# Severe shifts of *Zostera marina* epifauna: Comparative study between 1997 and 2018 on the Swedish Skagerrak coast

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## ARTICLE INFO

## ABSTRACT

The interaction between bottom-up and top-down processes in coastal ecosystems has been scarcely studied so far. Temporal changes in trophic interactions of *Zostera marina* along the Swedish west coast are relatively well studied, with the exception of epifaunal communities. Epifauna was used as a model study to explore resource (bottom-up) or predator (top-down) regulated in a vegetated ecosystem. We conducted a 21-year comparative study (1997 and 2018) using epifauna of 19 *Zostera marina* meadows along the Swedish Skagerrak coast. Large changes were observed in the composition of small (0.2–1 mm) and large (> 1 mm) epifauna. In the small-sized epifauna, the nematode *Southernia zosterae* and harpacticoids showed an increase of 90% and a decrease of 50% of their abundances, respectively. In the large-sized epifauna, the polychaete *Platynereis dumerilii* and chironomid larvae were absent in 1997 but thrived in 2018 (> 2000 ind. m$^{-2}$). Mesoherbivores (Idoteids and gammarids) were locally very abundant in 1997 but disappeared in 2018. An 83% decline of mytilids settling in *Zostera marina* leaves was observed. Our results showed that epifauna is predominantly top-down regulated. An integrative framework of the study area is outlined to shed light on the causes and consequences of the environmental shifts reported in *Zostera* meadows from the northern Skagerrak area throughout the last three decades.

## 1. Introduction

Coastal habitats experience extensive impacts from human activities (Halpern et al., 2015) and steady increase of stressors in the last decades (Butchart et al., 2011). These pressures have been extensively reported in sensitive ecosystems, e.g. coral reefs and seagrass meadows (Waycott et al., 2009). Previous studies have shown a declining trend of coral and seagrass cover along the coastlines of our planet, with several main responsible disturbances that are directly or indirectly caused by humans (Lotze et al., 2006, Orth et al., 2006, Halpern et al., 2019). Overfishing and nutrient pollution are expected to increase by human activities and climate factors with unknown ecological consequences (Lotze et al., 2006, Orth et al., 2006, Halpern et al., 2019).

Eutrophication - i.e. "increase in the rate of supply of organic matter to an ecosystem" (Nixon, 1995) - is a key environmental driver of seagrass cover loss (Orth et al., 2006). A combination of increased nutrients (bottom-up regulation) and the cascading trophic effects resulting from loss of top predators (top-down regulation) may enhance eutrophication through increased phytoplankton and fast-growing macroalgae production, underpinning a decrease of light and water transparency that suffocate the seagrass leaves (Hauxwell et al., 2001; Burkholder et al., 2007; Moksnes et al., 2008; Han and Liu, 2014). Hence, in areas subject to chronic eutrophication or subject to very sheltered conditions, e.g. fjords, a high increase of fast-growing filamentous algae favoured by the decrease of water quality is expected (Brodersen et al., 2015). In recent decades, filamentous algae have

increased dramatically on sublittoral sheltered areas, e.g. the Baltic Sea (Vahteri et al., 2000). It is known that algal mats constitute an important food source for grazers living on eelgrass leaves (Norkko et al., 2000; Jephson et al., 2008; Andersson et al., 2009). Epiphytic macroalgae may be responsible for more than 50% of primary productivity of seagrass (Borowitzka et al., 2006); and several species of grazers show preference for epiphytic algae over seagrass leaves (Jernakoff et al., 1996). Consequently, the associated epiphytic communities in seagrass and their function in the system should be analysed (Lavery et al., 2007), as well as the epifauna associated to epiphytes and eelgrass.

In the Skagerrak and northern Kattegat along the Swedish west coast, the filamentous algae were present in high amounts in 1997 but even more in the 2010s (BVVF, 2012). A number of contributions from field investigations as well as empirical field cage experiments have previously recorded the decline of *Z. marina* aerial extension (Baden et al., 2003; Moksnes et al., 2018) as well as profound changes in abundance and biomass of the associate fauna of *Z. marina* in the northern Kattegat and Skagerrak area (Baden et al., 2012; Boström et al., 2014; Moksnes et al., 2008). These studies show and test possible environmental drivers to the ecological changes occurring in the study area during the last decades. However, no comparative temporal and spatial study exists on the entire invertebrate epifauna communities, an important puzzle piece of the *Z. marina* ecosystem (Baden et al., 2012). Thus, there is no quantitative information available on the possible shifts occurring in the epifaunal community during the last two decades from this area.

In this study, we conduct a comparative study on the *Z. marina* and associated epifauna assemblages collected in 1997 and 2018 along the entire Swedish Skagerrak coast to identify any trend and/or shift on the structure of epifaunal community. Two fractions of epifauna were considered: small (0.2–1 mm) and large (> 1 mm), both occupy the lowest positions in the trophic chain (Baden and Pihl, 1984; Baden, 1990; Jephson et al., 2008). Field cage experiments carried out in the same area as the present investigation, revealed that the epifauna group would mainly increase in biomass (Moksnes et al., 2008; Baden et al., 2010). However, since experiments are simplifications of the ecosystem dynamics, Moksnes et al. (2008) also discussed a different possible scenario where shrimps and crabs may play a more important role as predators of the small epifauna and decrease the biomass of this group. Based on the results from the above experiments and since the investigated epifauna belongs to the two lowest trophic levels being mainly herbi- and detritivores, it is reasonable to hypothesize that the epifauna is primarily resource (bottom-up) than predator (top-down) regulated. Using the data from two extensive field surveys in 1997 and 2018, we thus predict ($H_0$) that this epifauna fraction has increased in biodiversity and abundance due to an increasing amount of organic production in the area.

## 2. Material and methods

### 2.1. Study area

Nineteen subtidal *Zostera marina* meadows were sampled along the Swedish Skagerrak coast in July 1997 (6th–29th) and July 2018 (8th–23th) (Fig. 1, Table 1), when the abundance and biomass of *Z. marina* and epiphytic fauna peaked (Baden and Pihl, 1984; Baden, 1990). These 19 meadows are distributed over a 200 km range and therefore exposed to different environmental conditions: from wave sheltered to wave exposed bays (effective fetch 0.17–13.90) and salinities between 10 and 31 PSU. The Swedish west coast is polyhaline since Baltic water mixes with north Atlantic water and the salinity depends on the prevailing wind and air pressure. For epifaunal comparative studies, 14 stations were included in the analysis since 5 of the 19 *Z. marina* meadows present in 1997 had disappeared in the 2018 survey, namely Valön, Åbyfjorden, Kovikshamn, Maleviken and Vendelsöfjorden (Fig. 1).

### 2.2. Field sampling

*Zostera marina* meadows were sampled between 1.5 and 3 m depth, which is the main depth distribution of eelgrass in the study area (Baden et al., 2003). Although *Z. marina* was the only reported seagrass, all sampled stations had other macroalgae species present within meadow such as, *Fucus vesiculosus*, *F. serratus*, *Chorda filum*, *Dictyota* sp., *Ascophyllum nodosum*, *Ruppia* sp., *Furcellaria* sp., *Sargassum* sp., *Ulva* sp., and *Spermatochnus paradoxus*. Water temperature did not show consistent variations between both sampling years (1997 and 2018) and ranged from 18 to 22 °C among stations. July was chosen as a sampling period since previous studies on the seasonal variation in epifauna abundance showed that in July the epifauna is represented by adult amphipods (before settling of numerous juveniles) and is right in the middle of *Mytilus* spp. settlement. The period between June and August constitutes the settlement peak of *Mytilus* spp. spat after which they move to other habitats or are preyed (Baden, 1990).

From both sampling years six randomly selected samples of eelgrass with associated fouling (detritus, epiphytes and fauna) per location were collected using a 200 μm mesh size plankton net on a frame enclosing an area of 35 × 35 cm (0.123 m$^2$). Each sample was spaced at least 5 m apart and was collected by snorkelling. Coverage of eelgrass and macroalgae was estimated in the field placing a 50 × 50 cm frame in the meadow, at least 5 m apart, where the coverage was classified as the percentage area cover within the quadrate.

