Vandfugles rolle som primærkonsumenter i lavvandede fjordområder

Waterfowl as primary consumers in shallow water fiord areas

PhD thesis
Preben Clausen
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Resumé

Sygdom i ålegræsset *Zostera marina* i Nordatlanten i 1930erne forårsagede at store submerse bevoksninger af ålegræs forsvandt fra bl.a. de danske fjord- og kystområder. Dette er blevet anført som hovedårsagen til at de Nordatlantiske bestande af knortegæs *Branta bernicla*, der især udnyttede denne habitat, kollapsede i de efterfølgende år. Man har dog diskuteret om det var ålegræssets forsvinden i sig selv, der forårsagede kollapsen, eller om det var en øget jagtlig mortalitet, som følge af at gæssene nu måtte søge føde på land. Diskussionen har imidlertid været ført uden en reel viden om gæssenes habitat- og fødeøkologi før ålegræssets forsvinden. Ålegræsbedene er nu reetableret i størstedelen af de danske fjordområder, og hovedformålet med mit PhD studie har været at tilvejebringe ny viden om vandfugles udnyttelse af og fødeøkologi på submerse ålegræsbede.

Det påvises at ålegræssets tilgængelighed for vandfuglene ofte begrænses af højvande forårsaget af vindforholdene. I perioder med favourable vandstandsforhold synes gæssene at foretrække ålegræsset fremfor deres alternative fødekilder på strandengene. Dette forklares ved at gæssene generelt har en bedre energetisk indtagelsesrate, og derfor forventeligt kan opnå en bedre forårsopfedning ved fouragering på ålegræsset. Samtidigt giver fouragering på vand en øget sikkerhed mod prædatorer som påvirker gæssene på landjorden. Den forbedrede forårsopfedning vil kunne påvirke gæssenes ynglesucces i positiv retning, hvis gæssene iøvrigt trækker til ynglepladserne under favourable vindforhold, og undgår prædation i yngleområdet. Det vises at reduktioner i udbuddet af ålegræs på en række lokaliteter i de senere år har forårsaget at gæssene må søge til andre habitater. Det antydes at gæssenes vinteroverlevelse i de senere år potentielt har været påvirket negativt af disse habitatskift, men at gæssene måske har løst problemerne ved at søge til andre lokaliteter med forekomst af ålegræs. Men da ålegræssets tilgængelighed altid vil være påvirkelig af svingninger i dets produktion og ufavourable vandstande, konkluderes det, at de optimale områder for knortegæssene udgøres af lokaliteter, der både indeholder (græssede) strandenge og ålegræsbede. Gæssenes græsning synes at påvirke ålegræssets frøproduktion, men skønnes iøvrigt ikke at have betydende effekt på vedligeholdelsen af eksisterende ålegræsbede, da denne primært foregår vegetativt.

Vandfugles græsning i Kertinge Nor estimeres til at udgøre 12% af årsproduktionen af ålegræs, hvilket er betydeligt højere end tidligere estimater fra submerse ålegræsbede. Det kan formentlig forklares ved en kombination af relativt høj fuglekoncentration (=høj fødekonsumption) og ringe ålegræs-produktion (=lav fødetilgang). Hermed har fuglene er betydelig indflydelse på omsætningen af næringsstofpuljerne i ålegræsset, men da disse kun udgør brøkdele af den totale næringsstof-omsætning i noret skønnes fuglenes betydning for næringsstof-omsætningen i et eutroft fjordområde alligevel at være ubetydelig.

Indledning

Denne rapport udgør min PhD-afhandling over emnet "vandfugles rolle som primærkonsumenter i lavvandede fjordområder". Den indledes med en synopse, der er en sammenfatning af baggrunden for PhD-studiet samt af den, igennem mine studier, nyerhvervede viden på området. Synopsen efterfølges af en samling af videnskabelige manuskripter; nogle er submittede til publicering i internationale tidskrifter, andre vil blive submittet indenfor den nærmeste fremtid, og ét er et udvidet resumé af undersøgelser, der endnu ikke er afsluttet. Referencer benyttet i synopsen og afhandlingerne er samlet bagest i rapporten, for at øge overskueligheden og for at spare papir, da der er mange reference overlaps mellem de forskellige afsnit i rapporten. Krydsreferencer mellem de forskellige afhandlinger er indført med romertal (f.eks. Clausen **III**; Clausen & Krause-Jensen **VI**).

Preface

This report is my PhD thesis over the subject 'waterfowl as primary consumers in shallow water fiord areas'. It is introduced with a synopsis (in Danish), which review the background for my PhD study and the new knowledge gained during the study, and is terminated with abstracts of each of the following scientific papers. Most of the essence of this section is also found in the introductive and discussive parts of the papers. The scientific papers are a collection of manuscripts in various stages of finishing, some are submitted, some will be submitted in near future, and the last one is an extended abstract of ongoing research. References used in the synopsis and the papers are placed together in the end of the report, aimed at enhancing readability and saving paper, as many references are used in several chapters. Crossreferences between chapters are quoted by Roman numerals, i.e. (Clausen **IV**; Clausen & Percival **V**).

Tak

Dette arbejde kan måske fremstå som et en-mands værk, bortset fra enkelte afsnit, der er medforfattere på. Men skindet bedrager. En første forudsætning for gennemførelse af et PhD-studie er financiering, og den bragte Jesper Madsen på plads, delvist gennem en Hav90 beviling. Tak for den chance du dermed gav mig, Jesper, og tak for fem års vejledning og samarbejde under mine speciale- og PhD-studier. Også tak til Søren Toft for vejledning undervejs.

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stadig ikke helt magter (knobene især!). Det samme gjaldt konstruktionen af alverdens forskellige "marine" bur og forsøgsfelter, disses etablering, opfølgning og nedtagning i Limfjorden, ved Nyord og ved Saltholm. Tak for alle turene 'derude' Ebbe og Jens Peder!.

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Tak til Øresundskonsortiet, der tillod mig at inkludere arbejdet fra Saltholm i rapporten. Tak til Danmarks Meteorologiske Institut for vejrdata, benyttet i **Appendix I** og afhandling **IV**.

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From my wintering in the Netherlands 1991/92 working with Whooper and Bewick's Swans I wish to thank several people. Even though the work I made there was not includeable in the subject of my PhD thesis, discussions with several people influenced my thinking and work with seagrasses and waterfowl later on. For this influence I thank Menno Zijlstra, Maarten Loonen, Kees Koffijberg, Mennobart van Eerden, Theo Vulink, Jouke Prop and Rudi Drent.

Special thanks goes to Menno & Donny Zijlstra and Maarten Loonen & Marion van Rijssel, who all acted as wonderful hosts every now and then, when I felt alone in a foreign country with an unpronounceable language. I surely will never learn to pronounce Almere Buiten (a town near Amsterdam), Groningen and van Gogh properly - fortunately I haven't heard a Dutchman pronounce LEGO (the famous Danish toys) properly, yet!.

1 Synopsis

Synopsen indledes med et overblik over de vigtigste resultater, der er nået ved forskningen i herbivore, dvs. planteædende, vandfugles rolle som primærkonsumenter på strandenge, på mudderflader, og i submerse akvatiske miljøer. Herefter gives et overblik over den viden, der er opbygget gennem denne undersøgelse.

1.1 Baggrund

Mit arbejde har taget udgangspunkter i tre forskningsområder indenfor herbivore vandfugles økologi, der i de seneste tyve år har bidraget med en øget forståelse af de faktorer, der påvirker de herbivore vandfugles (i de senere år ofte ændrede) habitatvalg, trækmønstre, tids- og energi-budgettering, samt populationsdynamik.

1.1.1 Vandfugles rolle som primærkonsumenter på strandenge

Det ene udgangspunkt er studier af vandfugles græsning på strandenge, hvorfra detail-undersøgelser af interaktioner mellem planterne og vandfuglene, samt vandfuglenes rolle i omsætningen af næringsstoffer også er udsprunget. Her er det især to velgennemførte studier af gæs, der udmærker sig ved målrettet forskning i herbivore vandfugles fødeøkologi og plante-herbivor interaktioner.

Det ene studium startede med hollandske undersøgelser af bramgæs *Branta leucopsis* og mørkbugede knortegæs *Branta bernicla bernicla*, der græsser på græsmarker og strandenge på øerne Schiermonnikoog, Terschelling og Texel i det hollandske Vadehav. Studierne er gennemført med fokus på faktorer, der påvirker gæssenes opfedning = konditionsopbygning om foråret, dennes betydning for ynglesuccessen, og dermed for bestandsudviklingen, og har fået mange "udløbere" i form af tyske undersøgelser af knortegæs i Vadehavet, danske undersøgelser af knortegæs på strandenge i Vadehavet, samt engelsk/hollandske studier af bramgæs, der græsser på engvegetation på småøer i Nordnorge, og på mosser og andre planter på Svalbard. Nedenfor vil jeg ofte begrænse mig til at omtale studier af mørkbugede knortegæs, da de i vid udstrækning er blevet brugt som støtte i mine egne problemformuleringer, analyser og konklusioner vedrørende de lysbugede knortegæs' *Branta bernicla hrota* økologi ved Agerø om foråret (Clausen **I**, **II**, **III**, **IV**).

Det andet studium er canadiske undersøgelser af små snegæs *Anser caerulescens caerulescens*, der græsser på lav-arktiske strandengsplanter.

Energi- og protein-optimering forklarer gæssenes habitat- og fødeskift

Drent, Ebbinge & Weijand (1978/79) fremførte en hypotese om at bram- og knortegæs skifter habitat eller trækker videre til andre lokaliteter i overvintringskvartererne, for at kunne fouragere i den habitat, hvor de får det største nettoindtag af energi (om efteråret-/vinteren) eller energi og protein (foråret). Habitatskiftene styres af fødens tilgængelighed, fordøjelighed, nærings- og energiindhold. Selvom hypotesen blev fremført med nogen evidens, er der *mange* antagelser i afhandlingen. Senere studier har dog med overbevisende styrke vist, at hypotesen generelt synes korrekt.

Drent *et al.* (1978/79) forudsagde at bramgæssene skiftede fra at fouragere på eng-rapgræs *Poa pratensis* og almindelig rajgræs *Lolium perenne* på gødede græsmarker (om vinteren) til fouragering på rød-svingel *Festuca rubra* på strandenge (om foråret) for at optimere energi- og protein-indtaget, og dermed opbygningen af fedt- og proteinreserver, og at de i april trak videre til rastepladserne på Gotland, når proteinindholdet i rød-svinglen blev for lavt.

Prins & Ydenberg (1985) viste, at bramgæssenes skift fra græsmarkerne til strandengene netop skete når proteinindholdet i fødeplanterne i de to habitater var identiske, men da proteinindholdet generelt er højere i planterne på græsmarkerne, må en præference for at fouragere på strandengene også være medvirkende til skiftet, måske fordi gæssene her kan fouragere uforstyrret, i modsætning til græsmarkerne hvor de jages bort af landmændene. Fortolkningen af mønstret var, at bramgæssene affinder sig med forstyrrelserne fra landmændene og fouragerer på græsmarkerne om vinteren indtil protein-indholdet i rød-svinglen når op på 20-25%. Dette niveau synes at være et minumumsnivea for gæssene, og når det nås skifter de til fouragering på *Festuca* på den uforstyrrede habitat. Når proteinindholdet i løbet af foråret igen falder under 25% trækker gæssene bort.

Prop, van Marken Lichtenbelt, Beekman & Faber (MS) har siden vist, at gæssene også forlader rastepladserne på Gotland, når proteinindholdet i *Festuca* falder under 25%, og at både de hollandske og gotlandske strandenge forlades når gæssene ikke længere kan øge deres kropsvægt ved fourageringen, grundet faldende næringskvalitet i og indtagelsesrate af den "aldrende" rød-svingel føde.

Drent *et al.* (1978/79) forudsagde også, at knortegæssene klarede problemet med det faldende energi- og proteinindtag ved fouragering på rød-svinglen ved at skifte til fouragering på planter i den lavere strandeng, især annelgræs *Puccinellia maritima* og strand-vejbred *Plantago maritima*.

Prop & Deerenberg (1991) viste, at det så afgjort er forklaringen, da gæssene i udpræget grad kan optimere deres energi- og proteinindtag ved at skifte til sidstnævnte planter, efterhånden som væksten af disse går igang. Især strand-vejbred og strand-trehage *Triglochin maritima* giver gæssene et stort netto energiindtag.

"Konditions-hypotesen": Knortegæssenes forårsopfedning

Flere undersøgelser har vist at ♀ gæssenes vægt ved ankomsten til ynglepladserne bestemmer deres ynglesucces, jo større vægt des større succes - underforstået, vægt opbygget andetsteds påvirker ynglesucces'en (f.eks. Ryder 1967).

Denne hypotese benævnte Ebbinge, St.Joseph, Prokosch & Spaans (1982) "konditions-hypotesen", og de fremførte samtidigt de første mere direkte beviser for, at konditions-opbygningen i hos mørkbugede knortegæs i Vadehavet om foråret gav sig udslag i ynglesucces'en, eksemplificeret med data fra 1977-79: Knortegæssene havde en total ynglefiasko i 1977, efter et forår med dårlig konditionsopbygning, og gode yngleår i 1978-79, efter forår med god konditionsopbygning.

Siden er det påvist, at selvom ♀'ernes gennemsnitlige kropsvægt afspejles i ynglesuccessen, så er det i virkeligheden kun en meget lille andel af individerne der får gæslinger, nemlig de der opnår den største kropsvægt sidst på foråret (Ebbinge & Spaans 1992). Forklaringen på disse individ forskelle følger nedenfor.

Det er karakteristisk at knortegæssene, når de græsser over et strandengsområde, stort set nedgræsser vegetationen (Drent & van Eerden 1980; Prop 1991). Det er kun de forreste gæs i flokken, og dermed en ganske lille andel af gæssene, der afgræsser strand-vejbred og strand-trehage (Teunissen, Spaans & Drent 1985; Prop & Loonen 1989). Dette forklares ved at disse er sjældne, og at gæssene har en stor præference for at fouragere på dem (Boudewijn 1984; Madsen 1987a). Resten af gæssene må nøjes med at fouragere på strand-annelgræs (Prop & Loonen 1989).

Teunissen *et al.* (1985) viste, at det er de stærkere individer og familier, der tilkæmper sig retten til at afgræsse strand-vejbred og strand-trehage, og at det sidenhen er disse individer der (gennemsnitligt) får flest afkom. Prop & Deerenberg (1991) kunne forklare denne forskel i ynglesucces ved, at gæs der udelukkende græsser på strand-annelgræs får en betydeligt lavere kropsvægt sidst i maj, når gæssene trækker til ynglepladserne, end gæs der supplerer med strand-vejbred og strand-trehage.

At det alligevel i nogle år ikke lykkes for gæssene at opbygge nok reserver til at gennemføre ynglen med succes kan forklares ved svigtende fødeudbud i kolde forår, idet disse fører til ringere produktion af strand-annelgræs (Madsen 1989)(og formentlig manglende udbud af strand-vejbred og strand-trehage, der har en senere vækststart end græsserne), hvorved gæssene tvinges til at fouragere på den mindre næringsrige rød-svingel (Madsen 1989, Prop & Deerenberg 1991).

Knortegæssenes ynglesucces og lemminger

I 1980erne var der en hed debat om, hvorvidt cykliske bestandssvingninger hos lemminger på de mørkbugede knortegæs' ynglepladser i Sibirien, havde større betydning for gæssenes ynglesucces end forårsopfedningen i Vadehavet. Summers (1986) og Summers & Underhill (1987) gjorde sig til talsmænd for, at svingninger i bestande af lemminger bestemte svingninger i polarrævenes antal, og dette igen bestemte det observerede mønster med næsten cykliske svingninger i knortegæssenes ynglesucces. Hypotesen var at lemmingernes antal kulminerede hvert tredie år, og i dette år fouragerede rævene udelukkende på lemminger, fik masser af hvalpe, og lod gæssene i fred, hvorved de fik en god ynglesucces. Næste år var lemmingerne borte, rævene (som der nu var mange af) skiftede til æg og gæslinger, og gæssenes ynglesucces kiksede. Det tredie år var mere uforudsigeligt.

Ebbinge (1989) afsluttede diskussionen ved at vise, at det ikke var et spørgsmål om *enten* forårsopfedningen *eller* lemminger og ræve; begge influerer på ynglesucces'en, og det gør vindforholdene under trækket til ynglepladserne også: Hvis der er for meget modvind taber gæssene sig for meget, og får derved en for ringe kondition ved ankomsten til ynglepladserne. Konditionsopbygningen *er* altså en forudsætning for en god ynglesucces, og hvis forudsætningen er i orden, så afgøres udkommet af prædationsraten på ynglepladserne.

Knortegæssenes effekt på deres fødeplanter

Gæssenes græsser ca. 30% af bladene på strand-vejbredens rosetter ved hvert græsnings besøg, hvorefter der går 4-7 dage før planten atter afgræsses (Drent & van Eerden 1980; Prins, Ydenberg & Drent 1980; Prop & Loonen 1989). Prins *et al.* (1980) simulerede græsningen ved at gennemføre klipningsforsøg, og påviste derved at afgræsning af ca. 30% af bladene gav den hurtigste genvækst af planten, sammenlignet med manglende klipning eller andre græsningsintensiteter. Gæssene synes med andre ord at optimere deres fouragering ved kun at afgræsse planterne hver 4-7 dage.

Siden er det vist, at gæssene også optimerer deres indtag når de græsser på strand-annelgræs. De besøger annelgræs-dominerede strandengsområder hver 1-2 dage, men de enkelte skud afgræsses først når de når en vis størrelse, hvilket i praksis betyder at den enkelte plante kun afgræsses ca. hver 20 dag (Prop 1991).

Ved systematisk at afgræsse planterne sikrer gæssene, at de kan afgræsse plantedele i vækst, dvs. ungt væv med højt proteinindhold og lavt fiberindhold (f.eks. Prins *et al.* 1980; Ydenberg & Prins 1981; Madsen 1989).

Gæssene græsser altså kun en vis andel af planterne hver gang de kommer forbi, men da det sker ofte bliver slutresultatet alligevel, at en betydelig andel af produktionen af fødeplanterne græsses. Madsen (1989) viste således, at knortegæssene på Langli græssede 85-87% af den overjordiske netto primær produktion (net above-ground primary production, NAPP) af annelgræs, og Prop & Loonen (1989) at knortegæssene tog 65% NAPP af strand-vejbred.

Græsningen synes at øge NAPP af strand-annelgræs, formentlig som følge af en gødskningseffekt fra gæssenes fækalier (Madsen 1989); mere herom nedenfor (snegåse-studierne).

Det er fornyligt påvist, at de græssende knorte- og bramgæs på øen Schiermonnikoog i Vadehavet sinker successionen (Olff, de Leeuw, Bakker & Platerink 1992). Resultatet af denne interaktion er, at plantesamfund, der domineres af græsnings tolerante plantearter, som samtidigt udgør hovedbestanddelen af gæssenenes føde (henholdsvis strand-annelgræs i den lave strandeng, og rødsvingel i den høje strandeng) trives på bekostning af græsnings intolerante arter som stiv kvikgræs *Elymus athericus* og strandmalurt *Artemisia maritima*. Gæssene er imidlertid ikke effektive nok til at stoppe successionen hen mod et kvik/malurt domineret samfund, og kan idag kun udnytte dele af strandengene på øen i kraft af kreaturafgræsning, der også favoriserer de planter gæssene foretrækker (Jensen 1985, Olff *et al.* 1992).

Snegæs og strandengsplanter

I 1979 indledtes et studie af interaktionen mellem græssende små snegæs og deres fødeplanter på lav-arktiske strandenge ved La Perouse Bay, på vestkysten af Hudson Bay, Canada. Her findes en stor ynglekoloni af lille snegås, der benytter området i den korte sommer fra juni til september. Andre gæs raster og fouragerer i området, på vej til og fra yngleområder længere mod nord. Gæssene fouragerer efter tøbruddet om foråret på rodstængler fra (især) tundra-star *Carex aquatilis*, disse graves frem med næb og fødder (betegnes "grubbing"). Om sommeren græsser gæssene især på to græsser, hylster-star *Carex subspatacea* og krybende annelgræs *Puccinellia phryganodes*.

Studierne indledtes med en påvisning af at jordbunden i strandengene var næringsfattig, og at væksten af hylster-star og krybende annelgræs kunne stimuleres ved gødskning med kunstgødning (Cargill & Jefferies 1984b) eller med gåsefækalier (Bazely & Jefferies 1985). Ved burforsøg vistes det, at gæssene fjernede en betydelig andel af den stående biomasse af hylster-star og krybende annelgræs, og at gæssenes græsning øgede NAPP (Cargill & Jefferies 1984a). Et længerevarende burforsøg påviste, at gæssene ved deres græsning stoppede, eller i hvert fald sinkede, successionen på strandengene (Bazely & Jefferies 1986), således at de foretrukne fødeplanter hylster-star og krybende annelgæs, der er pionérplanterne på strandengene, trivedes på bekostning af sekundære planter i successionen, bl.a. rød-svingel, strand-vejbred, Egedes potentil *Potentilla egedii*, rørhvenen *Calamogrostris deschampsoides* og ranke-fladstjerne *Stellaria humifusa*.

Ved detaljerede studier af planternes demografi fandt man ud af, at NAPP øgedes ved en kompensatorisk respons fra planterne på græsningen. Hylster-star reagerer på græsningen ved at danne flere blade på de græssede skud, og ved at øge vækstraten af de enkelte blade (Kotanen & Jefferies 1987). Krybende annelgræs reagerer ved at danne flere sideskud (udløbere), og ved øget bladproduktionen på sideskuddene (Bazely & Jefferies 1989a). Intensiteten og timingen af græsningen fandtes at have stor betydning for effekten af græsningen på krybende annelgræs, idet NAPP øgedes ved en lav til moderat græsning fra gæs, der græssede ved tre besøg med 12 dages intervaller. En lavere græsningsintensitet havde ingen effekt på NAPP, og en højere græsningsintensitet havde en negativ effekt på NAPP (Hik & Jefferies

1980; Hik, Sadul & Jefferies 1991). Denne respons fra planterne beskrives ved den såkaldte herbivor-optimerings kurve (Fig. 1).

