UNIVERSITEIT
GENT

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FLOATING SEAWEED AS EPHEMERAL NEUSTONIC HABITAT

Drijvend zeewier als efemeer neustonisch habitat

Sofie Vandendriessche

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Academic year 2006 – 2007

Thesis submitted in partial fulfillment of the requirements for the degree of
Doctor in Science (Biology)

Today I changed course for the first time since departing Gomera because the wind was variable and sometimes calm. I first sailed west by north and then WNW, making 21 or 24 miles. . . . The sailors caught a little fish, and we saw much weed of the kind I have already mentioned, even more than before, stretching to the north as far as you can see. In a way this weed comforted the men, since they have concluded that it must come from some nearby land. But at the same time, it caused some of them great apprehension because in some places it was so thick that it actually held back the ships.

Thursday, 20 September 1492

Christopher Columbus

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Friday, 15 December 2006 at 4.30 p.m.
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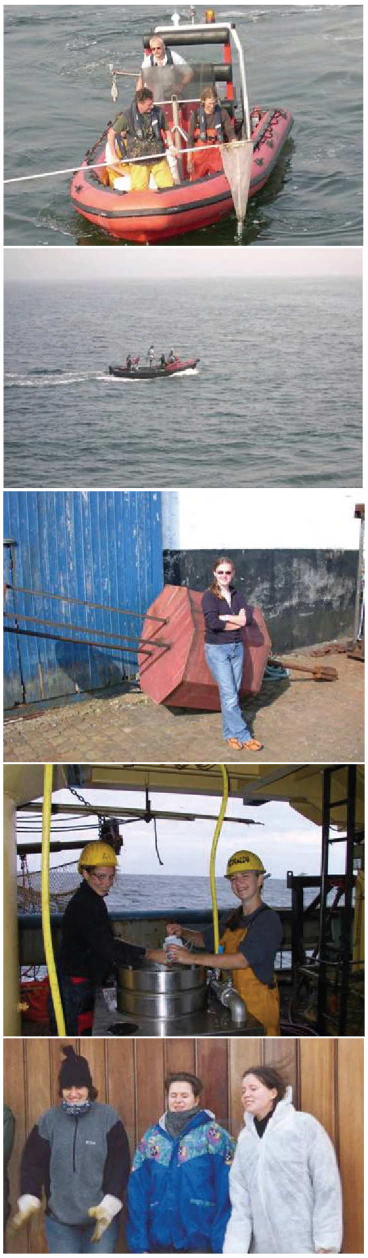
DANKWOORD

Dankwoord

Volgens velen is een doctoraat een periode van véél werk en véél stress. Dat is natuurlijk waar, maar ik kan me nochthans ook ontelbare momenten voor de geest halen waarvan ik dacht: “da’s nu ne keer ’t goe leven!” Zoals u misschien al kunt raden gaat het dan vooral over staalnames bij mooi weer, een spiegelgladde zee en een overvloed aan drijvende wierpakketten en dolfkes; maar ook daarbuiten heb ik mijn doctoraatsperiode ervaren als een leerrijke periode vol aangename samenwerkingen en interessante ervaringen.



Mensen die mij al langer dan 4 jaar kennen, zullen beamen dat ik volledig ‘gebeten’ was van mijn thesisonderwerp. Ik mag me dan ook gelukkig prijzen dat ik de kans heb gekregen om dat onderwerp verder uit te spitten, en dat ik alle mogelijkheden en steun heb gekregen om mijn studie tot een goed einde te brengen. Het schrijven van dit doctoraat zou onmogelijk zijn geweest zonder de hulp van collega’s, vrienden en familie. Hoog tijd dus voor een woordje van dank.

Vooreerst wil ik mijn promotoren Prof. Dr. Magda Vincx en Dr. Steven Degraer bedanken voor hun onophoudelijke steun tijdens de opbouw en het verloop van dit project. Alhoewel mijn doctoraat niet echt binnen het benthosonderzoek kadert, hebben ze me toch alle mogelijkheden geboden om het uit te werken, en hebben ze me steeds bijgestaan met advies en suggesties. Steven, merci voor alle uren lees- en denkwerk! Meestal had ik na een uurtje discussie met jou een nieuwe kijk gekregen op mijn data, en ging het verwerken en schrijven daarna een heel stuk vlotter.

Zoals ik al zei, heb ik fantastische herinneringen aan mijn staalnameperiode. Het succes van die staalnames hing grotendeels af van het weer en van de aanwezigheid van wiertjes, maar was ook afhankelijk van een goede organisatie. Daarom wil ik een woordje van dank richten tot het VLIZ en meer bepaald tot André Cattrijsse voor het organiseren (en vaak ook herorganiseren) van vaardagen met de Zeeleeuw, Zeehond en Zeearend, en voor de hulp bij de constructie van het neustonnet. Bedankt ook aan de bemanningen van de Zeeleeuw en Zeehond voor jullie enthousiasme en hulp bij het opvissen van ‘groene bloazen, drendels, orgasmewier en zèluzen’. De tochtjes in het loodsbootje waren meestal héél tof, maar soms was het ook berekoud en vrij lastig voor de maag, hetgeen vele staalname-vrijwilligers aan den lijve hebben ondervonden. Ontelbare mensen, zowel collega’s, studenten, vrienden als familie, hebben het gewaagd om bij alle soorten weersomstandigheden in dat bootje te stappen (ik ga geen poging ondernemen om ze allemaal op te noemen, want ik ga sowieso mensen vergeten). Ik ben jullie eeuwig dankbaar en ik hoop dat jullie er plezier aan hebben beleefd!

Uiteindelijk resulteerden de staalnames in een massa van potten en emmers vol wier en beestjes, die allemaal moesten verwerkt en geanalyseerd worden. Daarbij heb ik (gelukkig!) wat hulp gekregen van enthousiaste thesisstudenten (Marlies Messiaen & Gina De Keersmaecker) en maandwerkstudenten (Lien Steenhuyse, Matthew Lammertyn, Boris Pellegroms, Katrien Broekaert, Fréderic Leroux, Jelle Evenepoel). Daarnaast wil ik Danielle, Danny en Bart nog bedanken voor de asvrij-drooggewicht bepalingen, Annick en Danny voor de hulp in de klimaatkamers, Guy voor het scannen en Dirk voor de pigmentanalyses.

Het boekje dat u nu voor u hebt toont de resultaten van geslaagde staalnames en experimenten. Jammer genoeg hebben een aantal aspecten van de initieel geplande studie om practische redenen of tijdsgebrek niet de aandacht gekregen die ze verdienden. Eén van die aspecten is de studie over de dynamiek van drijvende wierpakketten die gebaseerd had moeten worden op de resultaten van een *in situ* experiment met een boei. Dat experiment is jammer genoeg niet geslaagd, ondanks de inspanningen van velen. Daarbij denk ik vooral aan José Reynaert en Jan Covemaecker (Ship Technics) die de boei hebben ontworpen en geconstrueerd, aan Jürgen die de experimentele opstelling heeft gemaakt en aan de bemanning van de Zeearend die de boei heeft geplaatst en jammer genoeg ook weer heeft moeten verwijderen. Een ander aspect van deze studie is de modellering van de trajecten die drijvende wierpakketten afleggen, hetgeen had moeten doorgaan in samenwerking met Serge Scory van de BMM. Serge, toch bedankt voor alle uitleg en voor je bijdrage aan mijn IWT-rapport! Terwijl ik bezig ben, wil nog enkele andere BMM-medewerkers bedanken voor hun bijdrage aan het opsporen van wierpakketten nl. Marisa Di Marcantonio en Benoit Loicq. Vooral een dikke merci om mij eens te laten meevliegen met de Britten Norman Islander. Ik heb toen wegens het slechte weer geen sprietje wier gezien, maar het was wel een toffe ervaring!

Voor het hoofdstuk over zeevogels geassocieerd met zeewier werden de data voorzien door de ESAS-partners, waaronder het Instituut voor Natuur- en Bosonderzoek. Vooral co-auteur Eric Stienen verdient een hartelijk woordje van dank voor het toeleveren van de data, voor het optreden als contactpersoon met de ESAS-partners en voor het lezen en bediscussiëren van het manuscript.

En dan kom ik bij de collega's van de Sectie Mariene Biologie... Dat ik zulke goede herinneringen overhoud aan mijn doctoraat is grotendeels aan jullie te danken. Ik heb het dan niet alleen over jullie bereidwilligheid om mee te gaan op zee, maar vooral ook over de collegiale en toffe sfeer tijdens practica, strand- en andere staalnames, de stages Wimereux, congressen, kwissen en andere evenementen. Een speciaal bedankje gaat naar Tim voor het opstellen van mijn databank, naar Marleen voor het nalezen van enkele van mijn manuscripten, naar Annelies G. voor de toffe staalnameweek op de Tridens, naar Wouter voor het maken van kaartjes, en naar mijn burogenootjes Saskia, Thomas en Sofie voor de babbels en eerste hulp bij computerproblemen.

Annelies DB, Eveline, Maarten en Saskia verdienen elk een gigantische dankuwelmerci voor het delen van lief en leed de afgelopen 7(!) jaar. Evenementen zoals 'de suikerkick', de reisjes naar Noorwegen en Etretat, de kennismaking met Yves Remère, mijn vrijgezellenavond (zonder Maarten uiteraard), en vele BBQ's en etentjes zijn in mijn geheugen gegrift. Vooral ook de wekelijkse badminton en de BBB-activiteiten stelden mij in staat om af en toe eens alle doctoraatsbeslommeringen te vergeten. Bedankt dus ook aan Ivan, Tom, Peter, Jan, Kris, Els, Jo, Xenia en David voor het incasseren en terugmeppen van de pluimpjes.

Uiteindelijk heb ik alles te danken aan mama en papa. Zij hebben me steeds alle kansen en steun geboden om mijn droom waar te maken: eerst om biologie te studeren, daarna om nog een jaartje MareLac bij te doen, en ten slotte om aan dit doctoraat te beginnen. Zonder jullie was dit nooit gelukt. Merci ook aan Steven, Sarah, An, Anneleen, Stijn, Hélène, Marita, François en de mémé's voor de interesse en alle aanmoedigingen.

Ten slotte moet ik nog één héél speciale ex-collega - waarmee ik bijzonder mooie momenten heb beleefd op de Zeeleeuw (geen details...) en die ik sinds april 2006 mijn echtgenoot mag noemen - bedanken. Gert, het is een bijzonder hectisch jaar geweest met jouw doctoraat, de trouw en huwelijksreis, en nu mijn doctoraat; maar ik had het voor geen geld willen missen. Merci voor alle steun, leeswerk, kusjes en kalmerende babbels. Ik besef dat het niet gemakkelijk kan zijn om met een zwangere vrouw met doctoraatskoorts te moeten samenleven. Ik kijk er al naar uit om samen met jou en ons klein prutske aan nieuwe uitdagingen te beginnen...

16 oktober 2006
Sofie Vandendriessche

De financiële steun voor dit doctoraatsonderzoek werd verschaft door het Instituut voor de aanmoediging van Innovatie door Wetenschap en Technologie in Vlaanderen (IWT) en door de Universiteit Gent (BOF GOA 12050398). Scheepstijd en logistieke steun werden voorzien door het Vlaams Instituut voor de Zee (VLIZ) en de Administratie Waterwegen en Zeewezen (AWZ).

SUMMARY

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SAMENVATTING

SUMMARY

Zaitsev (1970) defined the neuston 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 (Coston-Clements et al, 1991). 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 (Davenport & Rees, 1993, Ingólfsson, 1995). 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, such as 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 the 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 >1mm. Differences were less conspicuous in the 0.5mm-1mm fraction. Seaweed samples were characterised 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 (1mm 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 305 mg 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 showed 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 size distribution 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 the 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.

SAMENVATTING

Zaitsev (1970) definieerde het neuston als 'de planten en dieren die de oppervlaktelaag van de waterkolom bevolken'. De levensomstandigheden in die oppervlaktelaag verschillen substantieel van deze in diepere waterlagen. Daarom wordt de neustonische zone beschouwd als een beperkte niche die wordt ingenomen door een waaier van permanente of tijdelijke bewoners die aangepast zijn aan een leven in een stressvolle omgeving met een grote toevoer van organisch materiaal. De verspreiding van het neuston wordt vooral bepaald door vertikale migratie, en temporele en ruimtelijke variatie. Daarenboven kunnen de werkingen van wind en stromingen en de aanwezigheid van drijvend materiaal lokale accumulaties van neustonische organismen teweeg brengen. Vooral de neustonische gemeenschap geassocieerd met het permanent drijvende zeewier *Sargassum*, hetgeen abundant kan teruggevonden worden in de Sargassozee (Coston-Clements et al, 1991), is daar een goed voorbeeld van. Deze drijvende zeewiermatten dragen significant bij tot de primaire productie in de neustonische zone van de Atlantische Oceaan en ondersteunen bijgevolg een rijke gemeenschap van mariene organismen die het zeewier gebruiken als voedingsbron, beschutting, foerageergebied of vasthechtingsoppervlak.

Naast het permanent drijvende *Sargassum*, wordt het neuston ook sterk beïnvloed door het voorkomen van kleinere, meestal relatief kortlevende (= efemere) pakketten drijvend zeewier die bestaan uit van de kust losgeslagen wierfragmenten. Deze efemere wierpakketten herbergen een diverse fauna afkomstig van vastgehechte zeewiervelden, van op het strand aangespoeld wier, van de omringende en onderliggende waterkolom en vanuit de lucht (Davenport & Rees, 1993; Ingólfsson, 1995). De onderliggende redenen voor associatie met drijvende wieren zijn in de meeste gevallen de voedselvoorziening, het vasthechtingsoppervlak en de beschutting tegen predatoren. Het associatief gedrag van organismen die drijvende wieren koloniseren heeft enkele belangrijke ecologische gevolgen, zoals bijvoorbeeld de mogelijkheid van passieve verspreiding door middel van het zogenaamde rafting (= reizen per vlot).

Het overkoepelende doel van deze doctoraatsstudie was het bepalen van de ecologische impact van drijvende wierpakketten als efemere habitats en potentiële verspreidingsvectoren in de Noordzee. Omdat de informatie over het neuston in het algemeen en drijvende wierpakketten in het bijzonder in deze regio tot nu toe zeer schaars was, werden verschillende aspecten van de met drijvend zeewier geassocieerde ecologie in beschouwing genomen.

De impact van de aanwezigheid van drijvend zeewier op de soortensamenstelling en –rijkdom van het neuston aan de Belgische kust werd bepaald en gekwantificeerd in **hoofdstuk 2**. De analyses werden gebaseerd op zeewierstalen en controlestalen (i.e. oppervlaktewaterstalen zonder zeewier) die werden bemonsterd in de periode oktober 2002 – april 2003. De resultaten van de multivariate analyse toonden significante verschillen aan tussen de abundanties van macrofauna (> 1mm) in zeewierstalen en controlestalen. De verschillen waren minder duidelijk in de groottefractie 0.5 – 1mm. Over het

algemeen werden zeewierstalen gekenmerkt door de aanwezigheid van typische zeewierfauna zoals Acari, *Idotea baltica,* en *Gammarus* sp., terwijl controlestalen vooral Calanoida, Larvacea, Chaetognatha, en planktonische larven van Crustacea en Polychaeta bevatten. Zeewierstalen (1mm fractie) werden gekenmerkt door hogere diversiteiten (x3), densiteiten (x18) en biomassas (x49) in vergelijking met de omringende waterkolom (controlestalen). De impact van de aanwezigheid van drijvende wierpakketten op het neustonische milieu werd gekwantificeerd door het berekenen van de toegevoegde waarde met betrekking tot biomassa en densiteit. Deze berekeningen resulteerden in toegevoegde waarden van 311 Ind/m^2 in densiteit en 305 mg ADW/m^2 in biomassa. De graad van associatie per soort werd uitgedrukt als het gemiddelde percentage van individuen gevonden in zeewierstalen ten opzichte van alle gevonden individuen (zeewierstalen + controlestalen). Dertien soorten toonden een associatiegraad van meer dan 95% en kunnen dus beschouwd worden als leden van de fauna geassocieerd met drijvende zeewier.

De structurele variatie *binnen* de gemeenschap geassocieerd met drijvend zeewier werd onder de loupe genomen in **hoofdstukken 3 en 4**. De soortensamenstelling van de macrofauna geassocieerd met drijvende zeewierpakketten is zeer variabel en wordt beïnvloed door verscheidene factoren zoals ruimtelijke en temporele variatie, de tijd sinds de wieren werden losgeslagen, en waarschijnlijk ook de zeewiersoort. De aanwezigheid van mogelijke zeewierpreferenties, voornamelijk van de grazende crustaceeën *Idotea baltica* en *Gammarus crinicornis* **(hoofdstuk 3),** werd onderzocht door middel van *in situ* staalnames van drijvende wierpakketten gecombineerd met multiple-choice aquariumexperimenten in een gecontroleerde omgeving. De staalnameresultaten bevestigden de hypothese dat de soortensamenstelling van het zeewier een invloed heeft op de soortensamenstelling en abundantie van de geassocieerde fauna: stalen die vooral bestonden uit *Sargassum muticum* vertoonden hogere densiteiten, maar lagere diversiteiten dan stalen gedomineerd door *Ascophyllum nodosum* en *Fucus vesiculosus.* De aanwezigheid van zeewierpreferenties was ook duidelijk in de aquariumexperimenten, maar de resultaten kwamen niet exact overeen met die van de analyse van de stalen: (1) *I. baltica* vertoonde de hoogste densiteiten in zeewierstalen bestaand uit *F. vesiculosus* en *A. nodosum*, terwijl deze isopode in de experimenten het meest werd waargenomen op *Enteromorpha* sp. en *F. vesiculosus*, maar zich het meest voedde met *S. muticum, A. nodosum* and *Enteromorpha* sp.; (2) *G. crinicornis* vertoonde de hoogste densiteiten in zeewierstalen gedomineerd door *F. vesiculosus*, terwijl deze amphipode het meest werd waargenomen op *S. muticum*, maar zich het meest voedde met *A. nodosum* en *F. vesiculosus*. De experimenten toonden duidelijk aan dat de preferentie voor een bepaald habitat (beschutting) en een bepaalde voedselbron kan verschillen naargelang de zeewiersoort. Daarenboven blijken voedsel- en habitatpreferenties zeer moeilijk te bepalen omdat de preferenties van grazers kunnen variëren afhankelijk van het aantal keuzes, de grootte van de gebruikte grazers, en de aanwezigheid van competitoren en predatoren in het experiment. De effecten van de zeewiersamenstelling van drijvende wierpakketten worden hoogstwaarschijnlijk ook versluierd door de obligate opportunistische natuur van het merendeel van de geassocieerde fauna.

De studie beschreven in **hoofdstuk 4** is gebaseerd op een meer uitgebreide staalname (grotere ruimtelijk en temporele schaal). Het doel van deze studie was het bepalen van de drijvende krachten van de variatie aangetroffen binnen de geassocieerde gemeenschap van ongewervelden, en van hun relatieve belang. Daarenboven werd de temporele variatie binnen de populaties van *Gammarus* sp. en *Idotea* sp. geanalyseerd met betrekking tot lengte-frequentie distributie en seksuele maturiteit. De resulaten van de multivariate analyse toonden aan dat, naast de zeewiersamenstelling van de pakketten, vooral de ruimtelijke en temporele variatie belangrijke factoren zijn: de combinatie van de volumepercentages van *Fucus vesiculosus* en *Fucus spiralis,* de oppervlaktewatertemperatuur en de diepte gaf de hoogste coëfficiënt van overeenkomst in de BIO-ENV procedure (Rho = 0.26). Toch is deze coëfficiënt nogal laag, hetgeen impliceert dat andere factoren zoals de leeftijd en de reisgeschiedenis van de zeewierpakketten ook belangrijke invloeden kunnen uitoefenen op de samenstelling van de geassocieerde fauna. Een groot deel van de seizoenale variatie werd bepaald door de timing van de reproductieperiodes van de geassocieerde ongewervelden. Zowel *Gammarus* sp. als *Idotea* sp. bijvoorbeeld reproduceren het hele jaar door, met de hoogste intensiteit in de lente. Naast voorspelbare en meetbare factoren zoals oppervlaktewatertemperatuur, de grootte van de wierpakketten en de zeewiersamenstelling zijn er een aantal factoren die moeilijk (vb. leeftijd van de wierpakketten) of niet (vb. het voorkomen van stormen, uitwisselingen tussen pakketten) te kwantificeren zijn. Bijgevolg kunnen de samenstelling en densiteit van ongewervelden geassocieerd met drijvende wierpakketten slechts gedeeltelijk worden voorspeld of verklaard.

Door de voorziening van voedsel, beschutting, een visueel referentiepunt en de mogelijkheid tot passief transport worden drijvende wierpakketten beschouwd als een belangrijk habitat voor juveniele vissen. Het belang van de aanwezigheid van drijvende wierpakketten in de Noordzee voor juveniele neustonische vissen werd onderzocht in **hoofdstuk 5**. Daartoe werden zowel neustonstalen (zonder zeewier) als zeewierstalen geanalyseerd met betrekking tot de gemeenschapsstructuur van de vissen, en werden de voedingsgewoontes en lengte-frequentiedistributies van vijf vissoorten in detail onderzocht. In tegenstelling tot de neustonische visgemeenschap die vooral seizoenaal was beïnvloed, vertoonde de visgemeenschap geassocieerd met drijvend zeewier een meer complexe structuur: de respons van de geassocieerde vissoorten op de omgevingsvariabelen was soortsgebonden en was waarschijnlijk ook beïnvloed door interacties tussen soorten. Dit resulteerde in een grote multivariate afstand tussen de stalen gedomineerd door *Chelon labrosus* en de stalen gedomineerd door *Cyclopterus lumpus, Trachurus trachurus* en *Ciliata mustela*. De resultaten van de maaganalyses bevestigden dat *C. lumpus* aangepast is aan een leven in associatie met drijvende wierpakketten, aangezien deze soort een duidelijke ruimtelijke associatie vertoont met het drijvend zeewier en zich tevens intensief voedt met de geassocieerde ongewervelde fauna. Ook juvenielen van *C. mustela* voedden zich met deze fauna, maar op een meer opportunistische wijze. De vorm van de lengte-frequentie distributie wees in de richting van een versnelde groei bij zeewier-geassocieerde individuen. *Chelon labrosus* en *T. trachurus* waren over het algemeen groter in zeewierstalen, maar grote individuen werden ook regelmatig aangetroffen in de neustonstalen. Het aandeel van met drijvend zeewier geassocieerde ongewervelden in hun dieet was van minder belang vergeleken met het aandeel bij *C. lumpus*. Individuen van de zeenaald *Syngnathus rostellatus* voedden zich vooral met planktonische ongewervelden maar hadden een discontinue lengte-frequentie distributie. Dit kan een aanwijzing zijn dat sommige zeenaalden werden meegevoerd bij het loskomen van het zeewier en dat ze daarna geassocieerd bleven. Ter conclusie kan gesteld worden dat drijvende wierpakketten beschouwd moeten worden als efemere habitats die met verschillende intensiteiten en om verschillende redenen worden benut door verscheidene vissoorten (vooral juvenielen).

Drijvende wierpakketten voeren meestal een grote variëteit aan geassocieerde fauna, van kleine planktonische crustaceeën tot juveniele vissen, met zich mee. Daarom stelde de initiële hypothese van de studie beschreven in **hoofdstuk 6** dat de aanwezigheid van drijvende wierpakketten een kleinschalige patchiness (= ongelijkmatige verspreiding) kan induceren bij zeevogels door het signaliseren van abundante prooi. De invloed van drijvende wierpakketten op de verspreiding en het gedrag van zeevogels werd onderzocht door middel van de 'European Seabirds At Sea' databank (ESAS). De ratio van de frequentie van voorkomen in associatie met drijvend zeewier tot de totale frequentie van voorkomen verschilt tussen soorten en tussen groepen die werden afgebakend op basis van foerageerstrategie. De resultaten tonen aan dat vooral soorten die zich voeden aan het wateroppervlak en oppervlakkig duiken (sternen en de Middelste Zaagbek) baat hebben bij de aanwezigheid van drijvende wierpakketten en de geassocieerde ongewervelde fauna en visfauna. Soorten die zoeken naar pelagische en met de bodem geassocieerde prooi-organismen (duikers, zeekoeten, alken, papegaaiduikers, Jan-van-Genten en aalscholvers), en vooral benthosvoeders (zee-eenden en eidereenden) werden regelmatig waargenomen in associatie met drijvende wierpakketten, terwijl opportunistische soorten en aaseters zoals meeuwen en jagers slechts enkele keren werden waargenomen. Tenslotte werden stormvogels en pijlstormvogels (grijpen hun prooi aan het wateroppervlak of duiken erachteraan) zelden gezien in de omgeving van drijvend zeewier. Het meest voorkomende gedrag van zeevogels in associatie met drijvend zeewier was pikken aan het wateroppervlak, actief zoeken en achtervolgend duiken.

Een belangrijk gevolg van het associatief gedrag van vele mariene organismen is de mogelijkheid tot passief transport via rafting. Voor de studie beschreven in **hoofdstuk 7** werden laboratoriumexperimenten uitgevoerd om de levensduur, en bijgevolg ook de capaciteit als vlot te evalueren voor de wiersoorten *Fucus vesiculosus* en *Ascophyllum nodosum*. Het degradatieproces van de zeewierfragmenten en de activiteit van de grazer *Idotea baltica* werden sterk beïnvloed door de heersende temperatuur: alleen bij 5°C overtrof de groei het verlies aan gewicht. Bij hogere temperaturen zonken de zeewierfragmenten snel (binnen de 100 dagen bij temperaturen hoger dan 15°C). Het afbraakproces werd significant versneld door de aanwezigheid van *Idotea baltica*, hetgeen resulteerde in een afname van de levensduur van het vlot met 60-70%. Bij een constante temperatuur van 15°C en in afwezigheid van grazers bleven fragmenten van *A. nodosum* gemiddeld langer drijven

(45 weken) dan fragmenten van *F. vesiculosus* (15 weken). De resultaten van deze experimenten tonen aan dat zeewierfragmenten héél lang kunnen blijven drijven, maar dat de levensduur van vlotten bestaand uit drijvend zeewier sterk temperatuurafhankelijk is en wordt beperkt door de begrazing door geassocieerde herbivoren.

De resultaten van dit doctoraatsonderzoek tonen aan dat het habitat gevormd door drijvende wierpakketten zeer complex is. Alhoewel de aanwezigheid van drijvend wier op het wateroppervlak deels kan worden voorspeld (stormen, seizoenaal afwerpen van voortplantingsstructuren), is het habitat dat door deze wieren wordt gevormd zeer onstabiel en ongelijkmatig verspreid. Bijgevolg zijn de meeste soorten die met efemere wierpakketten zijn geassocieerd opportunistisch van natuur. Sommige van deze soorten vertonen een hogere mate van aanpassing aan dit habitat dan andere soorten, hetgeen wordt geïllustreerd door de continue reproductie met broedzorg bij *Idotea baltica*, het dieet bestaande uit zeewier-geassocieerde organismen bij *Cyclopterus lumpus*, en de verandering van gedrag naar pikken aan het wateroppervlak en onderdompelen bij *Sterna hirundo*. Het associatief gedrag van de aangetroffen fauna en hun al of niet optimale gebruik van het tijdelijke aanbod aan levensmiddelen hebben belangrijke ecologische gevolgen, zoals bijvoorbeeld de passieve verspreiding van geassocieerde fauna naar nieuwe, afgelegen plaatsen door middel van rafting. Het succes van rafting is sterk afhankelijk van de levensduur van de vlotten gevormd door drijvend zeewier, hetgeen op diens beurt significant wordt beïnvloed door temperatuur en begrazingsdruk. Toch kunnen drijvende wierpakketten in gunstige omstandigheden lange afstanden afleggen, waarbij ze de geassocieerde fauna die aangepast zijn aan een lang verblijf in het neuston met zich meevoeren.

CHAPTER 1

GENERAL INTRODUCTION AND OUTLINE

Sampling the neuston

1. THE NEUSTON AND ITS INHABITANTS

1.1. Definitions and sampling

The term 'neuston' originates from the Greek νεω, which means 'to swim'. In the beginning of the 20th century, it was mainly used to describe all micro-organisms inhabiting the surface film of a water body (Naumann, 1917). The general term was later broadened to include all animals and plants inhabiting the limnetic and oceanic surface layers (Zaitsev, 1970; Marshall & Burchardt, 2005) and was differentiated in subgroups depending on (a) the exposure to wind drift, hereby distinguishing *pleuston* (organisms exposed to wind drift because they are fixed to the surface by their own buoyancy) and *neuston s.s.* (organisms that stay close to the surface in a more temporary and variable manner), (b) the position of the organism with regard to the water surface (*hyponeuston*: submerged organisms – *epineuston*: organisms on top of the surface film), (c) the size of the organisms (*piconeuston* to *macroneuston*), and (d) the time spent in the neustonic layer, distinguishing *euneuston* or organisms that permanently inhabit the sea surface as adults, *facultative neuston* including organisms that are only found during a certain time of day, together with larval and juvenile stages of planktonic and benthic species, and *pseudoneuston* or organisms that are usually found in deeper water layers but occasionally occur at the surface (Zaitsev, 1970; Hempel & Weikert, 1972; Cheng, 1975; Marshall & Burchardt, 2005). Typical pleustonic forms include organisms like *Sargassum* (Fucales), *Physalia, Velella, Porpita* (Coelenterata), and *Janthina* (Gastropoda); a typically epineustonic organism is the water strider *Halobates* (Insecta). Temporary inhabitants (facultative neuston and pseudoneuston) of the hyponeuston, for example, include larvae of benthic animals, fish eggs and larvae, and a wide variety of crustaceans (Zaitsev, 1970, Cheng, 1975).

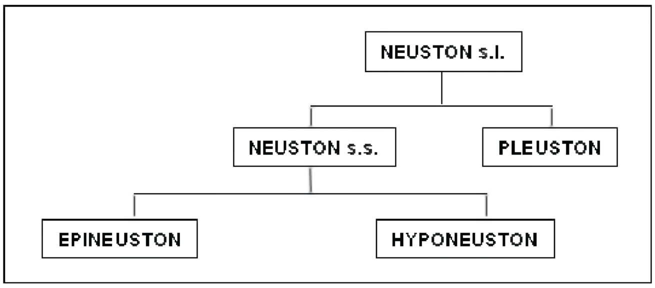

Fig. 1. Basic subdivisions of the neuston

The (macro)neuston is usually sampled with plankton nets of which the mouth is projected partially above and partially below the water surface (see picture on introduction title page). These nets are sometimes fitted with skis or floats and can be subdivided in different horizons, depending on the scale of the study and the water layer or organisms of interest. The sampling depth ranges from 5 cm to 90 cm; mesh size and towing speed are adapted to sampling conditions and the size and vulnerability of the investigated organisms (e.g. David, 1965; Zaitsev, 1970; Schram et al, 1981; Holdway & Maddock, 1983; Tully & O'Ceidigh, 1989; Doyle, 1992; Rawlinson et al, 2005, Vandendriessche et al, chapter 5). Given the method of sampling, studies of the neuston inevitably involve organisms from each of the neustonic categories described in the former paragraph (Cheng, 1975). Therefore, the term neuston should be interpreted as 'neuston s.l.' in the remainder of the text. More precisely, the term 'neustonic' will be used to refer to the surface fauna that are not associated with floating seaweed or other floating objects.

1.2. Ecological conditions in the marine neustonic environment

The living conditions in the upper layer of oceans and seas are considerably different from those in deeper water layers and are highly variable due to the proximity of the air-water interface. Important differences compared to deeper layers are (1) the high dissolved oxygen content, (2) the intensive absorption of solar radiation and (3) the consequent higher temperatures in the upper water layer, which may enhance local production (Zaitsev, 1970; Marshall & Burchardt, 2005). On the other hand, strong UV and IR radiation may have damaging effects (Hempel & Weikert, 1972), and surface water temperature may decrease due to evaporation and wind, making the surface layer a little colder than deeper layers (Cheng, 1975). Neustonic organisms are also exposed to dramatic changes in salinity after heavy rainfall or evaporation, and have to endure strong wave action during storms (Zaitsev, 1970, Marshall & Burchardt, 2005). Furthermore, contaminants such as heavy metals and various petroleum hydrocarbons are frequently introduced in the surface layer (e.g. river run-off and oil spills by ships) and generally reduce surface abundance and productivity (Hardy et al, 1985; Hardy, 1997; Wurl & Obbard, 2004). Next to the particular abiotic factors, life in the neuston is heavily influenced by biotic factors such as predation. Due to the close association with the sea surface, escape possibilities of neustonic organisms are reduced by half, while the predation pressure by fishes and birds is very high.

Notwithstanding the increased stress, the neustonic environment is densely populated with algae, bacteria and various life stages of zooplankton and fishes, which is mainly due to the high supply of nutrients. This nutrient supply supports an enriched productivity of the phytoneuston compared to the phytoplankton (Hardy, 1984), and supports large numbers of heterotrophic bacterioneuston (Zaitsev, 1970). A major input of organic matter is constituted by aerial precipitation onto the water surface. Insects blown out to sea, for example, are deposited on the sea surface and eventually die, but they do not immediately sink and play an important role in the feeding of neustonic fish (Zaitsev, 1970; Hempel & Weikert, 1972; Bowden & Johnson, 1976). Furthermore, aerial deposits of pollen, spores, cysts and other small particles contribute to the accumulation of terrigenic organic matter. Another important source of dead organic substances in the surface layer is the remains and excreta of aquatic animals and plants. Floating bird and mammal carcasses are quite

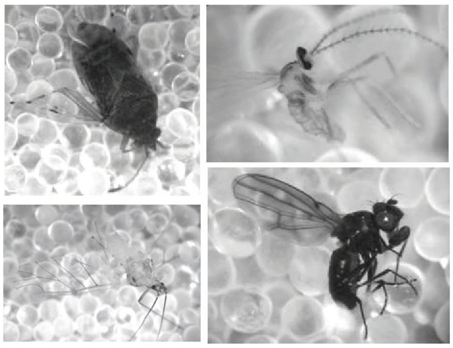

Fig. 2. Diptera and Hemiptera recovered from the sea surface (Belgian coastal zone)

common, but also decaying bodies of some crustaceans are known to become buoyant and rise to the surface. In addition to dead organic matter, the surface layer is rich in colloidal and dissolved organic matter like phosphates and organic nitrogen (Zaitsev, 1970; Cheng, 1975). Concentrations of organic matter of various origin may give rise to the formation of foam, which stimulates the development of a rich life by serving as food for heterotrophic organisms (Zaitsev, 1970).

The high amount of stress induced by biotic and abiotic factors gives rise to a number of adaptation strategies in neustonic organisms (Tully & O'Ceidigh, 1989). The part of pleustonic organisms (e.g. *Velella, Physalia*) that projects above the water, for example, can withstand prolonged dessication and exposure to direct solar irradiation (Zaitsev, 1970). Moreover, neustonic organisms often have a specific pigmentation, which can screen solar radiation and reduce predation (e.g. countershading with a blue colour on the upper side and a silvery colour on the lower side of the body – Zaitsev, 1970; Doyle, 1992). To maintain their position near the sea-surface, even in strong wave conditions, many organisms develop structures that promote buoyancy, such as fat inclusions in fish eggs and gas inclusions (e.g. air bladders in de seaweed *Sargassum,* air sac on the dorsal side of Mugilidae fry). Other organisms cling to floating objects and, in many cases, mimic their appearance (e.g. the Sargassumfish *Histrio histrio* – Coston-Clements et al, 1991).

1.3 Composition, structure and distribution

The composition of the (macro)neuston is highly variable and mainly depends on vertical migration (circadian rhythms), and temporal and spatial variation (e.g. Holdway & Maddock, 1983; Tully & O'Ceidigh, 1986; Locke & Corey, 1988; Rawlinson et al, 2005). The vertical distribution and migratory patterns of fauna are influenced by the light/dark cyclic periods perceived below the surface and the wavelengths discernable at various depths (Hempel & Weikert, 1972; Marshall & Burchardt, 2005). Especially UV-radiation and increased visibility to predators prevent most species from living near the sea surface during the day (Holdway & Maddock, 1983). Seasonal variation has been observed in most studies concerning the neuston, and is most pronounced in zones were temperature shows the largest amplitude (e.g. the littoral; Zaitsev, 1970). Generally, the neuston is richest and most abundant in summer due to the reproduction and larval development of many invertebrates and fishes in this period with optimal feeding conditions. By the time the surface temperature drops, most of these young organisms have recruited to deeper water layers or to the benthos.

As the permanent marine neuston mainly consists of thermo- and halophilic species (see table 1), largest diversities are reached in tropical waters and in temperate waters during summer. In temperate regions and at high latitudes, the temporary neuston shows a distinct circadian rhythm and generally constitutes the majority of the organisms, while specialised neustonts are rare (Zaitsev, 1970; Hempel & Weikert, 1972). The (sub)tropical neuston, on the other hand, is characterised by the presence of euneustonic species with a very strong affinity for the water surface, like the large marine water striders of the genus *Halobates*, and the molluscs *Glaucus* and *Janthina*. On a smaller geographic scale, the distribution of the neuston is highly influenced by winds and currents, which can disrupt the neustonic film and create local accumulations at surface slicks, fronts, eddies, upwelling regions and windrows (Shanks, 1983; Kingsford & Choat, 1986; Marshall & Burchardt, 2005). These accumulations are very conspicuous at the sea surface, because they contain foam and large numbers of floating objects.

Table 1. Composition of the hypo-, epi-, and phytoneuston, with examples per group (based on Zaitsev, 1970)

Group of Organisms	**Examples of Neustonic Representatives**
Hyponeuston	
Microorganisms	*Chromobacterium agarlyticum, C. rubidum, Micrococcus tetragenus, Sarcina citrina*
Protozoa	*Tintinnopsis kofoidi, Spumellaria* sp.
Small metazoans (invertebrates)	*Magelona rosea* (Polychaeta larvae), *Evadne tergestina* (Cladocera), *Oithina minuta* (Copepoda)
Large metazoans (invertebrates)	*Anomalocera patersoni* (Copepoda), *Gammarus locusta* (Amphipoda), *Bodotria arenosa* (Cumacea)
Fish eggs, larvae and fry	Mugilidae sp. eggs, Exocoetidae larvae
Epineuston	*Halobates* sp. (Insecta)
Phytoneuston	*Sargassum natans, S. fluitans*

Of special interest here is the neustonic community associated with the permanently floating seaweed *Sargassum (S. natans* and *S. fluitans)*, which is found in the Sargasso Sea and is subject to Langmuir currents (Johnson & Richardson, 1977; Coston-Clements et al, 1991; Woodcock, 1993). 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 structures (see section 2).

1.4 The role of the neuston in the marine environment

Due to the abundance of food and the stimulating light regime, the neuston mainly consists of early developmental stages of invertebrates and fishes, especially in temperate regions (Hempel & Weikert, 1972). In the Belgian part of the North Sea, for example, the fraction of eggs, larvae and juveniles amounted up to 95% of the total number of organisms (Messiaen, 2004). Consequently, the neustonic layer plays a key role in the growth and dispersal of a wide variety of marine organisms and in the regulation of recruitment to adult pelagic and benthic populations. This process of recruitment to deeper habitats is, together with the ascent of adults for spawning and the vertical migration of organisms that feed at the surface, responsible for the redistribution of the large amount of nutrients found in the neuston (Zaitsev, 1970). Additionally, the neustonic layer forms the contact zone between the marine environment, the air and the terrestrial environment: birds feed on neustonic prey but add nutrients in the form of carcasses and excretions, while in the littoral zone, there is an exchange of organic matter (e.g. beaching of carcasses and floating objects) and living organisms (e.g. settlement of benthic organisms).

To summarise, it can be stated that the neuston is a zone of intensive interaction with the air, the terrestrial environment and the deeper marine environment and that it plays a crucial role in the redistribution of organic matter and organisms which are adapted to a life in this habitat.

2. FLOATING OBJECTS AND THEIR POTENTIAL AS RAFTS

2.1 Fauna associated with floating objects

Within the quite uniform neustonic environment, floating objects are important sources of small-scale patchiness that significantly influence the faunal species composition of the neuston. Due to the provision of shelter from predatory fish and birds, the surface for attachment and in some cases even a food source, they attract a high variety of organisms ranging from stalked barnacles to harpacticoid copepods and turtles. Some neustonic animals are so specialised that they need floating objects for their survival. The grapsid crab *Planes minutus*, for example, is never collected from water that does not contain floating material like *Sargassum*, logs, pumice, cepalopod shells or tar balls, and has been shown to stay within 5cm of a floating object (Davenport, 1992). Another invertebrate with a clear dependency for floating objects is the harpacticoid copepod *Parathalestris croni*, which uses floating clumps of seaweed as 'nests' for its nauplii (Ingólfsson & Ólafsson, 1997).

Next to these highly specialised species, floating objects are colonised by many other invertebrate and fish species. Holdway and Maddock (1983), for example, found a high variety of epifauna (bryozoans, brachyuran megalopae, isopods, stalked barnacles, egg masses, polychaetes, etc.) associated with floating rubbish, pumice and tar on their journey from Fiji to the Bay of Biscay. A wide variety of fish taxa have a natural tendency to aggregate beneath or associate with floating structures such as plastic debris, floating seaweeds, pieces of wood, jellyfish, fish aggregation devices (FADs) and animal remains (e.g. Safran & Omori, 1990; Davenport & Rees, 1993; Moser et al, 1998, Masuda & Tsukamoto, 2000; Castro et al, 2001; Jaquemet, 2004; Thiel & Gutow, 2005 a, b). The presence of these high densities of associated fauna has been shown to attract larger predators such as seabirds (e.g. Haney, 1986; Arcos, 2000; Jaquemet et al, 2004).

The motives of invertebrates, fishes and birds for associating with floating objects are species-specific and many authors have already hypothesised on the advantages of this association behaviour. The most common motives are probably the availability of a surface for attachment, the provision of shelter from predators, and the presence of a food source (the substrate itself or the associated fauna) (Wright, 1989; Safran & Omori, 1990; Coston-Clements et al, 1991; Davenport & Rees, 1993;

Ingólfsson, 1998, Castro et al, 2001; Thiel & Gutow, 2005b). Other possible reasons are the functioning of floating objects as a substitution of the seabed or the littoral zone, as a spawning substrate and nursery area, as a meeting point for the formation and maintenance of schools, or as a cleaning station (Gooding & Magnuson, 1967; Coston-Clements et al, 1991; Castro et al, 2001; Masuda & Tsukamoto, 2000; Ólafsson et al, 2001). Although probably not a motive for association by itself, the possibility of rafting on floating objects is a major advantage for a lot of associated species. Rafting can greatly enhance their dispersal over distances beyond their swimming abilities (Dooley, 1972; Kingsford & Choat, 1985; Tully & O'Ceidigh, 1986; Locke & Corey, 1989; Wehrtmann & Dittel, 1990; Ingólfsson, 2000, Thiel & Gutow, 2005 a, b).

2.2 The principles of rafting

Many floating objects are highly buoyant and can travel huge distances under the influence of winds and surface currents. Consequently, the colonisation of floating objects by organisms from different origins creates the possibility of passive, long distance dispersal mediated by rafting. The process of rafting has been comprehensively reviewed in Thiel and Gutow (2005 a, b) and in Thiel and Haye (2006). The basic principles will be summarised in the following paragraphs (without unduly repeating these references).

Previous studies have shown that for a lot of marine species, the geographical distribution is wider than expected based on the dispersal potential, especially in the case of invertebrates with direct development (Johannesson, 1988). For some of these species, the expansion of their geographical range can be attributed to rafting-mediated passive dispersal (Helmuth et al, 1994). Martel and Chia (1991) demonstrated that several marine benthic molluscs lacking a planktonic larval stage disperse by drifting and subsequent rafting on floating objects, thus enhancing gene flow between populations. Additionally, the collection of floating objects worldwide has shown that many macro-invertebrates, fishes, and even terrestrial species like flightless insects and lizards can travel long distances and survive in association with these objects (e.g. Edgar, 1987; Helmuth et al, 1994; Peck, 1994; Smith, 2002).

The success of rafting and subsequent colonisation of new habitats mainly depends on three factors: (1) the adaptations of rafting organisms to survive the voyage, (2) the longevity, availability and quality of the raft, and (3) the ability of rafters to establish new populations upon arrival in a suitable habitat. The second factor will receive most attention in the present dissertation.

Floating items differ considerably in size, buoyancy, longevity and value as a food source (e.g. Kingsford, 1992; Hobday, 2000b), and can be subdivided in classes according to these qualities (Fig. 3). The most common natural rafts are constituted of plant debris such as seeds, wooden logs, seagrass fragments and seaweeds, which can provide food sources for rafting animals that feed on their rafts. Except for seaweeds with air bladders (pneumatocysts), these rafts usually have a low longevity because they easily sink or decompose. Significantly higher longevities are found for abiotic rafts (either natural or man-made) that are less prone to degradation by grazing or environmental influences (e.g. UV radiation).