### 2.3. Sample processing and analysis

In the laboratory, *Z. marina* leaves were washed with freshwater and detritus removed, epiphytes and fauna were sieved through a 1 mm sieve ("large epifauna") and retained on a 200 μm sieve ("small epifauna"). Both samples were stored in 70% ethanol and the small epifauna stained with Bengal Rose until sorting and morphological identification to the lowest taxonomic level possible. In each of the six replicates per location all epifauna > 1 mm was sorted macroscopically and identified under stereomicroscope if needed. Since the small epifauna fraction often are in abundance of thousands the abundance is based on means from three sub-samples, following Baden (1990). Identification of small epifaunal species was carried out using a stereomicroscope and a binocular microscope. Species were grouped into "morphospecies" (taxonomic identification of species based on morphological differences from related species) for comparative analysis between both field surveys (1997 and 2018), using the 14 meadows where *Z. marina* was reported.

Species richness and abundance of individuals per m$^2$ were calculated for each sampling station of *Z. marina* meadow for both study years ($n = 19$ in 1997 and $n = 14$ in 2018) to characterize the α diversity of epifauna and its spatial and temporal variations. Biomass (dry weight g m$^{-2}$) of the cleaned and dried *Z. marina* leaves as well as associated macroalgae were also estimated. Comparisons between the mean of cover percentages of 1997 and 2018 were carried out using the 14 meadows where *Z. marina* was reported in both field surveys. This comparative analysis was carried out using Student's *t*-test.

To assess patterns of epifaunal assemblage structure among the 14 sampled bays sampled in 1997 and 2018, nm-MDS (nonmetric multidimensional scaling) procedure was conducted based on Bray-Curtis similarity index on square-rooted transformed data.

A distance-based redundancy analysis (db-RDA, Legendre and Anderson, 1999) tested whether variation in any of the measured variables, i.e. eelgrass biomass, eelgrass coverage and accompanying algae coverage, significantly contributed to explain variation in epifaunal assemblage structure in the 19 eelgrass meadows. For multivariate multiple regression, a distance-based linear model routine (DISTLM) (Anderson, 2001) was used to assess the contribution of environmental factors on the epifauna abundance and composition using Akaike Information Criterion routine (AIC) as the selection criterion
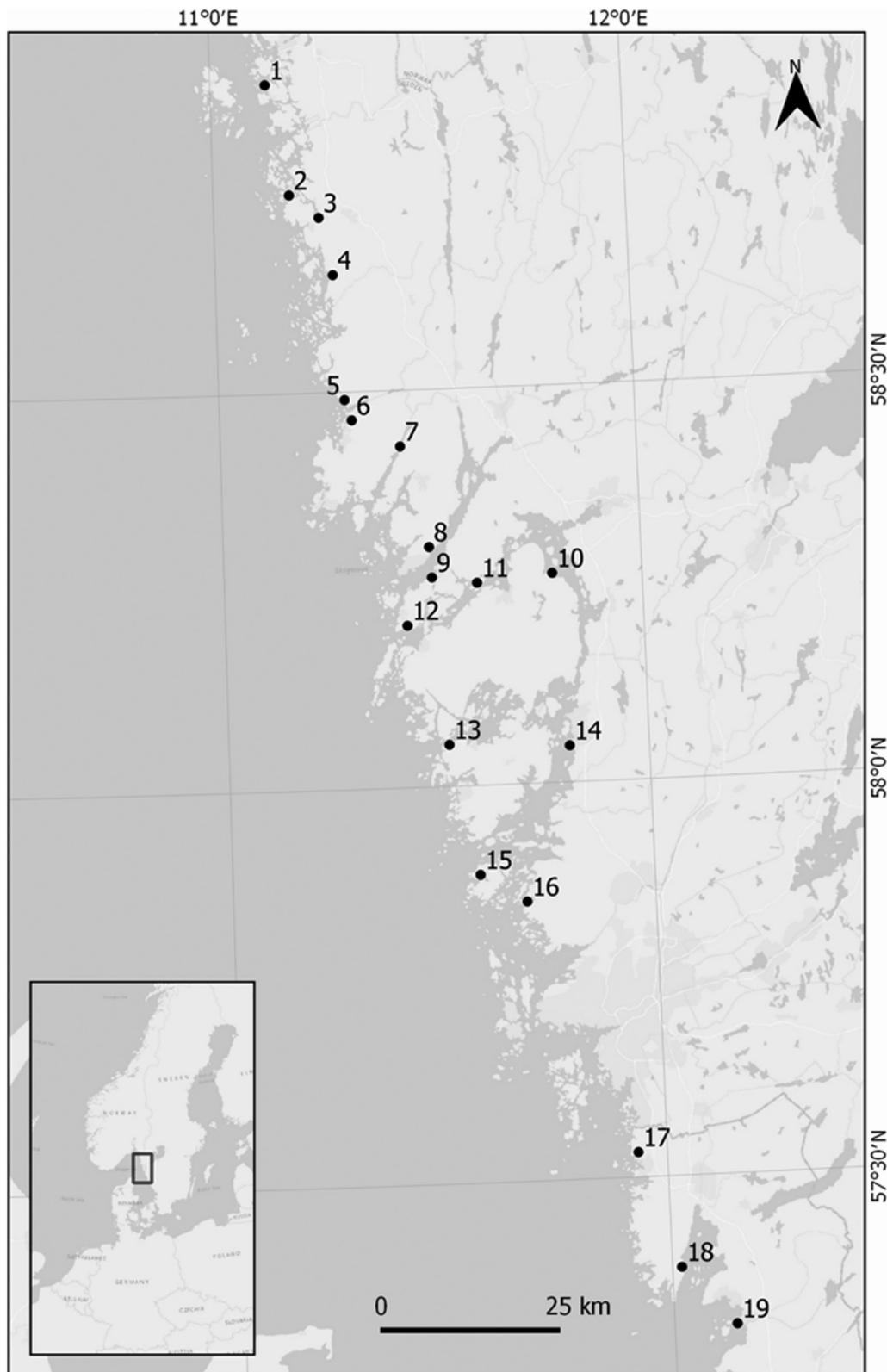
**Fig. 1.** Study areas where *Zostera marina* meadows were sampled in 1997 and 2018 along the Swedish west coast: 1-N. Lindholmen 2-Kvarnekilen; 3-S. Stridsfjorden (Sannäsfjorden); 4–Kämpersvik; 5–Valön; 6–Bottnefjord; 7–Åbyfjord; 8–Finsbo; 9–Lindholmen; 10–Slussen; 11–Hjältön; 12–Skallhavet; 13–Björnholmen; 14–Kåkenäs; 15–Marstrand; 16–Kovikshamn; 17–Maleviken; 18–Gottskärsviken; 19–Vendelsöfjorden.

([Legendre and Anderson, 1999](#)) to retain variables with good explanatory power, as a result of collinearity among variables. This analysis tested the significance of these relationships by fitting a linear model based on Bray-Curtis dissimilarities from square-root transformed abundance data.