Gæssenes fækalier gøder som nævnt jordbunden på strandengene. Men gæssene optager også betydelige mængder kvælstof fra planterne i form af proteiner, der benyttes til æglægning, indbygges i muskelvæv (gæslingernes vækst, og de voksne fugles opbygning af flyvemuskulatur til efterårstrækket) og indbygges i fjer (udskiftes om sommeren). Nettoresultatet er, at gæssene fjerner mere kvælstof fra strandengene end de tilfører til dem. Da strandengene som nævnt er næringsfattige synes denne herbivor-plante interaktion dødsdømt. Det er imidlertid blevet påvist, at kvælstoffixeringen fra atmosfæren er højere i græssede områder end i ugræssede områder, som følge af øget bakteriel aktivitet på i de græssede områder (Ruess, Hik & Jefferies 1989). Denne øgede kvælstoffixering er sammen med gæssenes fækalier grundlaget for den øgede NAPP (Bazely & Jefferies 1989b).

Studierne sidst i 1980erne har drejet sig om effekten af "grubningen" på strandengene. Det er vist, at denne form for "græsning" er destruktiv, og fører til store åbne eroderede partier uden vegetation (Kerbes, Kotanen & Jefferies 1990; Iacobelli & Jefferies 1991).

1.1.2 Vandfugles rolle som primærkonsumenter på tidevandspåvirkede mudderflader

Det andet udgangspunkt er britiske, hollandske og danske studier af græssende vandfugles, og det vil især sige knortegæs' og pibeænders *Anas penelope*, udnyttelse af dværg-ålegræs *Zostera noltii*, ålegræs *Zostera marina* (var. *angustifolia*) og rørhinde *Enteromorpha* spp. på mudderflader i britiske estuarier og i Vadehavet.

Disse områder er tidevandspåvirkede, hvilket betyder at vandfuglene fouragerer ved de to daglige lavvande og raster ved højvande (Madsen 1988, Summers 1990, O'Briain 1991).

Det er karakteristisk for knortegæssene, at de om efteråret foretrækker at fouragere på ålegræs eller rørhinde, og først skifter til strandenge, græsmarker eller landbrugsafgrøder hen på vinteren. I områder hvor både ålegræs og rørhinde forekommer synes der at være en præference for ålegræsset, der udnyttes før rørhinden (Ranwell & Downing 1959; Charman 1979; Tubbs & Tubbs 1982; O'Briain & Healy 1991).

Det er endnu ikke klarlagt hvad der gør at ålegræsset foretrækkes frem for rørhinde. I Mariager Fjord foretrækker de lysbugede knortegæs også at fouragere på ålegræs *Zostera marina* frem for søsalat *Ulva lactuca*, der først udnyttes hen på efteråret (Clausen 1991, Clausen & Ettrup in prep.). Drent *et al.* (1978/79) fandt at gæssene havde et større netto energi indtag ved fouragering på rørhinde (27 kcal time^{-1}) sammenlignet med fouragering på dværg-ålegræs (20 kcal time^{-1}). Madsen (1988) fandt et dagligt netto energi indtag på 986 kJ dag^{-1} for dværg-ålegræs fouragerende knortegæs, hvilket opnåedes ved 684 minutters fouragering, og derved kan omregnes til 20.7 kcal time^{-1}. Drent *et al.*'s ålegræs energi indtags estimat synes således korrekt, hvilket tyder på at rørhinde estimatet måske er for højt.

Vandfugles græsning på ålegræsbede på mudderflader

Det er gentagne gange vist ved burforsøg, at knortegæssenes græsning forårsager at den overjordiske del af vegetationen forsvinder hurtigere i græssede områder end i ugræssede områder (Jacobs, den Hartog, Braster & Carrière 1981; Tubbs & Tubbs 1983; Maheo & Denis 1987; Madsen 1988; Portig, Mathers, Montgomery & Govier 1994). Dvs. at gæssene afgræsser en betydelig del af biomassen, inden den visner/slåes af ved bølgeerosion om efteråret. Det samme gælder for den underjordiske andel af vegetationen, som gæssene graver efter ved at trampe i sedimentet (Jacobs *et al.* 1981; Madsen 1988; Portig *et al.* 1994). Denne fourageringsmetode stiger i intensitet med faldende tætheder af overjordisk biomasse (Madsen 1988)

Jacobs *et al.* estimerede at gæssene tog 51% af den maksimale stående biomasse af dværg-ålegræsset, svarende til 26% af årsproduktionen. Madsen (1988) beregnede tilsvarende estimater på 66-91% af maximum biomassen (33-45% af årsproduktionen); Portig *et al.* (1994) på 65-82% af maximum biomassen (svarende til 33-41% af årsproduktionen, med benyttelse af samme antagelse som Jacobs *et al.* (1981) og Madsen (1988) benyttede); og Baldwin & Lovvorn på 48% af maximum biomassen af *Zostera japonica* (24% af årsproduktionen, samme antagelse).

Det er også karakteristisk, at gæssene græsser vegetationen ned til en nedre tærskel-værdi, typisk 10-20% bunddække = ca. 5 til 10 g tørvægt m^{-2}, hvorefter de forlader ålegræsbedet (trækker videre eller skifter habitat)(Charman 1979; Jacobs *et al.* 1981; Madsen 1988).

Vandfugles græsning på rørhinde på mudderflader

Summers (1990) gennemførte det hidtil eneste studium af knortegæssenes græsning på et rørhinde bed. Resultatet er sammenligneligt med ålegræs-studierne; dvs. gæssene græsser en betydelig andel af rørhinden før det visner/fjernes ved bølgeerosion, og forlader rørhinde bedet når biomassen er græsset ned til ca. 1 til 5 g tørvægt m^{-2}.

1.1.3 Vandfugles rolle som primærkonsumenter i submerse akvatiske miljøer

Det tredie udgangspunkt er studier af vandfugle, der græsser på vandplanter i permanent submerse plantesamfund i søer og sublittorale brakke eller marine områder.

Vandfugles græsning på submerse plantesamfund

Der er gennemført en række burforsøg til belysning af om fuglenes græsning påvirker planternes vækst i submerse plantesamfund.

Burforsøg i søer har vist at vandaks arter voksede længere og dermed opnåede større biomasse, når de ikke afgræssedes af vandfugle (tråd-vandaks *Potamogeton filiformes* og børstebladet vandaks *Potamogeton pectinatus*, Jupp & Spence 1977; kruset vandaks *Potamogeton crispus*, Lauridsen, Jeppesen & Andersen 1993). Lauridsen *et al.* (1993) konkluderede derfor, at vandfuglenes græsning i Væng Sø forsinkede rekoloniseringen af planter i søen efter en hyper-eutrof periode. Mitchell (1989) beregnede at sorte svaner *Cygnus atratus* konsumerede 20-50% af årsproduktionen af *Ruppia polycarpa* og kransnålalger i en fersk lagune-sø i New Zealand.

Anderson & Low (1976) gennemførte burforsøg i Manitoba for at belyse vandfugles græsning på børstebladet vandaks. De estimerede at vandfugle græssede 40,4% af den maximale overjordiske biomasse.

Kiørboe (1980) gennemførte burforsøg på Tipper-grunden i Ringkøbing Fjord, men kunne ikke påvise en effekt af græsningen på biomasse udviklingen af planterne ved at sammenligne burfelter med græssede felter i et blandet makrofyt samfund (med forekomst af børstebladet vandaks, almindelig havgræs *Ruppia maritima*, langstilket havgræs *Ruppia cirrhosa*, vandkrans *Zannichellia palustris*, og kransnål-algerne *Chara aspera* og *Tolypella nidifica*). Jensen (1986) gentog forsøgene efter at makrofyt-samfundene i Ringkøbing Fjord var kollapset som følge af hypereutrofiering, og fuglebestandene på Tipper-grunden var gået drastisk tilbage. Han fandt beskedne effekter af græsningen på biomasse udviklingen af børstebladet vandaks, vandkrans og *Chara aspera*, men ikke på almindelig havgræs og *Tolypella nidifica*. Begge forfattere beregnede, at vandfuglene (på trods af de beskedne græsningseffekter) græssede en betydelig andel af årsproduktionen af makrofytterne på Tipper-grunden, nemlig 29% (15-60%) af produktionen i 1979 (Kiørboe 1980), 44% i 1984 og 16% i 1985 (Jensen 1986). Derved konsumerede vandfuglene betydelige mængder plantemateriale, der ellers ville være gået i forrådnelse, eller være blevet fjernet ved bølgeerosion.

Tilsvarende estimater er beregnet af Verhoeven (1980), der estimerede at blishøns *Fulica atra* konsumerede 25% af årsproduktionen af langstilket havgræs i en brakvands-lagune på Texel i Holland.

Effekten af vandfugles græsning på submerse ålegræs *Zostera marina* bede er generelt dårlig undersøgt. Thayer, Bjorndal, Ogden, Williams & Zieman (1984) estimerede at vandfugle kun græssede 3% af årsproduktionen af ålegræs i Chesakey Bay i USA, og fastslog derfor at vandfugles græsning i submerse ålegræs samfund var af ringe betydning for væksten og omsætningen af ålegræsset. Nienhuis & Groenendijk (1986) estimerede at 3.7% af årsproduktionen græssedes af vandfugle i Lake Grevelingen i Holland.

Vandfugles "graveaktiviteter" efter rhizomer og rodknolde

Ligesom på strandengene og mudderfladerne er der vandfugle, der graver efter de underjordiske dele af planterne. Estimaterne angivet ovenfor gælder effekter på over- og underjordisk biomasse kombineret. De fleste af de omtalte planter vokser med udløbere, og har et relativt spinkelt rodsystem, der går parallelt med bunden, umiddelbart under overfladen, og er derfor relativt dårligt fasthæftet. Formentlig vil f.eks. græssende svaner typisk rykke planterne op med rode.

En undtagelse udgøres af børstebladet vandaks, der har kraftigt udviklede rhizomer og rodknolde, der vokser relativt dybt. Enkelte vandfuglearter fouragerer på de underjordiske dele ved at grave huller i sedimentet, hvorved rhizomerne og rodknoldene frigøres og ædes. I Europa er det især svaner, i Nordamerika svaner og to arter af dykænder, canvasback *Aythya valisneria* og redhead *Aythya americana*, der graver efter de underjordiske dele.

Anderson & Low (1976) estimerede at vandfugle (især canvasback's) opgravede 42,9% af den maximale underjordiske biomasse af børstebladet vandaks. Generelt syntes der ikke at være nogen negativ effekt af "græsningen" og "gravningen" på biomasse udviklingen i det efterfølgende år. Men enkelte meget intensivt udnyttede områder opnåede ikke samme biomasse i det efterfølgende år, som de ubenyttede områder.

Nyere undersøgelser viser imidlertid, at graveaktiviteterne, som på strandengene, kan have en negativ effekt på biomasseudviklingen. Pibesvaner *Cycnus columbianus bewickii* i Holland udviser en stor præference for at fouragere på rhizomer og rodknolde af børstebladet vandaks (Dirksen, Beekman & Slagbohm 1991; Beekman, van Eerden & Diksen 1991). Svanerne græsser hurtigt rhizom- og rodknold biomassen ned til en tærskel-værdi på ca. 2 til 5 g tørvægt m^2 (Beekman *et al.* 1991; van Eerden, Scheffer & Munsterman MS), svarende til at 43-78% af den biomasse der var tilstede før svanerne ankomst fjernes, hvorefter svanerne skifter til fouragering på roe-marker m.m. Svanerne græsser især på de største rodknolde og rhizomer, og det vistes ved vækstforsøg at netop disse giver ophav til de største planter næste år (van Eerden *et al.* MS). Derved påvirker pibesvanerne deres egne muligheder for fouragering på børstebladet vandaks i efterfølgende år i negativ retning.

1.2 Resultater fra mit PhD studium

Der er stadig betydelige mangler i vor viden om vandfuglenes indtagelsesrater, energetik, eventuelle græsningseffekter, samt betydning for omsætningen af næringsstofferne i submerse plantesamfund.

Netop det faktum var en af grundene til, at mit forskningsfelt har været centreret om vandfugles udnyttelse af, og mulige interaktioner med, planter i submerse samfund i de lavvandede fjordområder, der i så udpræget grad er karakteristiske for det danske landskab.

Jeg har arbejdet med lysbugede knortegæs', knopsvaners *Cygnus olor*, og blishøns' græsning på (især) ålegræs *Zostera marina*, der typisk vokser i rene monokulturer, samt på planter i blandede almindelig havgræs, langstilket havgræs, børstebladet vandaks, vandkrans og kransnålalge *Charophyceae* samfund.

Her afrapporteres især studierne vedrørende de ålegræs fouragerende vandfugle, da de øvrige studier endnu kræver en del knofedt ved tastaturet, enkelte delresultater omtales dog hvor det skønnes relevant.

1.2.1 Vand som en komplicerende faktor

De færreste herbivore vandfugle henter deres føde ved dykning (i Vesteuropa er det kun blishøns og taffelænder *Aythya ferina* der gør det; Cramp & Simmons 1977, 1980). Resten må hente planterne mens de ligger på vandet, ved at tage dem fra vandoverfladen, ved at stikke hoved og hals ned i vandet, eller ved at vende rumpen i vejret ("up-ending"). Denne fourageringsmetode er besværet af at der konstant er "vand imellem", i sammenligning med fouragering på strandenge, der kun sjældent hindres af vand, og fouragering på mudderflader, der som oftest vil være tilgængelige ved lavvande (se dog Clausen & Fischer (1994), der viser at knortegæs i et efterår i Vadehavet gentagne gange skiftede til strandengsfouragering som følge af vedvarende højvande forårsaget af stormvejr).

Der er ikke hidtil gennemført undersøgelser til belysning af denne problemstilling.

1.2.2 Model-udviklinger og anvendelser

Jeg udviklede i forbindelse med mit speciale en model, der kunne belyse effekten af vandsstandssvingninger i Limfjorden på de lysbugede knortegæs' habitatvalg ved Agerø (Clausen 1991), fordi feltobservationer antydede at gæssene udnyttede ålegræsset når vandstanden var lav i Limfjorden og strandengene når den var høj. Tidevandsamplituden i Limfjorden er kun ca. 20 cm, og vandstandssvingningerne forårsages (især) af vindforholdene, idet østenvind giver lavvande og vestenvind højvande (Appendix I). En mere formel formulering af denne model findes i Clausen (I; Eqn. 1-3).

I løbet af mit PhD studium har jeg udviklet en ny model, der belyser tilgængeligheden af ålegræs i forhold til vandstanden/dybden i ålegræsbedet (Clausen I, Eqn. 4-8), for om muligt at kunne forklare mekanismen bag gæssenes vandstandsbetingede habitatskift.

Det påvises ved hjælp af de to modeller, at gæssene i foråret ved Agerø forlader ålegræsset som følge af at vandstanden stiger, og ålegræsset derfor bliver utilgængeligt, set ud fra gæssenes synspunkt. Det vises også, at der er signifikante forskelle imellem vandstandene, der forårsager skiftet i de undersøgte år. I det tidlige forår (subjektivt defineret som perioden fra 21. marts til 25. april) forlader gæssene ålegræsset når der er ca. 2 til 6 g tørvægt m^{-2} "tilbage", dvs. et niveau der stort set er sammenligneligt med tærskelværdierne beskrevet for de ålegræs og ørhinde fouragerende knortegæs på mudderflader. I det sene forår (26. april til 31. maj) er sammenhængen mellem vandstand og habitatvalg ikke så overbevisende, og tærskelværdien ligger noget højere, 55 til 80 g m^{-2}.

Fortolkningen af denne forskel mellem det tidlige og sene forår er, at gæssene i i det tidlige forår har en klar præferens for at fouragere på ålegræsset frem for på strandenge, senere er præferencen ikke så udtalt - mulige forklaringer på denne forskel gives nedenfor.

Den model, der belyser tilgængeligheden af ålegræs i forhold til vandstanden/dybden i ålegræsbedet, er også benyttet til belysning af begrænsninger i de fældende knopsvaners fouragering på henholdsvis ålegræs og havgræs/vandaks samfund ved Saltholm (Madsen, Clausen & Fox **VII**).

Knopsvanerne skiftede i 1993 ofte mellem at fouragere i de to samfund. Ved modellering fandt vi, at svanerne forlod ålegræsset som følge af stigende vandstand. Svanerne syntes således også at have en klar præferens for at fouragere på ålegræsset frem for på havgræs/vandaks, hvilket bl.a. kan forklares ved, at biomassetilgængeligheden i ålegræsbedene er betydeligt højere (100 til 225 g tørvægt m^{-2}) end i havgræs og vandaks samfundet (25 til 80 g m^{-2}), og svanerne derfor forventeligt får et større fødeindtag. Modelleringen viste også, at tilgængeligheden af ålegræs i løbet af sommeren faldt, både som følge af faldende biomasse i bedene, og stigende vandstande i Øresund. Svanernes vægttab i løbet af fældeperioden (indikeret ved abdominal-profil scores), kunne således muligvis tilskrives fødemangel.

1.2.3 Indtagelsesrater og forårsopfedning hos ålegræs fouragerende knortegæs

Standardmetoden for estimering af fødeindtagelsesrater hos herbivore vandfugle er at kombinere målinger af defækationsrater (antal fækalier/tid) med mål for fækaliernes vægt og fordøjelsesrater. Sidstnævnte beregnes ved at sammenligne koncentrationer af ufordøjelige markører (typisk "acid detergent fibres" ADF = cellulose og lignin) i føden og fækalierne. Defækationsrater er imidlertid svære at måle når fuglene fouragerer på vandet (man kan ikke se hvornår "det" sker), og der er ikke hidtil gennemført egentlige studier af fødeindtagelsesrater hos vandfugle, der fouragerer på submerse plantesamfund.

Gæssene ved Agerø afbryder ofte fourageringen på ålegræs for at raste, og går eventuelt ind til strandkanten for at pudse sig. Denne adfærd udnyttede jeg til at måle defækationsraten på gæs, der kom direkte ind fra fouragering til rast. Herved kunne jeg ikke kun beregne fødeindtagelsesraten, men også fuglenes brutto- og nettoenergiindtag, og daglige vægtændringer. Resultatet af beregningerne er beskrevet i Clausen (III).

Ved sammenligning med data fra Prop & Deerenberg (1991) vises det, at gæssenes netto energi indtag ved fouragering på ålegræsset generelt er højere end hvis gæssene fouragerer på rød-svingel og annel-græs på strandengene, men lavere end ved fouragering på strand-vejbred og strand-trehage. Da de sidstnævnte planter imidlertid er sjældne (især tidligt på foråret), og som tidligere nævnt kun udnyttes af en minoritet af gæssene, vil flertallet af gæssene generelt have en fordel ud af at fouragere på ålegræs frem for på strandengene, hvilket kan forklare den tidligere omtalte præference for ålegræs fouragering i denne periode.

Gæssene skal om foråret både opbygge en fedtreserve (brændstof til flyveturen til ynglepladserne på Svalbard) og en proteinreserve (opbygning af flyvemuskulatur, og reserver til æglægning på Svalbard). Derfor må både energi- og proteinindtag optimeres. Situationen i det sene forår kompliceres af at proteinindholdet i ålegræsset falder ned mod en nedre grænse på 15%, under hvilken gæssene næppe kan optimere deres proteinindtag (Prop & Deerenberg 1991). Heraf konkluderes det, at gæssene i det sene forår formentlig må skifte mellem strandengsfouragering (optimerer proteinindtaget) og ålegræsfouragering (optimerer energiindtaget), og det kan forklare den manglende sammenhæng mellem vandstandene og habitatvalget i denne periode.

Ved at estimere gæssenes daglige vægtændring ved fouragering på ålegræs vises det, ved sammenligning med Prop & Deerenberg (1991), at ålegræsfouragerende gæs sidst i maj vil kunne nå op på en kropsvægt på ca. 1500 g, hvilket er mere end hovedparten af gæssene på strandengene, der kun har adgang til at fouragere på strand-annelgræs (1400 g), men mindre end de dominante gæs, der supplerer med strand-vejbred og strand-trehage (1600 g).

1.2.4 Vand som en sikkerhedsfaktor

Vandfugle er generelt udsatte for to typer rovdyr: Rovfugle og pattedyr (især ræve). Begge typer har svært ved at gennemføre et succesrigt angreb på fugle, der fouragerer på vandet, og derfor kan submerse plantesamfund give fuglene en sikkerhed de ikke oplever på strandengene og mudderfladerne.

I Clausen (IV) vises det, at knortegæssene forstyrres ligeså ofte når de fouragerer på ålegræsset som på strandengene, men kun halvt så mange gæs reagerer på forstyrrelsen. Denne forskel er medvirkende til at gæssene flyver mindre når de fouragerer på ålegræs. En anden forskel er, at ålegræsfouragerende gæs græsser hen over bedet fra den ene ende til den anden, stort set uden at flyve op. Strandengsfouragerende gæs laver mange små flyveture, over hegn, mellem strandengsparceller, fra og til drikkesteder m.v. Resultatet er, at gæs på strandenge flyver otte gange så meget om dagen som gæssene på ålegræsset.

Flyvning er den energetisk dyreste form for aktivitet en fugl kan udøve. Typisk anslås omkostningen til 12½ til 15 gange BMR (basal metabolismen)(referencer i Clausen III), og alle andre aktiviteter ligger under tre gange BMR.

I Clausen (III) belyser jeg effekten af den mindre flyveaktivitet for ålegræs fouragerende gæs på konditionsopbygningen ved at korrigere det daglige energiforbrug. Ved hjælp af et konservativt estimat for flyveomkostningen finder jeg herved, at gæssene ved ålegræs fouragering alene kan opnå en vægt i slutningen af maj på 1600 g, dvs. det niveau som kun de dominante gæs kan opnå på strandengene.

1.2.5 Effekter af græsning på submerse ålegræsbestande

Der er ikke hidtil gennemført burforsøg til belysning af effekter af vandfugles græsning på submerse ålegræs samfund.

I Clausen (II) beskrives effekten af gæssenes fouragering på et ålegræsbed sydvest for Agerø, belyst ved burforsøg. Intensiv græsning i foråret 1993 forårsager, at ålegræsset i de græssede områder sammenlignet med burområderne øger den vegetative formering på bekostning af den generative formering (blomstringen). Forskellen forklares formentlig ved, at gæssene tager de længste/største skud, der er lettest at nå. Herved nedsættes skygningseffekten fra de større skud eller induceres øget dannelse af sideskud, hvilket fører til øget vegetativ produktion i ålegræsbedet. Da blomsterskuddene rekrutteres fra de store skud (Olesen 1993) forsinker gæssene samtidigt blomstringen i de græssede felter, og færre skud opnår en størrelse, der tillader blomstring. Forskellen imellem felterne udlignes dog hurtigt, og er borte i august.

