Short communication

Drift algae reduce foraging efficiency of juvenile flatfish

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Abstract

Although flatfish species utilise a wide range of habitats as adults, several species are confined to a very limited habitat as juveniles. Recruitment levels are dependent on the quality and quantity of these nursery areas and changes therein. In the Baltic Sea, these shallow environments are often subject to influxes of drifting macroalgae, which add structure to otherwise bare sandy substrate. Structure, such as vegetation, alters predator–prey interactions of a wide range of fauna and in an array of marine, freshwater, and terrestrial systems. The aim of our study was to assess the inhibition potential of drifting macroalgae on the foraging efficiency of juvenile flatfish (young of the year *Scophthalmus maximus* L., young of the year- and group 1 + *Platichthys flesus* L.) through a series of microcosm experiments. Our results show that foraging success is restricted by drift algae as predation efficiency of all predator species and size classes was negatively affected by the presence of macroalgae. Overall, there was a reduction in predation success by $80 \pm 12\%$ due to structural effects and/or the induced changes in water chemistry associated with the algae. Flatfish depend on shallow sandy areas as feeding and nursery grounds during their juvenile stage and frequently occurring macroalgal assemblages drastically change the features of the otherwise bare substrate, setting the stage for small-scale, localised processes potentially affecting population dynamics.
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1. Introduction

Many ecological interactions, such as those between predator and prey, are greatly influenced by habitat structure. At high densities, structures reduce foraging success (measured as growth rates, prey capture rates etc.) by increasing search and pursuit times and consequently lowering encounter and capture rates, compared to habitats with no or sparse structure (Crowder and Cooper, 1982; Diehl, 1992; Persson and Eklöv, 1995). The effects on predation success depend on the levels of complexity (Nelson and Bonsdorff, 1990; Bartholomew et al., 2000), such as density and species/features of the structure, and responses that are predator and prey specific in terms of size and species (Crowder and Cooper, 1982; Isaksson et al., 1994; Spitzer et al., 2000).

The shallow soft bottoms in the Baltic Sea have undergone dramatic changes in structural characteristics during the last decades due to increasing occurrences of drifting algal mats (Bonsdorff, 1992; Berglund et al., 2003). A macroalgal assemblage affects the biota through its physical presence but also by depletion of

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Table 1
Species composition of drifting macrophytes

Phaeophyceae
Pylaiella littoralis (L.) Kjellman / *Ectocarpus siliculosus* (Dillwyn) Lyngbye[d]
Dictyosiphon foeniculaceus (Hudson) Greville / *Stictyosiphon tortilis* (Ruprecht) Reinke[+]
Fucus vesiculosus L.[+]
Elachista fucicola (Velley) Areschoug
Chlorophyceae
Cladophora glomerata (L.) Kützing[d]
Ulva sp. (syn. *Entermorpha* sp.)
Cladophora rupestris (L.) Kützing
Rhodophyceae
Ceramium tenuicorne (Kützing) Waern[d]
Polysiphonia fucoides (Hudson) Greville
Rhodomela confervoides (Hudson) P.C. Silva
Furcellaria lumbricalis (Hudson) J.V. Lamoroux
Charophyceae
Chara aspera Willdenow
Haloragaceae
Myriophyllum spicatum L.
Zosteraceae
Zostera marina L.[+]

[d] =dominant species,[+] =commonly occurring species. The taxonomy follows Guiry and Guiry (2006).

oxygen during decomposition (Bonsdorff, 1992; Norkko and Bonsdorff, 1996a; Raffaelli et al., 1998). Juvenile flatfish, such as flounder, *Platichthys flesus* L., and turbot, *Scophthalmus maximus* L. (syn. *Psetta maxima*), are dependent on shallow soft bottoms as nursery and feeding grounds (Gibson, 1994). The prey utilised by these species include infaunal macroinvertebrates, which are, like the predators, directly impacted by occurrences of macroalgal mats and increased habitat structure. Several studies show macroalgal-induced changes in prey availability and foraging efficiency for benthic predators (Wilson et al., 1990; Isaksson et al., 1994; Norkko and Bonsdorff, 1996b; Norkko, 1998; Aarnio and Mattila, 2000; Andersen et al., 2005).

