Vlaanderen
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# Habitatmapping Sea Scheldt supralittoral

## Partim pioneer club-rush species

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**Way of quoting:**
Elsen R., Van Braeckel A., Vanoverbeke J., Vandevoorde  B. & Van den Bergh E. (2019). Habitatmapping Sea Scheldt supralittoral- partim pioneer club-rush species. Reports of the Research Institute for Nature and Forest 2019 (36). Research Institute for Nature and Forest , Brussels.
DOI: doi.org/10.21436/inbor.16164273

**D/2019/3241/259**
**Rapporten van het Instituut voor Natuur- en Bosonderzoek 2019 (36)**
**ISSN: 1782-9054**

**Responsible publisher:**
Maurice Hoffmann

**Cover photograph:**
*Schoenoplectus tabernaemontani* near Rupelmonde

**This research was carried out :**
Maritieme Toegang
Thonetlaan 102 bus 2
2050 Antwerpen
Belgium

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doi.org/10.21436/inbot.16854921
Rapporten van het Instituut voor Natuur- en Bosonderzoek 2019 (36)

# Dankwoord/Voorwoord

Dit door het INBO uitgevoerd onderzoek werd uitgevoerd in het kader van Habitatmapping supralitoraal Zeeschelde in opdracht van afdeling Maritieme Toegang (aMT). Waarvoor dank.

Aanvullende data over de Driekantige bies werd met toestemming ontleend uit de databank Waarnemingen.be van Natuurpunt VZW.

De dataverzameling op terrein gebeurde door Thomas Terrie, Dimitri Buerms en Joram De Beukelaer. Graag bedanken we jullie ook voor de achteraf geleverde expertise en inzichten.

# Samenvatting

De Vlaams- Nederlandse Scheldecommissie ontwikkelde in 2001 een langetermijnvisie met als doel het creëren van een gezond- multifunctioneel Schelde-estuarium. Om de ontwikkelingen op de voet op te volgen werd het monitoring programma MONEOS opgezet (Meire & Maris 2008). Binnen het MONEOS programma is INBO onder andere verantwoordelijk voor het opvolgen van de evolutie van de vegetaties langsheen de estuariene gradiënten in de Zeeschelde, het Vlaams gedeelte van het estuarium (Van Ryckegem et al, 2016). Naast loutere beschrijving van de evolutie is het voor het beleid ook interessant om inzicht te krijgen in de habitatvereisten en ontwikkelingskansen voor estuariene vegetaties onder gegeven abiotische omstandigheden. Gyselings R. et al (2011) en Van Braeckel A. et al (2008) ontwikkelden modellen voor schorvegetaties in de Zeeschelde op basis van ervaring en kennis en met behulp van de bestaande data, die echter niet met dat doel voor ogen verzameld waren. De resultaten van deze studies laten tot op zekere hoogte toe om functionele ecotopen te definiëren en af te bakenen maar voor koppeling aan abiotische factoren stootten ze op de limieten van de beschikbare data. De auteurs suggereerden om het onderzoek te vervolgen met beter, over de volledige abiotische gradiënten, gestratificeerde data en om naast vegetatiemodellen ook in te zetten op soortmodellen.

In deze vervolgstudie worden soortmodellen ontwikkeld voor planten uit de pionier- en lagere schorzones. Door oeverversteiling en –verharding en door toenemende hydrodynamiek staan deze zones onder verhoogde druk en zijn ze de meest kwetsbare in de Zeeschelde. De soortmodellen kunnen ingezet worden om ontwikkelingskansen voor deze ondervertegenwoordigde ecotopen in de Zeeschelde te verbeteren en om mogelijke gevolgen van inrichtings- en ontwikkelingsscenario's in te schatten.

Biezen hebben een sleutelrol in de vroege stadia van schorontwikkeling. Ze ontwikkelen op de grens tussen de litorale en supralitorale zone, reageren snel op subtiele omgevingswijzigingen en worden dan ook vaak “ecological engineers” genoemd. Voor bijna alle biezenpopulaties in de Zeeschelde werden precieze abiotische standplaatsdata verzameld om soortmodellen te maken. Ze groeien in populaties of zoden en men vindt ze langs de volledige zoutgradiënt van de Zeeschelde. De bestudeerde soorten zijn: Driekantige bies (*Schoenoplectus triqueter;* rodelijst soort in Vlaanderen (Van Landuyt et al. 2006)), Ruwe bies (*Schoenoplectus tabernaemontani*) en hun hybride Bastaardbies (*Schoenoplectus x. kuekenthalianus*) alsook Zeebies (*Bolboschoenus maritimus*), ook Heen genoemd.

Precieze standplaatsdata met betrekking tot groeilocaties werd verzameld in de zomers tussen 2013 en 2017. De exacte hoogte onderaan, bovenaan en centraal de pol werd opgemeten. Centraal de pol werd ook data van fysische groeikarakteristieken verzameld. Daarnaast werd ook informatie verzameld over de bodems waarin de soorten groeien. Deze data werd in GIS gekoppeld aan gemodelleerde getij-, saliniteit- en erosie gevoeligheid(schuifspanning) data van de groeilocaties. Met deze data kon per soort een distributie model worden opgesteld. Hiervoor werd het biomod2 package gebruikt dat in R software toegankelijk is. Omdat veranderingen in milieufactoren niet alleen het voorkomen maar ook de groeikenmerken van de plant kunnen beïnvloeden werden per soort ook deze relaties onderzocht.

De gemodelleerde distributie per soort toont aan dat saliniteit de belangrijkste verspreidingsfactor is voor de vier soorten, gevolgd door, afhankelijk van de soort, overspoelingsregime of erosiegevoeligheid. De soorten kunnen op basis van deze gegevens worden opgedeeld in twee functionele groepen. Enerzijds de meer brakke soorten Zeebies en Ruwe bies, anderzijds de zoetwater soorten Bastaardbies en Driekantige bies. In het brakke deel van het estuarium verdraagt Ruwe bies een hogere overspoelingshoogte dan Zeebies. Dit betekent dat eerstgenoemde soort in theorie lager op de oever dan laatstgenoemde kan groeien. In het zoete deel hebben Bastaardbies en Driekantige bies een vergelijkbare en eerder overlappende niche wat betekent dat ze eerder concurrerende soorten zijn.

De samengestelde distributie modellen bleken betrouwbaar te zijn om zowel de populatie- als de soortenverspreiding te voorspellen. Dit geldt zeker voor de zeldzame Driekantige bies. Naast distributie van de soorten werd ook gekeken naar de relatie tussen groeikarakteristieken (stengelhoogte, stengeldikte, densiteit van de stengels, bloeihoogte) en de verschillende milieufactoren. Door het tekort aan data voor Driekantige bies werd deze soort uit de analyse gelaten. Overspoelingshoogte beïnvloedt al de gemeten groeikarakteristieken. Populaties met een hogere overspoelingshoogte ontwikkelen een hogere stengeldensiteit en hebben langere en dikkere stengels. Dit leidt uiteindelijk tot een groter plant volume. Een uitzondering hierop is Bastaardbies die juist dunnere stengels ontwikkelt. Erosiegevoeligheid (slikhelling en schuifspanning) heeft slechts een kleine invloed op de groeikarakteristieken. De helling van het slik, een indicator voor erosiegevoeligheid, zorgt voor kortere stengels alsook een hogere stengeldensiteit. Schuifspanning heeft een negatief effect op de stengel dikte. Substraat type (al dan niet groeiend tussen breuksteen) heeft vooral een effect op Bastaardbies en Ruwe bies met dikkere stengels op breuksteen, wat ook het volume van de planten en/of de groeistrategie (verhouding tussen breedte en hoogte van de planten) kan beïnvloeden. Het al dan niet groeien op breuksteen beïnvloedt Zeebies slechts zeer beperkt.

Wijziging in verspreidingspatronen doorheen de tijd werden geëvalueerd door de huidige verspreiding naast de data van 1995 (Dekoninck, 1996), 2003 (Vandevoorde (2016) in Van Ryckegem et al. 2016 en Vandevoorde & Van Lierop (2018) in Van Ryckegem et al. 2018) en 2013 (Van Ryckegem et al 2018) te leggen. Het aantal populaties Zeebies bleef de voorbije 2 decennia nagenoeg het zelfde; Bastaardbies en Ruwe bies zijn momenteel wijder verspreid langsheen het estuarium, maar waar vroeger grotere aaneengesloten populaties voorkwamen zijn dit nu vaker kleinere populaties. Het oppervlakte areaal aan Ruwe bies nam af de voorbije 20 jaar. Driekantige bies verloor 1/3 van al de populatie en blijft nog steeds een zeldzame soort. Van al de soorten vinden we meer populaties lager in het getijvenster in vergelijking met 1995. Dit betekent ook dat de populaties in de zoetwaterzone weer tegen een grotere overspoelingshoogte bestand zijn, zoals dat ook in het begin van de 20e eeuw het geval was (Meire et al, 1992). Een mogelijke verklaring is de algemeen verbeterde waterkwaliteit.

Deze studie draagt bij tot het beter begrijpen van habitatvereisten voor vier biessoorten in de Zeeschelde. Onze resultaten voorspellen niet alleen habitatpotentie maar ook groeikarakteristieken op gedetailleerde schaal voor de verschillende biezensoorten. De ontwikkelde modellen kunnen worden ingezet voor scenario analysen met betrekking tot inrichting, beheer en klimaat.

# Aanbevelingen voor beheer en/of beleid

Ecotopenstelsels zijn belangrijke beleidsinstrumenten om te rapporteren over de evolutie van het ecosysteem en om effecten van abiotische veranderingen in te schatten, bijvoorbeeld bij scenarioanalyses. Schorren zijn in de Zeeschelde tot nu toe nog als één geheel gemonitord aangevuld met een schorvegetatiekartering. Binnen een schor kunnen echter verschillende abiotische vergelijkbare vegetatiezones onderscheiden worden die een gelijkaardige respons vertonen op veranderingen in stroomsnelheden, golven,...

Van Braeckel et al. (2008) karakteriseerde schorecotopen langs de volledige saliniteitsgradiënt van het Schelde-estuarium van monding tot Gent op basis van gebiedsdekkende maar ruimtelijk grovere abiotische informatie zoals het digitaal hoogtemodel en de vegetatiekaarten. Op basis van saliniteit en overstromingsfrequentie werd een onderscheid gemaakt tussen lage en hoge pionierzone, schorzone en hogere schorzone. De juiste grenswaarden langsheen de saliniteitsgradiënt bleken echter moeilijk af te leiden. Gyselings et al. (2011) zocht op basis van GPS-metingen en vegetatie-opnames in de Zeeschelde naar een betere en meer precieze afbakening. Uit de analyse bleek dat naast saliniteit en overspoelingsfrequentie, naar gelang het vegetatietype en/of kernsoort ook de geomorfologische eenheid (komgrond/oeverwal en afstand tot kreek) een belangrijke verklarende variabele is voor het voorkomen. Voor de minder frequent voorkomende vegetatietypes zoals pioniervegetaties bleek de dataset te beperkt om duidelijke grenzen af te bakenen. De auteurs suggereerden dan ook enerzijds om gericht het onderzoek verder uit te breiden met een betere stratificatie over de volledige abiotische gradiënten en anderzijds om naast vegetatiemodellen ook in te zetten op soortmodellen.

Deze studie geeft gevolg aan bovenstaande aanbevelingen en focust in de eerste plaats enkel op de meest kwetsbare ecotoop in de Zeeschelde, de pionierschorzone, waar biezen een prominente rol spelen. Biezen bezetten een zeer specifieke plaats op de overgang tussen slik en schor, zijn als kolonisatoren sleutelsoorten in schorvorming en vervullen een indicatorfunctie omdat ze gevoelig zijn voor subtiele omgevingswijzigingen. Deze studie onderzoekt de standplaatsfactoren die de ruimtelijke verspreiding bepalen, de invloed van milieufactoren op groeikarakteristieken en de evolutie sinds 1995 voor vier soorten biezen in de Zeeschelde. Voor elk van deze soorten werden verspreidingsmodellen opgesteld. Deze werden getest en bleken betrouwbaar te zijn om soortverspreiding in de Zeeschelde te voorspellen.

### Aanbevelingen

Uit deze studie van biezen in de Zeeschelde blijkt duidelijk dat dit pionierecotoop nog steeds onder grote druk staat, vooral in de zoete Zeeschelde. Nadat de biezengordels in de 20e eeuw bijna verdwenen, komen ze nu voorzichtig terug. De standplaatskenmerken verschillen echter van de vroegere of van standplaatskenmerken in referentiesituaties in andere estuaria zoals de Elbe, de Dordogne, de vroegere Biesbosch en Oude Maas en enkele Britse en Ierse estuaria. In de huidige Zeescheldehabitat zijn er steilere oevers, verdedigde schorplateaus, grotere getijamplitudes en grotere stroomsnelheden waardoor slechts een smallere groeizone overblijft voor deze biezen. Bovendien bestaat, vooral in de zoete zone, het huidig habitat voor een zeer groot deel uit breuksteen. Het is de vraag of alle soorten zich in de toekomst kunnen handhaven onder die omstandigheden. Meer ruimte creëren in het stroomopwaartse intertidaal deel zodat zacht hellende en minder dynamische slikken kunnen ontstaan, wordt sterk aanbevolen.

De driekantige bies (opgenomen als Rode Lijst-soort) is duidelijk de meest kwetsbare soort. Om deze soort van uitsterven in Vlaanderen te vrijwaren is het aangewezen om bij inrichting en beheer van de Zeeschelde rekening te houden met haar habitatvereisten. Een gericht actieplan dringt zich op, waar natuur- en rivierbeheerders samen hun schouders onder zetten.

Hiervoor kunnen de volgende stappen worden overwogen:

1. Nauwgezette monitoring van de aanwezige populaties in relatie tot (veranderende) omgevingsfactoren.

2. Zoeken naar en faciliteren van alternatieve groeiplaatsen buiten de vaargeul (ontpolderingen en GGG).
3. Bij dringende infrastructuurwerken kunnen bedreigde populaties als laatste redmiddel en met beperkte kans op succes, tijdelijk getransplanteerd worden eventueel aangevuld door restocking.

**Verdere stappen**

In deze studie kregen we inzicht in de heersende omgevingsfactoren die de standplaats van de huidige biezenpopulaties in de Zeeschelde bepalen. Verder werd reeds kort verkend hoe groeikarakteristieken wijzigen onder invloed van enkele stressfactoren en werden modellen ontwikkeld die de potentiële soortverspreiding in de Zeeschelde onder verschillende scenario's kunnen voorspellen.

Er zijn echter nog een aantal nader te onderzoeken aspecten met betrekking tot de mechanismen achter de verspreiding van biezen:

1. Omgevingsfactoren (zout, overspoelingsregime, helling, stroomsnelheid, waterkwaliteit, golfslag):
    - Het ecologische optimum voor elke soort
    - De ecologische grenzen voor elke soort

2. Competitiemechanismen die
    - spelen tussen de biezensoorten onderling
    - spelen tussen biezen en andere plantensoorten
    - potentieel een bedreiging vormen voor de meest kwetsbare soorten.

3. Functionele verschillen tussen de soorten

Binnen habitatmapping supralitoraal is het doel om ook de hogere schorecotopen te karakteriseren. Verdere stappen zijn enerzijds de koppeling van vegetatie aan een hydromorfologische model en anderzijds hydrologisch onderzoek in de schorren in relatie tot tijpostdata. Dit is al verkennend aangehaald in Gyselings et al. (2011) en kan sterk bijdragen tot een verbeterde schorecotoopafbakening.

**Evolutie in de tijd**

Meire et al. (1992) merkten op dat de toenmalige biezengordels in de oligohaliene en zoete zone van de Zeeschelde smaller en hoger in het tijvenster stonden dan in begin van de 20$^{e}$ eeuw. De hypothese van Meire et al. (1992) was dat waterkwaliteit en oeverstructuur hierin sturende factoren zouden zijn. Recent (2013-2017) bevinden de drie *Schoenoplectus* soorten zich gemiddeld ongeveer een halve meter lager in het tijvenster dan in 1995. Ze hebben dus hun bereik in het getijvenster opnieuw uitgebreid naar beneden. Tegelijk werden de populaties ook minder hoog in het tijvenster gevonden. De spreiding in het tijvenster is dus niet toegenomen, maar verschoven. Een mogelijke hypothese is dat verbeterde waterkwaliteit biezen terug toelaat om lager in het tijvenster te groeien en dat competitie (riet en concurrerende biezensoorten) van bovenuit de biezen lager in het getijvenster duwt.

Daarnaast stellen we ook vast dat meer dan de helft van de huidige biezenpopulaties in de Zeeschelde zich tussen de breukstenen bevindt. Breuksteen wordt vooral gestort op slikken die dynamischer worden t.g.v. een toenemende getijamplitude om erosie tegen te gaan. Van den Bergh et al. (2001) stelden dat biezen zich na het storten van breuksteen terug tussen breuksteen konden vestigen dankzij de relatieve beschutting en verbeterde verankeringsmogelijkheden. Ook deze stelling verdient nader onderzoek.

*Schoenoplectus triqueter* of driekantige bies

Driekantige bies, de zeldzaamste en kleinste van de vier soorten biezen, is een Rode Lijst-soort, komt in Vlaanderen enkel voor in de Zeeschelde en wordt beschouwd als één van de meest kenmerkende plantensoorten voor het zoetwatergetijdengebied. Deze bies kende een ruime verspreiding begin 20e eeuw. De verspreiding nu is beperkt tot het zoetwatergebied tussen Wetteren en Dendermonde. Driekantige bies is een typische pionier die gemiddeld bijna anderhalve meter onder gemiddeld hoogwater (GHW) groeit en dus bij elk getij overspoeld wordt. Tussen 1995 en 2003 nam het aantal populaties toe. Bij de laatste survey in 2013-2017 nam het aantal weer af tot amper 24, maar ze groeiden meer uit. Momenteel groeit een groot deel van de populaties op steile oevers tussen breuksteen. Historische en buitenlandse bronnen geven aan dat deze soort normaal op zacht glooiende hellingen met zacht substraat groeit. We tonen aan dat dit habitat binnen de Zeeschelde nog nauwelijks aanwezig is. Van de vier besproken soorten stelt driekantige bies de meest strikte habitateisen naar saliniteit, overspoelingsduur, -diepte en –frequentie, schuifspanning en maximale stroomsnelheid. Nauwgezette monitoring en extra aandacht voor deze soort bij de planning van infrastructuurwerken dringen zich op zodat ze niet helemaal uit Vlaanderen verdwijnt. Voor een betere bescherming is het ook aangewezen om de kiemings-, vestigings- en groeicondities in de Zeeschelde diepgaander te onderzoeken.

*Schoenoplectus x kuekenthalianus* of bastaardbies

Bastaardbies, de kruising tussen driekantige en ruwe bies, is minder zeldzaam dan driekantige bies. De overgrote meerderheid (enkele honderden populaties) komen verspreid voor tussen Gent en Kruibeke. Bij deze soort trad een daling van het aantal populaties op sinds 1995. De grootste verliezen situeren zich tussen Melle en Berlare, vermoedelijk door dijkwerken. De overgebleven populaties konden wel verder uitgroeien waardoor de oppervlakte tussen 2003 en 2013 stabiel bleef. Bastaardbies beslaat een bredere range in het getijvenster en stromingsvariatie dan de driekantige bies en kan dus als concurrerende soort beschouwd worden. Ook blijkt dat de slikken met een gemiddeld flauwere helling meer door bastaardbies begroeid zijn dan door driekantige bies. Ten opzichte van zeebies en ruwe bies zijn bastaardbiezen korter, maar de dichtheid aan stengels is groter.

*Schoenoplectus tabernaemontani* of ruwe bies

Ruwe bies gedijt van het Groot Buitenschoor tot Berlare. Deze brakke soort heeft dus een ruime saliniteitstolerantie dan de vorige ’zoete’ soorten. De verspreiding van ruwe bies in de Zeeschelde is echter niet geheel natuurlijk. Rond Antwerpen werden commerciële aanplanten onderhouden tot in de jaren 80-90 van de vorige eeuw en in 1993 werd er aan Appels en de Kramp ruwe bies aangeplant als experiment voor alternatieve oeververdediging. De oppervlakte ruwe bies daalt sinds 2003, mogelijk door concurrentie met andere soorten. Het aantal populaties is wel in stijgende lijn: van enkele tientallen in 1995 tot meer dan 130 bij de laatste survey, wat duidt op het opsplitsen van grote naar kleinere populaties. Uit DNA-onderzoek blijkt dat verspreiding vanuit de aanplanten optreedt (De Greef et al., 1999). Ruwe bies staat t.o.v. de twee vorige ‘zoete’ soorten doorgaans op locaties met een gemiddeld kortere overspoelingsduur, met minder steile hellingen en lagere maximale stroomsnelheden. Ook overspoelen niet alle standplaatsen bij ieder getij. Ruwe bies wordt in de Zeeschelde, net als de 2 ‘zoete’ soorten, gemiddeld minder hoog dan zeebies. Wel zijn de populaties ongeveer driemaal dichter.

*Bolboschoenus maritimus* of zeebies (heen)

Zeebies was wijd verspreid als pionier in de Zeeschelde bij het begin van de 20$^{e}$ eeuw maar was vooral kenmerkende soort voor de brakke zone. Ook in 1992 toen de eerste vegetatiekaart van de Zeeschelde gemaakt werd was deze soort overal aanwezig. Bij de laatste survey werden bijna 1500 populaties gekarteerd waarbij ook in de zwak brakke zone hoge aantallen werden geregistreerd. De ranges voor saliniteit, helling, schuifspanning en maximale stroomsnelheid zijn zeer gelijkend voor zeebies en ruwe bies. Ruwe bies verdraagt wel meer overspoeling en kan dus lager in het getijvenster gedijen. Zeebies heeft de langste en dikste stengels van al de onderzochte biezensoorten maar heeft ook de meest ijle populaties in de Zeeschelde.

## Voorspelde verspreiding van de plant in de Zeeschelde

Eén van de doelstellingen binnen deze studie was het opstellen van een soortverspreidingsmodel voor de 4 biezensoorten. Hieruit is afgeleid onder welke milieuomstandigheden de soorten groeien. Met deze voorspellingsmodellen werden de kans op voorkomen en de potentiële standplaatsen in de Zeeschelde nagegaan. Verder werd het ook toegepast om potenties te bekijken voor een toekomstscenario 2050 (Elsen 2018) afgeleid uit het Integraal Plan Zeeschelde. Hieruit bleek dat bij stijging van getijamplitude en zeespiegelstijging de potentie en verspreiding van alle onderzochte soorten sterk achteruit gaan. Zonder gerichte maatregelen zou tegen 2050 de driekantige bies uit de Zeeschelde kunnen verdwijnen.

## Invloed van omgevingsfactoren op groeikarakteristieken van de plant

Uit literatuur blijkt dat morfologische respons van planten vaak een indicator is van stress in zijn groeiomstandigheden. Daarom werd hier de relatie tussen groeikarakteristieken (stengelhoogte, stengeldikte, densiteit van de stengels, bloeihoogte) en enkele milieufactoren onderzocht. Omwille van het gering aantal populaties werd *S. triqueter* uit deze analyse gelaten.

Wanneer biezenpopulaties lager in het tijvenster staan (verhoogde overspoelingshoogte) vormen ze, zoals één van de vooropgestelde hypothesen stelde, een hogere stengeldichtheid alsook langere stengels. Bij de brakke biezensoorten zijn in dat geval de stengels ook dikker. De zoete Bastaardbies daarentegen ontwikkelt juist dunnere stengels. Ook een standplaats met een steilere helling draagt bij tot toenemende stress en resulteert in langere stengels en dichtere populaties. Op oevers met grotere schuifspanning hebben biezen een licht kortere stengel. Dit effect is het meest uitgesproken bij bastaardbies en het minst bij zeebies. Bastaardbies en ruwe bies gevestigd op breuksteen ontwikkelen dikkere stengels in vergelijking tot populaties op zacht substraat. Dit verschil in stengeldikte bepaalt mede het plantvolume alsook de plantstrategie.

# Summary

In 2001 the VNSC (Vlaams- Nederlandse Scheldecommisie) developed a long term vision for a healthy and multifunctional Scheldt Estuary ecosystem. The MONEOS monitoring program (Meire & Maris 2008) was designed to assess the developments towards this goal. In this program INBO monitors estuarine vegetations along the Sea Scheldt, the Flemish part of the estuary (Van Ryckegem et al, 2016). However, from a management point of view understanding and modelling habitat needs and potentials is a more interesting approach than just describing development observations. Gyselings et al.(2011) and Van Braeckel et al. (2008) were able to define functional tidal marsh ecotopes in the Sea Scheldt to a certain hierarchic level, based on monitoring data and expertise, but they hit the limits of the available data, not collected for that specific purpose. They also proposed to add species specific models.

In this study we elaborate on the above mentioned results. Additional data was collected specifically to model club-rush species, the more vulnerable category of pioneer species in the Sea Scheldt. The models can be used to design measures to enhance development potentials for these poorly represented ecotopes in the Sea Scheldt as well as for scenario analysis and assessments.

Tidal club-rush vegetation occupies a very specific ecotone, on the edge between the littoral and supra littoral zone, is often sensitive and quickly responds to subtle changes in the environment. Also called 'ecological engineers', club-rush species play a key role in early tidal marsh development. They grow in tufts or sods along the complete Zeeschelde salinity gradient. In this study species specific models could be generated by gathering high spatial resolution data for four club-rush species: Triangular Club-rush (*Schoenoplectus triqueter*), (listed as a threatened species in Flanders (Van Landuyt et al. 2006)), Grey Club-rush (*Schoenoplectus tabernaemontani*) and their cross-breed (*Schoenoplectus x. kuekenthalianus*) and Sea Club-rush (*Bolboschoenus maritimus*).

Data on these species was collected during summer field visits between 2013 and 2017. The exact locations and elevation of the lower and upper border and the central position were collected. Physical growth characteristics and information on the soil was collected from the central part of the tuft or sod. Subsequently, this data was linked in GIS to current and modeled environmental data such as tidal regime, salinity and erosion sensitivity (shear stress parameter). The dataset allowed to develop species distribution models using the biomod2 package in R software. Distribution and relative importance of environmental factors was assessed for each species as well as growth response to changes in environmental variables.

Evolution of species distribution in time was investigated in a comparison of the current situation to 1995 (Dekoninck, 1996), 2003 (Vandevoorde (2016) in Van Ryckegem et al. 2016 and Vandevoorde & Van Lierop (2018) in Van Ryckegem et al. 2018) and 2013 (Van Ryckegem et al 2018). This historical comparison of club-rush locations between 1995 and 2013 shows that *Schoenoplectus x kuekenthalianus* and *Schoenoplectus tabernaemontani* are now more widespread throughout the estuary but shifted from larger to smaller tufts. Both *Schoenoplectus triqueter* and *Schoenoplectus tabernaemontani* declined in surface area. *Schoenoplectus triqueter* remains a rare species. The *Bolboschoenus maritimus* population did not change so much. Compared to 1995, tufts of all species are again positioned lower in the tidal window in the fresh tidal zone as was the case in the early 20th century (Meire et al, 1992).

According to the species distribution models salinity is the most important species distribution factor in the Sea Scheldt followed by, according to species, inundation regime or erosion sensitivity. General distribution models predict fairly well population as well as species distribution, especially the rare *S. triqueter.*Two functional groups could be distinguished: *B. maritimus* and *S. tabernaemontani* as more brackish species and *S. x kuekenthalianus* and *S. triqueter* as freshwater species. *S. tabernaemontani*

can endure a higher inundation depth compared to *B. maritimus* meaning there is a vertical differentiation between the brackish species. *S. x kuekenthalianus* and *S. triqueter* have a similar inundation niche which means they are competitors. *S. x kuekenthalianus* is to a certain extent better adapted to a higher inundation depth.