Ved sammenligning med data fra 1992 og 1990 antydes det, at herbivor-optimerings kurven også gælder submerse ålegræs populationer.

Burforsøgene ved Saltholm viser også at knopsvanernes græsning forårsager en effekt på bladlængderne af ålegræsset. Ålegræsset ved Saltholm blomstrede (stort set) ikke i 1993, så en lignende effekt af græsningen kan ikke påvises herfra. På trods af effekten på bladlængderne kunne vi ikke påvise en effekt af græsningen på den vegetative biomasse udvikling af ålegræsset.

I Clausen & Krause-Jensen (VI) opstilles et årsbudget for ålegræssets produktion og vandfuglenes konsumption i Kertinge Nor. Det vises, at vandfuglene græsser 12% af årsproduktionen af ålegræs. Dette estimat er det hidtil højeste estimat for vandfugles konsumption på submerse ålegræsbede. Der synes at være flere forklaringer på, at fuglene græsser så stor en andel af ålegræsset: Der er en ringe produktion af ålegræs i noret, som følge af et meget højt eutrofieringsniveau; der er en relativt høj tæthed af herbivore vandfugle; og noret er lavvandet, hvilket betyder at en stor andel af ålegræsset vil være tilgængelig for fuglene, specielt fordi de to almindeligste herbivorer, knopsvaner og blishøns, er blandt de vandfugle der når længst ned under vandoverfladen.

1.2.6 Effekten af græsningen på gæssenes adgang til ålegræsset

Der produceres formentlig færre frø i de græssede områder ved Agerø som følge af græsningen, men effekten af græsningen på ålegræs bedet vurderes at være begrænset, dels fordi de fleste skud rekrutteres fra udløbere, de færreste fra frø (Olesen & Sand-Jensen 1994a), og dels fordi størstedelen af bedet ligger på dybder uden for gæssenes rækkevidde (under 70 cm dybde). Gæssenes græsning på bedet i et år har således næppe nogen effekt på deres muligheder for at afgræsse bedet i de efterfølgende år (Clausen II).

Gæssene nedsætter ved græsningen den gennemsnitlige bladlængde i ålegræs bedet. Ved hjælp af modellen, der belyser tilgængeligheden af ålegræs i forhold til vandstanden/dybden i ålegræsbedet vises det, at gæssene dermed forårsager en begrænsning af deres egen adgang til ålegræsset, svarende til at vandstanden sidst i april 1993 skal være 3 cm lavere før det kan betale sig for gæssene at skifte til ålegræsset, end hvis man forestillede sig at de ikke havde afgræsset bedet løbende igennem april måned (Clausen II).

Gæssene håndterer dette problem ved at flytte rundt mellem forskellige ålegræs bede. Da de længste blade om foråret også er de yngste, og dermed har det største proteinindhold, kan gæssene også optimere deres proteinindtag ved rotationen (Clausen III).

1.2.7 Hvorfor græsser gæssene ikke altid på ålegræsset?

Da vindforholdene afgør vandstanden i Limfjorden, og dermed om gæssene kan udnytte ålegræsset eller ej, vil variationer i vind- og vandstandsforhold fra år til år påvirke gæssenes muligheder for at fouragere på ålegræsset. Vejrforholdene er, som tidligere nævnt, samtidigt bestemmende for væksten på strandengene.

I Clausen (IV) sammenlignes gæssenes habitat udnyttelse ved Agerø i forårene 1989-93, og produktionen af henholdsvis ålegræs og annelgræs i tre af årene, og relateres til vejr- og vandstandsforhold. Det vises, at der er betydelige forskelle imellem gæssenes habitat udnyttelse i de undersøgte forår, og at gæssene i nogle forår har mindre adgang til ålegræs fouragering end i andre, som følge af vandstandsforholdene.

Produktionen af både ålegræs og annelgræs varierer betydeligt fra år til år. Gæssenes skift fra/til ålegræs/strandengs fouragering bestemmes af forholdet mellem tilgængelig biomasse og indtagsrater i de to habitater. F.eks. skiftede gæssene ved en relativt høj vandstand i 1990 (lav annelgræs og høj ålegræs produktion), og en relativt lav vandstand i 1993 (omvendt situation). Selvom ålegræs produktionen i nogle år er lavere, synes der generelt at være en mindst dobbelt så stor produktion af ålegræs sammenlignet med annelgræs, og der synes at være mindre år til år variation, formentlig fordi ålegræssets vækst primært bestemmes af solindstrålingen (der er relativt konstant fra år til år), og annelgræssets vækst af temperaturen (der varierer kraftigt fra år til år).

1.2.8 Ålegræsset og gæssenes bestandsudvikling

I 1930erne forsvandt store bestande af ålegræs på begge sider af Nordatlanten, formentlig som følge af sygdom forårsaget af inficering med *Labyrinthula macrocystis* eller som følge af en række år med usædvanligt høje vandtemperaturer; det var især de submerse *Zostera marina* bede der ramtes, hvorimod ålegræsset *Zostera noltii* og *Zostera marina* var. *angustifolia* på mudderfladerne påvirkedes i mindre omfang (reviews Cottam & Munro 1954; Rasmussen 1977; den Hartog 1987). I samme periode kollapsede bestandene af knortegæs på begge sider af Atlanterhavet (Cottam & Munro 1954; Salomonsen 1958). Der har været megen diskussion om hvorvidt det var ålegræssets forsvinden i sig selv, der forårsagede kollapsen, eller om ålegræssets forsvinden tvang gæssene ind på strandengene, og dermed udsatte dem for en øget jagtmortalitet, og denne forårsagede kollapsen (f.eks. Salomomsen 1958, Madsen 1987). Diskussionen er imidlertid ført uden et reelt grundlag til at evaluere betydningen af de submerse ålegræs bedes betydning for gæssenes bestandsudvikling, da der ikke hidtil er gennemført undersøgelser af knortegæssenes økologi i denne habitat.

Med mine undersøgelser (Clausen **I**, **II**, **III**, **IV**) er grundlaget betydeligt forbedret. Undersøgelserne viser samlet, at ålegræsset også om foråret er den foretrukne habitat for gæssene; at de ved at fouragere på denne generelt opnår et bedre energi indtag, og dermed gennemsnitligt kan opnå en bedre kropskondition sidst på foråret, hvilket øger gæssenes chance for en succesrig ynglesæson; og at ålegræsset giver en højere og måske mere stabil (føde)produktion. Da ålegræsset imidlertid ofte er utilgængeligt som følge af vandstandsforholdene er strandengene en nødvendig alternativ fourageringshabitat, måske også fordi gæssene sidst på foråret kan få problemer med at optimere protein indtaget på ålegræsset alene. Lokaliteter med udbud af både ålegræs og strandenge synes derfor at være nødvendige for at gæssene de fleste år kan opnå optimal forårsopfedning. Strandengene har formentlig også i 1930erne været et nødvendigt alternativ for gæssene, og de er derfor også blevet udsat for jagt på strandenge dengang.

Clausen & Percival (V) beskriver hvordan de lysbugede knortegæs siden 1970erne har været udsat for svindende ålegræs ressourcer i flere af de områder de benytter. Dette har forårsaget en betydelig ændring i gæssenes forekomst (antal og fænologi)(Madsen, Clausen, Percival & O'Connor in press), og deres detailudbredelse og habitatudnyttelse på de enkelte lokaliteter (Clausen & Percival V). Selvom ålegræssets forsvinden i flere af områderne formentlig skyldes ændrede eutrofieringsforhold og sedimentationsprocesser på de benyttede lokaliteter, kan den observerede respons fra gæssene måske på mange måder være sammenlignelig med situationen i 1930erne.

Det er for nyligt blevet vist, at bramgæssenes vægttab i senvinteren kan forklares ved at de sulter i denne periode (Owen, Wells & Black 1992), og da bramgæssene og knortegæssene har et sammenligneligt vægtforløb i løbet af vinteren (sml. Ebbinge 1989 med Owen *et al.* 1992), kan man antage at også knortegæssene taber sig som følge af at føden bliver knap, især hvis de som de lysbugede knortegæs stort set kun udnytter naturlige habitater. Bestandsudviklingen hos de lysbugede knortegæs har været meget langsom sammenlignet med de mørkbugede knortegæs' siden jagtfredningen i 1972. En mulig forklaring er at de lysbugede knortegæs generelt får færre unger end de mørkbugede knortegæs (gælder generelt for de gæs der yngler på Svalbard sammenlignet med Sibirien/Island; Madsen 1987).

I Clausen & Perrcival (V) sandsynliggøres det, at gæssene i de senere år ofte forlader rastepladserne når der er spist op, hvilket de formentlig ikke gjorde i samme omfang før reduktionerne i ålegræssets udbredelse. Dette fremføres som endnu en mulig forklaring på den lagsomme bestandsvækst, da gæssenes mortalitet i vinterhalvåret som følge heraf kan være øget. Da ålegræssygen jo nærmeste udryddede ålegræsset i 1930erne, kan man antage at denne effekt har været endnu mere udtalt dengang.

Jeg føler mig derfor overbevist om at ålegræs kollapsen både påvirkede gæssene i form af faldende ynglesucces; i form af en generel halvering af habitat udbuddet (bemærk at i de fleste af områderne hvor de lysbugede knortegæs forekommer, udgør ålegræs bedene mindst halvdelen af det "naturlige" habitat udbud; Clausen & Percival V); og i form af øget jagtmortalitet. Det er derfor som med lemmingerne/rævene *versus* konditionshypotesen ikke et spørgsmål om enten eller men *både og*.

1.2.9 Effekter af vandfugles graveaktiviteter på plantesamfundene

Vi gennemførte et studie ved Nyord i 1992/93, hvor svaners graveaktivitet efter rhizomer og rødder fra børstebladet vandaks fulgtes i løbet af efteråret og vinteren, og vegetationens respons herpå fulgtes den efterfølgende sommer. Resultaterne herfra kræver endnu en grundig fortolkning, men der synes at være evidens for at svanernes graveaktiviteter forårsager, at balancen mellem havgræs og vandaks forskydes, idet der i 'gravede' felter vokser mere havgræs og mindre vandaks end i 'ugravede' felter umiddelbart ved siden af. Svanernes graveaktiviteter kan således være en medvirkende faktor i den karakteristiske mosaik-struktur som oftest kendetegner de danske havgræs og børstebladet vandaks dominerede samfund på lavt vand.

1.2.10 Vandfuglenes græsning og næringsstofomsætningen

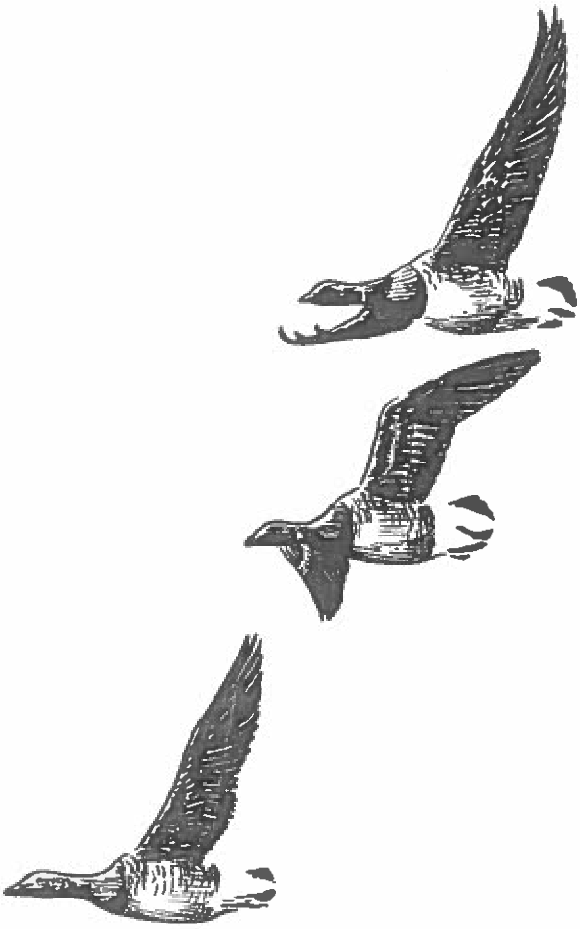
Årsbudgettet fra Kertinge Nor kan benyttes til et overslag over vandfuglenes græsnings betydning for omsætningen af næringsstoffer i et (eutroft) økosystem.

Vandfuglene græssede 51 tons ålegræs i 1991/92 (Clausen & Krause-Jensen VI). Ålegræsset i Kertinge Nor indeholder i gennemsnit ca. 3% N og 0,4% P (Christensen *et al.* 1994); konsumptionen kan således omregnes til 1,53 tons N og 0,20 tons P. Ca. 60% heraf returneres igen i form af fækalier og urinsyre; dvs. 0,91 tons N og 0,12 tons P.

Set i forhold til de totale næringsstofpuljer i noret er det ganske ubetydelige mængder af N og P vandfuglene dermed omsætter, også fordi ålegræsset typisk udgjorde under halvdelen af den totale makrofytbiomasse i noret. Der tilførtes i 1991 34,6 tons N og 1,6 tons P til noret (fra spildevand, vandløb og i nedbør), der var en nettotransport af 45 tons N og 7 tons P fra Kertinge Nor ud i Storebælt, der fjernedes 26 tons N ved denitrifikation, men tilførtes 17 tons N ved frigivelse fra bunden.

Vandfuglenes græsnings betydning for næringsstofomsætningen kan således negligeres i submerse samfund, i hvert fald i et eutroft økosystem. Da ålegræs produktionen forventeligt er betydeligt højere i et mindre eutrofieret økosystem (Sand-Jensen & Borum 1991), vil vandfuglenes betydning for stofomsætningen i et sådant system sikkert også kunne negligeres, med mindre der optræder betydeligt større tætheder af vandfugle i området. Sammenligningen med Nibe Bredning i Clausen & Krause-Jensen (VII) antyder, at det ikke nødvendigvis er tilfældet.

2 Afhandlinger/Papers



Paper I

Effects of water level changes in non-tidal areas on habitat choice and food quantity for *Zostera* feeding brent geese: a model approach.

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Summary

1. Brent geese spring fattening around Agerø (Denmark) alternate between feeding on saltmarshes and submerged *Zostera* beds in the Limfjord. It appeared from field observations that these alternations were depending on water level in the Limfjord.
2. A mathematical model was developed to assess the impact of water level fluctuations on the habitat use.
3. A second mathematical model was developed to test the impact of water level fluctuations on *Zostera* availability.
4. The first model was successful in demonstrating that fluctuations in water levels had considerable influence on habitat use by the brent geese, i.e. they fed on *Zostera* at low water levels and on saltmarshes during high water levels, particularly so in early spring, and that the switch between habitats occurred within a narrow water level span of c. 30 cm.
5. The second model demonstrated that the switch could be explained by lowered availability of *Zostera* as water levels increased.
6. By combining the output from the two models, differences between years could partly be explained by differences in *Zostera* availability in early springs (21 March - 25 April), whereas a more complicated situation was detected late springs (26 April - 31 May).

Keywords: Branta bernicla, eelgrass, waterfowl, mathematical models, weather, threshold, habitat switch.

Introduction

Waterfowl feeding on plants in intertidal areas must adapt their feeding behaviour to tidal fluctuations, which usually restricts food availability during a part of the tidal cycle. Examples include brent geese *Branta bernicla* and wigeon *Anas penelope* that feed in autumn on *Zostera* on intertidal mudflats in the Wadden Sea, and which can only reach to feed when *Zostera* beds are exposed at low tide; consequently, the birds have two daily feeding periods associated with the two low tides (Madsen 1988); an analogous situation was found by Summers (1990) in a study of brent geese feeding on *Enteromorpha* algal beds in Norfolk.

Another characteristic of waterfowl feeding on plants or algae on intertidal mudflats is 'giving up' thresholds, *i.e.* densities of *Zostera* or *Enteromorpha* coverage or biomass below which the brent geese abandon the mudflats as feeding habitat. Such tresholds have been reported from intertidal *Zostera noltii* beds by Charman (1979) and Madsen (1988); and from intertidal *Enteromorpha* beds by Summers (1990).

Superimposed on tidal fluctuations may be weather induced changes in water level, whereby wind or air pressure moves additional water into or out of tidal areas and modifies the overall water table behaviour (e.g. Huntley 1980; Pingree 1980). Dependent on wind strength and direction, this may increase or decrease the extent of habitat area exposed and thereby food availability during low tide (Evans 1981). Few studies of intertidal foraging have taken the weather factors into consideration, mainly because most intensive waterfowl and wader studies have been done in British estuaries and the Wadden Sea on genuinely intertidal habitats, where tidal amplitude exceeds 1 metre (Huntley 1980). In such areas, weather induced effects are of lower significance than the tidal effects on water levels, although storm surges occasionally overrule tidal fluctuations (Huntley 1980), with subsequent negative impact on the feeding performance of waders (Evans 1981), and on brent goose habitat use

(Clausen & Fischer 1994).

Large areas of the inner Danish waters and Baltic Sea are virtually non-tidal, with small tidal amplitude, e.g. 6 cm at Lolland in south-east Denmark (Eger 1985) and 4 cm in Szczecin Bay in Poland (Jasinska 1993). Here wind has a greater effect on water level than lunar tidal cycles, with water level ranging from -75 to 140 cm at Lolland (Eger 1985) and -134 to 196 cm at Szczecin Bay (Jasinska 1993). In non-tidal areas most seagrass beds in contrast to intertidal areas are permanently submerged, and this makes establishment of threshold values more complicated, because a part of the plant biomass may be unavailable for non-diving waterfowl.

This paper focuses on a situation where light-bellied brent geese *Branta bernicla hrota* in spring alternate between feeding on submerged *Zostera marina* beds and terrestrial habitats. The aim is to model the effects of changes in water levels on the habitat use of the brent geese, and on the food availability in the *Zostera* beds. By combining results from the two models, thresholds can be estimated, and it is assessed whether *Zostera* availability alone determines switches in habitat use.

Materials and methods

STUDY AREA

The study was conducted in March through May, 1989-93, in the Agerø area (56°43'N 8°33'E), in the western part of the Limfjord, Denmark (Fig. 1). This site is the most important spring fattening area for the Svalbard breeding population of light-bellied brent geese, with approximately 75% of the flyway-population found there in spring (Madsen *et al.* in press). While spring staging in the area, the brent geese alternate between feeding on submerged *Zostera* beds, saltmarshes, and (rarely) spring barley *Hordeum vulgare* fields. Both *Zostera* beds and saltmarshes are abundant habitats. The shallower parts of the Limfjord within the range used by the geese are dominated by *Zostera marina* beds at depths from approximately 30 to 300 cm, and with a total area of 12.0 km^2 (Drachmann, Mark & Clausen 1993, and unpublished data). The 7.5 km^2 of saltmarshes are dominated by *Puccinellia maritima* (lower marsh) and *Juncus gerardi* (upper) with regular presence of *Festuca rubra, Plantago maritima, Aster tripolium, Spergularia media*, and *Triglochin maritima*, all plants favoured by feeding brent geese (e.g. Boudewijn 1984). 89% of the salt marshes are grazed by cattle (Clausen & Percival V), hence believed to be highly attractive to feeding brent geese (e.g. Ebbinge 1992).

WATER LEVEL CONDITIONS

Data on water levels during September 1988 to September 1992 were obtained from Lemvig Harbour, approximately 40 km seaward of Agerø (Fig. 1). Although separated by the narrow strait of Oddesund (Fig. 1), water level changes recorded at Lemvig are believed to give a good estimate of water level changes at Agerø (Torben Larsen, hydraulic engineer, Department of Civil Engineering, University of Aalborg, personal communication).

An estimate of the average daily water level (ADWL) at Lemvig was calculated as the mean water level from the four daily tides (measured relative to DNN, 'Danish Ordnance Datum'), i.e. two low tides and two high tides. In order to estimate the ADWL on dates with three tides, the tide of the preceding or following date nearest to midnight was used as the fourth tide in the calculations. Calculations of ADWL was made for the periods September through May for the seasons 1988/89 to 1991/92.

As water level monitoring stopped in Lemvig in September 1992, supplementary data for September 1991 to May 1993 were obtained from Thisted Harbour, situated 30 km inland of Agerø (Fig. 1). The average of eight daily measurements (3 hour intervals) of water level at Thisted was used as estimates of ADWL for the periods September-May 1991/92 and 1992/93; the 1991/92 data for comparison with the Lemvig estimates of ADWL, and the 1992/93 data for use with the brent goose data.

Intra- and interseasonal variations in ADWL were tested by ANOVA's for samples with unequal numbers of observations and Duncan's multiple range tests (general linear models procedures; SAS Institute 1988).

COUNTS AND HABITAT USE OF GEESE

In 1989-90 and 1992-93 a minimum of three weekly counts were made of all brent geese found within the study area from the last week of March until the end of May, in 1991 coverage was slightly less intensive, with one to three weekly counts. The positions of goose flocks were drawn on field maps (scale 1:25,000), where notes on habitat choice, behaviour (feeding/roosting/flying etc.), and counting conditions (weather, disturbances etc.) were also recorded. For each count the proportion of brent geese feeding on the fjord (*i.e. Zostera*) was calculated.

Throughout this paper a distinction between two subjectively chosen periods is used, i.e. *early spring* (21 March - 25 April) and *late spring* (26 April - 31 May).

BIOMASS AND LEAF LENGTHS OF *Zostera*

The most important *Zostera* feeding site for brent geese is situated southwest of Agerø (Jørgensen, Madsen & Clausen 1994). Four *Zostera* samples were taken from this grazed study area on two occasions in 1992 and three in 1993 during early April to late May. Samples were taken by placing a 0.1 m^2 square steel frame on the bottom; *Zostera* plants growing inside the frame flattened when placing the frame were gently pulled inside, and plants growing outside were likewise pulled out. A square of *Zostera* turf was cut along the inside of the frame, and the whole turf removed to the surface in a sieve. All samples were sieved in saltwater through 1 mm mesh and the resulting material stored in plastic bags. In the laboratory samples were sorted into vegetative shoots, flowering shoots, rhizomes, and dead material, and shoot number counted; the number of leaves per shoot were counted and the length of all leaves measured from 15 or more randomly chosen vegetative shoots in each sample. All fractions were then oven-dried to constant weight at 70°C and weighed. Measured leaves were dried separately from unmeasured ones, enabling calculation of dry weight per cm leaf. As the brent geese only grazed on the above-ground plant parts, and flowering shoots were of no importance in the *Zostera* bed in spring (Clausen II), only data on vegetative shoots will be used here. All biomass data quoted hereafter refers to dry weight.

