

FLOATING SEAWEED AS EPHEMERAL NEUSTONIC HABITAT

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The neuston can be defined as 'those plants and animals inhabiting the surface film of the sea'. The living conditions in the upper layer of oceans and seas are considerably different from those in deeper layers. Consequently, the neustonic zone forms a restricted ecological niche inhabited by a wide range of permanent or temporary inhabitants, which are adapted to a stressful way of life in a region of a high organic matter supply. The distribution of neustonic organisms is mainly influenced by vertical migration and temporal and spatial variation. Additionally, winds, currents and the presence of floating objects can give rise to local accumulations of neustonic organisms. Of special interest is the neustonic community associated with the permanently floating seaweed *Sargassum*, which is abundantly found in the Sargasso Sea. Floating mats of these seaweed species significantly contribute to the primary production in the neustonic zone of the North Atlantic and consequently support a diverse community of marine organisms that use the seaweeds as food source, shelter, foraging grounds or surface for attachment.

Next to the permanently floating *Sargassum*, the neuston is also strongly influenced by the occurrence of smaller, and usually ephemeral floating patches composed of detached coastal seaweed fragments. Ephemeral floating seaweeds harbour a diverse fauna originating from attached seaweeds, the strandline of beaches, the surrounding and underlying water column, the seafloor or the air. These organisms colonise the seaweeds for various reasons, usually including the provision of shelter, food or attachment substrate. The association behaviour of these organisms and their use of the resources offered by floating seaweeds potentially have important ecological consequences, like the possibility of passive dispersal of associated fauna to new, distant locations by means of rafting.

The overall aim of this PhD study was to assess the ecological impact of floating seaweeds as ephemeral habitats and potential rafts in the North Sea. Because the information about the neuston and floating seaweed clumps in the North Sea was, up till now, very scarce, different aspects of raft-associated ecology were addressed.

In Chapter 2, the impact of the presence of floating seaweeds on the species composition and species richness of the neuston off the Belgian coast was assessed. Furthermore, the degree of association of the encountered species with the floating seaweed patches was quantified. The analyses were based on seaweed samples and control samples (i.e. surface water samples from a seaweed-free area) gathered in the period October 2002-April 2003. Multivariate analysis on neustonic macrofaunal abundances showed significant differences between seaweed and control samples, when considering the fraction > 1 mm. Differences were less conspicuous in the 0.5mm-

1 mm fraction. Seaweed samples were characterized by the presence of seaweed fauna e.g. *Acari*, *Idotea baltica*, *Gammarus* sp., while control samples mainly contained Calanoida, Larvacea, Chaetognatha, and planktonic larvae of crustaceans and polychaetes. Seaweed samples (1 mm fraction) harboured considerably higher diversities (x3), densities (x18) and biomasses (x49) compared to the surrounding water column (control samples). The impact of floating seaweeds on the neustonic environment was quantified by the calculation of the added values of seaweed samples considering biomass and density. These calculations resulted in mean added values of 311 ind.m⁻² in density and 305mg ADW.m⁻² in biomass. The association degree per species was expressed as the mean percentage of individuals found in seaweed samples in proportion to the total density and biomass of that species (seaweed samples + control samples). Thirteen species show an association percentage higher than 95%, and can therefore be considered as members of the floating seaweed fauna.

Chapters 3 and 4 focused on the structural variation within the seaweed-associated invertebrate macrofauna. The species composition of macrofauna associated with floating seaweed rafts is highly variable and influenced by many factors like spatial and temporal variation, period since detachment and probably also the seaweed species. The presence of seaweed preferences (Chapter 3) was assessed by a combination of *in situ* seaweed samplings and multiple-choice aquarium experiments in a controlled environment, using the seaweed-associated grazing organisms *Idotea baltica* and *Gammarus crinicornis*. Results from sampling data confirm that the seaweed composition has an effect on macrofaunal species composition and abundance: samples dominated by *Sargassum muticum* displayed higher densities but lower diversities compared to samples dominated by *Ascophyllum nodosum* and *Fucus vesiculosus*. Seaweed preference was also apparent from the multiple choice experiments, but did not exactly match the results of the community analysis: (1) *I. baltica* had high densities in seaweed samples dominated by *F. vesiculosus* and *A. nodosum*, while in the experiments this isopod was most frequently associated with *Enteromorpha* sp. and *F. vesiculosus*, and fed mostly on *S. muticum*, *A. nodosum* and *Enteromorpha* sp.; (2) *G. crinicornis* had high densities in seaweed samples dominated by *F. vesiculosus*, while in the experiments this amphipod was most frequently associated with *S. muticum*, but fed most on *A. nodosum* and *F. vesiculosus*. It is clear from the laboratory experiments that preference for habitat (shelter) and food can differ among seaweed species. However, food and habitat preferences are hard to assess because grazer preference may change if choices are increased or decreased, if different sizes of grazers are used, or if predators or other grazers are added to the experiments. Effects of seaweed composition may also be blurred due to the obligate opportunistic nature of a lot of the associated macrofaunal species.

The study described in Chapter 4 was more comprehensive and covered a larger temporal and spatial scale than in Chapter 3. The study aimed to determine what the driving forces of variation are within the invertebrate community associated with floating seaweeds, and what their relative importance is. Additionally, the temporal variation within the populations of *Gammarus* sp. and *Idotea* sp. was analysed on the levels of length and sexual maturity. The results of the multivariate analysis indicated that spatial and especially seasonal variation are important factors, next to the seaweed species composition of the clumps: the combination of the volume percentages of *Fucus*

vesiculosus and *Fucus spiralis*, sea surface temperature and depth resulted in the highest matching coefficient in the BIO-ENV procedure ($Rho = 0.26$). This coefficient, however, was still rather low, implying that other factors like seaweed age and travelling history strongly structure the assemblage. A large part of the seasonal variation was determined by the timing of the reproduction periods of the associated invertebrates. Both *Gammarus* sp. and *Idotea* sp., for example, reproduced all year round, with the highest intensity in spring. Next to predictable and measurable factors like sea surface temperature, clump volume and seaweed species composition, there are a lot of factors that are hard (e.g. clump age) or even impossible (e.g. occurrence of storms, exchanges between clumps) to quantify. Consequently, the composition and density of floating seaweed-associated macro-invertebrates can only partially be predicted or explained.