Besides species distribution we also investigated response of growth characteristics to different environmental variables. Growth characteristics are clearly influenced by inundation depth, erosion sensitivity and substrate. Inundation depth, affected by local tidal range, has a positive effect on all growth characteristics. In general the lowest tufts with higher inundation depth grow denser and have both thicker and longer stalks (with the exception for *S x. kuekenthalianus* that has, thinner stalks). Erosion sensitivity (slope and shear stress) plays a minor role for growth characteristics. Slope, an indicator of susceptibility of the river bank to erosion, leads to denser tufts with longer stalks. Modelled shear stress, another erosion indicator variable, has a negative effect on stalk thickness. On anthropogenic rip rap depositions *S. x kuekenthalianus* and *S. tabernaemontani* develop thicker stalks, which also influences plant volume and/or growth strategy (the ratio of plant thickness over length). The impact of the studied environmental factors on plant morphology for these species was more significant than anticipated.

This study contributes to a better understanding of habitat needs for these four species in the Sea Scheldt. Not only can our results predict habitat potential under changing conditions, e.g. in climate scenario's or management applications, it can at the same time estimate growth characteristics for these four species. Doing so we went into greater depth than Gyselings et al.(2011) an developed models that could be used for other species as well.

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# 1 Introduction

The Vlaams- Nederlanse Scheldecommisie (formerly Technische Schelde commissie) developed in 2001 a long term vision to develop a healthy and multifunctional Scheldt Estuary ecosystem by 2030. This long term vision includes both the Dutch and Flemish part of the estuary and tries to reach a sustainable balance between navigation for ships, recreation and ecosystem functioning while safety must be guaranteed (WenZ, 2013). In this study we focus on the inner estuary of the Scheldt named 'Sea Scheldt', running from Melle (near Gent) to the Belgian-Dutch border. It is characterised by a one-channel system and a salinity gradient of freshwater towards (beta-) mesohaline conditions at the downstream part. The habitats within the Sea Scheldt serve a range of ecosystem functions, encompassing water buffering and purification and recreation (Meire et al. 2005, Meire and Maris 2008). Tidal marshes and mudflats represent a total of 1254 ha of the Belgium Scheldt Estuary (Van Ryckegem et al. 2016).

To monitor the sustainability of the estuary, the MONEOS monitoring program was set up (Meire & Maris 2008). Within this monitoring program, INBO is monitoring geomorphology, habitats/ecotopes and tidal marsh vegetation (Van Ryckegem et al., 2016). Furthermore a research program 'Habitatmapping Zeeschelde' by order of Maritime Access focuses on the ecological validation and improvement of the currently used ecotopes. By developing habitat suitability models for macrobenthos and tidal marsh vegetation the objective is not only to improve the ecotope typology but also to develop decision support tools for estuarine management. The intensive use and maintenance of economic activity have had already severe impacts on the quality and quantity of these estuarine ecotopes, as exemplified in changes in the habitat composition (Van Braeckel et al. 2006, Van Kessel et al. 2010, IMDC and ARCADIS 2008). Additionally, climate change in particular sea level rise will increase flood volumes and erosion stress in the estuary (Monbaliu 2014). Therefore estuarine management can benefit from tidal marsh vegetation models for a better understanding of habitat changes and potential.

Gyselings et al. (2011) and Van Braeckel et al. (2008) already set up first modelled tidal marsh ecotope systems but mentioned drawbacks of available data and data precision for rare pioneer habitat types which form small fringes at the lower marsh edge. This study will focus especially on one of these pioneer tidal marsh types, more specific club-rush vegetation, growing at the lower marsh edge.

Van Braeckel et al. (2008) were able to delimit high and low pioneer zones in the tidal marshes as well as supralittoral vegetation types using inundation frequency as a key factor. The origin of the dataset was however rather rough using vegetation maps and digital elevation models. This was done for the major dominating key species along the complete salinity gradient from Vlissingen (NL) to Ghent (B). Gyselings et al. (2011) modelled different habitat types based on available vegetation plots and DGPS data but bumped on the limits of the available data which were not specifically collected for that purpose, and emphasized the potential use of species specific distribution modelling. Van Braeckel et al. (2008) suggested to look into presence and absence of pioneer club-rush species growing in pioneer habitats, as this habitat is among the most threatened in the Sea Scheldt. In this respect, club-rush species are especially relevant as they are among the first to colonize mudflats, key for marsh development (Zonneveld 1960, Hoffmann 1993 - a, Dekoninck 1996) and considered as 'ecosystem engineers' (Silinski et al. 2015, Schwarz et al. 2015). They play a role in river bank protection against erosion (Silinski et al. 2015, Coops et al. 1996) and can indicate sudden local environment changes. In the Sea Scheldt, the most characteristic club-rushes are 4 species known to grow in the narrow stretch between the marsh plateaus and the tidal mudflats although they can grow within higher marsh zones as a secondary succession stage form (Hoffmann 1993 - a, Hoffmann et al. 1996, Van Braeckel et al, 2008). These four species are: *Schoenoplectus triqueter* (driekantige bies, Triangular Club-rush) listed as a threatened species in Flanders; Van Landuyt et al. 2006), *Schoenoplectus tabernaemontani* (ruwe bies, Grey Club-rush), and their cross-breed *Schoenoplectus x kuekenthalianus* (bastaardbies, S.tr x S.tab) and *Bolboschoenus maritimus* (zeebies of heen, Sea Club-rush).

Few studies have been performed on club-rush species within the Scheldt Estuary. Some studies show different species morphological response to their environment (Dekoninck 1996, Hoffmann et al. 1997-a). Dekoninck (1996) already mentioned morphological responses related to the environment but did not study this in detail. In the meantime conditions in the estuary and the distribution of the club-rush species have changed drastically the last 2 decades. Water quality has considerably improved (Maris & Meire, 2011), the use of the waterway is intensified due to the 3rd widening of the navigation channel and new managed realignment sites were realised (Van Braeckel et al. 2014). All of these induced changes in the habitat range. Questions remain about the impact of environmental factors on the populations of pioneer species within the Scheldt Estuary and how this might have changed in the last twenty years.

The long-term formation and survival of pioneer habitat with these 4 club-rush species depends on (I) tidal regime such as inundation frequency and duration, tidal amplitude, (II) erosion sensitivity of the river bank, (III) salinity and (IV) competition with other tidal marsh species (Figure 1). Another factor which could not be ignored due to the vast occurrence in the smaller upper reaches of the Scheldt Estuary are hard defended anthropogenic shores or rip rap zones. This can alter habitat and growing conditions and characteristics. The 4 species are expected to have different critical values for these environmental variables in the Scheldt Estuary. Deegan et al. (2005) demonstrated that *S. tabernaemontani* and *B. maritimus* have a higher tolerance towards salinity than *S. triqueter*. Deegan et al. (2005) also hypothesized that *S. triqueter* is likely to be outcompeted by other species and can only be found in the narrow zone of its ecological optimum. Variation in salinity between river systems in Europe and Northern America explains difference in morphological response of *B. maritimus* (Lillebø et al. 2003). Inundation determines the species distribution across the shore (Dekoninck 1996; Deegan et al. 2005), where *S. tabernaemontani* is more tolerant to deep water than *B. maritimus* and *S. triqueter* is restricted to lower elevations due to competition with other species (Clevering A et al. 1996; Deegan et al. 2005). Surveys in the nighties found *Schoenoplectrus* species in the Sea Scheldt on rip rap in a narrow zone along the shoreline (Hoffmann 1993 –b; DeKoninck 1996 and Hoffmann et al. 1997-a). A study performed on *S. lacustris* by Coops et al. (1996) showed positive impact of waves higher than 23 cm on tuft erosion, where size of waves depended on the size of mudflats, ship size and frequency of ship passing. Silinski et al. (2016) made similar conclusions but focused more on settling of seeds and shoots. On the short term, vegetation formation of these 4 club-rush species is not only determined by survival but also by germination and settlement of the plants, which could be strongly hampered by high densities of macrobenthic species such as *Nereis diversicolor* (Zhu et al. 2016)

Environmental factors may not only determine the current and historical distribution but also the growth characteristics of the plant such as length of the stalk, thickness of the stalk, density of stalks, height of the fertile stem, biomass and growth strategy (Dekoninck 1996; Hoffmann et al. 1997- a). Lieffers & Shay (1981) showed negative effect of increasing inundation depth to the biomass and reproduction of *B. maritimus.* Dekoninck (1996) found similar indications for the *Schoenoplectus* genus but did not differentiate between species. Deegan et al. (2005) found negative effects of salinity and increasing inundation on the abundance and fitness of *S. triqueter*. Lillebø et al. (2003) did similar discoveries with *B. maritimus*. The biomass and stem density of *S. tabernaemontani* and *B. maritimus* decrease with increasing wave height and shear stress (Silinski et al. 2015).

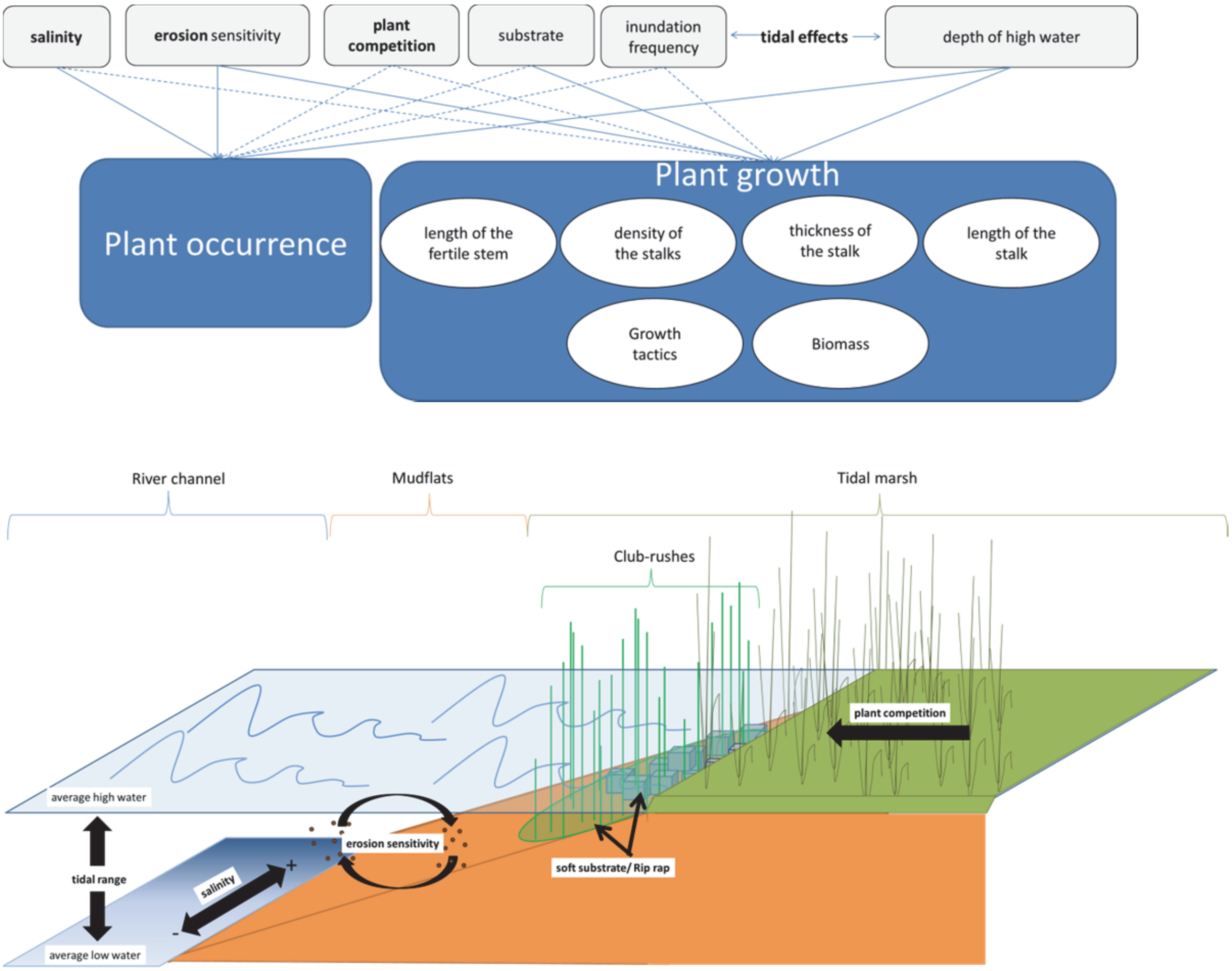


Figure 1: Conceptual model of the potential influence of environmental conditions on species occurrence and morphological response (effects indicated in the upper part by full lines are studied, effects indicated by dotted lines are not included in the study).

To gain insight in the key factors influencing the distribution of the 4 pioneer species, this study explores how environmental conditions in the Sea Scheldt affect the current and historical species distribution, using an explanatory species distribution model (SDM), as well as the morphological response to environmental condition, using linear regressions.

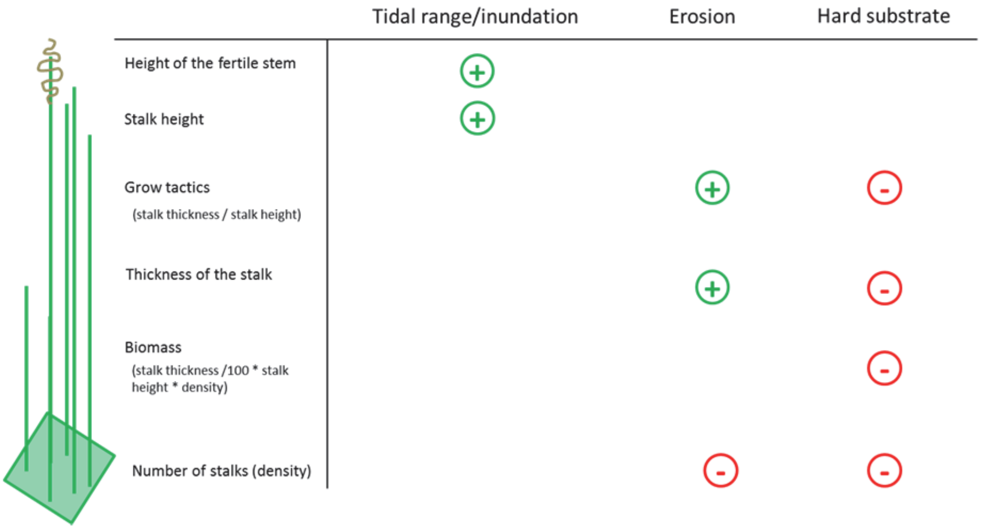
To study effects on plant distribution and morphological response the following **research questions** are considered:

A. In the general species distribution description we examine differences in cross shore distribution between the present distribution and those in 1995 (Dekoninck 1996). Does it stay the same (increase elevation similar to the mean high water rise) or are club-rush species growing lower in the tidal window, tolerating higher water depths?

B. Which environmental variables explain the spatial distribution of early successional club-rushes in the brackish and freshwater parts of the Scheldt Estuary?
    - Based on previous work and current occurrence, we hypothesise that *S. tabernaemontani* and *B. maritimus* will be associated with relatively high salinity levels, whereas *S. triqueter* and *S. x. kuekenthalianus* is/are expected to coincide with the lower range of the salinity gradient.

- We expect the club-rushes to occur within the relatively narrow inundation range indicative for the transition between mudflats and tidal marshes in the Sea Scheldt.

C. Which environmental variables explain the morphological response (physical growth characteristics) of early successional club-rushes in the brackish and freshwater parts of the Scheldt Estuary? Figure 2 gives an overview of the expected morphological responses with respect to different environmental variables.



| | Tidal range/inundation | Erosion | Hard substrate |
|---|---|---|---|
| Height of the fertile stem | + | | |
| Stalk height | + | | |
| Grow tactics (stalk thickness / stalk height) | | + | - |
| Thickness of the stalk | | + | - |
| Biomass (stalk thickness /100 * stalk height * density) | | | - |
| Number of stalks (density) | | - | - |

Figure 2: Hypothesized responses of physical growth characteristics to the investigated environmental variables.

# 2 Material and methods

## 2.1 Study area

The Scheldt Estuary, passing through Belgium and The Netherlands, is one of Europe's largest estuaries and has a total size of around 33.000 ha (Meire et al. 2005). Nature areas within the Scheldt Estuary are of international importance and some are part of the European Natura 2000 network (Decleer 2007). From the mouth in Vlissingen to Ghent, the Scheldt Estuary has a total length of 160 km. The focus area of this study is named 'Sea Scheldt' (blue section in Figure 3). This area is mainly characterized by a single channel system that stretches from the Dutch- Belgian border to Melle near Ghent, with a length of 100 km.

The Sea Scheldt has several tidal tributaries (Rupel, Durme,...) belonging to the estuary (Meire et al. 2005). The downstream part of the Scheldt in The Netherlands is called Western Scheldt. Both are excluded from this study (green sections in Figure 3).

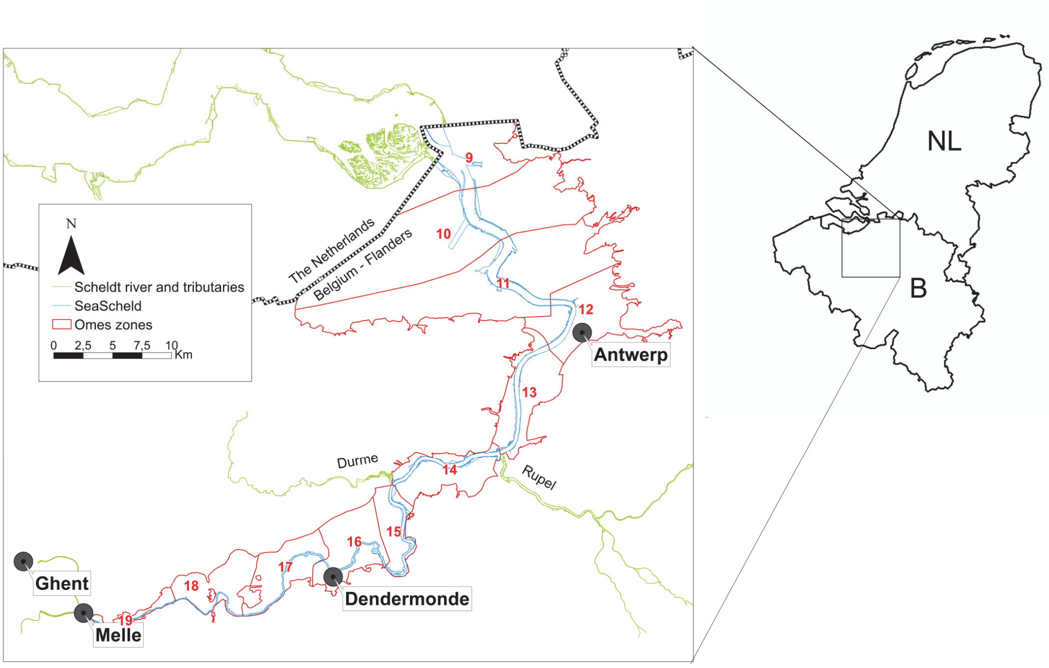


Figure 3: Situation of the Sea Scheldt and its tidal tributaries.

In recent years new managed realignment sites and wetland areas (Controlled Reduced Tide areas) have been connected to the estuary increasing new potential estuarine habitat (Van Ryckegem 2016). Only recent managed realignments are included in this study such as Paardeschor, Lillopolder, Paddebeek.

## 2.2 Studied species

The four species belong to two genera: *Schoenoplectus* and *Bolboschoenus,* and are known as club-rush species belonging to the *Cyperaceae* family. In literature due to the recent taxonomic changes both genera are often referred to as the genus *Scirpus*. Within the Scheldt Estuary hybridization between the 3 *Schoenoplectus* species occurs (De Greef 1999). Determination of the plants was done using an internal protocol of INBO (Research Institute for Nature and Forest , Belgium) that used examination of the stalk for determination based on the Belgian flora of Lambinon et al. (1998). Typically, *Schoenoplectus* species are leafless species growing in clumps/tufts, *Bolboschoenus* has long leaves and has a more sod like growing form. Within the *Schoenoplectus* genus, in general, *S. triqueter* has a sharp triangular stem, *S. tabernaemontani* has a cylindrical shoot while the crossbreed of both species *S. x kuekenthalianus* has rounded triangular stems. It is believed that dispersal of the 4 species is mainly vegetative by means of rhizomes (shoots). Dispersal by seeds is limited and rarely observed (Deegan et al. 2005, Dekoninck 1996). However, Meysman 1996 proofed that seed in the topsoil of the Sea Scheldt, found near club-rush populations could germinate. In his lab experiment germination of *S. triqueter* and *S. x kuekenthalianus* seeds proofed to be weaker than than seeds of *S. tabernaemontani*.

## 2.3 Overview of the analyses

After a general description of the species distribution, the historical distribution of *Schoenoplectus spp.* and *Bolboschoenus maritimus* is compared to estimate the historical and present population of all 4 club-rush species along the river (see 2.4.1).

Species Distribution modelling is used to predict current distribution of each club-rush species separately (see 2.5.4). Modelling is based on measured presence and random selected absence point data (see 2.4.4). The explanatory spatial variables are slope, mean inundation depth (MID) , maximum velocity, inundation time (IT) and frequency (IF).

Morphological responses of species defines how plant physical are challenged by environmental factors. Presence data was based on points measured in the field. Extracted environmental data was averaged per tuft. This data set was modelled in function of measured physical growth characteristics (2.5.5), such as 1) length of stalk, 2) height of fertile stem, 3) thickness of stalk and 4) density of stalks. Volume as measure for biomass, and an expression of grow strategy were derived of the physical growth characteristics.

## 2.4 Data collection and field measurements

### 2.4.1 General and historical description of the club-rush distribution

Historical distribution can be found in Dekoninck (1996) where a general overview is given of *Schoenoplectus* presence in 1995 , per 5 km river segments. This distribution data of Dekoninck is compared to the centroids of polygons extracted from a vegetation map of 2003 developed by Vandevoorde (2016) in Van Ryckegem et al. 2016 and Vandevoorde & Van Lierop (2018) in Van Ryckegem et al. 2018. As for *Bolboschoenus maritimus* the first comprehensive data on distribution is found in the vegetation map of 2003 (Vandevoorde (2016) in Van Ryckegem et al. 2016 and Vandevoorde & Van Lierop (2018) in Van Ryckegem et al. 2018). The 2003 vegetation map was remapped in 2013 (Vandevoorde in Van Ryckegem G et al. 2018). This created the possibility to compare surface area of the 4 club-rush species between these 10 years and even longer for the *Schoenoplectus* species.

Historical changes in elevation and mean inundation depth of 25 club-rush tufts of 1995 (Dekoninck 1996) of the *Schoenoplectus* genus is compared using data of 2013-2017 (*S. tabernaemontani* (n= 8), *S. x kuekenthalianus* (n= 9), *S. triqueter* (n= 8)) to explain changes in club-rush position in the tidal frame during the past 2 decades. Historical data on elevation and location was available in Dekoninck (1996). Historical data on mean high water of 1990 (source: Flanders hydraulics) was used to calculate historical mean inundation depth (MID).

### 2.4.2 Species occurrence

Before conducting field visits a comprehensive map was developed in early summer 2013 to have an indication about the distribution and exact location of tufts. This map originated from different data sources: it was based on the 2003 vegetation map (Vandevoorde (2016) in Van Ryckegem et al. 2016 and Vandevoorde & Van Lierop (2018) in Van Ryckegem et al. 2018) and was roughly updated with observations from a boat survey at low tide. The comprehensive map was digitized in GIS (ArcGIS, ESRI 2017) on a false colour image of spring 2013 (FCIR, resolution of 20x20cm) with an accuracy of 0.5m and later used during field visits.

During field visits, cross-shore width of the tufts was measured. This provided information on precise locations, size and elevation of the vast majority of club-rush tufts in the Sea Scheldt.

### 2.4.3 Field measurements

Field measurements were executed each year between 2013 and 2017 during a period of about 10 days in August. Between 2013 and 2016 almost all tufts belonging to the genus *Schoenoplectus* were located and measured. In 2017, measurements were primarily focused on the more common *Bolboschoenus maritimus,* but also the remaining *Schoenoplectus* tufts were measured. Due to time limits and the high abundance of *B. maritimus* only a subset of tufts were measured for this species. Therefore a stratified selection of tufts were visited that was based on population and OMES zones (shown in Figure 3) and substrate type (anthropogenic rock depositions (rip rap) versus soft substrate) based on an anthropological GIS geo-layer. The population stratum was discriminated using the following criteria: 1) populations were considered independent from each other if tufts were more than 100 m apart, 2) populations were independent when located on the other river bank.

<u>Elevation, exact position and substrate</u>: Elevation and position were measured on the lower, middle and upper part of each tuft (measuring transects, see Figure 4) using a RTK- Trimble R8 device that receives GPS and GLONAS satellites (minimal 4 satellites). When sods were long, measurements were repeated every few meters. For a more detailed description of the method see Annex 1. The measurements had a maximum horizontal precision of 1 cm and a maximum vertical precision of 1,5 cm. Due to a file error the data on precision for 2017 were missing, therefore the precisions of 2017 were not included. A summary of the measurements is available in Annex 2.

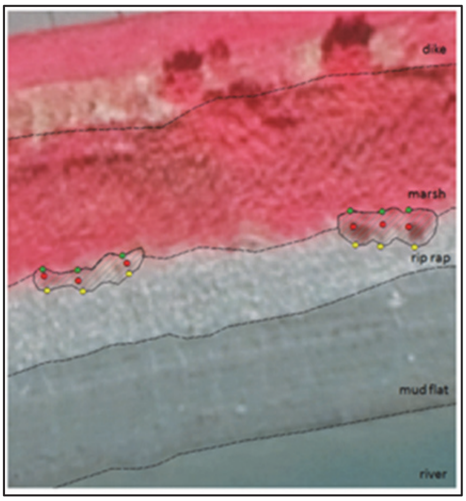


Figure 4: Visualization of field measurements of tufts. Yellow= lower measurement, Red = middle measurement, Green = upper measurement.

<u>Growth characteristics:</u> Data on growth characteristics were collected at a representative location at the centre of each tuft. Information was collected on length and thickness of one stalk (length starting at the base, diameter measured at the base), height of a fertile stem and number of stalks in a square of 20x20cm (density). The 20x20cm square was projected horizontally to standardize for possible impact of

the slope. Using these measurements volume was calculated as a measure for biomass: π* stalk thickness²*stalk height*stalk density. A second variable "growth strategy" was calculated (stalk thickness / stalk height) to indicate growth form.

### 2.4.4 Absence data

To develop a species distribution model (SDM) data are required on locations where species are present and absent. As our presence data provide quasi 100% coverage, absence locations to use in the analyses can be drawn randomly from the remaining area in the Sea Scheldt excluding the presence locations. Absence locations were drawn using a random stratified setup within an area between minimum 55% and maximum 5% inundation time (based on tide measurements of tidal gauges of 2011 until 2013). This is the inundated area where club-rush species were observed during field visits, rounded 5%. A five meter buffer zone around each observed tuft was excluded from random sampling of absences. Stratification was based on habitat type (tidal marsh and mudflats) and OMES zones to ensure scattered sampling. The randomly drawn absence locations were coupled with the vegetation map of 2013, which includes nearly all presences of the 4 club-rush species to check for possible overlap. A total of 10010 absence points were generated. This corresponds with the maximum number of measured points (455) of *S. tabernaemontani* within one OMES zone, multiplied by the number of OMES zones (11) and 2 for tidal marsh and mudflat habitat.

### 2.4.5 Habitat characteristics (GEOData)

According to the conceptual model (Figure 1) salinity, erosion sensitivity, plant competition, substrate (soft substrate or rip rap) and tidal effects (i.e. inundation and high water depth) are of importance to the plant growth and occurrence. Substrate was observed during field visits. Other data were available through raster or spatial data (GEOData) which were than extracted to the position measurements taken during field visits and generated absence data. The following paragraphs discuss the available raster data that could be linked to the variables in the conceptual model. An overview of the used environmental data is given in Table1.