In addition to these, data on leaf length and dry weights per cm leaf from 100 randomly taken *Zostera* shoots which were sampled by the author in early May 1991 in the northernmost end of the same *Zostera* bed are included.

Additional data on *Zostera* biomass and leaf lengths were obtained from the same area from spring 1990, collected during a study of population dynamics of *Zostera marina* (Olesen 1993, Olesen & Sand-Jensen 1994a, 1994b). Leaf lengths were provided as average lenght of the longest leaf per shoot. Average leaf length (of all leaves) were highly significantly positively correlated with average leaf length (of the longest leaf) in samples collected by the author in springs 1992-93 (Spearman Rank Correlation, $r_S=0.9940$, $n=8$, $P<0.0001$), and average leaf length (all leaves) was on average 71% (range 64-75%) of the average leaf length (longest leaf). Hence, average leaf length (all leaves) of samples from 1990 were estimated by multiplying average leaf length (longest leaf) with 0.71.

MODELLING EFFECTS OF WATER LEVEL ON HABITAT USE

During field work it seemed that the spring use of the *Zostera* beds coincided with periods of low water level, induced by easterly winds. The switch from saltmarsh to fjord or *vice versa* was not a simple linear response, i.e. flocks of brent geese gradually abandoned the saltmarshes to feed on *Zostera* as the water level fell. Instead it appeared that brent geese showed a discrete switch response within a very narrow water level range. An approximate test of this on/off response was made by use of a logistic model:

$$y=\frac{1}{1+\exp(c_1\cdot(x-c_2))} \qquad \text{eqn1}$$

where y is the proportion of brent geese feeding on the fjord, x is the ADWL, c_1 and c_2 constants. Implicit in this model is that y develops asymptotically towards 1 for falling water level and towards 0 for rising water level. The constant c_2 equates to the water level at which half of the brent geese are found on the fjord, and hence hereafter is termed the 'switch' water level, because when $x = c_2$ then:

$$y=\frac{1}{1+\exp(c_1\cdot(c_2-c_2))}=\frac{1}{1+\exp(0)}=0.5 \qquad \text{eqn2}$$

The constant c_1 determines the slope of the curve.

Rearranging and applying the natural logarithm throughout Eqn. 1 gives:

$$\ln(\frac{1}{y}-1)=c_1\cdot(x-c_2)=c_1\cdot x-c_1\cdot c_2 \qquad \text{eqn3}$$

which was used in an approximate test of the correlation between the ADWL and habitat choice, transforming the proportion of brent geese feeding on the fjord, y, to $\ln(1/y - 1)$. Tests were made for each year and period. Observations of all and none of the brent geese feeding on the fjord were taken as 0.9999 and 0.0001, respectively, because of the asymptotic requirements of the model. When the ADWL and the transformed proportion of brent geese feeding on the fjord were significantly correlated, the constants c_1 and c_2 were estimated from the transformed data by simple linear regression, and used in Eqn. 1 when fitting the curves of habitat use in relation to ADWL. Tests of equality of slopes, c_1, and intercepts, $-c_1\cdot c_2$, was made by multiple comparisons of linear regressions (Zar 1984).

MODELLING EFFECTS OF WATER LEVEL ON AVAILABILITY OF *Zostera*

Zostera leaves within a population on a sample date showed fairly constant widths and stood as tapes more or less vertical in the water column. This, with leaf length measurements allow for calculation of the proportion of the *Zostera* leaves that was actually available to the brent geese at different water depths, thereby enabling the construction of availability curves in relation to water level. Measures required for modelling are length of individual leaves, l_i, and a measure of the depth to which a brent goose can reach to feed by up-ending, r; input in the model as independent variable is water depth, x (Fig. 2).

Brent geese have a total body length of 56-61 cm (measured from bill tip to tail tip on fully stretched fresh specimen; Cramp & Simmons 1977); of this the leg to tail tip measures 17 cm (measured on a dead specimen in our department). A few centimetres of the belly in front of the legs remain above the water when brent geese up-end (from field observations). Hence it was estimated that a brent goose can reach approximately 40 cm below surface when up-ending, i.e. $r = 40$.

When the water depth is less than r the total leaf biomass is available to feeding brent geese, this can be quantified by leaf measurements as:

$$T=\sum_{i=0}^{n} l_i \qquad \text{for} \quad x \leq r \qquad \text{eqn4}$$

At water depths greater than r a part of the leaf biomass becomes unavailable to feeding brent geese. Two situations occur: one where brent geese can reach a part of the individual *Zostera* leaves, and the available leaf biomass can be quantified by leaf measurements as:

$$A_1=\sum_{i=0}^{n} l_i-(x-r) \qquad \text{for} \quad x>r \; ; \; l_i \geq x-r \qquad \text{eqn5a}$$

and one where the water depth is so large that the brent geese can not reach the individual *Zostera* leaves:

$$A_0=0 \qquad \text{for} \quad x>r \; ; \; l_i<x-r \qquad \text{eqn5b}$$

The proportion of the total leaf biomass available is P=1 for water depths less than the reach limit of the birds, $x \leq r$; at any water depth larger than the reach limit, $x>r$, the proportion is calculated as:

$$P=\frac{A_1}{T} \qquad \text{for} \quad x>r \qquad \text{eqn6}$$

The proportion of leaf biomass available was converted to biomass per unit area by multiplying P by unit biomass measured from the *Zostera* turves.

Modelling in relation to 'Ordnance Datum' water level measurements required a conversion factor to equate the depth in the sample area on any one date with simultaneous measurements of 'Ordnance Datum' water levels. Hence the variable x throughout Eqns. 4-6 was replaced by variable $d = x+x'$, where x' is determined by knowledge of the depth, x, at the sample site on a given date and of the 'Ordnance Datum' water level, d, at the same date, thus $x' = (d - x)$.

Average leaf length was used to calculate at which water level half of the biomass will be available, because when P=0.5 then:

$$P=\frac{A_1}{T}=\frac{n\times(\bar{l}-(x-r))}{n\times\bar{l}}=0.5 \qquad \text{eqn7}$$

where $\bar{l}$ is the average leaf length, and n is the number of leaves measured. This is easily rearranged to:

$$x=0.5\times\bar{l}+r \qquad \text{eqn8a}$$

and as $x = d - x'$ this can be rewritten in 'Ordnance Datum' terms to:

$$d=0.5\times\bar{l}+r+x' \qquad \text{eqn8b}$$

The median dates of early and late spring, as defined above, are 7 April and 13 May respectively. The available biomasses in relation to ADWL on 7 April 1992 was assumed equal to that sampled on 9 April 1992, and those on 7 April 1993, 13 May 1992, and 13 May 1993 were estimated by linear interpolation between surrounding sample dates. Availability curves so derived were used to estimate available *Zostera* biomasses when brent geese switched habitat (when ADWL = c_2).

Results

WATER LEVEL CONDITIONS

The tidal amplitude in the Western Limfjord is small; the measurements from Lemvig from September 1989 through May 1992 (excluding June through August all years) gave an average difference in water level between subsequent low and high tides of 21.1 ± 8.7 cm (Mean ± S.D., n=3999). Changes in weather conditions induced quite large changes in the water level even in spring, *i.e.* the lowest low tide and highest high tide measured at Lemvig in the period 21 March to 31 May, 1989-92, were -68 cm and 124 cm respectively, and the ADWL ranged from -56.5 cm to 85.0 cm (Fig. 3).

Comparisons between water level fluctuations in Lemvig and Thisted showed a highly significant correlation between the water levels measured at the two harbours both in early spring 1992 (R^2=0.978, t=16.434, P<0.0001, n=8) and late spring 1992

(R^2=0.971, t=32.337, P<0.0001, n=33)(Fig. 3), hence it was assumed that using the Lemvig water level measurements with the goose data for 1989-92 and the Thisted measurements for 1993 would only introduce a negligible error to year on year comparisons.

A two-way ANOVA found that significant effects of both year and period contributed to variations in ADWL ($F_{5,344}$=6.54, P<0.001), but found no significant year-period interactions. ADWL in early spring was significantly higher than in late spring (P<0.05, Duncan's multiple range test); ADWL in early spring 1989 and 1990 was significantly higher than in early spring 1991 and 1993 (P<0.05, Duncan's multiple range test), with 1992 intermediate and not significantly different from either of the two groups (Table 1); ADWL in late spring 1989 and 1992 were likewise significantly higher than in late spring 1991 and 1993 (P<0.05, Duncan's multiple range test), with 1990 intermediate (Table 1).

EFFECTS OF WATER LEVEL ON HABITAT USE

The tests by use of the logistic model found strong positive correlations between the ADWL and the transformed percentage of brent geese feeding on the fjord in early springs 1989-93, and late springs 1991-93, whereas no correlation was found in late springs 1989-90 (Fig. 4, Table 2). The interpretation of the modelling results is that geese do indeed shift habitat within a very narrow range of ADWL (Fig. 4). Calculations from the model (Eqn. 1), based on estimates of c_1 and c_2, revealed that the brent geese switch from >95% feeding on the fjord to >95% feeding on land within a 22.4 cm change in ADWL (Mean, range 14.5 to 29.8 cm, n=8).

The multiple comparisons between the eight significant regressions found no evidence for variance heterogeneity (Bartlett's test: B_c=6.51, df=7, P>0.25), and showed that the slopes c_1 of the regressions were not significantly different ($F_{7,115}$=1.326, P>0.10), whereas the intercepts $-c_1 \cdot c_2$ were ($F_{7,122}$=9.199, P<0.0005), *i.e.* c_2 differed between years. Pairwise comparisons of intercepts with Tukey q-tests gave ambiguous results with overlapping sets of similarities among incercepts (Table 2), consequently c_2 values can only approximately be ranked with early spring 1991 lowest, followed by late 1993, late 1992, early 1989, early 1993, late 1991, and early 1992 springs, and early spring 1990 highest (Table 2, compare with Fig. 4).

EFFECTS OF WATER LEVEL ON AVAILABILITY OF *ZOSTERA*

The comparison between water levels measured at the *Zostera* sample site and simultaneous measurements of water level at Lemvig/Thisted revealed that the value for *r* (40 cm for brent geese) at the sample site corresponded to an ADWL of -20.8 cm (Mean, range -23.5 to -17.6 cm, n=4).

The modelling of available *Zostera* based on leaf measurements showed that increases in water level above -20.8 cm had a large impact on *Zostera* availability (Fig. 5). An increase in ADWL of 9.2 cm (Mean, range 5 to 15 cm, n=6, 1991-93; only 1992-93 curves presented in Fig. 5) reduced available *Zostera* stocks by 50%, and an increase of 24.7 cm (range 15 to 38 cm, n=6, 1991-93) by 95%.

Conversion of *Zostera* availability to biomass per m^2 showed an increased impact of water level on availability of *Zostera*, due to large within- and between-years variations in *Zostera* biomass (5 sample dates 1992-93: $F_{4,15}$=37.66, P<0.0001)(Fig. 5). An increase in ADWL of 12.8 cm (Mean, range 5 to 20 cm, n=5) reduced available *Zostera* stocks to less than 16 g/m^2 (i.e. equivalent to 50% of the lowest initial biomass), and an increase of 22.8 cm (range 11-41 cm, n=5) to 5 g/m^2.

COMBINING OUTPUTS FROM THE TWO MODELS

The observed variation in *Zostera* biomass per m^2 may be caused by four parameters, *i.e.* the number of shoots per m^2, the number of leaves per shoot, the leaf length, and the width and thickness of leaves (=biomass per cm leaf). ANOVA's of these parameters based on raw data from six sample dates in 1991-93 found significant differences between sample dates in all four parameters: *i.e.* the average number of shoots ($F_{4,15}$=3.24, P<0.0418), the average number of leaves per shoot ($F_{5,513}$=33.62, P<0.0001), the average leaf length ($F_{5,2373}$=260.80, P<0.0001), and average biomass per cm leaf ($F_{4,13}$=20.94, P<0.0001).

For a feeding brent goose the most important of these parameters is believed to be the average leaf length, because this obviously has a great influence on the overall availability of the total *Zostera* biomass, whereas the other three parameters merely modify biomass density and therefore intake rates when water levels are sufficiently shallow for feeding brent geese.

Eqn. 8b was used to calculate the water levels at which half of the *Zostera* leaves would be available to feeding brent geese on sample dates, 1990-93. The outcome of the calculations is that the average leaf length in 1990 and 1992 was longer than that in 1993, and 1991 perhaps similar to 1993 (all samples significantly different, Duncan's multiple range tests, P<0.05, the 'perhaps' statement addressing the differences between years in timing of sampling dates)(Fig. 6). Consequently one could expect the brent geese to switch to feeding on the fjord at higher water levels in 1990 and 1992 than in 1993, with 1991 perhaps as intermediate, and they in fact did so in early springs, whereas no such relation was found in late springs (Fig. 4, Table 3).

Recalculating the results in the previous paragraph to *Zostera* biomass reveals a less clearcut pattern, due to effects of the observed variations in shoot densities, number of leaves per shoot and biomass per cm leaf. It turns out that in terms of biomass, 1990 was not different from 1993, whereas 1992 offered the brent geese much greater *Zostera* biomass (Fig. 6). When the available biomass in relation to ADWL was estimated for the median dates in early and late spring 1992 and 1993 and combined with 'switch' water levels, c_2, the biomass available at c_2 ranged from 1.7 to 79.9 g/m^2 (Fig. 7); an obvious relationship between the biomass available and the water level where the brent geese switched habitat was consequently not found.

Discussion

The first model (Eqns. 1-3) successfully demonstrated that water level fluctuations had a major impact on habitat use of the brent geese in early spring of all five study years (Table 2, Fig. 4), and that the brent geese switched from >95% feeding on the fjord to >95% feeding on land with a water level increase of 22.4 cm. The curves fitted by use of estimates of c_1 and c_2 and Eqn. 1 generally describe reality well, although the 1989 curve was affected by the presence of all geese on land at water levels below 0 cm (Fig. 4). This constrains the fitted curve to describe a habitat switch at a water level below those water levels where flocks of birds utilising both habitats actually were observed.

The first model also demonstrated significant effects of water level on habitat use in three of the five late springs studied. However, one would predict that the birds would switch at a higher water level in late spring than they had done in early spring of the same year. This is so because Danish *Zostera* stocks usually reach their lowest biomass in February-March, followed by very rapid growth from April to June-July due to the increased radiation in spring, and most of the increase in biomass is caused by leaf elongation (e.g. Sand-Jensen 1975; Wium-Andersen & Borum 1984; Pedersen & Borum 1993). Similar increases in average leaf length and biomass were also found in the *Zostera* bed used by the brent geese (Olesen & Sand-Jensen 1994a, Fig. 6). The expected observation of a late spring switch at a higher water level than that found in early spring was only observed in 1991 (Table 2), which also gave a good fit to the model (Fig. 4). In 1992, the geese switched at a significantly lower water level in late spring than in early spring, whereas no significant difference were found between switches in 1993 (Table 2). In late springs it was obvious that the brent geese on many days used both saltmarshes and *Zostera* beds over a wider range of water levels than they did in early springs (Fig. 4). A possible explanation of this observation, and the unexpected observation of switches at lower water levels in late springs will be given below.

The multiple comparisons of the regressions found significant differences in switch water levels, c_2, between early springs, with 1991 having the lowest value followed by 1989, 1993, 1992, and 1990 with the highest value (Table 2).

The second model (Eqns. 4-8) clearly demonstrated that increases in water level above -20.8 cm had a substantial impact on *Zostera* availability, and that the available *Zostera* biomass would be reduced to less than 5 g/m^2 after an increase of 22.8 cm to a water level of 2 cm (Fig. 5). The second model also demonstrated relatively large within- and between-year variations in declines of *Zostera* availability in relation to increasing water levels, due to variations in leaf length and biomass (Fig. 5, Fig. 6).

An evaluation of the results from the two models taken together reveals that water levels do affect the availability of *Zostera*, and that consequently the brent geese switch to feeding on land. This switch occurs within a water level range of between -20 and +10 cm (first model, Fig. 4), as predicted by the second model (Fig. 5). The observed switch at higher water levels in springs 1990 and 1992 compared to 1993 (Fig. 4) can be explained by the longer leaf lengths found in 1990 and 1992 (Fig. 6).

Studies of brent geese feeding on intertidal *Zostera noltii* beds in autumn have found 'giving up' thresholds, *i.e.* densities of *Zostera* coverage or biomass below which the brent geese abandon the *Zostera* as feeding habitat: Charman (1979) reported that brent geese left the *Zostera* beds when coverage fell below 15%; Madsen (1988) likewise found that the geese left the *Zostera* or switched to feeding on below-ground parts of the plants when coverage reached 10-20%, equivalent to 5.9 to 9.9 g/m^2; a similar result was obtained by a model approach on brent geese feeding on *Zostera* at Lindisfarne, England, where geese left when biomass fell below 4.5 g/m^2 (S. Percival, W.J. Sutherland & P.R. Evans, unpublished data). The data from early spring 1992 and 1993 suggest that a comparable threshold may be found in early spring, as the geese switched at biomasses of 1.7 g/m^2 in 1992 and 5.9 g/m^2 in 1993, but the threshold is much higher in late springs (Fig. 7).

The observations (i) that the geese would switch from >95% feeding on the fjord to >95% feeding on land with a water level change of 22.4 cm, (ii) that the *Zostera* biomass would be reduced to less than 5 g/m^2 with a water level increase of 22.8 cm, and (iii) that the average tidal amplitude of the Western Limfjord is 21.1 cm all indicate that the brent geese only use both habitats when the ADWL is in the range where they can not feed optimally on *Zostera* throughout the day, thus feed on *Zostera* during low tide and saltmarshes at high tide.

The late spring situation is, as stated above, puzzling. Brent geese are well known to optimize their feeding, in terms of energy and nutrient intake (Drent, Ebbinge & Weijand 1978/79; Prop & Loonen 1989; Prop 1991; Prop & Deerenberg 1991). This is especially important in spring when optimization of spring fattening is considered of major importance to subsequent breeding success (Teunissen, Spaans & Drent 1985; Ebbinge 1989; Prop & Deerenberg 1991). When feeding on the saltmarshes in spring, the bulk of food ingested by brent geese consist of two graminoids: *Puccinellia maritima* and *Festuca rubra* (Madsen 1989; Prop & Deerenberg 1991); the latter is gradually replaced by fleshy halophytes (*Triglochin maritima*, *Plantago maritima*, *Aster tripolium* and *Spergularia media*) as these emerge on the saltmarshes in late spring (Teunissen *et al.* 1985; Prop & Deerenberg 1991), particularly in years with an early start of vegetation growth (Prop & Deerenberg 1991). Although the dietary selectivity of brent geese on the Agerø saltmarshes have not been fully analyzed yet, there are good reasons to assume that similar patterns are found in this study area, due to observed habitat use within the saltmarshes (Clausen 1991), observed densities of droppings in different saltmarsh habitats, and bite marks on individual plants growing in the saltmarshes (P. Clausen, unpublished data). The reason for taking a still larger proportion of the fleshy halophytes is well documented: the halophytes have higher protein content, metabolisable energy content and gross intake rate, and therefore the geese achieve higher net energy intakes by feeding on the halophytes than when feeding on the graminoids (Prop & Deerenberg 1991). Within a group of brent geese, the fleshy halophytes are taken by a minor section of dominant individuals (Teunissen *et al.* 1985; Prop & Loonen 1989), and those are the ones with highest chance of successful reproduction (Teunissen *et al.* 1985). In terms of net energy intake rates it is now known that *Zostera marina* usually is a better forage than the graminoids, whereas it is comparable to the protein rich fleshy halophytes (Clausen III). But as protein levels falls in *Zostera* during spring, geese feeding on a pure *Zostera* diet in some years might run into a protein deficit (Clausen III). As a consequence one can expect the geese to prefer feeding on *Zostera* in early spring, when the only real alternatives are the graminoids; later in spring the balance is more difficult to predict, because in years with early growth there might be good reasons for feeding on fleshy halophytes on the saltmarshes, whereas in years with late growth, *Zostera* might still be preferred. This is supported by the observation in 1991 which was the year with latest onset of growth of the five years studied (Clausen IV), when the brent geese fed on *Zostera* as soon as it became available due to falling water levels, even in late spring (Fig. 4). The reason for the observed, and in terms of *Zostera* unpredictable, switch at shallower water levels in late spring during 1992 and 1993 compared to early springs in the same years (Fig. 4), and the apparent lack of water level fluctuations on habitat use in late spring of 1989-90 (Fig. 4), could be that in these four years, growth of the fleshy halophytes were good, and so the dominant brent geese switched between feeding on the fleshy halophytes and *Zostera*, as the halophytes become rapidly depleted during each grazing visit (Prop & Loonen 1989; Prop & Deerenberg 1991). The reason for the detected effects of water level fluctuations in late springs 1992 and 1993 might be that there still are good reasons for the less dominant brent geese to feed on *Zostera* compared to their alternative food *Puccinellia*, and their switch would be determined by a balance between biomass and intake rate derived in either of the habitats depending on water level: the shallower the water, the more geese feed on *Zostera*; in this context late spring 1993 was subject to the shallowest water levels observed in any year (Table 1). Also the effects of water levels fluctuations will only be manifest in years with a sufficient span between highest and shallowest water levels; in this context 1992 fits with the largest fluctuations in water levels (Fig. 3).

In conclusion, water level fluctuations in non-tidal areas may have a major effect on *Zostera* availability and thereby on the habitat use of brent geese. Two models were developed which can be used in predicting such effects, which may be of significance for many waterfowl feeding on submerged macrophytes in non-tidal habitats. The models in combination also can be used to determine biomass threshold values for *Zostera* feeding birds in submerged *Zostera* beds. Non-tidal habitats are found for example throughout the Baltic Sea (Eger 1985; Jasinska 1993), and in the Black Sea (Verkuil, Koolhaus & van der Winden 1993), and thereby may affect large numbers of waterfowl migrating from their wintering quarters in Western and Southern Europe, and Africa, towards their breeding grounds in Siberia.