Differences in epifaunal abundances from the 14 sampled bays between the studied years (1997 and 2018) were tested using one-way ANOVA after verifying normality and homoscedasticity of variances

**Table 1**
The mean abundance (ind m$^{-2}$) of large (> 1 mm body size) and small (0.2-1 mm) epifauna species, and mean dry weight per m$^2$ of *Z. marina* and respective standard errors (mean ± SE), per each of the 19 stations sampled along the Swedish west coast in July of 1997 and July 2018.

| Site N° | Site name | Latitude N | Longitude E | *Zostera marina* (g m$^{-2}$) | | Large epifauna (ind m$^{-2}$) | | Small epifauna (ind m$^{-2}$) | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | 1997 | 2018 | 1997 | 2018 | 1997 | 2018 |
| 1 | N. Lindholmen | 58°53′20.0 | 11°8′2.2 | 127 ± 23 | 235 ± 39 | 29 ± 14 | 859 ± 317 | 95,189 ± 28,286 | 35,975 ± 8851 |
| 2 | Kvarnekilen | 58°44′58.2 | 11°11′3.9 | 159 ± 29 | 201 ± 21 | 27 ± 10 | 4226 ± 1534 | 42,875 ± 12,797 | 73,023 ± 11,724 |
| 3 | S. Stridsfjorden | 58°43′12.4 | 11°15′16.1 | 144 ± 22 | 61 ± 15 | 143 ± 37 | 7396 ± 1777 | 19,950 ± 4494 | 134,237 ± 31,784 |
| 4 | Kämpersvik | 58°38′51.6 | 11°17′2.4 | 83 ± 12 | 113 ± 24 | 444 ± 51 | 270 ± 77 | 26,162 ± 5623 | 12,220 ± 1961 |
| 5 | Valön | 58°29′24.4 | 11°18′7.9 | 157 ± 22 | 0 | 263 ± 95 | 0 | 56,359 ± 8257 | 0 |
| 6 | Bottnefjord | 58°27′51.3 | 11°19′4.7 | 157 ± 15 | 226 ± 38 | 48 ± 40 | 1252 ± 359 | 27,251 ± 6324 | 38,504 ± 17,179 |
| 7 | Åbyfjord | 58°25′45.9 | 11°25′55.1 | 215 ± 11 | 0 | 10 ± 3 | 0 | 54,636 ± 6489 | 0 |
| 8 | Finsbo | 58°18′6.2 | 11°29′33.2 | 160 ± 22 | 286 ± 44 | 65 ± 29 | 971 ± 172 | 77,983 ± 13,289 | 51,179 ± 5663 |
| 9 | Lindholmen | 58°15′46.5 | 11°29′48.7 | 143 ± 13 | 205 ± 24 | 16 ± 4 | 36,029 ± 10,543 | 229,100 ± 40,042 | 80,027 ± 12,339 |
| 10 | Slussen | 58°15′45.9 | 11°47′5.6 | 212 ± 38 | 84 ± 18 | 49 ± 8 | 939 ± 347 | 44,432 ± 22,473 | 24,866 ± 3736 |
| 11 | Hjältön | 58°15′16.6 | 11°36′15.5 | 273 ± 49 | 21 ± 4 | 95 ± 19 | 885 ± 170 | 9101 ± 1834 | 30,630 ± 4360 |
| 12 | Skallhavet | 58°12′13.8 | 11°26′3.7 | 140 ± 15 | 31 ± 13 | 24 ± 5 | 3429 ± 1826 | 247,891 ± 53,235 | 72,784 ± 17,674 |
| 13 | Björnholmen | 58°3′8.2 | 11°31′26.3 | 209 ± 82 | 160 ± 33 | 27 ± 7 | 10,275 ± 6248 | 79,667 ± 15,598 | 89,056 ± 36,536 |
| 14 | Kåkenäs | 58°2′44.6 | 11°48′35.9 | 218 ± 23 | 85 ± 22 | 16 ± 5 | 268 ± 86 | 6326 ± 775 | 14,917 ± 2882 |
| 15 | Marstrand | 57°53′14.9 | 11°35′10.0 | 166 ± 50 | 94 ± 25 | 11 ± 3 | 22,091 ± 7583 | 37,558 ± 5158 | 116,319 ± 19,595 |
| 16 | Kovikshamn | 57°51′5.8 | 11°41′40.6 | 88 ± 14 | 0 | 31 ± 9 | 0 | 229,100 ± 40,042 | 0 |
| 17 | Maleviken | 57°31′52.0 | 11°55′53.4 | 97 ± 12 | 0 | 18 ± 7 | 0 | 21,459 ± 3981 | 0 |
| 18 | Gottskärsviken | 57°23′4.8 | 12°1′18.4 | 123 ± 11 | 77 ± 23 | 11 ± 4 | 3576 ± 1443 | 48,665 ± 9830 | 41,228 ± 9231 |
| 19 | Vendelsöfjorden | 57°18′38.1 | 12°8′43.4 | 175 ± 24 | 0 | 4 ± 3 | 0 | 6326 ± 775 | 0 |
| Total | | | | 160 ± 8 | 99 ± 10 | 70 ± 12 | 4781 ± 1108 | 63,408 ± 7255 | 42,896 ± 4822 |

using Kolmogorov-Smirnov and Levene's tests, respectively. Log (x + 1) transformation was carried out to fulfil ANOVA assumptions whenever necessary, and if not fulfilled the non-parametric Mann-Whitney test was used. The epifauna composition was tested by means of a permutational MANOVA (PERMANOVA) (Anderson et al., 2006), which allowed us to test the null hypotheses of no difference among the epifaunal communities through space and time. PERMANOVA allows meaningful analysis of variables with overdispersed or non-normal behaviour, i.e. zero-inflated data when comparing data from multiple species at the same time (Anderson, 2014). The factors considered were 'Meadows' (fixed) and 'Year' (fixed). All multivariate procedures were carried out via the PRIMER v6 (Clarke and Gorley, 2006) and PERM-ANOVA+ (Anderson et al., 2008) statistical package.

## 3. Results

### 3.1. Biomass and coverage of Zostera marina and epiphytic algae

Between 1997 and 2018 *Z. marina* was lost in 5 of 19 locations. The biomass of remaining *Z. marina* meadows showed no significant changes and ranged from 67 to 273 (mean: 160.3 ± 13.9 g DW m$^{-2}$) in 1997 and from 21 to 286 g (mean: 134.2 ± 22.3 g DW m$^{-2}$) in 2018 (Table 1). However, we found a spatial difference in the *Z. marina* biomass between the sampling years. A significant decrease of biomass was found in the southern meadows (1997: 170.1 ± 18.7 ($n = 10$); 2018: 78.89 ± 17.3 ($n = 7$)) (*t*-test, F = 7.89, p = 0.038). In the Northern meadows (sites n° 1–9) an increase of biomass from 149.4 ± 11.6 (1997) to 189.6 ± 29.1 g DW m$^{-2}$ (2018) was observed, though not significant (F = 3.45, p = 0.057). Notably, the meadows that had disappeared between 1997 and 2018 showed no signs of worse condition in *Z. marina* biomass or epifaunal abundance in 1997 (Table 1). The mean coverage of *Z. marina* showed a decrease throughout the study period, from 60% cover in 1997 ($n = 19$) to 48% in 2018 ($n = 14$) (*t*-test, F = 15.737, p < 0.001, Fig. 2). Cover of filamentous algae showed the opposite pattern, with a significant increase (*t*-test, F = 19.291, p < 0.001) in 2018 (17.7%) compared to 1997 (5.7%) (Fig. 2). The remaining recorded algae were scarce (< 5%), except *Fucus vesiculosus* in 1997 (5.8%) and *F. serratum* in 2018 (5.8%). In 2018, filamentous algae dominated the whole epiphytic algae composition > 60% cover in *Z. marina*, while in 1997, a high diversity of (non-filamentous) algae was identified (9 species), e.g. *F.
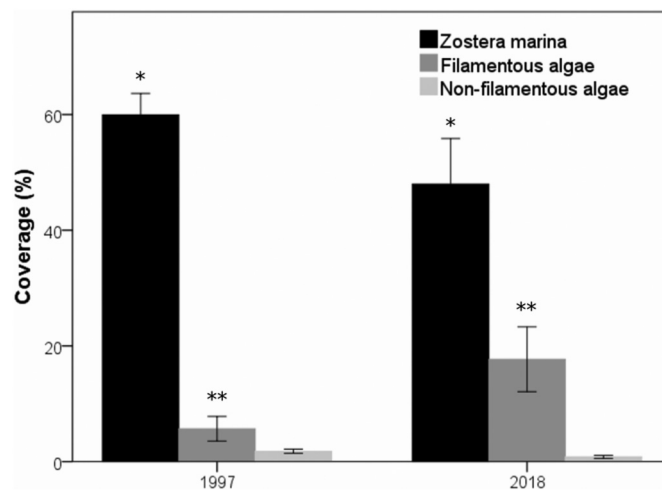


**Fig. 2.** Total mean percentage cover ( ± SE) of vegetation present in all of the 19 *Z. marina* meadows sampled in 1997 and the 14 meadows that were present in 2018. Significance: *p < 0.001, **p < 0.001.