#### *2.4.5.1 Inundation and tidal range*

Several studies indicate that tidal range and inundation regime determine species occurrence. A high inundation regime leads to the drowning of plants whereas in areas with a lower inundation regime species are outcompeted by other plants (Deegan et al. 2005, Dekoninck 1996).

<u>Inundation Frequency (IF):</u> Club-rush species grow in wet soil conditions and withstand some inundation. Inundation frequency is the percentage of the total number of flooding's. The frequency of flooding (in %) is based on tidal water level data (frequency data of 2010-2013 delivered by HIC of Flanders Hydraulic) and a Digital Terrain Model (DTM) of 2013.

<u>Inundation Time (IT):</u> The duration of flooding (percentages of total time) can determine the drowning probability of the species. Data is based on tidal water level data (frequency data of 2010-2013 delivered by HIC of Flanders Hydraulic) and DTM of 2013.

<u>Mean Inundation Depth (MID):</u> This variable describes the extent to which the plants are submerged during high water (in meter). MID is calculated as the mean high water level (MHW, 2010-2013) minus the elevation of the data points (location of presences and absences), both expressed in mTAW (height reference for Belgium).

#### 2.4.5.2 *Erosion sensitivity*

The survival of plants is partly determined by mortality due to erosion of tufts or sods.

Slope of the adjacent mudflat: Steep slopes are more subjective to erosion. A slope map (in %) was based on a 2013 DTM with a resolution of 1x1m and calculated using the slope tool (including eight neighbouring cells) in ArcGIS.

Maximum water velocity: Water velocity defines the physical challenge and the occurrence of uprooting of tufts. Two maximum water velocity maps were provided by Flanders Hydraulics in meters per second (m/s). One raster for flood and one for ebb tide. Data was based on the 2013-scenario output of a numeric 3D- SCALDIS model (Maximova et al. 2016). The maximum value of the combined raster was used.

Shear stress: Together with velocity, shear stress (N m$^{-2}$) determines the hydrodynamic pressure on the club-rush tufts. Raster data were used of the 50 percentile of bed shear stress derived from the same SCALDIS 3D-model.

#### 2.4.5.3 *Salinity*

Many studies indicate the importance of salinity for club-rush species distribution (Podleski 1982, Lillebø et al. 2003, Bakker et al. 1954, Deegan et al. 2004). Salinity is the main determinant of species occurrence along the river axis as there is a longitudinal gradient in salinity. Salinity data was based on raw data from 2010 until 2013 (units: chloride in mg/l) for 13 measuring stations distributed along the Sea Scheldt (OMES, 2015). For each year the maximum value between March and October (the growing season of the club-rush species) was extracted per station. An average of these values was used to develop a new raster layer. The data was then interpolated between measuring stations along the river axis and developed in a new salinity raster in ArcGIS (ESRI 2017).

#### 2.4.5.4 *Other data*

Other data on longitudinal distance to the sea, ship passage intensity (as proxy for wave intensity) and distance to low water were available but were left out due to poor data quality. Germination and shoot survival, as well as plant competition were not included in the analyses.

Table 1: Overview of data used for predictive model.

| | | |
|---|---|---|
| Inundation frequency | | 2010-2013[2] |
| Inundation time | | 2010-2013[2] |
| inundation depth: | Mean high water | 2010-2013[2] |
| | Elevation | 2013[3] |
| Slope | | 2013 [4] |
| Shear stress | | 2013[1] |
| Maximum velocity | | 2013[1] |
| Salinity | | 2010-2013[3] |

Data source:
[1] 3D-numeric model data from the Finel-model/Scaldis model
[2] Flanders Hydraulic
[3] De Vlaamse waterweg
[4] Developed at INBO

## 2.5 Data analyses

### 2.5.1 General and historical description of club-rush distribution

Historical data analyse: The distribution data of Dekoninck (1996) is compared to the centroids of tufts extracted from both 2003 and 2013 vegetation map in the same way Dekoninck (1996) did. The data are visualised with a resolution of 5km segments. Dekoninck (1996) did not publish data on *B. maritimus* but a comparison between the vegetation map of 2003 and 2013 is made instead. *B. maritimus*, however, often grows into large sods that can be over 100m long. To compare with *Schoenoplectus species*, which only grow in tufts of less than 50m, we divided sods into parts of maximum 50m length to have a comparable estimate of plant density. Every part was then regarded as a single entity, giving a more fair representation of the distribution along the river channel.

The method used in the previous paragraphs (same method used by Dekoninck 1996) is a good indicator to look at tuft distribution along the estuary channel but does not consider tuft size. Meaning one large tuft is equal to a small one and if tufts grow together they are becoming and counted as one. Therefore it is more reliable to estimate population size by surface area using the vegetation map of 2003 and 2013.

Historical shifts in inundation depth: To find out if tufts are found on a different elevation or whether or not they tolerate a different mean inundation depth a comparison was made between data of 1995 and data collected between 2013-2017. Dekoninck 1996 made a detailed description on the location and elevation of 25 *Schoenoplectus* tufts. This allows us to compare coupled locations of historical data from 1995 with data collected of nearby tufts from 2013-2017. Coupling of the locations takes care of standardising for differences in tidal range along the river axis. Data on mean high water of 1990 was available through Flanders hydraulics and extracted as explained in 2.4.5. We compared both elevation and mean inundation depth (MID) separately between historical and recent tufts using a linear mixed-effect model. Species, period (historical versus recent) and their interaction were included as factors. Location of the recent – historical tuft pairs was included as random grouping variable.

### 2.5.2 Data transformations

In order to comply with the assumptions of the modelling techniques used, data transformations were performed on the explanatory variables for the SDM and on the explanatory and response variables used in the physical growth characteristic modelling. Transformations were based on visual inspection of the response data and the relation between response data and explanatory variables.

The necessity for data transformation (no transformation, log10 or square root transformation) of the explanatory variables in the SDM analyses was checked by histograms of the values as well as by plotting the response (presence/absence - 1/0) in relation to each variable and fitting a smoothed line (Annex 3). To minimize skewness of the distributions and responses, all environmental variables were transformed using the square root with the exception of MID and IF, which were not transformed.

To minimize skewness of the distributions of the physical growth characteristics, histograms were made for each species and for different transformations (no transformation, log10 and square root transformation). Based upon the histograms the decision was made to log10 transform all physical growth characteristics with the exception of height of the fertile stem which was already normally distributed and growth strategy which was transformed using the square root. Histograms can be found in Annex 4.

To minimize skewness and maximize linearity of the responses to environmental variables, simple regressions were performed between each pair of physical growth characteristics and the original, log10 and squared environmental data. If the explained variation ($R^2$) of the linear regression on transformed data was considerably higher than on the original environmental data, the variable was transformed. Of all the environmental variables only shear stress was transformed using a square root transformation.

### 2.5.3 Multicollinearity

Prior to species distribution modelling explanatory variables were inspected for multicollinearity using Variance Inflation Factors (VIF). A threshold level of < 2 was used for all continuous variables. A higher threshold cannot guarantee independence of the environmental variables and makes results difficult to interpret. By dropping variables with the highest VIF, non-collinearity was preserved. After dropping variables, salinity could be combined witch shear stress, velocity, slope and MID.

For modelling morphological response, checking for multicollinearity was repeated as additional variables not used in the SDM were added (i.e. species identity, substrate (rip rap)). Here a GVIF (Generalized Variance Inflation Factors) was used. GVIF is based upon VIF but can also consider categorical variables (i.e. Species and rip rap). Salinity, MID, IF and IT were correlated with each other (GVIF > 2) and therefore could not be combined in one model. After dropping variables, MID could be combined witch shear stress, velocity, slope and the two fixed factors- species and rip rap.

### 2.5.4 Species distribution mapping

SDM analyses were performed in R (R Core Team 2013) using the biomod2 package (Thuiler et al. 2014). As mentioned in the previous section, the environmental variables salinity, shear stress, maximum velocity, slope and MID were used as explanatory variables. Points where information on environmental variables was missing due to incomplete raster data were left out of the analysis.

Seven modelling techniques were used to build Species distribution Models: a GLM-linear (including all two-way interactions), GLM-quadratic (including quadratic terms and all two-way interactions), GAM (3 knots), GAM (5 knots), maximum entropy (Maxent) and 2 machine learning methods: random forest (RF, 500 trees) and generalized boosting regression trees (GBM, 2500 trees).

By using different models, an informed choice on model selection can be made. In addition to the model fitting criteria for evaluation (see below), a visual inspection of the response curves was done to assess overfitting of models to the calibration dataset (Marmion et al. 2009). Later, the selected modelling techniques were examined for variable importance. For each of the explanatory variables an estimate was calculated to indicate the importance for predicting presence/absence of the species.

1. The complete dataset (presence and absence) was randomly split into two subsets: a calibration dataset which includes 80% of the data and the evaluation dataset containing the remaining 20%. **A first step** of calibration and validation consisted of repeated 'runs' in which the calibration set was further randomly subdivided in an inner-calibration dataset (70% of the data in the calibration dataset) and an inner-validation dataset (30% of the data in the calibration dataset) (Thuiller 2009, models Marmion et al, 2009). The inner-calibration dataset was used for estimating model parameters for each modelling technique and the inner-validation dataset to assess the predictive performance of each modelling technique by estimating AUC (Area Under the Curve) for predicted outcomes (probability of occurrence). For each modelling technique, twenty repetitions (so called "runs") were executed, and for each run a new inner-calibration and inner-validation set were randomly selected. Based on the average AUC over runs for each model, a first selection is made of the modelling techniques with the best predictive fit. **In a second step**, for each of the selected modelling techniques a 'full model' was constructed based on the full calibration set. This model was then evaluated based on

AUC calculated for the evaluation dataset, which consists of independent data that were never used for calibration.

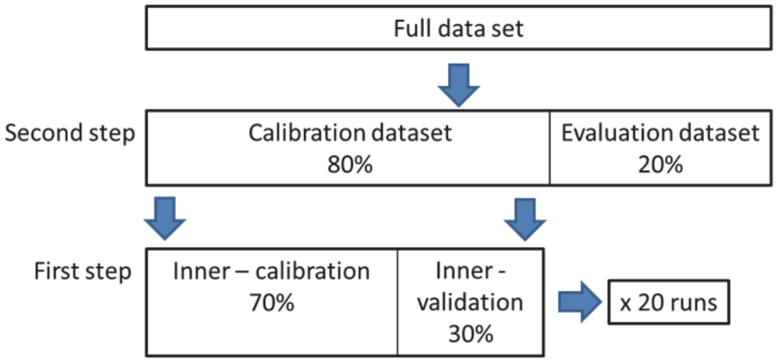


Figure 5: Model calibration and validation.

Relative Operating Characteristic (ROC) is the metric used to validate the 7 models on which the AUC is based. This is based upon the False Positive Rate (1-Specificity) and the True Positive Rate (Sensitivity). Specificity is the proportion of the predictions of the tested data correctly identified as absences. Sensitivity is the proportion of the predictions of the tested data correctly identified as present. The ROC describes the relation between False Positive Rate and True Positive Rate. The higher the area under the ROC curve (AUC), the better the prediction (see Figure 6). AUC values range between 0 and 1 where 0.5 indicates that one model is not better than the other or a random guess (see Figure 6).

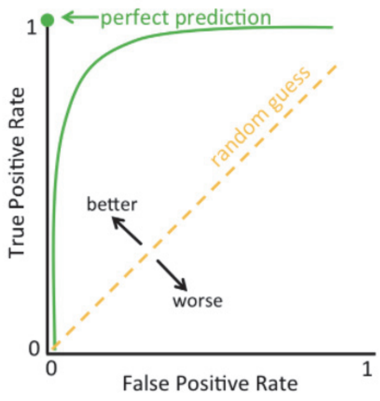


Figure 6: Figurative representation of ROC calculation (image adapted from Bccvl 2016).

Based on the average AUC calculated over the 20 runs for each modelling technique, a first selection of the most appropriate modelling techniques was made. For the most promising modelling techniques, response curves of species occurrence against each environmental variable were plotted. The plotted response curves were used to check for overfitting of the modelling techniques. After controlling for overfitting, the 2 most suited models were selected and used for predictions. Predictions of these selected models were calculated and plotted for the contemporary occurrence.

2. Variable importance (VI): Biomod2 uses variable importance to calculate the importance of environmental variables in explaining species occurrence. VI is defined in function of the correlation coefficient between the initial model prediction and the predictions from 100 runs where the environmental variable in question is randomly permuted between the data points (Thuiller et al. 2009,

Bucklin et al. 2015). The returned score is calculated as 1-the correlation coefficient. Variables with a high score are therefore more important to predict species distribution. VI scores were calculated for each environmental variable and compared between the selected modelling techniques.

### 2.5.5 Morphological response

After testing for non-collinearity, the selected environmental variables were used in linear models to test for their effect on plant growth characteristics. Species identity and substrate (rip rap) were included as categorical factors, the other environmental variables as continuous variables. Two-way interactions of species with all other variables were included. Due to insufficient data on *S. triqueter*, this species was left out of the physical growth analyses. Tukey post hoc tests were used to disentangle significant differences between species.

# 3 Results

## 3.1 General description

### 3.1.1 Species distribution along the salinity gradient

#### 3.1.1.1 *Schoenoplectus triqueter*

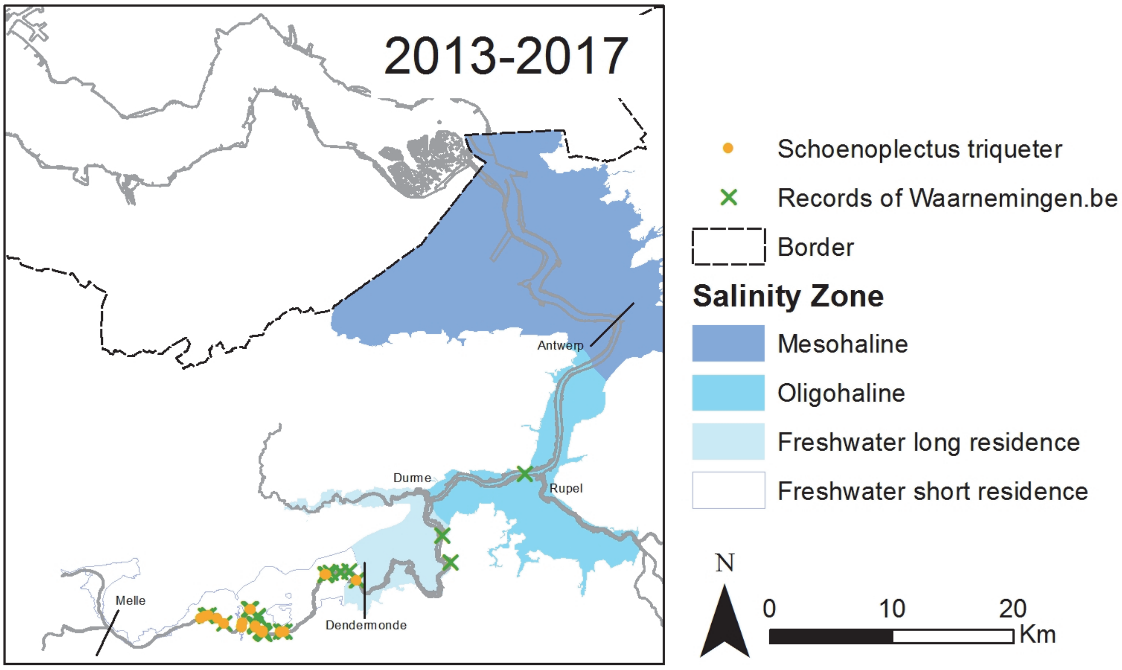


Figure 7: Distribution of *Schoenoplectus triqueter* between 2013 and 2017.

Around 1900, *Schoenoplectus triqueter* (driekantige bies, Triangular Club-rush)was rather common within the Sea Scheldt estuary and its tributary the Durme (Massart, 1907). In 1995 Dekoninck (1996) did an extensive inventory of this freshwater club-rush species in the Sea Scheldt and found 21 tufts between a distance of 70 to 90km from the Dutch-Belgian border. In the vegetation map of 2003 (Vandevoorde (2016) in Van Ryckegem et al. 2016 and Vandevoorde & Van Lierop (2018) in Van Ryckegem et al. 2018) 32 tufts were recorded and some ranged further upstream (up to km 95 from the Dutch-Belgian border) than the species was found in 1995. During field visits between 2013 and 2017 a total of 24 tufts were recorded, less than in 2003. All tufts were recorded in the freshwater zone between 70 and 90km from the border (see Figure 8). This confirms that this species is still rare in Belgium as the species is only present in the Sea Scheldt. Recent citizen science data (waarnemingen.be) has revealed some new observations. Even one tuft was observed in 2016 near the Rupel at 41km from the border (Figure 7). During field control in 2018 no rediscovery occurred indicating the ephemeral condition of the site in this oligohaline area.

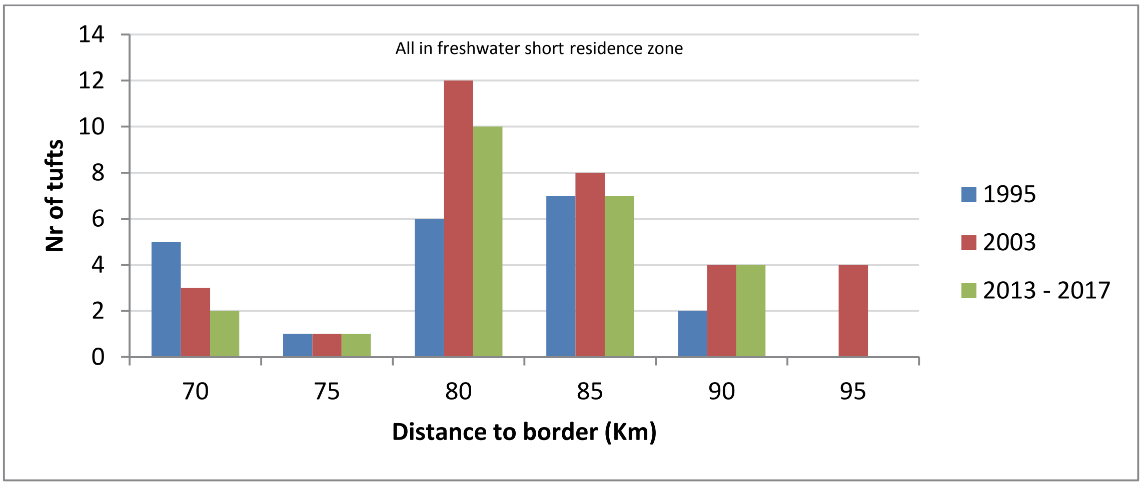


Figure 8: Historical distribution of *Schoenoplectus triqueter.*

### 3.1.1.2 *Schoenoplectus x kuekenthalianus*

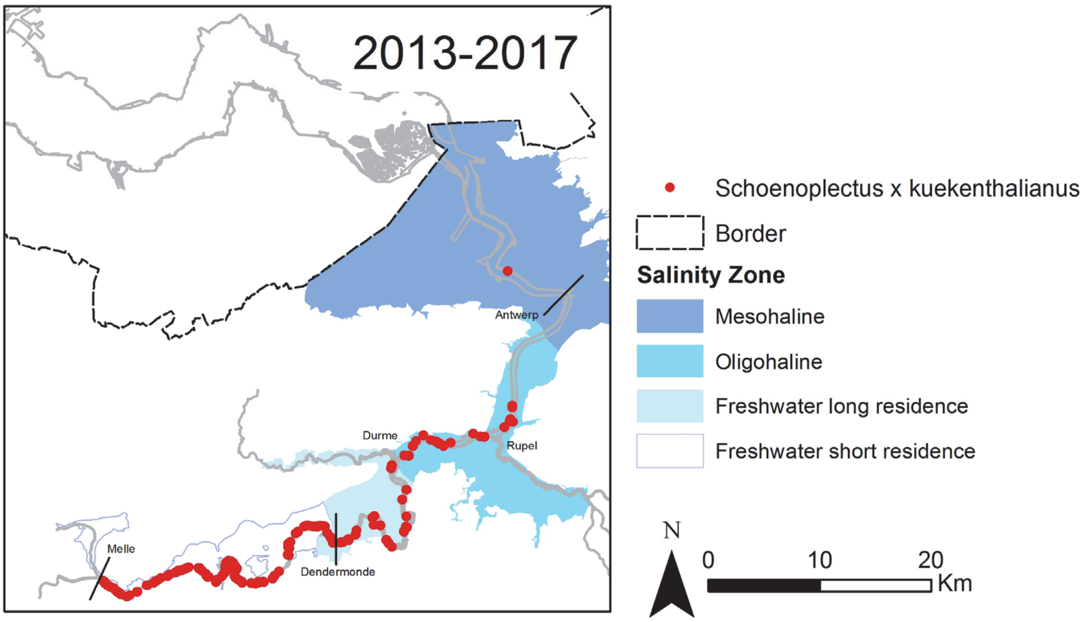


Figure 9: Distribution of *Schoenoplectus x kuekenthalianus* between 2013 and 2017.

In 1995, Dekoninck (1996) found a total of 423 tufts of *S. x kuekenthalianus* (bastaardbies, S.tr x S.tab). The highest abundance of tufts in 1995 was found in the freshwater zone with short residence, between 80 and 100km from the border. Yet, could be found up to 30km from the border. Between 1995 and 2003 the number of tufts declined to 351 but tufts were found more downstream than in 1995. The number of tufts continued to decline to 263 records between 2013 and 2017. The bigger loss of tufts was situated between 80 and 95km of the border (see Figure 10), probably due to dike reinforcements and reconstructions (Sigmaplan). The current range extends to 37km from the Dutch-Belgian border and even one isolated small tuft at 18km from the border into the mesohaline zone (see Figure 9).

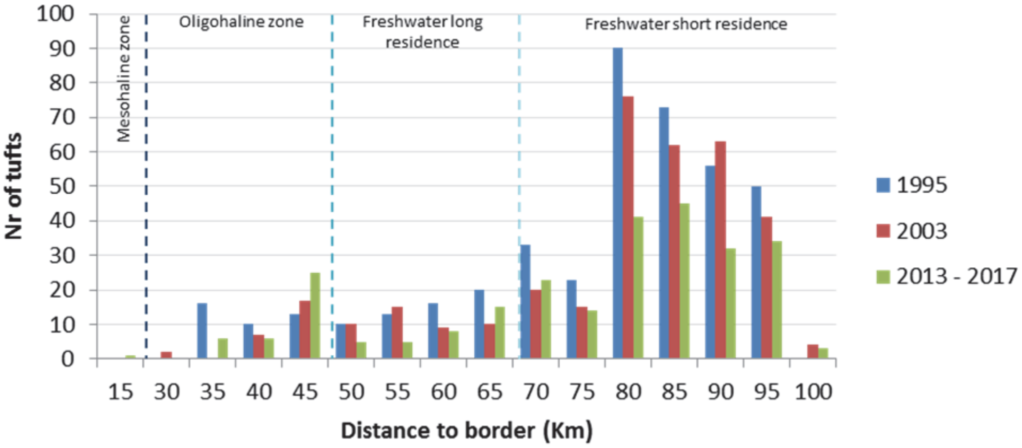


Figure 10: Historical distribution of *Schoenoplectus x kuekenthalianus*

### 3.1.1.3 *Schoenoplectus tabernaemontani*

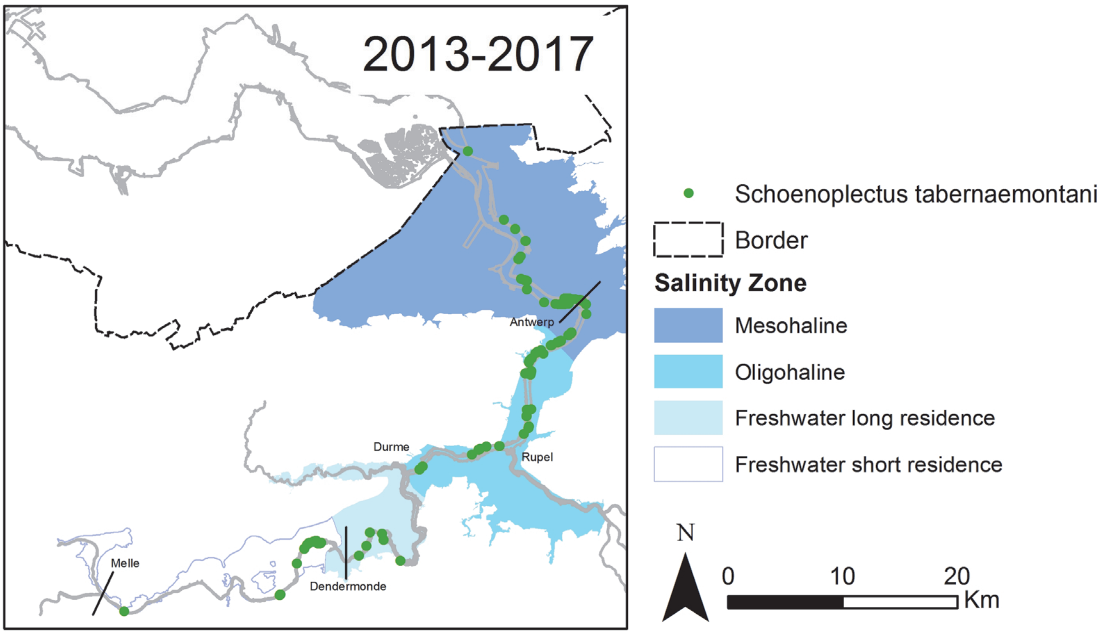


Figure 11: Distribution of Schoenoplectus tabernaemontani between 2013 and 2017.

The first record of *S. tabernaemontani* (ruwe bies, Grey Club-rush) was in 1860 (Hoffmann, 1993 -b). In 1979 the species was found in both brackish and freshwater parts of the Sea Scheldt but had his main niche between the border with the Netherlands and Burcht - at 25km from the border (Dekoninck 1996). Hoffmann et al. (1996), mentioned commercial planting in 1983 of the species downstream Antwerp. In 1993 *S. tabernaemontani* was planted as experiment for alternative shore protection near Appels, 74km from the border (Hoffmann 1996).

The inventory of Dekoninck (1996) in 1995 recorded 23 tufts, making the abundance rather limited. He did, however, not include the experimental and commercial plantings. The species had a wide range between 20 and 95km from the border where the majority of tufts were found upstream the plantings of 1983 (see Figure 12). Most tufts were recorded near the historical plantings (1993 and 1983). Hoffmann et al, 1997 -a expected genetic pollution between plantings and native population. DNA research of De Greef et al. (1999) showed that many tufts were originating from historical plantings. In 2003 the number of tufts has increased strongly up to 132 tufts (Vandevoorde (2016) in Van Ryckegem et al. 2016 and Vandevoorde & Van Lierop (2018) in Van Ryckegem et al. 2018).

Between 2013 and 2017, a total of 186 tufts were identified. Indicating that the number of tufts is still increasing. The most downstream record is at the 'Groot Buitenschoor' near the Dutch-Belgian border in the mesohaline zone (Figure 11), meaning the species can be found throughout the whole Sea Scheldt. The core of the species range is still near the historical plantings at the gradient of meso- to oligohaline zones. This demonstrates the importance of diaspora dispersal (Wolters et al. 2005) by large source populations facilitated by planting.