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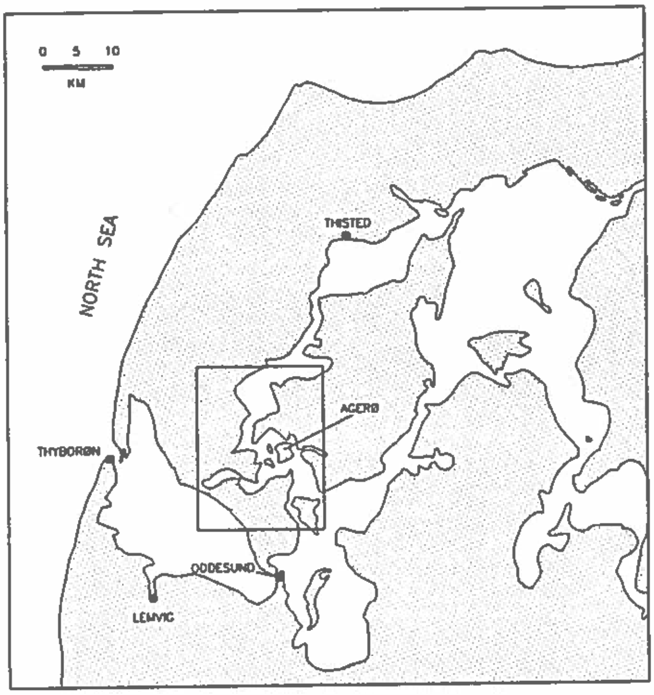

Fig. 1. Map of the Western Limfjord, Northwest Denmark, with the position of sites mentioned in the text. Open areas are the Limfjord and the North Sea, hatched areas the surrounding landscape. The approximate limits for feeding flocks of brent geese, that roost communally at Agerø, is given by the rectangle.

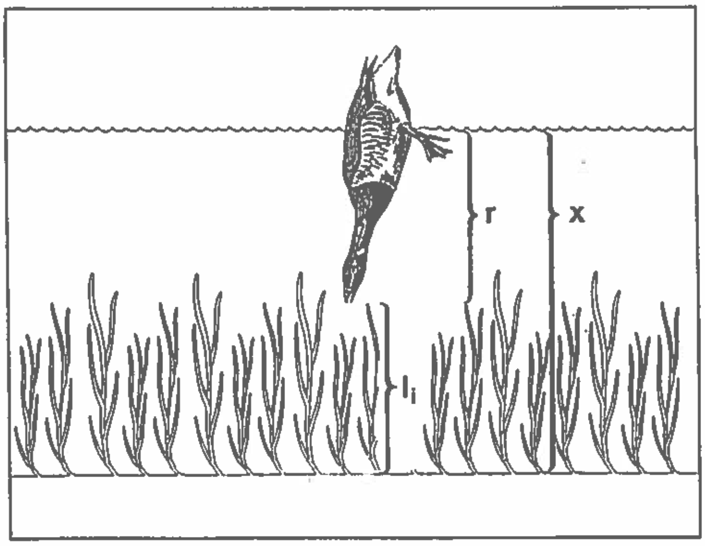

Fig. 2. Diagrammatic presentation of the basic parameters included in the model of effects on water level on *Zostera* availability. r = reach limit of a brent goose; l_i = the length of an individual *Zostera* leaf; x = the water depth.

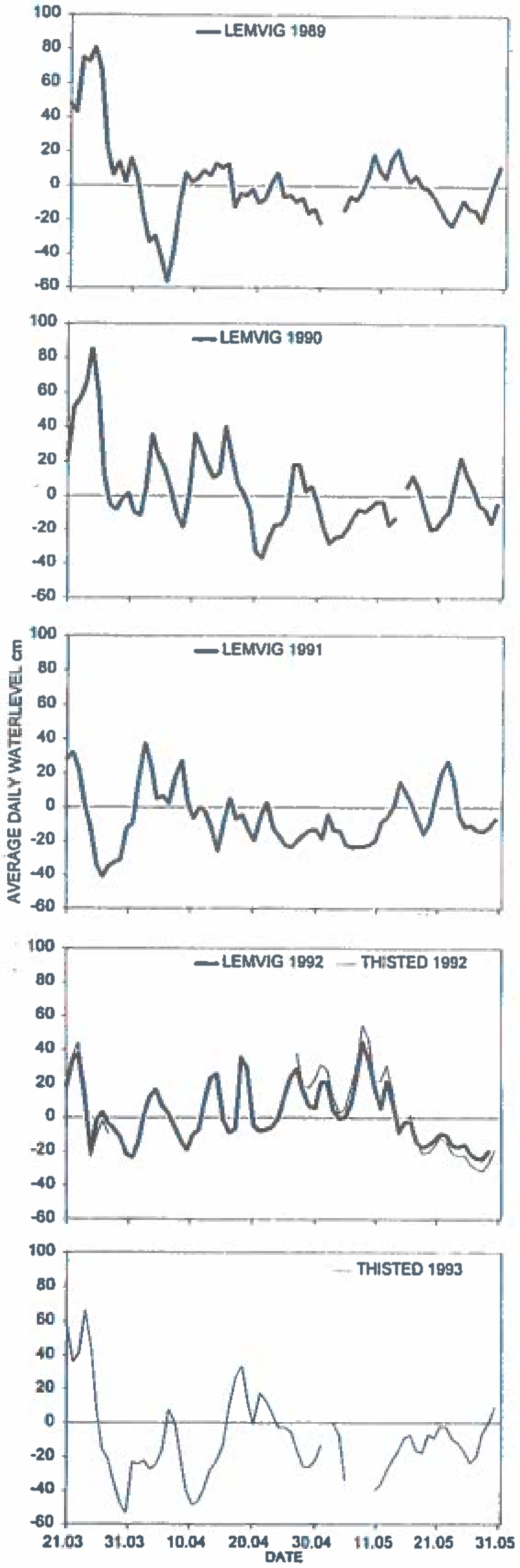

Fig. 3. Fluctuations in average daily water levels at Lemvig 1989-92 and Thisted 1992-93. Average daily water levels are relative to DNN ('Danish Ordnance Datum').

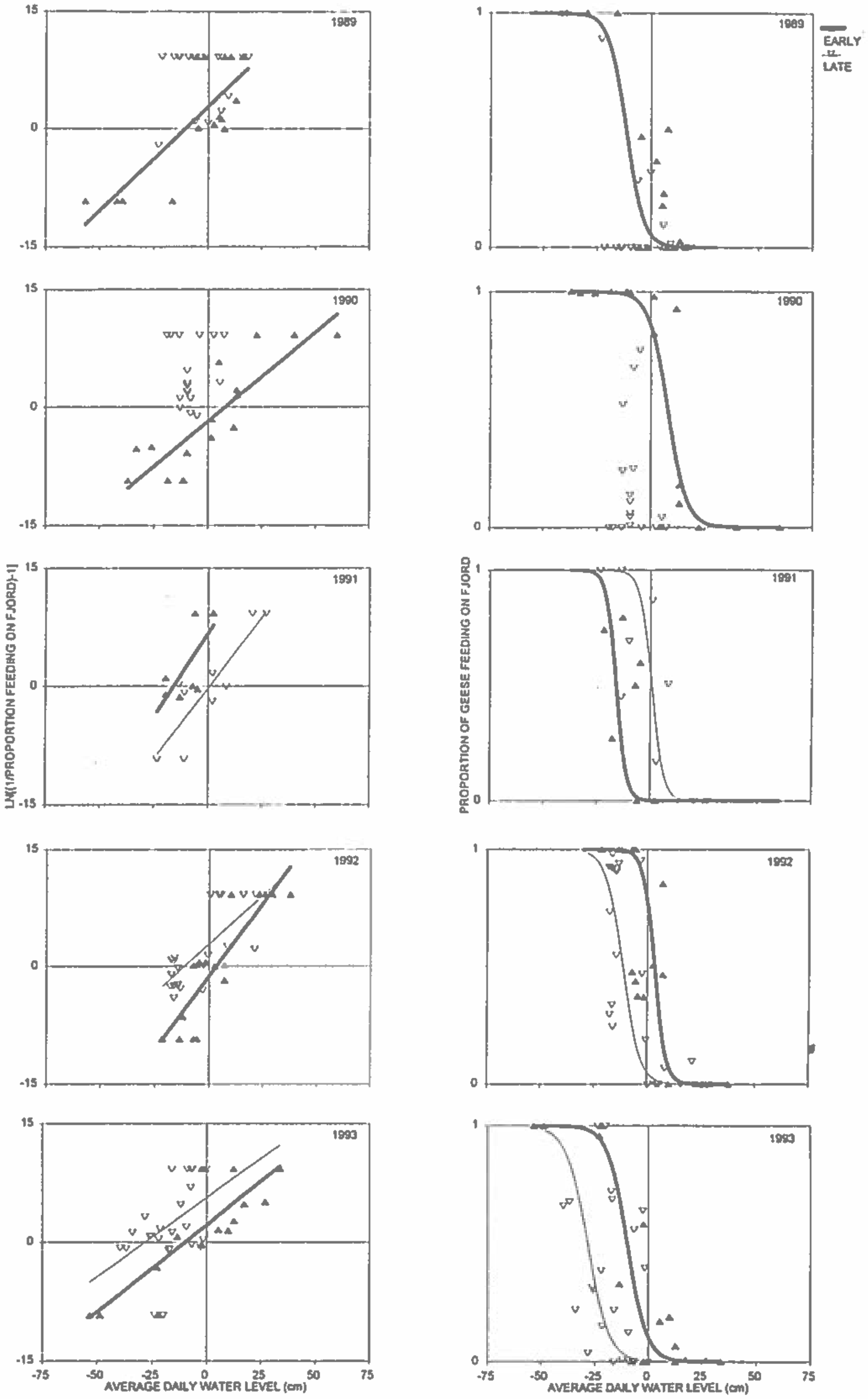

Fig. 4. Linear regressions of the natural logaritm of the transformed proportion of brent geese feeding on the fjord (1/y -1) in relation to the average daily water level (left), and curves of habitat choice of brent geese in relation to the average daily water level, fitted by estimates of constants c_1 and c_2 derived from the regressions (right). Only significant regressions and fits are shown. Early spring: 21 March - 25 April; late spring: 26 April - 31 May.

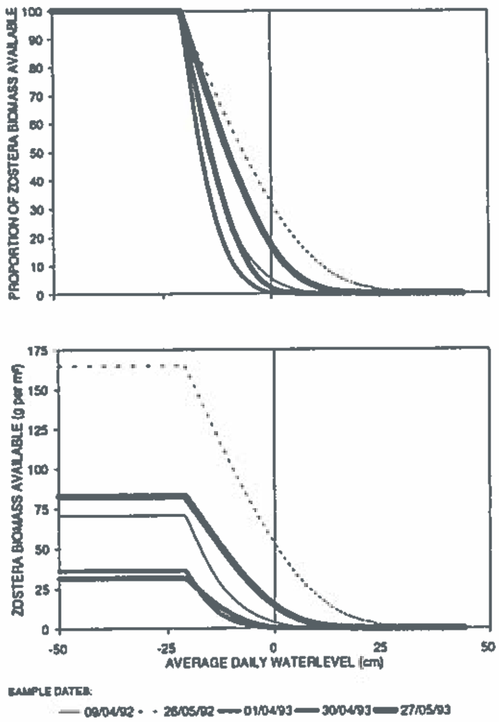

Fig. 5. Availability curves for *Zostera* in relation to water level on sample dates, 1992-93, based on the model of effects of water level on availability of *Zostera*. Both the proportional and biomass specific curves are shown.

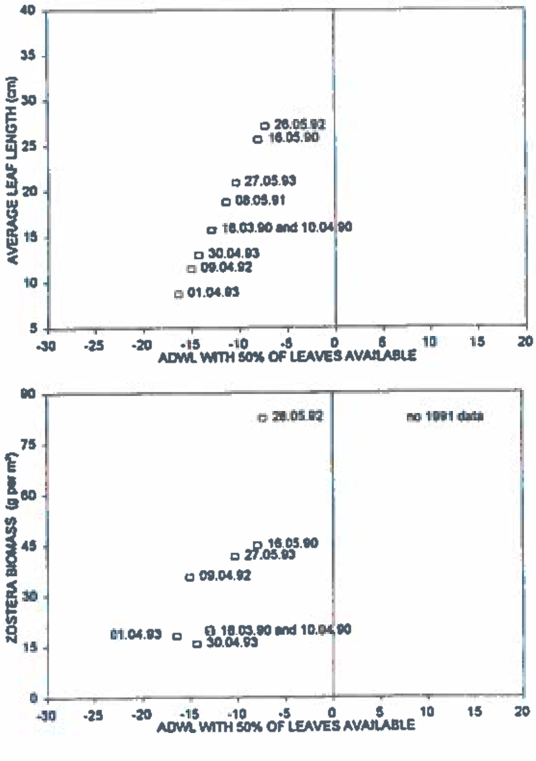

Fig. 6. The relationship between the average leaf length and the average daily water level at which 50% of the *Zostera* leaves would be available to the brent geese (upper), and the corresponding biomass of *Zostera* available, on sample dates 1990-93.

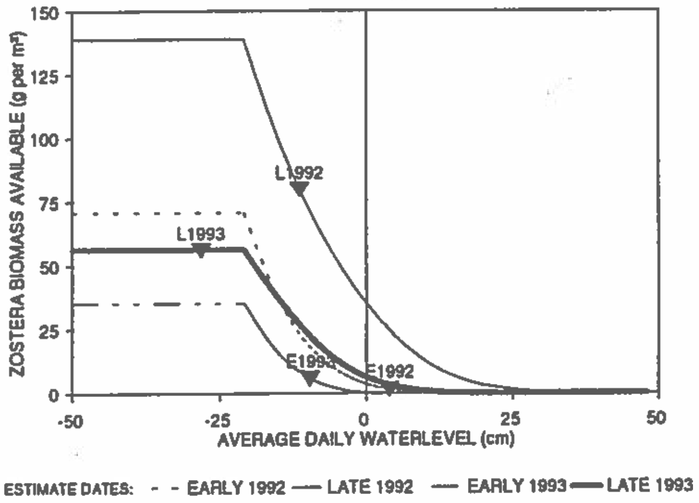

Fig. 7. Estimated availability curves for *Zostera* biomass on median dates for early (7 April) and late (13 May) springs 1992-93. Triangles gives the biomass at which the brent geese switched habitat, i.e. when the average daily water level were equal to c_2 for each period.

Table 1. Average water levels measured at Lemvig 1989-92 and Thisted 1993, and divided into early (21 March - 25 April) and late (26 April - 31 May) springs. Average water levels with the same letter are not significantly different (Duncan's multiple range tests, P>0.05).

Year	Mean early	N	P	Mean late	N	P
1989	7.05	36	AB	- 4.27	33	AB
1990	11.45	36	A	- 5.17	35	B
1991	- 3.07	36	B	- 8.80	36	BC
1992	1.91	36	AB	2.05	35	A
1993	- 5.09	36	B	-14.14	31	C

Table 2. Linear regressions of the natural logarithm of the transformed proportion of brent geese feeding on the fjord (1/y -1) in relation to the average daily water level, and parameter c_1 and c_2 estimates for early and late springs 1989-93. None of the slopes was significantly different from the others. Intercepts, and thereby c_2 estimates, that were not statistically significantly different are given the same letter in the column to the right (Tukey q-tests, P>0.05).

Period	Slope c_1	Intercept $-c_1 \cdot c_2$	N	Probability regression	Calculated c_2	Probability c_2
Early 1989	0.27	2.83	15	0.0003	-10.65	B D F
Early 1990	0.23	-1.80	16	0.0001	7.92	A C E G
Early 1991	0.42	6.65	8	0.0418	-15.80	B
Early 1992	0.38	-1.49	17	0.0001	3.89	A C FG
Early 1993	0.22	2.10	15	0.0002	- 9.62	B D FG
Late 1989			17	0.7577		
Late 1990			16	0.7527		
Late 1991	0.36	-0.29	11	0.0001	0.82	A D FG
Late 1992	0.25	2.84	24	0.0001	-11.34	B D
Late 1993	0.21	5.78	25	0.0354	-28.15	B

Appendix I

Effects of weather conditions on water level changes in the western Limfjord, Denmark.

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Summary

This section evaluates the effects of weather conditions (wind direction and speed, air pressure) on the water levels in the western Limfjord. By multiple regressions it is shown that the vast majority of changes in water levels can be explained by wind on the east-west axis, but also that time-lags, due to pent-up waters, has a major influence on water level in the Limfjord.

Introduction

Even though it was quite clear from observations during field work with Brent Geese around Agerø in springs, 1989-93, that easterly winds induced those low water periods essential for Zostera feeding, I felt quite unhappy without 'proving' that this was actually the case. For that reason I dived into the science of oceanography, and tried to model the water levels in the Limfjord in relation to weather conditions.

Materials and methods

Data relating to atmospheric air pressure and wind conditions, i.e. the averages of eight daily measurements of pressure, wind direction and wind speed (3 hour intervals), were obtained from a meteorological station in Thyborøn, situated where the Limfjord empties into the North Sea (see Fig. 1 in Clausen I), and data on water levels were obtained from Lemvig and Thisted (Clausen I).

The influence of weather conditions on water levels in spring were analyzed by stepwise multiple regression (SAS Institute 1988). Atmospheric pressure were provided as a daily average (mbar). Before entry into the regression models, this daily average pressure was converted by use of a simplified version of the 'inverse barometer law' (Huntley 1980), whereby the pressure-induced change in the water level, ΔH (cm), can be approximated:

$$\Delta H = (\overline{P_a} - P_a)$$

where $\overline{P}_a$ is the daily average pressure and P_a is the prevailing atmospheric pressure (1 atm = 1013 mbar). Wind direction were provided as mean angle (scaled North = 0°, East = 90° etc.) and wind speed in m/sec. Before entry into the regression models the wind direction was converted to a bivector axis system, variable x = cos(mean angle) (providing a vector in a North-South axis) and variable y = sin(mean angle) (vector in an East-West axis). The variables x and y were then multiplied by wind stress on the sea surface, τ:

$$\tau = C_D \rho_a W^2$$

where ρ_a is the density of air (taken as 1.25 kg/m^3), W is the wind velocity in m/sec, and C_D is the surface drag coefficient given by:

$$C_D = \begin{cases} 1.1 \cdot 10^{-3} & \text{for } W \leq 6 \text{ m/sec} \\ (0.61 + 0.063 \cdot W) \cdot 10^{-3} & \text{for } W > 6 \text{ m/sec} \end{cases}$$

whereby the effect of wind speed on water movements were incorporated (Li & Elliott 1993). Data entered into the first multiple regression model were ADWL at Lemvig 1989-92 and Thisted 1993 as dependent variable. Independent variables included: ΔH, τx and τy, and in order to evaluate time-lags of pressure and wind effects: ΔH, τx and τy variables for the previous four days, and year and period ('dummy variable', early=0, late=1, for the spring periods defined below) to evaluate seasonal effects. In a second multiple regression model, the effect of time-lags of pent-up waters were incorporated by adding the ADWL on the previous four days as four additional independent parameters.

Results

The stepwise multiple regression including only weather and seasonal effects found that seven wind variables, two pressure variables, and the year variable contributed significantly to and explained 85% of the variation in water level in the Western Limfjord (Table 1), of which wind on the previous day along the East-West axis alone explained 39%. Adding water levels from the previous four days to the regressions showed that water levels from the previous two days, wind along the East-West axis on the present and previous two days, wind along the North-South axis on the previous day, and pressure on the present and previous three days contributed highly significantly to and explained 93% of the variation in water level, of which water level on the previous day alone explained 69% (Table 1).

Discussion

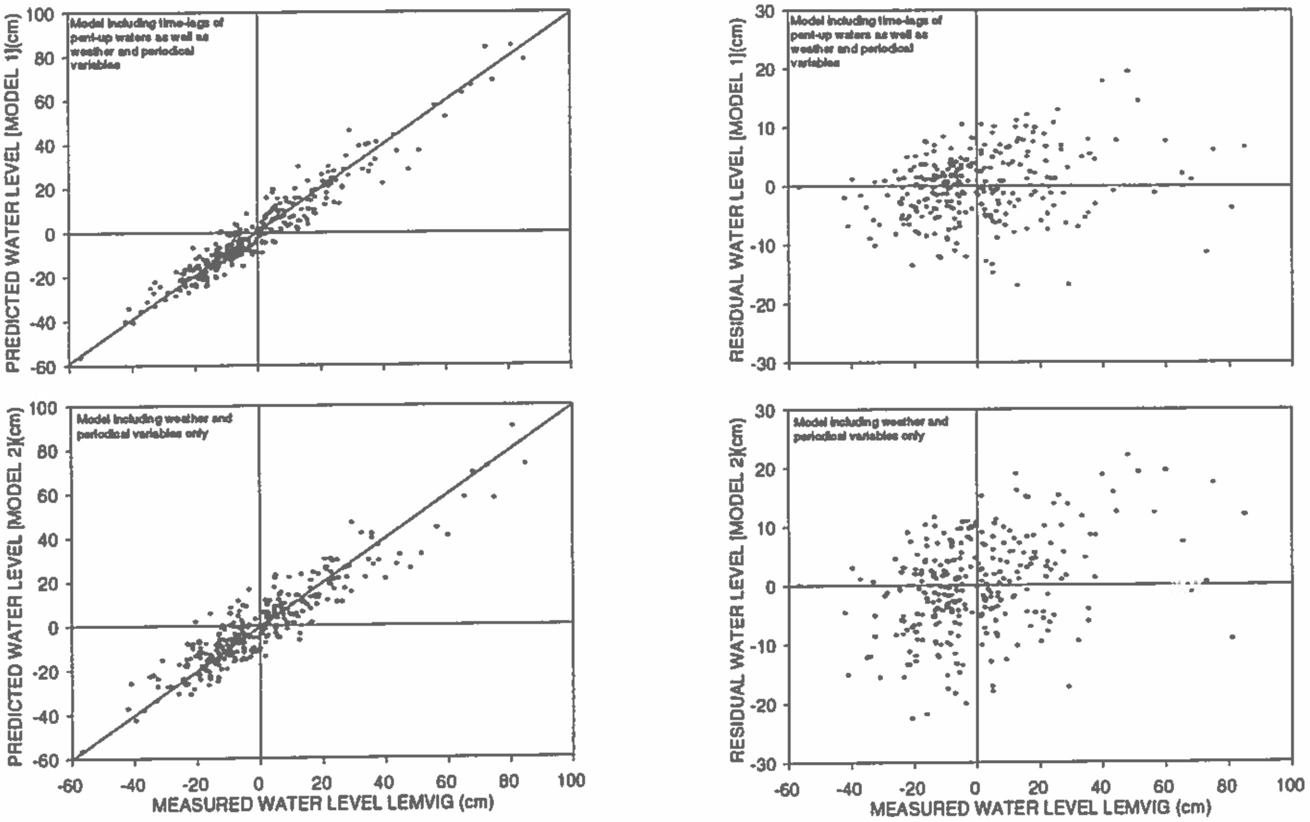
It is well known from oceanographic literature, that wind has a major effect on sea water level fluctuations (e.g. Pingree 1980; Bowden 1983), and that tides and water levels in narrow estuaries are partly distorted by physical effects on water movements caused by the surrounding landscape (Huntley 1980). The present evaluation of weather effects on ADWL in the Western Limfjord (Table 1) are in agreement with this, as this analysis found major time-lag effects by pent-up waters after periods of weather induced changes in water levels. Nevertheless, a large proportion of the variation in water level is caused by wind conditions - especially along the East-West axis (Table 1); a period dominated by easterly winds will give low water levels, one with westerly winds will give high water levels. This interpretation is supported by hydrometric studies which showed that a change from westerly winds (14 m/sec) to easterly winds (5 m/sec) in October 1991 caused a change in water movement through the Thyborøn channel from +8000 m^3/sec to -6000 m^3/sec (Bendtsen 1992). This study also showed, that during a week dominated by strong westerly winds, up to 10-25% of the 'normal' total water volume ($7 \cdot 10^9$ m^3) may be added to the Limfjord (Bendtsen 1992).