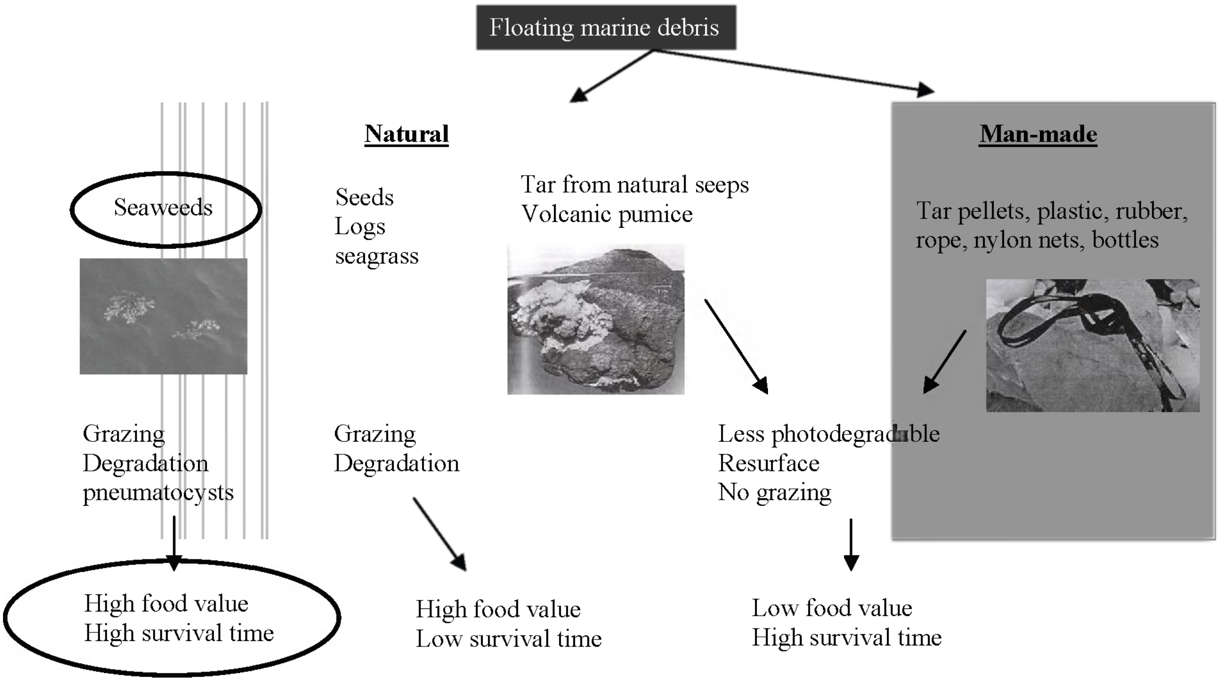

Fig. 3. Groups of floating objects in the marine environment based on their origin and characteristics (after Thiel & Gutow, 2005a). Pictures left to right: Vandendriessche (unpublished), Jokiel (1989), Barnes & Fraser (2003).

These abiotic rafts, however, are poor food sources for grazing fauna, so association is usually limited to filter-feeding animals or predators that can extract enough food from the surrounding water column. Bryozoans, serpulids and barnacles, for example, are common colonisers of plastic debris, (e.g. Winston, 1982; Barnes & Fraser, 2003), while herbivores like isopods and amphipods are abundantly found on seaweed rafts (e.g. Tully & O'Ceidigh, 1986; Ingólfsson, 1995 – 1998; Vandendriessche et al, 2006 a, b).

As for raft availability, macro-algae represent the quantitatively most important natural substrata in the world's oceans, especially when including the vast amounts of the permanently floating *Sargassum*. However, human activities such as tourism, commercial fishing and shipping have, in recent times, induced a spectacular increase of man-made floating objects mainly composed of plastic and tar. These objects have a high longevity and have presumably increased the chances of long-distance dispersal for a number of species. Consequently, the introduction of floating man-made debris has been the study object of a number of biogeographical investigations (e.g. Aliani & Molcard, 2003; Barnes & Fraser; 2003; Thiel et al, 2003).

Although many organisms have been found rafting on floating objects, they do not all possess the ability to survive on them for long periods of time. Helmuth et al (1994) indicated that reproduction by brooding young is an advantage for the rafting bivalve *Gaimardia trapesina*, which was later confirmed for other invertebrates (Thiel & Gutow, 2005b). Another advantage is mobility: mobile rafters can switch between floating items and reattach themselves after dislodgement. However, even if they survive the journey, rafters have to be able to survive the arrival in new habitats and establish a new population. Sessile rafters, for example, have only a limited capacity to detach and reattach and therefore have the highest changes of dispersal by releasing offspring from the raft, by sinking of the raft or by dislodgment from the raft (Jokiel, 1989). Mobile organisms, on the other hand, are well adapted to move from a raft to benthic habitats. The survival and establishment of these colonists in new habitats again depends on a number of factors such as the suitability of environmental conditions and the presence of competitors and predators. Furthermore, successful reproduction is essential, which implies that rafters either have to reproduce asexually, or that both sexes have to arrive simultaneously.

3. FLOATING SEAWEEDS

3.1 Permanently floating ráfts versus ephemeral ráfts

Based on their characteristics (high food value, relatively high longevity) and abundant availability, floating seaweeds are considered to be very suitable as rafts (Fig. 3). Consequently, seaweed rafts, their associated fauna and their characteristics were the focal points of this PhD work. The most thoroughly investigated neustonic seaweeds are undoubtedly the permanently pelagic rafts of *Sargassum natans* and *S. fluitans,* as they can be found in the Western North Atlantic (Thiel & Gutow, 2005a). *Sargassum* rafts provide a stable environment for their associated fauna and therefore harbour high diversities and numerous endemic species (e.g. Fine, 1970; Ryland, 1974; Stoner & Greening, 1984; Coston-Clements et al, 1991). More recently, several investigators also focused on uprooted coastal seaweeds floating at the surface like *Ascophyllum nodosum*, *Fucus vesiculosus, Himanthalia elongata, Chorda filum* and *Laminaria* spp. in the North Atlantic (Tully & O'Ceidigh, 1986; Davenport & Rees, 1993; Ingólfsson, 1995, 1998 & 2000, Ólafsson et al, 2001; Ingólfsson & Kristjánsson, 2002; Gutow, 2003), *Macrocystis pyrifera* and *Sargassum* sp. in the Northern Pacific (Kingsford, 1995; Safran & Omori, 1991; Kokita & Omori, 1998; Hobday, 2000a, b, c) and *Carpophyllum maschalocarpum, Macrocystis pyrifera* in the Southern Seas (Edgar, 1987; Kingsford, 1992; Helmuth et al, 1994). These uprooted coastal seaweeds get detached due to grazing damage (Hobday, 2000c; Viejo en Åberg, 2003), seasonal release of thalli and reproductive structures (Kingsford, 1992), and strong wave action during storms (Lenanton et al, 1982; van der Merwe & McLachlan, 1987; Hobday, 2000 a & c), and form aggregates that travel on the sea surface under the influence of prevailing winds and surface currents (Ingólfsson, 1995; Òlafsson, 2001). Other than

Sargassum rafts, these rafts composed of uprooted seaweeds are ephemeral and, depending on the associated fauna and environmental conditions, have a more or less limited longevity (see chapter 7).

3.1 Fauna associated with ephemeral seaweed rafts

Detached floating seaweeds harbour a fauna that differs from the associated fauna of attached seaweeds (Kingsford & Choat, 1985). A study of Ingólfsson (1995) indicated that four categories of associated fauna can be distinguished based on their origin: (1) species that inhabited the seaweed when it was still attached, and stayed associated when the seaweed was carried to sea, (2) species inhabiting cast-up seaweed, which were trapped on the seaweed when it was taken to sea by the tide, (3) subtidal, benthic and epibenthic species, colonising the seaweed when floating, and (4) planktonic and neustonic species that colonised the seaweed from the surrounding water column. The composition, density and diversity of the fauna have been shown to be influenced by a number of factors, of which clump size and spatial and temporal variation are recognised in most studies (Fine, 1970; Stoner & Greening, 1984; Kingsford & Choat, 1985; Tully & O'Ceidigh, 1986; Safran & Omori, 1990; Kingsford 1992; Druce & Kingsford, 1995; Ingólfsson, 1995 & 1998; Ingólfsson & Ólafsson, 1997, Ólafsson et al, 2001; Dempster & Kingsford, 2004; Ohta & Tachihara, 2004; Wells & Rooker, 2004; Salovius et al, 2005). A number of studies further indicate that raft age (Stoner & Greening, 1984; Edgar, 1987; Ingólfsson & Ólafsson, 1997; Ólafsson et al, 2001; Thiel, 2003; Thiel & Gutow, 2005b), seaweed species composition (Ingólfsson & Ólafsson, 1997; Ólafsson et al, 2001), disturbance and exchange between clumps (Ingólfsson, 1998) may also have considerable effects.

3.2 Floating seaweeds in the Belgian part of the North Sea

Notwithstanding the absence of natural rocky shores, clumps of detached coastal seaweeds are frequently encountered along the Belgian coast. These seaweeds probably originate from (1) the rocky coasts of northern France or southern England, passing by the Belgian coast by means of a residual current in a SW to NE direction through the English Channel; or (2) from the artificial hard substrates along the Belgian coast like harbour walls and groynes. Sampling of ephemeral floating seaweed clumps during a pilot study in 2000 yielded high densities of 55 invertebrate species and fishes (Vandendriessche et al, 2003). These results prompted a more detailed study about floating seaweeds as ephemeral habitats and rafting vectors.

4. OBJECTIVES AND THESIS OUTLINE

The overall aim of this study was to assess the ecological impact of floating seaweeds as ephemeral habitats and potential rafts in the North Sea. Because information on 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 first instance, the influence of the presence of floating seaweeds on the richness and composition of the neuston was assessed, followed by an analysis of environmental and biological factors structuring the seaweed-associated invertebrate community. Afterwards, the presence of high concentrations of prey available in the vicinity of floating seaweeds was related to the presence, abundance and behaviour of fish and marine birds. Finally, laboratory experiments were conducted to provide new information on seaweed raft longevity and consequently on the potential of floating seaweed clumps as vectors for long-distance dispersal in the North Sea.

Four chapters of this thesis and the addendum have already been published in international journals or were accepted for publication; the remaining chapters are submitted for publication. Each chapter is intended to be an autonomous part, which can be read separately from the other chapters. Consequently, a certain degree of overlap concerning introductions and methodologies is unavoidable. References are listed at the end of the thesis.

Chapter 2 presents the results of a baseline study, in which neustonic and seaweed-associated species assemblages were compared in terms of density, diversity and biomass. This study aimed to assess whether the presence of floating seaweeds alters the species composition and species richness of the neuston in the Coastal Bank and Flemish Bank area off the Belgian coast. Furthermore, an attempt was made to quantify the species-specific degree of association with the floating seaweed patches. This chapter has been published as *Vandendriessche S., Vincx M., Degraer S. (2006) Floating seaweed in the neustonic environment: a case study from Belgian coastal waters. Journal of Sea Research 55: 103-112.*

Chapter 3 focuses on the effects of the seaweed species composition of a floating seaweed clump on the associated macrofaunal assemblages. The presence of seaweed preferences and the mechanisms by which the seaweed species composition influences the macrofaunal composition (habitat and food choice) were assessed by a combination of *in situ* seaweed samplings in the Belgian coastal zone and of multiple-choice aquarium experiments in a controlled environment. This chapter has been published as *Vandendriessche S., De Keersmaecker G., Vincx M., Degraer S. (2006) Food and habitat choice in floating seaweed clumps: the obligate opportunistic nature of the associated macrofauna. Marine Biology 149: 1499-1507*

The study presented in **Chapter 4** synthesises and quantifies the effects of different sources of variation, based on data of ephemeral floating seaweed patches at the Belgian coast. In other words, the main question asked is 'What are the driving forces of variation within the invertebrate community associated with floating seaweeds, and what are their relative importances?' Furthermore, the temporal variation within populations of two abundantly encountered genera (*Gammarus* sp. and *Idotea* sp.) was analysed in terms of size-distribution and sexual maturity. This chapter has been submitted as *Vandendriessche S., Deprez T., Vincx M., Degraer S. Sources of variation in floating seaweed-associated macro-invertebrates. Marine Biology.*

Chapter 5 deals with the association between floating seaweeds and fishes. Although research about the importance of association behaviour is very important from the perspective of fisheries ecology, very little information is available concerning the relation between fishes and the highly dynamical floating seaweed clumps found in the North Sea. Therefore, the study presented in this chapter aimed to investigate the species composition and association behaviour of fishes associated with floating seaweeds. To this end, we identified neustonic fishes with a tendency to associate with floating objects, and investigated the variability within the fish community. For each of the associated fish species, the underlying motivation for association behaviour (food, shelter or other) was investigated. This chapter is in press as *Vandendriessche S, Messiaen M, O'Flynn S., Vincx M, Degraer S. Hiding and feeding in floating seaweed: floating seaweed clumps as possible refuges or feeding grounds for fishes. Estuarine, Coastal and Shelf Science.*

The influence of floating seaweed patches on the distribution and behaviour of seabirds forms the key issue addressed in **chapter 6**. Other than a few studies concerning *Sargassum* and some sporadic notes, few investigations have been done on the topic of seabirds associated with floating seaweeds. As a result, the study presented in this chapter aimed to examine the seaweed's possible attractions for seabirds in Northeast Atlantic waters, based on the European Seabirds At Sea database (ESAS). The main research questions of this study were: "Are there seabirds that are frequently seen associated with ephemeral patches of floating seaweed" and "Are these associations feeding mode-dependent?" This chapter has been submitted as *Vandendriessche S. Stienen E.W.M, Vincx M, Degraer S. Floating seaweeds: a source of small-scale patchiness in seabirds? Ardea.*

Chapter 7 discusses the results of an experimental study concerning the survival of floating seaweeds on the sea surface, which depends on several factors, including temperature, damage caused by sunlight, nutrient levels, epibiont growth, and grazing. However, the impacts and relative importance of these factors have not yet been quantified experimentally. In order to evaluate the rafting capacities of ephemeral seaweed patches, the study described in this chapter focused on the influences of temperature, grazing and clump size. The experimental study was carried out in a controlled environment reflecting North Sea (Belgian coastal zone) conditions in terms of salinity, temperature, seaweed species and grazer species. This chapter has been accepted for publication as *Vandendriessche S, Vincx M., Degraer S. Floating seaweed and the influences of temperature, grazing and clump size on raft longevity – a microcosm study. Journal of Experimental Marine Biology and Ecology.*

In the general discussion and perspectives for future research (**chapter 8**), key issues and considerations are deduced from the main results of the different chapters, and suggestions for future research topics are formulated.

Finally, the addendum reports on the observation of two specimens of juvenile long-snouted seahorses (*Hippocampus guttulatus*) in the neuston near the French-Belgian border. This short note has been published as *Vandendriessche S, Messiaen M., Vincx M., Degraer S. (2005) Juvenile* Hippocampus guttulatus *from a neuston tow at the French-Belgian border. Belgian Journal of Zoology 135(1): 101-102.*

CHAPTER 2

FLOATING SEAWEED IN THE NEUSTONIC ENVIRONMENT: A CASE STUDY FROM BELGIAN COASTAL WATERS

Multi-species seaweed clump (September 2003)

Paper published

Vandendriessche S., Vincx M., Degraer S. (2006)

Floating seaweed in the neustonic environment: a case study from Belgian coastal waters

Journal of Sea Research 55: 103-112

ABSTRACT

Floating seaweeds form the most important natural component of all floating material found on the surface of oceans and seas. Notwithstanding the absence of natural rocky shores, ephemeral floating seaweed clumps are frequently encountered along the Belgian coast. From October 2002 to April 2003, seaweed samples and control samples (i.e. surface water samples from a seaweed-free area) were collected every other week. Multivariate analysis on neustonic macrofaunal abundances showed significant differences between seaweed and control samples, when considering the fraction >1mm. Differences were less conspicuous in the 0.5mm-1mm fraction. Seaweed samples were characterised 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 (1mm 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 305 mg 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 showed an association percentage higher than 95%, and can therefore be considered as members of the floating seaweed fauna.

Keywords: Macrofauna; Neuston; Floating Seaweed; North Sea

1. INTRODUCTION

The paper at hand focuses on the organisms associated with floating seaweed. The most spectacular and most thoroughly investigated neustonic seaweeds are undoubtedly the truly pelagic rafts of *Sargassum natans* and *S. fluitans,* as they can be found in the Western North Atlantic (Thiel & Gutow, 2005a). *Sargassum* rafts provide a stable environment for their associated fauna and therefore harbour high diversities and numerous endemic species (e.g. Fine, 1970; Ryland, 1974; Stoner & Greening, 1984; Coston-Clements et al, 1991). More recently, several investigators also focused on uprooted coastal seaweeds floating at the surface like *Ascophyllum nodosum*, *Fucus vesiculosus, Himanthalia elongata, Chorda filum* and *Laminaria* spp. in the North Atlantic (Tully & O'Ceidigh, 1986; Davenport & Rees, 1993; Ingólfsson, 1995, 1998 & 2000, Ólafsson et al, 2001; Ingólfsson & Kristjánsson, 2002; Gutow, 2003), *Macrocystis pyrifera* and *Sargassum* sp. in the Northern Pacific (Kingsford, 1995; Safran & Omori, 1991; Kokita & Omori, 1998; Hobday, 2000a, b, c) and *Carpophyllum maschalocarpum, Macrocystis pyrifera* in the Southern Seas (Edgar, 1987; Kingsford, 1992; Helmuth et al, 1994).

Notwithstanding the absence of natural rocky shores, clumps of detached coastal seaweeds are frequently encountered along the Belgian coast. These seaweeds originate from (1) the rocky coasts of northern France or southern England, passing by the Belgian coast by means of a residual current in a SW to NE direction through the English Channel; or (2) from the artificial hard substrates along the Belgian coast like harbour walls and groynes. As there are only very few data on the fauna associated with these floating seaweeds, this paper aims to assess whether the presence of floating seaweeds alters the species composition and species richness of the neuston in the Coastal Bank and Flemish Bank area off the Belgian coast. Furthermore, an attempt is made to quantify the association of the encountered species with the floating seaweed patches.

2. MATERIALS AND METHODS

2.1 Sampling

During daylight hours, samples were collected from autumn to early spring (October 2002 until April 2003) on the Belgian continental shelf (BCS), in the southernmost part of the North Sea. Every other week, the RV Zeeleeuw sailed a trajectory of 60 nautical miles across the Coastal Bank and Flemish Bank area, thereby increasing the chance of floating seaweed encounters by sailing (as much as possible) perpendicular to the prevailing water currents (Fig. 1). Samples were collected at distances of 0.6 to 11.7 nautical miles from the coastline.

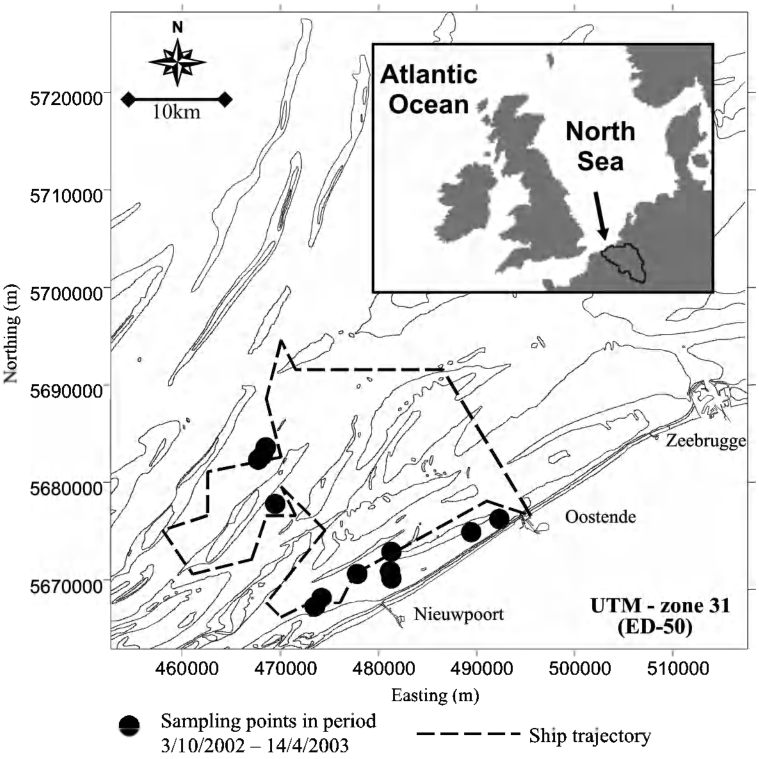

Fig. 1. Study area with indication of sampling occasions (black dots) and ship trajectory (interrupted line)

The search for seaweed was also supported by an airplane on pollution control missions (carried out by the Management Unit of the North Sea Mathematical Models). Persistent bad weather conditions prevented sampling on several dates; sampling was successful on 03/10/2002 – 12/11/2002 – 13/12/2002 – 07/02/2003 – 27/02/2003 – 21/03/2003 – 04/04/2003 – 14/04/2003. During these days, two scientists continuously looked out for seaweeds from the bridge of the research vessel. When clumps of floating seaweed were observed, a small assistance boat was lowered to the water surface and the seaweeds were gently approached, in order to avoid disturbance. Clumps of floating seaweed (minimum three per sampling occasion & 1 to 4 sampling occasions per sampling date) were collected using a 300 µm mesh dip net with a ring diameter of 40 cm. From a distance, the net was gently dipped under the clumps by means of an extensible handle. Three control samples (i.e. surface water samples without floating seaweed) were taken at each sampling position. After each haul, the net was emptied, rinsed and its contents preserved in an 8% buffered formaldehyde-seawater solution.

2.2 Data acquisition

In the laboratory, the preserved samples were rinsed in water, and sieved over a 1mm and 0.5mm sieve. After sorting, all organisms were identified – if possible – to species level. For certain taxa, further classification was done based on the life history stage, such as zoea, megalopa or post larval stage of decapods. All animals were counted on species or stage level. Certain species were reported on a higher taxonomical level (noted as 'sp.' – e.g. juveniles of the genera *Gammarus* and *Idotea* were grouped); these taxa are further also referred to as 'species'. Species occurring in a wide length range were measured (standard length from the rostral tip to the last abdominal segment for crustaceans) and their biomass was derived from regressions relating the standard length to Ash free Dry Weight (ADW). ADW was determined as the difference between dry weight (60°C for 5 days) and ash weight (650°C for 2 hours) for representative size distributions of the various species. For species caught in discrete life stages or occurring with a particular length, an average biomass value was assigned per stage or species. This value was determined by measuring the ADW of batches of animals belonging to a certain stage.

Densities and biomasses were expressed as individuals or mg ADW m^{-2} sea surface area, respectively, to enable comparisons between seaweed samples and control samples (sessile fauna such as barnacles and bryozoans were omitted from biomass analysis). Diversity was calculated and expressed as expected number of species (Hurlbert, 1971) in order to minimise the effect of variations in sample size. Averages of density, biomass and diversity are reported with standard error.

2.3 Data treatment

Univariate two-way analysis of variance (ANOVA - STATISTICA software) was used to test for differences in diversity, density and biomass between seaweed samples (SWS) and control samples (CS), taking into account the different sampling occasions (black dots in Fig. 1). If necessary, a log $(x + 1)$ transformation was performed to meet the required assumptions.

Species abundance data of SWS and CS were subjected to non-metric multidimensional scaling ordination (MDS) and cluster analysis using the Bray-Curtis similarity measure. ANalysis Of SIMilarities (ANOSIM) was used to test the statistic for significant differences ($p<0.05$) between groups and to identify the discriminating taxa (SIMilarity of PERcentages: SIMPER). Empty samples were excluded from the analyses and a presence-absence transformation was performed on the abundance data prior to the analyses. All community analyses were done using the Primer software (Clarke & Gorley, 2001).

Because the sampling strategy (dip net) always implies a "contamination" of seaweed samples with fauna from the surrounding water column, a bias is created in the dataset, which may obscure patterns in community composition. An attempt was made to filter out that bias in a quantitative way by calculating the 'added value', in terms of density and biomass, of seaweed samples according to the following procedure: (1) for each sample type (SWS & CS), different replicates were taken per sampling occasion, (2) Two-Way ANOVA analyses (2 sample types, 13 sampling occasions) were used to determine which species were found significantly more in SWS compared to CS, and can therefore be considered as seaweed fauna (if non significant, the species can be considered as member of the background neustonic fauna); (3) added values of densities and biomasses of the seaweed fauna are calculated by subtracting background neustonic values of density and biomass from seaweed sample values (per sampling occasion). These values can be used to study floating seaweed-specific processes in detail, without the bias caused by the presence of surface water fauna. Furthermore, they give an indication about the degree of association of the encountered species with clumps of floating seaweed. That association degree per species can also be expressed as a percentage: per sampling occasion and per species, the percentage of individuals and mg ADW found in SWS was calculated in proportion to the total density and biomass of that species (SWS + CS) on that sampling occasion. Averaging out these values over all sampling occasions yielded the association degree.

3. RESULTS

3.1 Neustonic fauna in presence and absence of floating seaweed

In total, 49 seaweed samples and 38 control samples were collected and analysed. Clumps of floating seaweed consisted of one or more seaweed species (*Fucus vesiculosus, Ascophyllum nodosum, Halidrys siliquosa*) and occasionally small amounts of other floating debris such as reed, feathers, plastic, nylon, wood and cardboard. Clump volume averaged 99 ml (range 8ml - 360ml).

During the initial analysis of both seaweed and control samples, analyses were performed on a dataset, in which the 0.5mm (0.5mm-1mm) and the 1mm (>1mm) fractions were pooled. This approach resulted in an indistinct grouping of seaweed samples and control samples (results not presented in this paper). Therefore, we split up the dataset in order to get a more detailed view of the differences.

3.1.1 1mm fraction

Diversity (Fig. 2A) showed significantly higher values in seaweed samples (mean ES(100)= 4.0) than in control samples (mean ES(100)= 1.5) (ANOVA $p<0.001$). The variation due to sampling occasion and the combined effect were both significant ($p<0.001$ and $p=0.003$, respectively). Although the species richness seems relatively low, a total of 44 species were found in SWS and a total of 23 species in CS. However, only a few species were common in all samples and most species were only sporadically found. This trend was even more pronounced in the control samples. *Density* (Fig. 2B) displayed the same trend as diversity: species abundances were significantly higher in seaweed samples (mean 404 ind m^{-2}) than in control samples (mean 23 ind m^{-2}) (ANOVA $p<0.001$).

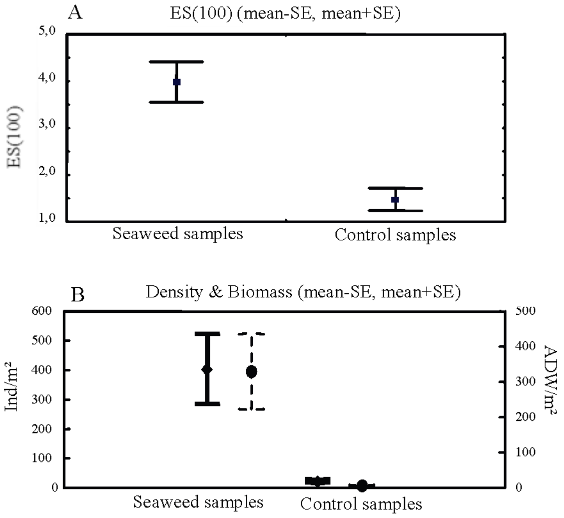

Fig. 2. Results of **1mm** fraction (A) plot of diversity expressed as expected number of species per 100 individuals (indication of mean and standard error), (B) plot of density expressed as individuals m^{-2} surface area (full line – left Y-axis - indication of mean and standard error); and biomass expressed as mg ADW m^{-2} surface area (dashed line – right Y-axis - indication of mean and standard error)

The variation due to sampling occasion was significant ($p=0.004$); the combined effect was not ($p=0.1$). High densities in seaweed samples were mainly due to the dominance of small barnacles, halacarid mites, isopods (mainly *Idotea baltica*) and amphipods (mainly *Gammarus locusta* and *Gammarus crinicornis*). *Biomass* (Fig. 2B) was substantially higher in seaweed samples (mean 329 mg ADW m^{-2}) than in control samples (mean 7 mg ADW m^{-2}) (ANOVA $p<0.001$), which was mainly due to the dominance of large isopods (*Idotea baltica* – 58% of the total biomass), large amphipods (mainly *Gammarus locusta* and *Gammarus crinicornis* – 10% of the total biomass) and a few fish (*Chelon labrosus* – 27% of the total biomass). The variation due to sampling occasion and the combined effect were both significant at $p<0.001$.

The cluster dendrogram and the MDS plot both revealed the same two groups (Fig. 3): (1) a group comprising the majority of seaweed samples (SWS) and (2) a group comprising most of the control samples (CS). ANOSIM analysis indicated that these groups were significantly different ($R=0.32$, $p<0.001$).

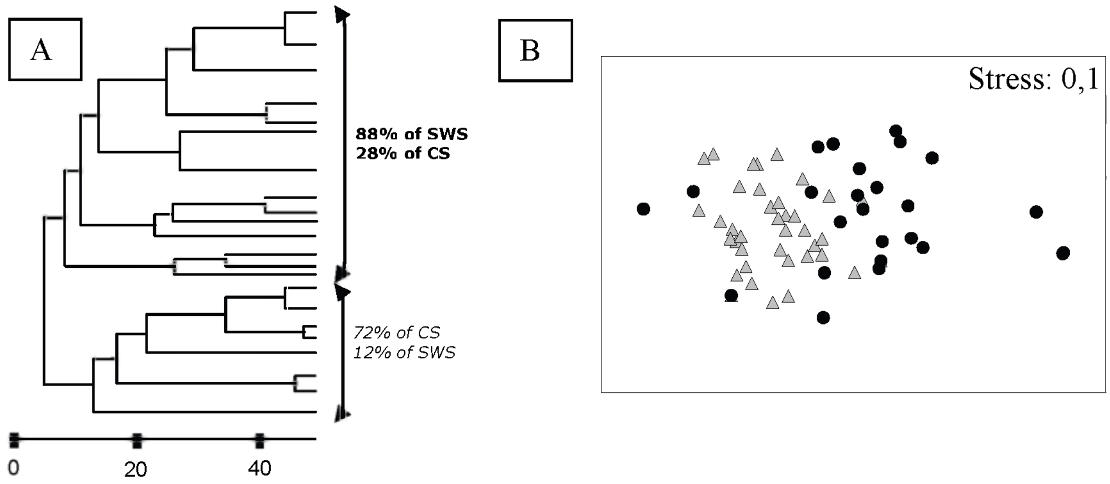

Fig. 3. (A) Simplified cluster (0-50% similarity): Bray-Curtis similarity / Presence-absence data / Group average sorting, (B) MDS plot: grey triangles represent seaweed samples (SWS); black dots represent control samples (CS)

3.1.2 0.5mm fraction

Diversity (Fig. 4 A) was higher in seaweed samples (mean ES(100)= 3.2) than in control samples (mean ES(100)= 2.4). This difference was not quite significant (two-way ANOVA, p=0.07). The variation due to sampling occasion was significant ($p<0.001$); the combined effect was not (p=0.4). *Density* (Fig. 4B) was higher in seaweed samples (mean 272 ind m^{-2}) than in control samples (mean 107 ind m^{-2}), but again, this trend was not confirmed by a two-way ANOVA (p=0.051). The variation due to sampling occasion was significant ($p<0.001$); the combined effect was not (p=0.9). *Biomass* (Fig. 4B) confirmed the trend observed in the 1mm fraction: biomass was higher (ANOVA p=0.01) in seaweed samples (mean 17mg ADW m^{-2}) than in control samples (mean 7mg ADW m^{-2}). Note, however, that the biomass was only 2.5 times higher, whereas in the 1mm fraction, biomass was almost 50 times higher.

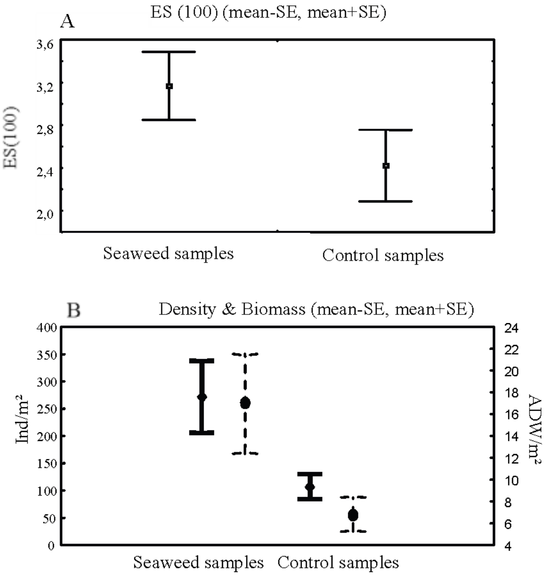

Fig. 4. Results of **0.5mm** fraction (A) plot of diversity expressed as expected number of species per 100 individuals (indication of mean and standard error), (B) plot of density expressed as individuals m^{-2} surface area (full line – left Y-axis - indication of mean and standard error); plot of biomass expressed as mg ADW m^{-2} surface area (dashed line – right Y-axis - indication of mean and standard error)

The variation due to sampling occasion and the combined effect were both highly significant ($p<0.001$).

Neither cluster analysis, nor MDS revealed the two groups established at the >1mm level (Fig. 5).

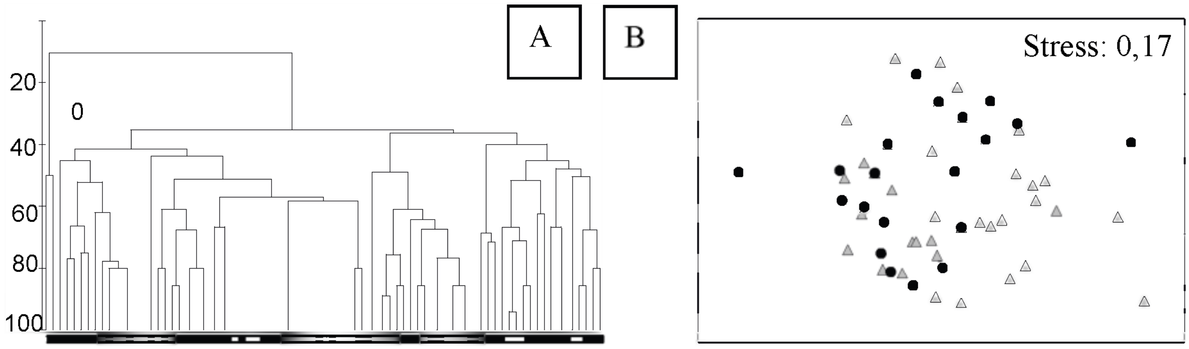

Fig. 5. (A) Simplified cluster (samples represented by black or white squares): Bray-Curtis similarity / Presence-absence data / Group average sorting. Black squares: SWS, white squares: CS, (B) MDS plot: grey triangles represent seaweed samples (SWS); black dots represent control samples (CS)

3.1.3. Species assemblages in fractions and groups

The differences in species composition between both fractions in the SWS and CS can be derived from Table 1: both fractions of the control samples and the 0.5mm fraction of the seaweed samples were mainly dominated by planktonic organisms like calanoid copepods, larvaceans, chaetognaths and invertebrate larvae (e.g. polychaete larvae and cypris larvae), while the 1mm fraction of SWS was mainly characterised by non-planktonic fauna e.g. Cirripedia, *Littorina mariae*, *Mytilus edulis*, Acari, *Gammarus locusta*, *Gammarus crinicornis*; *Idotea baltica*, *Idotea linearis* and *Idotea emarginata*. SIMPER analysis of 1mm data showed a very high average dissimilarity between seaweed samples and control samples (95.4%). The isopod *Idotea baltica* (seaweed samples) and calanoid copepods (control samples - not identified to species level) were the most discriminating taxa (contribution percentages: Table 2).

Table 1. Relative abundances of the 5 most important taxa in different fractions (1mm & 0.5mm) and groups (SWS & CS)

	1mm		**0.5mm**	
SWS	Cirripedia	25%	Calanoida	64%
	Acari	16%	Acari	13%
	Isopoda	15%	Cirripedia	5%
	Amphipoda	12%	Cypris	5%
	Cypris	11%	Larvacea	4%
	rest	21%	rest	9%
CS	Chaetognatha	22%	Calanoida	67%
	Insecta	10%	Larvacea	3%
	Ctenophora	14%	Cnidaria	10%
	Calanoida	12%	Polychaeta	5%
	Polychaeta (larvae)	19%	Ctenophora	10%
	Rest	23%	rest	6%

3.2 Added value of floating seaweed

In order to calculate the added values concerning density and biomass, Two-Way ANOVA analyses were performed on density and biomass data per species, taking into account two sampling types (SWS-CS) and 13 sampling occasions. The results concerning effect 1 (Table 2) indicate that some species always displayed higher densities and biomasses in SWS compared to CS, independent of sampling time and/or place. A calculation of the added values of these species clearly shows that *Idotea baltica* was not only a good indicator for seaweed samples (see SIMPER), it also seems to be an important contributor to the added values of seaweed samples (1mm fraction: Table 2). Other contributors to density (mean added value 311 Ind m^{-2}) and biomass (mean added value 305 mgADW m^{-2}) were amphipods (*Gammarus* sp., *G. locusta, G. crinicornis* and *Atylus swammerdami*), other idoteid isopods (*Idotea emarginata* and *Idotea* sp. juv.), fish (*Chelon labrosus*), barnacles, halacarid mites, mussels and even some insects. Other organisms (e.g. *Pleurobrachia pileus, Sagitta* sp., calanoid copepods and some insects) were not found significantly more in seaweed samples and can be considered as background fauna, with a 'uniform' distribution in the neuston of Belgian coastal waters.

Table 2. ANOVA results (effect of sample type: SWS vs. CS, effect of sampling occasion not represented) concerning density and biomass (significant values: $p<0.05$ – italic) per species.

	ANOVA (effect1: SWS / CS)		**Added value**		**Association**	**SIMPER**	
	density	**biomass**	**density**	**biomass**	**degree**	**Contribution %**	
	p-value	p-value	ind/m^2	mg ADW/m^2	percentage	SWS	CS
Elminius modestus	*<0.001*	nam	100,8	nam	95,8	10,9	nd
Acari sp.	*<0.001*	nam	63,5	nam	100	27,6	nd
Idotea baltica	*<0.001*	*<0.001*	40	177,9	97,2	37,5	nd
Sagitta sp.	0,54	0,58	bg	bg	bg	nd	24,2
Idotea sp. Juv.	*<0.001*	*<0.001*	17,8	4,2	95,8	8,7	nd
Atylus swammerdami	*<0.001*	*<0.001*	13,8	14,9	100	5,6	nd
Scatopsidae sp.	*<0.001*	0,08	12	bg	93,8	nd	nd
Sciaridae sp.	*0,02*	0,35	9,6	bg	83,8	nd	nd
Calanoida sp.	0,31	0,29	bg	bg	bg	nd	38,4
Pleurobrachia pileus	0,14	nam	bg	nam	bg	nd	18,7
mean added value / sample			**311,4**	**305,3**			

Only the 10 most abundant (> 2.5ind/m^2) and most frequently occurring (>10% of samples) species represented; species ordered by decreasing density - mean added values of all species with significantly higher density-biomass in SWS compared to CS, with their mean association degree (percent of the total number of individuals/mg ADW found in seaweed samples) - SIMPER contribution percentages of discriminating species per sample type.
nam: no avalaible measurements, bg: background values (ANOVA non-significant), nd: non-discriminating in SIMPER analysis.

The added value can be expressed as an absolute value: in density, for example, *I. baltica* had an added value of 40 ind m^{-2}, meaning that in the presence of seaweed, 40 more individuals can be found per m^2 than in the absence of seaweed. Another way of expression is by calculating the mean percentage of individuals and mg ADW found in SWS in proportion to the total density and biomass

(Table 2). For *Idotea baltica*, that mean density percentage was 97.2%, meaning that 97.2% of all individuals were found on floating seaweeds. Some species were even exclusively found in seaweed samples (100% association) and were completely absent from the surrounding surface waters (e.g. the amphipod *Atylus swammerdami*, the beetle *Helophorus aquaticus*, and halacarid mites).

4. DISCUSSION

4.1 Size fractions

In accordance with previous studies on the fauna associated with floating seaweed (Tully & O'Ceidigh, 1986; Ingólfsson, 1998 & 2000), all organisms larger than 0.5mm were rinsed from the seaweeds. In the present study, the 1mm and 0.5mm fractions were separated. Analysis of both fractions indicated substantial differences between seaweed samples and control samples in the 1mm fraction, whereas these differences were less pronounced in the 0.5mm fraction. The smallest fractions of seaweed samples and control samples were both characterised by high percentages of calanoid copepods (64% in SWS and 67% in control samples). These copepods were not identified up to species level, but variation at this level is improbable as this study and the study of Ingólfsson (1998) both indicate that calanoid copepods are not in essence associated with floating seaweed but are common in the surrounding neuston.

The similarity between taxa of SWS and CS at the 0.5mm level was probably due to the passive movement of the identified planktonic organisms in the water column. It is known, however, that smaller animals such as some species of harpacticoid copepods can cling to, or even seek passing seaweed clumps (Yeatman, 1962, Ingólfsson & Ólafsson, 1997; Ólafsson et al, 2001). In the present study, no such colonisers were encountered. Therefore, differences between control samples and seaweed samples are best discerned at the 1mm level.

In conclusion, it can be stated that the 0.5mm fraction of seaweed samples and control samples, and the 1mm fraction of control samples are mainly composed of 'background neustonic fauna', whereas the 1mm fraction of seaweed samples is populated by 'seaweed fauna'.

4.2 Seaweed samples versus control samples

Most authors acknowledge the effect of drifting vegetation on the habitat complexity in the neustonic environment and, consequently, on the neustonic species composition (Tully & O'Ceidigh, 1986; Locke & Corey, 1989; Davenport & Rees, 1993; Kingsford & Choat, 1985; Kingsford, 1992 & 1995; Shaffer et al, 1995, Ingólfsson, 1998, Hobday, 2000a, b). However, dip net control samples for statistical verification of the differences between seaweed fauna and surface water fauna have rarely been taken. Ingólfsson (1998) took a single control sample per sampling site and found that Calanoida, Decapoda larvae, Cirripedia larvae and Cladocera were not significantly more common in clumps of floating seaweeds than in the control samples. Shaffer et al (1995) collected five drift vegetation samples and five control samples per sampling date and found that seaweed samples were dominated by epiphytic organisms, while calanoid copepods were found significantly more in open water. In the study at hand, three control samples per sampling site were taken, in which Calanoida were also typically found. Kingsford & Choat (1985), Kingsford (1992) and Kokita & Omori (1998) collected seaweed samples and control samples, but used a purse seine net or a 2m diameter ring net and mainly focussed their research on fish. Consequently, their results are hard to compare with the results of this study. In general, the conclusions of Ingólfsson (1998), Shaffer et al (1995) and the present study are the same: there are significant differences between the species compositions and species abundances of seaweed samples and control samples.

The cluster dendrogram and MDS plot of Fig. 2 show a clear grouping of seaweed samples and control samples. However, some of the control samples resembled seaweed samples due to the presence of non-planktonic animals such as *Idotea baltica, Gammarus* juveniles and *Gammarus crinicornis*, while some of the seaweed samples resembled control samples due to the absence of seaweed species. If non-planktonic organisms were found in control samples, it was only in very low abundances (max 0.4 ind m^{-2}). Their presence may have been due to two factors: (1) *Idotea baltica* and *Gammarus locusta* were observed freely swimming at the surface (Tully & O'Ceidigh, 1986 and pers. obs.). So, *I. baltica* and *G. locusta* probably swim around at the surface in the vicinity of seaweed clumps and can therefore occasionally be found in control samples taken near floating seaweeds; and (2) some of the control samples contained small amounts of debris other than floating seaweed (e.g. reed, plastic and feathers), to which the non-planktonic species can cling. The absence of seaweed-associated species in some seaweed samples cannot be explained at present.

4.3 Diversity, density and biomass (1mm fraction)

An attempt was made to take variation due to differences in sampling occasion (spatial and/or temporal variation) into account by using a two-way ANOVA (2 groups, 13 sampling occasions). The 0.5mm fraction showed little difference in density, diversity and biomass between seaweed samples and control samples. There was, however, a significant effect of sampling occasion. In the 1mm fraction, both the effect of sample type and the effect of sampling occasion were significant. There was also a combined effect (except in density), which indicates that spatial and/or temporal variation intensified the differences between seaweed samples and control samples.