This study examined the impact of drifting algae on the foraging efficiency of *P. flesus* and *S. maximus*. We predicted that drifting algae would negatively affect the foraging efficiency (the number of prey items consumed in a given time period) of juvenile flatfish. We wanted to determine whether the effects of drifting algae differ based on predator species and size, which to our knowledge has not been addressed in the literature for juvenile flatfish prior to this study. We expected that smaller fish may be better able to manoeuvre in a structurally complex habitat, and as *S. maximus* have a larger gape size than *P. flesus* of the same length (Aarnio et al., 1996), they may be better equipped to utilise the food resources available.

2. Methods

2.1. Experimental organisms

Organisms were collected from Hinderbengtsviken Bay (60° 10′ N, 20° 32′ E), Åland Islands. *Platichthys flesus* (TL 39–96 mm) and *Scophthalmus maximus* (TL 26–43 mm) were collected using a beach seine (4 mm net, 2 mm mesh bag) and a push net (2 mm mesh). *Bathyporeia pilosa* Lindström is a common and often numerically dominant infaunal member on these sandy bottoms (Blomqvist and Bonsdorff, 1986), and constitutes an important food object for epibenthic predators such as *P. flesus* and *S. maximus* (Aarnio et al., 1996). *B. pilosa* (2.43 ± 0.04 mm) were collected with a shovel and a bucket sieve (1 mm). Drift algae, consisting of brown, green, and red algae (dominated by filamentous species) and some angiosperms (Table 1), were collected at the same site. After collection, the organisms were transported to the laboratory and placed in holding tanks. Fish were starved for at least 24 h prior to the start of a trial. Any associated animals were removed from the algae.

2.2. Laboratory experiment

The laboratory experiment was conducted at Husö Biological Station, Åland Islands, northern Baltic Sea, in summer 2005. The experimental set-up was a two factorial design with three structure levels (no structure/ artificial algae/drift algae) and two predator levels (present/absent). This set-up (with n replicates=3) was utilised in three consecutive runs varying predator sizes and species. We conducted trials using year 1+flounder (TL 80 ± 4 mm; hereafter 1+*P. flesus*), young-of-the-year flounder (TL 47 ± 2 mm; YOY *P. flesus*) and turbot (TL 33 ± 2 mm; YOY *S. maximus*). Aquaria ($16 \times 16 \times 9$ cm; 2.3 l) were filled with a 2.5 cm layer of sieved azoic sand and filtered (20 µm) seawater. Each tank contained 45 adult *B. pilosa*, approximating natural densities of 1642 ind m^{-2} (Blomqvist and Bonsdorff, 1986). The amphipods were acclimated to the tanks for at least one hour before predators and algae were added and the trial was started (Mattila and Bonsdorff, 1998). Predator treatments used one fish per tank. Algal treatments received 30 g wwt of drift algae, which is consistent with intermediate densities found in the natural environment (~1000 g wwt m^{-2}, Norkko and Bonsdorff, 1996b). To simulate algal structure in our artificial algae treatments, 9 g of filter wool (high-grade, saltwater-proof, synthetic fibres) was used. The amount was determined by visual approximation to the surface area and thickness of the layer created in our real algal

treatments. By using artificial structure we attempted to exclude chemical factors that might affect predation, such as algal exudates (possibly toxic) and/or algal-induced loss in dissolved oxygen.

At the start of each run, oxygen conditions were checked in one randomly selected tank from each treatment. The water chemistry (temperature, pH, O_2) of each tank was monitored at the end of each run. Water samples were taken 0.5 cm above the sediment surface with a siphon/suction tube. Trials were run at water temperature 15.0–17.5 °C and salinity between 5 and 6, for 6 h. After the water samples were taken, predators were removed and measured, and the algae were placed in zip lock bags for later analysis. The water and sand from each tank were passed through a 0.5 mm sieve and the surviving amphipods were counted. The algae were picked through and any amphipods in the algae were retrieved and counted. All fishes were released at the collection site at the end of the study.

2.3. Statistical analyses

All values are presented as mean±SE unless described otherwise. The data were tested for homoscedasticity with Cochran's test prior to analysis (all $p > 0.05$). A two way analysis of variance was performed on amphipod mortality for each predator using GMAV 5 (A.J. Underwood and M.G. Chapman, unpubl.). All factors are fixed and orthogonal. The two way ANOVAs were followed by Student-Newman-Keuls (SNK) tests to attribute differences between specific treatments and levels. As interactions were present, the p-values generated by post hoc analyses should be treated cautiously, but allow a ranking in factors (Underwood, 1997). Interspecific predation rates were analysed with one way ANOVAs followed by Scheffé post hoc analysis when appropriate. Regressions (curve estimation) were performed with SPSS 14.0 for Windows, after elimination of zero-values by addition of a constant (x + 1).