It is also evident that fluctuations in water levels caused by weather conditions are far more important than lunar tidal rhythms in determining the water level in the Limfjord.

Appendix I. Table 1. Stepwise regression models for the water level measured in Lemvig as function of weather and seasonal regressors (upper), and also including water levels on the previous days at Lemvig (lower). Day 0 = present day, day -1 the previous day etc.

Model parameters	Parameter estimate	F-value	Probability	Partial R^2	Model R^2
Intercept	82.51	3.99	0.0469		
Wind East-West day -1	-76.32	102.60	0.0001	0.39	0.39
Pressure day 0	0.68	58.35	0.0001	0.30	0.69
Wind North-South day -1	-65.97	39.95	0.0001	0.07	0.75
Wind East-West day -2	-39.37	28.52	0.0001	0.03	0.79
Wind North-South day -2	-54.80	26.55	0.0001	0.02	0.81
Wind East-West day 0	-37.95	34.34	0.0001	0.02	0.83
Pressure day -1	0.33	13.76	0.0003	0.01	0.84
Wind East-West day -3	-25.61	16.74	0.0001	0.006	0.84
Wind North-South day -3	-33.22	10.73	0.0012	0.006	0.85
Year	-0.95	4.37	0.0375	0.003	0.85

Model parameters	Parameter estimate	F-value	Probability	Partial R^2	Model R^2
Intercept	-1.42	13.00	0.0004		
Water level day -1	0.82	221.63	0.0001	0.69	0.69
Wind East-West day 0	-35.86	65.62	0.0001	0.10	0.79
Pressure day 0	0.86	170.35	0.0001	0.08	0.87
Pressure day -2	-0.34	12.12	0.0006	0.02	0.89
Wind East-West day -1	-43.96	61.82	0.0001	0.01	0.91
Wind North-South day -1	-52.22	51.79	0.0001	0.02	0.92
Wind East-West day -2	16.13	9.29	0.0025	0.002	0.92
Pressure day -3	0.29	9.52	0.0023	0.002	0.93
Pressure day -1	-0.33	8.25	0.0044	0.001	0.93
Water level day -2	-0.15	12.04	0.0006	0.001	0.93



Appendix I. Fig. 1. Plots of predicted (left) and residual (right) water levels by use of the models in Table 1 as a function of actually measured waterlevels in the western Limfjord, 1989-93.

Paper II

On the impact of spring grazing by brent geese on Zostera marina growth, reproduction, and availability as food resource.

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Summary

1. Brent geese that stage around Agerø, Denmark, in spring alternates between feeding on Zostera beds and saltmarshes. The Zostera beds are only accessible to feeding geese and thus used during low water level periods induced by easterly winds.
2. Impacts of brent goose grazing on Zostera marina growth and reproduction were assessed by exclosure studies in spring 1992 and spring through summer 1993.
3. The study in 1992 found minor, and that in 1993 major grazing impacts on Zostera. Brent geese grazed the whole 'residual' net above-ground primary production through April 1993, and thereby probably induced compensatory vegetative growth, with increased vegetative shoot production and decreased flowering shoot production in grazed compared to ungrazed plots through May and June. By August the difference between former ungrazed and grazed plots har almost disappered.
4. The influence of the grazing by brent geese on their subsequent access to Zostera food supply was modelled. The geese by grazing through April 1993 reduced average leaf lenghts by 2.5 cm. This lead to an increase of the 'threshold' water level above which they abandon feeding on Zostera by 3 cm, equivalent to 13% of the water level range within which Zostera gradually becomes unavailable to feeding geese. By the end of May the difference in 'threshold' water level was neglectable between grazed and ungrazed plots.
5. The geese by decreasing flowering and thereby probably seed production probably did not affect their opportunities for feeding in the same Zostera bed in coming years. They may, however, have a minor negative effect on dispersal of Zostera to new areas.

Keywords: Branta bernicla, grazing, herbivory, eelgrass, production, flowering.

Introduction

Studies of geese grazing on saltmarsh plants have shown that grazing not only removes above-ground plant material, but also can modify growth characteristics of their food plants and increase plant production (e.g. Prins, Ydenberg & Drent 1980; Jefferies 1988a), and may hamper succession (Bazely & Jefferies 1986; Hik, Jefferies & Sinclair 1992; Olff et al. 1992). When goose feeding activity includes grubbing for below-ground rhizomes and roots, it may reduce production and flowering (Giroux & Bédard 1987) and may even lead to destruction of their own feeding habitats (Jefferies 1988b; Iacobelli & Jefferies 1991; Kerbes, Kotanen & Jefferies 1990).

Other waterfowl studies have also demonstrated impacts of birds upon their food plants in aquatic habitats. Exclosure studies of waterfowl feeding on Zostera beds in autumn found that grazing increased the disapperance of above-ground plant parts in Zostera noltii Hornem. beds (Jacobs et al. 1981; Tubbs & Tubbs 1983; Madsen 1988; Portig et al. 1994), and Zostera marina L. beds (Tubbs & Tubbs 1983; Maheo & Denis 1987). Madsen (1988) and Portig et al. (1994) also demonstrated that the geese by trampling and digging in the sediment took a large part of the rhizomes of Zostera noltii. Thayer et al. (1984) and Nienhuis & Groenendijk (1986) estimated that birds only grazed 3.0-3.7% of the annual production of Zostera marina beds, and concluded that bird grazing was insignificant for Zostera marina growth and production.

Exclosure studies on Ruppia and Potamogeton dominated communities are less conclusive. Jupp & Spence (1977) found that Potamogeton filiformis Pers. and Potamogeton pectinatus L. grew longer and attained higher biomasses when protected from bird grazing. Lauridsen, Jeppesen & Andersen (1993) found a similar result in a study of Potamogeton crispus L., and concluded that the birds delayed recolonisation of plants in their study area, a former hypereutrophic lake during restoration. Exclosure studies in a multi-species community made by Kiørboe (1980) failed to detect any grazing effects, in the same area as Jensen (1986) found grazing effects of waterfowl on biomass of Potamogeton pectinatus, Zannichellia palustris L., and Chara aspera Deth. ex Willd., but no effects on Ruppia maritima L. and Tolypella nidifica (O.F. Müller). Both authors demonstrated, however, that the birds grazed 29% (range 15-60%) of the above-ground plant materials that would otherwise have disappeared anyway through winter storm action and plant senescence. Mitchell (1989) also estimated that 20-50% of the annual production of Ruppia polycarpa R. Mason and charophytes Charophyceae were eaten by black swans Cygnus atratus Latham.

Neither of the Zostera nor the Potamogeton or Ruppia studies, however, evaluated the possible impacts of the grazing activities on the subsequent development of the plant communities.

The present study aims to demonstrate spring grazing impacts by brent geese Branta bernicla L. on a Zostera marina bed, and to assesss the possible influence of grazing on the demography of their food plants. It also evaluates the subsequent effect of the grazing on the birds future grazing opportunities within the Zostera bed.

Materials and methods

STUDY AREA

A pilot study was conducted in spring 1992 and a more thorough study in spring and summer 1993 within the Agerø area (56°43´N 8°33´E) in the western Limfjord, Denmark (Fig. 1). This area is the most important spring feeding area for the Svalbard breeding population of light-bellied brent geese Branta b. hrota (O.F. Müller), with 2,200-3,100 geese (50-74% of the population), found there in recent years (Madsen et al. in press). When staging in the area the brent geese switch between feeding on submerged Zostera marina beds and saltmarshes. Zostera use depends on water levels in the Limfjord, as the geese only have access to Zostera during periods dominated by easterly winds that induce low water levels (Clausen I). Zostera beds dominate the submerged vegetation at depths from approximately 30 to 300 cm, covering an area of 12.0 km^2 within the range used by the geese (Drachmann, Mark & Clausen 1993 and unpublished data)(Fig. 1). Of these Zostera beds, the most important feeding area for brent geese are found southwest of Agerø (Jørgensen, Madsen & Clausen 1994), and this site was chosen for exclosure experiments (Fig. 1). The same site had been used for a study of population dynamics and demography of the Zostera marina population (Olesen 1993; Olesen & Sand-Jensen 1994a, 1994b).

ZOSTERA EXCLOSURE EXPERIMENTS

Four 2x2 m^2 exclosures of wooden poles and chicken wire (mesh size 8 cm) were erected in early April 1992 at c. 70 cm depth 100 m apart along a 300 m long transect parallel to the coast. Exclosure sites were choosen so that the exclosure and the adjacent 'grazed' sampling area appeared uniform in terms of shoot densities (i.e. bottom coverage) and leaf lengths of Zostera. In order to reduce microclimatic effects within the exclosures, 25-30 cm above the bottom was kept free of chicken wire, reducing exclosure effects on water circulation; in 1993 the wire was removed in late May, just after the geese had left the area. Zostera samples were taken initially 2-5 m outside each exclosure after they were established, and outside and inside (avoiding the 50 cm nearest to the exclosure to reduce any microclimatic effects) in late May 1992. Four new exclosures were erected (2-4 m away from the 1992 exclosure sites) and samples taken in early April 1993, and grazed and ungrazed samples were taken in late April, late May, early July and mid August. Brent geese were observed feeding right outside the exclosures at several occasions in both springs.

Samples were taken by placing a 0.1 m^2 square steel frame at the bottom; Zostera plants growing inside the frame pushed to the bottom when placing the frame were gently pulled inside, and plants growing outside were pulled out. A square of Zostera turf was cut along the inside of the frame, the whole turf sieved at the surface (1 mm mesh size) and materials collected by sieving stored in plastic bags. In the laboratory, samples were sorted into vegetative shoots and flowering shoots (all samples), rhizomes and dead material (most samples), and the numbers of vegetative and flowering shoots were counted (all samples). The number of leaves was counted and the length of all leaves measured from 15 or more randomly chosen vegetative shoots in all samples, with the leaves classified by age (1st leaf = the youngest, 2nd leaf = the second youngest etc., after Sand-Jensen 1975). All biomass fractions were dried to constant weight at 70°C in an oven and weighed. Measured leaves were dried separately from unmeasured ones, to derive dryweight per cm leaf. The dryweight per shoot (both vegetative and flowering) were calculated by dividing the dry weight in the sample with the number of shoots contained in the dried sample. All biomass data quoted hereafter refers to dry weight.

Paired sample t-tests (Zar 1984) were used when comparing biomasses per unit area and shoot densities from exclosures with those from grazed areas. This approach was chosen because Olesen (1993) and Olesen & Sand-Jensen (1994a, 1994b) found large demographic variations between Zostera sub-populations within the sampling area, i.e. an exclosure site was believed to be more similar in terms of biomass and shoot densities to its neighbouring grazed site than to other exclosure sites and grazed sites. Biomass per shoot was calculated by dividing biomasses per unit area with the shoot densities and were also compared by paired sample t-tests. All other parameters were compared by Student's t-tests (equal variances) or Welch's approximate t-tests (unequal variances).

COUNTS OF GEESE AND THEIR USE OF THE ZOSTERA BED

In both springs a minimum of three and usually four to six weekly counts were made of all brent geese found within the study area from the last week of March until the end of May. Goose flock positions and the numbers birds in flocks were drawn on field maps (scale 1:25,000), with notes on habitat choice, behaviour (feeding/roosting/flying etc.), and counting conditions (weather, disturbances etc.). During each count, numbers of brent geese feeding on the Zostera bed subject to exclosure studies were recorded, and converted to the number of goosedays used there. The number of goosedays between two counts was calculated as the average number of geese observed during two counts multiplied by the number of days between them. Goosedays were then summed to give the total number of goosedays, G, used over the entire period.

The total area of the Zostera bed where the exclosure study was performed is 84.58 ha (Drachmann et al. 1993), although only part of this is available to feeding brent geese. This is because brent geese can only reach 40 cm below surface when feeding (a depth found around the exclosures when a water level equivalent to -20.8 cm DNN 'Danish Ordnance Datum' occurs), and because all Zostera in spring becomes unavailable to feeding brent geese when the water level rises by an average of 22 cm (1.2 cm DNN)(Clausen I). Since water level rarely falls below -30 cm DNN (Clausen I), only Zostera found at water depths of approximately 0-70 cm is usually available to feeding brent geese. Since 7 of 34 plots sampled plots in a 100x300 meter grid within the Zostera bed occurred in this water depth range (0-70 cm, corrected for deviations from 'normal' i.e. 0 cm DNN; J. Drachmann, S. Mark & P. Clausen, unpublished data), the Zostera area available to feeding brent geese, Z_a, was estimated as: $Z_a = 7/34 \times 84.58$ ha = 17.41 ha.

CONSUMPTION OF ZOSTERA AND ESTIMATES OF NAPP IN GRAZED AND UNGRAZED PLOTS

The consumption of Zostera m^{-2} within the Zostera bed was calculated as: $C = G/Z_a \times GIR_d \times D \times P_f$, where G and Z_a are as defined above, GIR_d is the gross intake rate (dryweight) for brent geese feeding on Zostera (0.22 g min^{-1}; Clausen III), D is the mean day length (min day^{-1}), and P_f is the proportion of the day spent feeding by brent geese (0.784 from time-budgets; Clausen IV).

Estimates of net above-ground production (NAPP) in grazed and ungrazed plots were approximated by the method of Cargill & Jefferies (1984a): For ungrazed plots the vegetative shoot NAPP was calculated as: NAPP = $x_f - x_i$, where x_i is the vegetative shoot biomass present at start of the experiment and x_f is that sampled after the exclosure period. For grazed plots the vegetative shoot NAPP was calculated as: NAPP = $x_f - x_i + C$, where x_f and x_i are as defined above, and C is the amount consumed by the geese as defined above.

This calculation does not account for flowering shoots, which are shed and lost from the population. Olesen (1993) found that flowering shoots in the study area on average lasted 41 days from initiation of flowering to loss of shoots with ripe seeds. As I accidentally sampled Zostera with intervals of 41 days or more during the flowering period, NAPP of flowering shoots for summer 1993 was calculated as the sum of the biomass of flowering shoots.

The present approximation of NAPP does not include changes in dead above-ground biomass, and will probably give an underestimate. Dead biomass was excluded, because very many leaves are lost by wave action or shedding (a natural habit of Zostera by which loading of epiphytes are reduced; Sand-Jensen 1977) which may float around and decompose elsewhere in the Zostera bed, accumulate and decompose in deeper parts of the Limfjord, or wash onto surrounding beaches to decompose there. Consequently changes in dead biomass within the sample area might represent Zostera produced elsewhere, and introduce an inexpedient error in the NAPP estimate. Acknowledging this limitation of the calculations, the outcoming NAPP estimates will be termed residual net above-ground primary production rNAPP.

EFFECTS OF BRENT GOOSE GRAZING ON THEIR OWN FOOD SUPPLY

The brent geese by grazing the plants affect the biomass of Zostera available to themselves. The shorter the leaves, the less accessible they are subsequently to feeding brent geese in the following days, given constant water levels. The effect of grazing on food availability was assessed by use of the model developed in Clausen (I), whereby depletion curves of Zostera availability in relation to water level based on samples from grazed and ungrazed areas could be calculated and compared.

Results

DEVELOPMENT OF ZOSTERA SHOOT DENSITY, BIOMASS AND LEAF LENGTH IN GRAZED AND UNGRAZED PLOTS

The exclosure study in spring 1992 found that grazed plots had significantly higher vegetative shoot densities, rhizome biomass, and flowering shoot biomass than ungrazed plots after 40 days of grazing (Table 1). The higher biomass of flowering shoots was caused by significantly higher biomass per flowering shoot, as there was no significant difference in flowering shoot densities, nor in the vegetative shoot biomass, biomass per vegetative shoot or dead biomass (Table 1). Measurement of individual leaves on vegetative shoots found no significant difference between leaf lengths, neither between the number of leaves per vegetative shoot nor the biomass per cm leaf on vegetative shoots in grazed versus ungrazed plots (Table 1).

The full study in 1993 found significant effects after 29 days of grazing in late April, i.e. significantly lower vegetative shoot biomass (Fig. 2), fewer leaves on vegetative shoots (Fig. 2), and shorter leaves (Fig. 2), of which the 2nd, 3rd and 4th leaves were significantly shorter (Fig. 3), in grazed compared to ungrazed samples. No differences were detected in vegetative shoot densities and leaf biomass per cm leaf.

After 56 days of grazing in late May (departure time of the geese), the difference between vegetative shoot biomass in grazed and ungrazed plots had disappeared (Fig. 2). This was so despite significantly higher densities of vegetative shoots, higher number of leaves on vegetative shoots, and significantly higher leaf biomass per cm in grazed plots (Fig. 2); the effects of these on vegetative shoot biomasses were counteracted by significantly longer leaves (Fig. 2), of which the 1st, 2nd and 3rd leaves were significantly longer (Fig. 3), and significantly higher vegetative shoot biomass (Fig. 2) in ungrazed plots. Flowering started during May, and there were significantly higher densities and biomasses of flowering shoots in ungrazed plots (Fig. 2).

In early July, approximately 40 days after the geese left the area, most of the differences between the grazed and ungrazed plots had disappeared (Fig. 2, Fig. 3). However, there were significantly higher vegetative shoot densities and biomass, as well as flowering shoot densities in grazed plots (Fig. 2). These differences had disappeared by mid August (Fig. 2), when only significantly longer leaves were found in ungrazed plots (Fig. 2, Fig. 3).

COUNTS OF GEESE AND THEIR USE OF THE ZOSTERA BED

Between 2,600 (spring 1993) and 3,100 (spring 1992) brent geese stayed within the Agerø area from mid March until late May. Of these up to 70-75% were observed feeding within the Zostera bed subject to exclosure studies. Brent geese showed highly significantly different patterns of use of the Zostera bed in the two years (Table 2), with 27,000 goosedays spent on the Zostera bed from 1 April until departure in late May both years, but in 1992 49.4% of these were spent in April and 50.6% in May, whereas in 1993 67.5% were used in April and 32.5% in May (χ^2-test with Yates correction for continuity: χ^2=1836.53, df=1, P<0.001).

CONSUMPTION OF ZOSTERA AND ESTIMATES OF RNAPP IN GRAZED AND UNGRAZED PLOTS

Geese in the grazed areas during April and May 1992 consumed 21.0 g m^{-2} Zostera equivalent to 16.8% of the total rNAPP of 125.0 g m^{-2} in the same period; rNAPP in ungrazed plots was slightly less, 112.8 g m^{-2} (Table 3). 37.9 g m^{-2} or 33.5% of the total rNAPP was allocated to flowering shoots in the ungrazed plots, and 9.9 g m^{-2} or 7.9% in the grazed plots.

In 1993 brent geese consumed 15.3 g m^{-2} of Zostera in April; they removed all rNAPP in the grazed plots, since vegetative shoot biomass did not change in April 1993. In the ungrazed plots, rNAPP was estimated to be 22.8 g m^{-2} (Table 3). Through May, total rNAPP in the grazed plots was twice that in the ungrazed plots (Table 3); of which 39.0% of the total rNAPP was allocated to flowering shoots in ungrazed plots, compared to 7.9 % in grazed plots (Table 3). After the geese departed the production through June until early July in ungrazed areas almost stopped, and all of the negligible rNAPP was allocated to flowering; in the grazed plots vegetative and flowering production continued, with 10.5% of the total rNAPP allocated to flowering shoots (Table 3). From early July through mid August, the vegetative rNAPP in ungrazed plots was twice that of grazed plots, and flowering terminated in both ungrazed and grazed plots. The 'annual' (spring through summer) rNAPP estimate 1993 for the ungrazed plots was estimated at 116.5 g m^{-2} of which 14.5% were allocated to flowering shoots; and for grazed plots 148.0 g m^{-2} of which 6.4% were allocated to flowering. The annual flowering rNAPP in grazed plots was 56.2% of that found in ungrazed plots.

EFFECTS OF THE BRENT GEESE'S GRAZING ON THEIR OWN FOOD SUPPLY

The effect of the grazing by the brent geese through April on the Zostera leaf length distribution was that the average leaf length on 30 April in grazed areas were 2.5 cm (16.1%), and after one month of further grazing 3.5 cm (16.7%) shorter than in the exclosures (Fig. 2). Grazing geese thus created a more homogeneous stand of Zostera shoots in terms of leaf length, as confirmed by the higher variance of leaf lengths found in ungrazed plots compared to grazed plots (ANOVA, $F_{320,287}=1.60$, $P<0.001$ in late April and $F_{289,311}=2.14$, $P<0.001$ in late May; Fig. 4), a difference which persisted after the geese had left ($F_{320,329}= 1.67$, $P<0.001$ in early July, $F_{296,297}=1.34$, $P<0.001$ in mid August).

Also in late April fewer leaves were present on grazed shoots, a situation which was, however, reversed in late May (Fig. 2). The combination of fewer and shorter leaves in grazed areas in late April led to a 46.4% reduction of the available vegetative shoot biomass in grazed areas as compared to ungrazed areas, although disappeared by late May.