*vesiculosus*, *F. serratus*, *Chorda filum*, *Dictyota* sp., *Ascophyllum nodosum*, *Furcellaria* sp., *Sargassum* sp., *Ulva* sp. and *Spermatochnus paradoxus* (Fig. 2).

### 3.2. Large epifauna (> 1 mm) community of Zostera marina

A high variability in the community structure was observed in the studied *Z. marina* meadows, and specifically regarding the most abundant taxa (Fig. 3, Tables S1 and S2). These differences were also obvious when considering community descriptors, i.e. the number of morphospecies that greatly increased in 2018 (29 taxa) relative to 1997 (13 taxa) (Tables S1 and S2). In 1997, the large epifauna community was dominated by the anemone *Sagartiogeton viduatus* (57%), and to a lesser extent, by the shrimp *Palaemon adspersus* and the ascidian *Ciona intestinalis*, with 8% and 13% of overall abundance, respectively. In 2018, the large epifauna community was dominated by the polychaete *Platynereis dumerilii* and the Chironomid larvae that represented 31% and 40% of overall abundance, respectively. The remaining taxa minorly contributed to the overall community abundances (< 4% each
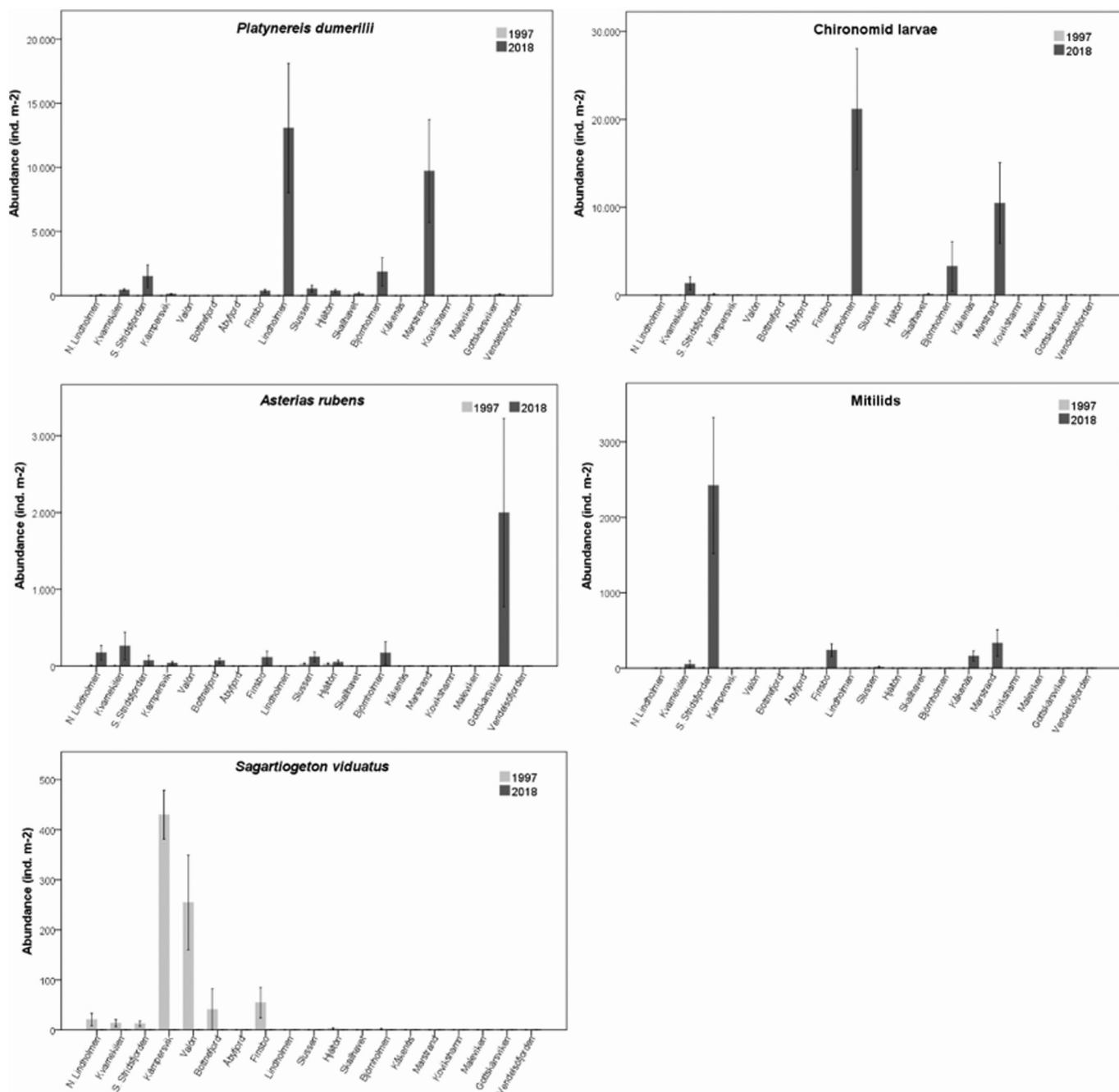
**Fig. 3.** Mean densities (ind. m$^{-2}$ ± SE) of the most abundant large epifauna (> 1 mm) in each of the 19 *Z. marina* meadows sampled in 1997 and 2018.

species). The large epifaunal community showed a high dissimilarity between the surveyed years (93.29%) and these differences were mainly explained by the lack in 1997 of the polychaete *P. dumerilii*, the chironomid larvae, and the mollusc *Tritia nitida*, as well as, the higher abundances of mytilids in 2018, belonging to larger individuals of the 0-age group also found in the small fraction (Fig. 3).

Differences between the large epifaunal community of both surveyed years were significant (pseudo-F = 10.253, p < 0.001) (Fig. 4a). This dissimilarity showed spatial variability among the sampled meadows (pseudo-F = 6.5083, p < 0.001) (Table 2), and these differences were consistent regardless temporal variations (Meadow x Year, pseudo-F = 6.3768, p < 0.001) (Table 3).

The total variation of large epifauna was fully explained by the first two db-RDA axes (99.9%), specifically by the first axis (99.7%) (Fig. 5a). The biomass of *Z. marina* was the variable that significantly

contributed to explain the epifaunal community structure in both surveys (1997 and 2018, Table 4). Differences in this variable were responsible for the dissimilarity between sampling stations.