3. Results

3.1. Experimental conditions

Experimental aquaria showed high initial O_2 levels (>90%), indicating that any changes in oxygen conditions were brought on by the treatments. pH ranged from 7.5 to 8.2. During the trials, O_2 levels decreased in treatments containing drift algae with a maximum reduction to 41% (range 41–97%), while good O_2 conditions (range 86–99%) prevailed in all other treatments.

Table 2

Two factor analysis of variance for effect of structure on foraging efficiency of (a) 1+ *P. flesus*, (b) YOY *P. flesus*, and (c) YOY *S. maximus*

Treatment	df	MS	F	p
a				
predation	1	636.056	23.850	**<0.001**
structure	2	155.056	5.810	**0.017**
predation × structure	2	218.722	8.200	**0.006**
Error	12	26.667		
Total	17			
SNK p(s)				
no structure:	no predation<predation			**
artificial algae:	no predation<predation			**
drift algae:	no predation=predation			ns
SNK s(p)				
no predation:	no structure=artificial			ns
	algae=drift algae			
predation:	no structure=artificial algae			ns
	no structure>drift algae			**
	artificial algae>drift algae			**
b				
predation	1	1352.000	190.125	**<0.001**
structure	2	68.667	9.656	**0.003**
predation × structure	2	68.667	9.656	**0.003**
Error	12	7.111		
Total	17			
SNK p(s)				
no structure:	no predation<predation			**
artificial algae:	no predation<predation			**
drift algae:	no predation<predation			**
SNK s(p)				
no predation:	no structure=artificial			ns
	algae=drift algae			
predation:	no structure=artificial algae			ns
	no structure>drift algae			**
	artificial algae>drift algae			**
c				
predation	1	68.056	6.282	**0.028**
structure	2	6.056	0.559	0.586
predation × structure	2	60.722	5.605	**0.019**
Error	12	10.833		
Total	17			
SNK p(s)				
no structure:	no predation<predation			**
artificial algae:	no predation<predation			*
drift algae:	no predation=predation			ns
SNK s(p)				
no predation:	no structure=artificial			ns
	algae=drift algae			
predation:	no structure=artificial algae			ns
	no structure>drift algae			*
	artificial algae>drift algae			*

Significant values are presented in bold.

3.2. Foraging efficiency

Some amphipod mortality was noted in non-predator treatments (overall mean 1±0.2), possibly due to counter-
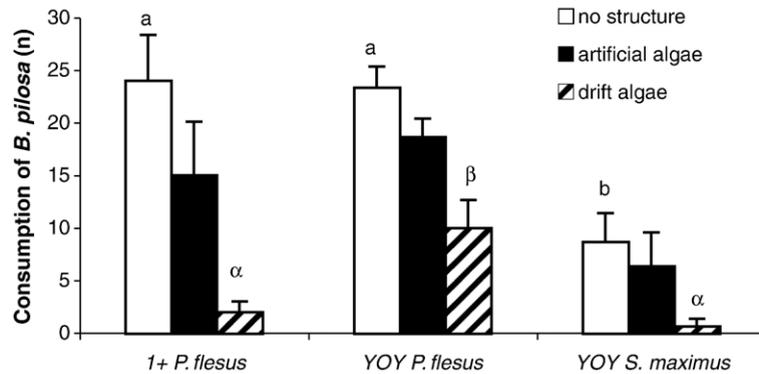
Fig. 1. Predator specific (1+*P. flesus*, YOY *P. flesus* and YOY *S. maximus*) consumption of *Bathyporeia pilosa* (n, mean±SE) in no structure-, artificial algae- and drift algae treatments. Different letters indicate statistically significant differences (ANOVA, Scheffé, p<0.05) among predator types within that particular treatment (Roman letters for no structure-, Greek letters for drift algae comparisons).