Clumps of floating seaweeds recovered off the Belgian coast seem to harbour a significantly higher species richness than the surrounding surface water (mean expected number of species per 100 individuals: 4.46 in SWS, 2.0 in CS; only 1mm fraction considered). Even though a high number of species were found in total (44 in SWS, 23 in CS), the majority of species were sparsely represented.

Individual samples, however, were often dominated by one of the minor species groups, especially in control samples. This pattern in species range could be attributed to the discontinuous distribution of neustonic fauna in the sea surface layer, for example due to swarming behaviour or the formation of windrows (Holdway and Maddock, 1983), and/or to the effect of spatio-temporal variation (see the previous paragraph).

Besides a higher number of species (x3), samples of floating seaweed off the Belgian continental shelf had significantly higher densities (x18) and biomasses (x49), than control samples. Both rocky shore fauna and colonising subtidal, benthic and epibenthic fauna contributed considerably to total densities, whereas high biomasses were mainly due to the abundant presence of actively colonising fauna (isopods, amphipods and fish). According to Ingólfsson (1998), some of these colonisers display a clump-seeking behaviour: they seek (1) shelter from predators such as large fish or birds (Kokita & Omori, 1998); (2) a food source: the associated macrofauna (Tully & O'Ceidigh, 1989) or the seaweed itself, although it should be noted that some herbivores like *Idotea baltica* destroy their own habitat by feeding on the seaweed (Gutow, 2003); or (3) a substrate for attachment. Other organisms, such as insects (Davenport & Rees, 1993), accidentally end up on floating seaweeds because of their tendency to seek or to hold on to vegetation. The success of these colonisers on floating seaweeds may be due to the lack of endemic neustonic species utilising the habitat (Locke & Corey, 1989).

4.4 Added value of floating seaweed

The analyses above clearly indicate that the presence of floating seaweed strongly increased the diversity, density and biomass of the neustonic macrofauna, especially in the 1mm fraction. However, due to the sampling method, floating seaweed samples are always 'contaminated' with fauna from the surrounding neuston. In future research on the macrofauna associated with floating seaweed (e.g. spatial and temporal variation), it is necessary to be able to determine the 'added value' of floating seaweed in the neuston concerning density and biomass; in this study averages of 311 Ind m^{-2}, and 305 mg ADW m^{-2}, respectively. These values were obtained by performing Two-Way ANOVA analyses and by subtracting background neustonic values of density and biomass from seaweed sample values (see data treatment). In this way, a distinction was made between "true seaweed fauna" such as *Idotea baltica, Atylus swammerdami* and *Gammarus crinicornis* and "background fauna" such as calanoid copepods, some insects, ctenophores, chaetognaths and pelagic larvae of barnacles and polychaetes. To be able to perform such an action, both floating seaweeds and the surrounding neuston should, as in the present study, be sampled in a representative way in order to compensate for aggregation behaviour of neustonic fauna and sampling artefacts. In this study, the Two-Way ANOVA analyses only yielded positively significant p-values, meaning that fauna are attracted to floating seaweeds.

The calculation of the added values in density and biomass provides not only a more accurate dataset to study seaweed specific fauna; it also gives an idea about the degree of association of the encountered species with the floating seaweeds. That degree of association can also be expressed as a percentage. The calculated percentages indicate that sixteen species* (>75% association) strongly depended on the presence of floating seaweed. This seaweed dependency was already clear for species such as *Idotea baltica, Idotea emarginata* and *Gammarus locusta* (e.g. Tully & O'Ceidigh, 1986; Davenport & Rees, 1993; Ingólfsson, 1995,1998,2000; Gutow, 2003; Gutow & Franke, 2003; Salovius et al, 2005), but has not yet been reported for *Gammarus crinicornis, Chelon labrosus* and *Helophorus aquaticus.* Their strong association degrees in this study are an invitation to more intensive samplings and to a detailed study of fauna associated with floating seaweed in Belgian coastal waters.

ACKNOWLEDGEMENTS

The first author acknowledges a specialisation grant from the 'Flemish Institute for the Promotion of Scientific-Technological Research' (IWT). The authors would like to express their gratitude to everybody who helped with the species identifications, and to colleagues and students for their support and help with the samplings (Eveline, Tom, Hannelore, Bea, Saskia, Miranda, Gert). Special thanks go to André Cattrijsse of the Flanders Marine Institute (VLIZ), to the crewmembers of the research vessel Zeeleeuw and to the people of MUMM (Marisa & Benoit). Furthermore, the authors would like to thank Peter Herman and Tom Ysebaert (NIOO-CEME) for their constructive comments on the concept of added value. M. Thiel, two anonymous referees and the editor (JJB) are acknowledged for their highly useful comments and corrections on earlier versions of the manuscript.

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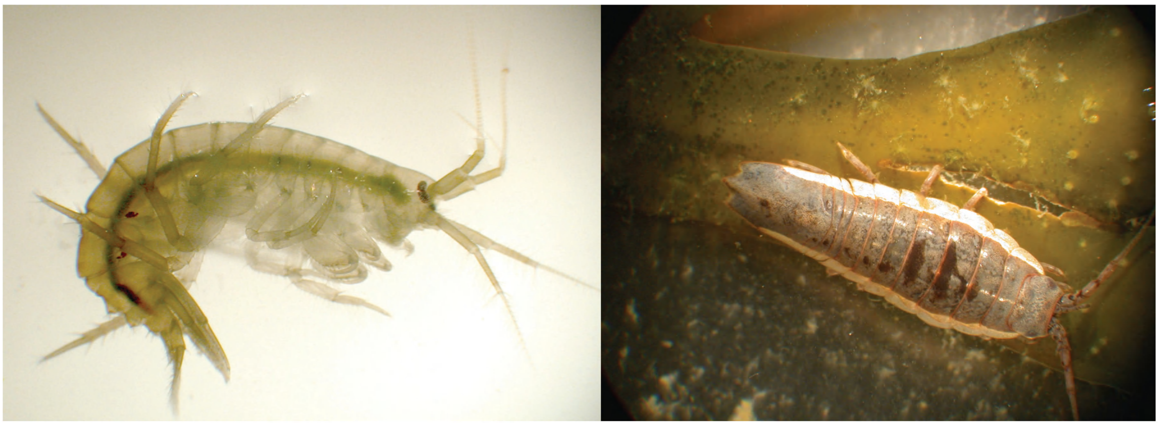
* *Gammarus locusta, G. crinicornis, Gammarus* sp. Juv., *Atylus swammerdami, Idotea* sp. Juv., *Idotea baltica, I. emarginata, Elminius modestus, Ostrea edulis, Helophorus aquaticus*, Psyllidae sp., Scatopsidae sp., Sphaeroceridae sp., Sciaridae sp., Acari sp., *Chelon labrosus.*

CHAPTER 3

FOOD AND HABITAT CHOICE IN FLOATING SEAWEED CLUMPS: THE OBLIGATE OPPORTUNISTIC NATURE OF THE ASSOCIATED MACROFAUNA



Gammarus sp. – *Idotea baltica*

Paper published

Vandendriessche S., De Keersmaecker G., Vincx M., Degraer S. (2006)

Food and habitat choice in floating seaweed clumps: the obligate opportunistic nature of the associated macrofauna

Marine Biology 149: 1499-1507

ABSTRACT

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 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 the sampling data confirm that the seaweed composition influences 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 (SWS) 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 SWS 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. The effects of seaweed composition may also be blurred due to the obligate opportunistic nature of a lot of the associated macrofaunal species.

Keywords: Macrofauna; Floating Seaweed; North Sea; Habitat Preference

1. INTRODUCTION

In recent years, many studies have focused on the fauna associated with floating seaweeds in temperate, (sub)tropical and even polar regions (reviewed by Thiel and Gutow, 2005a, b). Generally, the focal points of these studies are the possibility of rafting as a means of dispersal and the attraction of fish and invertebrates due to the provision of shelter, food and/or a substrate for attachment. Floating seaweeds generally harbour a diverse fauna of grazers that feed on their substrate (Thiel & Gutow, 2005a, b). Both the attractiveness and food value of seaweeds and the presence of pneumatocysts, which increase buoyancy, make them very suitable rafts. The fauna associated with these rafts initially consists of animals originally living on the seaweeds in situ and of a number of mobile species that quickly colonise the seaweeds from the surrounding water column (Ingólfsson, 1995 & 2000, Vandendriessche et al, 2006a). Especially the latter group is very persistent, whereas the number of intertidal species drops with time afloat (Ingólfsson, 1995).

The species composition of macrofauna associated with floating seaweed rafts is shown to be highly variable and influenced by many factors, from which spatial and temporal variations are most intensively studied: densities of associated fauna appear highly seasonal and related to geographic region, distance to shore or the nearest seaweed bank (e.g. Fine, 1970; Stoner & Greening, 1984; Kingsford & Choat, 1985; Tully & O'Ceidigh, 1986; Ingólfsson, 1995). There is, however, little information about the importance of the seaweed species as a structuring factor for the macrofaunal community. As different seaweed species exhibit varying levels of toughness, branching, chemical defenses against grazing, nutritional values and suitability for rafting, it can be expected that some of the seaweed-associated fauna have a preference for a certain seaweed species. As free-swimming associated species are able to move within clumps and between clumps, their seaweed preference (if present) is expected to be expressed in both macrofaunal abundances and seaweed consumption (Thiel & Gutow, 2005b).

Up till now, the relation between macrofaunal abundance and seaweed species composition in floating clumps of seaweed has received little attention. Kingsford & Choat (1985), for example, found significant differences in invertebrate abundances between seaweed species for attached plants, but that pattern was not found for floating seaweeds. They stated that on floating algae, differences between individual plants (e.g. age and origin) are probably a more important source of variation in invertebrate abundances than differences between species. Stoner & Greening (1984) and Ingólfsson (1998) did not find significant correlations between faunal densities and the relative weights of the main constituents (except for the species *Litopia melanostoma*, which was more abundant on *Sargassum natans* than on *S. fluitans* in the Sargasso Sea and the Gulf Stream). Ólafsson et al (2001), however, found significant correlations between diversity and density of harpacticoids and algal diversity, suggesting that the seaweed composition plays an important role in structuring the composition of the associated fauna.

Therefore, the objective of this study is to investigate whether the seaweed species composition of a seaweed clump influences the species composition of the associated macrofauna. The presence of seaweed preferences and the mechanisms by which seaweed species composition influence macrofaunal composition (habitat and food choice) were assessed by a combination of in situ seaweed samplings in the Belgian coastal zone and multiple-choice aquarium experiments in a controlled environment.

2. MATERIALS AND METHODS

2.1 Field data

On 18 May 2004, 23 samples of floating seaweeds were collected at the Belgian continental shelf (BCS), in the southernmost part of the North Sea. On that sampling date, two large seaweed aggregations were encountered, from which the samples were randomly taken. Samples 1-9 were gathered at a distance of 7 km from the coast (51° 11.45N – 2° 36.63E), whereas samples 10-23 were sampled 15 km from the coast (51° 12.87N – 2° 27.59E). The weather conditions were optimal and stable (mean wind speed 7.6 m/s, NW-NE wind, 12.9°C water temperature, humidity 86% and a mean salinity of 33.9 PSU). At the sampling sites, a small assistance boat was lowered from the RV Zeeleeuw to the water surface and the seaweeds were gently approached in order to avoid disturbance. Clumps of floating seaweed were collected using a 300 µm mesh dip net with a ring diameter of 40 cm. Three control samples (i.e. surface water samples without floating seaweed) were taken at each sampling position. After each haul, the net was emptied, rinsed and its contents preserved in an 8% buffered formaldehyde-seawater solution. Each haul was considered as a separate sample and used as such throughout the analyses.

In the laboratory, the preserved samples were rinsed over a 1mm sieve. The seaweeds were sorted and the volume of the algal constituents was recorded to the nearest millilitre, using a graduated cylinder as a measuring device. The macrofauna was identified to species level, wherever possible. For certain taxa, further classification was done based on the life history stage, such as zoea, megalopa or post larval stage of the decapods. Meiofauna and sessile organisms (such as harpacticoid copepods, acarines, nematodes, bryozoans and barnacles) were not counted. The densities were expressed as individuals per litre of seaweed and the diversity was calculated and expressed as expected number of species (per 100 individuals) (Hurlbert, 1971).

Prior to the analyses, the dataset was reduced to the species (1) accounting for > 3% of the total score in any one sample, and (2) found significantly more in seaweed samples compared to control samples. Univariate two-way analysis of variance (ANOVA) was used to test for differences in abundance between seaweed samples and control samples, taking into account the location. If necessary, a log (x + 1) transformation was performed to meet the required assumptions. In the cases were the assumptions were not met, a non-parametric Mann-Whitney U-test was applied.

Species abundance data of seaweed-associated fauna were subjected to non-metric multidimensional scaling ordination (MDS) using the Bray-Curtis similarity measure. ANalysis Of SIMilarities (ANOSIM) was used to test for significant differences ($p<0.05$) between groups, while the species contributing to dissimilarities between groups were investigated using a similarity-percentages procedure (SIMPER). The relationship between macrofauna densities and variables (sample site, sample volume and relative seaweed species abundance) was analysed using the Spearman rank correlation and the significance was determined using a permutation procedure (RELATE, Clarke & Warwick, 1994). The BIO-ENV procedure was used to define suites of variables that best determine the macrofaunal assemblages. All multivariate community analyses were done using the Primer v5.2.9 software package (Clarke & Gorley, 2001).

2.2 Experimental data

The seaweed preference of two abundant (see Vandendriessche et al, 2006a) floating seaweed-associated organisms from the Belgian coastal waters, *Idotea baltica* and *Gammarus crinicornis* (starved for 48h prior to the start of the experiments), was tested. During the experiments, the organisms were given the choice between five seaweed species that were also sampled on 18th May (see field data) and are commonly encountered in floating seaweed clumps in the English Channel region (Vandendriessche et al, 2006a – *Fucus vesiculosus*, *Himanthalia elongata*, *Enteromorpha* sp., *Ascophyllum nodosum*, *Sargassum muticum*) as well as a plastic aquarium plant as control. Cleaned fragments of the seaweeds of similar size (50 ± 0.5ml; freshly collected from Lake Grevelingen, or from fresh floating seaweed clumps in the case of *H. elongata*) were blotted dry and weighed prior the experiments. The seaweeds were randomly distributed over six compartments in a 1m x 0.3m x 0.4m aquarium and kept in place using nylon string and aquarium suckers. All multiple-choice experiments were conducted at a temperature of 15.5°C (± 1°C) in 34PSU aerated seawater, and the aquarium was provided with removable partitions and equally distributed oxygen sources.

Three types of experiment were carried out; each replicated three times and lasting for 12h (constant light): (1) seaweed preference of *Idotea baltica*, (2) seaweed preference of *Gammarus crinicornis*, and (3) seaweed preference of the two species put together, with possible preference shifts due to competition. The numbers of individuals used for the experiments were based on actual densities on floating seaweeds (83 Ind/l seaweed for *I. baltica* and 67 Ind/l seaweed for *G. crinicornis* on 18th May). Only adult individuals were used with mean lengths of 9 mm for *G. crinicornis* and 25 mm for *I. baltica.* In each experiment, the isopods and/or amphipods could graze and swim freely between the different algal species. Every 2 h, the number of swimming individuals was recorded. At the end of the experiment, the number of swimming and grazing individuals was recorded, the partitions were put in place and the number of individuals on each seaweed fragment was counted. Afterwards, the seaweeds were blotted dry and weighed again. Three control treatments (to check for autogenic weight loss of the algae) contained the same algae (except *Himanthalia elongata* due to a shortage of fresh material) but no isopods or amphipods. Wet weight of the control algae was determined before and after each experiment.

Differences between initial and final wet weight of the algae were used to calculate the percentage of algae consumed (± SD). Any negative weights were considered as non-grazing events and analysed as zero values (Goecker and Kåll, 2003). The presence of significant autogenic changes in the control treatments was tested with Wilcoxon matched pairs tests, taking into account the variation in initial weight.

All percentage data were arcsin transformed prior to the analyses. Variations in percent weight loss due to grazing, association frequencies of isopods and amphipods, and shifts in preferences of the grazers in the combined experiment compared to the experiments with one single grazer were investigated using Log-Linear Analysis of Frequency Tables, with seaweed species, treatment (single species or combined), and test (three replicates) as factors and association frequencies or weight loss as dependent variables.

3. RESULTS

3.1 Field data

The 22 analysed seaweed samples had an average seaweed volume of 327 ml, ranging from 30 ml to 7513 ml. Some SWS also contained floating debris other than seaweed (mean 22 ml - 6% of total volume) like nylon, feathers, plastic and oil. Three seaweed species predominated and were found on both sampling sites (Fig. 1): *Ascophyllum nodosum* (32% of total volume), *Fucus vesiculosus* (31%) and *Sargassum muticum* (22%). The species *Himanthalia elongata* (7%), *Fucus spiralis* (2%), *Cystoseira baccata* (0.3%), *Halidrys siliquosa* (0.1%) and *Enteromorpha* sp. (0.2%) were less common. All SWS, except two, consisted of more than one species, from which *F. vesiculosus* and *A. nodosum* were most frequently encountered (in 18 and 16 samples out of 22, respectively).

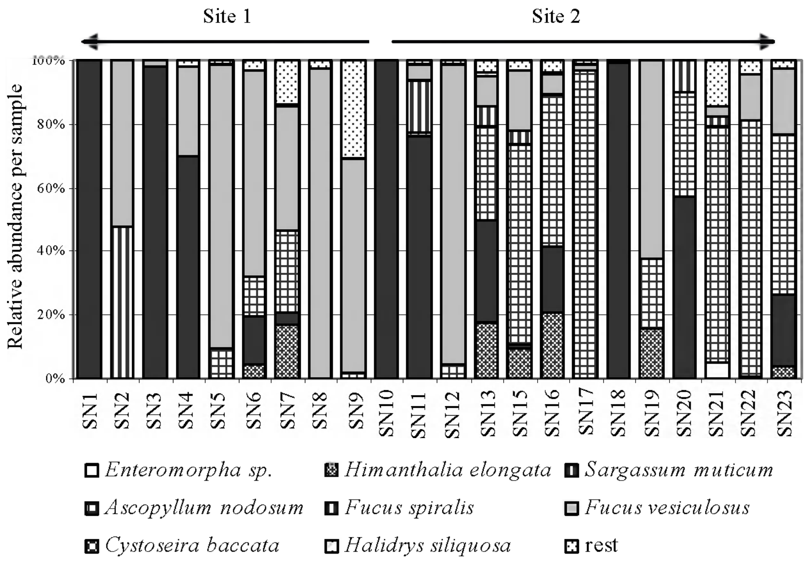


Fig. 1. Column chart showing relative abundances (%) of seaweed species per sample (SN_x), with indication of the sample site.

A total of 17148 organisms were identified, belonging to 78 taxa. From the 14 abundantly encountered taxa (> 3% of the total score in any one sample), ten were found significantly more in seaweed samples (SWS) compared to the surrounding water column (CS) (table 1).

Table 1. Univariate analyses p-values (effect of sample type: SWS vs. CS) concerning macrofaunal abundance (significant values: p<0.05 – italic) per species, with their mean association degree (percent of the total number of individuals found in seaweed samples) – designation to groups: bg = background fauna, sw = seaweed-associated fauna – mean density (individuals per liter of seaweed) of seaweed fauna

Group	**Species (and stage)**	**effect SWS/CS p-value**	**mean association %**	**group**	**Mean density Ind/l seaweed**
Polychaeta	*Autolytus prolifer* (polybostrichus)	0,214	73,7	bg	-
Insecta	Aphididae sp.	*0,001*	73,1	sw	35.86
Insecta	Formicidae sp.	0,194	75,0	bg	-
Insecta	Chironomidae sp.	*0,000*	75,0	sw	10.62
Crustacea	Calanoida sp.	0,157	29,3	bg	-
Crustacea / Decapoda	*Liocarcinus holsatus* zoea	0,935	45,0	bg	-
Crustacea / Decapoda	*Liocarcinus holsatus* megalopa	*0,000*	73,7	sw	345.74
Crustacea / Decapoda	*Liocarcinus holsatus* juv.	*0,001*	75,0	sw	15.60
Crustacea / Isopoda	*Idotea baltica*	*0,000*	75,0	sw	69.50
Crustacea / Isopoda	*Idotea* sp.	*0,039*	74,9	sw	21.95
Crustacea / Amphipoda	*Stenothoe marina*	*0,000*	75,0	sw	36.13
Crustacea / Amphipoda	*Gammarus crinicornis*	*0,000*	74,8	sw	40.01
Ascidiacea	Larvacea sp.	*0,001*	0,0	bg	-
Osteichthyes / Gadiformes	*Ciliata mustela*	*0,010*	75,0	sw	7.69

When only considering the seaweed-associated fauna, density of the SWS averaged 583 Ind/l (range 136-1609 Ind/l), while the ES (100) averaged 7.2 (range 5-9). Significant correlations were found between volume of the clumps and density of the associated macrofauna (R: -0.55, p: 0.008); and between volume of the clumps and diversity of the associated macrofauna (R: 0.49, p: 0.02). The effect of clump volume was not the same for all the species: some species exhibit a positive relation with clump volume (*Idotea baltica*, *Idotea* juveniles*, *Ciliata mustela*) while others show a negative relation (Aphididae sp., Chironomidae sp., *Stenothoe marina*, *Liocarcinus holsatus* megalopae* and juveniles*, *Gammarus crinicornis*) (asterisks indicate significant correlations at the level $p<0.05$).

MDS and ANOSIM ($p= 0.146$) analyses based on densities (Ind/l) of the seaweed-associated fauna (Bray-Curtis similarity) indicated no differences between the two sampling points (samples 1-9 and 10-23). Groups defined according to the dominant seaweed species in the samples (highest relative abundance – all seaweed species and fraction of debris considered) do show differences in macrofaunal species composition (Fig. 2; Table 2).

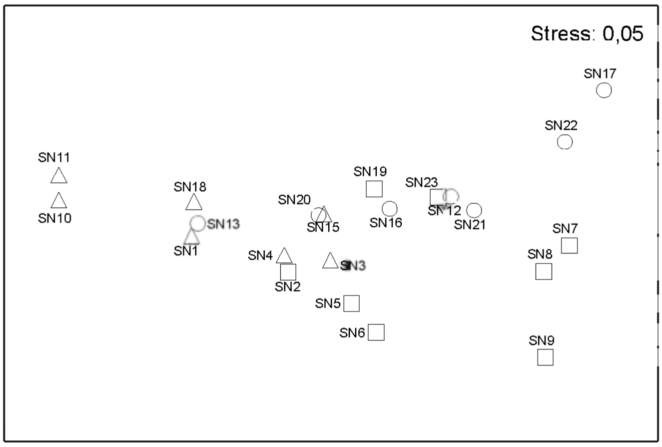


Fig. 2. MDS plot (Bray-Curtis similarities) of samples based on species densities, with indication of dominant seaweed species (highest relative abundance in each sample). *Sargassum muticum* = triangle, *Fucus vesiculosus* = square, *Ascophyllum nodosum* = circle

Results of pair-wise tests reveal significant differences between the *S. muticum* dominated group and the groups dominated by *F. vesiculosus* and *A. nodosum* (dissimilarities of 61% and 53%, respectively - Table 2). The SIMPER-analysis indicated that the dissimilarity between the *S. muticum* dominated group and the *F. vesiculosus* dominated group is mainly due to the abundant presence of *Liocarcinus holsatus* megalopae (percentage contribution: 63%) and *Stenothoe marina* (8%) in the first group and of *Gammarus crinicornis* (9%), *Idotea baltica* (5%) and *Idotea* juveniles (4%) in the second group. Similarly, the differences between the *S. muticum* dominated group and the *A. nodosum* dominated group are caused by the higher abundances of *L. holsatus* megalopae and juveniles (66% and 5%) and *S. marina* (8%) in the first group and of *I. baltica* (5%) and Aphididae sp. (5%) in the second group. Densities of the discussed macrofaunal species per seaweed group are displayed in Fig. 3.

Table 2. Results of ANOSIM and pair-wise tests for differences in macrofaunal community structure depending on the dominant seaweed species in a sample. R-values and p-values are reported.

Community structure of seaweed-associated fauna		
	R-value	p-value
Global test	0.277	*0.004*
Groups compared		
S. muticum – F. vesiculosus	0.414	*0.003*
S. muticum – A. nodosum	0.349	*0.021*
F. vesiculosus – A. nodosum	0.076	0.175

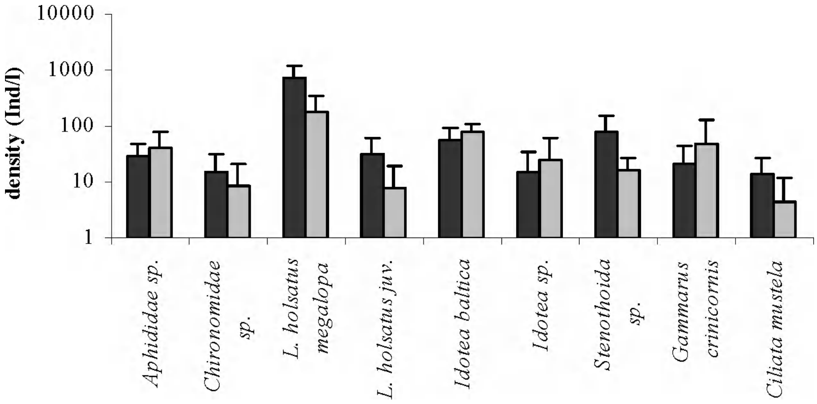


Fig. 3. Column chart showing mean densities (Ind/l - indication of SD – logarithmic scale) of the discussed macrofaunal species for the *Sargassum muticum* group (black) and the *Fucus vesiculosus / Ascophyllum nodosum* group (grey)

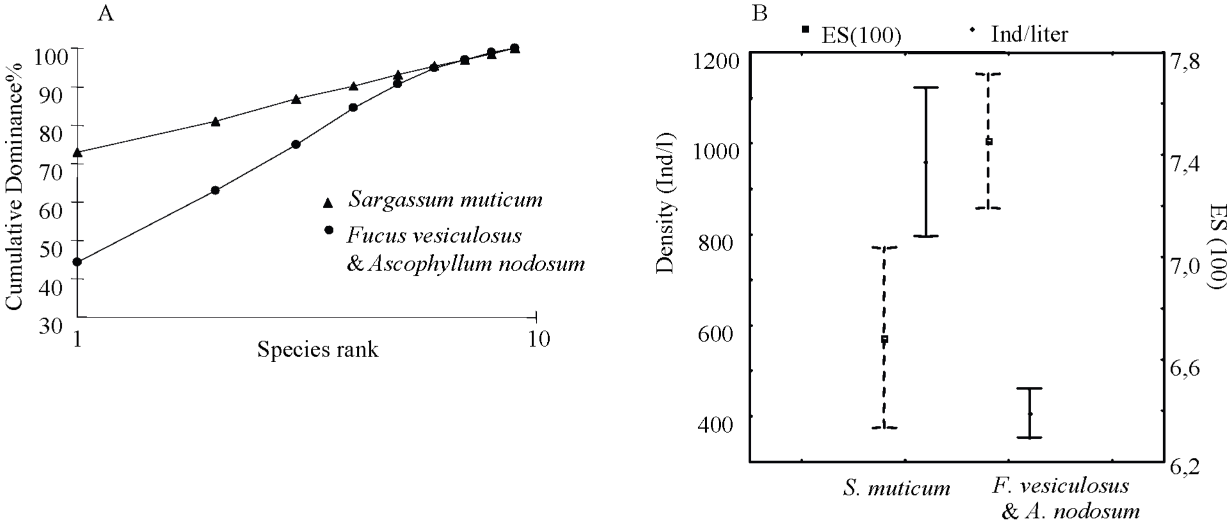


Fig. 4. A. K-dominance curves for the two significantly different sample groups (*S. muticum* and *Fucus vesiculosus/Ascophyllum nodosum*) – B. Whisker plots of density (Ind/l – left Y) and diversity (ES(100) – right Y), with indication of mean and standard error.

As multivariate analysis only indicates differences between *S. muticum* dominated samples and samples dominated by other seaweeds, density and diversity are discussed for two groups. When comparing density and diversity data of *S. muticum* dominated samples with samples dominated by *F. vesiculosus* or *A. nodosum*, we found that: (1) density was significantly higher (MWU p= 0.001) in *S. muticum* dominated samples (mean 960 Ind/l) compared to *F. vesiculosus*/*A. nodosum* dominated samples (mean 407 Ind/l); (2) the Expected Number of Species was higher in *F. vesiculosus* / *A. nodosum* dominated samples (mean 7.5 vs. 6.7), however not significantly (MWU p= 0.18); (3) next to a higher diversity, *F. vesiculosus* / *A. nodosum* dominated samples also exhibited a much higher evenness (Fig. 4a).

Results from the RELATE and BIO-ENV analyses confirmed the influences of seaweed species and volume on the macrofaunal assemblages. RELATE indicated a significant correlation between the standardised Euclidian distance matrix of the variables (sample site, sample volume and relative seaweed species abundance) and the similarity matrix of macrofaunal data ($p<0.005$). The draftsman plot and the associated correlation matrix showed no evidence of collinearity, so all variables were used in the BIO-ENV analysis. Within the analysed SWS, a combination of five variables (volume and relative abundances of *S. muticum, A. nodosum, F. vesiculosus* and the debris fraction) best explained the macrofaunal assemblages ($\sigma = 0.557$). Correlation analyses between the five selected variables, density and diversity reflect the results discussed in previous sections and in Fig 4b: volume has a negative effect on density and a positive effect on diversity; increasing relative abundances of *F. vesiculosus* and *A. nodosum* have a positive effect on diversity and a negative effect on density, while it is the other way round for *S. muticum*. The effect of an increasing rest fraction (positive for diversity, negative for density) is similar to the effect of *F. vesiculosus* and *A. nodosum*.

3.2 Experiments

Control samples showed no significant weight loss (*Enteromorpha* sp. p= 0.14; *Sargassum muticum* p= 0.07; *Fucus vesiculosus* p= 0.7; *Ascophyllum nodosum* p= 0.14) for the examined seaweed species. Therefore, a correction factor for autogenic changes of the seaweeds during the experiments was not used (Petersen & Renaud, 1989).

The preference order of *Idotea baltica* based on the association percentage was: *Enteromorpha* sp. (27%), *F. vesiculosus* (26%), *S. muticum* (9%), plastic (8%), *H. elongata* (7%) and *A. nodosum* (7%). An average of 5% of the population was swimming at the end of the experiments. Although a preference (effect seaweed Chi-sqr.: 52.6; $p<0.001$) was shown for some seaweed species, this preference was not reflected in the weight loss due to grazing (Fig. 5). As a food choice, *S. muticum* (14% weight loss), *A. nodosum* (13% weight loss) and *Enteromorpha* sp. (11% weight loss) seem to be more attractive (effect seaweed: Chi-sqr.: 167.9; $p<0.001$).

The weight loss effect due to the grazing activity of *Gammarus crinicornis* was smaller (mean weight loss: 2%) compared to the one of *I. baltica* (mean weight loss: 7%). *G. crinicornis* showed a clear preference for *S. muticum* with 44% of the population found on this seaweed species (effect seaweed Chi-sqr.: 68.3; $p<0.001$). In spite of this high association percentage, the mean weight loss (2.8%) is slightly lower compared to the ones found for *A. nodosum* (3.8%) and *F. vesiculosus* (2.9%) (effect seaweed Chi-sqr.: 158.2; $p<0.001$).

The experiments in which both species were used (Fig. 6), show moderate shifts in association percentages of both species, compared to the experiments concerning a single grazer (Fig. 5) (Log-Linear Analysis *Idotea baltica* (a) effect seaweed p< 0.001, (b) effect test p= 0.5 (c) effect treatment p= 0.29, (c) all combined effects p> 0.05 – *Gammarus crinicornis* (a) effect seaweed p< 0.001, (b) effect test p= 97, (c) effect treatment p= 0.15, (d) combined effects p> 0.05). For both species, there are no significant changes due to the presence of another grazer. As no distinction could be made between the grazing marks of both species in the combined experiment, no conclusions can be made about shifts in grazing effects on the different seaweed species.

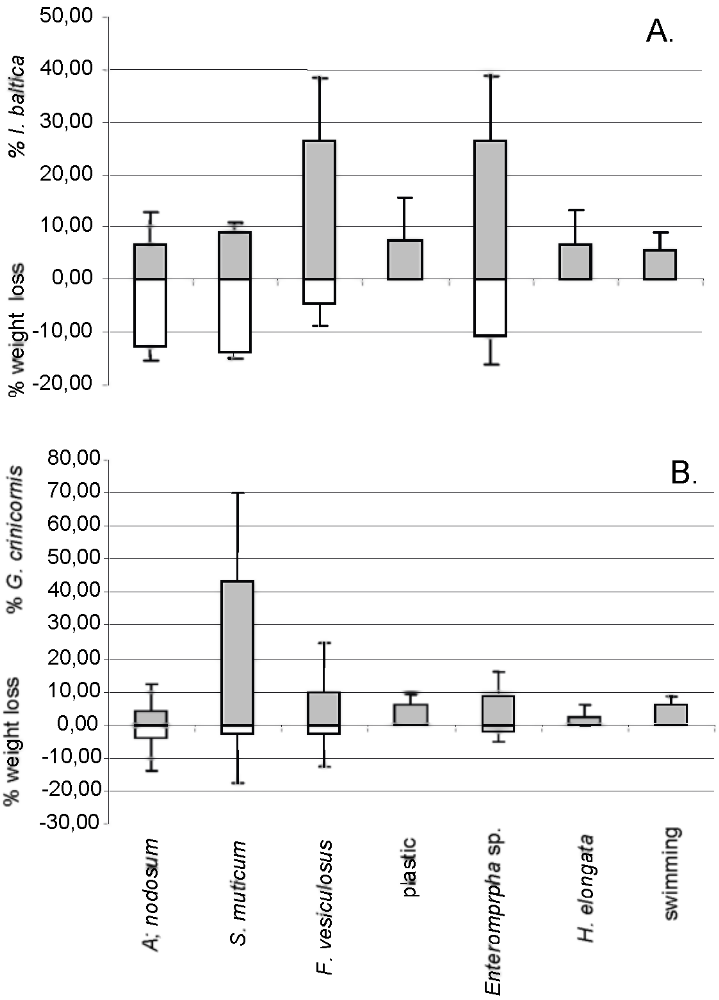


Fig. 5. Seaweed choice of *Idotea baltica* (A) and *Gammarus crinicornis* (B), expressed as the mean percentage (± SD) of the population per seaweed species, and the mean percentage of each seaweed species grazed (± SD)

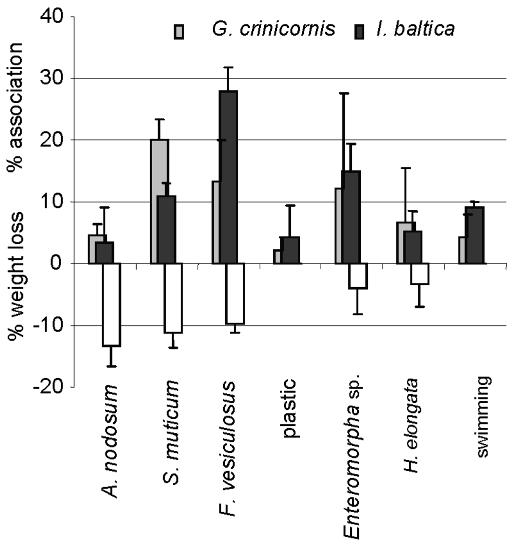


Fig. 6. Seaweed choice of *Idotea baltica* and *Gammarus crinicornis* in a combined multiple-choice aquarium experiment, expressed as the mean percentage (± SD) of the population per seaweed species, and the mean percentage of each seaweed species grazed (± SD)

4. DISCUSSION

The main objective of this study was to assess the importance of the seaweed species in structuring the species composition, density and diversity of the seaweed-associated macrofauna. Therefore, an attempt was made to minimise spatial and temporal variation in the field study. A factor that could not be eliminated from this study, however, was the variation in clump size. Some authors have found positive relationships between the abundance of associated fauna and clump size (Fine, 1970; Stoner & Greening, 1984; Kingsford & Choat, 1985; Safran & Omori, 1990; Kingsford 1992; Druce & Kingsford, 1995; Ingólfsson, 1995 & 1998; Ólafsson et al, 2001, Thiel & Gutow, 2005a,b), which may be due to greater protection from predators in larger clumps, reduced danger of dropping off the clumps, a higher food supply compared to the surrounding water column and more surface for attachment. In this study, only few species were found to show such a correlation and therefore it is likely that correlations vary greatly depending on the origin of the seaweeds and the association degree and behaviour of the associated species. A positive correlation between species richness and clump size was not found in Fine (1970), but was found to be significant in Ingólfsson (1995 & 1998), Ólafsson *et al* (2001) and the present study. Thiel and Gutow (2005a) mention a positive correlation between the surface area and the species richness, for at least some floating items. Surface area can be substantially higher for seaweeds with a complex 3D structure. The higher structural complexity of *Sargassum muticum*, compared to *Fucus vesiculosus* and *Ascophyllum nodosum*, may be responsible for differences in density and diversity of the associated macrofauna. The amphipod *Stenothoe marina*, for example, is known to associate with highly branched structures such as seaweeds and hydroids (Bradshaw et al, 2003) and may therefore display higher densities in *S. muticum*. Furthermore, varying levels of toughness, chemical defenses against grazing, nutritional values, value as a refuge and suitability for rafting of different seaweed species (Ragan & Jensen, 1977; Salemaa, 1987; Hay et al, 1988; Tuomi et al, 1988; Denton & Chapman, 1991; Hemmi & Jomalainen, 2004; Thiel & Gutow, 2005a) are expected to result in preferences of macrofaunal species for certain seaweed species in clumps of floating seaweeds. In literature, however, little evidence can be found for the confirmation of this hypothesis (Stoner & Greening, 1984; Kingsford & Choat, 1985; Ingólfsson, 1998; Ólafsson et al, 2001). However, interesting results were obtained when reducing the number of variables in a study. Ingólfsson & Ólafsson (1997) focused on only one species, the harpacticoid *Parathalestris croni*, and found a clear preference for floating thalli of *A. nodosum* and its epiphyte *Polysiphonia lanosa*, to which the copepods can easily cling. In the present study, reduction of macrofaunal data to the clearly associated organisms (see table 1) and minimisation of spatial and temporal variation resulted in clear patterns of seaweed preference. Seaweed preference was also apparent from the results of the multiple choice experiments, but did not exactly match the results of the community analysis: (1) *Idotea baltica* had high densities in seaweed samples dominated by *Fucus vesiculosus* and *Ascophyllum 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) *Gammarus 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*. Neither the present study, nor literature provides a definite answer about the preference of these species. It is clear from the laboratory experiments, however, that preference for habitat (shelter) and food can differ among seaweed species. Orav-Kotta and Kotta (2004), for example, found a significant correlation between distributions of *I. baltica* and *F. vesiculosus* in the Baltic Sea, but a shift towards filamentous macro-algae in case of eutrophication. In multiple-choice experiments, it seemed that *F. vesiculosus* was selected as shelter, while filamentous algae were preferred as food when both seaweed species were offered. A similar food preference for filamentous algae was found by Goecker and Kåll (2003) for *I. baltica* and *Gammarus oceanicus*, while Jormalainen et al (2001) and Schaffelke et al (1995) found that *I. baltica* preferred *F. vesiculosus* over other algae, including *Enteromorpha* sp. In a host plant preference experiment including *Fucus serratus* and the red alga *Polysiphonia fucoides*, *I. baltica* was evenly distributed between the host plants, but grazed more on *F. serratus* (Svensson et al, 2004). Pavia et al (1999) performed multiple-choice experiments on *Idotea granulosa* and *Gammarus locusta* and found that the isopods grazed heavily on apices of *A. nodosum*, while the amphipods preferred macro-epiphytes.

Previous studies have suggested that habitat choice of grazers is mainly a function of algal morphology (e.g. Nicotri, 1980) and colour (Salemaa, 1987), while they prefer to feed on filamentous algae due to a higher nutritional value (Boström & Mattila, 1999; Pavia et al, 1999). 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 (Hay et al, 1988; Arrontes, 1990; Schaffelke et al, 1995; Pavia et al, 1999; Boström & Mattila, 1999). The effect of the presence of a second grazer was not significant in the present study, although Pavia et al (1999) and Viejo and Åberg (2003) already suggested that superficial wounds inflicted by isopods could facilitate the feeding of gammarid amphipods. Salemaa (1987), on the other hand, only found negligible competitive effects when using three *Idotea* congeners in different microhabitats.

Although seaweed preference of the associated macrofauna appears highly variable, it is clear that the macrofaunal species composition is strongly influenced by the size and seaweed composition of the clumps. However, these factors do not explain all the variation in species associations, densities and species richness, so it is very likely that, next to spatial and temporal variation (minimised in the present study), the period since detachment (Stoner & Greening, 1984; Edgar, 1987; Ingólfsson, 1995 & 1998; Ingólfsson & Ólafsson, 1997; Ólafsson *et al*, 2001; Thiel, 2003) or the event of washing onto a beach and refloating (Kingsford & Choat, 1985) may also be major structuring factors. The discrepancies between habitat choices found in floating seaweeds and laboratory experiments may, in part, be due to the history of the seaweeds: the stress of floating at the surface (higher temperatures and UV radiation compared to attached algae) can have a significant effect on the palatability of the algae (Cronin & Hay, 1996) and therefore also on the food choice of the species. Effects of seaweed composition may also be blurred due to the obligate opportunistic nature of a lot of the associated macrofaunal species. The survival of some of these species (e.g. flying insects that were blown offshore and land on floating seaweeds – juvenile fish that need shelter from larger predators) depends on the food, shelter and attachment space offered by the seaweeds. The seaweed-associated fauna therefore takes advantage of the presence of all alternative habitats in the neustonic environment, regardless of the seaweed composition. Eventually, only species/individuals with a good swimming ability (e.g. *I. baltica, G. crinicornis*) can move to a clump with more favourable conditions (higher nutritional value or more shelter) whenever such clumps are available. The availability of the preferred seaweeds is in turn highly dependent on seasonal factors, such as fragmentation at the end of the growing season, variation in the amount of grazing damage and the occurrence of storms (Thiel & Gutow, 2005a). In short, the transient and unpredictable nature of floating seaweed clumps (and their constituent species) is believed to induce an opportunistic behaviour in the associated fauna ensuring their survival but obscuring their food and/or habitat preferences.

In the case of floating seaweeds off the Belgian coast, where few seaweed species (mostly *F. vesiculosus* and *Enteromorpha* sp.) are encountered on the artificial hard substrates, the input of several seaweed species from neighbouring coastlines results in an increased structural complexity of the neustonic layer in the Belgian coastal zone and consequently in higher faunal densities and diversities. Especially the presence of the invading seaweed species *S. muticum* seems to have a significant effect on the encountered species assemblages. The growing importance of this structurally complex seaweed species may enhance the rafting opportunities of high densities of several macrofaunal species that are not commonly encountered in other seaweed clumps.

5. CONCLUSION

In this study, it is clearly shown that the macrofaunal species composition was influenced by the species composition of the seaweeds; and that in some cases the effect of seaweed species may be stronger than competition and spatial distribution. Food and habitat choice are the main mechanisms influencing the seaweed preference of associated macrofauna. However, interpretation of the sample data and experimental outcome, in the light of seaweed preferences, should be done with care. Food and habitat preferences are highly dependent on the offered choices. Preference sequences may alter completely when omitting one or more seaweed species in the experiments, or by changing seaweed abundance. The same is true if the abundance and number of seaweed species to choose from is lower in one seaweed clump compared to another. Another factor to consider, when studying effects of seaweed preference in the field, is the obligate opportunistic nature of some of the associated species:

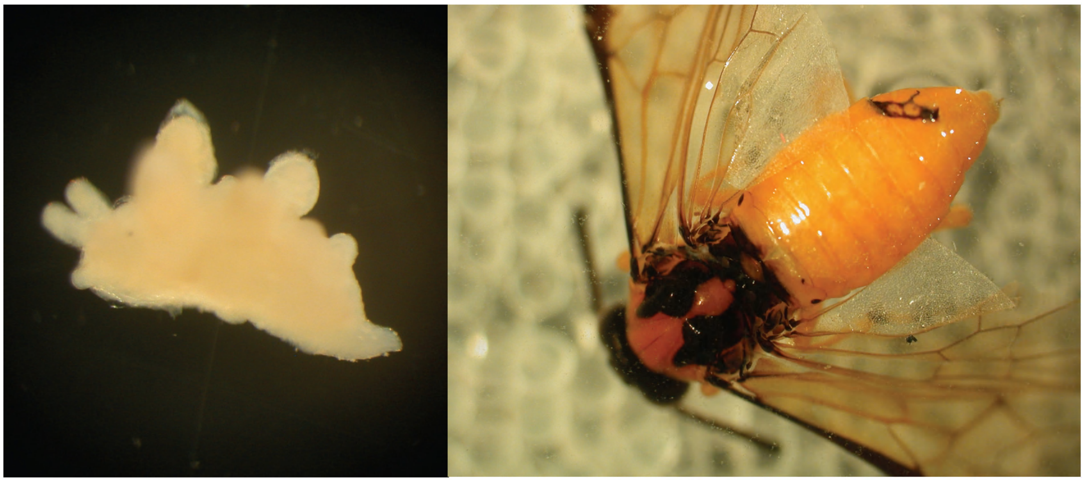
due to the transient nature of floating seaweed clumps, associated fauna have to be able to survive in sub-optimal conditions concerning food and/or habitat.