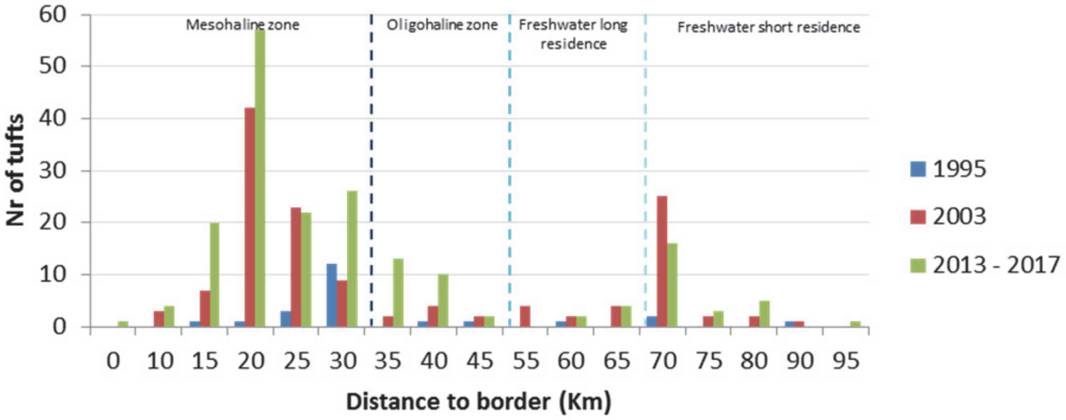


Figure 12: Historical distribution of *Schoenoplectus tabernaemontani*.

**Historical planting of *Schoenoplectus tabernaemontani* in the Sea Scheldt.**

In 1983 commercial planting of *Schoenoplectus tabernaemontani* was done downstream of Antwerp on both sides on the shore line (Linkeroever and Oosterweel). Annually stalks were cut near ground level and used for wickerwork (Hoffmann 1993 - b). Relics of these populations can still be found today and are still the only large contiguous sods of this species found in the estuary. Smaller plantings near Kallo and Burcht were also established. The latter have disappeared due to a historical sand dump (Hoffmann 1993 - b). The plantings near Kallo have been lost, Hoffmann (1993 - b) also pointed at the poor growing of these tufts. Plantings where always done within the growing range of the species. Other small plantings, not for commercial use, with *S. tabernaemontani* happened on the left bank near the 'Kennedy tunnel' and the new managed realignment 'Ketenisse polder'(Vandevoorde 2019) and are still present.

Some experiments with not native *S. tabernaemontani* plant material, from the Ijselmeer and Oude Maas, occurred to test its potential as ecological shore protection in 1993 (Hoffmann et al. 1997-a). Two sites were planted, one at 'De Kramp' downstream Dendermonde and a second at 'Nieuw Schor van Appels' (Hoffmann et al. 1997-b, Hoffmann et al. 1997-a). The planting sites of the 'De Kramp' have disappeared but marshland has extended. This could either be due to or the combination of the historical plantings or the establishment of alternative shore protection. The Appels population has largely been reduced but still persists. After planting, not native tufts wiredraw to higher elevation than nearby native populations as planted tufts could not withstand the inundation depth that native tufts experience (Hoffmann et al. 1997-a). From the 21th century onwards. Losses occurred by succession to reed land and marsh erosion at more high dynamic areas.

#### 3.1.1.4 *Bolboschoenus maritimus*

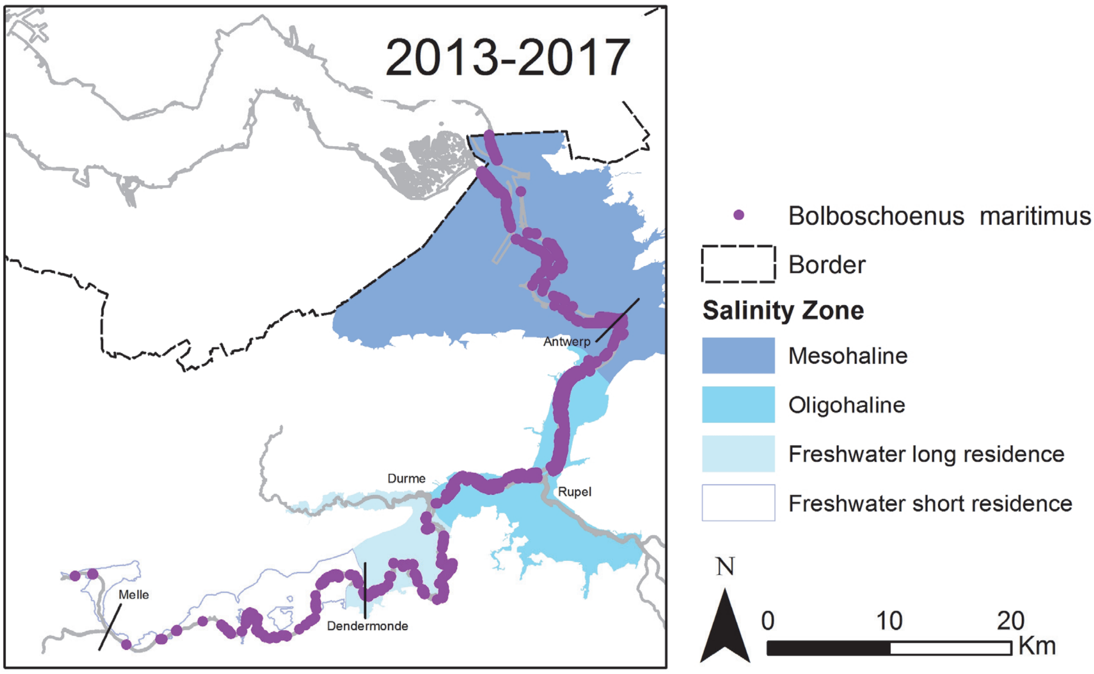


Figure 13: Distribution of *Bolboschoenus maritimus* between 2013 and 2017

Of all species covered in this study, *Bolboschoenus maritimus* (heen, Sea Club-rush) is most spread throughout the estuary. Historical evidence of 1904 show the abundance of large tufts, expanding over the low sloping mudflats downstream Antwerp in 1904 (Image 1) and the Notelaer in 1954 (Image 2).

Image 1: *Bolboschoenus maritimus* near Antwerp in 1904 (Massart 1907, 1908)

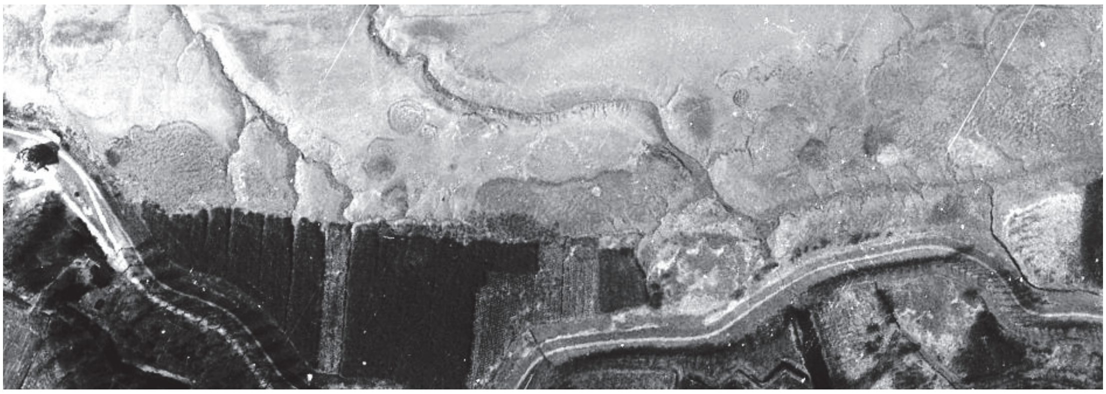


Image 2: Pioneering *Bolboschoenus maritimus* tufts adjacent to the old Notelaer tidal marsh in 1954 (Van Braeckel et al. 2006).

Dekoninck (1996) did not investigate this species in 1995. Yet, Hoffmann (1993 a and b) clearly indicates that the species could be found throughout the estuary in 1992 and preferred the more brackish waters. In 2003 *B. maritimus* appeared to be widely spread throughout the estuary. At the vegetation maps of 2003, 1286 tufts were recorded. Many recorded tufts appeared to grow together into large sods. In the vegetation map of 2013 (Van Ryckegem et al. 2018), 1491 tufts were mapped. This signifies the increasing population of the species. Although the species is in recent years more bound to the upper parts of mudflats, in contrast to historical information, this species is still very well spread throughout the estuary.

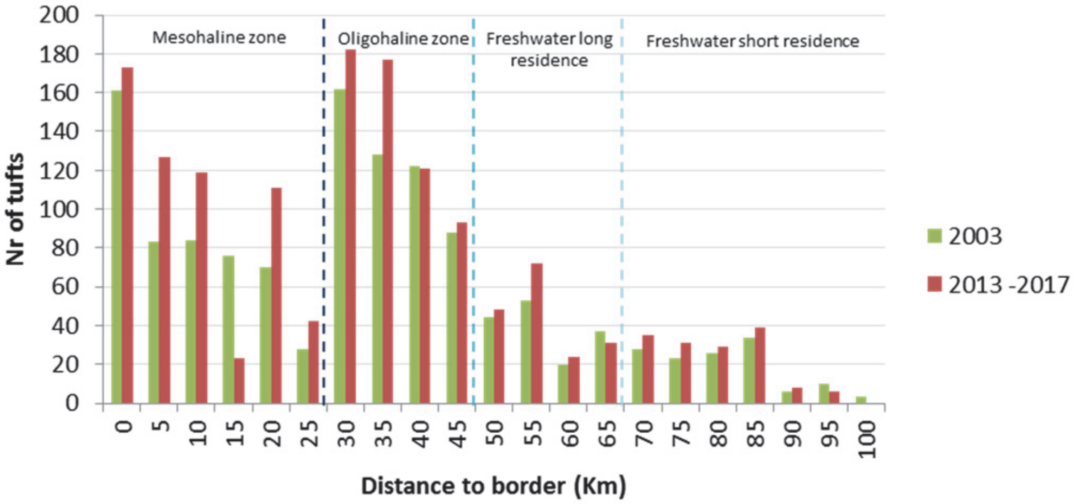


Figure 14: Historical distribution of *Bolboschoenus maritimus*

### 3.1.1.5 *Changes in surface area of club-rush species in the Sea Scheldt*

No high resolution data on surface area between 1990 and 2000 is available. Therefore it is difficult to construct an overall estimation of the total population size of club-rush species before the year 2000. A vegetation map covering the whole Sea Scheldt was made in 2003 (Vandevoorde (2016) in Van Ryckegem et al. 2016 and Vandevoorde & Van Lierop (2018) in Van Ryckegem et al. 2018). This map was revised to the situation in 2013 (Van Ryckegem et al. 2018) and allows to take a closer look at surface increase or decrease of club-rush species and is presented in Table 2.

Table 2: Surface area of club-rush species in the Sea Scheldt estuary between 2003 and 2013.

| **Species** | **2003 (ha)** | **2013 (ha)** | **Δ ha** |
|---|---|---|---|
| *S. triqueter* | 0.03 | 0.02 | -0.01 |
| *S. x kuekenthalianus* | 0.38 | 0.42 | 0.04 |
| *S. tabernaemontani* | 1.87 | 0.66 | -1.21 |
| *B. maritimus* | 17.41 | 17.70 | 0.29 |

## 3.1.2 Tidal elevation in time for the 3 Schoenoplectus species

To find out if the general distribution of tufts on the cross shore profile has changes both elevation and MID were studied. Historical data of tufts (Dekoninck 1996) was coupled to nearby present tufts locations that were measured between 2013-2017. Using coupled data we standardises for the spatial effect of the tidal range along the river axis. This data was used to study changes in both elevation and mean inundation depth between 1995 and 2013 – 2017. To study changes in mean inundation depth, mean high water levels of 1990 and 2013 was used as data of 1995 was not available.

### *3.1.2.1 Elevation*

The elevation of tufts has changed during the last 23 years. All 3 species are found on lower elevation in 2013 than in 1995 (linear mixed model, $P < 0.001$). Furthermore, *S. tabernaemontani* grows on higher elevation than *S. triqueter* and *S. x kuekenthalianus* ($P < 0.05$), see Figure 15. An interaction between species and the different measured years was not significant (normal distribution of residuals and fitted data, see Annex 7). Table 3 shows the absolute change in mean elevation (Δ m) on the tufts locations between 1995 and 2013 and is equal to 27cm for *S. triqueter*, 30cm for *S. x kuekenthalianus* and 58cm for *S. tabernaemontani*.

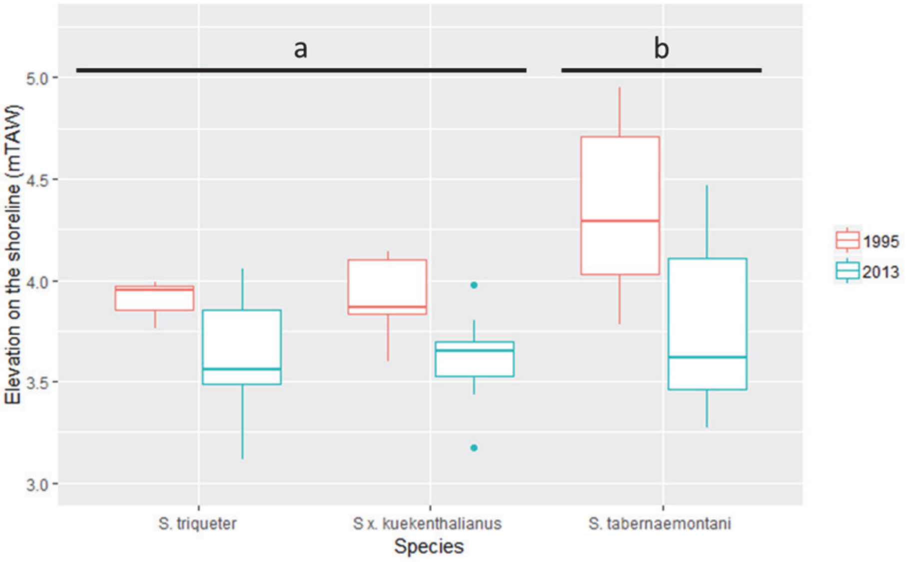


Figure 15: Changes in tuft elevation between 1995 and 2013 where (b) *S. tabernaemontani* is significantly different than (a) *S. triqueter* and *S. x kuekenthalianus* ($P > 0.05$).

### *3.1.2.2 Mean inundation depth*

As explained in previous paragraph species are growing at lower absolute elevation. This could either mean that mean high water decreased so species experience a lower MID and therefore allow them to grow at lower elevation. In the contrary, measurements show an average increase of mean high water of 57 cm at the studied locations. A second explanation would be that the club-rush species are growing at lower elevation and experiencing a higher mean inundation depth (MID) than 23 years ago.

Figure 16 shows the difference in MID between 1995 and 2013 and is significant ($P<0.001$), meaning tufts are enduring a higher MID in 2013 (normal distributed of residuals and fitted data, see Annex 7). Table 3 suggest that the difference between elevation and MID range could also be determent by a higher water level (as Δ mean elevation ≠ Δ MID range, but higher). The same trend is seen for the lower and higher points of tufts, meaning that tufts in a whole moved lower in the tidal window.

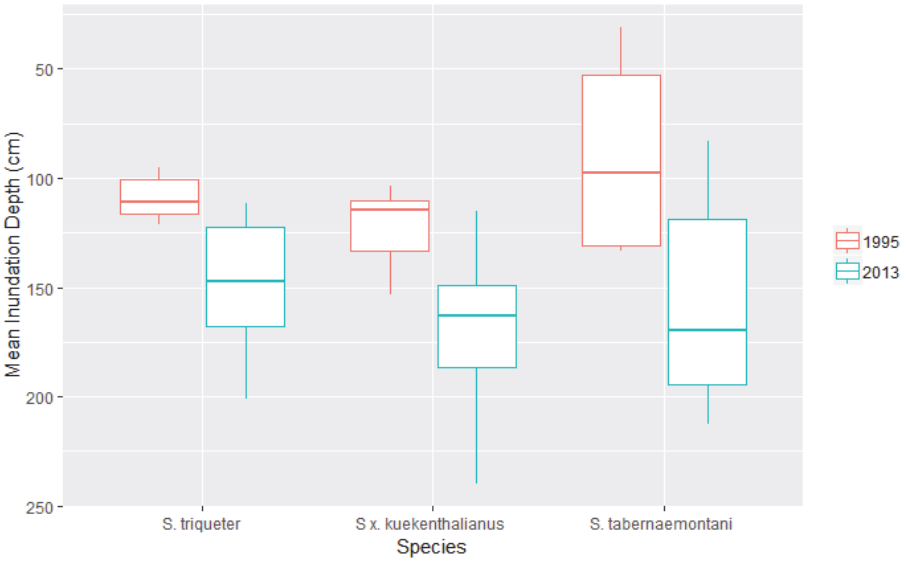


Figure 16: Changes in MID between 1995 and 2013.

Table 3: Change in mean elevation and MID on 26 tufts between 1995 and 2013, low point is the lowest point in a tuft, high point is the highest point in a tuft (MID of 1995 was based on tidal data of 1990).

| **Mean (mTAW)** | | **Mean elevation (mTAW)** | | | **MID range (cm)** | | | **MID low point (cm)** | | | **MID high point (cm)** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | n | 1995 | 2013 | Δ (m) | 1995 | 2013 | Δ | 1995 | 2013 | Δ | 1995 | 2013 | Δ |
| ***S. tabernaemontani*** | 8 | 4.35 | 3.77 | 0.58 | 90 | 158 | 69 | 138 | 198 | 60 | 41 | 110 | 69 |
| ***S x. kuekenthalianus*** | 9 | 3.92 | 3.62 | 0.3 | 121 | 168 | 47 | 177 | 220 | 42 | 63 | 117 | 55 |
| ***S x. triqueter*** | 8 | 3.91 | 3.64 | 0.27 | 95 | 150 | 55 | 143 | 190 | 47 | 58 | 109 | 51 |

As explained above, club-rush species are found lower on the cross shore and endure a higher MID. In theory, this would indicate that the potential habitat range has increased as plants can endure a higher inundation depth (or wider range of MID) and extend their population downwarts the cross shore. Yet, Table 3 (MID low point and MID high point) shows that the tufts extent in its whole did not increase, rather moved to a greater MID or lower elevation. This is very likely due to the competition with other marsh plants that grow above club-rush species.

The theoretical changes in habitat range is exampled in (Figure 17), here elevation and mean inundation depth of all coupled tufts are compared between 1995 and 2013. In case of *S. triqueter* the potential habitat range would theoretical increase downwards the shoreline. The width of the habitat range of *S. tabernaemontani* did not change but shifted downwards. The response of *S. x kuekenthalianus* is different as data of elevation in relation to mean inundation depth of 1995 and 2013 does not show a clear decreasing linear pattern in 1995. This is due to 3 tufts that are found on an elevation higher than 4 mTAW and have a higher inundation (indicated with purple circle in Figure 17) than expected with a linear relationship. This exceptional high growing site in 1995 is a yard that was part of the Sigma dike constructions. This site could be easily colonized by club-rush in the absence of other competitive species. Excluding these sites, the species theoretical habitat range did increase between 1995-2013, similar to the two other *Schoenoplectus* species, downwards the shoreline.

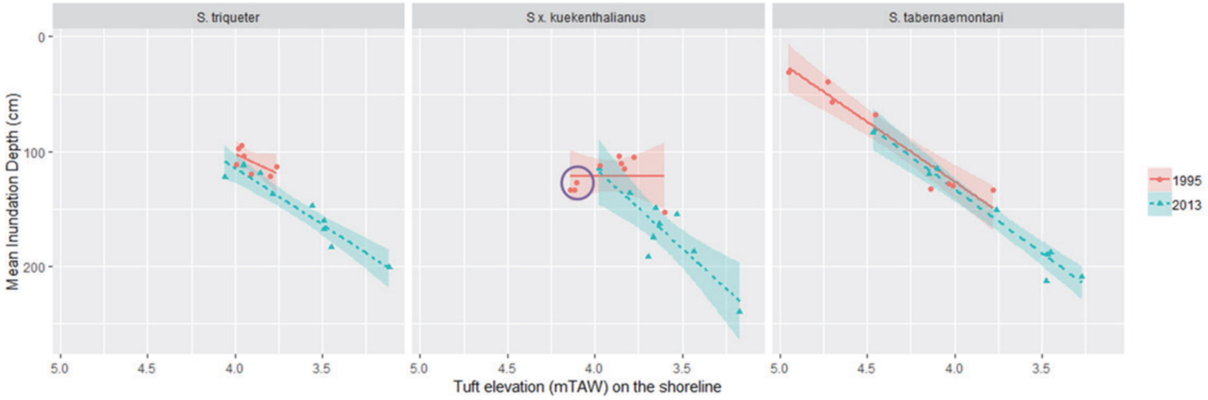


Figure 17: Relation between the elevation of tufts and mean inundation depth between 1995 and 2013. Points within the purple circle represent temporary exceptional high pioneer zones between 1990 and 1995 created after dike constructions.

## 3.2 Species distribution modelling

### 3.2.1 Data exploration and model selection

#### *3.2.1.1 Exploration of the environmental ranges*

Exploratory data analysis suggests that in the Sea Scheldt *Bolboschoenus maritimus* is found in both freshwater and brackish environments with an overall wide range of mean inundation depth (MID) and inundation frequency (IF) (Figure 18). However its vertical range in the tidal window shifts upward towards the higher salinity zones due to salt stress (Van Braeckel et al, 2008). The core the *B. maritimus* population of is located in the downstream brackish areas with lower mean high water levels and inundation time and a gentle slope. Within the *Schoenoplectus* genus, *S. tabernaemontani* has a wider salinity range, similar to *B. maritimus*, with the core of the population in the brackish zone. *S. tabernaemontani* is lower in the tidal window compared to *B. maritimus*.

Both *S. triqueter* and *S. x kuekenthalianus* are freshwater species and occur mainly on upstream, steeper river banks almost only at locations with a 100% inundation frequency and a greater MID. In case of shear stress and maximum water velocity (indicators of erosion sensitivity) there is no clear difference between species but the range is wider for *S. x kuekenthalianus,* S. *tabernaemontani* and *B. maritimus*. This could be related to their wider salinity range and the changes in these characteristics along the salinity gradient.

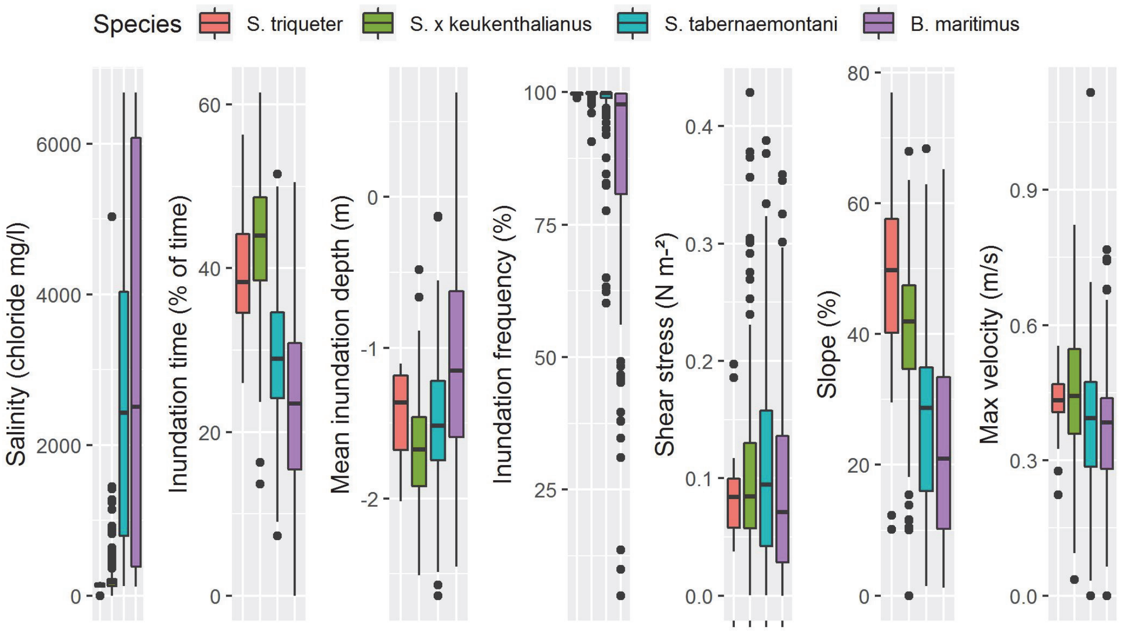


Figure 18: Boxplots showing environmental ranges

For all 4 club-rush species a large part of the field occurrence is on rip rap (Figure 19). Rip rap can therefore not be ignored in the morphological response modelling. *S. x. kuekenthalianus* was found relatively more on rip rap than the other species.

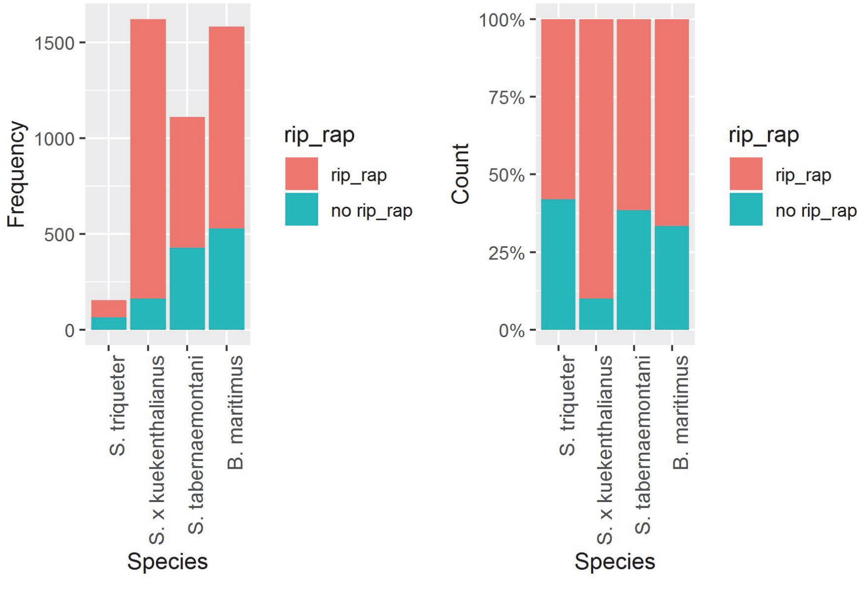


Figure 19: RTK point distribution on rip rap and no rip rap, left the total number of measured points, right the relative frequency of the measurements.

#### *3.2.1.2 Analysis of multicollinearity*

Before developing a regression model explanatory variables are checked on their correlation. This is done using the variance inflation factor (VIF) for multicollinearity. The (G)VIF comparisons of the environmental variables are given inTable 4. The VIF comparison (selection of variable set with all VIF < 2) for the species distribution (presence and absence dataset) dataset resulted in the selection of salinity, shear stress, velocity, slope and mean inundation depth (MID) (Figure 20). Inundation time (IT) and inundation frequency (IF) were both strongly correlated with MID. We opted to keep MID as explanatory variable as data of IT was less precise (5% interval) and IF data was based on interpolated raster data. MID however was partly based on detailed field data. Also MID is less studied in literature while often suggested to be of high importance.

The selection of variables (GVIF, same threshold as for VIF) used in the morphological response modelling (only presence data) resulted in the selection of shear stress, velocity, slope and MID together with species identity and rip rap. Salinity was highly correlated with nearly all other variables and therefore not included. In addition morphological response of club-rush species in relation to salinity is already studied frequently (Podleski 1982, Lillebø et al. 2003, and Deegan et al. 2004). The reason for correlation of salinity for the morphological response and not in the species distribution is due to the increase in data points for the SDM.

Complementary to GVIF a comparison between the continuous environmental data and the presence or absence of rip rap was done using boxplots (see Annex 5). Results show that environmental ranges did not differ drastically between tufts found on or off rip rap.