error or handling. During predator absence, no differences in amphipod mortality between the structure treatments were found (two way ANOVA, SNK, p>0.05, Table 2a–c), indicating that predator presence caused virtually all amphipod mortality. However, significant predation × structure interactions occurred (two way ANOVA, p=0.006, p=0.003 and p=0.019, Table 2a–c). All predator types showed responses to drift algae (Fig. 1), with a mean reduction in foraging of 80±12%, suggesting that algae strongly inhibit predator success. Amphipod mortality in drift algae treatments was independent of predator presence (1+*P. flesus* and YOY *S. maximus*). Predation by YOY *P. flesus* occurred even though drift algae were present, but fewer amphipods were consumed than in the no structure or artificial algae treatment (p<0.01, Table 2b). Still, the consumption by YOY *P. flesus* in the presence of drift algae was considerably greater than by the other predator types (one way ANOVA, df=2, MS=76.444, F=9.053, p=0.015, Scheffé post hoc p<0.05, Fig. 1). Artificial algae induced non-significant reductions in foraging efficiency of 28±5%. *S. maximus* displayed lowest amphipod consumption (one way ANOVA, df=2, MS=225.333, F=7.375, p=0.024, Scheffé post hoc p<0.05), while both size classes of *P. flesus* ate similar amounts when no structure was present (Scheffé post hoc p=0.989, Fig. 1). The same trend emerged in the treatments with artificial algae, but here *S. maximus* differed non-significantly (one way ANOVA, df=2, MS=120.333, F=2.992, p=0.126).

When the data on dissolved oxygen were included as covariates in the model predicting amphipod mortality, there was no significant effect of oxygen levels (p>0.05) and the data on oxygen were therefore excluded from the analysis presented above. However, dissolved oxygen was significantly positively related to predation efficiency of all predator types (p=0.002, p=0.001, and p<0.001,

for 1+*P. flesus*, YOY *P. flesus* and YOY *S. maximus*, respectively, Fig. 2), although structure may have influenced these results.

4. Discussion

4.1. Predation success inhibited by drift algae

Mechanisms underlying lowered foraging success in habitats with structure include increased amounts of refuges for prey and physical/visual obstruction of predators (Orth et al., 1984; James and Heck, 1994; Laegdsgaard and Johnson, 2001; Finke and Denno, 2002). Our study confirms findings that drifting algae at intermediate amounts induce a drastic drop in the predation efficiency of juvenile flatfish (Aarnio and Mattila, 2000). Similar results have been obtained for
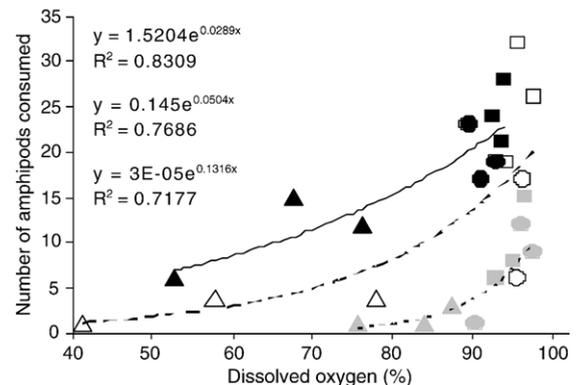

Fig. 2. Amphipod consumption (n) as a function of dissolved oxygen (%). Black symbols and solid line=1+*P. flesus*, white symbols and dashed line=YOY *P. flesus*, grey symbols and dotted line=YOY *S. maximus*. Squares indicate no structure, circles show artificial algae treatments, and triangles drift algae treatments. All relationships are significant (p<0.01).

other epibenthic predators (Wilson et al., 1990; Isaksson et al., 1994; Norkko, 1998). Using one predator type only (*P. flesus*), Aarnio and Mattila (2000) focused on shelled prey, species which may actively utilise the algal habitat for protection. The present study concerned interactions with a prey species unable or unwilling to migrate into the algal material. Algae can harbour large abundances of invertebrates (Vetter, 1995; Norkko et al., 2000), but benthic species show highly specific responses to drifting algal mats, with the main beneficiaries being mobile, opportunistic taxa, such as Chironomidae, Ostracoda and *Hydrobia* spp., while infaunal species such as *B. pilosa* are less capable of utilising the algal mats, and are primarily negatively affected by them (Norkko et al., 2000). The organisms used in this study are mainly found on bare substrate, and this may accentuate the effect of the drift algae on these species and their interactions (Isaksson et al., 1994). To the best of our knowledge, drift algal assemblages as a source (rather than a sink) of algal-associated invertebrate prey for flatfish predators have not been quantified, although the assemblages may increase benthic prey availability.

All predators used in this experiment should have been equally able to utilise the prey offered; however, lower predation occurred in the trial utilising *S. maximus* as predator. Of the two species used, *S. maximus* has the bigger gape size and begins to consume macrofauna immediately after settling (Gee, 1989), so lower predation was not expected. The low consumption by *S. maximus* could be a consequence of using small individuals with a lower energy demand than the bigger *P. flesus*. In addition, the *S. maximus* individuals used in our trial were at a length (≥ 30 mm) when they reduce the amount of amphipods in their diet in favour of fish (Aarnio et al., 1996), which may have influenced our results. In contrast to the other predator treatments, YOY *P. flesus* continued to consume *B. pilosa* even though drift algae were present, albeit at a lower rate. Perhaps the smaller *P. flesus* were less physically hindered by the structure in the drift algae treatment. Differing feeding behaviour between age groups has been shown in past studies (Summers, 1980).