ACKNOWLEDGEMENTS

The first author acknowledges a specialisation grant from the 'Institute for the Promotion of Innovation through Science and Technology in Flanders' (IWT). The authors would like to express their gratitude to Saskia Van Gaever and Jeroen Speybroeck for their help with the samplings; and to Dries Bonte for the introduction to Log-Linear Analysis. Special thanks go to André Cattrijsse of the Flanders Marine Institute (VLIZ), and to the crewmembers of the research vessel Zeeleeuw. Marleen De Troch, two anonymous referees and the editor are acknowledged for their highly useful comments and corrections on earlier versions of the manuscript.

CHAPTER 4

SOURCES OF VARIATION IN FLOATING SEAWEED-ASSOCIATED MACRO-INVERTEBRATES



Tergipes tergipes and Tenthredinidae sp.

Paper submitted

Vandendriessche S., Deprez T., Vincx M., Degraer S.

Sources of variation in floating seaweed – associated macro-invertebrates

Marine Biology

ABSTRACT

The species composition and density of fauna associated with floating seaweeds is highly variable and influenced by many factors such as spatial and temporal variation, period since detachment and seaweed species composition. Based on data from floating seaweeds in the Belgian coastal zone, the present 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 size distribution 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.

Keywords: Macrofauna; Floating Seaweed; North Sea; Spatial and Temporal Variation

1. INTRODUCTION

The presence of floating seaweeds on the sea surface has an important impact on the species composition and diversity of the neustonic fauna. Not only do floating seaweeds carry littoral fauna that stayed associated after detachment, they also attract fauna from the surrounding and underlying water column due to the provision of shelter, a food source, surface for attachment and a means of passive long distance dispersal (Tully & O'Ceidigh, 1986; Ingólfsson, 1995, 1998, 2000; Ólafsson et al, 2001; Thiel & Gutow, 2005a). This process of continuous colonisation results in substantial increases in diversity, density and biomass of the surface layer fauna (Kingsford & Choat, 1985; Druce & Kingsford, 1995; Vandendriessche et al, 2006a). However, floating seaweed clumps are complex systems, in which the species assemblages are influenced by a wide range of factors. The effects of raft age, origin and distance travelled reflect the process of succession during the voyage of floating seaweed clumps after the event of detachment (Stoner & Greening, 1984; Ólafsson et al, 2001, Thiel & Gutow, 2005a). During the drift, the seaweeds and their associated epiphytes and fauna change markedly, altering the living conditions for other colonisers (Edgar, 1987; Ingólfsson & Ólafsson, 1997, Thiel, 2003). The effects of variation linked to the size of the clumps were not straightforward throughout the different studies in the past: some authors have found positive relationships between the abundance of associated fauna and clump size (Fine, 1970; Stoner & Greening, 1984; Kingsford & Choat, 1985; Safran & Omori, 1990; Kingsford 1992; Druce & Kingsford, 1995; Ingólfsson, 1995 & 1998; Ólafsson et al, 2001), which may be due to greater protection from predators in larger clumps, reduced danger of dropping off the clumps, a higher food supply compared to the surrounding water column and more surface for attachment. In Highsmith (1985) and Vandendriessche et al (2006b), only few macrofaunal species were found to show such a correlation and therefore it is likely that correlations vary greatly depending on the origin of the seaweeds and the association degree and behaviour of the associated species. A positive correlation between species richness and clump size was not found in Fine (1970), but was found to be significant in Ingólfsson (1995 & 1998), Hobday (2000b), Ólafsson et al (2001) and Vandendriessche et al (2006b). The effects of seaweed species composition have already been confirmed in Iceland (Ingólfsson & Ólafsson, 1997; Ólafsson et al, 2001) and in the southern part of the North Sea (Vandendriessche et al, 2006b), where some invertebrates show a preference for a certain seaweed species as habitat or food source. However, due to the ephemeral status of floating seaweed patches and the opportunistic nature of the associated fauna, seaweed preference is often not expressed. Influences of spatial and temporal variation on the associated fauna have already been established in studies throughout the world: densities of associated fauna appear highly seasonal and related to geographic region, distance to shore or the nearest seaweed bank (Fine, 1970; Stoner & Greening, 1984; Kingsford, 1992; Kingsford & Choat, 1985; Tully & O'Ceidigh, 1986; Ingólfsson, 1995;

Ingólfsson & Ólafsson, 1997, Dempster & Kingsford, 2004; Ohta & Tachihara, 2004; Wells & Rooker, 2004; Salovius et al, 2005).

Most studies about fauna associated with floating seaweeds focus on a limited number of variation sources: Wells and Rooker (2004), for example, only discussed spatial and temporal variation, while Thiel (2003) focused on the age of seaweed rafts and temporal succession, and Vandendriessche et al (2006b) dealt with the impact of variations in seaweed species composition. The aim of the present study is to synthesise and quantify the combined effects of different sources of variation (depth, temperature, salinity, sample site and date, sample volume, relative seaweed species abundance, clump age), based on data of ephemeral floating seaweed patches at the Belgian coast. In other words, the main question asked is 'What are the driving forces of variation within the invertebrate community associated with floating seaweeds, and what are their relative importances?' Furthermore, the temporal variation within populations of two abundantly encountered genera (*Gammarus* sp. and *Idotea* sp.) was analysed on the levels of size distribution and sexual maturity.

2. MATERIALS AND METHODS

2.1 Sampling

Monthly samples were collected from October 2002 until September 2004 on the Belgian Continental Shelf (BCS), in the southernmost part of the North Sea. Every other week, the RV Zeeleeuw sailed trajectories of ± 60 nautical miles across the Belgian part of the North Sea, thereby increasing the chance of floating seaweed encounters by sailing (as much as possible) perpendicular to the prevailing water currents. Samples were collected at distances of 0.6 to 19.3 nautical miles from the coastline, and were grouped according to their origin into (1) near shore samples (NS) from the Coastal Banks (<10 km off shore), and (2) off shore samples (OS) from the Flemish Banks and Hinder Banks (> 10 km off shore; Fig. 1). Sampling intensity was not equal over the seasons because bad weather often prevented the search for floating seaweeds (especially in the period Oct – Jan). For successful samplings (25 sampling days), the mean number of sampling points (and hence the amount of encountered seaweed clumps) was highest in the periods Feb-Apr and Jun-Sep. During these days, two scientists continuously looked out for seaweeds from the bridge of the research vessel. When clumps of floating seaweed were observed, a small assistance boat was lowered to the water surface and the seaweeds were gently approached, in order to avoid disturbance. Clumps of floating seaweed (minimum three per sampling occasion, and 1 to 4 sampling occasions per sampling date) were collected using a 300 µm mesh dip net with a ring diameter of 40 cm. The maximal size of the clumps was determined by the diameter of the dip net. As they could not be adequately sampled, larger seaweed clumps were left undisturbed. Three control samples (i.e. surface water samples without floating seaweed) were taken at each sampling position (>10 metres away from the nearest seaweed clump). After each haul, the net was emptied, rinsed and its contents preserved in an 8% buffered formaldehyde-seawater solution.

Environmental variables measured included depth (Marimatech SeaSound 206C), sea surface temperature and salinity (thermosalinograph SBE21).

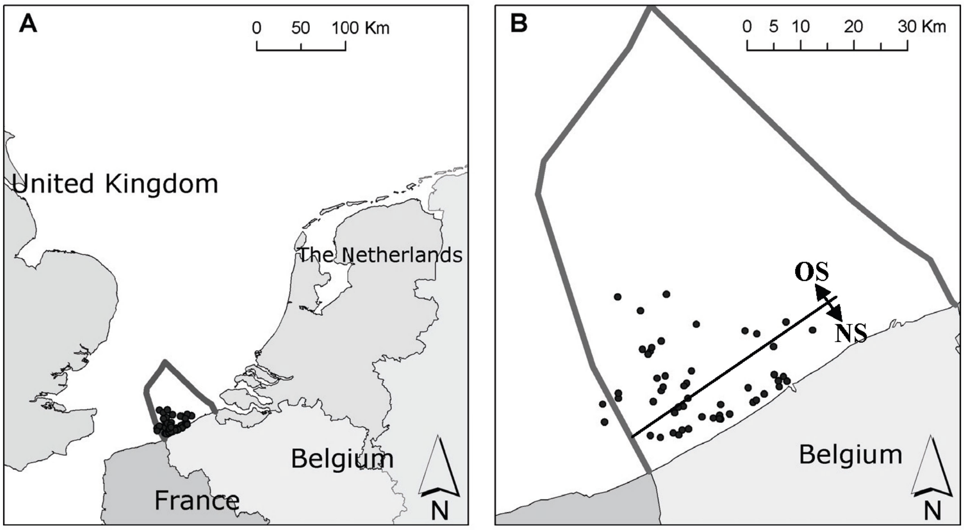


Fig. 1. Map of the sampling area (Belgian Continental Shelf) with indication of the sampling points (black dots) and the grouping of near shore samples (NS) and off shore samples (OS) (black line, B).

2.2 Data acquisition

In the laboratory, the preserved samples were rinsed in fresh water and sieved over a 1mm sieve (cf. Vandendriessche et al, 2006a). After sorting, all non-colonial and mobile macrofauna were identified – if possible – to species level. For certain taxa, further classification was done based on the life history stage, such as zoea, megalopa or post larval stage of decapods. Meiofauna and sessile organisms (such as harpacticoid copepods, acarines, nematodes, bryozoans and barnacles) were not counted. Certain species were reported on a higher taxonomical level (noted as 'sp.' – e.g. juveniles of the genus isopod *Idotea* were grouped); these taxa are further also referred to as 'species'. Species occurring in a wide length range were measured (standard length from the rostral tip to the last abdominal segment for crustaceans).

Raft volumes were quantified by water displacement per seaweed species. Floating objects other than seaweeds were lumped and referred to as 'rest'. The dominant species of seaweed were classified into two categories based on their color and epiphyte load (only determined for samples Oct

2002 – Sept 2003): recently detached or new seaweed (green, few epiphytes), and old seaweed (reddish brown, considerable epiphyte cover) (cf. Stoner & Greening, 1984; Parsons, 1986).

2.3 Data treatment

Prior to the analyses, the dataset was reduced to the species (1) accounting for > 3% of the total score in any one sample, and (2) found significantly more in seaweed samples compared to control samples: univariate two-way analysis of variance (ANOVA) was used to test for differences in abundance between seaweed samples and control samples, taking into account the date and location (49 sampling occasions, 2 sample types). If necessary, a log $(x + 1)$ transformation was performed to meet the required assumptions. Of all species, the added value of density was calculated by subtracting background neustonic values from seaweed sample values per sampling occasion (see Vandendriessche et al, 2006a). These values were expressed as individuals per litre of seaweed, and were further used in the analysis of the macrofaunal data.

Effects of spatial (near shore, off shore) and temporal (seasonal) variation on the densities (added values) of the seaweed-associated species were examined using the non-parametric Kruskal-Wallis (KW) and Mann-Whitney U test (MWU), because the assumptions for parametric testing were not fulfilled. As only two samples represented the off shore autumn group, all autumn samples were excluded from the statistical analyses.

The assemblage structure of the seaweed-associated invertebrate fauna was investigated using non-metric multidimensional scaling ordination (MDS) using the Bray-Curtis similarity measure. ANalysis Of SIMilarities (ANOSIM) was used to test for significant differences ($p<0.05$) between groups, while the species contributing to dissimilarities between groups were investigated using a similarity-percentages procedure (SIMPER). Patterns of association between macrofaunal abundances and environmental factors (depth, temperature, salinity) and other variables (sample site and date, sample volume and relative seaweed species abundance, clump age) were analysed using the Spearman rank correlation and the significance was determined using a permutation procedure (RELATE, Clarke & Warwick, 1994). The BIO-ENV procedure was used to define suites of variables that best determine the macrofaunal assemblages. All multivariate community analyses were done using the Primer v5.2.9 software package (Clarke & Gorley, 2001).

3. RESULTS

3.1 Environmental conditions

Seasonal variations in temperature and salinity were pronounced. Sea surface temperatures increased from a minimum of 5.5°C in winter to a maximum of 22.4°C in summer (KW $p < 0.001$ in both NS and OS samples). Winter temperatures differed significantly between OS and NS (MWU $p = 0.002$); no significant differences were observed in spring and summer samples (MWU $p = 0.12$ and 0.72, respectively). Salinity decreased from winter to spring, and increased again in summer (KW NS $p = 0.01$, OS $p < 0.001$). Significant effects of spatial variation were observed in summer samples, in which the salinity was higher in the OS samples (Table 1, MWU $p = 0.001$); no significant differences were observed in winter and spring samples (MWU $p = 0.64$ and 0.34, respectively).

Depth averaged 14.7 ± 0.6 m in near shore samples and 19.6 ± 0.6m in off shore samples ($p< 0.001$).

Table 1. Average sea surface temperatures (°C) and salinities (PSU) per sampling area and per season, reported with their standard error.

	season	**N**	**surface temperature**	**salinity**
Near shore	autumn (25/9 – 3/10)	13	16,9 ± 0,3	32,6 ± 0,4
	winter (7/2 – 27/2)	11	7,3 ± 0,2	33,7 ± 0,3
	spring (21/3 – 20/6)	27	14,8 ± 0,6	32,3 ± 0,3
	summer (1/7 – 4/9)	18	19,2 ± 0,4	33,4 ± 0,2
Off shore	autumn (25/9)	2	17,9	32,6
	winter (18/2 – 27/2)	7	5,7 ± 0,2	33,9 ± 0,1
	spring (4/4 – 5/6)	45	13,5 ± 0,5	32,6 ± 0,2
	summer (21/6 – 5/9)	60	18,8 ± 0,2	34,0 ± 0,1

3.2 Seaweed clumps

Clumps of floating seaweed consisted of one or more seaweed species like *Fucus vesiculosus* (Fv), *Ascophyllum nodosum* (An), *Halidrys siliquosa* (Hs), *Fucus spiralis* (Fs), *Himanthalia elongata* (He), *Cystoseira* sp. (Csp), filamentous green algae (fil. gr. algae), *Chorda filum* (Cf) and *Sargassum muticum* (Sm), and small amounts of other floating debris like reed, feathers, plastic, nylon, wood and cardboard.

During the sampling period, there were clear seasonal shifts in the relative abundances of the dominant seaweed species in both near shore samples and off shore samples (Fig 2). In the near shore samples, *A. nodosum* and *H. elongata* were quite abundant in autumn and winter samples, while spring and summer samples were mostly dominated by *F. vesiculosus* and *F. spiralis* (KW Fv $p = 0.003$, An p < 0.001, He p = 0.003, Fs p = 0.02). In the off shore samples, *A. nodosum*, *H. elongata* and *F. vesiculosus* were dominant in autumn (few samples) and winter, while the abundances of *F. spiralis* and *S. muticum* became more important in spring and summer (KW Fv p = 0.007, An p = 0.19, He p = 0.18, Fs p < 0.001, Sm p = 0.001). Spatial differences were significant for Fv (MWU p = 0.002) and An (p = 0.002) in winter; for Fv (p = 0.03), An (p = 0.002), He (p = 0.07) and Sm (p = 0.004) in spring; and for Fv (p = 0.03) in summer.

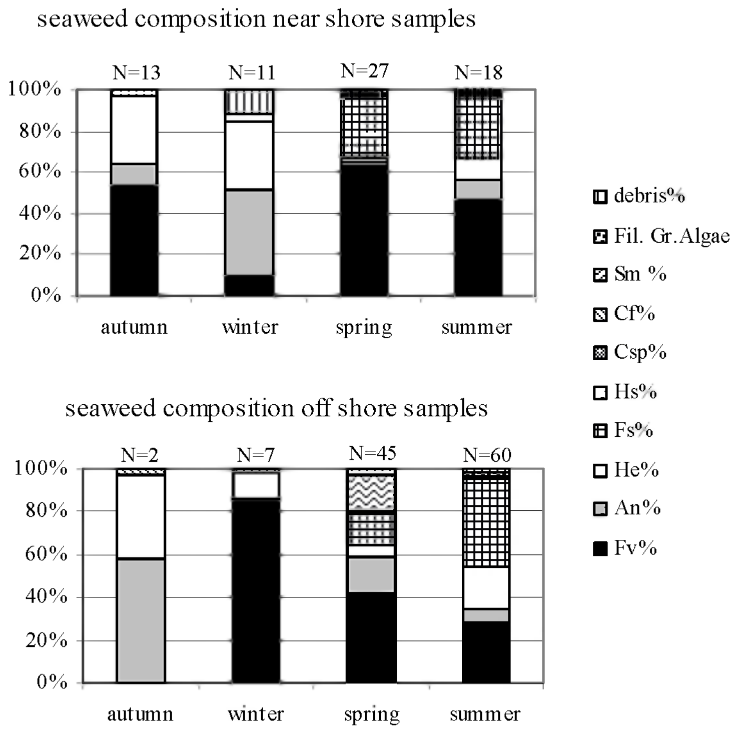


Fig. 2. Bar charts representing seaweed species composition (volume %) of floating seaweed clumps in the near shore and off shore region per season. *Fucus vesiculosus* (Fv), *Ascophyllum nodosum* (An), *Halidrys siliquosa* (Hs), *Fucus spiralis* (Fs), *Himanthalia elongata* (He), *Cystoseira* sp. (Csp), Filamentous green algae (Fil. Gr. Algae), *Chorda filum* (Cf), *Sargassum muticum* (Sm)

3.3 Invertebrate macrofauna

A total of 137 invertebrate taxa were recorded, of which 51 were terrestrial organisms. Forty-four species occurred frequently within floating seaweed patches; and 21 species were significantly more abundant within seaweed samples compared to control samples. Dominant taxa of the seaweed-associated fauna included gammarid amphipods (22% of added value), idoteid isopods (13%), decapod larvae and juveniles (63%), and insects (1%).

A negative correlation existed between seaweed volume and total invertebrate density in both the near shore and off shore samples (NS: Spearman R = -0.37, p = 0.002; OS: Spearman R = -0.41, p < 0.001) and in all seasons (all p < 0.01). Few species showed a significant correlation with seaweed volume: *Idotea emarginata* showed a positive correlation with seaweed volume in the near shore samples (Spearman R= 0.37, p = 0.002), while in the

Table 2. Results of Kruskall-Wallis and Mann-Whitney U tests for all seaweed-associated species, based on added values of densities. P-values in italics are significant. Nd: not determined (one of the groups has only zero-values)

	Kruskall - Wallis near shore	Kruskall - Wallis off shore	Mann - Whitney U winter	Mann - Whitney U spring	Mann - Whitney U summer
Total density (added value)	*0,02*	*< 0,001*	0,16	*0,02*	0,99
Amphipoda					
Gammarus locusta / G. crinicornis	*< 0,001*	*< 0,001*	0,28	0,27	*0,02*
Atylus swammerdami	0,22	0,44	0,37	0,95	*0,04*
Jassa sp.	*0,001*	0,7	0,21	0,13	0,1
Stenothoe marina	0,58	*< 0,001*	nd	*< 0,001*	0,58
Isopoda					
Idotea sp. Juv.	*< 0,001*	*0,03*	0,75	*0,003*	0,11
Idotea linearis	*< 0,001*	0,58	0,21	0,17	*< 0,001*
Idotea baltica	*< 0,001*	*0,03*	*0,026*	*< 0,001*	*0,01*
Idotea emarginata	*< 0,001*	0,79	*0,003*	0,62	0,77
Decapoda					
Liocarcinus holsatus MG	*< 0,001*	*0,001*	nd	0,13	*0,02*
Liocarcinus holsatus Juv.	*0,02*	*0,04*	nd	0,5	0,34
Pisidia longicornis MG	*0,016*	0,09	nd	0,76	*0,02*
Carcinus maenas MG	*< 0,001*	0,29	nd	*< 0,001*	0,94
Hippolyte varians PL	*0,03*	*< 0,001*	nd	0,39	0,28
Palaemon elegans PL	*0,001*	*< 0,001*	nd	0,19	0,89
Insecta					
Helophorus aquaticus	0,9	*< 0,001*	0,07	0,84	0,07
Psyllidae sp.	0,12	*< 0,001*	*0,03*	nd	nd
Scatopsidae sp.	*0,01*	*< 0,001*	*0,04*	0,27	0,58
Sciaridae sp.	0,47	*0,001*	0,07	0,67	0,43
Aphididae sp.	0,1	*< 0,001*	nd	*0,01*	0,21

off shore samples, *Stenothoe marina* (Spearman R = 0.21, p = 0.03) and juveniles of *Idotea baltica* (Spearman R = 0.25, p = 0.008) showed a positive correlation, and postlarvae of *Palaemon elegans* (Spearman R = -30, p = 0.001), Psyllidae (Spearman R = -19, p = 0.04) and Aphididae (Spearman R = 0.21, p = 0.02) showed a negative correlation.

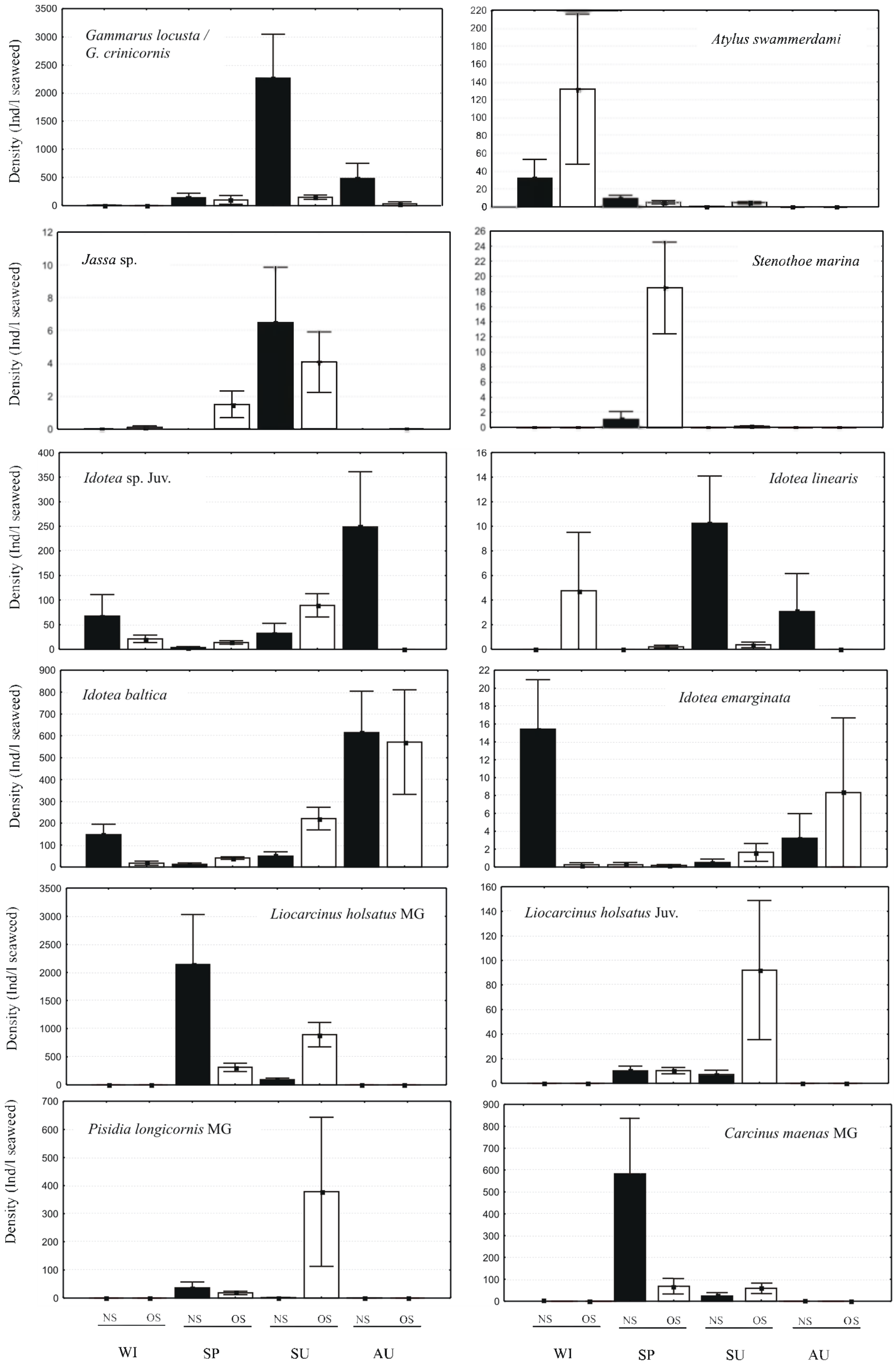
The overall correlation between seaweed volume and diversity (ES(100)) was positively significant (Spearman R = 0.29, p < 0.001). When regions and seasons were analysed separately, positive significant correlations were only encountered in the off shore samples (Spearman R = 0.36, p < 0.001) and in spring (Spearman R = 0.49, p < 0.001).

For most of the associated species, there was a clear temporal variation in their abundance, although the intensity of the variation in some cases varied depending on the sampling area (Fig. 3 & Table 2). The overall density was highest in the near shore samples (mean 2104 Ind/l vs. 1364 Ind/l), and increased from winter (mean 33 Ind/l) to summer (2167 Ind/l). The most abundant amphipods, *Gammarus locusta / G. crinicornis*, showed a significant seasonal signal in both sampling areas with highest densities in summer. Summer densities, however, were significantly different between sampling areas (MWU p = 0.02). Differences between seasons were only significant in near shore samples for *Jassa* sp. (KW p = 0.001), whereas seasonality in *Stenothoe marina* was most pronounced in the off shore samples (KW p < 0.001), where highest densities were recorded in spring (mean 18 Ind/l).

Temporal variation was pronounced in both sampling areas for *I. baltica* and *Idotea* juveniles, but was only significant in near shore samples for *I. linearis* and *I. emarginata.* Spatial variation was obvious in *I. baltica*, for which significant differences in abundance between sampling areas were observed in winter (MWU p = 0.03), spring (MWU p < 0.001) and summer (MWU p = 0.01). Seasonal patterns in abundance were similar for *I. baltica, I. emarginata* and *I. juveniles*, with high abundances in autumn and winter, while *I. linearis* was found more sporadically.

The occurrence of crab larvae was highly seasonal: they appeared in spring, in very high densities for *Liocarcinus holsatus* and *Carcinus maenas* (mean 997 Ind/l and 261 Ind/l, respectively), and were found until the end of summer. Crab juveniles (*L. holsatus*) and postlarvae of prawns (*Hippolyte varians* and *Palaemon elegans*) also started to appear in spring but reached their highest densities in summer. Spatial variation was not significant for prawn larvae and juvenile crabs, but was present in summer for megalopae of *L. holsatus* and *Pisidia longicornis* (MWU p = 0.02 for both) and in spring for *C. maenas* (MWU p < 0.001).

Only few insect taxa were found significantly more in seaweed samples compared to the surrounding water column, and these were only found on a few occasions. Generally, the densities were higher in off shore samples: spatial variation was significant for Psyllidae sp. and Scatopsidae sp. in winter (MWU p = 0.03 and 0.04, respectively), and for Aphididae sp. in spring (MWU p = 0.01).


Gammarus locusta / G. crinicornis
Atylus swammerdami
Jassa sp.
Stenothoe marina
Idotea sp. Juv.
Idotea linearis
Idotea baltica
Idotea emarginata
Liocarcinus holsatus MG
Liocarcinus holsatus Juv.
Pisidia longicornis MG
Carcinus maenas MG
Density (Ind/l seaweed)
NS
OS
WI
SP
SU
AU

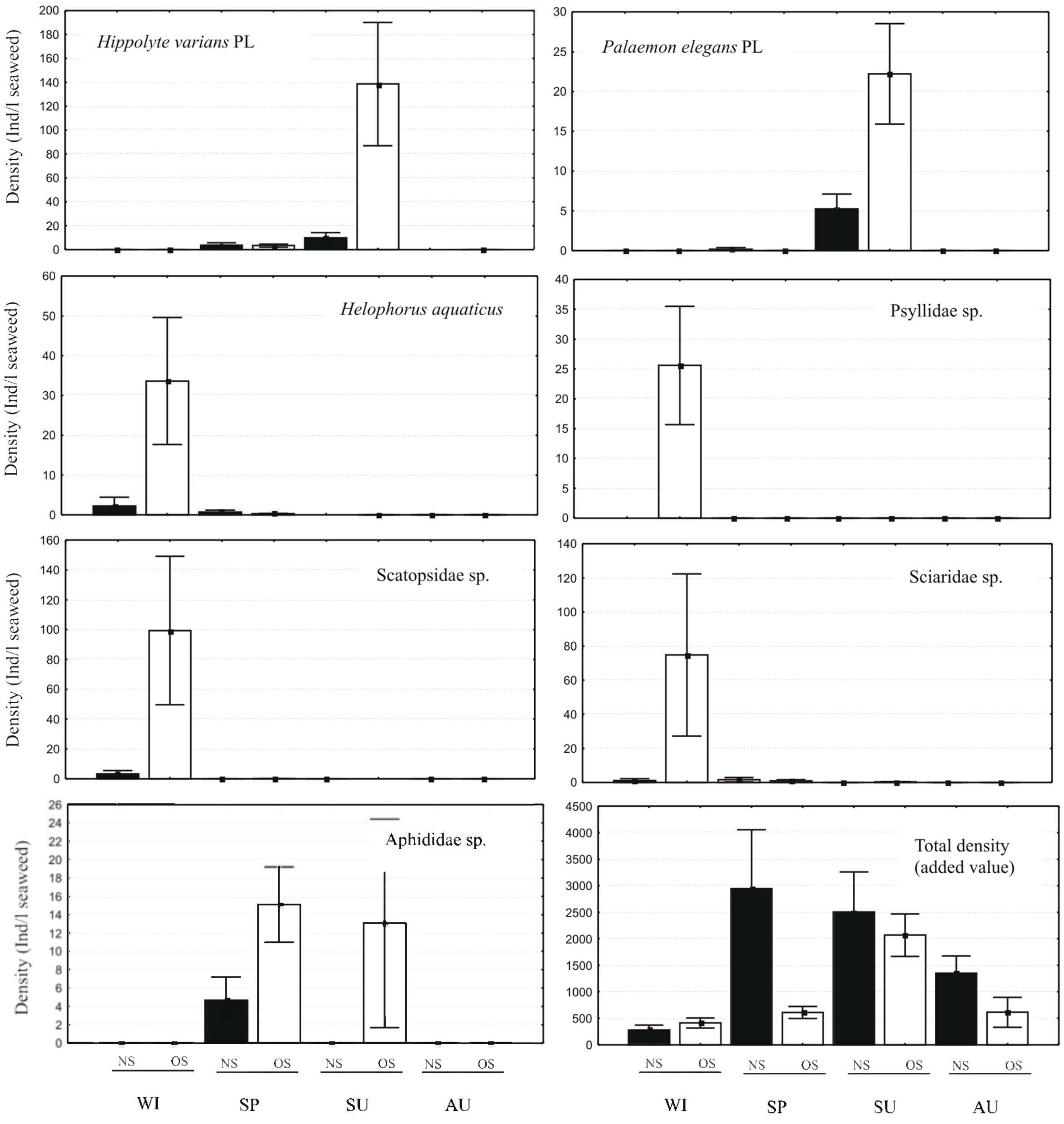


Fig. 3. Spatial (near shore = black bars, off shore = white bars) and temporal variation within abundances of invertebrate macrofauna, with Y-error bars representing standard error.

3.4 Community structure

A two-way ANOSIM based on the densities (added values) of seaweed-associated invertebrate macrofauna revealed significant differences between seasons and sampling areas (R = 0.26 and 0.22, respectively, with a significance level of 0.1% in both cases). Pairwise tests between seasons indicated that the degree of separation between seasons (R –values ranging between 0.29 and 0.68) is, except for the comparison spring-summer (R = 0.14), higher than between sampling areas. The MDS plot with seasons as factors reflected the temporal variation, but indicated that there is a larger variability within the spring samples (average similarity 28.5%) compared to the other seasons (average similarity autumn: 48.4%, winter: 34.7%, summer: 32.5%) (Fig. 4). SIMPER analysis showed that the contributions to similarities between seasons can be attributed to the presence and abundance of (1) *I. baltica*, *Idotea* juveniles and *G. locusta* / *G. crinicornis* in autumn, of (2) *I. baltica*, *I. emarginata*, *Idotea* juveniles and *A. swammerdami* in winter, of (3) *L. holsatus* megalopae and juveniles, *I. baltica*, *Idotea* juveniles, *G. locusta* / *G. crinicornis*, *C. maenas* megalopae and *Aphididae* sp. in spring, and of (4) *L. holsatus* megalopae and juveniles, *I. baltica*, *Idotea* juveniles, *G. locusta* / *G. crinicornis* and *H. varians* postlarvae in summer. As for sampling areas, *G. locusta* / *G. crinicornis*, *I. baltica* and *L. holsatus* megalopae contributed for 75% to similarity between groups, but near shore samples were additionally characterised by *Idotea* juveniles and *C. maenas* megalopae, while off shore samples also contained *L. holsatus* juveniles, *P. longicornis* megalopae and *A. swammerdami*.

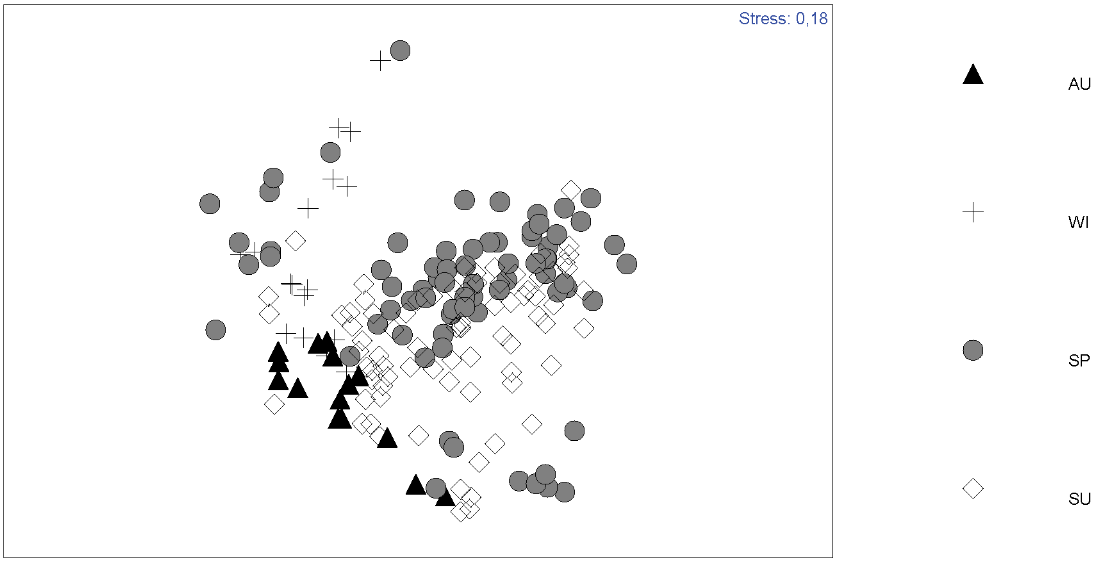
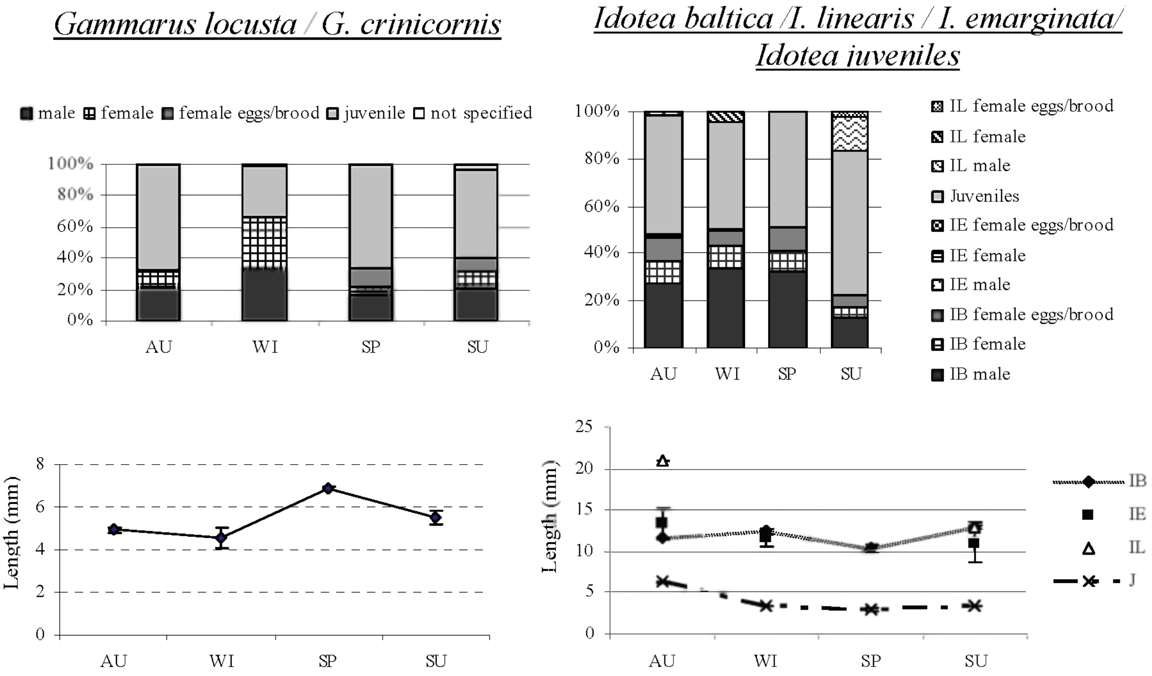


Fig. 4. MDS plot of seaweed samples, with seasons as factors.

The multivariate patterns of invertebrate density data were compared to environmental parameters (seaweed volume, relative abundances of seaweed constituents, surface water temperature and salinity, distance to shore and depth). RELATE indicated a significant correlation between the standardised Euclidean distance matrix of the variables and the similarity matrix of macrofaunal data (p = 0.003). The draftsman plot and the associated correlation matrix showed no evidence of collinearity, so all variables were used in the BIO-ENV analysis. Within the analysed samples, a combination of four variables best explained the macrofaunal assemblage: % *Fucus vesiculosus*, % *F. spiralis*, sea surface temperature and water depth. However, the matching coefficient was rather low (Rho = 0.26), implying that there were other factors that strongly structured the assemblage. One of these factors might be the age of the seaweeds, which was investigated using a subset of the data (Oct 2002 – Sept 2003). The ANOSIM results, however, indicated a minor impact of seaweed age (R = 0.1).

3.5 Gammarus sp. / Idotea sp.

Two crustacean genera were abundantly associated with floating seaweeds all through the year: *Gammarus* with mixed populations of *G. crinicornis* and *G. locusta*, and *Idotea* with *I. baltica, I. emarginata* and *I. linearis*. *Idotea* juveniles (<7mm) were grouped because the different genera were hard to distinguish at small sizes. The temporal variation within the populations of these two genera was investigated on the levels of size distribution and sexual maturity (data autumn 2002 – spring 2004).



Gammarus locusta / G. crinicornis

Idotea baltica /I. linearis / I. emarginata/ Idotea juveniles

Fig. 5. Left: bar chart of population composition and line plot of seasonal variation in length (mean and standard error) in *Gammarus locusta / G. crinicornis*. Right: bar chart of population composition and line plot of seasonal variation in length (mean and standard error) in *Idotea baltica* (IB), *I. emarginata* (IE), *I. linearis* (IL) and *Idotea* juveniles (J)

In the analysed specimens of *Gammarus*, sexes were generally first recognised from a size of 2 - 5mm. Maximum sizes were 22mm in males and 15.4mm in females. A high percentage of juvenile individuals were present in *Gammarus locusta / G. crinicornis* all through the year (31 – 67%) with highest numbers in spring. Nevertheless, mean length increased by 2 mm in spring, compared to autumn and winter, indicating the presence of larger adults. The bar chart in Fig. 5 indicates that reproducing adults (large males and females carrying eggs and embryos) were found in highest relative abundances in spring and summer, whereas especially reproducing females were virtually absent in autumn and winter. Males and ovigerous females were generally larger (mean lengths of 8.2 and 8.8mm, respectively) compared to immature adults (mean 6.2mm).

Of all encountered idoteid isopods, *Idotea emarginata* and *I. linearis* only constituted a small proportion (0.8 and 0.5%, respectively), so it can be assumed that juveniles (43.8%) were almost all *I. baltica* (56.5% adults). *Idotea linearis* was only sporadically found (males and non-reproducing females in autumn and winter), but were most abundant in summer (16.2% of total *Idotea* population). In summer, all females were carrying eggs or embryos. As for *I. emarginata*, males were only found in small proportions (0.02 – 0.7%) in autumn, winter and summer, while non-reproducing and reproducing females were only found in autumn and summer (0.02 – 0.18% and 0.23 – 0.02%, respectively). Adult length stayed within the range of 10-15mm all year through.

Idotea juveniles were found in large numbers throughout the year, with the highest mean relative abundance in summer (61%). Similarly, the presence of reproducing adults was continuous, indicating a year-round reproduction. The average lengths of adults and juveniles were highest in autumn (11.6 and 6.3mm) and lowest in spring (10.3 and 3mm), in which the reproduction was most intense.

4. DISCUSSION

The observed seasonal patterns within seaweed-associated communities are due to a combination of physical and biological processes, including seasonal shifts in water temperature and reproduction periods, which regulate the availability of larvae and juveniles (Dempster, 2005). At the Belgian coast, invertebrate densities generally increased after winter to peak in spring (near shore samples) and summer (off shore samples). This pattern is very pronounced for the different species of decapods: crab megalopae and juveniles, and prawn postlarvae started to appear in spring and were found abundantly throughout the summer. However, adults were seldomly found in the vicinity of floating seaweeds and were not found significantly more than in the surrounding water column, suggesting that megalopae and juveniles leave the floating seaweeds to recruit to the water column or the benthos. Crab larvae and prawn postlarvae are known associates of floating seaweeds and drift seagrass (e.g. Kingsford & Choat, 1985; Franke et al, 1999), on which they hitchhike to shallow coastal waters before metamorphosis (Wehrtmann & Dittel, 1990; Thiel & Gutow, 2005b).

In gammarid amphipods and idoteid isopods, all developmental stages of maturity were represented, and most species were found throughout the year. *Atylus swammerdami* was found abundantly in off shore winter samples, but showed no significant seasonal pattern. *Jassa* sp. and *Stenothoe marina* were found more sporadically, in summer and spring, respectively. The *Gammarus crinicornis / G. locusta* species group was found throughout the year, with highest densities in summer. The increase in densities followed an increase in the proportion of reproducing adults in spring, resulting in a considerable input of juveniles in summer. Similarly, the highest proportions of

Idotea juveniles were also found in summer (61%), as reproduction was most intense in spring, although continuous throughout the year like in other idoteids (e.g. Healy & O'Neill, 1984; Salemaa, 1986; Tully & O'Ceidigh, 1986; Abello & Frankland, 1997). However, overall *Idotea* densities were highest in autumn and winter, unlike in other idoteid populations with continuous reproduction (e.g. Healy & O'Neill, 1984), where highest densities were reached in May-September. Apparently, the densities of *I. baltica* and *I. emarginata* were not correlated with water temperature, and high numbers of adults and juveniles per litre of seaweed could be found, even in winter (Tully & O'Ceidigh, 1986). The high densities in autumn can partly be attributed to the recruitment of the new generation to the seaweed, but may also result from new recruitments from the littoral zone (Salemaa, 1979; Tully & O'Ceidigh, 1986). It has been reported that *I. baltica* migrates to over-winter in off shore sublittoral waters, during which they may encounter floating seaweeds with which they stay associated (Salemaa, 1986). The reproduction of gammarid amphipods and idoteid isopods by incubating developing embryos is an advantageous strategy for rafting organisms, since it allows the persistence of local populations on a floating item (Highsmith, 1985; Helmuth et al, 1994; Thiel & Gutow, 2005b).