Table 4: (G)VIF values for species distribution and morphological response modelling

| **Distribution** | | | | **Growth characteristics** | | | |
|---|---|---|---|---|---|---|---|
| All variables | VIF | Selected variables | VIF | All variables | GVIF | Selected variables | GVIF |
| Salinity (sqrt) | 2 | Salinity (sqrt) | 1.3 | Species | 1.61 | Species | 1.31 |
| Shear stress (sqrt) | 1 | Shear stress (sqrt) | 1.3 | Rip rap | 1.27 | Rip rap | 1.19 |
| Max velocity (sqrt) | 1 | Max velocity (sqrt) | 1.2 | Shear stress (sqrt) | 1.57 | Shear stress (sqrt) | 1.56 |
| Slope (sqrt) | 2 | Slope (sqrt) | 1.3 | Slope | 1.92 | Slope | 1.58 |
| Inundation depth | 10 | Inundation depth | 1.1 | Max velocity | 1.63 | Max velocity | 1.56 |
| Inundation time (sqrt) | 18 | | | Inundation depth | 3.24 | Inundation depth | 1.42 |
| Inundation frequency | 5 | | | Inundation frequency | 2.4 | | |
| | | | | Salinity | 4.02 | | |
| | | | | Inundation time | 5.54 | | |

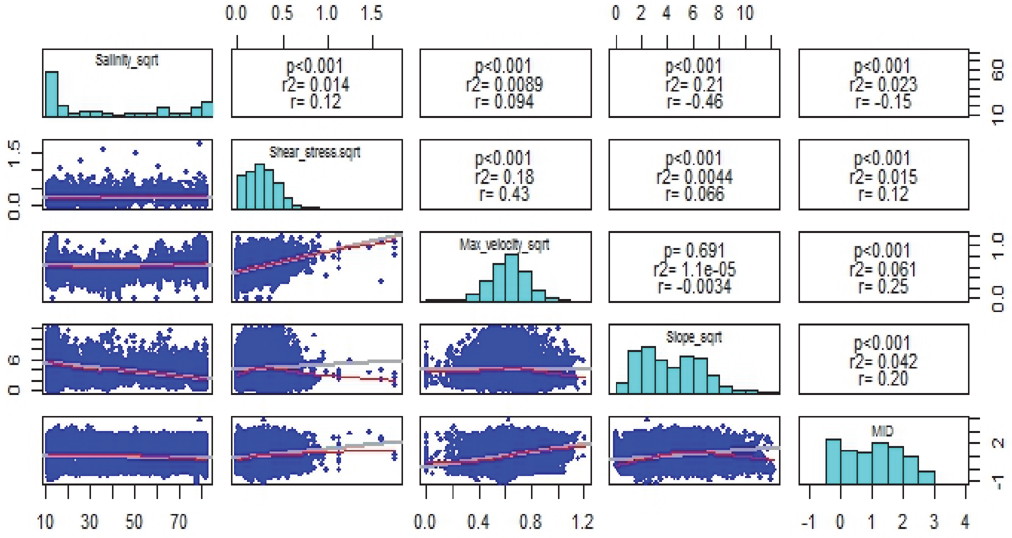


Figure 20: Correlations between selected environmental variables for species distribution modelling

#### 3.2.1.3 *Model selection*

Seven modelling techniques, available in the biomod2 package, were used to build species distribution models for each species. The predictive performance (AUC) of the seven modelling technique for each species is summarized in Table 5. Based on the average AUC over replicate runs, both the machine learning models (RF and GBM) were performing extraordinarily well. These 2 machine learning techniques had an Area Under the Curve (AUC) higher than 0.89 for all species (see Table 5). The Maxent model technique had the lowest AUC for all species. The two GAM models scored differently but increasing the knots from 3 to 5 lead to a higher AUC. The quadratic GLM (GLMq) performed better for all species when compared to the linear GLM (GLMs), and performed comparable to the GAM with 3 knots. After dropping the Maxent algorithm due the low AUC, the decision was made to select the best performing GLM and GAM together with the machine learning techniques. This lead to the selection of GAMk5, GLMq, GBM and RF (bold in Table 5). For these models, the validation (using AUC) of the "full model" was comparable to the average of the calibration runs (Table 5).

Table 5: Predictive model performance (expressed as AUC) of the different modelling techniques both for the full model and the calibrated runs (black coloured cell's). The colour range indicates performance (red = worse, green = better). Model names in bold are the selected models (based on the average performance over runs) for further analysis.

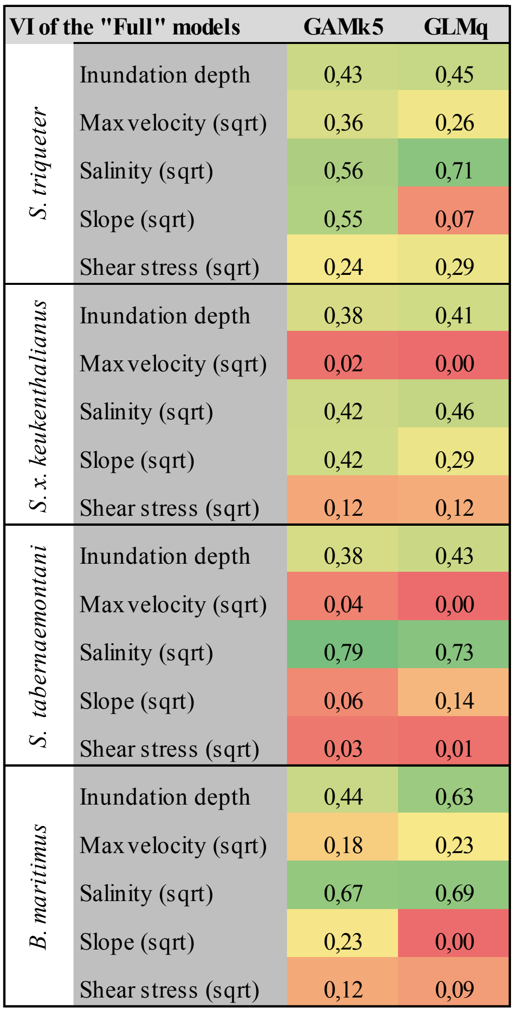
| | | GAMk3 | **GAMk5** | GLMs | **GLMq** | MAXENT | **GBM** | **RF** |
|---|---|---|---|---|---|---|---|---|
| *S. triqueter* | Full model | 0,960 | 0,970 | 0,904 | 0,962 | 0,897 | 0,994 | 0,999 |
| | Avg. RUN | 0,951 | 0,965 | 0,914 | 0,949 | 0,912 | 0,993 | 0,997 |
| | Min RUN | 0,923 | 0,949 | 0,895 | 0,937 | 0,887 | 0,986 | 0,988 |
| | Max RUN | 0,959 | 0,975 | 0,930 | 0,965 | 0,934 | 0,998 | 1,000 |
| *S. x. kuekenthalianus* | Full model | 0,925 | 0,938 | 0,902 | 0,922 | 0,875 | 0,949 | 0,977 |
| | Avg. RUN | 0,922 | 0,936 | 0,902 | 0,921 | 0,882 | 0,949 | 0,973 |
| | Min RUN | 0,916 | 0,930 | 0,896 | 0,912 | 0,875 | 0,943 | 0,970 |
| | Max RUN | 0,927 | 0,944 | 0,910 | 0,931 | 0,894 | 0,956 | 0,976 |
| *S. tabernaemontani* | Full model | 0,862 | 0,881 | 0,804 | 0,857 | 0,629 | 0,928 | 0,994 |
| | Avg. RUN | 0,859 | 0,877 | 0,806 | 0,861 | 0,655 | 0,927 | 0,984 |
| | Min RUN | 0,847 | 0,857 | 0,789 | 0,835 | 0,640 | 0,911 | 0,978 |
| | Max RUN | 0,873 | 0,895 | 0,829 | 0,876 | 0,668 | 0,943 | 0,990 |
| *B. maritimus* | Full model | 0,778 | 0,822 | 0,707 | 0,766 | 0,629 | 0,905 | 0,989 |
| | Avg. RUN | 0,764 | 0,794 | 0,698 | 0,750 | 0,635 | 0,890 | 0,980 |
| | Min RUN | 0,755 | 0,771 | 0,679 | 0,723 | 0,603 | 0,870 | 0,975 |
| | Max RUN | 0,779 | 0,808 | 0,717 | 0,766 | 0,658 | 0,907 | 0,984 |

When inspecting the response curves for each variable (shown in Annex 6) of all species, it can be argued that the machine learning algorithms (GBM and RF) are too flexible and subject to overfitting of the calibration data of all variables. Therefore both GBM and RF were not selected for further model predictions. This leads to the final selection of the quadratic GLM (GLMq) and GAM (knots= 5) (GAMk5).

Variable importance: Both selected modelling techniques (GAMk5 and GLMq) predict salinity as the main factor determining the distribution of each species (Table 6). Likewise, mean inundation depth

(MID) shows to be of importance for all species modelling. In general shear stress is of least importance for species distribution. The importance of slope and maximum velocity depends on the species (Table 6). Maximum velocity is relatively important for *S. triqueter* and *B. maritimus*. The importance of slope is less clear as the results greatly differ between the modelling techniques. Only for *S. x kuekenthalianus* there is a clear (but moderate) importance of slope.

Table 6: VI for the selected modelling techniques. A higher score means a higher importance (green coloured), the lower the score the less important (red coloured).



| **VI of the "Full" models** | | **GAMk5** | **GLMq** |
|---|---|---|---|
| *S. triqueter* | Inundation depth | 0,43 | 0,45 |
| | Max velocity (sqrt) | 0,36 | 0,26 |
| | Salinity (sqrt) | 0,56 | 0,71 |
| | Slope (sqrt) | 0,55 | 0,07 |
| | Shear stress (sqrt) | 0,24 | 0,29 |
| *S. x. keukenthalianus* | Inundation depth | 0,38 | 0,41 |
| | Max velocity (sqrt) | 0,02 | 0,00 |
| | Salinity (sqrt) | 0,42 | 0,46 |
| | Slope (sqrt) | 0,42 | 0,29 |
| | Shear stress (sqrt) | 0,12 | 0,12 |
| *S. tabernaemontani* | Inundation depth | 0,38 | 0,43 |
| | Max velocity (sqrt) | 0,04 | 0,00 |
| | Salinity (sqrt) | 0,79 | 0,73 |
| | Slope (sqrt) | 0,06 | 0,14 |
| | Shear stress (sqrt) | 0,03 | 0,01 |
| *B. maritimus* | Inundation depth | 0,44 | 0,63 |
| | Max velocity (sqrt) | 0,18 | 0,23 |
| | Salinity (sqrt) | 0,67 | 0,69 |
| | Slope (sqrt) | 0,23 | 0,00 |
| | Shear stress (sqrt) | 0,12 | 0,09 |

## 3.2.2 Predicted species distribution of the club-rush species

### 3.2.2.1 *Schoenoplectus triqueter predictions*

Predictions of *S. triqueter* (driekantige bies, Triangular Club-rush) occurrence are slightly different between the 2 models. Using the GLMq model, probabilities of occurrence higher than 0 started at around 55km from the border with the Netherlands and reached the highest predictions (+/-30%) around 87km. More upstream the probabilities dropped to near zero around 95km and increased again to approximately 13% at the upstream reach. Predicted probability of the GAM5k model increased more downstream starting around 50km and reached a local peak of 75% at 75km from the border. Upstream 75km probabilities were generally higher using the GAM5k model than the GLMq model but fluctuated widely up to 87km, where they stagnated at around 13%. Field observations started upstream around 72km from the border.

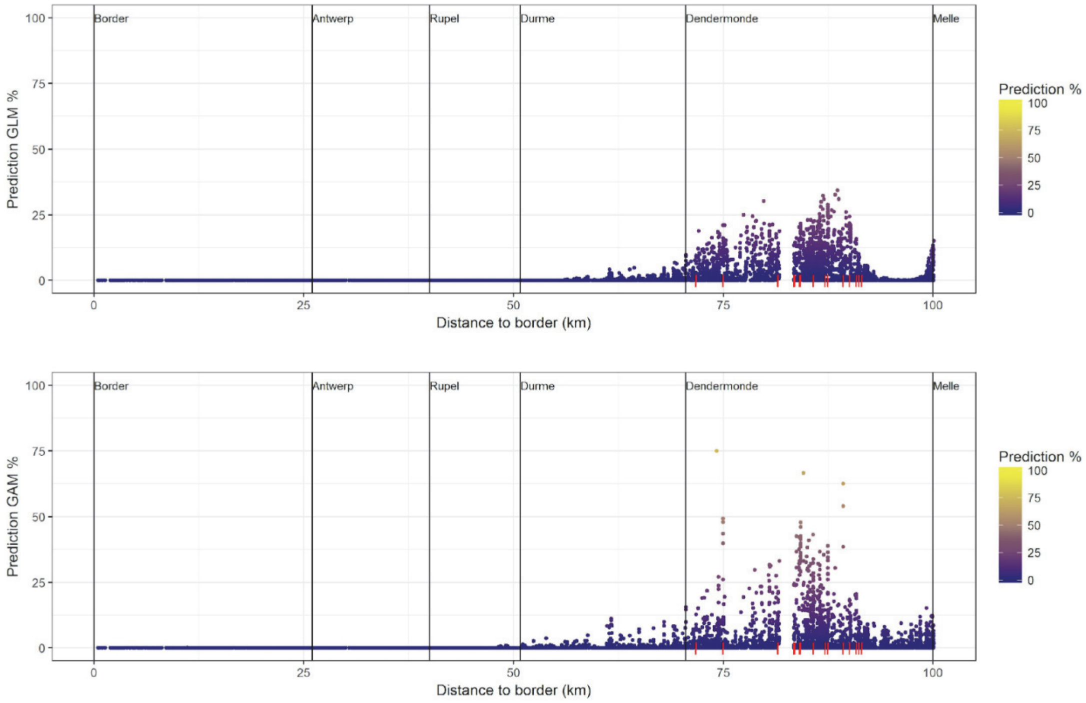


Figure 21: Predicted probability of occurrence along the river axis (from downstream to upstream) for *Schoenoplectus triqueter* using a quadratic GLM model (upper) and a 5k GAM model (lower).

#### 3.2.2.2 *Schoenoplectus x kuekenthalianus predictions*

Occurrence of *S. x kuekenthalianus* (bastaardbies, S.tr x S.tab) was predicted to increase upstream from 25km (GLMq) and 30km (GAM5k) upstream the Dutch-Belgian border in the mesohaline zone. Increase in prediction values stagnated in the fresh water zone near the Durme conjunction( 50km) at around 70-75%.

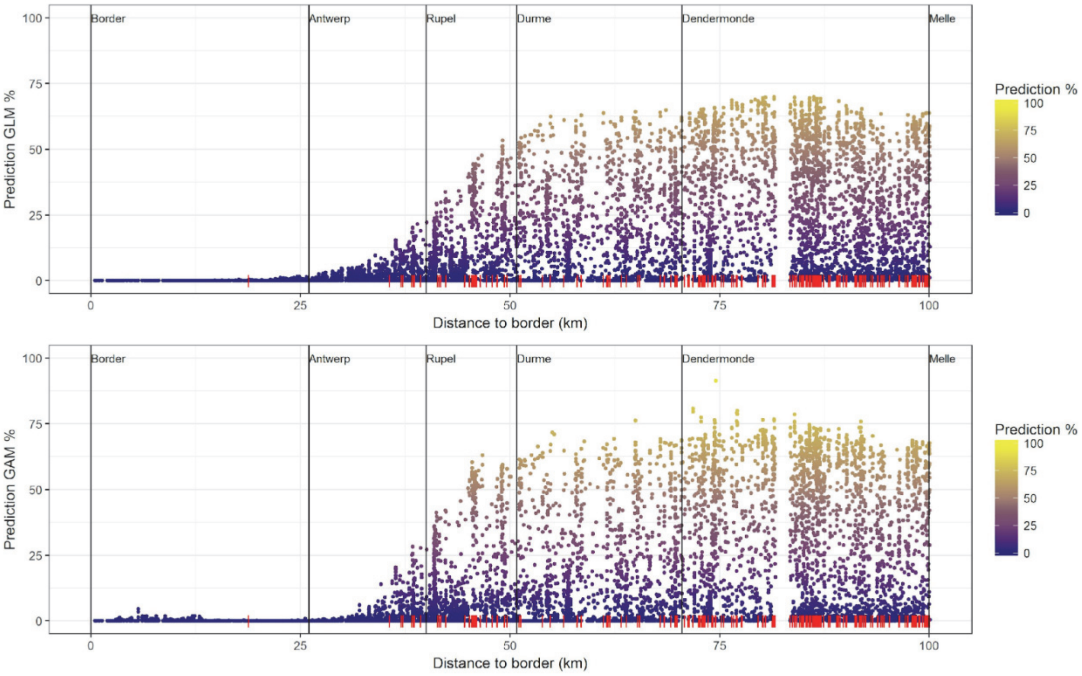


Figure 22: Predicted probability of occurrence along the river axis (from downstream to upstream) for *Schoenoplectus x kuekenthalianus* using a quadratic GLM model (upper) and a 5k GAM model (lower).

#### 3.2.2.3 *Schoenoplectus tabernaemontani predictions*

The GLMq predicted the highest probability of occurrence of *Schoenoplectus tabernaemontani* (ruwe bies, Grey Club-rush) (+/- 60%) upstream 26km, whereas the highest predictions for GAM5k (+/-75%) were found at Antwerp (26 km from the border). Predictions correspond with the core of the present population. GAM5k yielded generally higher predictions across the river section except for the downstream part between the border and 20km. Both model predictions were lower than 12% upstream 50km of the border.

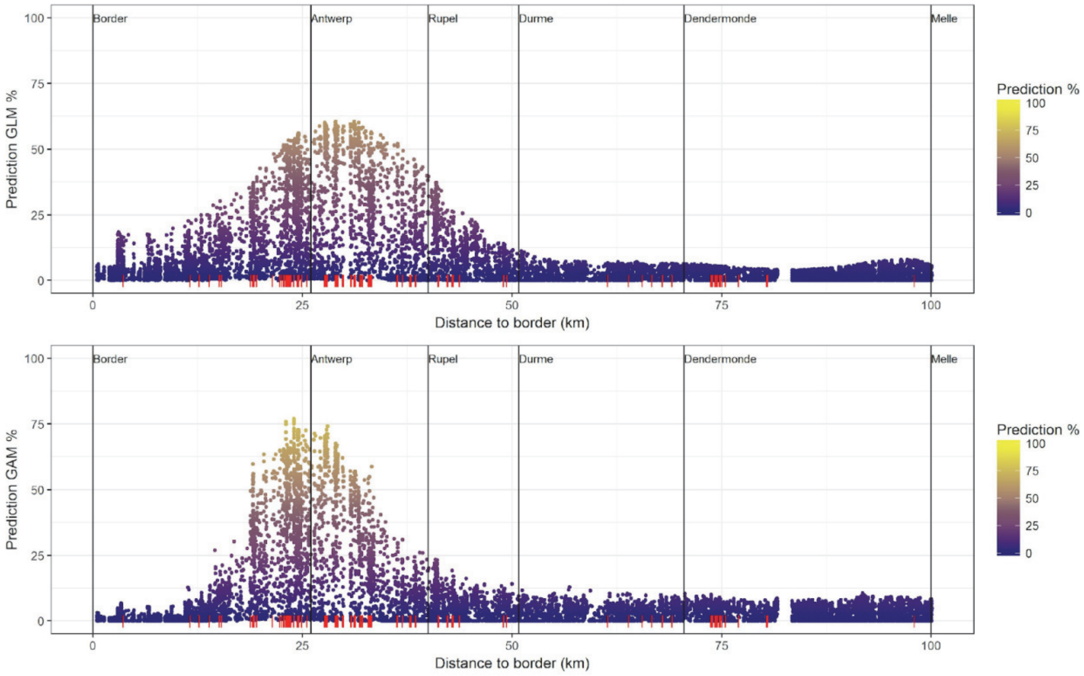


Figure 23: Predicted probability of occurrence along the river axis (from downstream to upstream) for *Schoenoplectus tabernaemontani* using a quadratic GLM model (upper) and a 5k GAM model (lower).

#### 3.2.2.4 *Bolboschoenus maritimus predictions*

Both models predicted a reasonable probability for current occurrence of *B. maritimus* (heen, Sea Club-rush) across the entire study area. Yet predictions are lower (+/-25%) in the fresh water part 50km upstream the border, which correspond with the field observations. The GLMq predicted generally a lower probability of occurrence than the GAM5k model. The highest prediction of the GLMq was 68% and is situated around 26km from the border. The GAM5k model predicted at one point a 96% chance of occurrence at 12km.

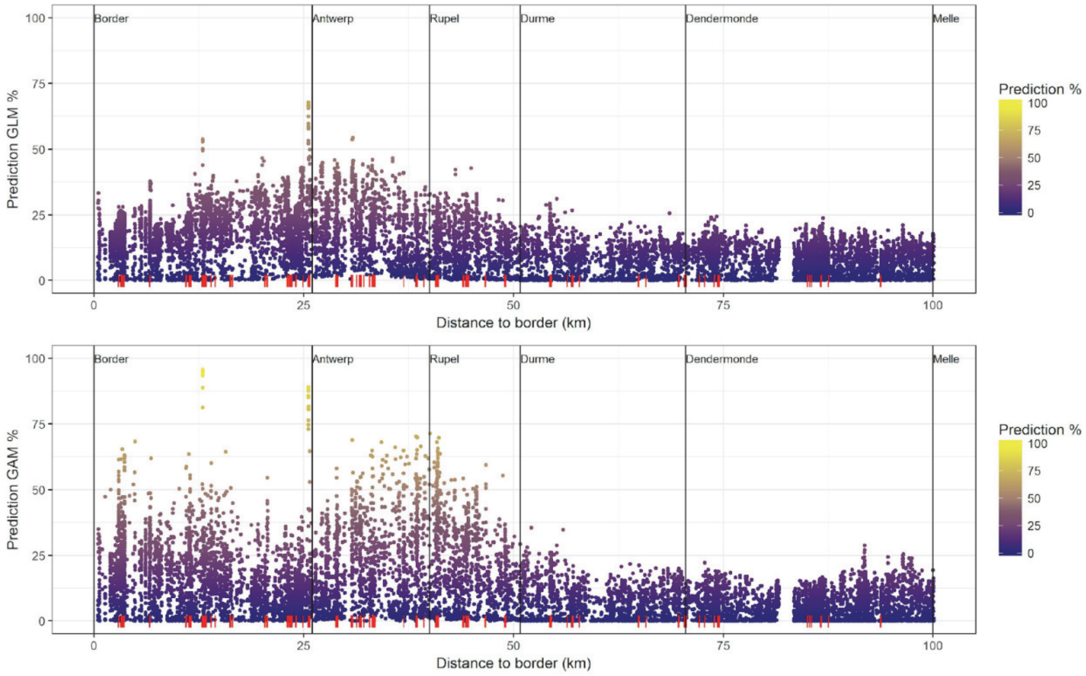


Figure 24: Predicted probability of occurrence along the river axis (from downstream to upstream) for *Bolboschoenus maritimus* using a quadratic GLM model (upper) and a 5k GAM model (lower).

## INTERMEZZO Model predictions of species distribution for a 2050 situation

The obtained species distribution models for the four species can be used to study occurrence probabilities with different sets of environmental data. Consequently the potential for this pioneer ecotope of the tidal marsh can be estimated. Climate scenarios, such as sea-level rise, and different management alternatives can be compared with current predictions using the regression models obtained in this study (see 3.2.1.3).

Within the research framework of 'Integraal plan Boven-Zeeschelde' a first attempt of future 2050 scenario was tested with a 40cm sea level rise in Vlissingen and an increase of the tidal amplitude (Van Braeckel et al. 2019). As morphological responses of the estuary are uncertain, a 2013 bathymetry was used as the basis for the digital elevation model and slope calculations. Mean inundation depth, shear stress and maximum velocity were derived from the 3D-numeric Finel-model, SCALDIS model, developed by Flanders Hydraulics (Smolders et al., 2016). Furthermore tidal marsh plateaus in this inner reach of the Schelde Estuary, de Zeeschelde, are expected to grow steadily with the rise of the mean high water (Temmerman et al. 2004). Therefore the elevation of tidal marsh plateaus wider than 75m were raised according to the expected local high water rise (Figure 25).

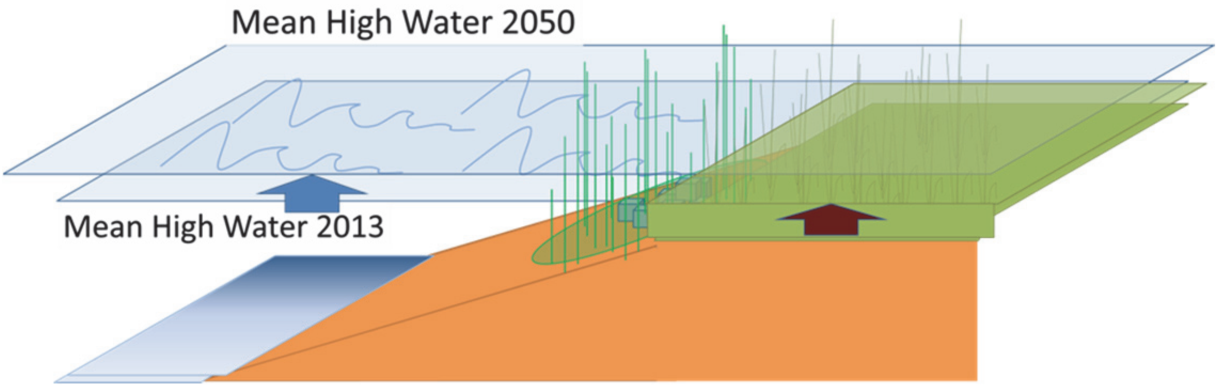


Figure 25: Raise in elevation of the tidal marsh plateau in the used digital elevation model (adapted from Elsen 2018).

Combining this environmental data, the potential occurrence of the 4 club-rush species is modelled for the climate scenario 2050. The result of the modelled species distribution is shown in Figure 26 (adapted from Elsen 2018) where current distribution (faded colours) is compared with the investigated climate scenario anno 2050. Predictions were based on the full GAM5k model.

Based on these results the typical fresh water species, *Schoenoplectus triqueter* and *Schoenoplectus x. keukenthalianus* are severely threatened in this scenario, while the brackish species *Schoenoplectus tabernaemontani* and especially *Bolboschoenus maritimus* still show higher probabilities of occurrence.

To conclude when high mudflats would not raise comparable to the tidal marsh plateaus and the upper estuary is kept in his corset, the survival of *Schoenoplectus triqueter* and *Schoenoplectus x. keukenthalianus* is at stack. Therefore it is necessary to allow natural development of the river banks near the channel to prevent the populations of 'drowning'. Measures such as widening of the river by relocations of the dike is recommended. Planning measures in direct connection to the channel is important to maintain a moderate hydromorphological dynamic level as the chances for pioneer marsh ecotope decreases in time at low dynamic sites due to accelerated tidal marsh vegetation succession with more competitive tidal marsh species.