4.2. The experimental set-up; structural and chemical impact on foraging

Limitations of small-scale short-term experiments (including low replication) need to be taken into account when interpreting the results. The use of small experimental arenas may have affected the behaviour of the predators, in particular the larger *P. flesus*. Unpublished results show a lower, albeit non-significant (p > 0.05) rate of consumption (%) over 5 h by *P. flesus* in smaller experiment containers (256 cm^2) compared to larger ones (602 cm^2) (Nordström et al., unpubl.). Even though this difference disappears when experimental time is prolonged to 10 h, it indicates that some restriction on foraging may have occurred here, possibly adding to the effect seen in drift algae treatments. Although limiting extrapolation to larger scales and natural conditions, microcosms this size have been useful in previous studies (Boström, 2002) and minimise scale-dependent co-aggregative behaviour of predators and prey which may lead to overestimation of prey mortality (Bergström and Englund, 2002).

This study did not effectively separate the structural and chemical impact of the treatments on predation efficiency due to discrepancies in characteristics (volume, wwt, density, rugosity) between the real and the artificial structure. Our results indicated reductions in foraging efficiency by artificial algae, but these were not significant. The density of the structure was probably too low to provide a protective refuge for the prey (Heck and Thoman, 1981; Nelson and Bonsdorff, 1990). Although R^2 values for the equations indicated high predictive power, the regression analyses on foraging efficiency vs. oxygen concentration also showed a grouping of the different values according to treatments, thus confounding the impact of oxygen levels on foraging with that of structure (Fig. 2). The trial performed with *S. maximus* indicates that, in this case, structure was the important factor as foraging ceased at relatively good oxygen conditions (75–87% saturation). This was not as evident in the trials with *P. flesus*.

Changes in the chemical properties (oxygen deficiency, toxic substances) of the sediment and bottom water are an important feature of drifting algal mats, and further add to alterations in predator–prey relationships. These alterations can include increased or diminished predator foraging efficiency, or increased prey availability (Norkko and Bonsdorff, 1996b; Tallqvist et al., 1999; Tallqvist, 2001). The macroalgal-induced physical and chemical changes in the habitat may lead to synergistic effects on ecological interactions, and must together be acknowledged when evaluating the effects of drifting algae.

4.3. Altered food preferences of juvenile flatfish

Although adults occur over a wide range of habitats, juvenile *S. maximus* and *P. flesus* are confined to a very limited nursery area, and ultimate recruitment levels are dependent on the quality and quantity of sites suitable for juvenile survival (Gibson, 1994). The presence of

structure alters the accessibility of prey and subsequently the diet of benthic fish (Aarnio and Mattila, 2000; Andersen et al., 2005; this study). Changes in structural characteristics may alter the suitability of a habitat as a nursery area (Gibson, 1994). The effects on the fish may be size-dependent (Wennhage and Pihl, 1994) and may or may not translate to a change in growth rates (Meng et al., 2000; Andersen et al., 2005). *P. flesus* is able to utilise a wide array of benthic food items, and specialises on preferred prey only when these are abundant (Mattila and Bonsdorff, 1998; Andersen et al., 2005). *S. maximus* quickly enters the piscivorous life stage and is therefore less dependent on zoobenthos than *P. flesus* (Aarnio et al., 1996). Nevertheless, both species are potentially confined to bare substrate immediately after settlement (Wennhage and Pihl, 1994).

5. Conclusions

Drift algae inhibit the foraging efficiency of juvenile flatfish. While we did not manage to separate the structural and chemical effects of the macroalgae, it was evident that predation success was hampered for both predator species (*Platichthys flesus* and *Scophthalmus maximus*), and size classes (+1 and YOY *P. flesus*). However, YOY *P. flesus* was the only predator able to continue feeding successfully in the presence of drift algae. Our study confirms that drift algae may have effects on predation rates and trophic transfer of energy through the food web in areas essential for flatfish recruitment in the Baltic Sea. The potential impacts of this effect are made greater by the system's low species diversity and relatively simple food web. The future challenge lies in determining the long-term effects of drifting algae on trophic interactions in the Baltic Sea.

Acknowledgements

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