A few insect families were found significantly more in seaweed samples compared to control samples. The presence of insects was sporadic and probably the result of swarming during a period of off shore winds, driving the insects to sea (Bowden & Johnson, 1976). Unable to return, the insects are forced to land on the sea surface. The presence of living insects on floating seaweeds and their absence in the neuston may be the result of three mechanisms: (1) insects land equally on seaweed and surface water but the ones on the seaweed can survive longer, (2) insects are preprogrammed to land on a vegetation-like surface and avoid landing on the water surface or (3) insects were associated with beached seaweed and were trapped when the seaweed became resuspended. As the abundant insect species (*Helophorus aquaticus*, Psyllidae sp., Aphididae sp., Scatopsidae sp. and Sciaridae sp.) were winged and are not typically seen on decaying seaweed, aerial introduction is most probable. Insects blown out to sea provide a considerable amount of organic matter to the surface water, and if associated with drifting vegetation, they might colonise distant shores (Bowden & Johnson, 1976; Peck, 1994). Because the association of insects is quite coincidental, the properties of the seaweed clumps will be of little importance. The most important cause of variation is probably the aerial insect composition at the time of off shore winds.

The BIO-ENV analysis confirmed the role of surface temperature as a driving factor for seasonal variation, but also put forward the relative abundances of *Fucus vesiculosus* and *Fucus spiralis* in the individual seaweed clumps. Results showed that the availability of these seaweed species is spatially and temporally influenced (*F. vesiculosus* had high relative abundances in autumn, spring and summer in near shore samples, and in winter, spring and summer in off shore samples; whereas *F. spiralis* showed considerable proportions in spring and summer only, in both regions). The spatial and temporal limitations in the availability and abundance of these seaweeds may in turn influence the abundance and presence of invertebrate macrofauna that prefer these species above others as food and/or habitat (cf Vandendriessche et al, 2006b).

A final factor selected during the BIO-ENV was depth, which is linked to the spatial variation between seaweed samples. It is highly unlikely that depth itself is a major factor influencing the invertebrate species assemblage, as most species colonised the floating seaweeds from the surrounding water column. Depth, however, reflects the spatial differences between sampling areas; in the present study the different sandbank systems. These sandbank systems are prone to different current regimes, and the sampled seaweed clumps may therefore have entirely different origins, ages and traveling trajectories. Moreover, because the Belgian coastline possesses no natural hard substrates of itself (seaweeds only grow on harbor walls and groynes), it is doubtful that distance to shore shows any relation with distance traveled. So it can be hypothesised that in this case, spatial variation is a function of raft history, which is likely to be highly complex given the tidal regime at the English Channel and the Belgian coast.

An attempt was made to assess the impact of seaweed age by grouping the dominant seaweeds (usually *F. vesiculosus* or *A. nodosum*) per clump according to colour and epiphyte load. The age groups, however, only showed minor differences between the invertebrate communities, which was to be expected as most clumps were composed of more than two algal species. Because seaweed clumps often converge or break up, the constituting seaweeds of a clump may have different ages and origins, so age of the seaweeds may differ even within clumps (Ingólfsson, 1998). Although age and origin of a clump are, in most cases, hard to assess, they may still be of great importance to colonising invertebrates, especially to herbivores feeding on epiphytes and on the seaweeds themselves. Stoner and Greening (1984), for example, found that the effects of age on the permanently floating *Sargassum* were more important than the effects of clump size, and were mainly due to a higher degree of food availability and shelter resulting from a larger epiphyte load in older plants. Furthermore, Cronin and Hay (1996) stated that the susceptibility of seaweeds to herbivores is largely dependent on the history (dessication, UV-exposure) of the seaweeds.

Based on the invertebrate species composition of the analysed floating seaweed clumps, it can be assumed that the clumps were in an advanced successional stage (Ingólfsson, 1995; Thiel, 2003; Thiel & Gutow, 2005b): there were only few littoral species (e.g. *Mytilus edulis, Tergipes tergipes*) left and new colonisers (e.g. *Idotea baltica, Gammarus crinicornis / G. locusta*) were abundant and reproducing.

Although the effect of variation linked to the size of the clumps was a major factor following the BIO-ENV analysis in Vandendriessche et al (2006b), it was not selected as important structuring variable in the present study. Again, only few species were found to show a positive correlation; and the positive correlation was significant for species richness and clump size. Similar results were obtained by Ingólfsson (1998), who found a positive correlation between density and clump size for intertidal species, but not for benthic or pelagic species. In that particular study, the correlation between clump size and diversity of the associated species was also highly significant. These findings affirm the hypothesis that correlations vary greatly depending on the origin of the seaweeds and the association degree and behaviour of the associated species, and that they are probably a reflection of the history of the clump rather than being the result of its structural complexity (Ingólfsson, 1998; Vandendriessche et al, 2006b).

When investigating fauna associated with floating seaweeds, a number of structuring factors can be discerned like spatial and temporal variation, clump size and composition, age and origin. Still, there always remains a proportion of the variation that can only result from coincidences during the course of the journey of the floating seaweeds (e.g. washing ashore, convergence with and exchange between other clumps, disturbance during storms). Furthermore, some factors can be discerned but are hard to quantify (e.g. age and traveling history). Consequently, floating seaweeds constitute a complex system in the neuston, with varying but still considerable effects on the associate invertebrate fauna. Of all variation, only a part can be quantified and attributed to measurable sources of variation (matching coefficient of only 0.26 in the present study), while a large part of the variation results from structuring factors that are hard (e.g. clump age) or even impossible (e.g. number of convergence or divergence events between clumps) to quantify.

As a conclusion, it can be stated that, in the present study, the sea surface temperature and the seaweed species composition were important sources of variation, while variation in depth reflected the traveling history of the seaweed clumps. The clump volume also played a role in structuring the invertebrate assemblages, but that effect was very species-specific. Other factors like clump age, the occurrence of storms, convergences or divergences of clumps and beaching incidents were hard or even impossible to measure, but probably had considerable consequences with regard to the associated invertebrates. These results reflect the complexity of the habitat formed by floating seaweed clumps at the sea surface.

ACKNOWLEDGEMENTS

The first author acknowledges a specialisation grant from the 'Institute for the Promotion of Innovation through Science and Technology in Flanders' (IWT). The authors would like to express their gratitude to colleagues and students for their support and help with the samplings. Special thanks go to André Cattrijsse of the Flanders Marine Institute (VLIZ), to the crewmembers of the research vessel Zeeleeuw and to the people of MUMM (Marisa & Benoit). Furthermore, the authors would like to thank Gert Van Hoey and Marleen De Troch for their useful comments on earlier versions of the manuscript.

CHAPTER 5

HIDING AND FEEDING IN FLOATING SEAWEED: FLOATING SEAWEED CLUMPS AS POSSIBLE REFUGES OR FEEDING GROUNDS FOR FISHES

Juvenile lumpsucker

Paper in press

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Hiding and feeding in floating seaweed: floating seaweed clumps as possible refuges or feeding grounds for fishes

Estuarine, Coastal and Shelf Science
Doi: 10.1016/j.ecss.2006.09.017

ABSTRACT

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 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.

Keywords: Juvenile Fish; Floating Seaweed; Refuge; North Sea

1. INTRODUCTION

A wide variety of fish taxa throughout the world's oceans have a natural tendency to aggregate beneath or associate with floating structures such as plastic debris, floating seaweeds, pieces of wood, jellyfish, fish aggregation devices (FADs) and animal remains (e.g. Safran & Omori, 1990; Davenport & Rees, 1993; Moser et al, 1998, Masuda & Tsukamoto, 2000; Castro et al, 2001; Thiel & Gutow, 2005 a, b). Generally, the fish community is found to be more diverse below floating seaweeds than below other floating items (Fedoryako, 1989). According to Kingsford (1995), the increased diversity in the presence of floating seaweeds compared to the surrounding water column can be attributed to the substantial increase in habitat complexity of the pelagic environment.

Many authors have already attempted to classify fish based on the spatial and temporal relation between the fishes and the floating object. Castro et al (2001) distinguished 'associated' fishes (circulate around the structure and do not show any dependence) and 'aggregating' fishes (live close to the floating object and depend on it). Dooley (1972) separated coincidentally associated fishes with rare occurrence, moderately associated fishes, seasonally occurring fishes, and closely associated fishes. Hirosaki (1960 - in Thiel & Gutow, 2005b), proposed a classification in (1) fishes that stay within the branches of the algae, (2) fishes that remain underneath the floating patch, and (3) fishes that swim around the patch with close association; and Gooding and Magnuson (1967) discerned transients (no response to and no contact with the floating object), visitors (response but no contact) and residents (response and contact). Although different classifications have been used in literature, they all distinguish groups based on the dependency of the fishes to the floating object and are therefore relatively comparable and applicable in new studies.

Floating seaweed is considered to be an important habitat for juvenile fish. Masuda and Tsukamoto (2000) found that the onset of the association behaviour already starts at an early stage in some fish species (at 12mm TL for *Pseudocaranx dentex*) and is probably triggered by visual and mechanical stimuli. The advantages of associating with floating seaweeds are numerous (reviewed in Castro et al, 2001): (1) the benefits of living in the shade in relation to predators and detection of prey (Kingsford, 1992), (2) the presence of abundant food sources like smaller fish, associated macrofauna or the seaweed itself (Safran & Omori, 1990; Davenport & Rees, 1993; Wright, 1989), (3) the shelter from piscivorous fish and birds (Wright, 1989; Kokita & Omori, 1998), (4) the potential for passive transport (Dooley, 1972), (5) the meeting point function for the formation and maintenance of schools or for spawning (Masuda & Tsukamoto, 2000), (6) the substitution of the seabed for non-pelagic fish, and (7) the function of floating objects as cleaning stations (Gooding & Magnuson, 1967). Accordingly, aggregative and associative behaviour of juvenile fish can be the expression of convergent behaviours resulting from different motivations (Castro et al, 2001).

Different studies indicate that the association between most fish species and floating seaweeds is of a temporary nature, particularly in the juvenile stages (e.g. Davenport & Rees, 1993; Castro et al, 2001; Ingólfsson & Kristjansson, 2002). Furthermore, Shaffer et al (1995) described that the function of floating seaweed with regard to juvenile fish may change seasonally. Juvenile *Sebastes diploproa*, for example, finds refuge from predators in spring and summer, whereas in autumn, the seaweed increasingly serves as a prey habitat. Several studies reported higher fish densities in summer months, probably due to the increased availability of floating seaweed in that period (Kingsford, 1992; Thiel & Gutow, 2005b). Next to temporal variation, variations in the size of floating seaweed patches strongly influence the densities and species composition of the associated ichthyofauna (Hunter & Mitchell, 1967; Dooley, 1972, Nelson, 2003; Moser et al 1998). Because effects of seaweed species composition, distance to shore and raft age (increased epibiont load) have already been reported for rafting invertebrates (Fine, 1970; Ólafsson et al, 2001; Ingólfsson, 2000; Castro et al, 2001; Thiel & Gutow, 2005b; Vandendriessche et al, 2006b), these factors are also likely to apply to rafting fish.

Although research about the importance of association behaviour is very important from the perspective of fisheries ecology, very little information is available concerning the relation between fishes and the highly dynamical floating seaweed clumps found in the North Sea. Therefore, the present study aims to investigate the species composition and association behaviour of fishes associated with floating seaweeds. To this end, we identified neustonic fishes with a tendency to associate with floating objects, and investigated the variability within the fish community. For each of the associated fish species, the underlying motivation for association behaviour (food, shelter or other) was investigated.

2. MATERIALS AND METHODS

2.1 Sampling

Based on literature (e.g. Dooley, 1972; Ingólfsson, 1995; Cho et al, 2001) and personal experience, a neuston net and a dip net were found to be the most effective net types for sampling neustonic (not associated with floating objects) and seaweed-associated juvenile fish communities, respectively. This approach, however, was expected to result in variations concerning net efficiency, and therefore in differences concerning the fish species and sizes caught. In the present study, we took into account the variation in net efficiency by analysing the quantitative data from the two sampling methods separately.

2.1.1 Neuston net samplings

A year-round survey of the neuston (monthly samplings) was carried out in the Belgian part of the North Sea (BPNS) (6 sampling stations, Fig. 1) in the period July 2003 – June 2004. Samples were taken with a rectangular net (2 m x 1 m, 1 mm mesh), of which only the lower half was immersed, thereby sampling the upper 0.5 m of the water column. After a tow of 15 minutes (average filtered volume: 2623m³, average speed: 1.5 knots), the net was emptied and rinsed, while the contents were preserved in formalin solution. All fishes were first anaesthetised in a benzocaine (Ethyl amino-4-benzoate)-water solution to prevent regurgitation of the stomach contents.

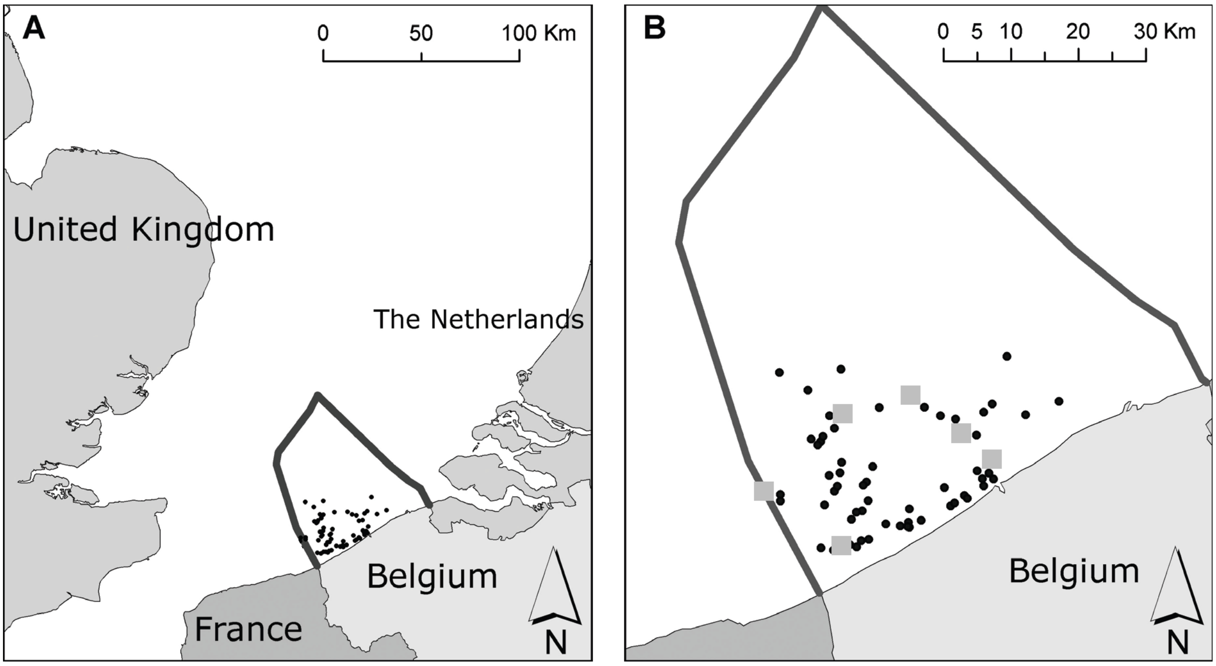


Fig. 1. Map of the southern part of the North Sea (A) and the Belgian continental shelf (B; delimited by black line), with indication of neustonic sampling stations (grey squares) and seaweed sampling sites (black dots).

2.1.2 Dip net samplings

Seaweed samplings were conducted from October 2002 to September 2004 in the BPNS. The RV ‘Zeeleeuw’ was used to collect patches of floating seaweed using a 40 cm diameter dip net with 300 μm mesh, ensuring that the captured fish had a spatial affinity with the seaweed. During the sampling period, 249 seaweed samples from 60 sampling sites (Fig. 1) were collected along with their associated macro-invertebrates and fish fauna. Three control samples (i.e. surface water samples without seaweeds) were taken at each sampling site. The size of the seaweed samples was dictated by the diameter of the sampling net used. In the field, all fishes were anaesthetised in a benzocaine - water solution and preserved in formalin solution together with the rest of the associated fauna.

Sampling intensity was not equal over the seasons because bad weather often prevented the search for floating seaweeds (especially in the period October – January). For successful samplings, the mean number of sampling points (and hence the amount of encountered seaweed clumps) was highest in the periods February - April and June - September. Clumps of floating seaweed consisted of one or more seaweed species like *Fucus vesiculosus* (Fv, mean 30% of total clump volume), *Ascophyllum nodosum* (An, mean 10%), *Halidrys siliquosa* (Hs, mean <1%), *Fucus spiralis* (Fs, mean 29%), *Himanthalia elongata* (He, mean 20%), *Cystoseira* sp. (Csp, mean <1%), Filamentous green algae (Fil. Gr. Algae, mean <1%), *Chorda filum* (Cf, mean <1%) and *Sargassum muticum* (Sm, mean 8%), and small amounts of other floating debris (mean 3%) like reed, feathers, plastic, nylon, wood and cardboard. Most clumps (85%) were composed of more than one seaweed species.

2.2 Laboratory treatment

Neuston- and seaweed samples were rinsed over a 1 mm sieve and the associated fishes and macro-invertebrates were removed. The volume of the seaweed constituents (and other debris) was recorded to the nearest millilitre, using a graduated cylinder. All fishes were counted and identified, and the total length (± 1mm) of each individual was recorded. The macro-invertebrates found in seaweed samples were counted and identified.

2.3 Analysis of seaweed-associated macro-invertebrate data

Prior to the analyses, the dataset was reduced to the species (1) accounting for > 3 % of the total abundance in any one sample, and (2) found significantly more in seaweed samples compared to control samples. Univariate two-way analysis of variance (ANOVA, 41 sampling occasions, 2 sample types) was used to test for differences in abundance between seaweed samples and control samples. If necessary, a log (x + 1) transformation was performed to meet the required assumptions. Of all invertebrate species that were found significantly more in seaweed samples, the added value was calculated by subtracting background neustonic values from seaweed sample values per sampling occasion (see Vandendriessche et al, 2006a). These values were further used in the analysis of the fish data.

2.4 Stomach content analysis of seaweed-associated and neustonic fish

Diverse larval and juvenile fish species were recorded in the surface 0.5 m of water, and were either neustonic or associated with floating seaweed patches. The species *Trachurus trachurus*, *Chelon labrosus, Ciliata mustela*, and *Syngnathus rostellatus* were frequently and abundantly found in both sample types and were selected for stomach analysis. *Cyclopterus lumpus* was only found in association with floating seaweeds and was also included. For each of the selected fish species, the stomach contents of neustonic and seaweed-associated individuals were examined per 5 mm length class (for individuals >1.5 cm in *C. lumpus*, > 2 cm in *C. labrosus, C. mustela* and *T. trachurus*, > 6 cm in *S. rostellatus*). Length classes with fewer than 5 fish were omitted from all analyses. The intact stomachs were removed under a stereoscopic microscope, by cutting above the oesophagus and below the large intestine (for Syngnathidae, the entire gut was examined). An incision was made along the longitudinal axis and the contents emptied onto a Petri dish with a few drops of deionised water. All prey items encountered in the stomachs were counted, identified (if possible to species level), and measured. The biomass (mg Ash Free Dry Weight/m^3) of each prey item was computed with length-AFDW regressions established formerly in the laboratory. Both fish and stomach contents were placed into separate vials for potential further investigation and subsequent drying. After identification and measuring, the stomach contents were placed in pre-weighed aluminium foil cups, dried at 110°C for 5 hours, incinerated in ceramic cups at 550°C for 15 minutes, and cooled to room temperature in a dessicator for 2 hours before weighing in order to obtain AFDW.

For the quantitative analysis of the stomach contents, the fullness index (FI) was used:

$$FI = \frac{S_i}{W_i} x100$$

where S_i is the AFDW of the stomach content in milligram (mg) and W_i is the AFDW of the fish (mg). As a qualitative measure, the Shannon-Wiener index (H') of the stomach contents of the common fish species was calculated as $H' = -\sum p_i x \ln p_i$

where p_i is the proportion of the individuals found in the 'i'th species.

Furthermore, frequencies of occurrence and numerical and gravimetrical percentages were calculated to characterise the stomach contents (Hyslop, 1980). The frequency of occurrence (*FO%*) calculates the percentage of the total number of stomachs in which the specific prey species occur. The numerical percentage (*N%*) reflects the proportion (percentage) of the total individuals an all food categories, whereas the gravimetric percentage (*G%*) reflects the proportion of the total weight (expressed as AFDW).

The degree of dietary overlap was calculated using the Schoener index (1970):

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} \left| p_{xi} - p_{yi} \right|\right)$$

where p_{xi} and p_{yi} are the proportions of the 'i'th prey category for the species pair x and y, and n the number of prey categories. The index ranges from 0 for no diet overlap to 1 for complete diet similarity.

2.5 Data treatment

Differences in fish species compositions between neustonic samples and seaweed samples were examined using non-metric MultiDimensional Scaling ordination (MDS) using the Bray-Curtis similarity measure. ANalysis Of SIMilarities (ANOSIM) was used to test for significant differences ($p<0.05$) between groups (defined *a priori*), while the species contributing to dissimilarities between groups were investigated using a SIMilarity-PERcentages procedure (SIMPER). The relationship between seaweed-associated fish densities (individuals per litre of seaweed) and variables (seaweed volume, relative abundances of the seaweed constituents per sample, surface water temperature and salinity, distance to shore, atmospheric pressure and humidity) was analysed using the Spearman rank correlation and the significance was determined using a permutation procedure (RELATE, Clarke & Warwick, 1994). The BIO-ENV procedure was used to define suites of variables that best determine the macrofaunal assemblages. Empty samples were excluded from the analyses and a square root transformation was performed on the abundance data prior to the analyses. All multivariate community analyses were done using the Primer v5.2.9 software package (Clarke & Gorley, 2001).
The univariate non-parametric Mann-Whitney U-test (MWU) was used to test for differences in stomach content parameters of fish found in neustonic samples and seaweed samples.

3. RESULTS

3.1 Neustonic Fish

ANOSIM revealed significant seasonal differences between samples (Global R: 0.206; significance level $p = 0.001$, Fig. 2); and pairwise tests showed that all seasons differed significantly, except summer samples and autumn samples. The MDS plot and the SIMPER analysis both indicated a large variability in the summer samples (average similarity: 34%), compared to the other seasons (average similarity autumn: 64%, winter: 54%, spring: 60%). Postlarvae and juveniles of *Ammodytes tobianus / Hyperoplus lanceolatus* and *Clupea harengus / Sprattus sprattus / Engraulis encrassicolus* were abundant throughout the year, but there were considerable differences in the seasonal occurrences of other fish species (Table1). Effects of sampling station (spatial variability) and effects of the presence of small amounts of floating seaweed and debris were not significant.

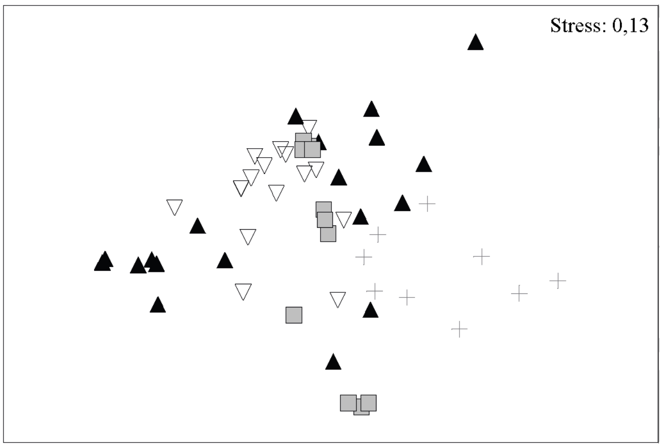


Fig. 2. MDS of neustonic fish data (sqrt transformation, Bray-Curtis similarity): black triangles = summer samples, white triangles = autumn samples, crosses = spring samples, squares = winter samples

	seasonal occurrence				length range (cm)	# caught
	spring	**summer**	**autumn**	**winter**		
Ammodytes tobianus / Hyperoplus lanceolatus	■	■	■	■	0.3 – 12.2	884
Arnoglossus laterna		■			0.5	1
Belone Belone		■			0.9 – 3.7	69
Chelon labrosus		■	■	■	0.3 – 3.8	1591
Ciliata mustela	■	■			0.4 – 3.6	405
Clupea harengus / Sprattus sprattus/ Engraulis encrassicolus	■	■	■	■	0.4 – 9.3	2257
Cottidae sp.		■	■	■	0.2 – 1.2	290
Echiichthys vipera		■			0.4 – 1.6	45
Hippocampus guttulatus			■		2.9 – 3.5	2
Labrus bergylta		■			0.6 – 1.1	2
Merlangius merlangus	■				0.6 – 4.1	10
Pleuronectidae sp.	■	■			0.7 – 1.3	3
Pollachius pollachius	■				3.2	1
Pollachius virens		■			2.5	1
Scophthalmus maximus	■	■			1.6 – 2.1	4
Solea solea	■	■	■	■	0.3 – 0.8	14
Syngnathus acus		■	■	■	2.9 – 5.5	7
Syngnathus rostellatus	■	■	■	■	1.0 – 5.7	28
Trachurus trachurus		■		■	0.3 – 4.2	258

Table 1. List of fish species encountered in neuston samples, with indication of seasonal occurrence, length range (cm) and numbers caught.

3.2 Macro-invertebrates and fish associated with floating seaweed

Several macrofaunal invertebrates were found significantly more in dip net seaweed samples than in dip net control samples. Harpacticoid copepods, crab megalopae, gammarid amphipods, idoteid isopods and postlarval prawns constituted 95% of the added value (Fig. 3). Of all analysed seaweed samples, 41% contained fishes (590 specimens in total, Table 2), while control dip net samples only yielded two *Platichthys flesus* larvae.

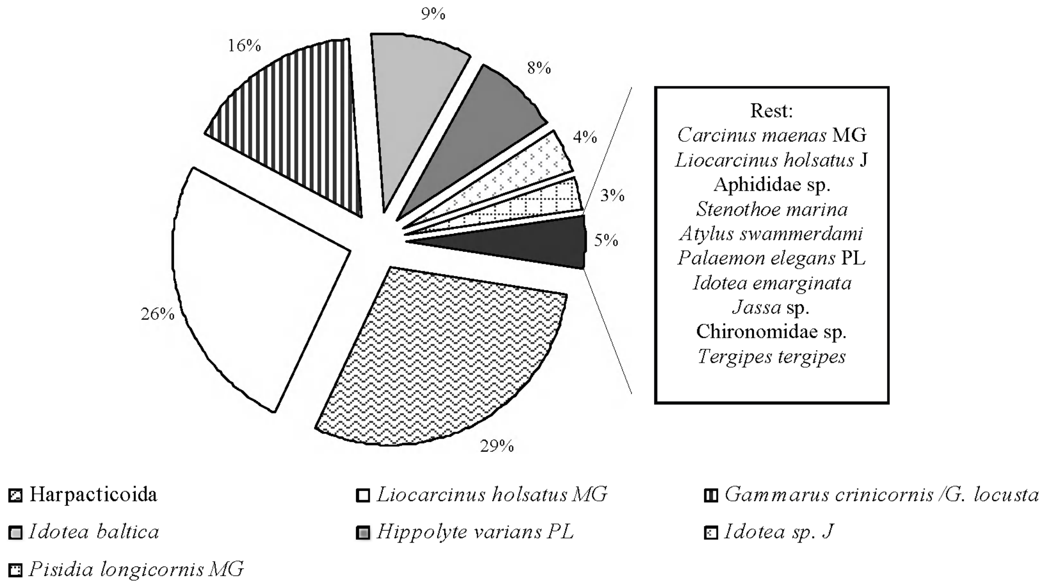


Fig. 3. Pie chart representing relative abundances of seaweed-associated macro-invertebrates (MG: megalopa; J: juvenile, PL: postlarva)

	Seasonal occurrence				**Length range (cm)**	**# caught**
	spring	**summer**	**autumn**	**winter**		
Belone belone		■			4.0	1
Blennidae sp.		■			1 – 1.2	2
Callionymus lyra	■				-	1
Chelon labrosus		■	■		0.7 - 2.8	202
Ciliata mustela	■	■			1.0 - 4.0	147
Cottidae sp.		■			0.8 – 1.7	13
Cyclopterus lumpus	■	■	■	■	0.6 – 4.9	97
Entelurus aequorius	■	■		■	13.6 - 15	6
Gobiidae sp.		■			1.1 – 1.2	2
Merlangius merlangus		■			3.4	1
Nerophis lumbriciformis	■				5	1
Pollachius pollachius	■				2.3 – 2.6	11
Pollachius virens	■				2.3	1
Syngnathus acus		■			7.4 - 14.4	2
Syngnathus rostellatus		■			3.7 – 12.2	7
Trachurus trachurus		■			0.7 – 4.3	147

Table 2. List of all fish species encountered in dip net seaweed samples, with indication of seasonal occurrence, length range (cm) and numbers caught.

MDS based on seaweed-associated fish data (Fig. 4) revealed four groups (ANOSIM R: 0.8, p = 0.001): a group of seaweed samples that exclusively contained *Chelon labrosus* (average similarity: 69%), and three other groups that were dominated (highest densities) by *Ciliata mustela* (average similarity: 48%), *Cyclopterus lumpus* (average similarity: 62%), or *Trachurus trachurus* (average similarity: 56%). These last three groups were more closely related and frequently contained other fish species. The multivariate pattern of the fish data were compared to the environmental data (seaweed volume, relative abundances of the seaweed constituents per sample, surface water temperature and salinity, distance to shore, atmospheric pressure and humidity, added values of associated macro-invertebrates). RELATE indicated a significant correlation between the standardised Euclidian distance matrix of the variables and the similarity matrix of macrofaunal data (p = 0.001). The draftsman plot and the associated correlation matrix showed no evidence of collinearity, so all variables were used in the BIO-ENV analysis. Within the analysed seaweed samples, a combination of all variables best explained the macrofaunal assemblages, but the matching coefficient was very low (σ = 0.23). This implies that only a part of the biotic structure is explained by the measured variables, and that there are other factors that strongly structure the fish assemblages.

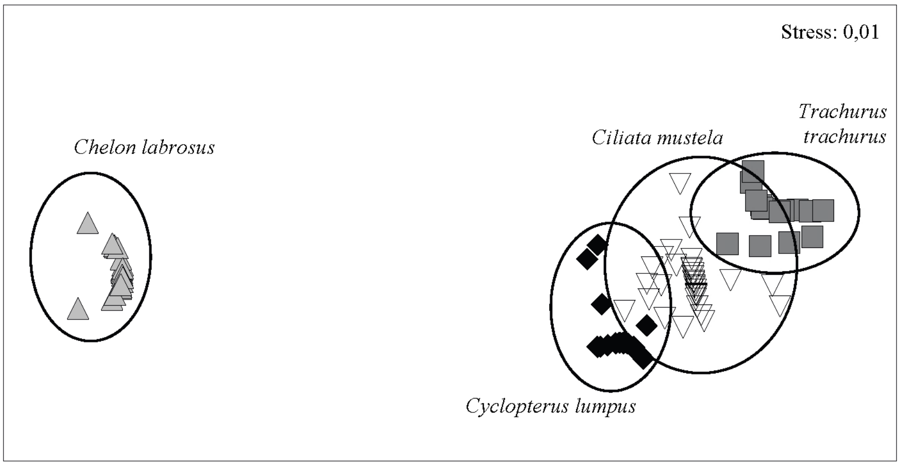


Fig. 4. MDS plot (Bray-Curtis similarities) of samples based on fish densities in seaweed samples, with indication of dominant fish species.

Correlation analyses between density data of abundantly and frequently occurring fish species and variables (Table 3) indicated different responses of the fish species: *Cyclopterus lumpus* was strongly associated with the occurrence of large clumps of *A. nodosum* and *H. elongata* and was most abundantly found in winter. *Trachurus trachurus* was associated with *F. spiralis*, *A. nodosum* and *H. elongata*, but showed a negative correlation with clump volume. This species was usually found off-shore in summer. *Chelon labrosus*, on the other hand, was abundantly found in near-shore stations in summer, but also showed a negative correlation with clump volume. *Syngnathus rostellatus* was found frequently, but in low abundance, in summer samples and showed a slight affinity for *F. spiralis*. Finally, *Ciliata mustela* showed a strong positive correlation with the seaweed *S. muticum*, and was abundantly found in spring samples close to the shore. For all fish species, there seemed to be no straightforward links between the added values of potential invertebrate prey items and fish densities, especially in the light of the stomach analyses results (see below).

Table 3. Results of Spearman rank correlations between fish densities and environmental variables and prey densities. Results indicate positive (+) or negative (-) correlations and the significance level (* significant p< 0.05, ** highly significant p< 0.01, ***very highly significant p< 0.001). Abbreviations: *Fucus vesiculosus* (Fv), *Ascophyllum nodosum* (An), *Halidrys siliquosa* (Hs), *Fucus spiralis* (Fs), *Himanthalia elongata* (He), *Cystoseira* sp. (Csp), Filamentous green algae (Fil. Gr. Algae), *Chorda filum* (Cf) and *Sargassum muticum* (Sm).

	% Fv	% An	% He	% Fs	% Hs	% Csp.	%Cf	% Sm	% Fil. Gr. Algae	% Debris	Total vol. (ml)
Cyclopterus lumpus	/	+***	+***	/	+*	+*	/	/	+*	/	+***
Trachurus trachurus	-*	-**	-**	+***	/	/	/	/	/	-*	-*
Chelon labrosus	/	/	/	/	/	/	+***	-*	/	/	-*
Syngnathus rostellatus	/	-*	/	+*	/	/	/	/	/	/	-*
Ciliata mustela	/	/	-*	/	/	/	-*	+***	/	/	/

	Distance to shore (km)	Atm. Pres. (Pa)	Humidity (%)	Water temp. (°C)	Sal. (PSU)	*Gammarus locusta / G. crinicornis*	*Atylus swammerdami*	*Jassa* sp.	*Stenothoe marina*	*Idotea* sp. J	*Idotea baltica*
Cyclopterus lumpus	/	/	/	-***	+***	-***	-**	/	/	/	/
Trachurus trachurus	+**	-**	/	+***	+***	/	/	/	-*	/	/
Chelon labrosus	-**	/	-***	+***	-***	+***	/	/	-*	+*	/
Syngnathus rostellatus	/	-**	/	+**	+*	/	/	/	/	/	/
Ciliata mustela	-**	+**	+***	-***	-**	/	/	/	+***	/	/

	Idotea emarginata	*Liocarcinus holsatus* MG	*Liocarcinus holsatus* J	*Pisidia longicornis* MG	*Carcinus maenas* MG	*Hippolyte varians* PL	*Palaemon elegans* PL	*Tergipes tergipes*	Chironomidae sp.	Aphididae sp.	Harpacticoida sp.
Cyclopterus lumpus	+*	/	-*	-**	/	-*	-*	/	/	/	/
Trachurus trachurus	/	+**	+*	+***	/	+***	+***	/	-*	-**	-*
Chelon labrosus	-*	-**	-*	-**	/	/	/	+*	-*	-**	-**
Syngnathus rostellatus	/	+*	+*	+**	/	+**	+***	/	/	/	/
Ciliata mustela	/	/	/	/	+**	/	-*	/	/	+***	+***

3.3 Stomach analyses

3.3.1 Cyclopterus lumpus

Large numbers of young lumpsuckers (up to 13 per clump) were frequently encountered in floating seaweed clumps (in 10% of all seaweed samples, 16% of total number of fish). Most lumpsuckers were juveniles in their first (0.6 – 3 cm) or second (ca. 3.5 cm) year according to the estimates of Davenport and Rees (1993) and Ingólfsson and Kristjánsson (2002). The largest individuals were found in winter (mean length 3.5 cm); the smallest in spring (mean length 1.9 cm). Although 18 different prey items (mainly amphipods, isopods, decapod larvae, copepods and fish eggs) were found in the stomachs, the average Shannon-Wiener index was generally low (range 0.12 – 0.34; Table 4). Most fish had a full stomach (only two stomachs were empty), but only 1 to 4 different prey species could be distinguished per stomach. The average fullness index was positively correlated with the total length of the juvenile fish (Spearman R: 0.26; p= 0.01) and ranged between 0 and 18.3.

	length classes	Shannon-Wiener diversity index		Fullness index	
	(cm)	Neuston	Seaweed	Neuston	Seaweed
Cyclopterus lumpus	1.6 - 2	/	0.29 ± 0.44	/	5.86 ± 2.39
	2.1 – 2.5	/	0.13 ± 0.18	/	5.70 ± 2.87
	2.6 - 3	/	0.18 ± 0.27	/	6.46 ± 3.72
	3.1 – 3.5	/	0.34 ± 0.43	/	9.75 ± 5.01
	3.6 - 4	/	0.22 ± 0.28	/	8.30 ± 4.39
Ciliata mustela	2.1 -2.5	0.32 ± 0.31	/	1.51 ± 1.14	/
	2.6 - 3	0.23 ± 0.3	0.16 ± 0.28	1.47 ± 0.91	1.28 ± 1.07
	3.1 – 3.5	0.41 ± 0.32	0.21 ± 0.32	0.91 ± 0.64	1.38 ± 1.17
	3.6 - 4	/	0.46 ± 0.31	/	1.81 ± 1.24
Chelon labrosus	2.1 – 2.5	/	0.17 ± 0.16	/	3.80 ± 1.52
	3.1 – 3.5	0.02 ± 0.02	/	4.17 ± 2.74	/
Trachurus trachurus	2 .1- 2.5	0.25 ± 0.34	0.12 ± 0.24	0,29 ± 0,01	2.57 ± 1.53
	2.6 -3	0.72 ± 0.4	0.21 ± 0.3	1.34 ± 1.25	1.46 ± 0.56
	3.1 – 3.5	0.81 ± 0.08	0.11 ± 0.28	0.46 ± 0.46	0.59 ± 0.54
	3.6 – 4	0.65 ± 0.39	/	0.30 ± 0.31	/
Syngnathus rostellatus	< 8.1	0.0	0.0	0.0	3.32 ± 3.16
	>8.1	/	0.13 ± 0.08	/	2.04 ± 1.53

Table 4. Shannon-Wiener diversity index and Fullness index based on stomach content data per length group of fish species, for each of the sample groups (mean and standard deviation).

The qualitative stomach analysis (Fig. 5, only gravimetric percentage represented; frequency of occurrence and numerical percentage showed the same trends) showed a shift in dominant prey with increasing length of the juveniles, from a dominance of *Liocarcinus holsatus* megalopae, calanoid and harpacticoid copepods and small gammarid amphipods (mainly *Gammarus* sp. juveniles) in the smallest length class to *Idotea baltica*, fish eggs, calanoids and large gammarid amphipods

(*Gammarus locusta* and *G. crinicornis*) in the larger length classes (rest: *Palaemon* postlarvae, small fish, *Sagitta* sp., *Idotea emarginata*, *Idotea linearis*, *Jassa* sp. and *Carcinus maenas* megalopae).

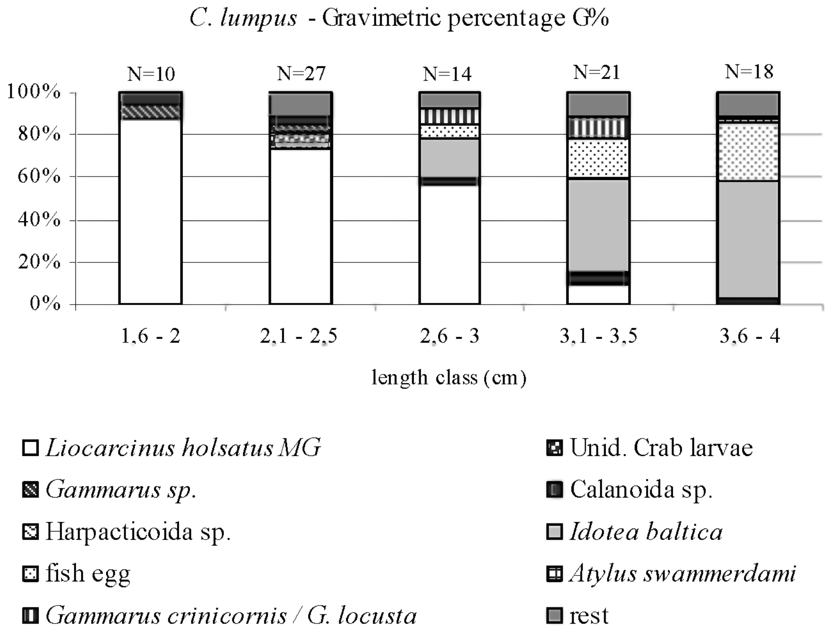


Fig. 5. Bar chart of the mean gravimetric percentages of the different prey items of *Cyclopterus lumpus* per length class in seaweed samples

3.3.2 Ciliata mustela

Fivebeard rocklings were encountered in both neustonic and seaweed samples. However, the size distributions of both sample groups showed substantial differences: rocklings from seaweed samples were generally larger (2.5 – 4 cm) than specimens from neustonic samples (0.5 – 3 cm) without seaweed (Fig. 6). The food consumption of individuals in size classes found in both sample types (2.6 -3 cm, 3.1 – 3.5 cm) will be further discussed. The Shannon-Wiener indices and fullness indices of both size classes did not differ significantly between seaweed fish and neustonic fish (MWU, $p > 0.4$ in all cases). In both size classes of neustonic and seaweed-associated fish, calanoid copepods were the dominant prey item (Fig. 7). Neustonic fish also fed intensively on fish eggs and, as they grew, they started feeding on larger prey items like crab megalopae. The diet of the seaweed-associated fish was more variable and also comprised considerable amounts of harpacticoid copepods, small gammarid amphipods and invertebrate eggs (probably from isopods and amphipods).

3.3.3 Chelon labrosus

Chelon labrosus was found abundantly in seaweed samples (summer and autumn) and neuston samples (summer, autumn and winter), with the dominant size class being 0.5 cm larger in seaweed samples (1.6 – 2 cm), compared to neuston samples (1.1 – 1.5 cm) (Fig. 6). As only few individuals

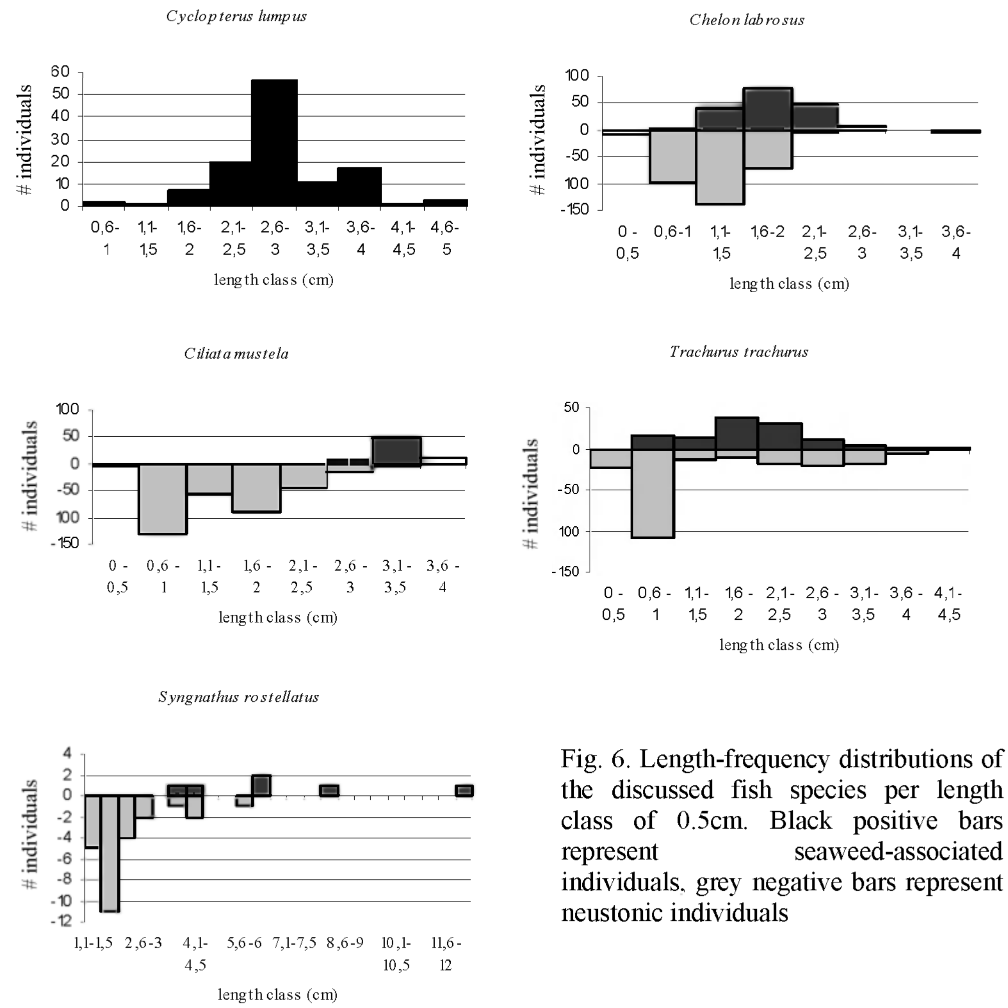


Fig. 6. Length-frequency distributions of the discussed fish species per length class of 0.5cm. Black positive bars represent seaweed-associated individuals, grey negative bars represent neustonic individuals

(17) larger than 2 cm were found, the results of the stomach content analysis will only be briefly discussed. Mullets from seaweed samples (2.1 – 2.5 cm, mean FI: 3.8) most frequently fed on calanoid (all stomachs, N%: 95, G%: 99%) and harpacticoid copepods (54% of all stomachs, N%: 3.9, G%: <0.1), and on dipteran insects (27% of all stomachs, N%: 0.6, G%: <0.1). Calanoid copepods were also the main prey (found in all stomachs, N% & G% >99) for mullets from neuston samples in the 3.1 – 3.5 cm length class (mean FI: 4.17). Dipteran insects and cypris larvae were rarely found; harpacticoid copepods were absent in stomachs of neustonic fish.