### 3.3. Small epifaunal (0.2–1 mm) community of Zostera marina

The small epifaunal community present in *Z. marina* suffered substantial changes during the study period (Table 1, Fig. 6, Tables S3 and S4). The mean number of morphospecies remained equal (21 taxa) in 1997 and 2018 stations (Tables S3 and S4). The most abundant taxa in 1997 were the harpacticoid copepods, the nematode *Southernia zosterae*, the amphipod *Erichthonius difformis* and mytilid plantigrades (mean size 1.2 mm) that constitute 84% of the overall abundance. In 2018, the nematode Enoplidae sp1, the harpacticoid copepods, and the amphipod *Monocorophium insidiosum* made up 72% of the overall
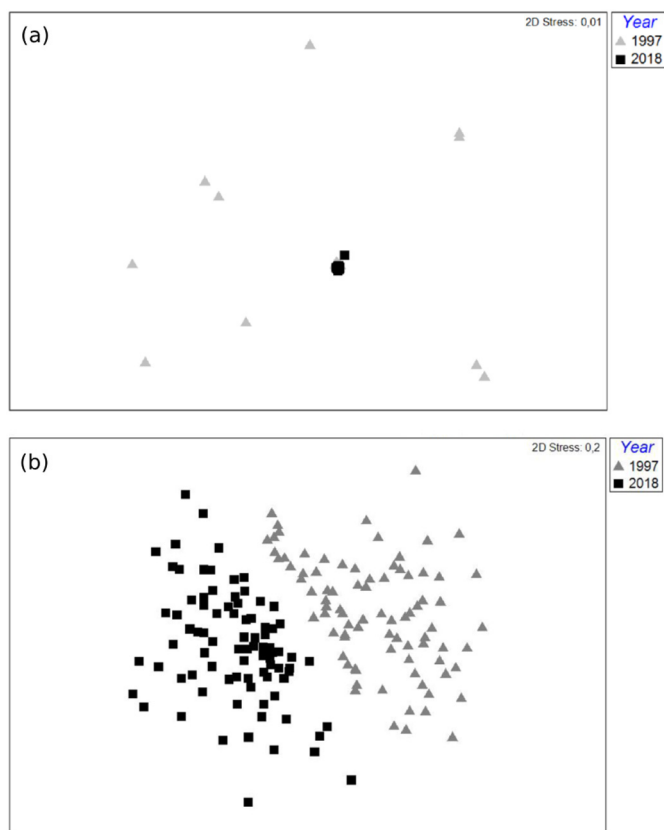
Fig. 4. MDS of the sampled *Zostera marina* meadows showing a) a large (> 1 mm body size), and b) a small (0.2–1 mm) epifaunal assemblage composition in 1997 and 2018.

abundance (Fig. 6). Both years showed a high dissimilarity (81.47%) in their epifaunal community, mostly explained by the lack of the nematode Enoplidae sp1 in 1997, and the decrease of harpacticoid abundances and the nematode *Southernia zosterae* in 2018 (Table 2). Also, the similarities of epifaunal composition within each surveyed year remained low, namely 33.1% and 39% in 1997 and 2018, respectively. These percentages were mostly explained by the high variability of harpacticoid copepods and nematodes (Fig. 6).

Significant differences were found when comparing the epifaunal composition of both years (pseudo-F = 17.475, p = 0.001), and also spatial variability was among the sampling stations (pseudo-F = 10.719, p = 0.001, Fig. 4b). These differences were consistent regardless the time gap between both surveys (1997–2018) (Location*Year, Pseudo-F = 8.505, p = 0.001, Table 3).

The first two db-RDA axes explained a ca. 67.5% of the total variation observed in epifaunal community structure (Fig. 5b), the greatest contribution coming from the first axis (63.5%) and a scarce 4% to the second axis. The variables that mostly contributed to explain these differences were the biomass of *Z. marina* and the cover of filamentous algae, where several species were pooled to adequately compare data of both surveys (1997 and 2018) (Table 4).

### 3.4. Changes of epifauna composition between 1997 and 2018

The present comparative study was carried out using the 14 sampling stations where *Z. marina* meadows were present in both surveys (1997 and 2018). The 0-group mytilids (small and large epifaunal fractions together) on eelgrass leaves showed an 83% decrease in 2018 (14 stations) compared to 1997 abundances (19 stations). These differences were significantly different (F = 10.444, p = 0.002). The overall abundance of small epifauna (Table 2, S3, S4) decreased 18% from 1997 to 2018, with no significant differences between them (One-way ANOVA, F = 0.573, p = 0.479). These differences in abundances were mainly due to a decrease of 83% of the amphipod *Erichthonius difformis* populations from 1997 to 2018 though no significant differences were found due to the high heterogeneity among stations (Mann-Whitney test, U = 3065, p = 0.139). This was also explained by ca. 50% decrease of harpacticoids abundances in 2018, with significant differences between both years (F = 10.764, p = 0.001). In contrast to other taxonomic groups, the amphipod *Monocorophium insidiosum* showed a 22% increase in abundance in 2018 but with no significant differences in time (F = 0.417, p = 0.519). The nematodes, mainly constituted by taxa belonging to Enoplidae and the species *Southernia zosterae*, showed an increase of 90% in 2018, that was consistently significant (F = 49.282, p ≤ 0.0001). Interestingly, mesoherbivores i.e. Idoteids and Gammarids were abundant (ca. 200–1100 ind. $m^{-2}$) in four of the most southern localities in 1997 whereas they had disappeared completely in 2018 (Tables S3 and S4).

Large epifauna abundances (Tables 2, S1, S2) were 90 times higher in 2018 compared to 1997, being significantly different between both

### Table 2

Large (> 1 mm body size) and small (0.2–1 mm) epifauna species contributing the most to differences between years. Important species determined using SIMPER analysis in PRIMER. Mean abundances of each large and small epifauna species in the 1997 and 2018 are included. Mean contribution of each species to the dissimilarity between the 2 years in study and this mean value divided by its SD (Dissimilarity/ SD) are also reported. Dissimilarity/SD represents the consistency with which each species contributes to overall dissimilarity (i.e. how good it is as a discriminator). Percent contribution of each large and small epifauna species to the dissimilarity and its cumulative contribution are also included.

| Epifauna size | Species | Mean abundance (ind m$^2$) | | Mean contribution to dissimilarity | Dissimilarity/SD | Contribution % | Cumulative % |
|---|---|---|---|---|---|---|---|
| | | 1997 | 2018 | | | | |
| Large | *Platynereis dumerilii* | 0.00 | 2015.79 | 23.18 | 1.02 | 23.37 | 23.37 |
| | Chironomid larvae | 0.00 | 2603.05 | 12.36 | 0.57 | 12.46 | 35.82 |
| | *Asterias rubens* | 5.83 | 219.14 | 8.87 | 0.52 | 8.94 | 44.77 |
| | Mytilids | 0.39 | 229.48 | 8.43 | 0.42 | 8.50 | 53.26 |
| | Cnidaria sp1 | 0.00 | 128.32 | 6.57 | 0.30 | 6.62 | 59.88 |
| | *Mya arenaria* | 0.00 | 160.99 | 4.01 | 0.39 | 4.04 | 63.92 |
| | *Palaemon adspersus* | 5.54 | 119.03 | 3.93 | 0.54 | 3.96 | 67.89 |
| | *Crangon crangon* | 0.00 | 93.43 | 3.74 | 0.39 | 3.77 | 71.65 |
| | *Rissoa* sp. | 0.00 | 74.00 | 6.61 | 0.35 | 3.64 | 75.29 |
| Small | Enoplidae sp1. | 0 | 25957.33 | 22.06 | 1.29 | 27.08 | 27.08 |
| | Harpacticoids | 24109.58 | 12027.45 | 15.97 | 1.19 | 19.6 | 46.68 |
| | *Southermia zosterae* | 14324.96 | 1245.95 | 10.08 | 0.88 | 12.37 | 59.05 |
| | Mytilids | 8287.84 | 1325.34 | 7.93 | 0.62 | 9.73 | 68.77 |
| | *Erichtonius difformis* | 13109.5 | 2228.09 | 7.81 | 0.62 | 9.59 | 78.37 |

**Table 3**

Results of PERMANOVA for differences in large (> 1 mm body size) and small (0.2–1 mm) epifaunal community composition considering sampled meadows ("Meadow", fixed factor) and Year ("Year", fixed factor) pressure in coastal stations. Significant differences (p < 0.05) are highlighted in bold.

| Epifauna size | Source of variation | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|---|
| Large | Year | 1 | 1.1297e5 | 1.1297e5 | 10.253 | **0.0002** | 4985 |
| | Meadow | 13 | 1.4619e5 | 11,246 | 6.5083 | **0.0002** | 4950 |
| | Year x meadow | 13 | 1.4324e5 | 11,018 | 6.3768 | **0.0002** | 4936 |
| | Residual | 140 | 2.419e5 | 1727.9 | | | |
| | Total | 167 | 6.443e5 | | | | |
| Small | Year | 1 | 75,083 | 75,083 | 17.475 | **0.001** | 999 |
| | Meadow | 13 | 70,398 | 5415.3 | 10.719 | **0.001** | 997 |
| | Year x meadow | 13 | 55,855 | 4296.6 | 8.5047 | **0.001** | 996 |
| | Residual | 140 | 70,728 | 505.2 | | | |
| | Total | 167 | 2.7206E5 | | | | |

years (F = 265.88, p < 0.0001). This sharp increase was explained by the abundance increase of the most important components of this epifaunal fraction in 2018. Specifically, large-sized mytilids showed an increase of abundances, being significantly different (U = 2709, p = 0.00001) whilst the remaining dominant species, e.g. the polychaete *Platynereis dumerilii* and chironomid larvae were absent in 1997, but showed high abundances in 2018. In addition, the important intermediate predator the shrimp *Palaemon adspersus* showed a significant 21-fold increase of abundances in 2018 (U = 3843, p < 0.00001) (Tables 2, S1 and S2).