Floating seaweed is considered to be an important habitat for juvenile fishes due to the provision of food, shelter, a visual orientation point and passive transport. The importance of the presence of the highly dynamical seaweed clumps from the North Sea to juvenile neustonic fishes was investigated in Chapter 5 by analysing both neuston samples (without seaweed) and seaweed samples concerning fish community structure, and length-frequency distributions and feeding habits of five associated fish species. While the neustonic fish community was mainly seasonally structured, the seaweed-associated fish community was more complex: the response of the associated fish species to environmental variables was species specific and probably influenced by species interactions, resulting in a large multivariate distance between the samples dominated by *Chelon labrosus* and the samples dominated by *Cyclopterus lumpus*, *Trachurus trachurus* and *Ciliata mustela*. The results of the stomach analysis confirmed that *C. lumpus* is a weedpatch specialist that has a close spatial affinity with the seaweed and feeds intensively on the seaweed-associated invertebrate fauna. Similarly, *C. mustela* juveniles also fed on the seaweed fauna, but in a more opportunistic way. The shape of the size-frequency distribution suggested enhanced growth when associated with floating seaweed. *Chelon labrosus* and *T. trachurus* juveniles were generally large in seaweed samples, but large individuals were also encountered in the neuston. The proportion of associated invertebrate fauna in their diet was of minor importance, compared to the proportions in *C. lumpus*. Individuals of *Syngnathus rostellatus* mainly fed on planktonic invertebrates but had a discontinuous size-frequency distribution, suggesting that some of the syngnathids were carried with the seaweed upon detachment and stayed associated. Floating seaweeds can therefore be regarded as ephemeral habitats shared between several fish species (mainly juveniles) that use them for different reasons and with varying intensity.

Because floating seaweeds generally carry a wide variety and large densities of associated fauna, ranging from small planktonic crustaceans to juvenile fishes, the initial hypothesis of the study described in Chapter 6 therefore stated that, if present, floating seaweeds may signal the presence of abundant prey to seabirds and induce small-scale patchiness. The influence of floating seaweed patches on the distribution and behaviour of seabirds was investigated using the European Seabirds At Sea database (ESAS). The ratio of frequency of occurrence in association with floating seaweed to total frequency of occurrence differed between species and seabird groups based on their foraging strategies. The results indicated that surface feeding species that

make shallow dives (terns and red-breasted mergansers) benefit most from the presence of floating seaweeds and their associated macro- and ichthyofauna. Species hunting for pelagic and bottom-dwelling prey (divers, guillemots, razorbills, puffins, gannets and cormorants), and especially benthos feeders (scooters and eiders) were frequently seen in association with floating seaweeds, while opportunists and scavengers like gulls and skuas were recorded on few occasions. Finally, petrels and shearwaters (surface-seizing, pursuit-plunging, pursuit-diving) were seldomly seen in association with floating seaweeds. The most common behavioural activities of the birds associated with floating seaweed were found to be surface pecking, actively searching, and pursuit plunging.

An important consequence of association behaviour of marine organisms is the possibility of passive dispersal by means of rafting. For the study described in Chapter 7, laboratory experiments were conducted to evaluate the longevity, and consequently also the rafting capacity of the brown seaweeds *Fucus vesiculosus* and *Ascophyllum nodosum*. The seaweed degradation process and the activity of the grazer *Idotea baltica* were strongly influenced by temperature: only at 5°C, the seaweed growth exceeded the weight loss. At higher temperatures, seaweed fragments sank quickly (within 100 days at temperatures higher than 15°C). This process was significantly accelerated in the presence of *Idotea baltica*, resulting in a decrease of raft longevity of 60-70%. At a constant temperature of 15°C and in the absence of grazers, fragments of *A. nodosum* floated longer (mean 45 weeks) than fragments of *F. vesiculosus* (mean 15 weeks). The results indicate that floating seaweeds have the potential to stay afloat for a long time, but that their longevity is temperature-dependent and strongly reduced by grazing activity of associated herbivores.

The results of this PhD thesis demonstrate that the habitat formed by floating seaweeds is very complex. Although the presence of floating seaweeds in the neuston can, to a certain degree, be seasonally predicted (storms, seasonal release of fertile structures), the habitat that they form is still very patchy and unstable. Consequently, most species found in association with ephemeral floating seaweed patches are opportunistic of nature. However, some species display a higher level of adaptation to this habitat than other species, which is manifested in the reproduction by continuous brooding in *Idotea baltica*, the diet consisting of seaweed-associated macrofauna in *Cyclopterus lumpus* and the behavioural shift towards surface pecking and dipping in *Sterna hirundo*. The association behaviour of the encountered species and their (optimal) use of the transient resources offered by floating seaweeds potentially have important ecological consequences, like for example the passive dispersal of associated fauna to new, distant locations by means of rafting. The process of rafting strongly depends on the longevity of the seaweed raft, which is in turn significantly influenced by temperature and grazing pressure. In favourable conditions, seaweed rafts can potentially cover great distances, carrying with them rafting fauna that are able to survive a long journey in the neuston.