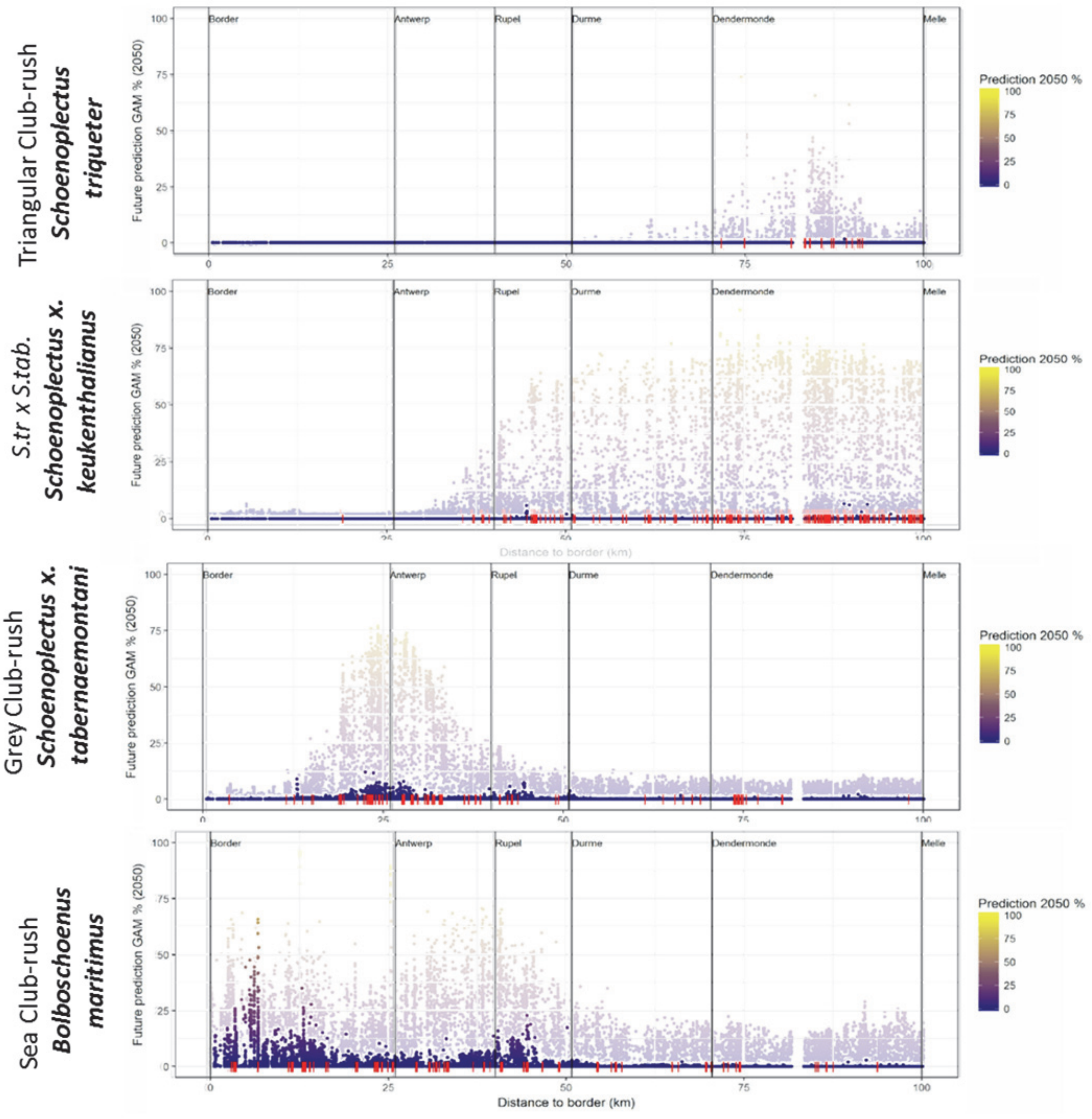


Figure 26: Current (faded colours) and future predicted probability of occurrence for the 4 club- rush species using a GAM5k model (adapted from Elsen 2018).

## 3.3 Environmental effects on physical growth characteristics

After studying the current distribution of the 4 club-rush species the selected environmental variables were used in linear models to study effect on plant morphological response. As mentioned in 3.2.1.2 species identity and rip rap were included and salinity was dropped. Due to insufficient data on *S. triqueter*, this species was left out of the linear modeling. The data on all physical growth characteristics of all species are shown in the histograms of Annex 3.

### 3.3.1 Effects of mean inundation depth

Mean inundation depth (MID) affected all the studied growth characteristics. The morphological response of *B. maritimus*, *S x kuekenthalianus* and *S. tabernaemontani* to a higher MID is similar (except for thickness of the stalks and growth strategy). Shoots of all species increase in length with an increasing mean inundation depth (MID), both for height of stalks ($p < 0.001$, Figure 27-B and) and fertile stems ($p < 0.01$, Figure 27-D and Table 7). Also overall volume ($cm^3$ per 20x20cm) ($p < 0.001$, Figure 27-E and Table 7) and density ($p < 0.01$, Figure 27-C and Table 7) increase with a deeper MID.

A different reaction to an increasing MID is observed for the freshwater species *S. x kuekenthalianus* compared to *B. maritimus* and *S. tabernaemontani* concerning the stalk thickness and growth strategy. While *B. maritimus* and *S. tabernaemontani* grow thicker stalks with deeper MID, *S. x kuekenthalianus* grows thinner stalks ($p < 0.001$, Figure 27-A and Table 7). This also affects the response of growth strategy (stalk thickness/height) to MID For *B. maritimus* and *S. tabernaemontani no clear effect is observed, but* for *S. x kuekenthalianus* there is a clear effect of lower stalk thickness over height with increasing MID ($p < 0.05$, Figure 27-F and Table 7) due to higher and thinner stalks.

### 3.3.2 Effects of substrate

There is a significant effect of the presence/absence of rip rap on the thickness of the stalk depending on the species (interaction effect, $p < 0.001$, see Figure 27 and Table 7). On rip rap stalks of *S. x kuekenthalianus* are clearly thicker. Also stalks of *S. tabernaemontani* are thicker on rip rap, but the difference between presence/absence of rip rap is smaller than for *S. x kuekenthalianus.* For *B. maritimus* the effect of rip rap on thickness of the stalk is very limited. Rip rap also affects plant volume and growth strategy. For plant volume the interaction with species is only marginally significant ($p = 0.06$), but Figure 27 suggests that only for *S. x kuekenthalianus* the volume of the plants is higher on rip rap. For growth strategy the effect significantly depends on the species with a higher thickness over length ratio on rip rap for *S. tabernaemontani* and *S. x kuekenthalianus* and slightly lower ratios on rip rap for *B. maritimus*.

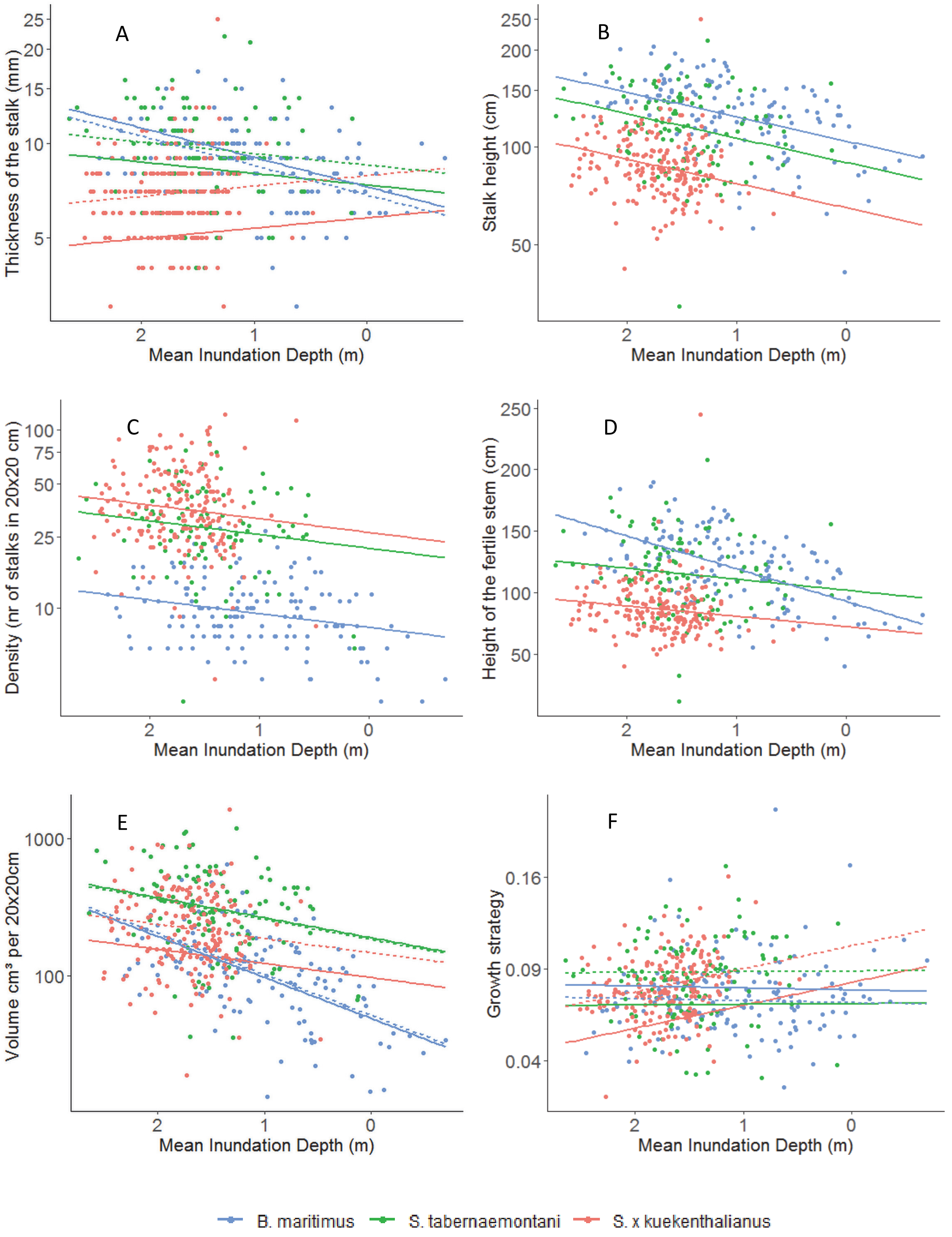


Figure 27: Relations between mean inundation depth and all growth characteristics (reversed x-axis); A: thickens of the stalk, B: stalk height, C: density, D: height of the fertile stem, E: volume cm³ per 20x20cm² (dotted line - stalk thickness on rip rap, full line - stalk thickness on soft substrate), F: growth strategy. Dotted line - effect of rip rap, full line - effect of soft substrate.

### 3.3.3 Effects of erosion sensitivity

The survival of these pioneer plants is partly determined by mortality due to erosion of tufts or sods. Habitat characteristics such as slope of the adjacent mudflat and modelled shear stress (TAU50%) could indicate higher vulnerability to erosion.

Slope:

Slope affects stalk height, density and growth strategy. Stalk height increases slightly with an increase in slope ($p < 0.05$, Figure 28 and Table 7). Slope also has a positive effect on the number of stalks per area unit ($p < 0.05$, Figure 28 and Table 7). Growth strategy is negatively affected by an increasing slope ($p < 0.001$, Figure 28 and Table 7).

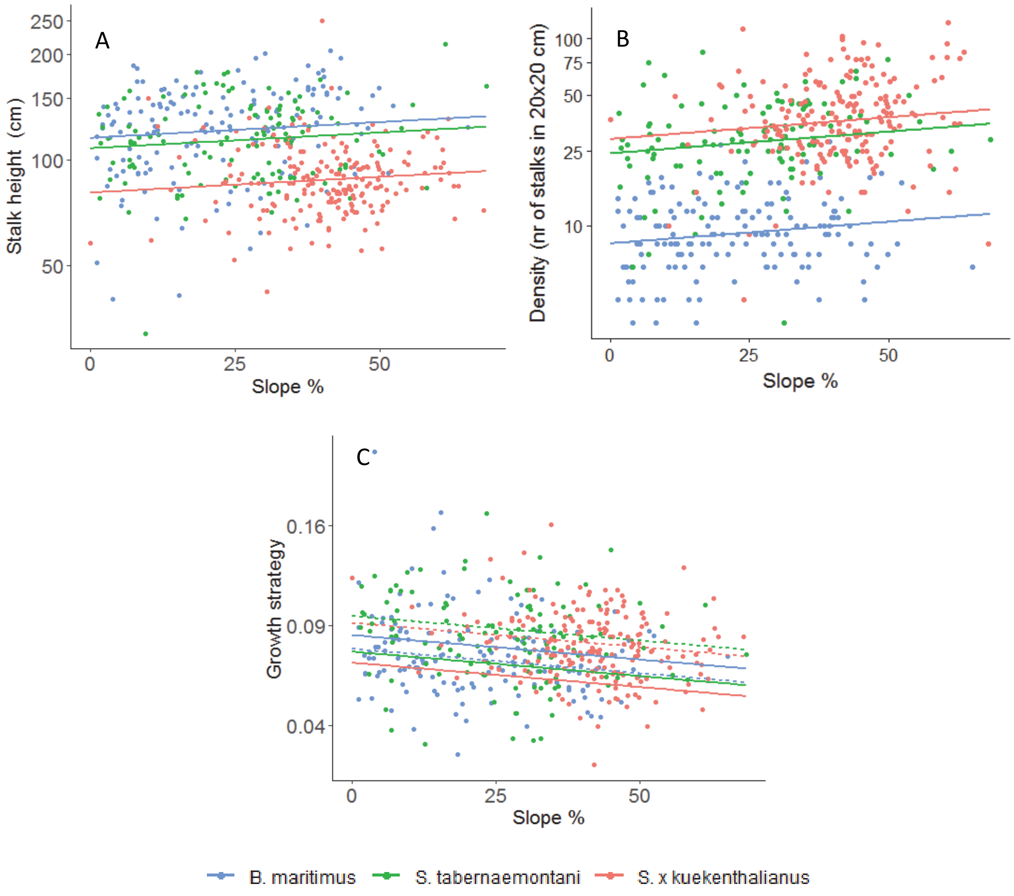


Figure 28: Relation between slope of the river bank and (A) stalk height, (B) density and growth strategy (C). Dotted line – effect of rip rap, full line – effect of soft substrate.

## Shear stress:

The only significant effect of an increase in shear stress is a slight reduction of the stalk height ($p < 0.05$, Figure 29 and Table 7).

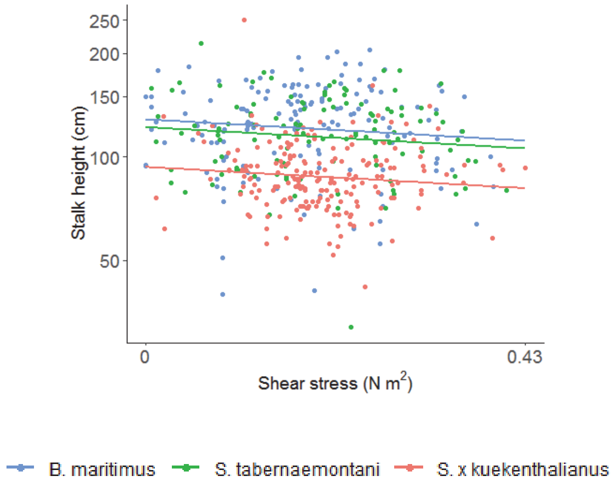


Figure 29: Relation between shear stress and stalk height.

Table 7: Summary of the LM analyses for growth morphological response. Bold are significant effects and interactions; Signif. codes: '.': 0.5 > p ≤ 1; '*': p ≤ 0.05; '**': p ≤ 0.01; '***': p ≤ 0.001

**thickness of the stalk (log10)**

| ANOVA | Sum Sq | f | p | |
|---|---|---|---|---|
| **Species** | 1,453 | 47,900 | 0,000 | *** |
| **rip_rap** | 0,161 | 10,608 | 0,001 | ** |
| **MIDmTAW** | 0,201 | 13,241 | 0,000 | *** |
| Shear_stress.sqrt | 0,039 | 2,555 | 0,111 | |
| Slope | 0,028 | 1,849 | 0,175 | |
| Max_velocity | 0,007 | 0,463 | 0,497 | |
| **Species:rip_rap** | 0,223 | 7,335 | 0,001 | *** |
| **Species:MIDmTAW** | 0,203 | 6,686 | 0,001 | ** |
| Species:Shear_stress.sqr | 0,063 | 2,078 | 0,126 | |
| Species:Slope | 0,022 | 0,709 | 0,493 | |
| Species:Max_velocity | 0,006 | 0,212 | 0,809 | |

Residuals: 7.1733 Adjusted R²: 0.246

**height of the stalk (log10)**

| ANOVA | Sum Sq | f | p | |
|---|---|---|---|---|
| **Species** | 2,174 | 90,595 | 0,000 | *** |
| rip_rap | 0,002 | 0,177 | 0,674 | |
| **MIDmTAW** | 0,355 | 29,606 | 0,000 | *** |
| **Shear_stress.sqrt** | 0,056 | 4,692 | 0,031 | * |
| **Slope** | 0,054 | 4,493 | 0,035 | * |
| Max_velocity | 0,001 | 0,070 | 0,791 | |
| Species:rip_rap | 0,040 | 1,645 | 0,194 | |
| Species:MIDmTAW | 0,032 | 1,351 | 0,260 | |
| Species:Shear_stress.sqrt | 0,021 | 0,858 | 0,425 | |
| Species:Slope | 0,001 | 0,045 | 0,956 | |
| Species:Max_velocity | 0,005 | 0,203 | 0,817 | |

Residuals: 5.3638 Adjusted R²: 0.384

**number of stalks (log10) - density**

| ANOVA | Sum Sq | f | p | |
|---|---|---|---|---|
| **Species** | 17,658 | 193,610 | 0,000 | *** |
| rip_rap | 0,027 | 0,600 | 0,439 | |
| **MIDmTAW** | 0,448 | 9,827 | 0,002 | ** |
| Shear_stress.sqrt | 0,016 | 0,357 | 0,550 | |
| **Slope** | 0,287 | 6,291 | 0,012 | * |
| Max_velocity | 0,002 | 0,033 | 0,856 | |
| Species:rip_rap | 0,086 | 0,942 | 0,390 | |
| Species:MIDmTAW | 0,008 | 0,091 | 0,913 | |
| Species:Shear_stress.sqr | 0,034 | 0,367 | 0,693 | |
| Species:Slope | 0,191 | 2,094 | 0,124 | |
| Species:Max_velocity | 0,055 | 0,600 | 0,549 | |

Residuals: 20.293 Adjusted R²: 0.598

**height of the fertile stem**

| ANOVA | Sum Sq | f | p | |
|---|---|---|---|---|
| **Species** | 119481,000 | 101,953 | 0,000 | *** |
| rip_rap | 440,000 | 0,750 | 0,387 | |
| **MIDmTAW** | 25752,000 | 43,949 | 0,000 | *** |
| Shear_stress.sqrt | 1775,000 | 3,030 | 0,082 | . |
| Slope | 1154,000 | 1,970 | 0,161 | |
| Max_velocity | 1136,000 | 1,938 | 0,165 | |
| Species:rip_rap | 1171,000 | 0,999 | 0,369 | |
| **Species:MIDmTAW** | 7082,000 | 6,043 | 0,003 | ** |
| Species:Shear_stress.sqrt | 889,000 | 0,759 | 0,469 | |
| Species:Slope | 1974,000 | 1,684 | 0,187 | |
| Species:Max_velocity | 908,000 | 0,775 | 0,461 | |

Residuals: 246103 Adjusted R²: 0.361

**volume (log10)**

| ANOVA | Sum Sq | f | p | |
|---|---|---|---|---|
| **Species** | 13,587 | 47,673 | 0,000 | *** |
| **rip_rap** | 0,720 | 5,054 | 0,025 | * |
| **MIDmTAW** | 4,504 | 31,604 | 0,000 | *** |
| Shear_stress.sqrt | 0,223 | 1,566 | 0,211 | |
| Slope | 0,296 | 2,078 | 0,150 | |
| Max_velocity | 0,000 | 0,004 | 0,953 | |
| Species:rip_rap | 0,798 | 2,799 | 0,062 | . |
| **Species:MIDmTAW** | 0,870 | 3,053 | 0,048 | * |
| Species:Shear_stress.sqr | 0,223 | 0,784 | 0,457 | |
| Species:Slope | 0,030 | 0,106 | 0,899 | |
| Species:Max_velocity | 0,115 | 0,403 | 0,668 | |

Residuals: 63,414 Adjusted R²: 0.275

**growth strategy (sqrt)**

| ANOVA | Sum Sq | f | p | |
|---|---|---|---|---|
| **Species** | 0,035 | 13,127 | 0,000 | *** |
| **rip_rap** | 0,018 | 13,528 | 0,000 | *** |
| **MIDmTAW** | 0,004 | 2,814 | 0,094 | . |
| Shear_stress.sqrt | 0,000 | 0,220 | 0,640 | |
| **Slope** | 0,015 | 11,290 | 0,001 | *** |
| Max_velocity | 0,000 | 0,374 | 0,541 | |
| **Species:rip_rap** | 0,036 | 13,741 | 0,000 | *** |
| **Species:MIDmTAW** | 0,012 | 4,655 | 0,010 | ** |
| Species:Shear_stress.sqrt | 0,001 | 0,561 | 0,571 | |
| Species:Slope | 0,001 | 0,531 | 0,588 | |
| Species:Max_velocity | 0,000 | 0,025 | 0,975 | |

Residuals: 0,03632 Adjusted R²: 0,139

### 3.3.4 Difference in growth characteristics between species

Species differences in responses are analysed using Tukey tests. Mean stalk height is significantly different (p <0.001, Figure 27-B, Table 8) between the downstream species *S. tabernaemontani* and *B. maritimus* on one hand and the fresh water species *S. x kuekenthalianus* on the other.

All three species differ significantly in density of stalks from each other (p <0.001, Figure 27-C,Table 8). *B. maritimus* has a low stalk density compared to *Schoenoplectus* species of which fresh water *S*. x *kuekenthalianus has the highest density* . Because of the complexity of interactions between species and MID (see 4.4), Tukey tests between species were not performed for thickness of the stalk, length of the fertile stem, volume and growth strategy.

Table 8: Difference in growth characteristics between species

| **Height of the stalk** | Species | mean (cm) | mean (log10) | std | n | group |
|---|---|---|---|---|---|---|
| | *B. maritimus* | 121,06 | 2,08 | 0,13 | 151 | a |
| | *S. tabernaemontani* | 114,02 | 2,06 | 0,12 | 120 | a |
| | *S. x keukenthalianus* | 87,50 | 1,94 | 0,10 | 194 | b |
| **Number of stalks - density** | Species | mean (n) | mean (log10) | std | n | group |
| nr of stalks in 20x20 | *B. maritimus* | 9,04 | 0,96 | 0,20 | 151 | a |
| | *S. tabernaemontani* | 27,93 | 1,45 | 0,23 | 118 | b |
| | *S. x keukenthalianus* | 36,14 | 1,56 | 0,23 | 194 | c |

# 4 Discussion

## 4.1 Historical and current species distribution of the 4 club-rush species.

The population of *S. triqueter* (driekantige bies, Triangular Club-rush) was already small in 1995 and lost 1/3 of its total area since 1995. The species distribution models predicted a probability of occurrence, albeit low, in the area downstream our mapped populations until the confluence with the Rupel. This would mean that the potential distribution area for *S. triqueter* is wider spread throughout the fresh water part of the estuary. This modelled result is confirmed by the temporary observations from waarnemingen.be (Figure 21). It might also be that this species is a bad competitor and loses competition with other plants quickly, even with other club-rush species as hypothesized by Deegan et al. (2005). Protection of the present populations and opening of new managed realignment sites within the potential occurrence zone are offering new uncolonised frequently flooded river banks could alter the threatened status.

The number of tufts of *S. x kuekenthalianus* (bastaardbies, S.tr x S.tab) have been declining since 1995. Hoffmann (1993 b) and Dekoninck (1996) mentioned that all tufts were found only on rip rap. Likewise between 2013 and 2017 the vast majority of tufts were found on rip rap (90%). The decline between 2003 and 2013 is likely due to recent dike reinforcements and reconstructions as the concentration of lost populations matches the same extent. Yet, between 2003 and 2013 the surface area stayed more or less the same (+0.04ha). The reason of the decline in numbers of tufts but increase in surface area is most likely due to expansion and connection of tufts into larger sods in the more downstream areas.

The number of tufts of *S. tabernaemontani* (ruwe bies, Grey Club-rush) strongly increased since 1995. Although there is a higher abundance of tufts, the surface area of this species has declined with 1,22ha. This is most likely due to the separation of bigger tufts into smaller ones, by expansion of- and competition with reed (*Phragmites australis*) and *B. maritimus* and limited expansion possibilities downwards the mudflats as MID increases. A second reason why the number of tufts have increased will be the establishment of new tufts facilitated by plantings around Antwerp and Appels in the eighties and nineties. De Greef et al. (1999) found, based on genetic analyses, that many tufts originated from these historical plantings as Hoffmann et al, 1997 -a expected. Also, the number of tufts is higher near these planted sites.

*Bolboschoenus maritimus* (heen, Sea Club-rush) is a species that has been historically abundant in the brackish and fresh water part of the estuary and it still is today. The number of tufts did increase the last decade but the total area covered by the species is substantially the same, even increased slightly between 2003 and 2013 . This due to the combination of the expansion of tufts, and the loss by competition with other marsh plants as reed.

## 4.2 Changes in vertical position of the club-rushes between 1995 and 2013

Changes in vertical plant position of the genus *Schoenoplectus* were studied based on elevation and mean inundation depth (MID) using 25 historical records from Dekoninck (1996) coupled to nearby present locations (records from 2013-2017). The same trend for all 3 *Schoenoplectus* species was found: plants grow lower on the shoreline and experience a greater MID. This is likely due to changes in environmental conditions between 1995 and 2013. One reasons could be the improving water quality of the Sea Scheldt since the 90’s (Maris & Meire, 2011 and suggested by Meire el. al., 1992). Another reason could be increased sedimentation rates on the higher mudflat, as shown by Van Braeckel et al. (2014), resulting in better wave and current attenuation (Coops et al. 1996).

This expansion to lower tidal elevations would mean that club-rush species are able to grow on both (historical and present) inundation depths and, theoretically, could have expanded their habitat range along the shoreline. Yet, the surface area of all species did not change drastically since 1995. Table 3 indicates that also the higher limit moved down in the tidal frame. Other factors, possibly competition (e.g. *Phragmites australis*), force the club-rushes to lower tidal elevations (Figure 17). Doing so, they are clearly pioneer species facilitating marsh expansion. Real increase in club-rushes habitat will only be possible in new pioneer areas where club-rushes can settle and cannot be out competed.

## 4.3 Predicted spatial distribution and morphological response of club-rush species

Spatial distribution and differences of habitat range between *B. maritimus, S. x kuekenthalianus, S. tabernaemontani* and *S. triqueter* was explored using Species Distribution Modelling (SDM). The environmental variables used in the modelling clearly influence the species distribution and the morphological responses. Unfortunately, in every graph under 3.2.2 missing data creates a gap around 80km from the border near Wetteren.

The main factor determining the club-rush species distribution along the Sea Scheldt river is salinity. *Bolboschoenus maritimus* was found in higher abundance in more brackish zones but has a broad range of salinity tolerance and can also be found in the upstream freshwater areas. *S. tabernaemontani* is found more in mesohaline and oligohaline environments. The niche of *S. x kuekenthalianus* ranges from oligohaline to freshwater environments while the niche of *S. triqueter* is restricted to narrow stretches in the freshwater zone (Rich et al. 2002, Deegan et al. 2004). Therefore this species is pinched in between competition of larger more adapted freshwater and brackish water club-rush species. Salinity ranges of species do differ (Podleski 1982, Lillebø et al. 2003, Bakker et al. 1954 and Hong-li Li et al. 2011, Deegan et al. 2004) between river systems as other factors in the local environmental conditions can interact and influence the salinity ranges (Deegan et al. 2004).

Together with salinity, the mean inundation depth (MID) is the most important variable to determine occurrence of the club-rushes along the river bank. This is in line with the conclusions of Deegan et al. (2004), Lillebø et al. (2003) and Clevering et al. (1996). *Bolboschoenus maritimus* has a wider range than the 3 *Schoenoplectus* species and is found more frequently higher up the riverbank (Figure 18). However this should be studied in each salinity zone separately, in general this species is found higher up in the tidal frame in de mesohaline zones compared to the situation in de lower salinity zones due to salt stress (Van Braeckel et al, 2008). *Schoenoplectus x kuekenthalianus* can endure the greatest MID. This means that this species can grow on places with a lower tidal elevation and therefore can colonize lower mudflats than other club-rush species. Both *S. triqueter* and *S. tabernaemontani* are more intermediate species.

MID affects the plants growth characteristics. The morphological response of *B. maritimus, S x kuekenthalianus and S. tabernaemontani* to a greater inundation depth are similar (except for thickness of the stalks). All species increase in length with increasing MID, both for the height of stalks and fertile stems which confirms the hypotheses. The ecological rationale would be that plant stalks need to have access to oxygen to respire and keep seeds above water. Therefore plants will grow taller with increasing MID. This is in line with ecological interpretations of Clevering et al. (1996), Deegan et al. (2005) and Dekoninck (1996) and would lead to increased plant volume. Physical growth modelling of *S. triqueter* was impossible because available data was insufficient. Yet, data on growth characteristics is shown in Annex 4.