## 4. Discussion

The best possible estimates of seagrass distribution reveal a global decline with about 30% over 140 years (Waycott et al., 2009) and a net loss of European seagrass with 29% and *Z. marina* with 57% between 1869 and 2016 (De los Santos et al., 2019). The areal distribution of *Zostera marina* along the Swedish Skagerrak coast had a 59% decline between the mid-1980s and 2000 (Baden et al., 2003; Nyqvist et al., 2009) and is reported to have decreased further with additional 79% in the Southern part of the area (Moksnes et al., 2018). We found a total loss of 5 meadows (out of 19) between 1997 and 2018, and a sharp decrease (54%) of *Zostera* biomass in the southern meadows. The increase of epiphytic algae in the studied *Zostera marina* meadows, underpinned still ongoing deterioration of the *Z. marina* meadows. This finding is in accordance with the loss found by Baden et al. (2003) with the largest loss in the southern part of the study area but with no clue to when this occurred between the mid-1980s and 2000. The present investigation may narrow this time interval since *Z. marina* was still found in 1997, but had disappeared in the 2000 investigation (Baden et al., 2003). The mean *Z. marina* biomass in remaining meadows remained constant (about 150 g DW m$^{-2}$) over two decades. Historically this can be compared with biomass values from 1926 with a mean of 520 g DW m$^{-2}$ ($n$ = 5) (Gislén, 1928), i.e. a 60% loss in biomass per m$^{-2}$. Further, in 1926, *Z. marina* meadows extended from 0.9 to 8.4 m (Gislén, 1928), whereas now the mean max. depth is ca. 4 m (Baden et al., 2003;
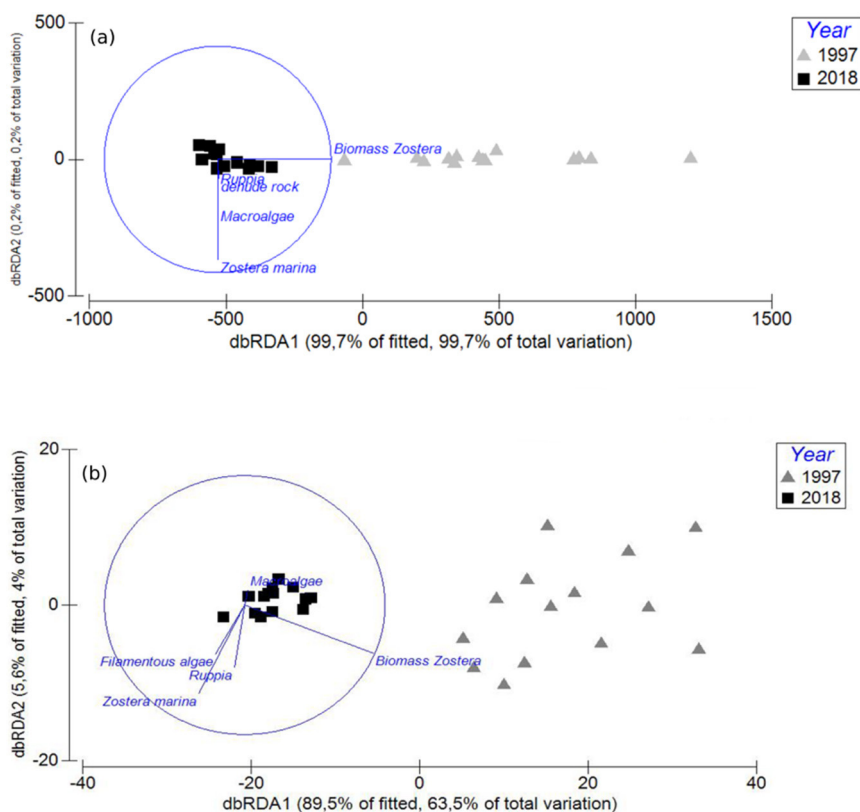


**Fig. 5.** Distance-based redundancy analysis (dbRDA) biplot of the first and second axes relating those environmental variables that affected significantly (see Table 4) the s assemblage structure of large (> 1 mm body size) (a) and small (0.2–1 mm) (b) epifauna located at different *Z. marina* meadows in 1997 and 2018.

**Table 4**
Results of multivariate regression testing the relationship between the seagrass and macroalgae species and the large (> 1 mm body size) and small (0.2–1 mm) epifauna assemblage structure. To retain variables with explanatory power, the AIC procedure was chosen as model selection criterion (sequential tests, Legendre and Anderson, 1999).

| Epifauna size | Variable | AIC | SS (trace) | Pseudo-F | p | Proportion of explained variation | Proportion of accumulative explained variation |
|---|---|---|---|---|---|---|---|
| Large | +Biomass *Z. marina* | 141.65 | 7.4453e6 | 55,518 | 0.0002 | 0.92832 | 0.99962 |
| Small | +Biomass *Z. marina* | 0.57118 | 7602.8 | 31.469 | 0.0002 | 0.49979 | 0.63471 |
| | +Filamentous algae | 0.64359 | 1139.1 | 5.6728 | 0.0004 | 7.4883E-2 | 0.70959 |

Moksnes et al., 2018) which decreases the areal extension of *Z. marina* on the Swedish Skagerrak coast even more compared to 1926.

Despite the similar species richness, the eelgrass epifauna experienced drastic temporal (1997–2018) and spatial (200 km) shifts. Small epifauna shifted to a community dominated by the nematode Enoplidae sp1 and the amphipod *Monocorophium insidiosum,* and a sharp decrease of the amphipod *Erichthonius difformis* and harpacticoids occurred. Large epifauna drastically increased their abundances. Several species

