). *Zostera* biomass declined with depth (Fig. 2c) but since seagrass is known to provide refuge for fauna (Heck et al., 2003; Thormar et al., 2016), it is possible that this facilitative effect was accentuated with depth in such that fauna accumulated around the available structure deeper down, whereas at shallower depths where more structure was available, the fauna was more evenly spread out. Also, when standardizing to m^2, epifaunal abundance was highest at intermediate depths (7 m, Fig. 4c). Here as well as at 11 m, the total abundance was dominated by the small gastropod *Lacuna* sp. (> 50% dominance, Fig. 4 a, Table S5). Such small gastropods are known to drift by water currents in search of suitable microhabitats and can thus accumulate in for example, macroalgal beds and seagrass meadows (Martell and Diefenbach, 1993; Fredriksen et al., 2005). Our study may have coincided with a stochastic accumulation of snails at certain depths, which further resulted in elevated total abundances of epifauna. An even more plausible explanation to low diversity and density of fauna in the Finnøya *Zostera* bed is the occurrence of high cover of ephemeral macroalgae. Pihl et al. (1995), and Christie et al. (2009) reported lower diversity and density of invertebrates and fish associated with increasing amount of ephemeral macroalgae on seagrass than on perennial macroalgae. In the Finnøya locality the DW ratio of epiphytic and unattached ephemeral macroalgae to *Zostera* being maximum 1.38 at 3.5 m (Fig. 2 c & d) was associated with a minimum of faunal abundance (Fig. 4 b & c) and similar to findings in a highly eutrophicated. Swedish locality for comparable depths (Pihl et al., 1995).

The stomach analysis of the thornback ray revealed that they favour amphipod and isopod mesoherbivores of 2–3 cm and nereid polychaetes of 4–6 cm as prey items, suggesting some top-down control of the faunal assemblage. Despite the relatively large specimens investigated of about 70 cm total length the food choice consisted of small species compared to thornback rays of the Adriatic (max length 55 cm) preferring crabs and shrimps (Santic et al., 2012). The stomach content may represent the most abundant species available rather than an active choice of food. Unfortunately, the stomachs of all other fish species were empty which could be an effect of continued digestion of fast digested prey e.g., fish during the night after being caught in the survey net.

The fish community in the *Zostera* bed differed to the fish fauna found in the kelp forest nearby (Norderhaug et al., 2005). In the kelp forests the rays were hardly caught, while different species of labrids (wrasses) were numerous, as well as three species belonging to the cod family.

4.4. Aquaculture and fishery

The unexpected high occurrence of opportunistic ephemeral macroalgae in the Finnøya *Zostera* resembles the conditions found in *Zostera* along the coast of the Kattegat and Skagerrak. Here, eutrophication caused by a surplus of nutrients and lack of fish top predators promotes overgrowth of ephemeral algae able to suffocate *Zostera* (Baden et al., 2012; Östman et al., 2016). Finnøya belongs to the Norwegian region Møre-Romsdal (Fig. 1) producing 13% of farmed salmonids in Norway (national production≈1 billion tonnes). From aquaculture in Møre-Romsdal an annual release of total nitrogen and phosphorous amounts to 6224 t and 1076 t in 2012 (Guerrero and Sample, 2021). These nutrient amounts are equivalent to 1.25 million population equivalents (pe) raw sewage of nitrogen (5 kg tot-N per person per year) and 0.65 million pe raw sewage of phosphorous (0.6 kg tot-P per person and year) being 60% and 83% (2012) of the total anthropogenic nitrogen and phosphorous, respectively. The nutrient release has increased at a constant rate since the introduction of aquaculture in the mid 1980s without any other sources changed (Guerrero and Sample, 2021). Locally, about 10 aquaculture units are within 20 km from Finnøya. Close to Finnøya the nitrate concentrations of the sea water have more than tripled between 1995 and 2012 (See 4.1 for details). In the same period the nitrogen and phosphorous release from aquaculture in the Møre-Romsdal region have tripled and doubled, respectively (Guerrero and Sample, 2021).