3.3.4 Trachurus trachurus

High numbers of juvenile horse mackerels were found in the neustonic environment in summer (only few individuals in winter). The individuals caught in association with floating seaweed clumps were generally larger (dominant size classes 1.6 – 2.5 cm) than the ones found in seaweed free areas (dominant size class 0.6 – 1 cm). The size classes between 2 and 3.5 cm were found in both sample types. The Shannon-Wiener index per size class was generally higher in neuston samples

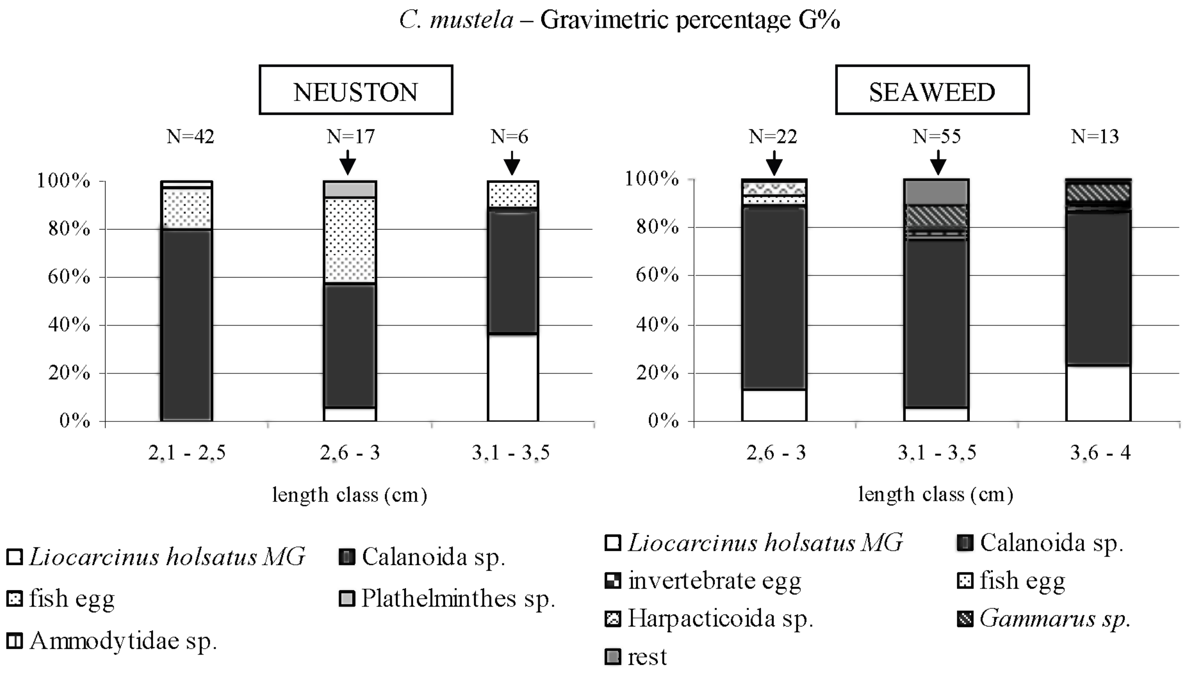
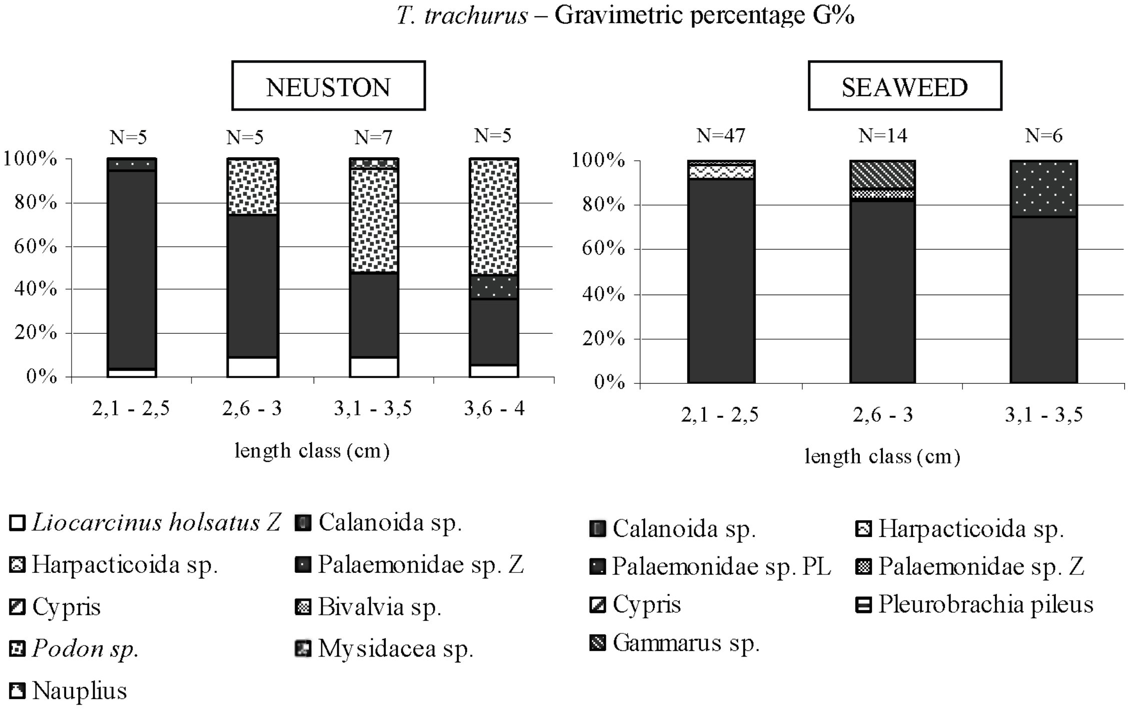


Fig. 7. Bar charts of the mean gravimetric percentages of the different prey items of *Ciliata mustela* per length class in neustonic samples and seaweed samples



compared to seaweed samples (Table 4); these differences were significant in the 2.6 – 3 cm and 3.1 – 3.5 cm length classes (MWU p= 0.05 and 0.002, respectively). Although the mean fullness index in seaweed samples was higher than in neuston samples, the difference was only significant in the 2.1 – 2.5 cm size class (MWU p= 0.003). Figure 8 shows that the diet from neustonic individuals was more varied than from seaweed-associated individuals: neustonic fish fed on 9 different planktonic prey species, mostly copepods, cladocerans and pelagic larvae of barnacles, crabs, prawns and bivalves. Seaweed-associated fish, on the other hand, predominantly fed on harpacticoid and calanoid copepods, but occasionally ingested larger prey items like postlarval prawns and gammarid amphipods.

3.3.5 Syngnathus rostellatus

Individuals of the pipefish *S. rostellatus* were encountered in 17% of the neuston samples and mainly consisted of small juveniles (dominant size class: 1.6 – 2 cm). The individuals found in seaweed samples were considerably larger / older and had a discontinuous size distribution ranging between 3.5 and 12.5 cm. In general, pipefish which were smaller than 8 cm exclusively fed on calanoid copepods (mean FI: 3.32). The two larger individuals (8.4 cm & 12.2 cm) recovered from seaweed samples also ingested some harpacticoid copepods and crab megalopae (*Liocarcinus holsatus* and *Carcinus maenas*) (mean FI: 2.04).

3.4 Diet overlap

Table 5. Schoener's index of diet overlap using percent by number. Bold: seaweed fish, underlined: neuston fish

	Cyclopterus lumpus	***Chelon labrosus***	***Trachurus trachurus***	***Ciliata mustela***	***Syngnathus rostellatus***	*Chelon labrosus*	*Trachurus trachurus*	*Ciliata mustela*	*Syngnathus rostellatus*
Cyclopterus lumpus	/	0.08	0.10	0.16	0.07	/	/	/	/
Chelon labrosus	/	/	0.90	0.73	0.96	0.97	/	/	/
Trachurus trachurus	/	/	/	0.80	0.86	/	0.56	/	/
Ciliata mustela	/	/	/	/	0.69	/	/	0.60	/
Syngnathus rostellatus	/	/	/	/	/	/	/	/	/
Chelon labrosus	/	/	/	/	/	/	0.55	0.55	/
Trachurus trachurus	/	/	/	/	/	/	/	0.51	/
Ciliata mustela	/	/	/	/	/	/	/	/	/
Syngnathus rostellatus	/	/	/	/	/	/	/	/	/

The calculated index of diet overlap (Schoener, 1970) indicated a relatively low overlap between the trophic spectrum of the seaweed-associated fish species *C. lumpus* and those of the other seaweed-associated species (overlap values 0.07 – 0.16; Table 5). Significant overlap (> 0.6) was apparent between *C. labrosus, C. mustela, T. trachurus* and *S. rostellatus* (0.69 - 0.96) in seaweed samples. The diet overlaps of *C. labrosus, C. mustela* and *T. trachurus* were lower in the neuston samples (0.51 - 0.55) than in the seaweed samples. The feeding habits of *C. labrosus* were almost identical in both sample types (0.97), while the diets of *C. mustela* and *T. trachurus* were clearly influenced by the presence of floating seaweed.

4. DISCUSSION

4.1 Fish communities

The presence of high concentrations of small juvenile fish in the upper layer of the water column is a known phenomenon (e.g. Zaitsev, 1970; Castro et al, 2001). The distribution of this ichthyoneuston is strongly influenced by the occurrence of floating objects, around which young fish tend to aggregate. These floating structures can serve as feeding or cleaning stations, shelters, rafts and meeting points for young conspecifics (review in Castro et al., 2001).

In the present study, we focused on juvenile neustonic fish which showed an affinity for floating seaweed clumps in the Belgian coastal area. The five fish species that were frequently and abundantly encountered in and near floating seaweed patches are known residents or visitors in the neustonic layer. Juveniles of *Ciliata mustela*, for example, were found abundantly during a neuston survey in Galway Bay, Ireland (Tully & O'Ceidigh, 1989), while *Cyclopterus lumpus* has been recorded in association with floating seaweed on many occasions (Tully & O'Ceidigh, 1989; Davenport & Rees, 1993; Ingólfsson, 1995 – 1998 - 2000). Juvenile mullets (*C. labrosus* in the present study) are known to have protective coloration adapted to a neustonic life and to develop an air sac near the dorsal fins to enable them to remain near the surface (Zaitsev, 1970). Together with horse mackerels (*T. trachurus* in the present study), mullets have frequently been reported as being associated with floating structures like fish farms (Dempster et al, 2005), FADs and drift algae (Dooley, 1972; Lenanton et al, 1982; Kingsford & Choat, 1985; Kingsford, 1992; Castro et al, 2001). Young pipefish (Syngnathidae) have been recorded in association with both permanently floating *Sargassum* (Fine, 1970; Kingsford, 1992; Cho et al, 2001; Ohta & Tachihara, 2004, Wells & Rooker, 2004) and ephemeral seaweed patches (e.g. Kulczycki et al, 1981).

The observed temporal variation in presence and abundance of neustonic fish is in accordance with the findings of Hempel and Weikert (1972), who found that temperature, wave action and solar radiation are the most important structuring factors. Similarly, the seasonal variation plays a major role in seaweed associated fish, as can be derived from Table 2 and the significant correlations with surface water temperatures in Table 3. However, there are other factors structuring the species composition, such as the floating seaweed presence and species composition, clump volume, distance to shore and the densities of the seaweed-associated invertebrate fauna (Safran & Omori, 1990; Ingólfsson, 1995 & 2000; Vandendriessche et al, 2006b). The low matching coefficient between fish data and environmental data indicates that only a part of the biotic structure is explained by the measured variables. These results do not agree with previous studies about fishes associated with floating objects, in which generally clear patterns of spatial and temporal variation could be observed (e.g. Wells & Rooker, 2004 a, b; Dempster & Kingsford, 2004). The lack of spatial patterns in the present study may be due to the limited spatial scale of the samplings, which was also reflected in the community analysis of the neustonic assemblages; and the sampling area can therefore be considered as a single geographical entity. The large multivariate distance between the samples dominated by *C. labrosus* and samples dominated by *C. lumpus*, *T. trachurus* and *C. mustela* could be caused by species interactions (e.g. territorialism (Ingólfsson, 2000) or predation (Dempster, 2005)), although the results of the stomach content analysis and diet overlap do not support the presence of such interactions between the investigated species. The data rather suggest that fish species associated with floating seaweeds have somewhat different nutritional requirements and feeding strategies. There may have been (large) predatory fish that were not sampled with the used net, but did have an influence on the species composition of the associated fish fauna. However, Nelson (2003) hypothesises that there may be insufficient time or stability for factors as competition and predation to influence size and diversity of the fish fauna associated with floating objects.

The community analyses of neustonic and seaweed-associated fish show that the presence of floating seaweeds in the neuston influences the species composition of the fish fauna. One striking feature is the abundant presence of juvenile *C. lumpus* and its total absence in the neuston samples. These functionally benthic juveniles (floating seaweed provides a substitute for the seabed in the pelagic zone – Davenport & Bradshaw, 1995) show adaptations of appropriate form and colour to the habitat: they have a ventral sucker which is suitable for adhering to the seaweed surface, and they are cryptically coloured (Davenport & Bradshaw, 1995). Similar adaptations are found in the *Sargassum* fish *Histrio histrio* displaying weed-like coloration and appendages. Some of these adaptations have also been reported for facultative rafters, which may enhance their survival in an environment with high predation pressure (Thiel & Gutow, 2005b). The impact of the presence and constitution of floating seaweed clumps, however, varies with the fish species (Dempster & Kingsford, 2004). Some species, like *C. lumpus*, are influenced by the volume and seaweed species composition of the clumps, while poor relationships were observed in the case of schooling fish like *T. trachurus* (similar observations in Druce & Kingsford, 1995). There were no straightforward correlations between fish densities and densities of available prey species in any of the fishes.

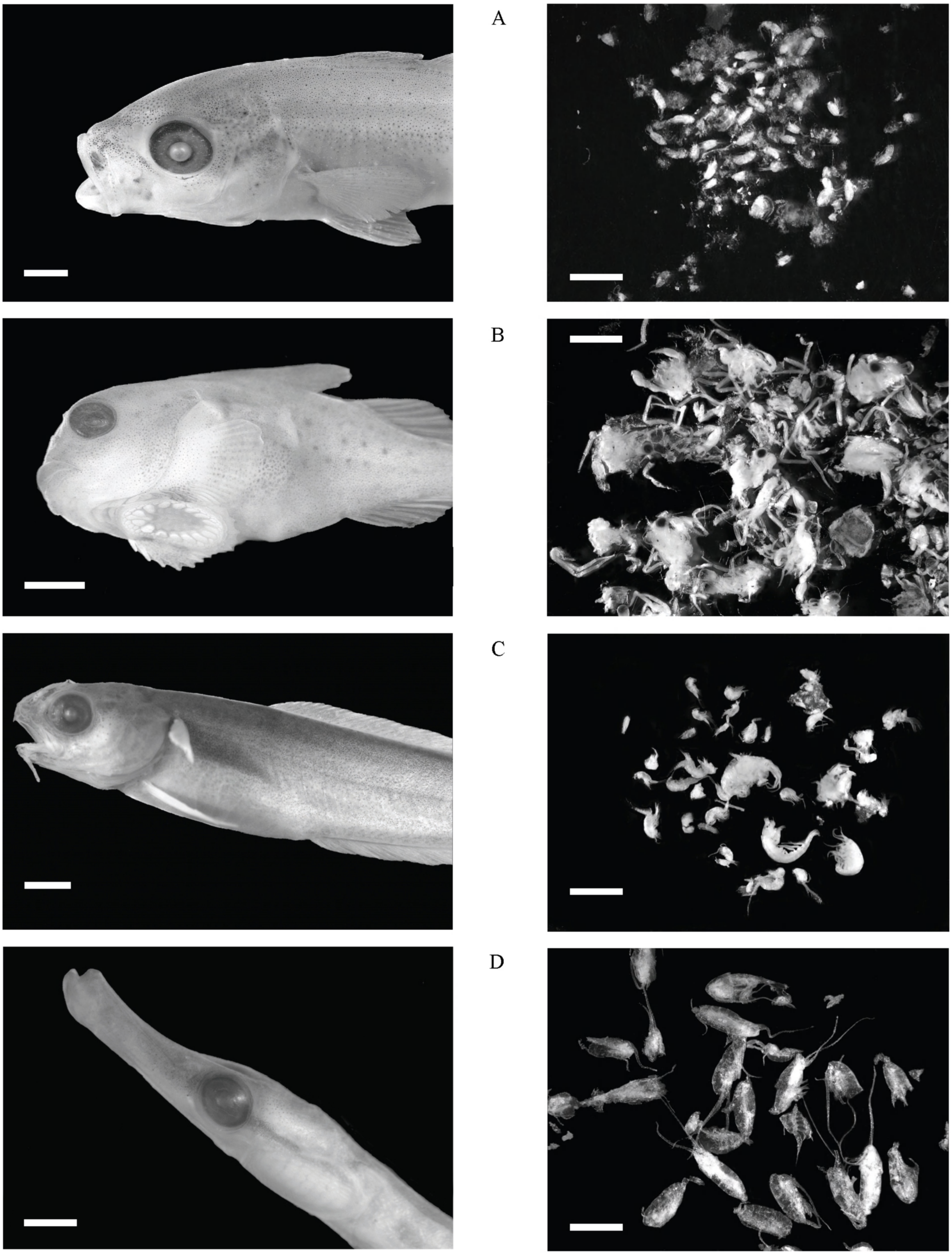


Fig. 9. Four fish species encountered in floating seaweed clumps and an example of their stomach contents (scale bar equals 2mm in each picture). A/ *Trachurus trachurus* - calanoid copepods; B/ *Cyclopterus lumpus* – megalopa larvae of *Liocarcinus holsatus* and a head of *Idotea baltica*; C/ *Ciliata mustela* – harpacticoid and calanoid copepods, *Stenothoe marina, Jassa herdmani* and the head of an unidentified amphipod, D/ Syngnathidae sp. – calanoid copepods

4.2 Feeding habits and length-frequency distributions

Generally, dietary shifts were observed during the growth of the different fish species. Especially the diet of *C. lumpus* changed markedly with increasing length of the fish, which was also observed in Ingólfsson and Kristjánsson (2002), where larger individuals switched from crustacean larvae and halacarid mites to harpacticoids, isopods, amphipods and smaller conspecifics. To a lesser extent, gradual changes were also observed in *C. mustela, T. trachurus* and *S. rostellatus*. These fish species tend to switch from smaller prey like copepods to larger prey items like crab megalopae, prawns and amphipods. According to Tully and O'Ceidigh (1989), larger individuals of *C. mustela* ate higher numbers of prey, rather than switching to other prey items.

Next to dietary changes with fish size, there were also clear differences between the diets of fish feeding in the neuston and in floating seaweed patches. Juvenile rocklings (*C. mustela*) from seaweed samples, for example, had a more variable diet compared to conspecifics feeding in the neuston. Seaweed-associated fauna like harpacticoid copepods, idoteid isopods and gammarid amphipods (*Gammarus* sp.) were obviously suitable prey items for the associating fish species. The advantage of ingesting these prey items is reflected in the length-frequency distributions: juvenile fish from seaweed samples were generally larger than specimens from neustonic samples, which was also reported in Kingsford (1992). This may be due to (1) the fact that seaweed samples are colonised by older fish that can ingest larger (seaweed-associated) prey and can withstand possible harsh hydrodynamic conditions in order to stay associated with floating seaweed clumps; or (2) the fact that juvenile fish grow faster when associated with floating seaweeds due to the provision of shelter (i.e. lower energy expenditure) and high densities of potential prey items (i.e. ideal feeding conditions). Based on the absence of 3 – 3.5 cm individuals in the neuston, it can be hypothesised that the latter may be true for the species *C. mustela*. However, a detailed analysis of growth parameters is needed to confirm this hypothesis. The larger size classes of *T. trachurus* and *C. labrosus* were found in both the neuston samples and seaweed samples (although in varying numbers), suggesting a turn-over of seaweed-associated fish (Safran & Omori, 1990). The discontinuous length distribution in *S. rostellatus* suggests that most of the seaweed associated specimens were caught in the seaweed upon detachment, instead of having colonised the seaweed from the surrounding neuston. As a result of their vulnerability in the surface water, they probably stay associated with the floating seaweed to avoid predators. From the presence of adult sygnathids, Kingsford & Choat (1985) concluded that floating seaweeds may provide a dispersal mechanism for this less mobile group.

4.3 Association behaviour

The absence of juvenile lumpsuckers (*C. lumpus*) outside floating seaweed patches and the composition of their diet (mainly seaweed-associated macro-invertebrates, especially in the larger size classes) confirm the findings of Davenport and Rees (1993) and Ingólfsson and Kristjánsson (2002): postlarval and juvenile lumpsuckers are predators specialised on floating seaweed patches in the Northeast Atlantic, attaching themselves to seaweed fronds with their ventral sucker (pers. obs.) and feeding on prey concentrated beneath the weed cover. Therefore, they can be regarded as aggregated, closely associated residents that stay within the branches of the seaweeds (Gooding & Magnuson, 1967; Dooley, 1972; Castro et al, 2001). *Ciliata mustela, Trachurus trachurus, Chelon labrosus* and *Syngnathus rostellatus* were found in both seaweed samples and neuston samples, so their association with floating seaweeds is of a more opportunistic nature and they can be regarded as being associated (Castro et al, 2001). *Ciliata mustela* seems to have most benefit of association with floating seaweeds: the juveniles clearly feed on the buffet of associated macro-invertebrates and length distribution data suggest that their growth is enhanced compared to neustonic conspecifics. The advantages for *T. trachurus* (transient visitors according to Langtry & Jacoby, 1996) and *C. labrosus* do not seem to be of similar importance: these species predominantly feed on planktonic prey, presumably in deeper layers (Hempel & Weikert, 1972) and there is no evidence of enhanced growth. Still, these species may benefit from association with floating objects for reasons other than prey availability: both species are schooling and may use floating objects as shelters, meeting points or transports to enriched convergence zones, surface slicks or near shore habitats (Kingsford & Choat, 1985; Kingsford, 1992; Shanks, 1983; Castro et al, 2001; Thiel & Gutow, 2005b). *Chelon labrosus* commonly enters brackish lagoons and freshwater, but spawns offshore. Consequently, floating seaweeds may serve as a means of transport, thereby enhancing the survivorship of larval and juvenile species as they move from offshore waters into bays and estuaries (Wells & Rooker, 2004a). Postlarval *Syngnathus rostellatus* largely depend on floating seaweeds for their survival in the neustonic layer. Young individuals and adults of this demersal species are probably carried with the seaweed after detachment from the substrate, and stay within the seaweed branches to ensure protection from predators. For this particular species, floating seaweeds serve as substitutes of the seabed (Hunter & Mitchell, 1967 in Castro et al, 2001), thereby increasing chances of survival.

4.4 Conclusions

The neustonic fish community at the BPNS is mainly seasonally structured, but is also strongly influenced by the patchy occurrence of floating objects. Floating seaweeds can be regarded as temporary and unpredictable habitats shared between several fish species (mainly juveniles) that use them for different reasons and with varying intensity. Accumulations of floating seaweeds can increase the survival of young fish through avoidance of predators (larger predatory fish and diving birds), and the associated macrofauna can serve as a food source for fish, as was the case for *Cyclopterus lumpus*. This may result in an enhancement of survival and growth of juveniles of the different fish species. For some fish species, like *Trachurus trachurus, Syngnathus rostellatus* and

Chelon labrosus, raft associated food items appear to represent opportunistic prey items. The association of these fish with floating seaweeds may result from other motivations like the formation of schools, transport to a more suitable habitat or survival in a habitat resembling the sea bed.

ACKNOWLEDGEMENTS

The first author acknowledges a specialisation grant from the 'Institute for the Promotion of Innovation through Science and Technology in Flanders' (IWT). The authors would like to express their gratitude to colleagues and friends for their help with the samplings, to Danielle Schram, Danny Peelaers and Bart Beuselinck for the weighing of the fish and their stomachs, to Wouter Willems for making the maps, and to Gina De Keersmaecker, Boris Pellegroms, Matthew Lammertyn, Frederic Leroux and Katrien Broekaert for the processing of a large amount of samples. Special thanks go to André Cattrijsse of the Flanders Marine Institute (VLIZ), and to the crewmembers of the research vessel Zeeleeuw. Dr. Gert Van Hoey, Dr. Peter Nelson and the anonymous referees are acknowledged for their constructive comments on earlier versions of the manuscript.

CHAPTER 6

FLOATING SEAWEEDS: A SOURCE OF SMALL-SCALE PATCHINESS IN NORTHEAST ATLANTIC SEABIRDS?

Fulmarus glacialis

Paper submitted

Vandendriessche S., Stienen E.W.M., Vincx M., Degraer S.

Floating seaweeds: a source of small-scale patchiness in Northeast Atlantic seabirds?

Ardea

ABSTRACT

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 differs between species and seabird groups based on their foraging strategies. The results indicate 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.

Keywords: Seabirds; Floating Seaweed; Northeast Atlantic, Feeding Strategy

1. INTRODUCTION

Large-scale variations in seabird distributions are mainly caused by environmental heterogeneity resulting from physical oceanographic processes (Haney 1987 & references therein) and pervasive anthropogenic disturbance (Jackson et al. 2001, Camphuysen 2005). However, patchiness in seabird distribution may also occur at smaller scales due to species-specific responses to the environment (e.g. Garthe 1997, Wanless et al. 1997, Boyd et al. 2006). Likewise, the presence of surface features (e.g. floating wood, debris, seaweed, buoys, and fronts) may determine seabird distribution as they provide resting places and can temporarily increase available food sources, to which seabirds can quickly respond. Haney (1987), for example, described patchiness due to the visible surface manifestations (slicks alternating with ripples of rough water) of internal waves. The seabird patchiness was probably due to qualitative differences in prey composition as most birds were actively foraging or feeding. Similar observations were done at fronts (e.g. Haney 1985, Balance & Pitman 1999, Spear et al. 2001), due to the locally elevated level of prey biomass. Especially the distribution of phalaropes (mostly feeding or resting) has been linked to the presence of large and persistent oceanic fronts and other oceanographic features that concentrate zooplankton at the surface (e.g. Haney 1985 & 1986, Lee 1987, Brown & Gaskin 1988).

On an even smaller scale, a wide variety of floating objects have been reported to attract seabirds: Cadée (2002) reports on peckmarks on and ingestion of debris like plastic, styrofoam and cuttlebones in the North Sea; Arcos (2000) observed an alternative feeding strategy of Balearic shearwaters involving capture of fish under floating objects; and floating seaweeds in the Bay of Fundy (Canada) are shown to attract seabirds such as phalaropes, gulls and terns (Parsons 1986, Huettmann pers.com.).

The influence of floating seaweed patches on the distribution and behaviour of seabirds forms the key issue of the present study. Floating seaweeds, both the permanently floating *Sargassum* and ephemeral patches composed of different species, are shown to teem with small marine animals seeking food and refuge, including crustaceans and fish (e.g. Fine 1970, Tully & O'Ceidigh 1986, Coston-Clements et al. 1991, Ingolfsson 1995, Kingsford 1995, Vandendriessche et al. 2006a, Vandendriessche et al, in press). The increased biomass in invertebrates and fish compared to the surrounding water column may constitute an important (more or less predictable) source of extra food, although probably exploited in an opportunistic way (Arcos et al. 2000). In the Sea of Okhotsk, for example, dunlins were seen feeding on rafts of floating seaweed, probably on snails and insects (Huettmann pers.com.). Furthermore, floating seaweeds could play an important role by signalling suitable feeding areas to birds since they tend to accumulate in biologically rich water masses (Arcos et al. 2000).

From the observations listed above, it is clear that seabirds are attracted to surface phenomena like floating seaweeds. Other than a few studies concerning *Sargassum* and some sporadic notes, however, few investigations have been done on the topic of seabirds associated with floating seaweeds. As a result, the present study aims to examine the seaweed's possible attractions for seabirds in Northeast Atlantic waters, based on the European Seabirds At Sea database (ESAS). The main research questions of this study are: "Are there seabirds that are frequently seen associated with ephemeral patches of floating seaweed" and "Are these associations feeding mode-dependent?"

2. MATERIALS AND METHODS

The seabird data used in the analyses were extracted from the European Seabirds At Sea database, which is composed of seabird observations collected and coded using standardised survey techniques (Tasker *et al.* 1984, Camphuysen *et al.* 2004). The database was established in the early 1980's and contains results of ship-based and aerial seabird surveys in Northwest European waters (Camphuysen & Garthe 2004). Of special interest for this study is the use of standardised coding of behaviour types in the database. The coding system, for example, introduced specific coding of associations of birds with certain surface phenomena and emphasises on feeding behaviour and foraging interactions. Association codes have been devised for birds associating with near-surface fish shoals or marine mammals, with floating objects such as wood, rubbish, oil slicks and seaweeds, and with fronts, buoys, markers, vessels, offshore installations, sea-ice or land. The associated birds are further described according to behaviour, which can be flying towards the surface phenomenon, scavenging, searching for prey, feeding, or resting. Furthermore, the description of the foraging behaviour is detailed and distinguishes between 20 behavioural codes like holding fish, aerial pursuit, scavenging at fishing vessel, surface pecking, and actively searching. The great benefit of detailed behavioural coding is that it provides insight in potential correlations between seabird presence and oceanographic or other factors driving prey, and that it allows discrimination between real associations and coincidental observations (Camphuysen & Garthe 2004).

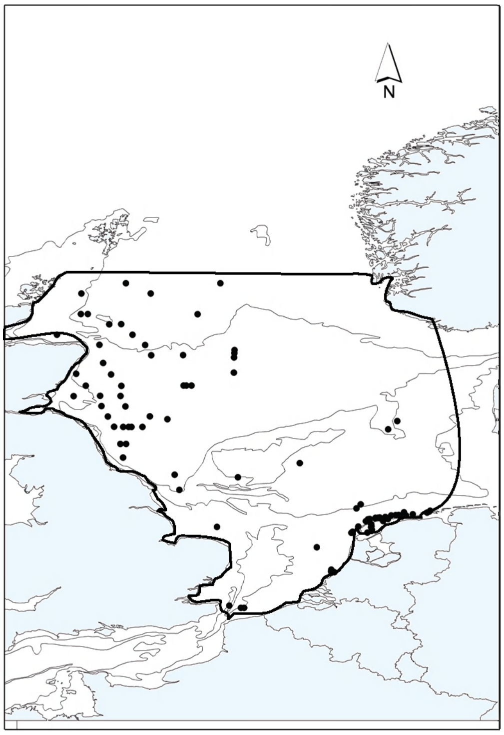


Fig. 1. Map indicating the observation points (212) of seabirds associated with floating seaweed and the delimitation of the study area.

The used data originated from the period 1979 – 2000. Detailed association codes were only recorded in < 1% of all records. Because the coding system was not always used at the same level of detail (e.g. a large proportion of the records only distinguished between 'associated with fish shoals', 'approaching observation base' and 'pattering'), a quantitative analysis of the importance of floating seaweeds was biased. However, as this bias depended on the observers and circumstances per trip, it was assumed that the bias was straightforwardly applied to the entire dataset, enabling comparisons between species. Consequently, it should be taken into account that the numbers resulting from the analyses are for inter-species comparison purposes only, and that they do not give reliable estimates of real seaweed-associated densities.

Although the database contained data about all Northwest European waters, the data about seaweed-associations in seabirds were concentrated in the North Sea. Therefore, only the seabird data from that region (59.17 – 51.26 N and 2.47 W – 6.58 E, see Fig. 1) were extracted and used in the analyses. Only data of common seabirds were included; rare seabird species (less than 300 records) and terrestrial birds were excluded. All abundances of seabirds were expressed as frequencies of occurrences to correct for aggregation behaviour.

Seabird species were grouped *a priori* according to foraging behaviour based on literature (Cramp et al. 1978-1997). The non-parametric Kruskal-Wallis test was applied to test for differences between multiple independent groups. Pairwise tests were done using the multiple comparisons procedure (Conover 1971).

3. RESULTS

Floating seaweed accounted for 2% of all observations of surface phenomena (Fig. 2A; large man-made objects like buoys, platforms and vessels not taken into account) and for 4% of all seabird counts in association with these phenomena. These percentages, however, are likely to be underestimated because floating seaweed is often an important constituent of patches of floating matter and lines in sea, and because floating seaweeds often converge at fronts.

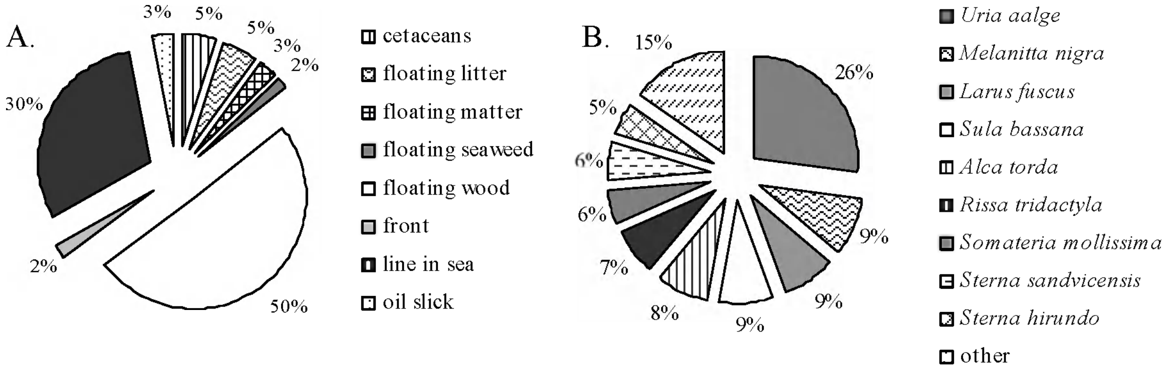


Fig. 2. A. Pie chart of relative importance of surface phenomena, based on frequencies of occurrences. B. Pie chart showing the top-10 observation frequencies of seabirds in association with floating seaweed.

The most common visitors of floating seaweed patches were guillemots (*Uria aalge*), common scoters (*Melanitta nigra*), gulls *(Larus fuscus, Rissa tridactyla*), gannets (*Sula bassana*), razorbills (*Alca torda*), eiders (*Somateria mollisima*), and terns (*Sterna sandvicensis, Sterna hirundo*) (Fig. 2B). Occasional visitors included other gulls (*L. argentatus, L. canus, L. marinus, L. ridibundus*) and terns (*S. paradisaea*), fulmars (*Fulmarus glacialis*), skuas (*Stercorarius skua*), cormorants (*Phalacrocorax carbo*) and red-breasted mergansers (*Mergus serrator*). In order to quantify the importance of floating seaweeds to the observed seabird species, the ratios of frequency of occurrence in floating seaweeds to total frequency of occurrence in the study area was calculated per species (Fig. 3).

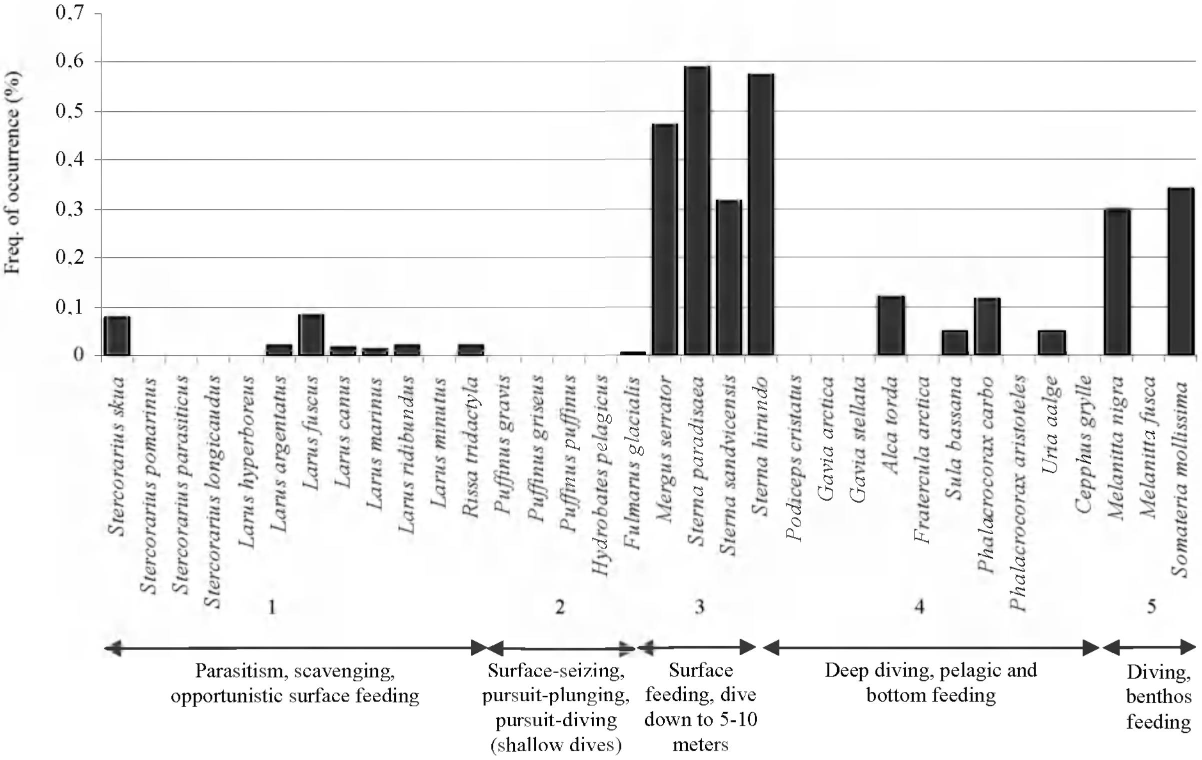
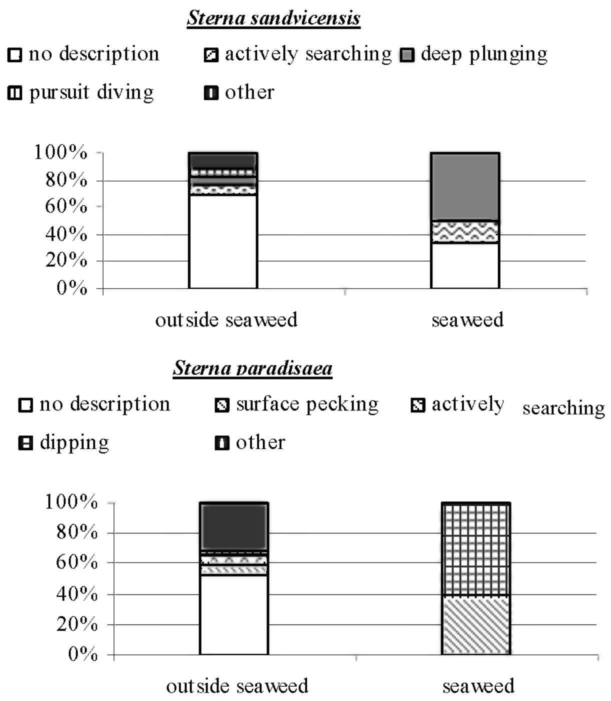


Fig. 3. Bar chart showing the ratio of frequency of occurrence in association with floating seaweed to total frequency of occurrence per seabird species. Arrows indicate foraging habits of the discussed species (5

The ratio of frequency of occurrence in association with floating seaweed to total frequency of occurrence (FO ratio) differed between species and seabird groups based on their foraging strategies. A Kruskal-Wallis test showed significant differences between the groups (df = 4, p = 0.03) and especially between groups 2 & 3 and 2 & 5 (Multiple Comparisons $p < 0.05$). The highest FO ratios were observed in group 3 (mean 0.49%), followed by groups 5 (mean 0.21%), 4 (mean 0.03%), 1 (mean 0.02%) and 2 (mean <0.001%) (Fig.3). These results indicate 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 and actively searching (mainly gulls and terns), and pursuit plunging (mainly cormorants) (Table 1.). The activities of razorbills, fulmars, seaducks and guillemots were seldomly recorded, but were mostly pursuit-plunging or actively searching.

Because foraging behaviour in terns was regularly described, we compared their behaviour around seaweeds to their behaviour outside seaweed patches (Fig. 4.). The three tern species were most commonly associated with fish shoals (up to 20%) and their top-3 foraging activities varied when comparing seaweed-associated birds with the rest of the observed birds. *Sterna paradisea* was mainly seen dipping and surface pecking in the vicinity of floating seaweeds, which is similar to other cases, in which they were mainly seen surface pecking, actively searching and dipping. Foraging behaviour was quite similar in *S. sandvicensis* as well: in both cases the main activities were actively searching and deep plunging. Considerable differences, however, could be observed in *S. hirundo*, which was mainly seen surface pecking and dipping around floating seaweeds, but was actively searching, pursuit diving or scavenging in most other cases. These results indicate that, especially in the case of *S. hirundo*, the presence of floating seaweed patches may influence foraging behaviour and therefore also prey choice.



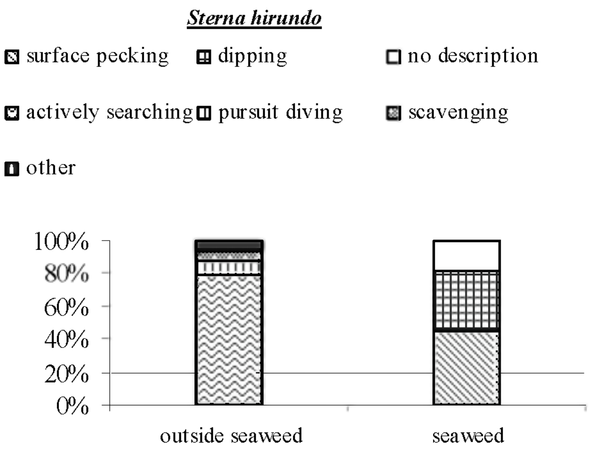


Fig. 4. Comparison concerning foraging behaviour in three tern species: at floating seaweed vs. outside floating seaweed

Table 1. Behavioural activities of birds associated with floating seaweeds, expressed as percentage of total observations (frequency of occurrence) per species

	approach obs base	*actively searching*	*scavenging*	*surface pecking*	*surface seizing*	*dipping*	*deep plunging*	*plunge-diving*	*pursuit plunging*	*no description*
Alca torda									5,5	94,5
Fulmarus glacialis		20								80
Larus argentatus		28,6		28,6						42,9
Larus canus										
Larus fuscus		38,9	5,6	13,3	22,2					22,3
Larus marinus		33,3					33,3			33,3
Larus ridibundus										100
Melanitta nigra										100
Mergus serrator										100
Phalacrocorax carbo									100	
Rissa tridactyla		13,3		13,3	13,3	6,7				53.4
Somateria mollissima									16,7	83,3
Stercorarius skua			100							
Sterna hirundo				45,5		36,4				18,2
Sterna paradisaea				40		60				
Sterna sandvicensis		16,7					50			33,3
Sula bassana		16,7					16,7			66.7
Uria aalge	3,6								3,6	89,7

4. DISCUSSION

4.1 Seaweed-associated birds and their foraging behaviour

Of a few of the species that were (occasionally) found associated with floating seaweeds in the present study, some reports already exist in literature concerning association of conspecifics or congeners with floating seaweeds. Of other species, only sporadic notes about behaviour or diet indicate a possible interest for floating objects as foraging grounds. Finally, for some species, there are no indications other than the association percentages in the present study for attraction to floating seaweed patches.

As could be expected from their foraging habits (parasitism, scavenging, and opportunistic surface feeding), gulls and skuas (*Stercorarius* sp., *Larus* sp., *Rissa tridactyla*) were only occasionally observed in the vicinity of floating seaweeds. Only *L. argentatus, L. fuscus* and *R. tridactyla* were observed while surface pecking or surface seizing (table 1). Skuas and gulls also appeared in low numbers around *Sargassum* mats, where they only occasionally fed (Haney 1986).