By reducing average Zostera leaf length and biomass the geese also reduced their own subsequent feeding opportunities, since these are determined by available leaf lengths and the water levels in the Limfjord (Clausen I). The effect of their grazing on their own food supply was modelled by use of the method developed in Clausen (I). It was found that the geese in late April, if one assumes that the geese would start grazing on the Zostera beds when more than 5.9 g m^{-2} of Zostera were available (a threshold established for early spring 1993, Clausen I) the geese in the grazed areas should switch from feeding on saltmarshes to feed on Zostera at a water level of -2 cm DNN, in ungrazed areas at 1 cm DNN, i.e. a 3 cm higher water level (Fig. 5). Computed likewise for late May 1993, and assuming a threshold of 56.2 g m^{-2} (Clausen I), the shift in ungrazed areas would occur at a 1 cm higher water level. In late May 1992 there was no difference between grazed and ungrazed areas (Fig. 5).

Discussion

DEVELOPMENT IN ZOSTERA SHOOT DENSITY, BIOMASS, LEAF LENGTH AND RNAPP

The use of residual net above-ground primary production estimates, based on sampled Zostera biomass, as an indicator of production differences between grazed and ungrazed areas, may cause some interpretive limitations, due to the high leaf and shoot turnovers of Zostera marina populations. In the present study area brutto above-ground primary production was 3.6 times the maximum above-ground biomass in 1990 (Olesen & Sand-Jensen 1994a). Observed differences in rNAPP may, however, reflect goose grazing for two reasons:
1) The high leaf turnover is caused by a continous growth of new leaves and shedding of old leaves (Sand-Jensen 1975), with decreasing nitrogen content in older leaves (Pedersen & Borum 1993, Olesen 1993, Clausen III), partly because nitrogen from older leaves are translocated to younger ones (Pedersen & Borum 1992). 2) The brent geese in the study area were almost always observed feeding by submerging their necks or up-ending, i.e. most likely feeding on attached leaves or shoots, as detached older leaves would float around or fall to the bottom, and most likely would be avoided as forage due to their lower nutritive value. In this context it must be kept in mind that brent geese are highly specialized herbivores, which crop specific parts of their food plants to optimise intake rates in terms of quantitative and nutritive value (e.g. Prins et al. 1980, Prop & Loonen 1989, Prop 1991, Prop & Deerenberg 1991).

Initial sampling did not include samples from both the exclosure and the grazed areas, hence it could be that the observed differences in late April and late May were caused by initial differences. Hovever, Olesen (1993) found that Zostera populations with high densities of shoots had short leaves and those with low densities long leaves early in spring, and this difference persisted throughout the growing season. The observed differences in April-May, which disappeared during June-August are more likely to be effects of grazing, because it is unlikely that all four sets of exclosure+grazed areas should all have been established in areas with long leaves (exclosures) and with short leaves (grazed areas) respectively. As tests are performed by pair-wise comparisons (biomass) or overall populations (leaf lengths) differences due to population specific characters are also minimised.

Grazing by brent geese during April and May 1993 significantly affected the growth characteristics of Zostera. Geese by intensive grazing removed all rNAPP through April, since average leaf length, number of leaves per shoot, and thereby vegetative shoot biomass were reduced in grazed plots as compared to ungrazed plots in late April. During May, when partially released from heavy grazing, Zostera in the grazed plots increased rNAPP through vegetative growth, by increasing the number of vegetative shoots and number of leaves per shoot which, in spite of persistently shorter average leaf lengths in grazed areas, led to the dissappearance of any difference between grazed and ungrazed vegetative shoot biomass by the end of May. This was also partly a result of the greater investment in sexual production which occurred in the ungrazed plots. After the geese departed, vegetative production continued through June, resulting in a substantial difference between ungrazed and grazed vegetative shoot densities and biomass found in early July. Due to increased rNAPP in the former ungrazed plots through July and August, almost all differences had disappeared between the former grazed and ungrazed plots in mid August, after almost three months without grazing.

The observed vegetative growth response may be seen as a compensatory growth response of the grazed Zostera. Support for this can be found in literature dealing with geese grazing on saltmarsh graminoids and dealing with Zostera demography.

The vegetative response of Zostera to grazing by brent geese may be comparable to that of Carex subspatacea grazed by lesser snow geese Anser caerulescens L., i.e. increased NAPP by increased leaf turnover and leaf production per main shoot (Kotanen & Jefferies 1987), and that of grazed Puccinellia phryganodes, i.e. increased NAPP by increased axillary shoot production and increased leaf production on axillary shoots (Bazely & Jefferies 1989a). Zostera plants in this study were not divided into main and axillary shoots, hence it is not possible to conclude whether the Zostera response was a "Carex type" or a "Puccinellia type" response, or a combination of both. The increase in NAPP of Carex and Puccinellia is believed to be partly caused by the fertilising effects of droppings and increased bacterial nitrogen fixation in open areas created by grazing and grubbing geese (Bazely & Jefferies 1985; Bazely & Jefferies 1989b; Ruess, Hik & Jefferies 1989). Such an explanation does not explain compensatory growth of Zostera in this study, because Zostera in the generally eutrophic Limfjord are unlikely to be nitrogen limited, especially in spring and early summer. Indeed, Pedersen & Borum (1993) found no evidence of nitrogen limitation in the same period in a Zostera population which is more dense than the one subject to grazing (compare Pedersen & Borum 1993; Olesen & Sand-Jensen 1994a; Fig. 2), and their study was conducted in an area with lower nitrogen concentrations in the water column than those found in the western Limfjord (compare Pedersen & Borum 1993; Limfjordsovervågningen 1992a). Olesen & Sand-Jensen (1994a) found that many vegetative shoots throughout the year developed on side-branches of the main Zostera shoots, especially in May-June, but many of these later died due to shading from the larger shoots, i.e. shoot densities were regulated by self-thinning. If geese graze the largest shoots (as suggested by the observed significant grazing impacts on the longest leaves in April and May, Fig. 3), a possible explanation is that the shading effect is reduced in the grazed plots, whereby more vegetative shoots formed on side-branches survive, leading to increased production. An alternative explanation would be that grazing on large shoots induce increased side-branching.

The observed larger investment in flowering in ungrazed areas is believed to be an effect of grazing on vegetative shoots in grazed plots, rather than an effect of grazing on flowering shoots. This is so for more reasons: 1) Flowering shoot densities were low in April, when the most intensive grazing activity took place. 2) Flowering shoots have a low nitrogen (i.e. protein) content (73% of that found in vegetative shoots, Olesen 1993). 3) Protein contents of vegetative shoots during May 1993 approached 15% (Clausen III), a value considered to be a lower threshold for optimisation of protein intake (Prop & Deerenberg 1991), and it is unlikely that the brent geese should feed on the less nutritious flowering shoots during spring, when the geese build up a protein reserve necessary for the subsequent breeding season, i.e. their potential reproductive success. 4) The delay of flowering and the reduction in flowering shoot biomass in grazed plots can also be explained by the geese taking the larger shoots, as flowering shoots are recruited from larger plants (Olesen 1993). The studies of grazing by lesser snow geese found no effects on flowering, since Carex and Puccinellia rarely or never flowered in the Canadian study area (Cargill & Jefferies 1984). However, it is well documented that intensive herbivory reduces or even prevents flowering and subsequently seed production of terrestrial plants (e.g. Rockwood 1973; Bentley, Whittaker & Malloch 1980; Stephenson 1982; Briggs 1991).

The demographic studies by Olesen (1993) and Olesen & Sand-Jensen (1994a, 1994b) found highly variable individual developments and intensive early flowering. This suggests that their study in 1990 was less affected by grazing, as grazing in the present study in 1993 made a homogeneous stand of Zostera shoots (Fig. 4) and delayed flowering (Fig. 2). In favour of this interpretation is that only 2,200 brent geese used the Agerø area in 1990. They spent 16,356 goosedays (76.7% in April, 23.3% in May in the Zostera bed through April and May 1990 (Clausen IV), i.e. 60.8% of the goosedays spent there in 1993, and the geese grazed an estimated 13.2% of rNAPP in 1990 (Clausen IV). The production in 1990 was probably comparable to or higher than that observed in 1993, because of a very early spring with higher radiation that year (Clausen IV), and radiation is known to be the main growth regulator in temperate Zostera marina beds (e.g. Sand-Jensen 1975; Wium-Andersen & Borum 1984).

The 1992 study found some grazing impacts on Zostera (Tables 1 and 3), despite the lower grazing intensity (16.8% of rNAPP grazed in 1992; 31.6% in 1993). Although less conclusive than those found in 1993, they followed similar pattern, i.e. decreased flowering and increased vegetative growth in grazed plots.

The studies in 1990-1992 and 1993 may suggest that the herbivore optimization curve (i.e. no effect of low intensity grazing, stimulative effect of medium intensity grazing, and adverse effect of high intensity grazing on growth of the food plants) found in the Puccinellia phryganodes/lesser snow geese studies (Jefferies 1988a; Hik & Jefferies 1990; Hik et al. 1991), may operate in Zostera marina populations too. A demonstration of negative effects with very intensive grazing regimes, however, can only be made by more studies in forthcoming years, if goose numbers continue to increase around Agerø as they did in recent years (Jørgensen et al. 1994) whereby an expected increase in grazing pressure also will occur.

EFFECTS OF THE BRENT GEESE'S GRAZING ON THEIR OWN FOOD SUPPLY

By reducing average leaf lengths by 2.5 cm in April 1993, the geese affected the water level at which they would switch to feeding on Zostera by 3 cm. This may seem a small range, however, as the Zostera is reduced to thresholds below which the geese abandon feeding on it with a water level rise of 22.8 cm, 3 cm is equivalent to a 13.2% reduction of the water level range giving access to Zostera feeding. The brent cope with this problem by rotating between feeding on different Zostera beds in the area (Clausen III). In May, with increased production, more biomass in grazed areas, and with generally longer leaves, most of the impact by the geese on their access to the Zostera supply disappeared.

Most differences between grazed and ungrazed areas had disappeared in August. This suggests that goose grazing in one year do not affect their grazing opportunities in the following year. The maximum above-ground vegetative biomass values of 136 g m^{-2} and 151 g m^{-2} in the formerly grazed and ungrazed areas in August 1993 were low compared to those found by Olesen (1993) in the same study area in 1990 (mean 229, range 188-303 g m^{-2}). This is probably explained by a very cold and windy summer with low solar radiation in 1993 (Danish Meterological Institute; monthly reports), which may have had led to adverse effects on Zostera developments over summer.

The reduction in flowering and thereby probably seed production presumably has little effect on subsequent food supply either. Olesen & Sand-Jensen (1993a) found that the vast majority of shoots in the Zostera bed was recruited from vegetative growth, and that only very few seedlings survived in established beds. However, the reduction potentially could influence establishment of Zostera beds in new areas within the Limfjord, as they solely are recruited from seeds (Olesen & Sand-Jensen 1993b). This influence is, however, probably also of minor importance, as most of the Zostera beds (below c. 70 cm depth) are out of reach of the geese and thus free of grazing impacts. With the present goose use, where the whole rNAPP was taken in April and 13.1% of the total rNAPP in May of 1993, there is still space for expanded use of Zostera by the brent geese in coming years.

Acknowledgements

My sincere thanks goes to Jan Drachmann and Morten J. Hansen who made the bulk of goose counts in 1992 and 1993 respectively; also to Jan Drachmann and Susanne Mark for a great work with the mappings of Zostera around Agerø; to Birgit Olesen, Tony Fox, and Jesper Madsen who reviewed a draft of the manuscript; and the Danish Research Academy who funded a part of my PhD study.

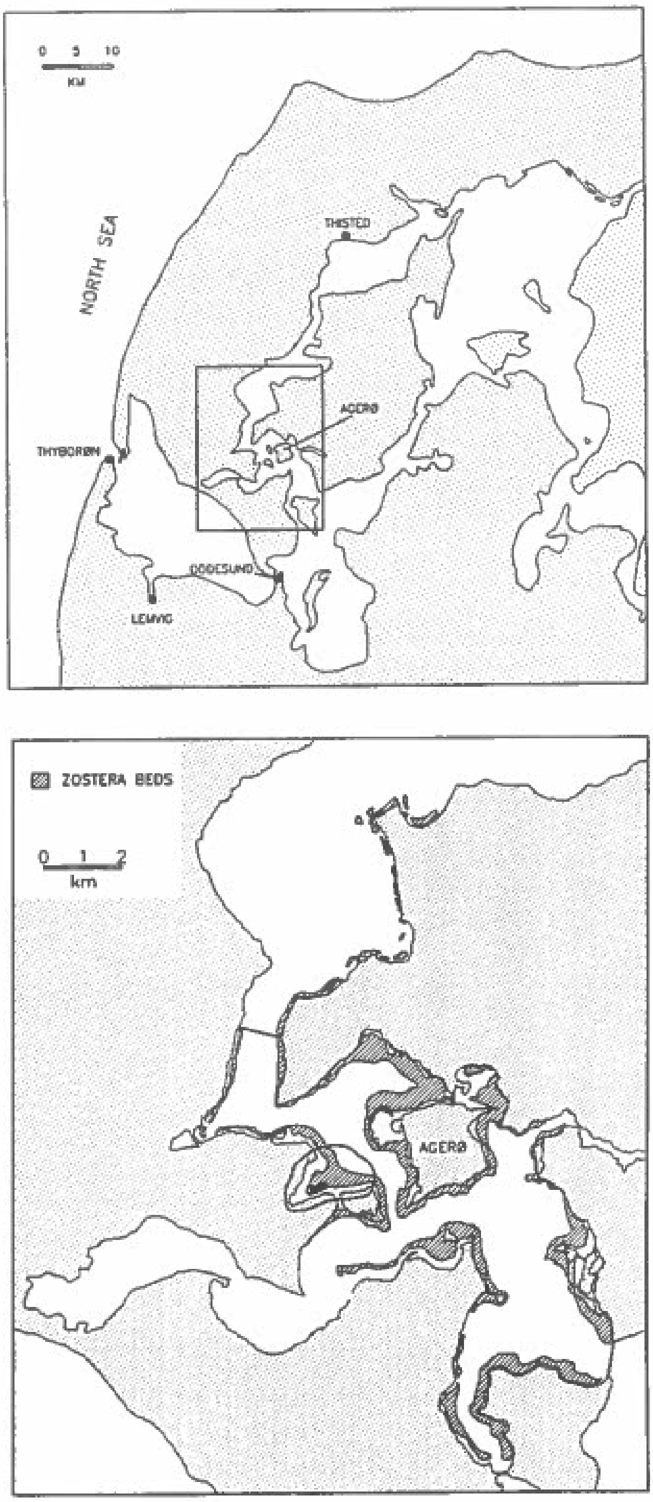

Fig. 1. The western Limfjord, Northwest Jutland, Denmark (left). Open areas are the Limfjord and the North Sea, dotted areas the surrounding landscape; the rectangle surrounds the area used by feeding flocks of brent geese that roost communally at Agerø. Zostera marina beds found within this area is hatched (right; from Drachmann, Mark & Clausen 1993). The position of the Zostera marina exclosure study site is given by the tiny black rectangle; and the limit of the Zostera bed for which goosedays calculations was made by surrounding solid line.

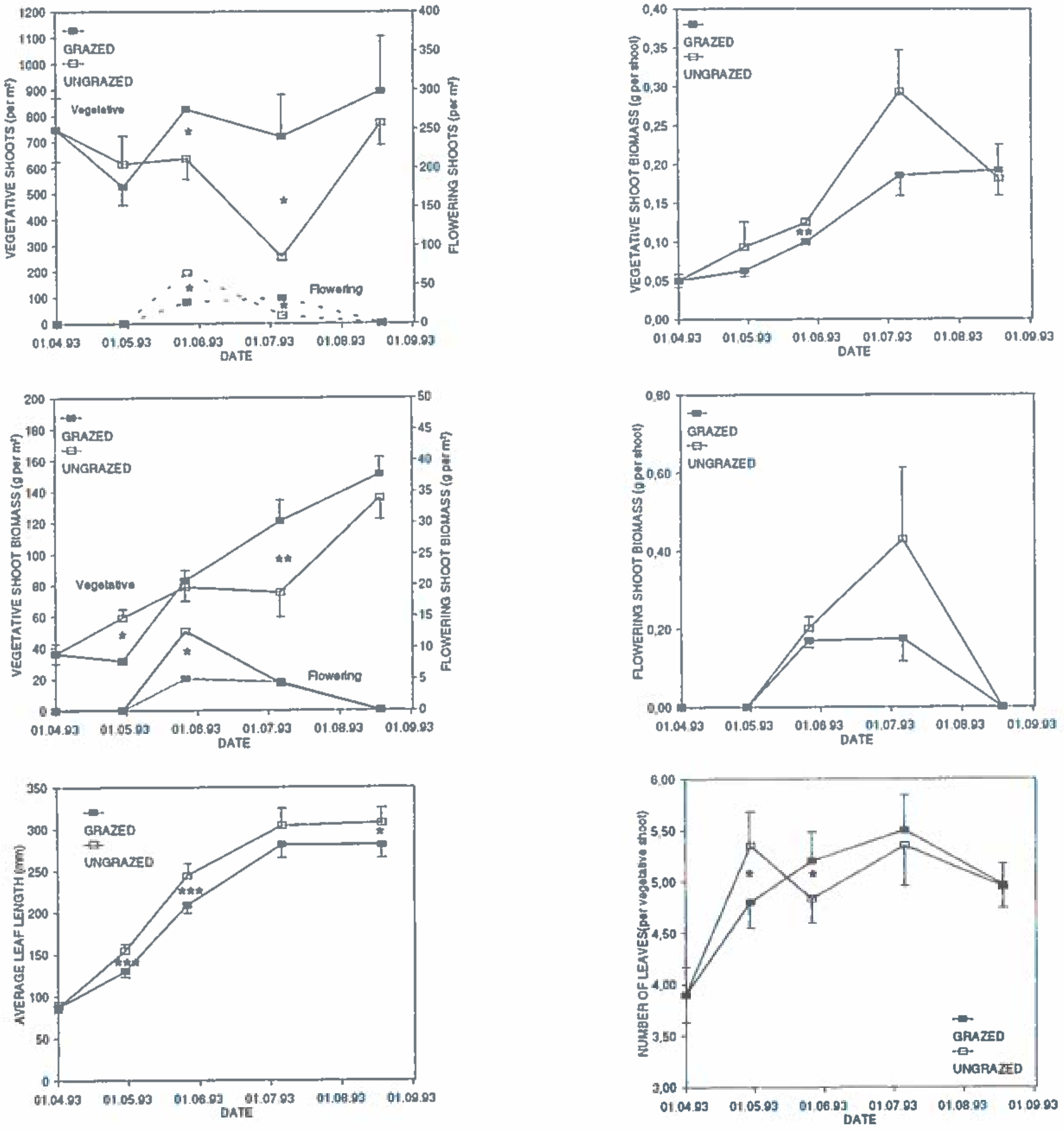

Fig. 2. Development in biomass and density parameters and leaf lengths of Zostera marina in grazed and ungrazed plots, April through August, 1993. The figure shows the development in mean values, with bars giving S.E. (all but leaf lengths) and 95% confidence limits (leaf lengths) respectively. Significantly different means are marked by asterisks, * $p<0.05$, ** $p<0.01$, *** $p<0.001$. Tests were paired t-tests (one-tailed)(all but leaf lenghts), and Student's t-tests (samples with equal variances) or Welch's approximate t-tests (samples with unequal variances)(leaf lenghts)(both two-tailed).

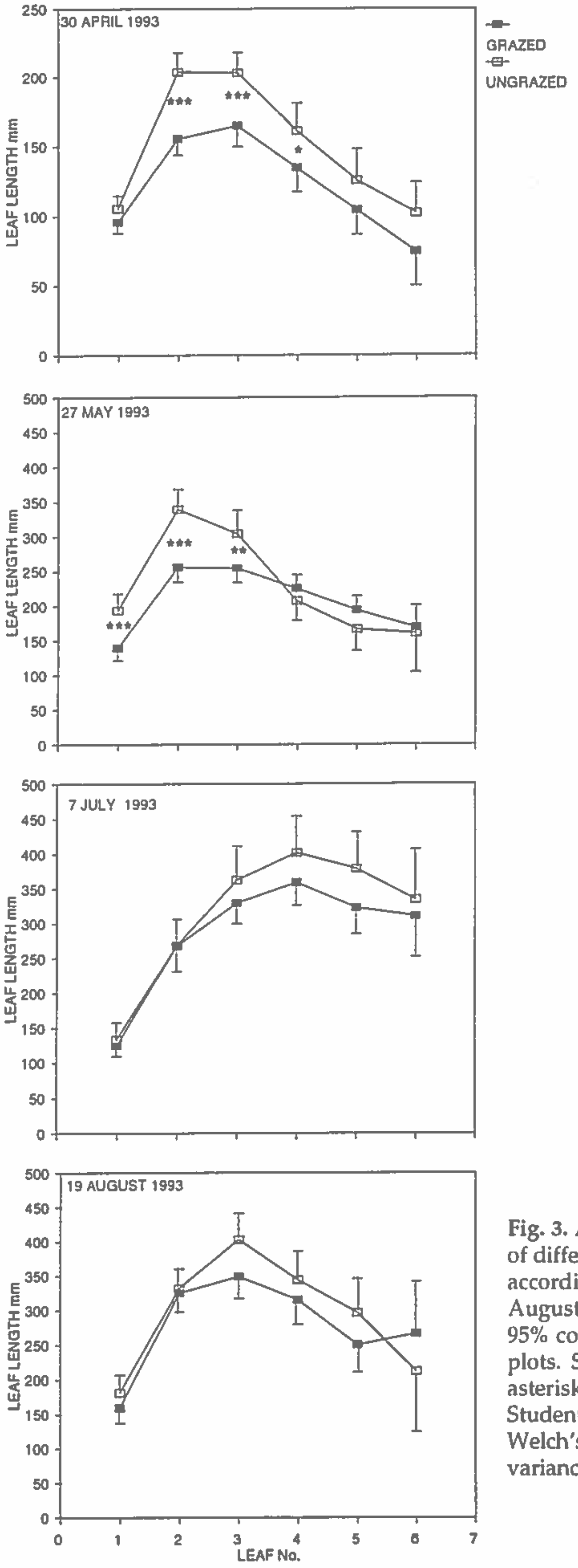

Fig. 3. Average leaf lengths of Zostera marina leaves of different age (1= 1st leaf = youngest leaf and so on according to Sand-Jensen (1975)), April through August, 1993. The figure shows mean values with 95% confidence limit bars for grazed and ungrazed plots. Significantly different means are marked by asterisks, * $p<0.05$, ** $p<0.01$, *** $p<0.001$. Tests were Student's t-tests (samples with equal variances) or Welch's approximate t-tests (samples with unequal variances)(both two-tailed).