Coastal cod and other gadoids potentially exert top-down regulation on coastal ecosystem. Although gadoids are reported numerous in the kelp forest (Norderhaug et al., 2005) the overall status of the standing stock of the dominant coastal cod north of 62°N is a significant decline of spawning stock biomass (SSB) with about 50% since the 1980s and 66% since a peak in the 1990s (ICES, 2014, 2018). This contrasts with the SSB of both demersal and pelagic fish species in the more off-shore NE Atlantic that have shown an increase of about 40%. We found abundant thornback rays as intermediate predators in the Finnøya *Zostera* bed and they seem to be a natural part of the coastal and not least the *Zostera* ecosystem. This species is registered as by-catch that show great variations between years but with no temporal trend.

From the above data on nutrient release and fish catch we find it likely that the relatively large biomass of ephemeral macroalgae, normally indicating eutrophication of the seagrass area, derives from the steadily increasing nutrient release and the relatively high nutrient concentrations found during our investigation. The decline in coastal cod SSB may have affected the top-down regulation of the *Zostera* ecosystem and exaggerated the eutrophication as also found in Baden et al. (2012) in *Zostera* on the Swedish west coast. However, Jiménez-Ramos et al. (2019) found empirical evidence that the top-down control of filamentous algae from herbivores was minimized with sparse *Zostera* density and high exposure. Since the Finnøya *Zostera* is both a sparse and high current velocity meadow it is likely that the bottom-up effect (nutrients) is a more determinant factor than the top-down effect.

4.5. The Finnøya Zostera ecosystem interpreted from stable isotopes

All macroalgae and most of the herbivores have about the same $\delta^{15}N$ signal around 4–6‰. The $\delta^{13}C$ signal, however, was between −13 to −22 for green and brown algae whereas the signal for red algae was much lower −19 to −32. This difference among algal groups is also reported from the Norwegian kelp forest (Fredriksen, 2003) but not from a Danish *Zostera* meadow where red algae had a max $\delta^{13}C$ signal of −20 (Thormar et al., 2016). The low isotopic signal may be related to their predominantly use of CO_2 rather and HCO_3^- in photosynthesis of some species of red algae (Maberly et al., 1992; Valiela et al., 2018).

Gastropods are grazers of epiphytes and *Zostera* itself which explains their $\delta^{13}C$ value close to *Zostera* $\delta^{13}C$. The amphipods, however, are strictly macroalgal eaters with same $\delta^{13}C$ as a mean of all the macroalgae, even red algae. Decapods are mainly invectivores and they have a

$\delta^{15}N$ signal above the herbivore /detrivores and lower than the intermediate fish and piscivores. The clam is a filter feeder, and the high $\delta^{15}N$ signal may indicate that it filters not only phytoplankton, but even zooplankton. This is all consistent with the findings of Jephson et al. (2008) and Thormar et al. (2016) from *Zostera* in S Sweden and Denmark.

The finding of a small number of predatory fish and nereid polychaetes in ray stomachs explains why the thornback ray has a higher $\delta^{13}C$ signal (14‰) than other intermediate predators (the 0-group pollocks, some predatory polychaetes and crabs) of around $\delta^{15}N$ of 10‰ but not at the same high level of ^{15}N accumulation as the true piscivores cod with $\delta^{15}N$ of 18‰. (Fig. 6, Table S6).

4.6. Conclusions

Given the remote location close to the polar circle this deep *Zostera* bed was expected to reflect pristine conditions. However, our study showed the biomass of ephemeral macroalgae was equal to or even exceeded the biomass of the seagrass at all depths suggesting strong effects of eutrophication. We postulate that the high abundance of macroalgae caused poorer habitat conditions, and that the algal growth was supported by the general high discharges from salmon aquacultures in the region and even more locally, potentially exaggerated by a 50% decline in the coastal cod. Coastal cod are dominant fish predator in shallow coastal areas. A lack of predators may affect the top-down regulation, but likely to a lesser degree in sparse and exposed meadows like the Finnøya *Zostera*. Relationships between surplus of nutrients from fish farms, overfishing of coastal cod and reduced ecosystem services of *Zostera* should be documented in more detail for better management actions.

Author contributions and financial support

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2022.113497.

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