In the present study, shearwaters (*Puffinus gravis, P. griseus, P. puffinus*), fulmars (*Fulmarus glacialis*) and storm-petrels (*Hydrobates pelagicus*) showed little or no affinity for floating seaweeds, although their foraging behaviour includes surface-seizing. In the Mediterranean, however, Arcos et al. (2000) reported on an alternative feeding strategy of Balearic shearwaters (usually plunge-diving, pursuit-diving and surface-seizing of small fish; or interaction with subsurface predators), involving capture of fish under floating objects, both biotic and abiotic. Stomach analysis from Manx shearwaters (*Puffinus puffinus*) off the south-eastern USA suggested foraging around floating *Sargassum* mats (Lee 1995), a feeding behaviour also commonly exhibited by Audubon’s shearwaters (*P. lherminieri*) (Haney 1986). Similar behaviour or evidence from stomach contents have not yet been reported for shearwaters in the North Sea. Fulmars were in a few cases seen while actively searching in the vicinity of floating seaweeds. Although Cadée (2002) reports on peckmarks on and ingestion of debris in the North Sea, and Zaitsev (1971) described surface-feeding on neustonic invertebrates, the only real evidence that fulmars feed on floating object - associated fauna is the presence of the isopod *Idotea metallica* in their diet (Furness & Todd 1984) as this isopod exclusively establishes populations on objects drifting on the sea surface (Gutow 2003).

The group of surface feeding, shallow divers (terns and red-breasted mergansers) showed the highest association percentages with floating seaweeds. Furthermore, the feeding behaviour of *Sterna hirundo* showed a shift from actively searching, pursuit diving or scavenging to surface pecking and dipping in the vicinity of floating seaweeds. This shift indicates that this species feeds on the invertebrates and/or small fish that are associated with the seaweeds. The interest of terns (species not specified) for seaweed-associated fauna was already observed in Canada, where they were seen plunge-diving in the immediate vicinity of floating seaweed patches (Parsons 1986). Another observation of seaweed-association was done in South Africa, where Antarctic terns (*Sterna vittata*) frequently roosted at sea on floating wood or floating kelp stipes (Tree & Klages 2004). Similarly, bridled terns (*S. anaethetus*) and black terns (*Chlidonias niger*) frequently used floating *Sargassum* as roost sites and foraging habitat in Haney (1986).

The association of red-breasted mergansers (*Mergus serrator*) with floating seaweed has not yet been reported, but is not surprising given its diet and method of feeding: primarily fish obtained by foraging from the surface with head and eyes immersed and subsequent diving. Next to fish, seaweed-associated invertebrates like *Idotea, Palaemon* and *Gammarus* have been described as prey (Cramp et al. 1978 – 1997).

Of the group consisting of deep-diving, pelagic and bottom feeding species, razorbills (*Alca torda*), gannets (*Sula bassana*), cormorants (*Phalacrocorax carbo*) and guillemots (*Uria aalge*) were occasionally observed in association with floating seaweeds. The behaviour of these species was only recorded in a few cases, in which they were mostly pursuit-plunging. Especially gannets and cormorants are known to pick up floating debris from the sea surface, which they use as nesting material together with, or instead of seaweed (Podolsky & Kress 1989, Tasker et al. 2000). Cormorants and gannets are mainly piscivores feeding on a variety of pelagic and benthic species (e.g. gadoids, herring, eel, labrids, flatfishes), but some records also mention the ingestion of the pelagic/neustonic lumpsucker (*Cyclopterus lumpus*) (Lilliendahl & Solmundsson 2006 for cormorants, Burton 1980 for gannets). The juveniles of this fish species are known associates of floating seaweeds in north-western Europe (Davenport & Rees 1993, Ingólfsson & Kristjánsson 2001, Vandendriessche et al. in press). Their occurrence in cormorant and gannet stomachs may indicate the use of floating seaweeds as foraging grounds.

An unexpected outcome of this study was that common scooters and eiders showed relatively high association percentages (mean 0.21% in group 5, Fig. 3) with regard to floating seaweeds. As these species are benthos feeders (primarily molluscs; Cramp *et al.* 1978 – 1997), it is unlikely that they are attracted due to the high densities of seaweed-associated fauna. No other reports about associations of these species with floating structures were found, so the meaning of the high association percentages in the present study remains unclear.

4.2 Advantages of floating seaweed presence for seabirds

The results of the present study and comparison with literature about conspecifics or congeners indicate that some seabirds are attracted by floating seaweeds. Generally, seabirds with the greatest affinities for floating seaweeds were surface-feeding and plunge diving species (cf. Haney 1986), indicating that these species are attracted by the increased prey concentration associated with floating seaweed patches. Given the seasonal and ephemeral character of such patches in the study area (contrary to the permanently floating *Sargassum*), the seaweed-associated fauna can only be exploited in an opportunistic way. Still, they can temporarily constitute an important and predictable source of extra food. At the same time, floating seaweeds and other floating objects can signal suitable feeding areas, since they tend to accumulate in biologically rich waters such as convergence fronts (Arcos et al. 2000). Another use of floating seaweed patches was mainly described in *Sargassum* patches, were some tern and phalarope species often roost on the semi-solid surface, probably allowing them to conserve energy while they are not foraging (Haney 1986, pers. obs.). Similar behaviour was however not described in the study area. To summarise, it can be stated that the increased structural complexity and food supply in ephemeral floating seaweed patches may enhance foraging conditions for some seabird species depending on their preferred prey and foraging strategy, which consequently increases small-scale patchiness in seabird distribution.

4.3 Methodology and research outlook

As pointed out in the material and methods section, the bias in the used database does not allow us to make reliable quantifications of seaweed-association in seabirds. Furthermore, the description of seabird behaviour in the vicinity of floating seaweeds was not straightforwardly recorded with the same level of detail, and some entries of behavioural codes seem extremely unlikely (e.g. pursuit diving in *Sterna sandvicensis* and *S. hirundo*). These factors call for caution in the interpretation of the data. However, the general message of the present study is not affected by this bias: the results indicate that some seabirds show a real interest in floating seaweeds as foraging or resting grounds. Consequently, it would be worthwhile to focus on the association between seabirds and seaweeds in the future, with a high level of detail concerning behaviour. Additionally, the effects of seasonal variation and variation in size of floating seaweed patches should be investigated.

ACKNOWLEDGEMENTS

This study would have been impossible without the consent to use the European Seabirds At Sea database. Therefore, the authors would like to thank all ESAS-partners for approving to the use of the data for this research topic. The first author acknowledges a specialisation grant from the ‘Institute for the Promotion of Innovation through Science and Technology in Flanders’ (IWT). The study was conducted within the framework of GOA 1205398 and GOA-BBSea 01GZ0705 (Ghent University), and the European networks MarBEF and ENCORA. Dr. G. Van Hoey is acknowledged for his constructive comments on earlier versions of the manuscript.

CHAPTER 7

FLOATING SEAWEEDS AND THE INFLUENCES OF TEMPERATURE, GRAZING AND CLUMP SIZE ON RAFT LONGEVITY – A MICROCOSM STUDY

Adult *Idotea baltica*

Paper in press

Vandendriessche S., Vincx M., Degraer S.

Floating seaweeds and the influences of temperature, grazing and clump size on raft longevity – a microcosm study

Journal of Experimental Marine Biology and Ecology

ABSTRACT

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 indicated that floating seaweeds have the potential to stay afloat for a long time, but that their longevity is temperature-dependent and can be strongly reduced by grazing activity of associated herbivores.

Keywords: Floating Seaweed; North Sea; grazing, temperature

1. INTRODUCTION

Floating seaweeds are abundantly found in surface waters of the Belgian coastal zone and other regions of the world due to the presence of buoyant tissue or gas filled bladders. After detachment as a result of grazing damage, wave action during storms or seasonal release of thalli or reproductive structures (Lenanton et al., 1982; van der Merwe & McLachlan, 1987; Hobday, 2000 a , b, c; Viejo & Åberg, 2003; Thiel & Gutow, 2005a), these algae and other debris form ephemeral rafts of various sizes and shapes, which can travel considerable distances due to tidal and non-tidal (e.g. wind induced and density-driven currents) drift of surface waters (Parsons, 1986). The seaweed rafts influence the distribution of species by providing fauna with a substrate for attachment, protection, a food source and a means of dispersal (Thiel & Gutow, 2005b). The process of rafting has been intensively studied in recent years and appears to be an advantageous strategy for enhancing survival and dispersal of seaweeds and their associated fauna (Dayton, 1973; Parsons, 1986; Macaya et al., 2005, Salovius et al., 2005; Thiel & Gutow, 2005b).

Although the importance of rafting as a dispersal mechanism is widely accepted, indications about raft longevity and travel distance in literature are usually limited to rough estimates. Strong indications for longevity of floating seaweeds come from studies in which entire plants or parts were tethered in coastal areas (reviewed in Thiel, 2003). The drawback in these studies is that tethering may not be representative of the open ocean situation, as the seaweeds are not allowed to be free floating and are therefore restricted in their response to prevailing environmental conditions (winds, currents, wave surges). Other authors used distance to the nearest potential source region as an estimate for floating duration (Ingólfsson, 1995). This approach, however, cannot be used in regions where current patterns are so complex that unravelling the origin of seaweed patches is still to be challenged (e.g. Belgian coast). Another method is based on the size and growth rate of sessile rafters like stalked barnacles (e.g. Helmuth et al., 1994; Macaya et al., 2005), which were not found on floating seaweeds recovered off the Belgian coast (Vandendriessche et al., 2006a). Finally, estimates were also made based on colour and blade length of the seaweeds themselves (Ryland, 1974; Stoner & Greening, 1984; Parsons, 1986; Helmuth et al., 1994; Hobday, 2000c). Although these methods provide data about the age of the rafts, an answer to the question 'How long can floating seaweeds stay buoyant?' can only be obtained experimentally by maintaining them in seawater in a laboratory, like it has been done in the past for a number of drift plant seeds and fruits (e.g. Skarpaas & Stabbetorp, 2001; Lacap et al., 2002; Thiel & Gutow, 2005a).

Macaya et al. (2005) stated that the survival of floating seaweeds on the sea surface depends on several factors, including temperature (Hobday, 2000c), damage caused by sunlight (Jokiel, 1980), nutrient levels (Edgar, 1987), epibiont growth (Parr, 1939) and grazing (Thiel & Gutow, 2005a). However, the impacts and relative importance of these factors have not yet been quantified experimentally, as was suggested in Thiel and Gutow (2005a). Parsons (1986) stated that exudation and weight loss can and probably do occur while the seaweed is floating, but did not make measurements. In order to evaluate the rafting capacities of ephemeral seaweed patches, the present study focused on the influences of temperature, grazing and clump size on raft longevity. The experimental study was carried out in a controlled environment reflecting North Sea (Belgian coastal zone) conditions considering salinity, temperature, seaweed species and grazer species.

2. MATERIALS AND METHODS

2.1 Experiment I: influence of temperature and grazing

The experiment was carried out in 4 climate chambers with constant temperatures (5°C, 10°C, 15°C and 18°C) and a 12:12h light:dark cycle (constant light intensity, Philips TL-D 18W, 840). In each climate room, 12 plastic containers (25cm diameter) were filled with 1.5 litres of artificial seawater (34 ± 0.5 PSU) and provided with an air source. The temperature and salinity conditions are based on typical values from water mass characteristics from the North Sea (salinity 34 – 35 PSU, mean water temperatures 6°C in winter to 17°C in summer). Fresh *Fucus vesiculosus* and *Ascophyllum nodosum*, harvested from Lake Grevelingen and the Paulina saltmarsh (The Netherlands), were thoroughly rinsed in order to remove associated fauna and filamentous algae. Pieces of seaweed (6 x *Fucus*, 6 x *Ascophyllum*) with an initial blotted wet weight of 10 to 12.5 grams were randomly distributed into the containers in each climate chamber. Five adult individuals of the herbivorous isopod *Idotea baltica* (18 – 31 mm standard length) were randomly added to 6 containers (3 x *Fucus*, 3 x *Ascophyllum*) in each climate chamber. This isopod number roughly corresponds with densities of 300-500 individuals per litre of seaweed, which is quite high but still realistic (see chapter 4). Two to five times a week (more frequently at the higher temperatures), the seaweed fragments were blotted dry and weighed to the nearest milligram. The number of isopods in each container was checked and dead individuals were immediately replaced. Twice a week, the seawater was replaced. The experiments at 10, 15 and 18°C ran until all seaweed fragments had sunk; the experiment at 5°C was stopped after 211 days (all fragments were still floating).

The choice of *Idotea baltica* as test organism for grazing is based on the fact that the genus *Idotea* is one of the most abundant taxa found on a wide variety of floating items (Thiel & Gutow, 2005b). *Idotea baltica* is very abundant and dominant on algal rafts in the North Sea, indicating the importance of floating substrata for this species (Locke & Corey, 1989; Vandendriessche et al., 2006a). Contrary to its congener *Idotea metallica*, this species grazes heavily on its rafting substrate, thereby shortening the longevity of the raft and eventually destroying it (Gutow, 2003). Nevertheless, this species is considered to be a successful rafter due to its ability for local recruitment (reproduction by incubating embryos in the marsupium), enabling the maintenance of local populations when the duration of the journey exceeds the typical lifetime of the species (Thiel & Gutow, 2005b). Furthermore, *Idotea baltica* grows quite fast on floating items (0.37 mm per day; Gutow, 2003) and can strongly cling to its substrate. The species is also very motile and can switch between floating items in favorable conditions.

2.1 Experiment 2: influence of clump size

This experiment was carried out in a 15°C climate chamber with a 12:12h light:dark cycle (constant light intensity, Philips TL-D 18W, 840). Twenty-four aerated containers were filled with artificial seawater and fresh fragments of *Fucus vesiculosus* and *Ascophyllum nodosum* of different size, which were thoroughly rinsed in order to remove associated fauna and filamentous algae. Fragments of both seaweed species with an initial wet weight of 20, 40, 80 and 160 grams (± 0.5 g; 3 replicates each) were randomly distributed in the containers. The initial numbers of air bladders and reproductive structures were counted. Every week, the seawater was replaced and the seaweed fragments were blotted dry and weighed to the nearest milligram. The experiment was stopped after one year and five months, when only six fragments were still floating.

2.3 Data treatment

The effects of seaweed species and grazing treatment per temperature were investigated using a 3-Way ANOVA based on log (x+1) data of raft longevity (days) and final weight (no test for data from 5°C because the experiment was stopped after 211 days). The effects of seaweed species and grazing treatment per temperature on rate of weight loss were investigated using a 2-Way ANOVA and Spearman rank correlations because, in this case, the assumptions did not fulfil the requirements for a 3-Way ANOVA. Parametric T-tests were used to examine differences in mortality of *Idotea baltica* in the two seaweed treatments per temperature. Two-Way ANOVA was also used to examine the effects of initial clump weight and seaweed species on the longevity and the rate of weight loss in the second experiment. The significance of correlations was tested using the Spearman rank procedure.

Due to the use of artificial seawater, fouling of the seaweed fragments was not detected during the course of both experiments and was not considered in further analyses.

3. RESULTS

3.1 Experiment I: influence of temperature and grazing

3.1.1 Raft longevity

The raft longevity of the seaweed was not significantly different between *Fucus vesiculosus* and *Ascophyllum nodosum* in this first experiment (3-Way ANOVA $F_1 = 2.8$, $p = 0.1$). The effects of grazing, however, were more important ($F_1 = 21.7$, $p < 0.0001$). In the presence of the isopod *Idotea baltica*, seaweed fragments sank significantly faster, which was most pronounced at the highest temperatures: seaweed fragments stayed afloat for a mean of 16.8 days in the presence of isopods and for a mean of 55.3 days in the absence of isopods at 15°C, while they floated for a mean of 24.4 days in the presence of isopods and for a mean of 61.3 days in the absence of isopods at 18°C. This means that the floating capacity of the seaweed fragments decreased with 60-70% in the presence of the used isopod density (Figure 1).

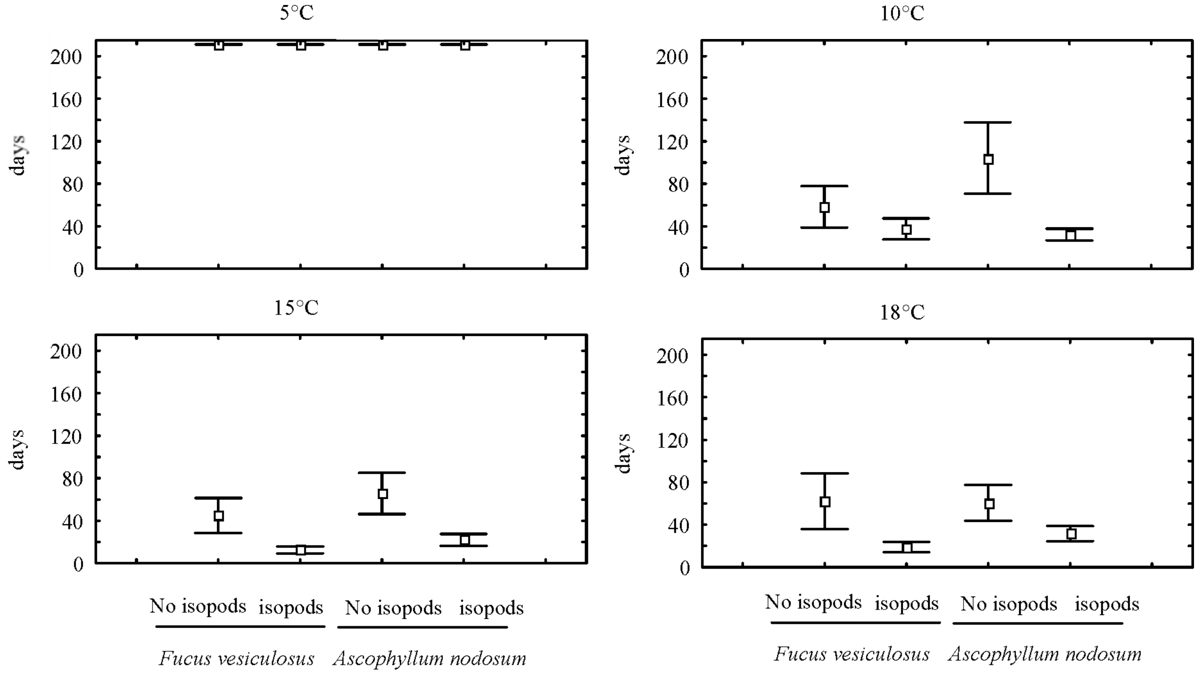


Fig. 1. Whisker plots (mean ± SE) of raft longevity (days) per treatment (2 seaweed species – presence or absence of grazing isopods)

Next to a negative effect of grazing, the raft longevity also suffered a negative effect (however not significant in 3-Way ANOVA: $F_2 = 2.9$; $p = 0.07$) of increasing temperature (Figure 2A). For the two treatments (grazing / no grazing), the correlation between floating capacity (expressed as days afloat) and temperature was significantly negative (Spearman $R = -0.66$, $p < 0.001$

in both cases). While seaweed fragments were still floating after 211 days at 5°C, they sank within a 100 days above 15°C in the absence of isopods and even faster in their presence (in less than 45 days).

All interaction effects between temperature, grazing treatments and seaweed species were not significant (3-Way ANOVA $F_2 = 0.12$ for temp. x seaweed species, $F_2 = 0.55$ for temp. x grazing treatment, $F_1 < 0.00$ for seaweed species x grazing treatment, $F_2 = 0.77$ for temp. x grazing treatment x seaweed species, $p > 0.05$ in all cases).

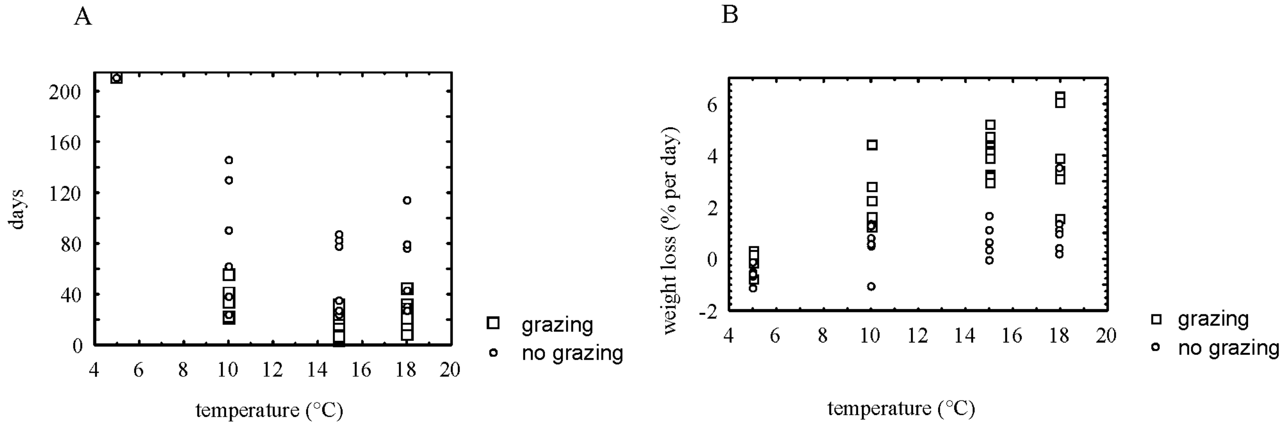


Fig. 2. Scatterplots of (A) raft longevity (days) vs. temperature (°C), and (B) rate of weight loss (% per day) vs. temperature (°C) per grazing treatment (2 series)

3.1.2 Weight loss

The effects on the rate of weight loss are similar to those on floating capacity: grazing significantly increased weight loss at all temperatures (reduced seaweed growth at 5°C), while the seaweed species did not account for any differences (Table 1). Differences in the rate of weight loss between treatments (grazing / no grazing) increased with temperature: the rate of weight loss was 1% higher at 5°C in the case of grazing, 2% at 10°C and 3% at 15 and 18°C. The correlation between temperature and weight loss was stronger in the treatments subjected to grazing (Spearman R = 0.71, $p < 0.001$) than in the treatments without grazing (Spearman R = 0.62, $p = 0.001$) (Figure 2B).

Table 1. Results of Two-Way ANOVA regarding effects of seaweed species (*Ascophyllum nodosum – Fucus vesiculosus*), the presence of grazing and the interaction of both factors per temperature on the rate of weight loss.

Temperature	TWO-WAY ANOVA F_1- and p-values					
	Effect seaweed		Effect grazing		interaction	
	F_1	p	F_1	p	F_1	p
5°C	0.53	0.49	*6.86*	*0.031*	2.54	0.15
10°C	1.95	0.20	*7.77*	*0.02*	<0.01	0.95
15°C	1.39	0.26	*80.93*	*0.000002*	*5.44*	*0.039*
18°C	0.11	0.75	*16.81*	*0.0026*	*5.39*	*0.045*

In the no-grazing treatments, seaweed fragments slowly lost weight until they sank (Figure 3). In a few cases, the weight stabilised and the formation of reproductive structures was observed. Only at the lowest temperature (5°C) was significant growth seen (up to 335% of the initial weight). Weight increased, although less spectacularly, in the grazing treatments at 5°C. At higher temperatures, however, the grazing by isopods augmented the rate of weight loss (up to five times faster). The results indicated a higher grazing activity of *Idotea baltica* at higher temperatures, but also a faster decomposition of the seaweed fragments due to fragmentation and degradation. Only at a temperature of 5°C was the growth of the seaweed large enough to compensate for the grazing pressure.

The weight at which the seaweed fragments sank was highly variable (range 1-100% of initial weight) and was not influenced by temperature (3-Way ANOVA $F_2 = 0.69$, $p = 0.51$), while significant effects were observed considering seaweed species and grazing (3-Way ANOVA $F_1 = 4.54$, $p = 0.04$ and $F_1 = 8.64$, $p = 0.06$, respectively). Fragments of *F. vesiculosus* sank at a larger size (mean 46% of initial weight) compared to fragments of *A. nodosum* (mean 22%). On average, seaweed fragments sank at 29-42% of the initial weight, but the variations were very high.

3.1.3 Mortality of Idotea baltica

Differences in the mortality of isopods were not significant between seaweed treatments ($p > 0.25$ at all temperatures). There was, however, a positive significant relationship between isopod mortality and temperature (Spearman $R = 0.51$, $p = 0.01$). Average mortality ranged from an average of 0.05 individuals per day at 5°C, over 0.09 Ind/day at 10° C, 0.33 Ind/day at 15°C to 0.22 Ind /day at 18°C.

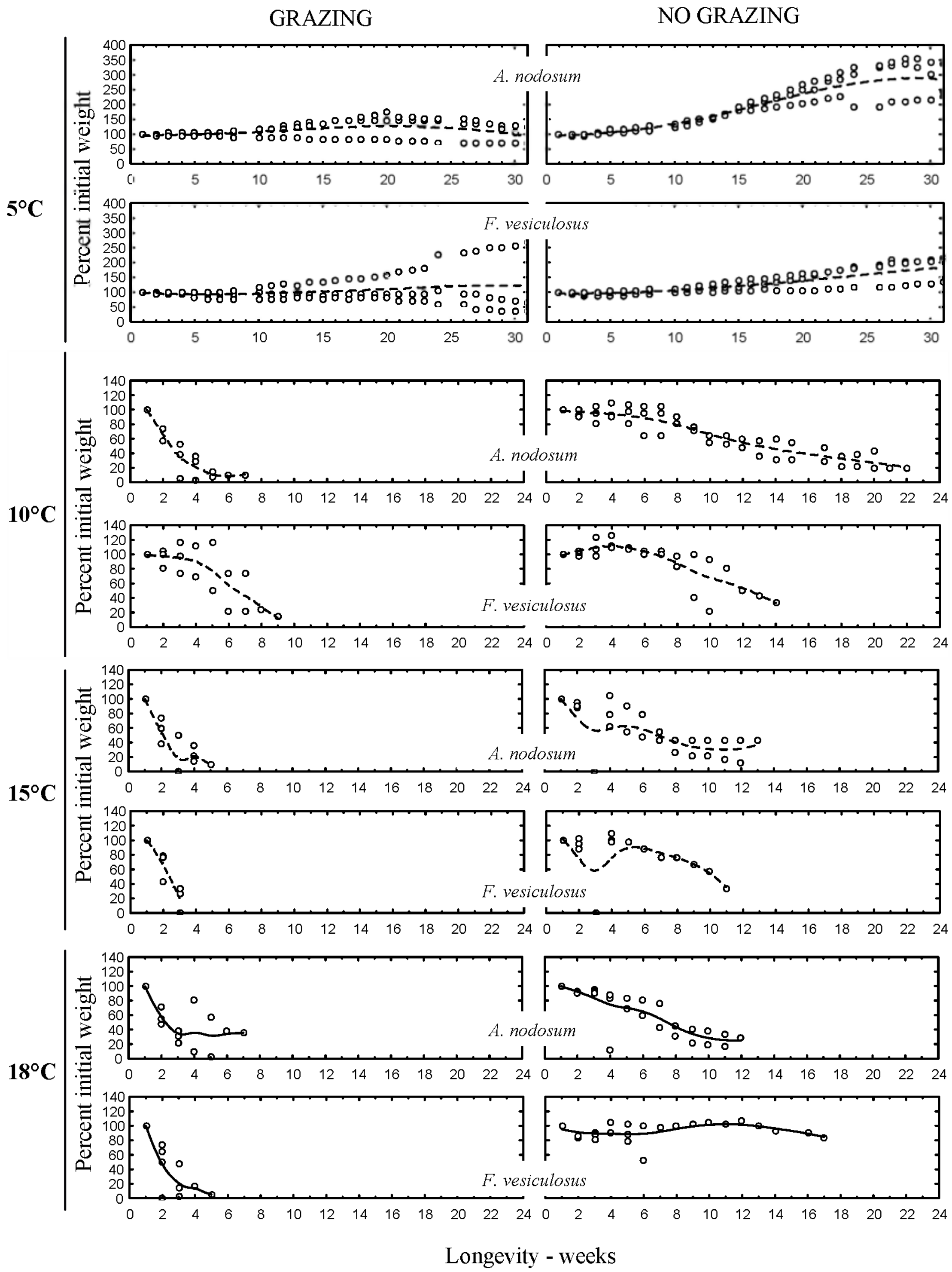


Fig. 3. Scatterplots of percent initial weight as a function of time (weeks) per temperature and per treatment. Trendline = distance weighted least squares

3.2 Experiment 2: influence of clump size

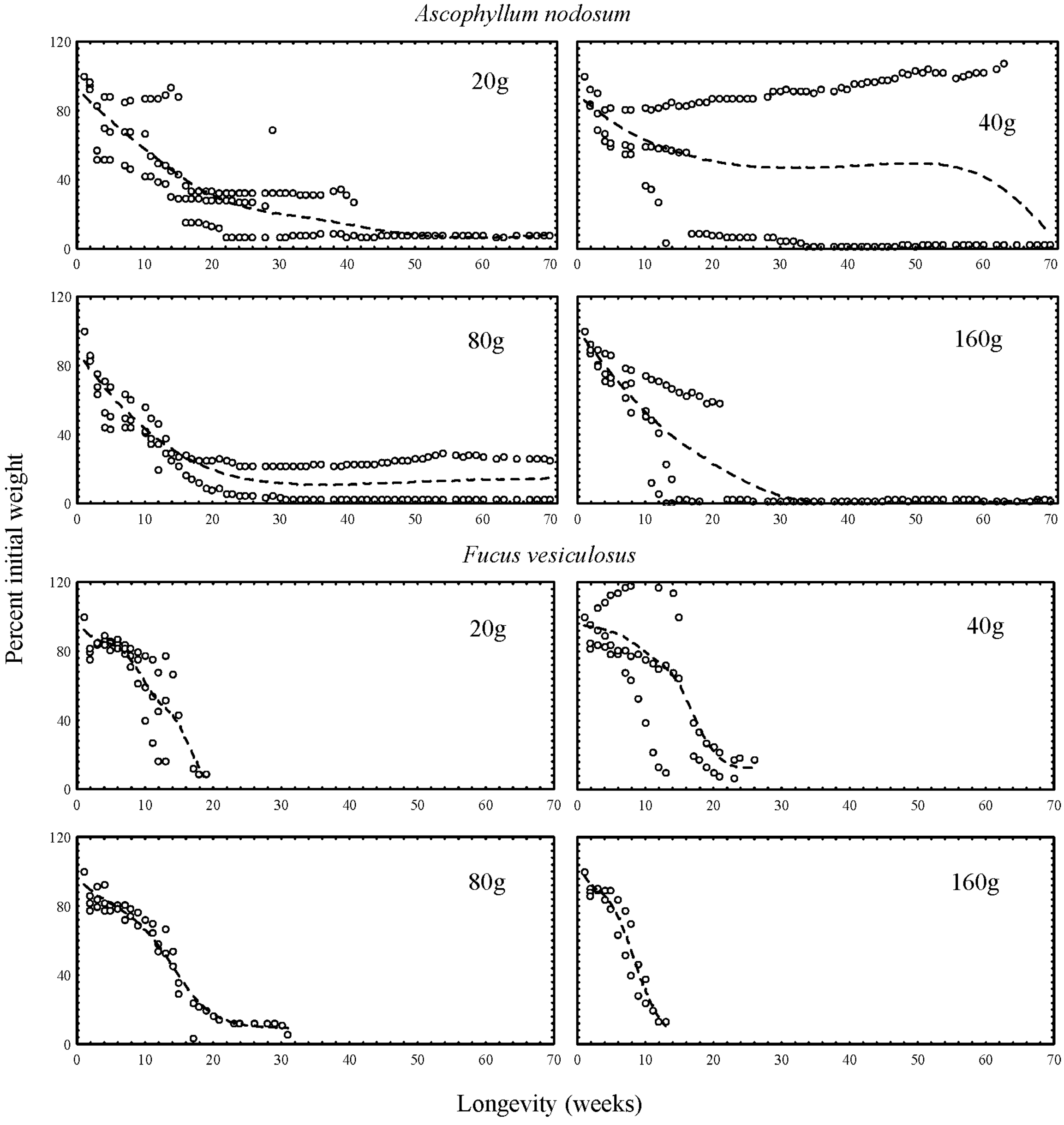
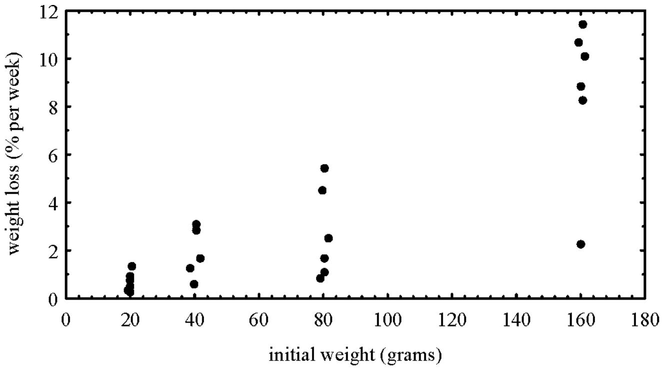


Fig. 4. Scatterplots of percent initial weight as a function of time (weeks) per seaweed species and per treatment (4 initial fragment sizes). Trendline = distance weighted least squares

The effect of seaweed species on floating capacity was significant in this second experiment (2-Way ANOVA $F_1 = 11.06$, $p = 0.005$), while the initial weight of the seaweed fragments was not (2-Way ANOVA $F_3 = 0.49$, $p = 0.41$). Fragments of *Ascophyllum nodosum* stayed afloat for an average of 45 weeks (± 26 weeks), while fragments of *Fucus vesiculosus* stayed at the water surface for an average of only 15 weeks (± 9 weeks) (Figure 4). Apparently, there was no significant correlation between floating capacity and the number of air bladders and reproductive structures for both species (*F. vesiculosus*: Spearman $R = 0.12$, $p = 0.69$; *A. nodosum*: Spearman $R = -0.21$, $p = 0.50$).

The rate of weight loss, however, was strongly influenced by the initial size of the seaweed fragments (Spearman R = 0.84, $p < 0.001$): the 20g fragments decreased with a mean of 0.7% per week; the 40g fragments with 1.6% per week, the 80g fragments with 1.7% per week and the 160g fragments with 8.6% per week (Figure 5). The evolution in weight loss of the fragments, however, was very variable (Fig. 4). In *A. nodosum*, there usually was an initial decrease of weight (all reproductive structures were gone after 2 weeks) after which a lot of the fragments sank or fragmented (signs of decay were obvious after 6 weeks; fragmentation of the remaining fragments was advanced after 12 weeks). Small fragments had the capacity to stay afloat for a long time (up to 70 weeks). Only few fragments showed temporary increases of weight, which was mainly due to the formation of new reproductive structures (between week 40 and 48). Fragments of *F. vesiculosus* quickly showed signs of decay, but fragmentation was less frequent. Just like in *A. nodosum* fragments, temporary increases in weight could be observed due to the formation of shoots (week 16 in 80g fragments) and reproductive structures (from week 19 in two 40g fragments).

Fig. 5. Scatterplot of the rate of weight loss (% per week) as a function of initial weight (grams).



4. DISCUSSION

4.1 Experiments

Rafting is regarded to be an important dispersal mechanism in the marine environment, but its success largely depends on the quality of the floating substrate. Floating seaweeds probably represent the quantitatively most important biotic substrates and they are very well suited for rafting due to their buoyancy (pneumatocysts) and food value (Thiel & Gutow, 2005a). Grazing on the seaweeds themselves allows herbivores to temporarily survive on seaweed rafts, but the presence of (high densities of) a voracious grazer may have detrimental effects on buoyancy and even destroy the raft. This is clearly demonstrated by the study of Gutow (2003) and the results of the present study, in which grazing by the common isopod species *Idotea baltica* shortened the period of buoyancy by 60-70%. While *I. baltica* itself and other mobile rafters may seek new rafts (e.g. in convergence zones), less mobile and sessile rafters will inevitably perish. The degradation speed and grazing activity, however, were strongly influenced by temperature (cf. Paalme et al., 2002): weight loss and subsequent sinking was fastest at higher temperatures (15-18°C), but was substantially slower at lower temperatures. The rate of weight loss was even exceeded by growth at 5°C: seaweed fragments substantially increased in weight. These results agree with the findings of Hobday (2000c) and Salovius and Bonsdorff (2004) that the decomposition rate of floating seaweed rafts is temperature dependent. In the study of Hobday (2000c), observations showed that the aging rate of *Macrocystis* was low below 20°C, but that there was a dramatic increase at higher temperatures. A lower consumption rate in cold conditions also explains the absence of signs of decay on floating *A. nodosum* in Iceland after 40 days (Ingólfsson, 1998), while grazing experiments with *I. baltica* in the North Sea resulted in rapid degradation and weight loss (Gutow, 2003; Vandendriessche et al., 2006b). Contrary to ephemeral seaweed rafts, the permanently floating *Sargassum* has an optimal survival in high water temperatures (Dooley, 1972; Thiel & Gutow, 2005a).

The size of seaweed rafts can vary from a few centimetres (seaweed fragments) to tens of meters (large entanglements of a high number of different plants, e.g. Helmuth et al., 1994). Fell (1967) stated that rafting by brown algae is more significant in the southern hemisphere because kelp species are generally larger there and thus more persistent. The influence of clump size on the persistency of rafts and thus on the period of buoyancy was investigated in the second experiment, which indicated that initial weight of the detached seaweeds does not significantly influence the period of buoyancy. Moreover, larger seaweed fragments lost weight faster than smaller fragments. Rather than being the result of initial fragment size, the higher persistency of large rafts (Fell, 1967) is more likely to result from entanglement of new seaweed fragments that maintain the buoyancy of the raft and provide additional food resources for rafting organisms.

In this experiment, the difference between seaweed species was more important than the differences in fragment size: fragments of *Ascophyllum nodosum* stayed afloat longer (mean 45 weeks) than fragments of *Fucus vesiculosus* (mean 15 weeks). This difference can be explained by differences in the degradation process: *A. nodosum* fragmented quite quickly, after which a large proportion of the smaller fragments sank. The remaining fragments that were equipped with large air bladders were able to stay afloat for a long time and sometimes even formed reproductive structures. These small fragments, however, cannot support the initially high densities of rafters and their importance as rafts for associated fauna probably diminishes dramatically. However, as they are still able to become fertile, these fragments may still promote the dispersal of the seaweed itself (cf. Dayton, 1973; Deysher & Norton, 1982; Macaya et al., 2005). In rafts of *F. vesiculosus*, fragmentation was less frequent and the degradation process quickly affected the air bladders, causing the fragments to sink. In both species, however, the variability in the degradation process was very high: while there was apparent weight loss in most fragments, some fragments did not show any signs of decay and grew substantially. Although all seaweed plants were collected at the same site and at the same time, small variations in age, toughness and size of the bladders may have influenced floating capacity. The fact that the seaweed species had no significant effect on raft longevity in the first experiment may be due to the small size of the used fragments and the substantial effect of grazing.

4.2 Implications for the rafting process

The estimates of floating capacity obtained in the present study (*Ascophyllum nodosum* and *Fucus vesiculosus*) reached a maximum of one year and five months at a constant temperature of 15°C (probably even more at 5°C, but the experiment was stopped after 211 days). Taking into account a mean raft velocity of 0.5 – 1.0 km per hour for floating objects (Thiel & Gutow, 2005a), a seaweed raft has the potential to travel 6180 – 12360 km. However, these estimates are significantly shortened (decrease with 60-70%: 1854 – 4944 km) due to the presence of grazers, which cause the rafts to decrease in size and sink much faster. Furthermore, raft longevity will, in open ocean conditions, even more be shortened due to epibiont load (Dooley, 1972) and fragmentation and loss of buoyancy as a result of wave action (Johnson & Richardson, 1977; Shaffer et al., 1995), effects of dessication and high UV-radiation (Cronin and Hay, 1996), and the occurrence of storms, during which massive amounts of seaweeds sink or wash ashore. The persistence of pelagic rafts in inshore areas also appears to be related to the proximity of surrounding land (Parsons, 1986). The movement of seaweed in a bay, for example, is probably very restricted and the majority of floating seaweeds probably beach shortly after detachment. Consequently, rafting is very likely to be more limited than expected based on floating capacity of the freshly detached seaweeds, and persistence estimates for *A. nodosum* and *F. vesiculosus* of 10 - 12 days (Parsons, 1986 – Canada) to more than 43 days (Ingólfsson, 1998 – Iceland) are probably more realistic. Ideally, the differences between potential and real raft longevity could be investigated using satellite tracking of freshly released rafts (Hobday, 2000a).

Although the results of the present study indicated that the longevity of a raft composed of floating seaweeds is in the order of magnitude of weeks to a few months rather than a year or more, the potential success of rafting via floating seaweeds should not be minimised or dismissed: in a few weeks time, a raft can still travel considerable distances, especially when the raft is caught in strong (tidal) currents or internal waves, or is driven by strong winds (Kingsford & Choat, 1986; Helmuth et al., 1994; Thiel & Gutow, 2005a, Thiel & Haye, 2006). Additionally, low temperatures enhance raft longevity, potentially increasing rafting success in winter conditions and at high latitudes. Finally, not all rafters have a destructive effect on their raft, which was clearly shown for the isopod *Idotea metallica*, a rafter that only minimally feeds on the seaweeds (Gutow, 2003). Hence, many studies provide evidence supporting long-distance dispersal mediated by seaweed rafts, ranging from hundreds of kilometres (e.g. Hobday, 2000c; Macaya et al., 2005) to intercontinental travel (e.g. Yeatman, 1962; Ingólfsson, 1992; Franke et al., 1999).

The increase of raft longevity with decreasing temperatures in the present study strengthens the hypothesis that rafting by organisms on ephemeral floating seaweeds is much more important at higher latitudes (Fell, 1967; Helmuth et al., 1994; Thiel & Gutow, 2005a), at which production and growth of the seaweeds can exceed weight reduction due to grazing, and at which macro-algae are more abundant (compared to the tropics; Highsmith, 1985). Although long-distance rafting by means of seaweeds is less probable at lower latitudes, the dispersal of rafting fauna and flora has probably increased dramatically in the last decades due to the increase of long-lived man made rafts (e.g. plastic, tar balls, rubber), which are not prone to grazing and which are less sensitive to temperature and UV-radiation mediated decay (e.g. Aliani & Molcard, 2003; Thiel et al., 2003; Barnes & Milner, 2005). Man-made flotsam carrying persistent colonisers has even been reported from the Southern Ocean and the Arctic (Barnes & Fraser, 2003; Barnes & Milner, 2005), and is very likely altering the process of marine rafting in terms of increased opportunities for rafting and shifts in rafting species (Winston, 1982; Thiel & Haye, 2006).

4.3 Conclusion

Floating seaweeds can, at low temperatures, continue to grow during their journey and constitute a continuously replenished food source for some rafting animals. However, the presence of high densities of grazing organisms substantially contributes to the destruction of the rafts. Consequently, the period in which a raft can support a rafting community (including grazers) is shorter than expected based on the estimation of the floating capacity of fresh seaweed fragments. The temperature-dependency of degradation and grazing activity implies that long-distance dispersal by means of rafting on floating seaweeds has the highest chances of success at higher latitudes.

ACKNOWLEDGEMENTS

The first author acknowledges a specialisation grant from the 'Institute for the Promotion of Innovation through Science and Technology in Flanders' (IWT). The authors would like to thank Sofie Derycke and Carl Van Colen for providing the fresh seaweed, and Jelle Evenepoel, Annick Van Kenhove and Danny Peelaers for their assistance with the experiments. Dr. G. Van Hoey and Dr. I. De Mesel are acknowledged for their useful suggestions and comments.

CHAPTER 8

GENERAL DISCUSSION AND PERSPECTIVES FOR FUTURE RESEARCH

Floating *Fucus vesiculosus*

1. GENERAL DISCUSSION

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. The thesis dealt with different aspects of raft ecology and, based on their key issues, can roughly be divided in three main parts being (1) a part describing the effects of seaweed presence in the neuston and the structural variation within floating seaweed-associated fauna in chapters 2-4; (2) a part describing the importance of floating seaweeds and their associated fauna for higher trophic levels i.e. birds and fishes in chapters 5-6; and (3) a part examining the potential of floating seaweeds as rafts mediating long-distance dispersal of associated fauna in chapter 7.

1.1 Floating seaweeds and the structural variation within the associated fauna

The encounter rate of floating seaweeds along the Belgian coast

Ephemeral clumps of detached coastal seaweeds are frequently encountered along the Belgian coast. Based on the sampling data, a rough estimate of the encounter rate of floating seaweeds can be made (Fig. 1). During the sampling period for the present study, floating seaweeds were found on few occasions in autumn and winter, usually following a storm. The encounter rate increased in spring and peaked in summer, in which up to four seaweed aggregations could be encountered per sampling day (on average 60 nautical miles sailed per sampling day). The number of individual seaweed clumps per encounter varied enormously (from one to hundreds of clumps of different sizes). Because the research vessel was stopped at almost every encounter, the amount of floating seaweeds could not be quantified in a standardised way.