that previously showed rather low densities, e.g. mytilids (larger but still 0-group), or even absent, e.g. the polychaete *Platynereis dumerilii* and chironomid larvae, were more abundant in 2018. From the dbRDA analysis the epifaunal abundance relates mostly to the biomass of *Z. marina* and ephemeral algal. These results may be explained by the composition and functional diversity of sessile epibionts, also observed by Momota and Nakaoka (2017) in *Zostera marina* seabeds on the northeastern coast of Japan. The sessile epibiosis may affect the
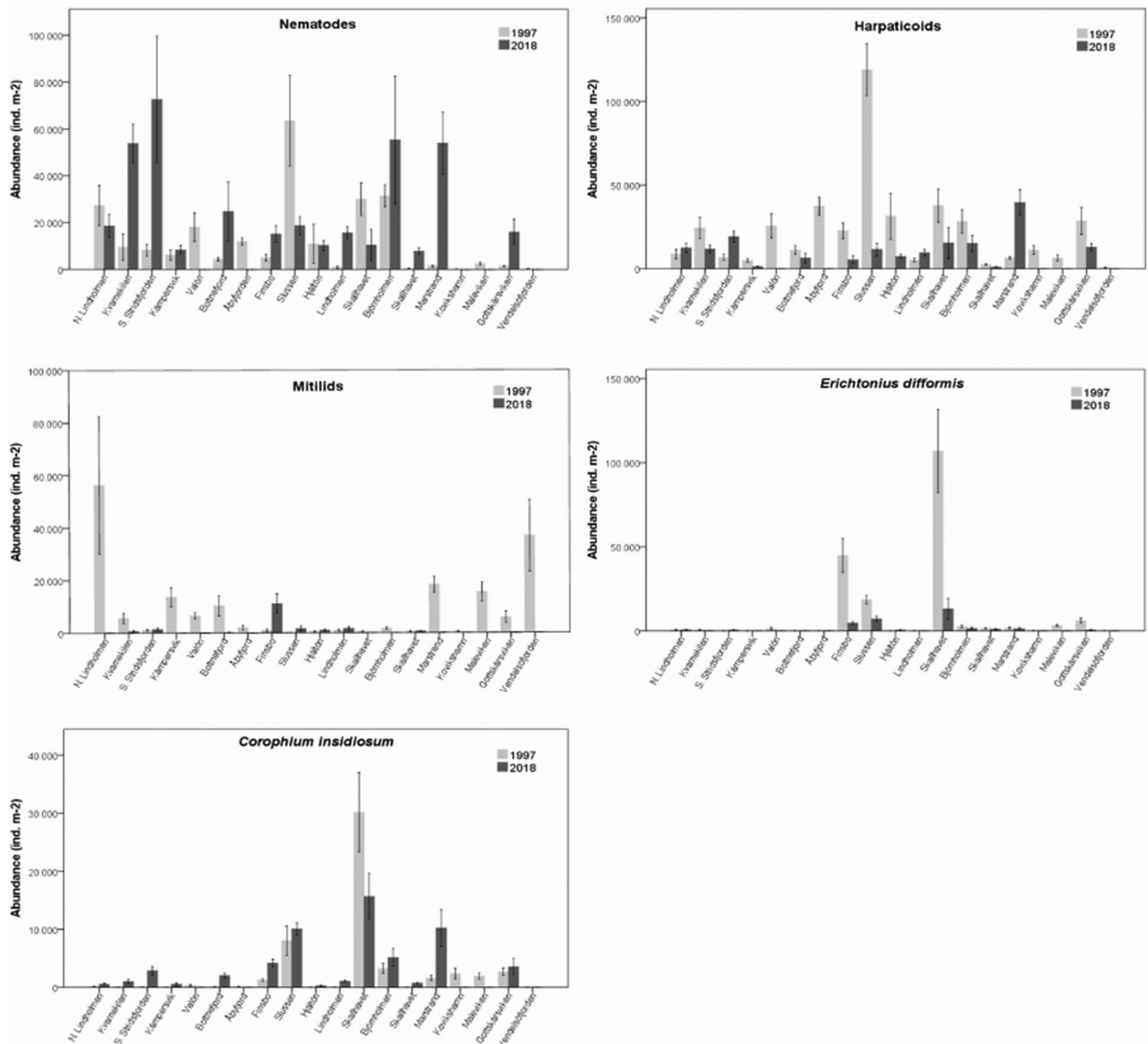


**Fig. 6.** Mean densities (ind. m$^{-2}$ ± SE) of the most abundant small epifauna (0.2–1 mm) in each of the 19 *Z. marina* meadows sampled in 1997 and 2018.

biomass and diversity of mobile epifaunal invertebrates and this relationship indicates the importance of non-trophic animal-plant interactions in this japanese coastal ecosystem since eelgrass meadows are utilized as habitat by epifauna (Momota and Nakaoka, 2017).

A sharp reduction of 83.4% in mean mytilid abundance from 1997 to 2018 was observed. Seagrass is an important temporary (June–August) substrate for mytilids along the Swedish west coast. Densities of up to 25,000 plantigrades $m^{-2}$ in *Z. marina* adjacent to site 8 (Finsbo) were recorded in July 1986 (Baden, 1990). To minimize food competition and cannibalism from adult mytilids the plantigrades grow to ca. 2 mm length in *Z. marina* before byssus drifting to the adult mussel beds close to *Z. marina* (De Blok and Geelen, 1958; Bayne, 1964; Sigurdsson et al., 1976). This decrease is in accordance with the catch statistics of wild mussels from the North Sea, Baltic and Kattegat and Skagerrak decreasing to one third since 1973, from ca. 150.000 t to 50.000 t, being more accentuated after 2000 (Sandström et al., 2018). Explanations to the decrease of mytilids in the Skagerrak have got public attention but have yet to be scientifically analysed and verified. Although *Z. marina* is not the only substrate for plantigrade mytilids (Bayne, 1964) it is definitely important and a habitat close to adult mussel banks. Thus, lack of plantigrade substrate could be an additional explanation to mytilid decline.

This study shows that in 1997 important mesograzers, such as the amphipod *Gammarus* spp. and the isopod *Idotea* spp., were abundant in 7 of 19 meadows along the Skagerrak coast and mainly restricted to the southern part of the study area (Table S3). These meadows were inhabited by surprisingly high densities of mesograzers (ca. 200–1100 ind. $m^{-2}$), similar to those previously found in *Z. marina* meadows free of filamentous algae in the Baltic archipelago (Baden et al., 2010; Boström et al., 2014). In 2018, however, all mesograzers were missing in the investigated meadows. During the mid-1980s Baden and Pihl (1984) and Baden (1990) found mesograzers densities of ca. 100 ind. $m^{-2}$, in meadows in the middle part of the study area. In the 2000s all mesograzers had disappeared from this area as well (Baden et al., 2012). Mesograzer species have a pivotal role to control the growth of epiphytic and filamentous macroalgae, and thus, crucial to avoid the severe shift herein observed (Moksnes et al., 2008; Andersson et al., 2009; Svensson et al., 2012). High predation pressure from intermediate predators on these species underpinned an extensive overgrowth of ephemeral algae that has occurred since the mid-1980s (Baden et al., 2012) and a further increase of ca. 50% filamentous algae biomass is documented from the area between 1998 and 2012 (BVVF Hydrogis, 2012). The ephemeral and epiphytic algae in both living and decomposing condition constitute the main food source of small cryptic epifauna (1–0.2 mm), mostly herbivores and detritivores (Jephson et al., 2008; Thormar et al., 2016) (Fig. 7). An increased abundance of these herbivores could thus be expected when the algal production increases, but on the contrary, this group has also decreased.

Intermediate predators on the Swedish west coast (mainly gobiids and sticklebacks) appear to be the main group controlling populations of mesograzers like gammarids and idoteids since these mesoherbivores are larger and thus preferred prey items (Fig. 7). When missing, the intermediate predators including the shrimp *Palaemon adspersus* eat smaller epifauna as found using stable isotope analysis (Jephson et al., 2008; Thormar et al., 2016). In Danish *Z. marina* Thormar et al. (2016) found that polychaetes, mainly Nereids, which are abundant in *Z. marina*, are a common food item for small fish. Meiofauna, like harpacticoids, are found in stomachs of small intermediate fish predators (< 4 cm) and larger crustaceans (shrimps and crabs) (Moksnes et al., 2008; Jephson et al., 2008; Thormar et al., 2016). The abundance of intermediate fish predators in *Z. marina*, e.g. black goby, *Gobius niger*, and three-spined stickleback, *Gasterosteus aculeatus* and two-spotted goby (*Gobiusculus flavescens*) along the Swedish west coast, has increased with a factor of 10 due to overfishing of top-predators, e.g. cod (*Gadus morhua*) since the 1980s (Wennhage and Pihl, 2002; Svedäng and Bardon, 2003; Baden et al., 2012; Boström et al., 2014). Annual cod

catch in the Skagerrak decreased from 400 kt. in the beginning of 1980s to 175 kt. in 1997. In 2018 the catch (and quota) was only 50 kt. (Sandström et al., 2018), showing a decrease of 71% between 1997 and 2018 since the populations have been overexploited. This is the most probable explanation to the dramatic increase of intermediate predators found by Baden et al. (2012) and also reported from the Baltic proper, where sticklebacks have increased in abundance with a factor of 2–3 between early 2000s to mid-2010s (Olsson et al., 2019). The intermediate invertivore shrimp *Palaemon* has an increase of 21-fold in abundance between 1997 and 2018. The same trend was found for the crab *Carcinus maenas*, but their abundances were only spatially-limited to a certain number of meadows. The increase of the former two species is substantially higher than those found in Baden et al. (2012). Top-down effects have recently shown to play important roles in seagrass ecosystems (Valentine and Duffy, 2006; Lewis and Anderson, 2012; Burkholder et al., 2013; Östman et al., 2016) including the *Z. marina* meadows on the Swedish west coast between mid-1980s to mid-2000s (Baden et al., 2012). During these two decades, there is no actual data revealing when the dramatic flip occurred in faunal composition and the cascade consequences resulting in 60% loss of *Z. marina* (Baden et al., 2003; Nyqvist et al., 2009). We showed that *Z. marina* and numerous mesoherbivores are still present in the southern part of Skagerrak in 1997 but disappeared in 2018.