Environmental variables indicating erosion sensitivity such as slope, shear stress and maximum current velocity have relatively less impact than salinity and MID. However, this response is species specific. For *S. triqueter* and *S. x kuekenthalianus* slope is important. These 2 freshwater species are found more frequently on steeper slopes. Most likely other, competitive species cannot settle or grow lateral on these steep slopes under high environmental pressure with high inundation depth and often covered in rip rap. A steeper slope results in taller stalks and an increase in stalks density, the latter is according to the hypothesis. By an increase in slope the above surface space for stalk growth decreases, stalks will be closer to one another. This can lead to individual stalk competition for light (see Figure 30, below) which leads to higher stalks.

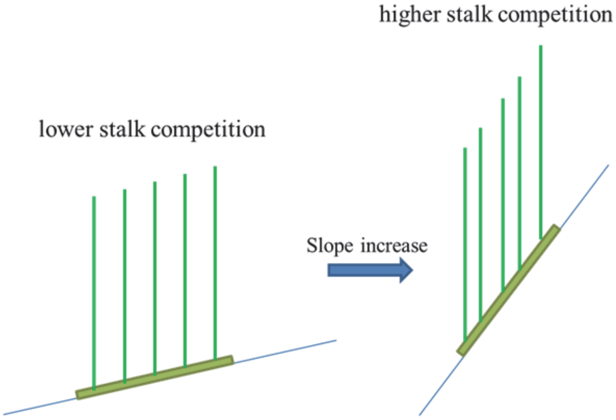


Figure 30: Effect of slope on competition of stalk height.

Effects of erosion sensitivity as indicated by shear stress are noticeable by a slight but significant reduction in stalk height. This more compact growth form could indicate an increase in stress and may result in a change of growth strategy by investing in root development to improve root anchoring. This is however not studies in this paper.

Considering substrate or the difference between soft bottom and hard anthropogenic shores (rip rap) as a factor influencing distribution and morphological response is new. No study has been found including this topic. As a large part of the tufts in the Sea Scheldt are found on rip rap (see Figure 19) it becomes a relevant factor. According to the results of this study growing on rip rap increases the thickness (higher thickness over length ratio) of the stalks for *S x. kuekenthalianus* and *S. tabernaemontani* (Figure 27), and can contribute to an increase in the above ground plant volume (*S x. kuekenthalianus*). *B. maritimus*, in contrast, develops a slightly lower ratio on rip rap than on soft sediments.

Heuner et al. (2015) and Gevers et al. (2012) conclude that changes in morphological response of *S. tabernaemontani* and *B. maritimus* are in fact indications of environmental stress. To fully understand increase in stress on plant performance due to the aquatic environment, growth characteristics could be modelled in function of position towards the river channel or studied by means of controlled experiments.

## 4.4 Study limitations and further research

Van Braeckel et al. (2008) tried to define tidal marsh ecotopes based on salinity and inundation frequency for each OMES zone (Figure 3) separately. However, foolproof abiotic characterization of tidal marsh vegetation's along the complete salinity gradient was not possible based on these two variables solely. Gyselings et al (2011) analyzed all available data, albeit not collected for that purpose, in search for the right abiotic determinants. Their study showed that inundation frequency is not the only important tidal variable and that key abiotic variables vary along the salinity gradient and among vegetation types and species. They suggested well stratified targeted data collection across abiotic gradients, modeling within smaller upstream-downstream ranges and also species models in addition to vegetation model. This study tries to implement these suggestions for the most vulnerable ecotope in the Sea Scheldt: club-ruches in the pioneer zone. More detailed data on environmental variables was collected for each club-rush population along the river gradients and reliable species specific models could be built. However, the number of observations per species was too small for small range models which might yield even better results. Step by step a similar approach can be applied to other key species and vegetation types and ultimately all models combined could yield a complete vegetation model along the Sea Scheldt gradients. However as we move up in the tidal frame also other forcing factors such as soil characteristics, drainage and hydrologic regime increasingly prevail and will call for closure studies. Future studies should focus on these environmental variables on a smaller and local scale, preferably including seasonal changes.

In the previous sections distribution by salinity, tidal effect and erosion were discussed as well as the growth response to these environmental variables. But as Xinhai LI et al. 2013 explains it is highly recommended to discuss limitations of SDM models and the data used. We will not discuss the relevance of SDM for ecology and management as this has been debated in numerous other papers (Xinhai LI et al. 2013, Barbet-Massin et al. 2012, Zimmermann et al. 2009, Guisan et al. 2000). Yet, we will discuss some decisions made during the modelling. It is well documented that machine learning methods (RF and GBM) are performing very well (Marmion et al 2009). They often outperform other modelling techniques (Bucklin et al 2015). However, these techniques are sensitive to overfitting meaning realistic predictions with these techniques are less sustained. Often it is more advised to use techniques generating continuous curves, such as a GLM or GAM (Thuiller et al 2004). This supports the decision to drop the machine learning models in this study for reasons of overfitting. Predictions on rare species distributions are often more accurate than predictions on more common species (Bucklin et al 2015). In this study the AUC for the rare species *S. triqueter* scored indeed higher than the models of more common club-rush species, *B. maritimus*.

Contrary to measurements taken in situ (often more accurate), raster data can contain spatially more extended data or comprises a longer period (e.g. 2011 - 2013). For pioneer species, restricted to small ridges along the tidal marsh raster data is often to coarse (Gyselings et al. 2011) and therefore inaccurate for these club-rush species. In this study, data on environmental extremes (maximum values) where used which increases accuracy of the SDM (Bucklin et al. 2015, Zimmermann et al. 2009). For modelling morphological responses of plants such as growth characteristics in situ measurements of current velocity and wave actions are needed. This could improve the understanding of species reactions to environmental conditions. Further research on morphological responses should focus on precise environmental field data that can be directly related to the growth positions on micro scale. This could be done using proper lab experiments.

Several studies show a potential impact of climate change upon the Belgium coast and the Scheldt estuary (Monbaliu et al. 2014, Lebbe et al. 2008) but never indicate potential shifts in ranges for pioneer species within the estuary. Such information is essential to detect areas for potential march development, and can play a crucial role in nature management decisions for the Sea Scheldt. Data that represent future environmental changes due to climate change or changes in river management is available for such scenario from an ongoing project where future 2050 system scenarios are investigated (Integrated Plan Upper-Sea Scheldt or IP 2050 (WenZ 2013)). Biomod allows predictive modelling of different scenarios, as demonstrated in the “INTERMEZZO ” using the current obtained models. The comparison between current and future scenario occurrence can indicate survival of species under different future management or climate scenarios as explained in more detail in Elsen (2018) and Van Braeckel et al. (2019) were also the future survival probability of *Schoenoplectrus triqueter* is discussed in greater detail.

Future studies can focus on the importance of competitive species like reed or on the co-occurrence of club-rush species on the cross shore distribution in relation to environmental variables. Our field dataset did not allow such research as data on plant competition was not available and co-occurrence was rather rare. A comparison using the survival probability of the predicted species distribution, obtained after SDM, can already give first insights but would be better examined using field experiments. Co-occurrence of different club-rush species can reveal functional differences between species in function to march erosion by wave as Coops et al. (1996) showed using *Schoenoplectrus lacustris* and *Phragmites australis.*

# 5 Conclusions and management recommendations

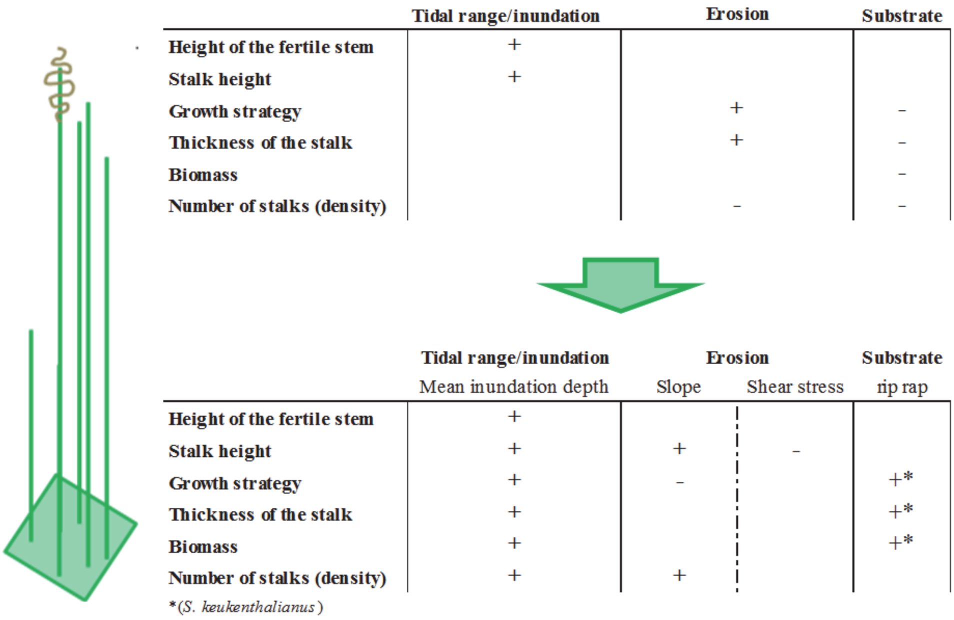
## 5.1 Conclusions

This research characterizes habitat suitability for 3 *Schoenoplectus spp*. and *Bolboschoenus maritimus* within the Belgian Sea Scheldt estuary and studies current and historical population. In the general description we assessed the evolution of the population size over the last 2 decades. *Schoenoplectus x kuekenthalianus* and *Schoenoplectus tabernaemontani* are more widespread throughout the estuary since 1995 but likely have shifted from more large tufts to smaller tufts. *Schoenoplectus triqueter* stays a rare species. The population *Bolboschoenus maritimus* did not change drastically the last 2 decades. Difference in club-rush position along the shoreline between 1995 and 2013 changed. Nowadays tufts are found at a lower elevation than in 1995. Doing so, tufts experiencing a higher inundation depth. In general, the status of the club-rush species is improving, especially in the more downstream area of the Sea Scheldt. This might be due to a better water quality and/or sedimentation on the higher mudflatzone.

Yet, the *Schoenoplectus* species may experience more stress due to competition with other more common tidal marsh species and a changing environment other than water quality. Leading to a practical status quo in population size. As changes in environment (other than water quality) are crucial for the more rare species, like *Schoenoplectus triqueter,* modelling of future scenarios is performed in Elsen (2018).

A second objective was to develop a species distribution model (SDM) for all 4 club-rush species in the Sea Scheldt Estuary in Belgium. This SDM was used to indicate the main factors determining distribution and predict possible distribution. Predicted distribution corresponds with the field observations indicating a good fit of these models. Therefore the method used proofed to be useful for habitat modelling of species. Salinity and mean inundation depth were the 2 major factors determining distribution. The importance of velocity, shear stress and slope to the species distribution were different between species.

Besides species distribution, response of growth characteristics to environmental factors were clearly defined by inundation depth, erosion sensitivity and substrate. Interesting enough environment variables have more influence on the growth characteristics than expected. Mean inundation depth had a positive effect on all growth characteristics. In general plants standing at deeper inundation depth grow in denser tufts and have thicker and longer stalks (with the exception for *S x. kuekenthalianus*). Erosion as well as substrate plays a minor role in shaping growth characteristics. Slope, a variable believed to stimulate erosion, lead to denser tufts with longer leaves. Shear stress, another erosion variable, has a negative effect on stalk height. On anthropogenic rock depositions (rip rap) *S. x kuekenthalianus* and *S. tabernaemontani* develop thicker stalks which changes the plant volume and/or growth strategy. These changes in morphology could indicate stress conditions.



| | Tidal range/inundation | Erosion | Substrate |
|---|---|---|---|
| **Height of the fertile stem** | + | | |
| **Stalk height** | + | | |
| **Growth strategy** | | + | - |
| **Thickness of the stalk** | | + | - |
| **Biomass** | | | - |
| **Number of stalks (density)** | | - | - |

| | Tidal range/inundation | Erosion | | Substrate |
|---|---|---|---|---|
| | Mean inundation depth | Slope | Shear stress | rip rap |
| **Height of the fertile stem** | + | | | |
| **Stalk height** | + | + | - | |
| **Growth strategy** | + | - | | +* |
| **Thickness of the stalk** | + | | | +* |
| **Biomass** | + | | | +* |
| **Number of stalks (density)** | + | + | | |

*(*S. keukenthalianus*)

Figure 31: summary of hypotheses and conclusions

This study is a another step towards a better understanding of changing habitats within the Sea Scheldt. The fact that club-rush species nowadays are found throughout the estuary makes it easy to assess the probability of pioneer-marsh development. Our results can not only be used to detect changes in population due to a changing environment but also predict potential habitat.

## 5.2 Management recommendations

Clubrush vegetations almost disappeared in the 20th century and, especially in the fresh tidal part of the Sea Scheldt, they currently experience severe environmental pressure. In the last two decades an hesitating recovery process shows but habitat characteristics differ greatly from the historical situation or from 'references' in other estuaries such as the Elbe, Dordogne, former Bieschbos or oude Maas as well as some British and Irish estuaries. Steeper slopes, defended shores, bigger tidal amplitudes and current velocities, smaller growing spaces and hence different stress and competition conditions characterize the current club-rush habitat. In the fresh water parts of the Sea Scheldt, current habitat are existing almost only out of rip rap. The question remains if in the future these club-rush species can survive this environment. Creating more suitable intertidal habitats with gentle and less dynamic slopes is therefore highly recommended.

The protected *Schoenoplectus triqueter* is found to be the most vulnerable species in the Sea Scheldt. To prevent its extinction in Flanders special attention should be paid to its habitat needs and the protection of the few existing populations:

1. Detailed monitoring of the remaining populations in relation to (changing) environmental conditions.
2. Study and facilitate alternative habitats outside the estuarine channel (new managed realignment sites or flood controlled areas)
3. If populations are threatened by infrastructure works, tufts can temporarily be transplanted with limited success. Aiding by restocking can help survival.

We improved our knowledge on environmental conditions for the current club-rush populations in the Sea Scheldt, their morphological response to certain stress factors and models were developed that can to a certain extent predict spatial population and species distribution under different scenario's .

However, some aspects still need more clarification :

1. Key forcing factors (salt, inundation regime, slope, current velocity, water quality, wind and ship waves):
    - Species specific ecological optimum,
    - Species specific ecological boundaries.
2. Competition strategies
    - Between different club-rush species.
    - Between club-rushes and other vegetation types.
    - That might threaten the most vulnerable species.
3. Functional differences between club-rush species.

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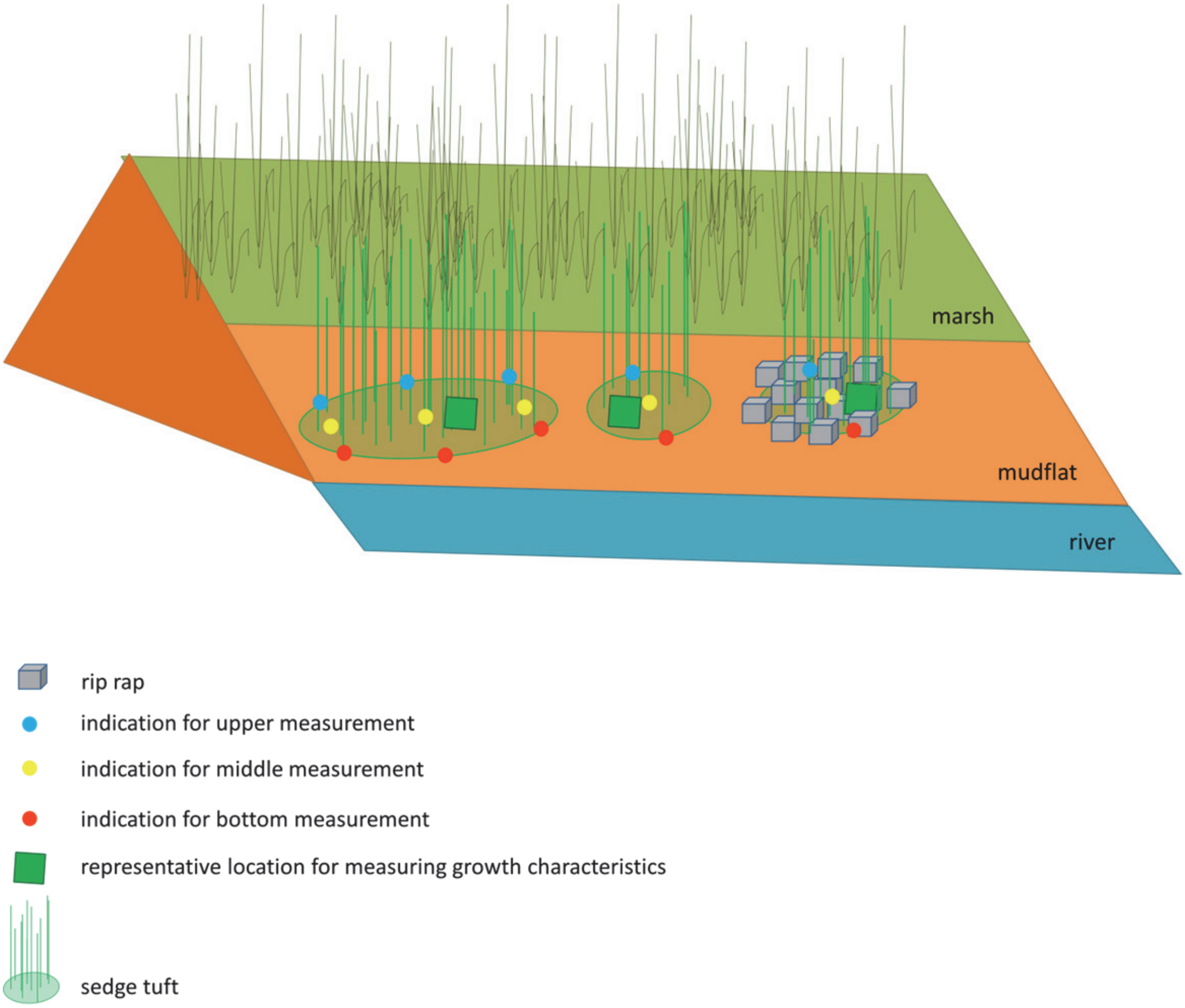
## 6.1 Annex 1: Field method



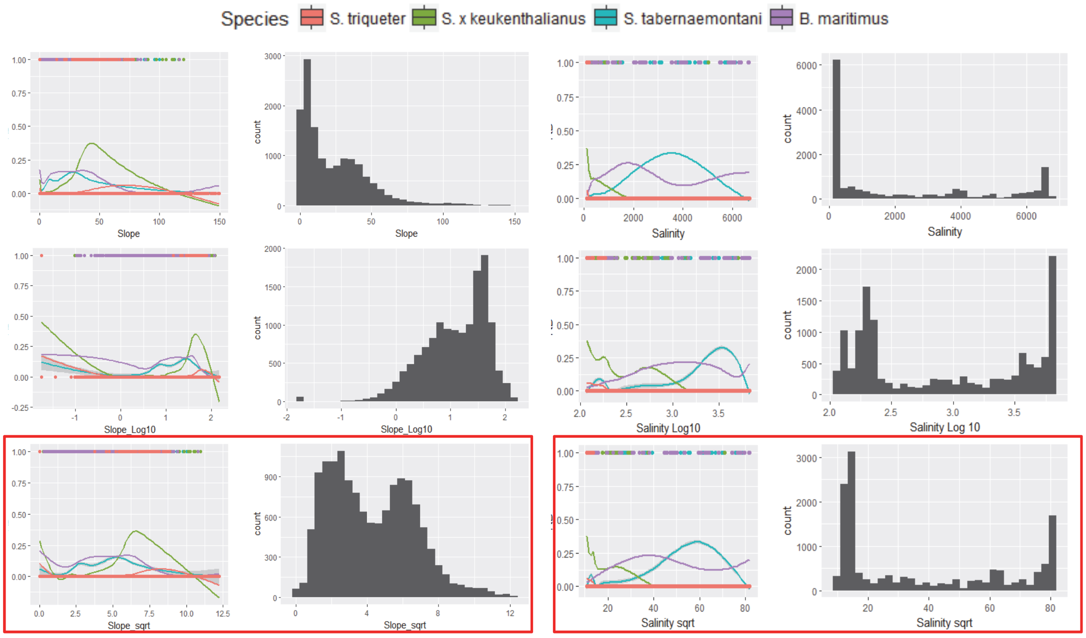
## 6.2 Annex 2: Summary of the field measurements

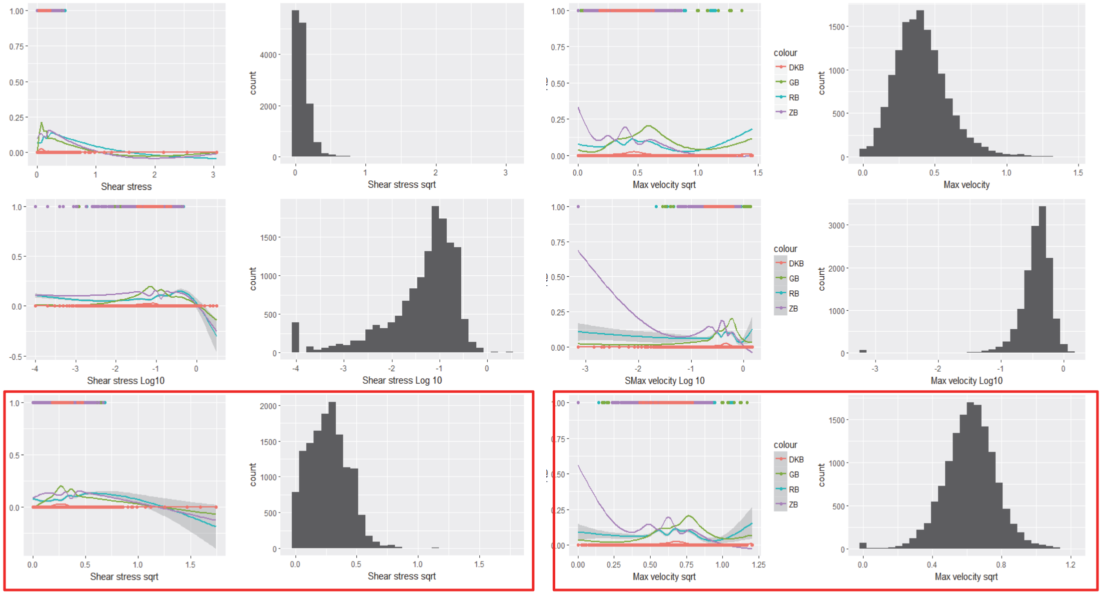
| | | | Number of tufts measured | Number of measured points |
|---|---|---|---|---|
| 2013 | *S. triqueter* | no rip rap | 10 | 69 |
| 2013 | *S. kuekenthalianus* | no rip rap | 16 | 117 |
| 2013 | *S. tabernaemontani* | no rip rap | 16 | 219 |
| | | **Total** | **42** | **405** |
| 2014 | *S. triqueter* | rip rap | 1 | 6 |
| 2014 | *S. kuekenthalianus* | rip rap | 24 | 129 |
| 2014 | *S. kuekenthalianus* | no rip rap | 2 | 9 |
| 2014 | *S. tabernaemontani* | rip rap | 25 | 147 |
| 2014 | *S. tabernaemontani* | no rip rap | 9 | 96 |
| | | **Total** | **61** | **387** |
| 2015 | *S. triqueter* | rip rap | 2 | 18 |
| 2015 | *S. kuekenthalianus* | rip rap | 42 | 441 |
| 2015 | *S. tabernaemontani* | rip rap | 63 | 447 |
| 2015 | *S. tabernaemontani* | no rip rap | 11 | 120 |
| | | **Total** | **118** | **1026** |
| 2016 | *S. triqueter* | rip rap | 10 | 66 |
| 2016 | *S. kuekenthalianus* | rip rap | 116 | 885 |
| 2016 | *S. kuekenthalianus* | no rip rap | 4 | 36 |
| 2016 | *S. tabernaemontani* | rip rap | 15 | 87 |
| | | **Total** | **145** | **1074** |
| 2017 | *S. kuekenthalianus* | rip rap | 2 | 18 |
| 2017 | *S. tabernaemontani* | rip rap | 1 | 3 |
| 2017 | *B. maritimus* | rip rap | 107 | 1056 |
| 2017 | *B. maritimus* | no rip rap | 50 | 543 |
| | | **Total** | **160** | **1620** |

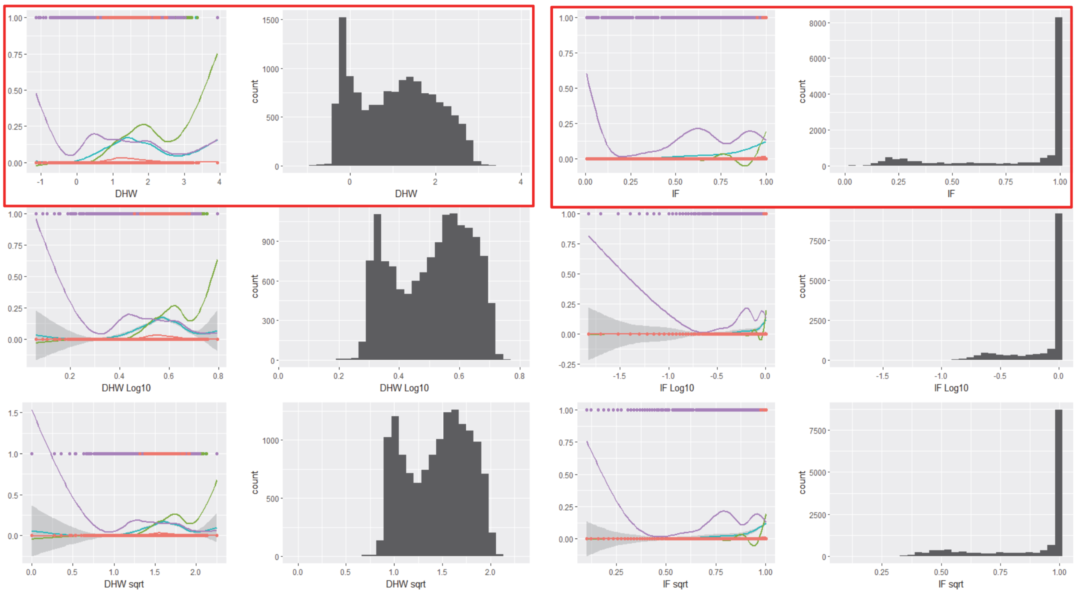
| | | | |
|---|---|---|---|
| 2013-2017 | **Total** | **526** | **4512** |

## 6.3 Annex 3: Transformations SDM

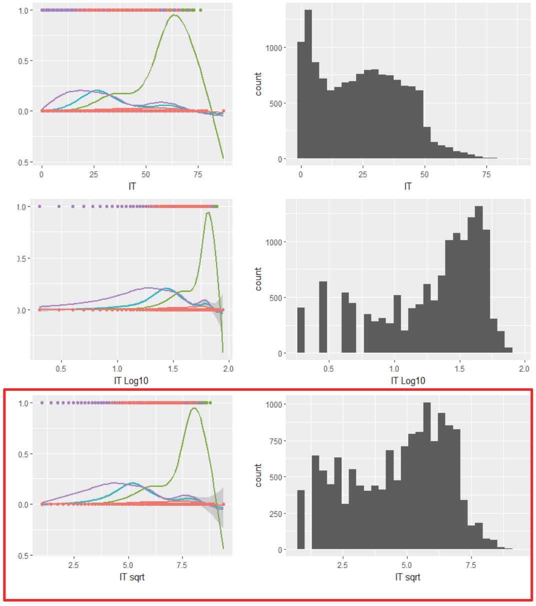
As explained under 2.5.2, data transformations of the environmental variables for the species distribution model was based both histograms of the values as well as by plotting the response (presence/absence - 1/0) in relation to each variable and fitting a smoothed line. These graphs are presented below. Red aligned are resemblance the chosen transformations.