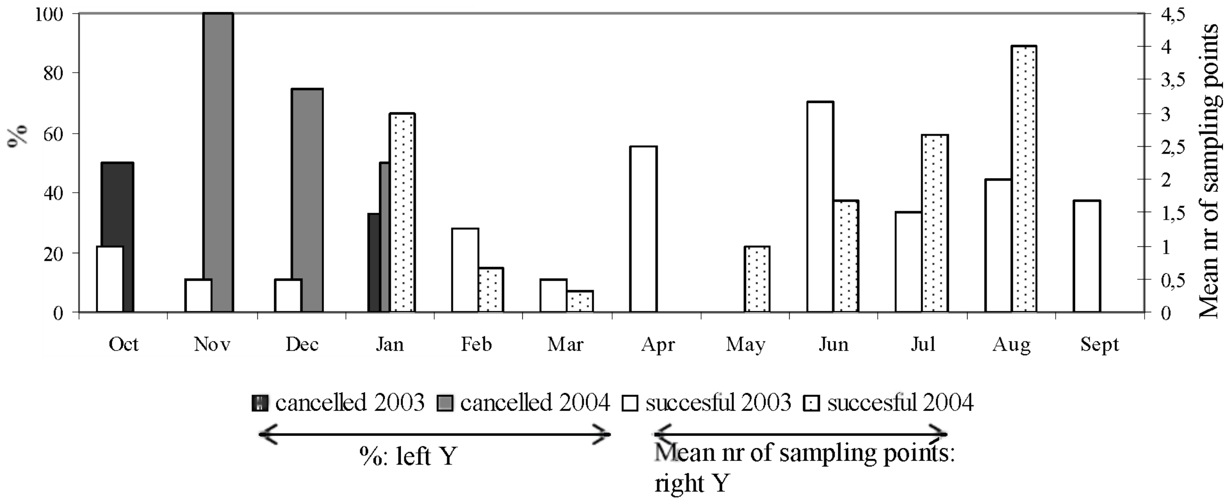


Fig.1. Column chart showing the percentage of unsuccesful samplings (left Y) and the mean number of sampling points for the successful samplings (right Y) for the years 2003 and 2004.

Furthermore, the ship trajectory was designed for a maximal chance of seaweed encounters by sailing (as much as possible) perpendicular to the prevailing water currents. The only way to obtain reliable estimates of floating seaweed abundance (e.g. kg/km²) is by performing transect counts in a predefined grid, thereby recording position, size, seaweed species and distance from the research vessel (see perspectives for future research). Alternatively, estimates could be made from an airplane, but in that case, clump size and seaweed species are harder to assess (personal obs.).

The added value of floating seaweed in the neustonic environment

The presence of floating seaweeds on the sea surface has an important impact on the species composition, abundance and diversity of the neustonic fauna. Not only do floating seaweeds carry littoral fauna that stayed associated after detachment, they also attract fauna from the surrounding and underlying water column due to the provision of shelter, a food source, surface for attachment and a means of passive long distance dispersal (Tully & O'Ceidigh, 1986; Ingólfsson, 1995, 1998, 2000; Ólafsson et al, 2001; Thiel & Gutow, 2005a, b). This process of continuous colonisation results in substantial increases in diversity, density and biomass of the surface layer fauna (Kingsford & Choat, 1985; Druce & Kingsford, 1995, Vandendriessche et al, 2006a). In the case study conducted in the Belgian coastal zone (chapter 2), diversity, density and biomass of seaweed-associated fauna were, respectively, 3, 18 and 49 times higher compared to the surrounding water column. These high values were mainly due to the abundant presence of large, mobile fauna (> 1mm, e.g. *Idotea baltica* and *Gammarus* sp.), which were termed seaweed fauna because they were found significantly more in seaweed samples than in the surrounding water column. The composition, abundance and biomass of smaller organisms (0.5 – 1 mm; e.g. Calanoida sp. and larval polychaetes) were similar to those of the surrounding water column; these fauna were termed background neustonic fauna. The success of large fauna colonising ephemeral floating seaweed patches is probably due to the lack of endemic neustonic species utilising the habitat (Locke & Corey, 1989), which is caused by its instability and patchiness.

Although the effect of the presence of floating seaweeds in the neuston dominated all other effects in the analyses of chapter 2, the community structure already revealed possible influences of spatial and temporal variation. The sources of variation within the seaweed-associated invertebrate community were closely investigated in chapters 3 and 4 (the variation within the fish community was dealt with separately, see chapter 5 and the following section). The results of both chapters and other studies described in literature showed that floating seaweed clumps are complex systems, in which the species assemblages are influenced by a wide range of factors.

Seaweed preference and the opportunistic nature of fauna associated with floating seaweeds

On a small spatial and temporal scale (chapter 3), the volume and the seaweed species composition of the clumps turned out to be main sources of variation: (1) volume had a negative effect on density and a positive effect on diversity; (2) increasing relative abundances (%) of *Fucus vesiculosus* and *Ascophyllum nodosum* had a positive effect on diversity and a negative effect on density, while it was the other way round for *Sargassum muticum*, and (3) the effect of an increasing rest fraction (positive for diversity, negative for density) was similar to the effect of *F. vesiculosus* and *A. nodosum*.

The effect of clump volume, however, was clearly species - dependent, which may explain varying hypotheses concerning the effects of clump volume in other studies. Some authors have found positive relationships between the abundance of associated fauna and clump size (Fine, 1970; Stoner & Greening, 1984; Kingsford & Choat, 1985; Safran & Omori, 1990; Kingsford 1992; Druce & Kingsford, 1995; Ingólfsson, 1995 & 1998; Ólafsson et al, 2001), which may be due to greater protection from predators in larger clumps, reduced danger of dropping off the clumps, a higher food supply compared to the surrounding water column and more surface for attachment. In Highsmith (1985) and Vandendriessche et al (2006b; chapter 3), only few macrofaunal species were found to show such a correlation and therefore it is likely that correlations vary greatly depending on the origin of the seaweeds and the association degree and behaviour of the associated species. A positive correlation between species richness and clump size was not found in Fine (1970), but was found to be significant in Ingólfsson (1995 & 1998), Hobday (2000b), Ólafsson et al (2001) and Vandendriessche et al (2006b; chapter 3).

The importance of the seaweed species composition found in the community analysis of chapter 3, agrees with the results of Ingólfsson and Ólafsson (1997), which showed that the harpacticoid copepod *Parathalestris croni* had a preference for *A. nodosum* and its epiphyte *Polysiphonia lanosa*. Based on the importance of the seaweed species composition in the field data analysed in chapter 3, multiple-choice experiments were designed to further investigate the mechanisms by which the seaweed species composition influenced the macrofaunal composition (habitat and food choice of *Idotea baltica* and *Gammarus crinicornis*). Seaweed preference was also apparent from the results of these experiments, but did not exactly match the preferences observed in the field. The experiments, however, did show that preference for habitat (shelter) and food can differ among seaweed species and that the preference for a certain seaweed species is influenced by the offered choices, the presence of other grazers and predators (see also Schaffelke et al, 1995; Pavia et al, 1999; Jormalainen et al, 2001; Goecker & Kåll, 2003; Orav-Kotta & Kotta, 2004; Svensson et al, 2004). In general, the underlying causes for habitat choice in grazers are believed to be algal morphology (e.g. Nicotri, 1980) and colour (Salemaa, 1987), whereas the food choice is mainly determined by nutritional value of the available seaweed species (Boström & Mattila, 1999; Pavia et al, 1999). In the case of fauna associated with floating seaweeds, however, the effects of seaweed species composition may be blurred due to the obligate opportunistic nature of a lot of the associated macrofaunal species. The survival of some of these species depends on the food, shelter and attachment space offered by the seaweeds. The seaweed-associated fauna therefore takes advantage of the presence of all alternative habitats in the neustonic environment, regardless of the seaweed composition. Eventually, only species/individuals with a good swimming ability (e.g. *I. baltica, G. crinicornis*) can move to a clump with more favourable conditions (higher nutritional value or more shelter) whenever such clumps are available. The availability of the preferred seaweeds is in turn highly dependent on seasonal factors, such as fragmentation at the end of the growing season, variation in the amount of grazing damage and the occurrence of storms (Thiel & Gutow, 2005a). In short, the transient and relatively unpredictable nature of floating seaweed clumps (and their constituent species) is believed to induce an opportunistic behaviour in the associated fauna ensuring their survival but obscuring their food and/or habitat preferences.

The complexity of the habitat formed by floating seaweeds

In a more comprehensive study (chapter 4), the seaweed species composition of the clumps (especially the relative abundance of *Fucus vesiculosus* and *F. spiralis*) again appeared to be an important structuring factor within the associated invertebrate community. However, spatial and especially seasonal variation had a more important impact. At the Belgian coast, invertebrate densities generally increased after winter to peak in spring (near shore samples) and summer (off shore samples). These results agree with numerous other studies, in which densities of associated fauna appeared highly seasonal and related to geographic region, distance to shore or the nearest seaweed bank (Fine, 1970; Stoner & Greening, 1984; Kingsford, 1992; Kingsford & Choat, 1985; Tully & O'Ceidigh, 1986; Ingólfsson, 1995; Ingólfsson & Ólafsson, 1997, Dempster & Kingsford, 2004; Ohta & Tachihara, 2004; Wells & Rooker, 2004; Salovius et al, 2005). Although the results of the analysis in chapter 4 clearly indicate the importance of variations related to geographical position, season and seaweed species composition, they also show that these factors explain only part of the variation (± 26%).

One factor that could account for another part of the variation is the age of the seaweed clumps, and consequently also the distance travelled. This factor is a reflection of the process of succession during the voyage of floating seaweed clumps after the event of detachment (Stoner & Greening, 1984; Ólafsson et al, 2001, Thiel & Gutow, 2005b). During the drift, the seaweeds and their associated epiphytes and fauna change markedly, altering the living conditions for other colonisers (Edgar, 1987; Ingólfsson & Olafsson, 1997, Thiel, 2003). In the present study, however, different age groups (based on colour and epiphyte load of the dominant seaweeds) only showed minor differences concerning invertebrate composition, which was to be expected as most clumps were composed of more than two algal species. Because seaweed clumps often converge or break up, the constituting seaweeds of a clump may have different ages and origins, so age of the seaweeds may differ even within clumps (Ingólfsson, 1998). Although age and origin of a clump are, in most cases, hard to assess, they may still be of great importance to colonising invertebrates, especially to herbivores feeding on epiphytes and on the seaweeds themselves (e.g. Stoner & Greening, 1984; Cronin & Hay, 1996). The only reliable clue to the age of the seaweed clumps in the present study is the invertebrate species composition: the presence of only few littoral species (e.g. *Mytilus edulis, Tergipes tergipes*) and the abundant presence of new, reproducing colonisers (e.g. *Idotea baltica, Gammarus crinicornis / G. locusta*) indicate that most of the clumps were in an advanced successional stage and had already been floating around for a long time (Ingólfsson, 1995; Thiel, 2003; Thiel & Gutow, 2005b).

The remainder of the variation in invertebrate species composition is probably due to coincidental events occurring during the journey of the floating seaweed clumps, like beaching and subsequent resuspension, convergence with and exchange between other clumps, and disturbance (e.g. storms, passing ships).

1.2 Floating seaweeds, birds and fishes

The varying intensity of association with floating seaweeds in juvenile fishes

Within the quite uniform neustonic environment, floating objects are important sources of small-scale patchiness that significantly influence the faunal species composition of the neuston, which was clearly shown for invertebrates in chapters 2-4. However, these effects also apply to a wide variety of fish taxa (especially juveniles – chapter 5) which have a natural tendency to aggregate beneath or associate with floating structures, including floating seaweeds (e.g. Safran & Omori, 1990; Davenport & Rees, 1993; Moser et al, 1998, Masuda & Tsukamoto, 2000; Castro et al, 2001; Jaquemet, 2004; Thiel & Gutow, 2005 a, b). The fish classifications proposed by Hirosaki, (1960 - in Thiel & Gutow, 2005b), Gooding and Magnuson (1967), Dooley (1972) and Castro et al (2001), which are based on the closeness of the association between fishes and a floating object, indicate that the response to and dependency on floating seaweeds is species specific. Furthermore, several hypotheses about the motivations of fishes to associate with floating structures have been proposed (reviewed in Castro et al, 2001), including the benefits of living in the shade in relation to predators and detection of prey (Kingsford, 1992), the presence of abundant food sources like smaller fish, associated macrofauna or the seaweed itself (Safran & Omori, 1990; Davenport & Rees, 1993; Wright, 1989), the shelter from piscivorous fish and birds (Wright, 1989; Kokita & Omori, 1998), the potential for passive transport (Dooley, 1972), the meeting point function for the formation and maintenance of schools or for spawning (Masuda & Tsukamoto, 2000), the substitution of the seabed for non-pelagic fish, and the function of floating objects as cleaning stations (Gooding & Magnuson, 1967). In the study described in chapter 5, the dependency and motives for association were investigated for five fish species (*Cyclopterus lumpus, Trachurus trachurus, Ciliata mustela, Chelon labrosus, Syngnathus rostellatus*) found in floating seaweeds along the Belgian coast.

The analysis of the fish species composition confirmed the patterns observed for associated invertebrates (chapters 2-4): the presence of floating seaweeds in the neuston influences the species composition of the fauna, and the seasonal variation is of great importance, but only part of the biotic structure can be explained by the measurable variables.

Differences in the diets and the shapes of the length-frequency distributions clearly reflect the varying intensity of resource utilisation in floating seaweeds by the different fish species. The absence of juvenile lumpsuckers (*C. lumpus*) outside floating seaweed patches and the composition of their diet (mainly seaweed-associated macro-invertebrates, especially in the larger size classes) confirm that postlarval and juvenile lumpsuckers are predators specialised on floating seaweed patches in the Northeast Atlantic (Davenport & Rees, 1993; Ingólfsson & Kristjánsson, 2002). *Ciliata mustela, Trachurus trachurus, Chelon labrosus* and *Syngnathus rostellatus* were found in both seaweed samples and neuston samples, so their association with floating seaweeds is of a more opportunistic nature. Juveniles of *Ciliata mustela* clearly feed on the buffet of associated macro-invertebrates and the length distribution data suggest that their growth is enhanced compared to neustonic conspecifics. The advantages for *T. trachurus* and *C. labrosus* do not seem to be of similar importance: these species predominantly feed on planktonic prey, presumably in deeper layers (Hempel & Weikert, 1972) and there is no evidence of enhanced growth. Still, these species may benefit from association with floating objects for reasons other than prey availability: both species are schooling and may use floating objects as shelters, meeting points or transports to enriched convergence zones, surface slicks or near shore habitats (Kingsford & Choat, 1985; Kingsford, 1992; Shanks, 2000; Castro et al, 2001; Thiel & Gutow, 2005b). Postlarval *Syngnathus rostellatus* largely depend on floating seaweeds for their survival in the neustonic layer. Young individuals and adults of this demersal species are probably carried with the seaweed after detachment from the substrate, and stay within the seaweed branches to ensure protection from predators.

The results of the present study in the North Sea confirm the general importance, although species specific, of floating objects for the survival and development for a wide variety of fish species. Therefore, I consider a thorough knowledge about the implications of association behaviour to be very important with regard to fisheries ecology, and recommend a more detailed investigation in the North Sea (see perspectives for future research).

The feeding mode-dependent use of floating seaweeds by seabirds

Although they are ephemeral and transient, floating seaweeds generally carry a wide variety and large densities of associated fauna, ranging from small planktonic crustaceans to juvenile fishes (chapters 2-5). 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. This hypothesis was tested using the North Sea data, and more precisely the association coding system of the European Seabirds at Sea database (ESAS).

Analysis of the relative frequency of occurrence data indicated that several species of seabirds are indeed attracted to floating seaweed patches and that the degree of association of seabirds with these floating seaweeds is feeding-mode dependent. Generally, seabirds with the greatest affinities for floating seaweeds are surface-feeding and plunge diving species (cf. Haney 1986), in the present study illustrated by the high relative frequency of occurrence of red-breasted mergansers (*Mergus serrator*) and terns (*Sterna* sp.). The feeding behaviour of the common tern *Sterna hirundo* even showed a shift from actively searching, pursuit diving or scavenging to surface pecking and dipping in the vicinity of floating seaweeds, indicating that this species feeds on the invertebrates and/or small fishes that are associated with the seaweeds.

Given the seasonal and ephemeral character of seaweed patches in the study area (contrary to the permanently floating *Sargassum*), the seaweed-associated fauna can only be exploited in an opportunistic way. Still, they can temporarily constitute an important and predictable source of extra food, or indicate the presence of suitable feeding areas since floating seaweeds tend to accumulate in biologically rich waters (Arcos et al. 2000). In other studies, mainly concerning *Sargassum* patches, some tern and phalarope species were often found roosting on the semi-solid surface, probably allowing them to conserve energy while they are not foraging (Haney 1986, pers. obs.), but such behaviour was not described in the study area. Consequently, the small-scale patchiness in seabird distribution induced by floating seaweeds in the North Sea is believed to be the result of the increased structural complexity and food supply in ephemeral floating seaweed patches, which may enhance foraging conditions for some seabird species depending on their preferred prey and foraging strategy.

1.3 Floating seaweeds as rafts

Reduced longevity of seaweed rafts due to grazing and high temperatures

From the introduction (chapter 1) and discussion in chapter 7, it should be clear that the study of the rafting process is associated with a lot of IFs: rafting can be successful IF long-living rafts are available, IF rafting fauna can survive during transportation and arrival, and IF they are able to establish new populations and successfully interact with local populations (Thiel & Gutow, 2005b). To elucidate a part of the first conditional factor (longevity), the experiments discussed in chapter 7 were designed to provide quantitative data about the longevity of floating seaweed rafts and the effects of temperature, grazing and clump size. The results indicated that floating seaweeds of the species *Fucus vesiculosus* and *Ascophyllum nodosum* have the potential to stay afloat for more than a year and, at a mean raft velocity of 0.5 – 1.0 km per hour (Thiel & Gutow, 2005a), can travel thousands of kilometres. However, they are not able to maintain a rafting community consisting of grazers that intensively feed on the raft itself: at high densities of the grazer *Idotea baltica*, the raft longevity decreased with 60-70% in the present study (see also Gutow, 2003). The rate of weight loss due to grazing and decomposition was especially high at higher temperatures (>15°C), while a viable raft could be maintained at 5°C, even in the presence of destructive grazers. On top of the clearly negative effects of grazing and increased temperatures, raft longevity is probably significantly reduced as a result of epibiont load (Dooley, 1972), fragmentation and loss of buoyancy as a result of wave action (Johnson & Richardson, 1977; Shaffer et al, 1995), effects of dessication and high UV-radiation (Cronin & Hay, 1996), and the occurrence of storms, during which massive amounts of seaweeds are sunken or washed ashore. Consequently, rafting is very likely to be more limited than expected based on floating capacity of the freshly detached seaweeds, and persistence estimates for *A. nodosum* and *F. vesiculosus* of 10 - 12 days (Parsons, 1986 – Canada), more than 43 days (Ingólfsson, 1998 – Iceland) and 77 – 412 days (present study, only considering effects of temperature and grazing) are probably more realistic.

Still, the potential success of long-distance dispersal via floating seaweeds should not be minimised or dismissed. In a few weeks time, a raft can travel considerable distances, especially when the raft is caught in strong (tidal) currents or internal waves, or is driven by strong winds (Kingsford & Choat, 1986; Helmuth et al, 1994; Thiel & Gutow, 2005a, Thiel & Haye, 2006). Additionally, low temperatures enhance raft longevity, potentially increasing rafting success in winter conditions and at high latitudes. Furthermore, raft longevity can substantially increase when 'young' seaweed fragments merge with 'older' rafts, thereby contributing to the buoyancy and providing new food sources for the associated fauna (Fell, 1967). Finally, not all rafters have a destructive effect on their raft, which was clearly shown for the isopod *Idotea metallica*, a rafter that only minimally feeds on the seaweeds (Gutow, 2003).

Many studies provide (circumstantial) evidence supporting the possibility of long-distance dispersal mediated by seaweed rafts, ranging from hundreds of kilometres (e.g. Hobday, 2000c; Macaya et al, 2005) to intercontinental travel (e.g. Yeatman, 1962; Ingólfsson, 1992; Franke et al, 1999). So, although more information on the conditions for successful rafting is needed (see research outlook and Thiel & Haye, 2006), long-distance algal rafting is a process that seems to work on a geological time scale. Furthermore, frequent rafting on ephemeral seaweed patches can have significant effects on the population connectivity within regions (estuaries, lagoons, bays – Thiel & Haye, 2006).

The threats of man-made floating objects

Up till now, this discussion was limited to rafts composed of buoyant seaweeds. There are however, numerous other natural substrates that are able to carry adapted rafters to potential new habitats: pumice, wooden logs and sea grass leaves to name a few (Jokiel, 1989, Wehrtmann & Dittel, 1990, Thiel & Gutow, 2005a). Together with floating seaweeds, they offer uncountable rafting possibilities, albeit restricted by food value and buoyancy, and consequently enhance the chances of the introduction of non-native species in distant habitats. Up to this point, the introduction of new species can still be regarded as a natural process. However, as already pointed out in chapter 7, man-made debris (mainly plastic) is abundantly available these days and has the potential to stay adrift for years. Consequently, the possibilities for rafting has dramatically increased for some species (e.g.

bryozoans; Winston, 1982), especially in areas where natural floating substrates are less abundant (Barnes, 2002). Therefore, the supply of plastic, nylon and other persistent substances to the marine environment should, next to shipping and aquaculture (e.g. Reise et al, 1999; Gollasch, 2006), be considered as a threat with regard to the introduction of non-native and possibly even invasive species.

Another threat of man-made debris in the marine environment, and more specifically in the neuston, is the ingestion of or entanglement in these items. In chapter 6, it was indicated that many bird species are attracted to features on the sea surface because of the possible concentrations of prey items in their vicinity. This attraction may be fatal when seabirds land on the sea surface and get entangled in discarded nylon fishing nets or if they ingest floating tar balls or pieces of plastic (Dunnet et al, 1990; Tasker et al, 2000). During the sampling campaigns for this PhD study, it became clear that floating man-made debris is a major problem at the Belgian coast: 21% of the analysed seaweed clumps contained substances like plastic, nylon, cardboard, rubber, rope, tar or synthetic ribbon. On a few occasions, entangled carcasses of guillemots (*Uria aalge*) were encountered in seaweed clumps containing nylon remains of fishing nets. Even rafting invertebrates are negatively affected by floating plastic and tar. Figure 2, for example, shows idoteid isopods stuck to the surface of tar balls. From these examples, it should be clear that floating marine debris does not consist of harmless substances that eventually wash ashore and can be cleaned up by machines, but that they influence the dispersal and survival of many marine organisms. This is one more reason to strive for the reduction of the input of abiotic garbage in the marine environment.

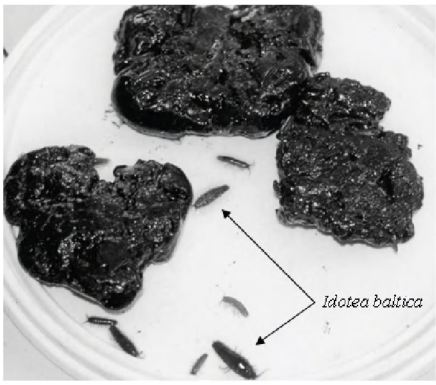


Fig. 2. Tar recovered from clumps of floating seaweed, with numerous isopods stuck to the surface (Belgian coast, September 2003).

1.4 General conclusion

As a general conclusion of this PhD study, it can be stated 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, an endemic fauna like the one associated with the pelagic *Sargassum* species cannot be found in the North Sea. Most species found in association with ephemeral floating seaweed patches are opportunistic of nature, and profit of any increase of structural complexity in the neustonic layer, regardless of its nature. Of course, 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 an increased survival and growth of young fishes, and 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 (> 1000 km in a few months time, based on the estimates in the present study), carrying with them rafting fauna that are able to survive a long journey in the neuston.

2. PERSPECTIVES FOR FUTURE RESEARCH

The results presented in this PhD-study provide new and detailed information about the importance of floating seaweeds in the neustonic environment, about the lives and habits of the associated fauna and their predators, and about the possibilities of associated fauna to colonise new habitats by means of rafting. However, a number of questions remain unaddressed and during the processing of the samples and the subsequent research, new questions have arisen. The purpose of this research outlook is therefore to make suggestions for future research topics that rank high on my priority list.

1. The importance of seaweed within the neuston

The analysis of neustonic samples in the present PhD-study was designed to provide data about the importance of floating seaweeds for neustonic fishes (chapter 5). However, a lot of basic information about the neuston in the Belgian coastal zone is still lacking. In the present study, for example, the sampling depth of the neuston was predefined to 0.5m in order to compare with seaweed samples. Unfortunately, this approach did not allow evaluating population distributions within the water column compared to sub-surface layers, as was recommended in Hempel & Weikert, (1972) and Marshall and Burchardt (2005). Furthermore, variations in the depth of the neustonic layer resulting from diel variation, and seasonal and other factors were not taken into account and merit a more detailed study.

The results of chapter 2 clearly show that floating seaweeds increase the complexity of the surface layer of the sea and consequently alter the species composition and richness of the neuston. However, the assessment of their ecological value is incomplete without data about the abundance of floating seaweeds, which are usually obtained by transect counts recording position, size, seaweed species and distance from the research vessel (e.g. Kingsford & Choat, 1985; Hinojosa et al, 2005). Density data of seaweed rafts, together with satellite tracking of seaweed clumps in the English

Channel would also allow estimations of the chances of successful transit from the Atlantic Ocean to the North Sea.

2. Fish associated with floating seaweeds and other floating objects

The results of chapter 5 about the attractiveness of floating seaweeds to fishes indicate that there are several fish species that use floating seaweeds either as feeding grounds, substrates for attachment, hiding places or meeting points. One of the hypotheses addressed in the discussion was that some fish species grew faster in association with floating seaweeds, when compared to their neustonic conspecifics. Unfortunately, the data were insufficient to confirm that hypothesis. One of the suggestions is therefore to conduct a detailed cohort-analysis with subsequent age-estimations of a limited number of fish species.

Another suggestion relates to the sampling techniques in the conducted neustonic- and seaweed surveys: although the neuston net and dip net are believed to be the most suitable devices for adequately sampling juvenile neustonic and seaweed-associated fishes, I believe that larger (predatory) fishes were missed. In order to gain more information about fishes that are more loosely associated with floating seaweeds, it would be interesting to analyse underwater footage containing recordings of the underside and close vicinity of a seaweed patch. Very interesting results based on video imagery were already obtained with respect to fishes associated with pelagic *Sargassum* by Moser et al (1998).

The effects of floating objects with regard to fishes are not limited to floating seaweeds, but also (partly) apply to buoys, fish farms and other man-made structures (e.g. Gooding & Magnuson, 1967; Castro et al, 2001; Deudero, 2001; Nelson, 2003; Dempster & Kingsford, 2004; Dempster, 2005; Dempster et al, 2005). Because the presence of floating seaweed is quite unpredictable in space and time, man-made objects are excellent alternatives to study the behaviour of neustonic fishes (e.g. interspecific trophic relationships) in relation to surface structures (see Druce & Kingsford, 1995). At the Belgian coast, a possible study site could be the recently developed *Mytilus edulis* cultures at Nieuwpoort.

3. Birds and floating seaweeds

The use of association codes in a database with standardised recordings of seabirds is an excellent means of examining associations between seabirds and floating objects. However, in the database (ESAS) used for the analyses in chapter 6, detailed association codes were only recorded in < 1% of all records. Because the coding system was not always used at the same level of detail, a quantitative analysis of the importance of floating seaweeds was biased. Consequently, the results from the analyses did not give reliable estimates of real seaweed-associated seabird densities. In order to obtain the necessary data, a quantitative study (limited in time and space) of seabird association should be conducted, thereby making detailed records of seabird behaviour, distance to the shore and the size and composition of the seaweed patches. Furthermore, the term 'association' should be better defined depending on the closeness of the association of seabird species with floating seaweeds (e.g. feeding within a range of 10m of the seaweeds or resting on the seaweeds). Defining the term 'association' for seabirds could be based on the classification systems already existing for associated fishes (Gooding & Magnuson, 1967; Dooley, 1972; Castro et al, 2001).

4. Rafting-mediated dispersal

Although the process of algal rafting is a central theme in the present doctoral dissertation, the presented results only give more information about the value and potential of floating seaweeds as oceanic rafts. However, even if a raft is suitable to support a diverse rafting community, rafting can only be successful if the rafting organisms are able to establish persistent new populations upon arrival in new habitats (Thiel & Gutow, 2005b). An excellent tool to study connectivity, dispersal directions and relationships between and within populations is molecular analysis. Real proof of rafting can be expected if both rafting and coastal specimens were to be included in the same molecular analysis (Thiel & Haye, 2006). Based on the work of Wares (2001), it can be assumed that the isopod *Idotea baltica* is a suitable subject for analysis of population connectivity through rafting. Another possible approach to study the arrival of rafting fauna is by describing the beaching process of floating seaweed clumps, which can be achieved by sampling floating seaweeds in a transect from the beach to coastal waters.

The results of chapter 7 and the findings of other recent studies (e.g. Aliani & Molcard, 2003; Barnes & Fraser, 2003; Thiel et al, 2003; Barnes & Milner, 2005) indicate that the increased input of rubbish in the marine environment has induced changes (rafting fauna, frequency of rafting, rafting success) in the rafting process. Therefore, it appears necessary to pay special attention to anthropogenic floating substrata in the North Sea. One question to be tackled is: 'Are there differences in species composition in rafts when comparing natural and man-made rafts?'

ADDENDUM

JUVENILE *HIPPOCAMPUS GUTTULATUS* FROM A NEUSTON TOW AT THE FRENCH-BELGIAN BORDER

Juvenile long-snouted seahorse

Paper published

Vandendriessche S., Messiaen M., Vincx M., Degraer S.

Juvenile *Hippocampus guttulatus* from a neuston tow at the French-Belgian border

Belgian Journal of Zoology 135(1): 101-102

SHORT NOTE

The long-snouted seahorse *Hippocampus guttulatus* Cuvier, 1829 occurs mostly in shallow inshore waters among algae and eel grass (*Zostera* or *Posidonia*) and also in littoral lagoons (Lelong, 1995). The species can be found in the Eastern Atlantic from the British Isles to Morocco, including the Canary Islands, Madeira and the Azores (Lourie et al, 1999). The presence of the long-snouted seahorse in Belgian waters was already suspected (see CITES appendix II) but never confirmed. *Hippocampus ramulosus* Leach, 1814 is regarded as an invalid synonym of this species, although this name is still widely used for what is now *H. guttulatus* (Lourie et al, 1999).

The sampling station where *Hippocampus guttulatus* was found is situated between the sandbanks Buiten Ratel en Oost Dyck (UTM 5674450 - 460236.7), on the French-Belgian border (Fig. 1). This station was investigated during a sampling campaign on August 20th (2003) with the research vessel 'Zeeleeuw'. The sample was taken with a rectangular neuston net (2m x 1m, 1mm mesh) from which only the lower 50cm is immersed, thereby sampling the upper 50cm of the water column. Identifications of the specimens, which were preserved in a 10% formaldehyde-seawater solution, are based on characteristics described by Lourie et al (1999).

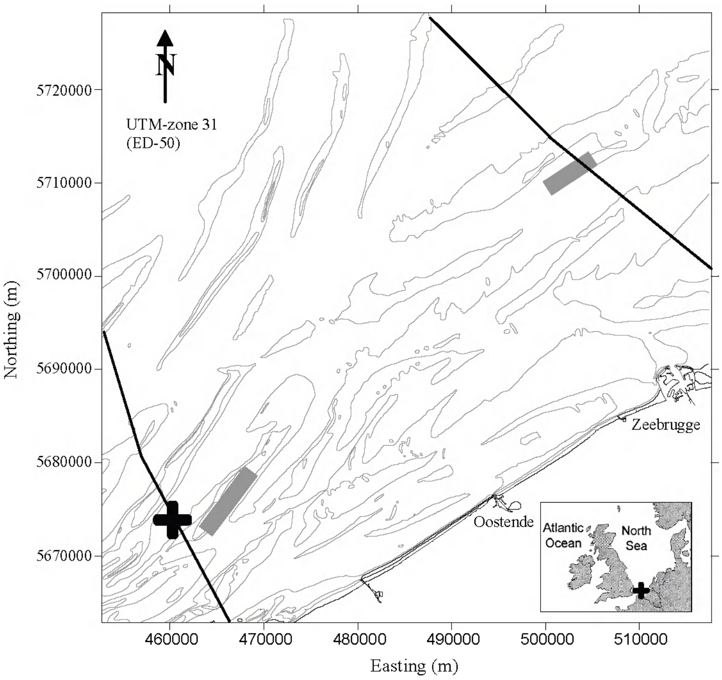


Fig. 1. - Sampling station *Hippocampus guttulatus* (black cross) and fishermen's catches of *Hippocampus hippocampus* (grey areas) in Belgian marine waters (border represented by black lines)

The neuston sample contained two well-preserved juveniles (approximately 3 to 4 weeks old) of the species *Hippocampus guttulatus.* Most of the examined characteristics (Table 1) are within the range for both *Hippocampus guttulatus* and *H. hippocampus* (i.e. number of trunk rings, number of tail rings, number of pectoral fin rays, number of dorsal fin rays). However, the ratio of snout length to head length (> 1/3) certainly suggests that these specimens are *H. guttulatus* or the European long-snouted seahorse, and the number of pectoral fins on one of the specimens is consistent with it being *H. guttulatus*. Both specimens lack a mane of thick skin fronds on neck and head, usually seen in adults (Fig. 2).

	Specimen 1	Specimen 2
Overall height	2.93 cm	3.51 cm
Number of trunk rings	11	11
Number of tail rings	36	37
Snout length / head length	0.42	0.42
Coronet	Rounded knobs	
Spine development	Blunt and well-developed	
Pectoral fin rays	15	16
Dorsal fin rays	18	18
Cheek spine	Low and blunt	
Eye spine	Prominent, rounded	

Table 1. Examined identification characteristics for both specimens

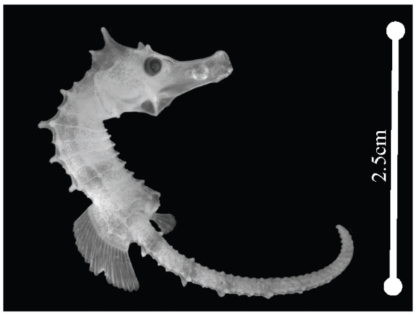


Fig. 2. - Photograph of specimen 2

Year	***Date***	***Number***	***Method of capture / vessel***	***Capture site***	***Destination of sea horses***	***remarks***
1997	May	4	Coastal fisheries	-	Oostende North Sea Aquarium	alive
1998	14-20 March	1	-	3 nautical miles from Zeebrugge	-	-
1998	24 July	1	Shrimp fisheries / O.211	-	Died and was discarded	During night
1998	22 September	7	Gill net / N.95	Between 51 12.70 N- 02 29.70E and 51 15.43N – 02 32.99E	released	Associated with *Alcyonidium*
1998	23 September	14			Aquarium of skipper-ship owner	
1998	24 September	33			Oostende North Sea Aquarium	
1998	25 September	66			Sealife Blankenberge	
1999	24 June	1	Coastal fisheries / O.101	-	-	-
1999	10 July	1	Coastal fisheries / O.152	-	-	Dead but no signs of decay
1999	14 July	1	O.20	-	-	Pregnant male
1999	-	-	N.95	Between 51 12.70 N- 02 29.70E and 51 15.43N – 02 32.99E	-	Skipper is convinced of the presence of a local population
2000	28 September	1	O.190	Westpit fishing grounds	-	Dead
2001	17 February	1	Gill net / O.369	-	-	-
2001	18 August	1	Coastal fisheries / O.190	-	-	-
2001	25 September	1	Coastal fisheries / O.190	-	-	male
2002	11 September	1	O.191	Fishing grounds near Oostendebank	-	-
2004	20 April	1	O.190	Wenduinebank	-	-
2004	21 May	1	O.20	3 nautical miles from Oostende	-	alive

Table 2. Recent seahorse catches (*Hippocampus hippocampus*) by local fishermen in Belgian marine waters

This is the first reported catch of *Hippocampus guttulatus* for the Belgian waters, and the origin of the specimens is unclear. Although there are numerous records for southern Britain, it is unlikely that specimens could reach the Belgian coast due to their poor swimming ability and the lack of assisting currents (Garrick-Maidment, 1998). On the other hand, the presence of a local population seems unlikely because from 1997 onwards, only *Hippocampus hippocampus* was occasionally caught by local fishermen (Table 2, Fig. 1). As the specimens were caught near the sea surface, it is likely that they were carried to the Belgian coastal zone through the English Channel in association with floating debris (the sample contained decaying duckweed, plant seeds and pieces of plastic). However, the presence of seahorses (and their fry) in the neuston is quite uncommon. Only *Hippocampus erectus* has already been reported from the neuston in association with floating debris and vegetation (Powell et al, 2000; Castro et al, 2001; Teixeira & Musick, 2001).

As the entire genus *Hippocampus* is listed in Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) and both *H. guttulatus* and *H. hippocampus* are listed as Data Deficient by IUCN (World Conservation Union), it is most important to gather information on the presence and persistence of local populations of seahorse species to form the basis of legal protection and conservation. Hopefully, this note will be the starting point for a detailed record of Belgian seahorse catches.

ACKNOWLEDGEMENTS

First, the authors would like to show their gratitude to Neil Garrick-Maidment, Sara Lourie and Janelle Curtis for their assistance with the species identifications and to Hans Hillewaert for editing the fotograph. The list of seahorse catches by fishermen was composed by Eddy Eneman from the Oostende North Sea Aquarium. Special thanks go to André Cattrijsse of the Flanders Marine Institute (VLIZ) and to the crewmembers of the research vessel Zeeleeuw. The first author acknowledges a specialisation grant from the 'Flemish Institute for the Promotion of Scientific-Technological Research' (IWT).

ERRATUM

The statement that this is the first reported catch of *Hippocampus guttulatus* for the Belgian waters is not correct: Holly (1936) already mentioned the presence of one individual of *H. guttulatus* from a shrimp net tow near Oostende. With thanks to Simon Claus for bringing this reference to the author's attention.

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APPENDIX: SPECIES LIST

I. Fauna from dip net samples (seaweed-associated fauna + background neustonic fauna)

Phylum Cnidaria
Classis Hydrozoa
Abietinaria abietina
Aglaophenia pluma
Bougainvillia sp. (medusa)
Clytia hemisphaerica
Coryne muscoides
Eutonina indicans (medusa)
Hydrallmania falcata
Laomedea flexuosa
Lizzia blondina (medusa)
Obelia dichotoma
Obelia sp.
Obelia longissima
Obelia geniculata
Phialidium hemisphericum (medusa)
Phialopsis diegensis (medusa)
Podocoryne sp.
Steenstrupia nutans (medusa)
Classis Scyphozoa
Chrysaora hysoscella
Classis Anthozoa
Actiniaria sp.
Phylum Ctenophora
Classis Tentaculata
Beroe sp.
Pleurobrachia pileus
Phylum Nematoda
Nematoda sp.
Phylum Annelida
Classis Polychaeta
Autolytus sp.
Autolytus prolifer (polybostrichus)
Harmothoe sp.
Lanice conchilega (larva)
Magelona johnstoni
Nereis sp.
Ophiodromus flexuosus
Pectinaria koreni (larva)
Phyllodoce maculata
Sabellidae sp.
Spionidae sp.
Spirorbis sp.
Syllidae sp.
Phylum Arthropoda
Subphylum Hexapoda
Classis Insecta
Ordo Diptera
Agromyzidae sp.

        Cecidomyiidae sp.
        Chironomidae sp. (larva + adult)
        Chloropidae sp.
        Empididae sp.
        Ephydridae sp.
        Lonchopteridae sp.
        Muscidae sp.
        Otitidae sp.
        Phoridae sp.
        Psychodidae sp.
        Scatopsidae sp.
        Sciaridae sp.
        Sphaeroceridae sp.
        Tipulidae sp.
    Ordo Hymenoptera
        Formicidae sp.
        Ichneumonidae sp.
        Tenthredinidae sp.
    Ordo Coleoptera
        Cantharidae sp.
        Chrysomelidae sp.
        Coccinellidae sp.
        Endomychidae sp.
        Helophorus aquaticus
        Scarabeidae sp.
        Staphylinidae sp.
    Ordo Hemiptera
        Aphididae sp.
        Cercopidae sp.
        Cicadellidae sp.
        Corixidae sp.
        Lygaeidae sp.
        Psyllidae sp.
    Ordo Neuroptera
        Chrysopidae sp.
    Ordo Thysanoptera
        Thysanoptera sp.
Subphylum Chelicerata
  Classis Arachnida
    Ordo Acarina
        Acari sp.
    Ordo Araneae
        Araneae sp.
Subphylum Crustacea
  Classis Copepoda
        Calanoida sp.
        Harpacticoida sp.
        Siphonostomatoida sp.
  Classis Cirripedia
        Elminius modestus
        Semibalanus balanoides
  Classis Malacostraca
    Ordo Decapoda
        Carcinus maenas (zoea, megalopa, juvenile)
        Galathea intermedia (megalopa)

Hippolyte varians (postlarva)
Liocarcinus holsatus (zoea, megalopa, juvenile)
Necora puber (megalopa, juvenile, adult)
Palaemon elegans (postlarva, adult)
Palaemon serratus (adult)
Pisidia longicornis (zoea, megalopa)
Thia scutellata (megalopa)

Ordo Mysidacea
- *Mesopodopsis slabberi*

Ordo Cumacea
- Cumacea sp.
- *Pseudocuma longicornis*

Ordo Isopoda
- *Idotea baltica*
- *Idotea emarginata*
- *Idotea granulosa*
- *Idotea linearis*
- *Idotea pelagica*
- *Jaera* sp.

Ordo Amphipoda
- *Atylus swammerdami*
- *Corophium acherusicum*
- *Gammarellus angulosus*
- *Gammarus locusta*
- *Gammarus crinicornis*
- *Hyale nilssoni*
- *Jassa* sp.
- *Orchestia gammarellus*
- *Stenothoe marina*

Phylum Mollusca
- Classis Gastropoda
  - *Facelina bostoniensis*
  - *Littorina mariae*
  - *Tergipes tergipes*
- Classis Bivalvia
  - *Mytilus edulis*
  - *Ostrea edulis*

Phylum Bryozoa
- *Bowerbankia sp.*
- *Electra pilosa*
- *Flustra foliacea*

Phylum Chaetognatha
- *Sagitta* sp.

Phylum Echinodermata
- Classis Ophiuroidea
  - Ophiuroidea sp. (larva)
- Classis Asteroidea
  - Asteroidea sp. (larva)
- Classis Echinoidea
  - Echinoidea sp. (larva)

Phylum Chordata
- Subphylum Urochordata
  - Classis Larvacea
    - Larvacea sp.

Subphylum Vertrebrata
Classis Osteichthyes (juveniles)
Belone belone
Blenniidae sp.
Callionymus lyra
Chelon labrosus
Ciliata mustela
Cottidae sp.
Cyclopterus lumpus
Entelurus aequorius
Gobiidae sp.
Merlangius merlangus
Nerophis lumbriciformis
Platichthys flesus (larva)
Pollachius pollachius
Pollachius virens
Syngnathus acus
Syngnathus rostellatus
Trachurus trachurus

II. Fish fauna from neuston net samples

Phylum Chordata
Subphylum Vertebrata
Classis Osteichthyes (juveniles)
Ammodytes tobianus
Arnoglossus laterna
Belone belone
Chelon labrosus
Ciliata mustela
Clupea harengus
Cottidae sp.
Echiichthys vipera
Engraulis encrassicolus
Hippocampus guttulatus
Hyperoplus lanceolatus
Labrus bergylta
Merlangius merlangus
Pleuronectidae sp.
Pollachius pollachius
Pollachius virens
Scophthalmus maximus
Solea solea
Sprattus sprattus
Syngnathus acus
Syngnathus rostellatus
Trachurus trachurus

III. Seabirds associated with floating seaweeds (ESAS-database)

Phylum Chordata
  Subphylum Vertebrata
    Classis Aves
      Alca torda
      Fulmarus glacialis
      Larus argentatus
      Larus canus
      Larus fuscus
      Larus marinus
      Larus ridibundus
      Melanitta nigra
      Mergus serrator
      Phalacrocorax carbo
      Rissa tridactyla
      Somateria mollissima
      Stercorarius skua
      Sterna hirundo
      Sterna paradisaea
      Sterna sandvicensis
      Sula bassana
      Uria aalge