In coastal Skagerrak, the top-down effect exacerbates the bottom-up effect which seems to be due to nutrient enrichment but even to the sedimentation of allochtonous particulate organic matter in coastal bays from agriculture and domestic run-offs (Aure et al., 1996; Skogen et al., 2014). The remineralization of organic matter and posterior release of nutrients in the water column and sediments may trigger an enhanced nutrient concentration in coastal ecosystems (e.g. Glud et al., 1998; Bourgeois et al., 2017). This nutrient enrichment seems to be a driver of overgrowth of filamentous algae on *Z. marina* meadows (Pihl et al., 1995, 1996, 1999), and in manipulative field experiments (Moksnes et al., 2008). Spatial variability in the cover of filamentous algae may be expected since it greatly depends on site-specific conditions such as, topography, hydrodynamic exposure, water exchange, run-offs, among others (Pihl et al., 1999; Rasmussen et al., 2013).

The interaction of top-down (predation-controlled) and bottom-up (nutrient-controlled) processes determine key interactions among species and their responses to human-induced stressors, specifically fishing pressure and coastal surplus of nutrients in the Skagerrak (Baden et al., 2012). Trophic cascades are susceptible to occur in this scenario, as formerly observed in eelgrass beds from Baja California (Jorgensen et al., 2007), with low predator abundances and coastal nutrient enrichment. Models have been developed to highlight direct and indirect pathways through the trophic net from a marine ecosystem to identify wider effects of natural and anthropogenic pressures (Lynam et al., 2017). We identify that the observed shift in epifauna composition is not only directly affecting the eelgrass bed ecosystem assembly, but indirectly mediated by shifts in the relative importance of both forces, top-down, through the decrease of mesograzers (large-sized epifauna mainly composed by amphipods and isopods) by intermediate predators (i.e. small fish, shrimps and crabs), and bottom-up, through surplus of nutrients resulting in the overgrowth of filamentous algae and suffocation of *Z. marina* (Fig. 7).

We found a largely changed epifauna between 1997 and 2018 where the abundance of mesograzers decreased, large epifauna (intermediate invertebrate predators) increased and small epifauna species (herbi-and detritivores) decreased. Despite the low trophic level of the herbi- and detritivorous epifauna it seems that the epifauna does not benefit from the surplus of epiphytes but rather decreases in abundance. This indicates that in the balance between bottom-up and top-down effects the top-down effect is more pronounced, and small epifauna is over-predated by high abundances of intermediate invertebrates and fish. This is in accordance with manipulative field experiments where nutrient addition and grazer exclusion affected the
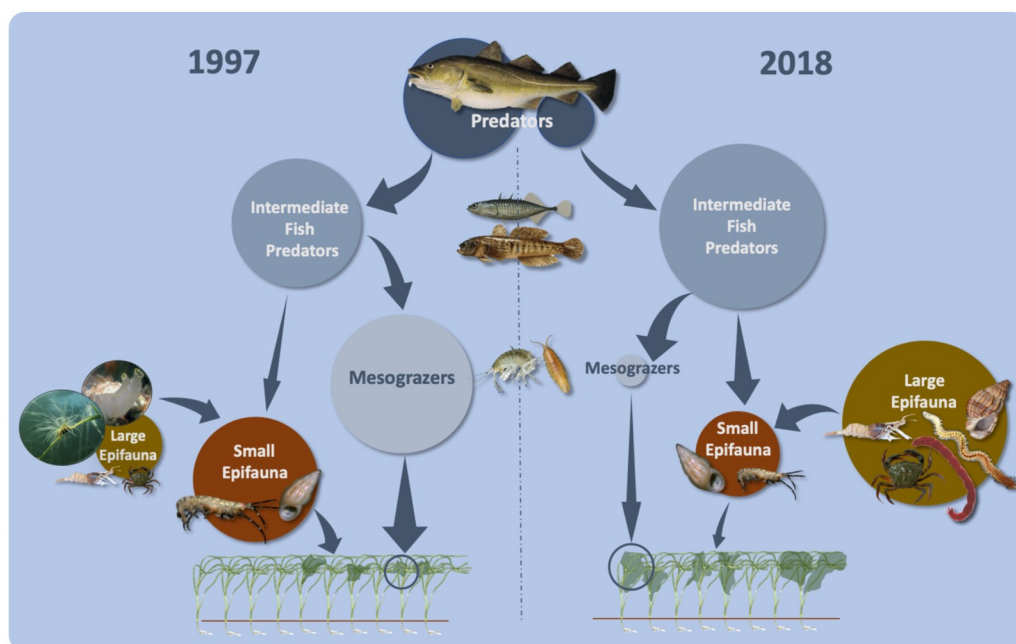
**Fig. 7.** Conceptual model of the regime shift observed in the *Z. marina* meadows between 1997 and 2018 in the Skagerrak. The percentage changes found within each group (circle) is shown with the largest circle being 100% and the smaller circle is a percentage area of the 100% circle. The low densities of top predators, e.g. cod (*Gadus morhua*) (Baden et al., 2012; Sandström et al., 2018) directly exert control on the abundances of intermediate predators dominated by sticklebacks (*Gasterosteus aculeatus*), gobies (*Gobius niger* and *Gobiusculus flavescens*) and *Palaemon adspersus* (Baden et al., 2012). The fish species preferably preyed on mesograzers (*Gammarus* spp. and idoteid isopods) in 1997 but turn to small amphipods, harpacticoids and nereidids in 2018. Mesograzers are pivotal to control overgrowth of filamentous algae on *Z. marina* leaves (Svensson et al., 2012). The densities of mesograzers greatly affect the structure of large epifauna, with a good representation of sessile filter feeders in 1997 (e.g. the anemone *Sagartiogeton viduatus* and the ascidian *Ciona intestinalis*) and generalist vagile species in 2018 (the polychaete *Platynereis dumerilii* and chironomid larvae) that may prey on small epifauna, mainly nematodes + harpactioids. The current contribution of both epifaunal fractions (large and small) to maintain low levels of filamentous algae seems to be minor compared to grazing pressure of mesograzers in 1997.

epifauna composition and abundance (Mosknes al. 2008; Duffy et al., 2015). The later study used 15 seagrass beds from the whole *Zostera marina* distribution area as a model study. We can thus reject our H₀ hypothesis that the epifauna community benefits from increased filamentous algae.

To conserve and restore *Z. marina* beds and associated seagrass ecosystem services a better coastal management is needed. To achieve this, a co-management of fishing activities and nutrient pollution from agriculture and domestic run-offs in the studied region needs to be integrated (Baden et al., 2010, 2012; Eriander et al., 2016).

**CRediT authorship contribution statement**

**Rodrigo Riera:** Data curation, Writing - original draft. **Joana Vasconcelos:** Data curation, Investigation, Writing - original draft.**Susanne Baden:**Data curation, Supervision, Conceptualization, Writing - review & editing.**Linda Gerhardt:**Data curation.**Ricardo Sousa:**Formal analysis, Writing - review & editing.**Eduardo Infantes:**Conceptualization, Resources, Writing - review & editing.

**Declaration of competing interest**

The authors declare no conflicts of interest.

**Acknowledgements**

**Funding**

**Appendix A. Supplementary data**

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2020.111434.

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