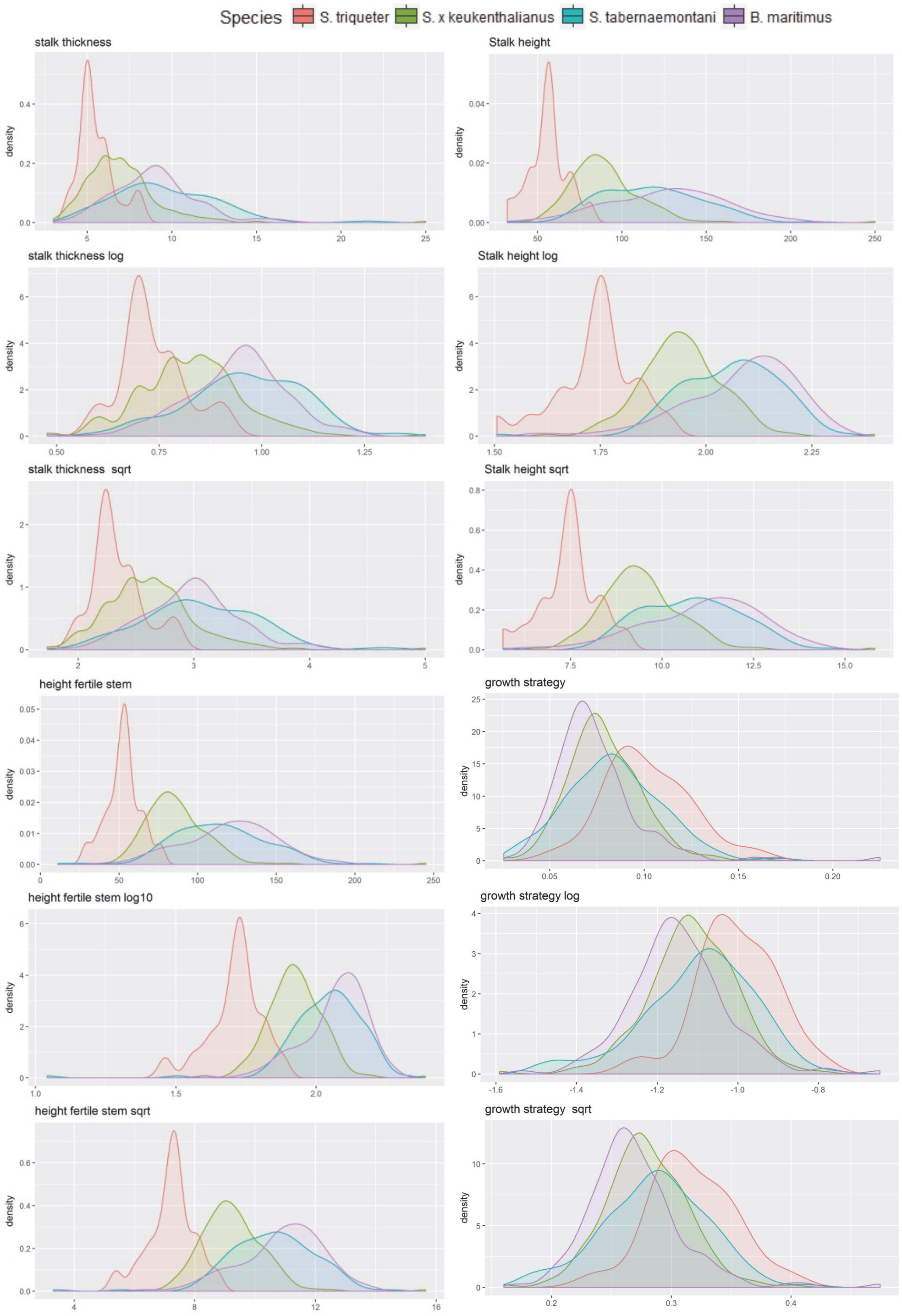


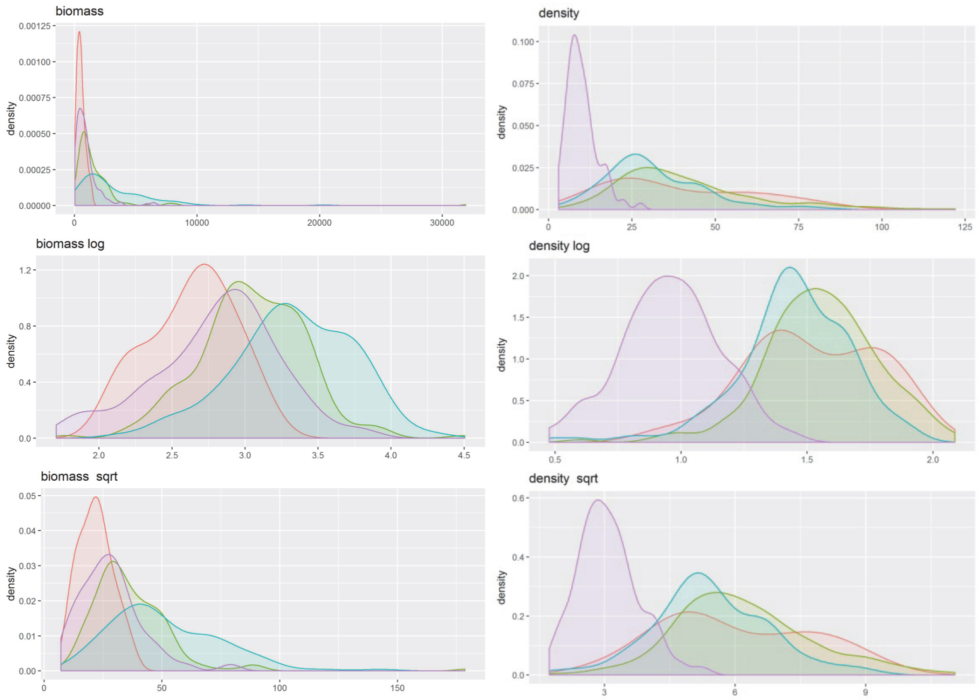
DHW
count
DHW
IF
count
IF
DHW Log10
count
DHW Log10
IF Log10
count
IF Log10
DHW sqrt
count
DHW sqrt
IF sqrt
count
IF sqrt



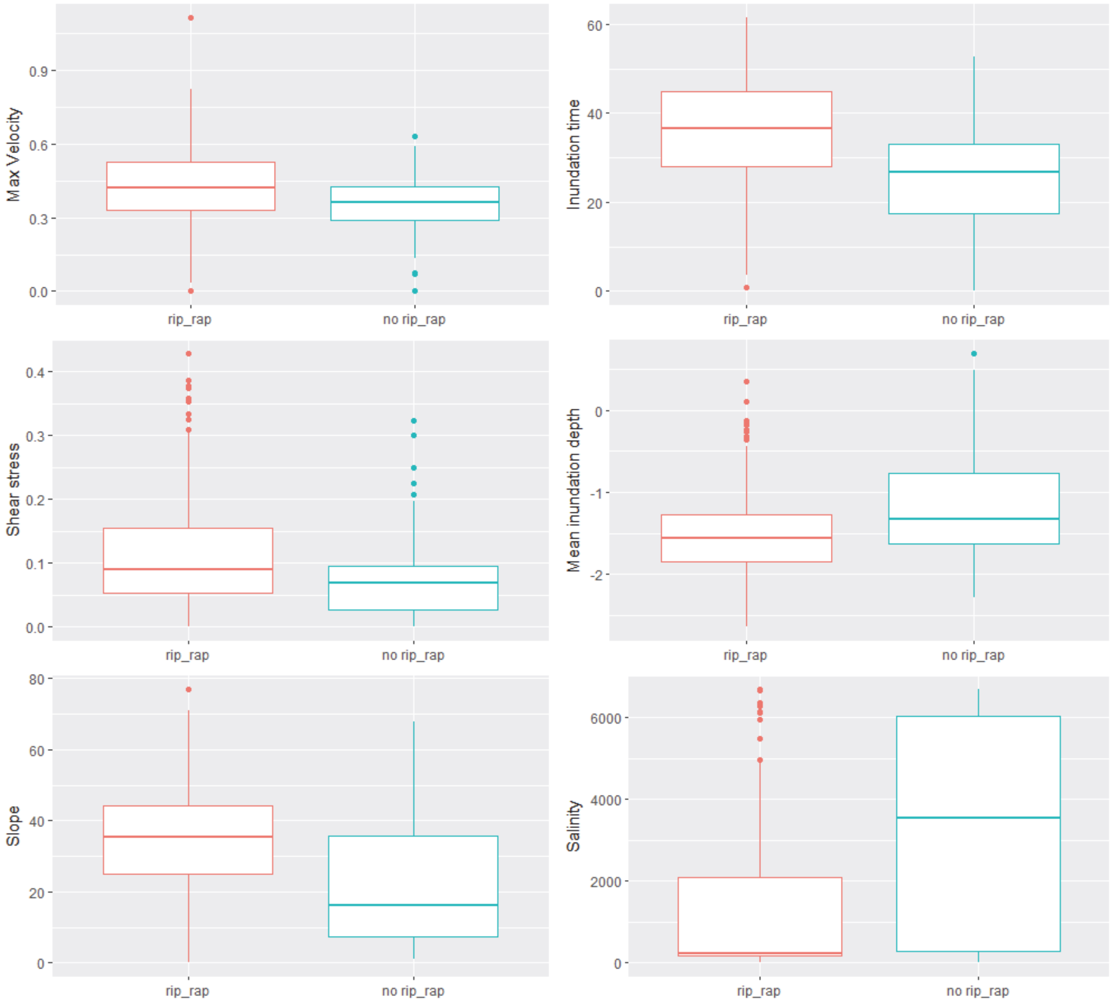
IT
count
IT
IT Log10
count
IT Log10
IT sqrt
count
IT sqrt

## 6.4 Annex 4: Transformation growth characteristics



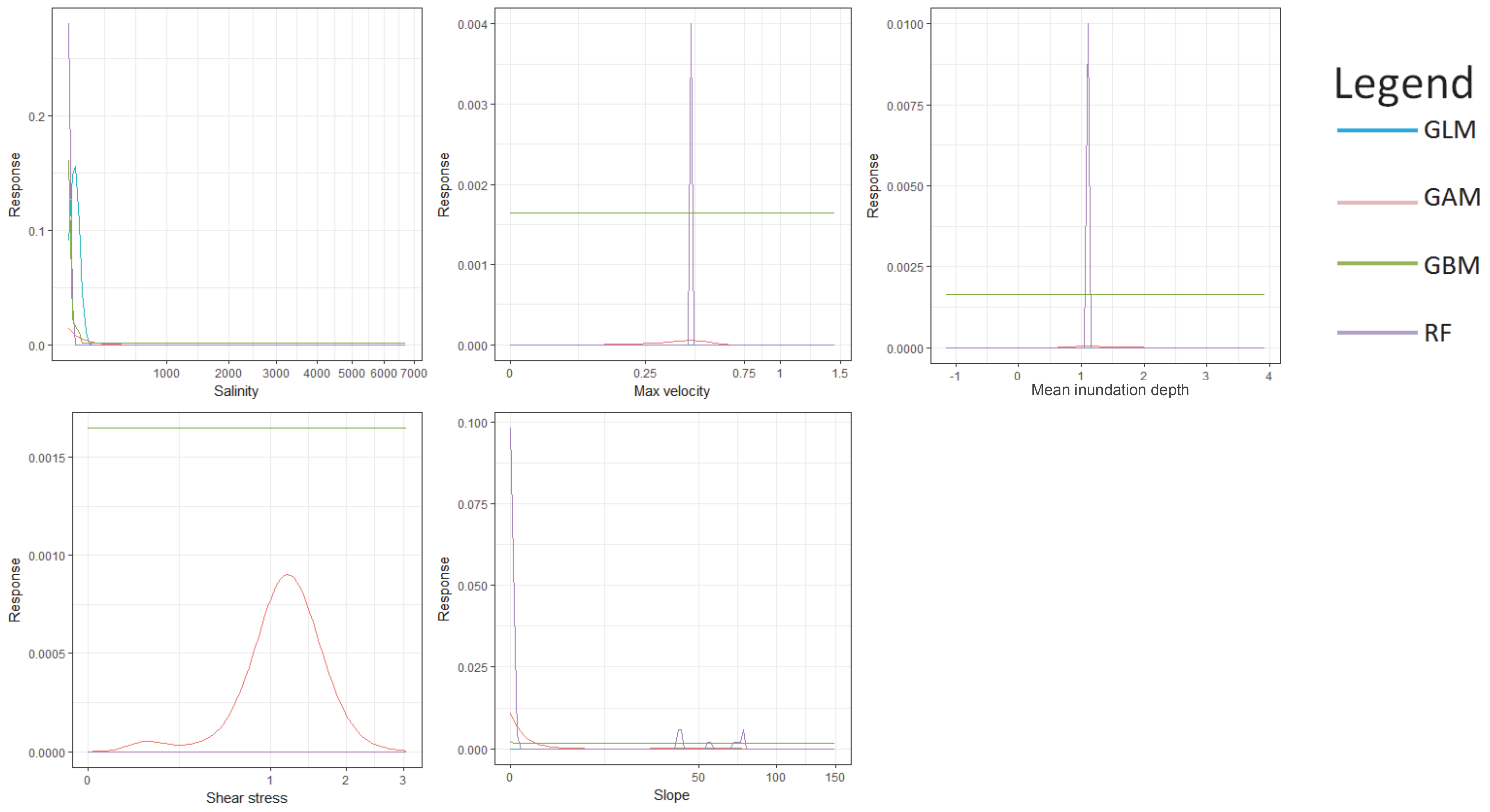

biomass
density
0.00125
0.00100
0.00075
0.00050
0.00025
0.00000
0
10000
20000
30000
density
density
0.100
0.075
0.050
0.025
0.000
0
25
50
75
100
125
biomass log
density
1.2
0.8
0.4
0.0
2.0
2.5
3.0
3.5
4.0
4.5
density log
density
2.0
1.5
1.0
0.5
0.0
0.5
1.0
1.5
2.0
biomass sqrt
density
0.05
0.04
0.03
0.02
0.01
0.00
0
50
100
150
density sqrt
density
0.6
0.4
0.2
0.0
3
6
9

## 6.5 Annex 5: Environmental variables in relation to rip rap

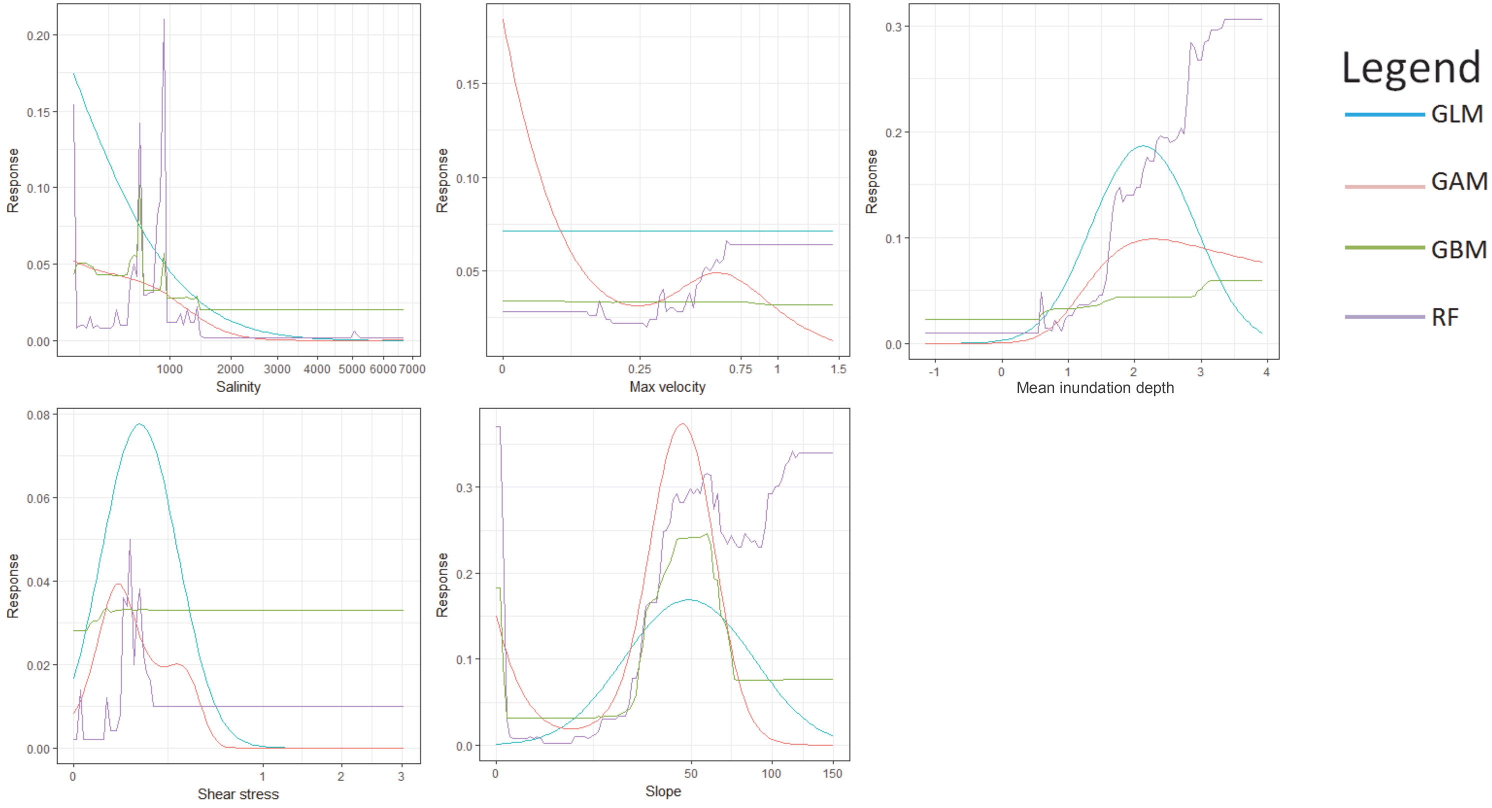


## 6.6 Annex 6: Response curves

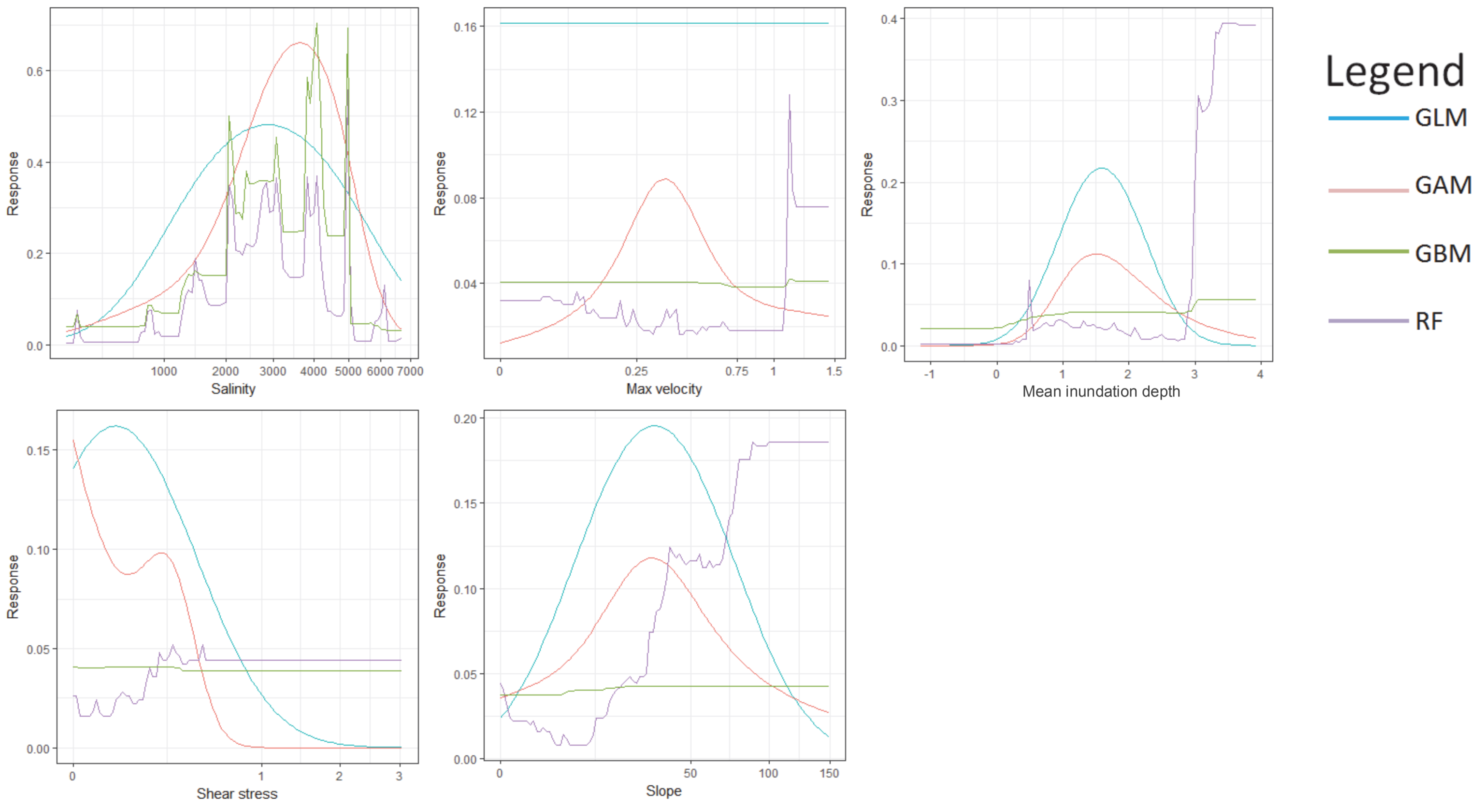
Response curves *Schoenoplectus triqueter*



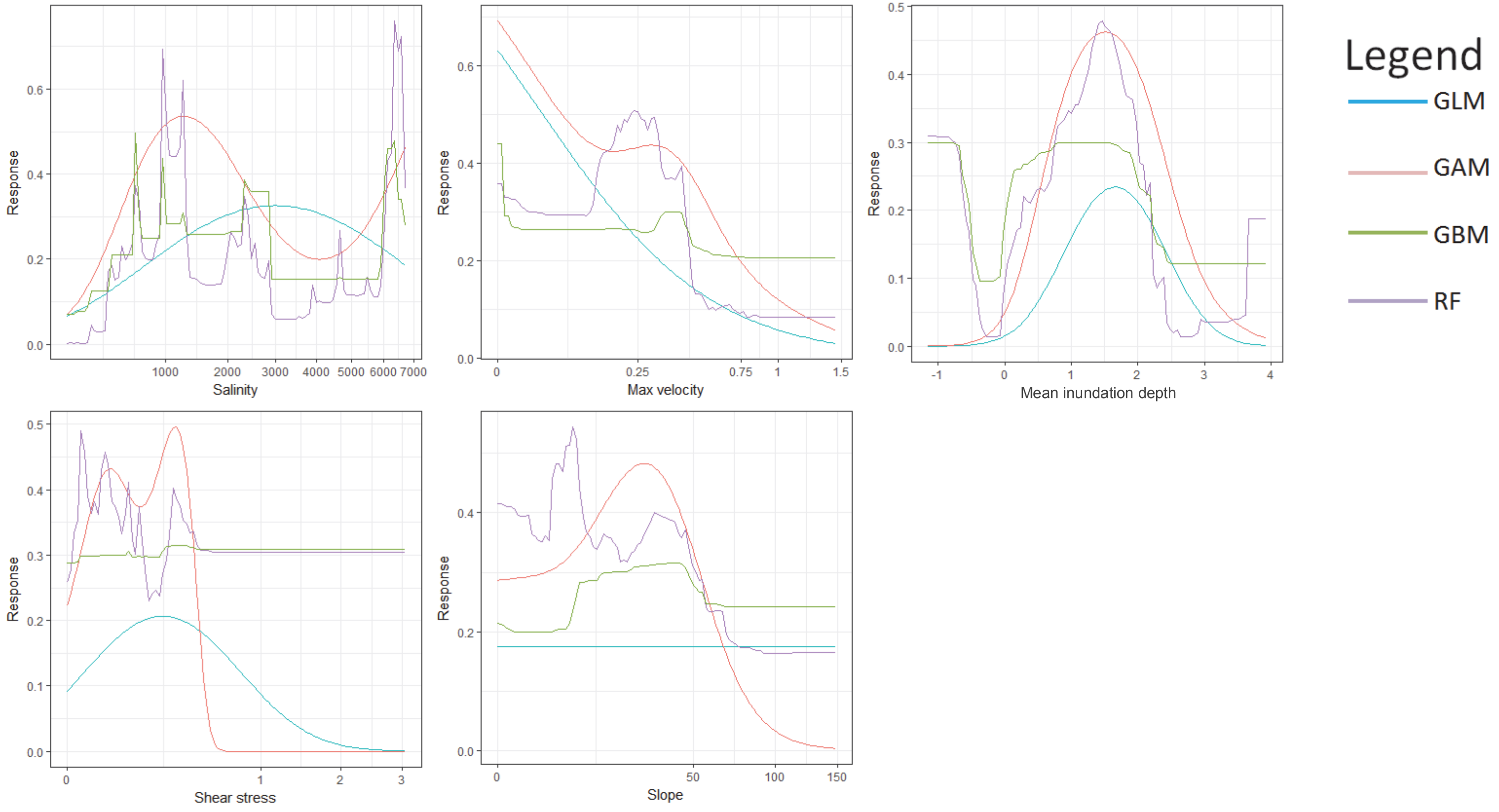
Response curves *Schoenoplectus x kuekenthalianus*



Response curves *Schoenoplectus tabernaemontani*



Response curves *Bolboschoenus maritimus*



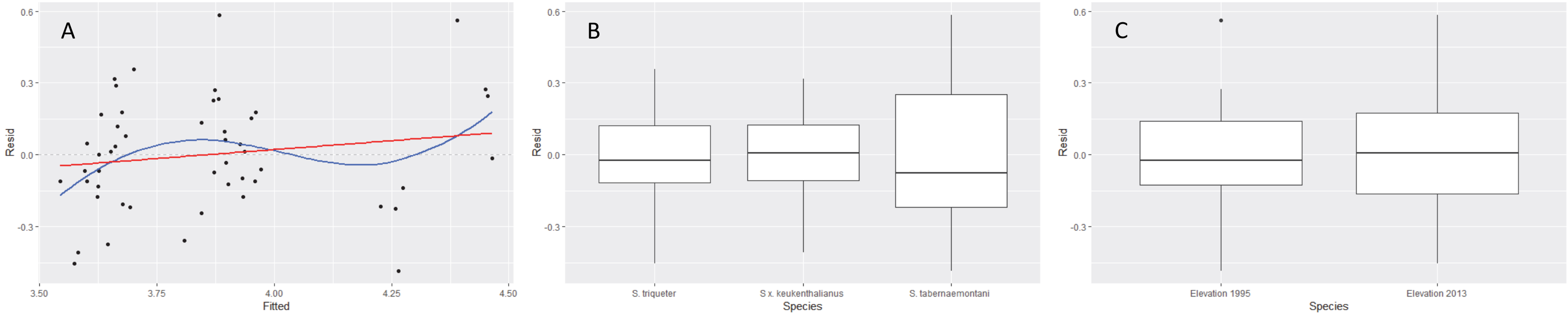
## 6.7 Annex 7: Normal distribution historical analyses

A= Residuals in function of fitted values, red smoothed line, bleu smooth line

B= Boxplot off residuals for every species

C= Boxplot of residuals for elevation of mean inundation depth (MID)

Elevation:



Mean inundation depth (MID):