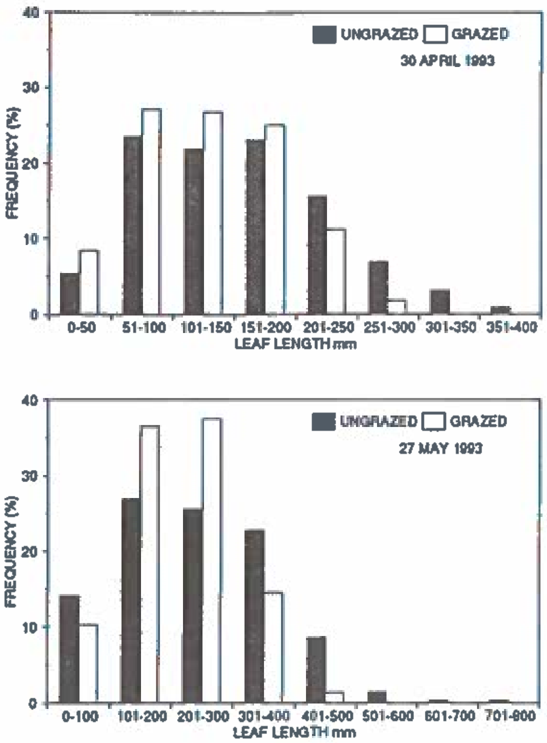

Fig. 4. Frequency distributions of Zostera leaves in grazed and ungrazed plots, based on measurements of of all leaves from 60 randomly choosen shoots late April and May 1993.

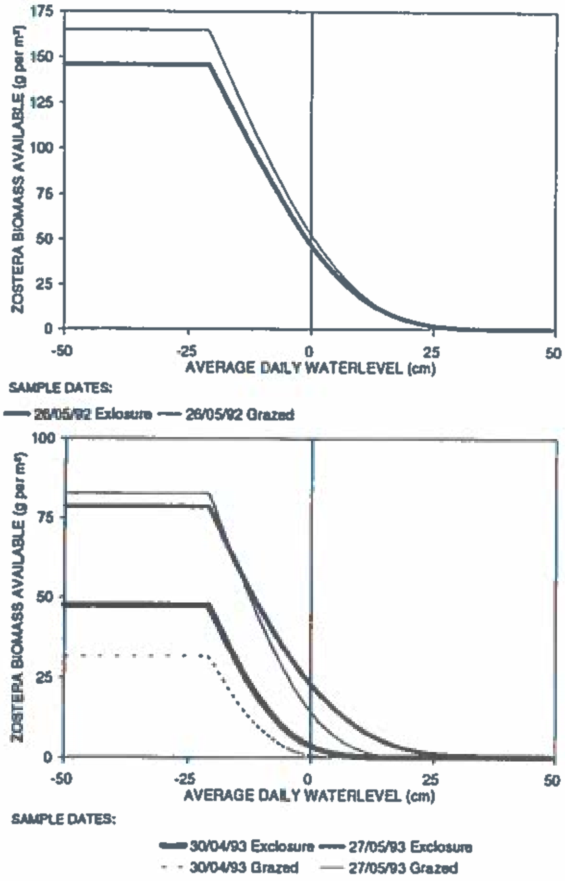

Fig. 5. Depletion curves of available Zostera biomass in relation to water level on sample dates, 1991-93, in grazed and ungrazed plots. The curves were derived by use of a model of effects of water level on availability of Zostera biomass (from Clausen I).

Table 1. Zostera marina biomass and density parameters and leaf lengts of vegetative shoots in grazed and ungrazed (exclosure) plots 26 May 1992 after 40 days of grazing. Differences between biomass and density data were tested by paired t-tests (one-tailed), those between leaf lengths by Student's t-tests (two-tailed).

	Ungrazed Mean (N)	Grazed Mean (N)	t	P
Biomass and density parameters				
Vegetative shoot biomass (g dryweight m^{-2})	145.77 (4)	165.02 (4)	-2.38	n.s.
Vegetative shoot density (shoots m^{-2})	615 (4)	900 (4)	3.06	<0.05
Vegetative shoot weight (g dryweight $shoot^{-1}$)	0.25 (4)	0.20 (4)	1.82	n.s.
Vegetative leaf biomass (mg dryweight cm^{-1})	1.28 (4)	1.28 (4)	0.04	n.s.
No. of leaves per vegetative shoot	5.43 (60)	5.75 (60)	-1.56	n.s.
Flowering shoot biomass (g dryweight m^{-2})	37.91 (4)	9.88 (4)	2.84	<0.05
Flowering shoot density (shoots m^{-2})	145 (4)	45 (4)	2.17	n.s.
Flowering shoot weight (g dryweight $shoot^{-1}$)	0.29 (4)	0.21 (4)	2.62	<0.05
Rhizoms+root biomass (g dryweight m^{-2})	10.78 (2)	16.00 (2)	-16.71	<0.025
Dead Zostera biomass (g dryweight m^{-2})	1039.86 (2)	618.52 (2)	0.76	n.s.
Leaf lengths				
Average leaf length - all leaves (mm)	277.60 (326)	270.85 (345)	0.72	n.s.
Average leaf length - 1st leaf (mm)	228.43 (60)	215.35 (60)	0.78	n.s.
Average leaf length - 2nd leaf (mm)	330.52 (60)	328.10 (60)	0.12	n.s.
Average leaf length - 3rd leaf (mm)	338.00 (60)	357.26 (58)	-0.92	n.s.
Average leaf length - 4th leaf (mm)	303.82 (56)	306.83 (58)	-0.15	n.s.
Average leaf length - 5th leaf (mm)	239.06 (48)	255.58 (55)	-0.77	n.s.
Average leaf length - 6th leaf (mm)	213.70 (30)	161.88 (43)	2.25	n.s.
Average leaf length - 7th leaf (mm)	143.18 (11)	124.70 (10)	0.48	n.s.

Table 2. Brent goose use of the Zostera marina bed where the exclosure experiment were carried out, the spring period was divided into April and May.

	1992			1993		
	April	May	Total	April	May	Total
Total number of brent geese using the Agerø area	3,100	3,100		2,600	2,600	
Peak count of geese feeding on Zostera on bed	2,320	1,810		1,830	1,500	
Goose-days spent feeding on Zostera within bed	13,655	13,973	27,628	18,158	8,734	26,892
Size of Zostera bed (water depths 0-70 cm): 172,450 m^2						
Goose-days spent feeding on Zostera per m^2	0.08	0.08	0.16	0.11	0.05	0.16
Zostera ingestion per minute feeding: 0.22 g/min						
Approximate daylength (min)	843	971		843	971	
Proportion of day used for feeding: 0.78						
Total ingestion (g/m^2)	11.5	13.6	25.1	15.3	8.5	23.8

Table 3. Residual net above-ground production (rNAPP) of Zostera marina in grazed and ungrazed plots, spring 1992, and spring-summer 1993; mean values of Zostera biomass (SE in brackets).

Plot type year Sample date	Vegetative shoot biomass g m^{-2} Mean(SE)	Flowering shoot biomass g m^{-2} Mean(SE)	rNAPP Vegetative g m^{-2}	rNAPP Flowering g m^{-2}	Consumption g m^{-2}	rNAPP g m^{-2}	Total
Grazed 1992							
9 April	70.9 (14.4)	0					
26 May	165.0 (9.0)	9.9 (4.9)	94.1	9.9	21.0[1]	125.0	
Ungrazed 1992							
9 April	70.9 (14.4)	0					
26 May	145.8 (22.1)	37.9 (9.8)	74.9	37.9	0	112.8	
Grazed 1993							
1 April	36.3 (6.3)	0					
30 April	31.6 (2.1)	0	- 4.6	0	15.3	10.7	
27 May	82.8 (7.0)	5.1 (2.2)	51.2	5.1	8.5	64.7	
7 July	120.9 (13.5)	4.5 (0.7)	38.1	4.5	0	42.6	
19 August	151.0 (11.1)	0	30.0	0	0	30.0	
'Year' total				114.7	9.5	23.8	148.0
Ungrazed 1993							
1 April	36.3 (6.3)	0					
30 April	59.0 (5.7)	0	22.8	0	0	22.8	
27 May	78.7 (9.0)	12.6 (3.2)	19.7	12.6	0	32.3	
7 July	75.1 (15.6)	4.3 (3.3)	- 3.6	4.3	0	0.7	
19 August	135.8 (13.6)	0	60.7	0	0	60.7	
'Year' total				99.6	16.9	0	116.5

[1] The consumption estimate for 1992 was based on goosedays used in the period 9 April - 26 May, and is thus slightly lower than that calculated for the whole April - May period in Table 2.

Paper III

Exploitation patterns, intake rates and spring fattening of Zostera feeding Brent Geese.

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Summary

The exploitation patterns, intake rates, metabolisable energy and potential body mass increments of Zostera marina feeding Brent Geese Branta bernicla in a Danish spring staging area was studied during spring, 1990-93. It was found that the Brent Geese by a rotational use of different Zostera beds could crop the most nutritious leaves. Gross intake rates of Zostera feeding Brent Geese was comparable to those of Brent Geese feeding on Puccinellia maritima and Festuca rubra, but lower than those feeding on Plantago marina and Triglochin maritima, reported elsewhere. However, as Zostera generally had higher metabolisable energy than these other plants, the net energy intake of the Zostera feeding Brent Geese was higher, especially in early spring. In late spring, with declining protein concentrations, Zostera may be a less favourable food plant than the better saltmarsh plants, i.e. Plantago and Triglochin. Hence, it is hypothesized that the Brent Geese in that period may optimise energetic intake by feeding on Zostera and protein intake by feeding on saltmarsh halophytes. However, as only a minority of the saltmarsh feeding Brent Geese have access to feeding on the rapidly depleted Plantago and Triglochin plants, most geese can expect a better accumulation of body reserves by feeding on Zostera, especially when calculations of body mass increments were adjusted for the lower flying activities of Zostera feeding Brent Geese.

Keywords: Branta bernicla, eelgrass, intake rates, metabolisable energy, body mass increments, spring fattening.

Introduction

Major declines of Zostera marina, caused by the socalled 'wasting disease', occurred along the Atlantic coasts of North America and Europe in the 1930s (reviews Cottam & Munro 1954, Rasmussen 1977, den Hartog 1987). These declines may have caused population breakdowns, which during the 1930s and 1940s affected all Brent Goose populations found on both sides of the North Atlantic, as Zostera marina was known to have had high importance for feeding Brent Geese Branta bernicla (discussed in Cottam & Munro 1954, Salomonsen 1958, Madsen 1987).

Zostera marina has become reestablished in many of those areas where it disappeared, particularly in Denmark (compare Rasmussen 1977, Ærtebjerg et al. 1993), and Zostera marina beds are now frequently used by Brent Geese in Danish waters in spring. In other areas, Zostera marina populations still are few and restricted in distribution, e.g. in the Netherlands. Dark-bellied Brent Geese Branta bernicla bernicla staging in the Dutch Wadden Sea are thus obliged to feed on habitats other than Zostera beds. In spring they feed on saltmarshes where their feeding efficiency in terms of energy and nutrient (especially protein) intake, which lead to a massive increase in body weight in that period, is of crucial importance for the reproductive success of the Brent Geese (Teunissen et al. 1985, Ebbinge 1989, Prop & Deerenberg 1991).

Brent Geese in spring optimise their foraging by visiting specific patches of vegetation with intervals of a few to several days, dependent on forage species. Their visits are scheduled to get the highest possible intake in terms of quantity and nutritive value, without destroying their food plants (Prins et al. 1980, Prop & Loonen 1989, Prop 1991, Prop & Deerenberg 1991).

Despite the possible importance of the link between Brent Goose populations and Zostera beds, very few studies have been made on intake rates and energetics of Zostera feeding Brent Geese, and all were made on Brent Geese feeding on intertidal Zostera noltii beds in autumn and winter (Charman 1979, Drent et al. 1978/79, Madsen 1988).

This paper assesses exploitation patterns, intake rates and energetics of Brent Geese that feed on submerged Zostera marina beds in spring. By comparison with evidence published from studies of saltmarsh grazing Dark-bellied Brent Geese in the Wadden Sea the importance of the Zostera beds as alternative feeding habitat to saltmarshes is discussed in relation to spring fattening and reproductive output of Brent Geese.

Study area and methods

The Brent Geese in this study belong to the Svalbard breeding population of Light-bellied Brent Geese Branta bernicla hrota. The study was conducted in springs 1989-93 (March-May) in the Agerø area (56°43'N 8°35'E), in the Western Limfjord, Denmark (Fig. 1). In recent years this area has been used by 2200-3100 geese, representing 50-75% of the population throughout the spring fattening period (Madsen et al. in press). Staging Brent Geese roost communally northwest of the island Agerø, and disperse during the daytime to feeding on submerged Zostera beds and saltmarshes.

Zostera beds occur at depths from approximately 30 to 300 cm and dominate the submerged vegetation of the Limfjord. They cover an area of 12.0 km^2 within the range used by the geese (Drachmann et al. 1993 and unpublished data)(Fig. 1). Among the Zostera beds the four most important feeding areas for Brent Geese are found southwest, north, east and south of Agerø (Jørgensen et al. 1994)(Fig. 1) and these sites were used for scoring dropping rates, and for sampling of plants and droppings for chemical analyses. Brent Geese only feed on Zostera at low water levels, induced by wind and air pressure conditions (Clausen I).

The vegetation of the 7.5 km^2 of saltmarshes (Fig. 1) is dominated by Puccinellia maritima (lower marsh), and Juncus gerardi and Festuca rubra (upper marsh). Locally, halophytes such as Plantago maritima, Aster tripolium, Spergularia media, and Triglochin maritima are found abundantly in mosaic areas, with Juncus and the halophytes growing in tussocks and Puccinellia in between. 89% of the saltmarsh area is managed by cattle grazing (Clausen & Percival V), hence considered of high quality for feeding Brent Geese (cf. Ebbinge 1992).

COUNTS AND MAPPINGS OF GEESE

In all years except 1991 a minimum of three and usually four to six weekly counts were made of all Brent Geese found within the study area from the last week of March until the end of May; in 1991 coverage was slightly less, with one to four counts weekly. A full count of the area can be made with telescopes from eight observation points in less than three hours, so counts were frequently made both in the morning and evening. Positions of flocks and numbers of geese were drawn on field maps (scale 1:25,000).

For each count the Brent Goose flocks were summed, and the proportions of these feeding on saltmarshes, in each of the four most important Zostera beds, and in the remaining Zostera beds were calculated.

DIET AND DROPPING RATES ON ZOSTERA BEDS

When feeding on the Zostera beds it was assumed that the Brent Geese exclusively fed on Zostera, because the beds in shallow water used by the Brent Geese use are practically free of alternative food resources, with low densities of algae covering less than 5% and Zostera comprising more than 60% (up to 100%) of the bottom in the beds (J. Drachmann, S. Mark & P. Clausen unpublished data). Hundreds of observations at close range showed that Brent Geese fed on Zostera leaves, which are easily recognisable when ingested. Only twice were small flocks of Brent Geese observed feeding at alternative food resources in the Limfjord, i.e. a flock feeding on the green alga Monostroma grevillei and the brown alga Petalonia fascia in March 1991, and a flock that fed on Zostera and the red alga Porphyra purpurea in April 1992.

Dropping rates of feeding geese should preferably be measured when intake rates balance output rates (Bédard & Gauthier 1986). This is difficult with Brent Geese feeding on water, as the cloacal region of the abdomen is invisible. However, occasionally flocks went ashore to roost or preen for a short time, and when doing so abdomens of individual geese were observed and the time between excretion of the first and second dropping was measured with stopwatch. These measuments were only made on flocks that had been feeding continously for at least 1½ hour and went directly in to roost from the feeding area, and so it was assumed that their guts were filled, and output rates balanced their intake rates.

COLLECTION AND CHEMICAL ANALYSIS OF ZOSTERA AND DROPPINGS

When flocks went ashore, 30 or more droppings were collected on the beach and Zostera leaves plucked from where the geese had been feeding.

Wet weights of droppings and Zostera samples were determined, and samples dried for 48 hours at 40°C in an oven, cooled in an exicator, and dry weights determined. Dry weight per dropping were calculated by dividing the dry weight per dropping sample with the number of droppings contained in it. Samples of droppings and Zostera were analysed (duplicate, occasionally single or triplicate dependent on the amount collected) at the Central Laboratory of the National Institute of Animal Science. At the laboratory, samples were ground through a Viley mill (1 mm mesh) and analyzed. Chemical analyses included Kjeldahl nitrogen, cell wall components (neutral detergent fibre (NDF), acid detergent fibre (ADF) and lignin), ash, sand (all concentrations measured as % of sample). In addition samples from 1992 and 1993 were analyzed for (crude) fat (ether extracted), and dropping samples were analyzed for nitrogen of urinary origin (Terpstra & de Hart 1974); average values for fat and urinary nitrogen from 1992 and 1993 were used as estimates for concentrations of these in calculations with samples from 1990 and 1991.

Additional Zostera samples (ungrazed and grazed) from an exclosure study area (Clausen II) were also analyzed for Kjeldahl nitrogen, and four samples taken in early June 1993, just after departure of the geese, were sorted in leaves of different age (1st leaf = the youngest, 2nd leaf = the second youngest and so on after Sand-Jensen 1975) and analyzed separately for Kjeldahl nitrogen.

CALCULATIONS OF INTAKE RATES AND METABOLISABLE ENERGY

Gross intake rates (dryweight) (GIR_d) of Zostera feeding Brent Geese were calculated as:

$$GIR_d=\frac{D_r\times D_w\times 100}{(100-R)}\qquad where\qquad R=(1-\frac{M_{fdw}}{M_{ddw}})\times 100$$

D_r is the dropping rate (droppings min^{-1}), and D_w is the dropping weight (g dryweight $dropping^{-1}$). R is the retention rate, based on concentrations of markers in the food and droppings, M_{fdw} and M_{ddw} (on dry weight basis), respectively (Drent et al. 1978/79). ADF was choosen as the most reliable marker (Prop & Deerenberg 1991), because a significant cellulose digestion (part of ADF) could be considered unlikely. The Brent Geese on average ingest 0.22 g Zostera dry weight min^{-1} (results below), and Zostera contains 84% water (P. Clausen, unpublished data). This ingestion rate equals 1.38 g wet weight min^{-1}. The digestive capacity of Brent Geese (maximum load in intestinal system) is 150 g fresh weight (Prop & Deerenberg 1991). Hence throughput time on average is 150 g/1.38 g min^{-1} = 109 min (Prop & Deerenberg 1991). According to Prop & Vulink (1992) cellulose digestion is negligible, when throughput time is less than two hours. Gross intake rates (dryweight) GIR_d were recalculated to gross intake rates (ashfree weights)(GIR_{afd}) by:

$$GIR_{afd}=GIR_d\times\frac{100-ash\%}{100}$$

where ash% is the ash contents (% of dryweights) in Zostera samples.

The calculations below are in agreement with those made by Prop & Deerenberg (1991), whereby basis for direct comparisons with their results is founded.

(Crude) protein concentrations of Zostera were calculated as 6.25×Kjeldahl nitrogen, and those of droppings as 6.25×(Kjeldahl nitrogen - nitrogen of urinary origin). Hemicellulose content was calculated as %NDF - %ADF. Soluble cell contents was calculated as 100% - %NDF, and soluble carbyhydrates as 100% - %NDF - %fat - %protein. All contents were recalculated to proportions of organic matter (ash-free dry weight).

The (apparent) digestibility of component i (DC_i) in the food was calculated as:

$$DC_i(\%)=\frac{[Cf_i-(Mf/Md)\times Cd_i]}{Cf_i}\times 100$$

where Cf_i is the concentration of component i in the food (%), Cd_i is the concentration of component i in the droppings (%)(excluding urinary matter), and Mf and Md are the concentrations (ashfree dryweight basis) of an indigestible marker (ADF).

The metabolisable energy (ME) contents of Zostera (kJ g^{-1}) was calculated as:

$$ME=\sum\frac{(Cf_i\times DC_i\times EC_i)}{10^4}$$

where energy values EC_i of plant component i was taken as 39.3 kJ g^{-1} (fat), 17.8 kJ g^{-1} (protein) and 17.6 kJ g^{-1} (structural and soluble carbohydrates)(after Schmidt-Nielsen 1975).

CALCULATION OF DAILY ENERGY BALANCE AND MASS CHANGE I

Light- and Dark-bellied Brent Goose have comparable body mass and size (Fog 1967, Cramp & Simmons 1977). The daily existence energy (DEE) of Light-bellied Brent Geese was therefore expressed in terms of metabolic mass of Dark-bellied Brent Geese as:

$$DEE=647\times M^{0.74}\ (kJ\cdot day^{-1})$$

where M is the body mass (in kg) of the geese (Boudewijn 1984). As the brent geese undergo a dramatic mass change in spring (Ebbinge 1989), an adjustment for this was made by assuming that the geese had a body mass of 1200 g by 10 April (Ebbinge 1989), equivalent to a DEE of 740 kJ/day. DEE later in spring was calculated adding mass changes (see below) achieved per five-day period, and adjusting DEE to the new body mass. This procedure is similar to that used by Prop & Deerenberg (1991; J. Prop personal communication).

The body mass change (MC g day^{-1}) of Zostera feeding Brent Geese can then be calculated as:

$$MC\ (g\ day^{-}1)=\frac{Productive\ energy\ PE(kJ\ day^{-}1)}{Energy\ required\ per\ g\ mass\ increment}$$

where PE = (Net energy intake NEI, kJ day^{-1}) - (daily existence energy DEE, 837 kJ day^{-1}); NEI was calculated as NEI = (Feeding time, min day^{-1})×(Net energy intake rate, NIR, kJ min^{-1})(Prop & Deerenberg 1991). The feeding time was estimated as 78.4% of the daylength (from Clausen IV, based on timebudgets). The energy required per g mass change was taken as 25.5 kJ g^{-1} (Prop & Deerenberg 1991).

Net energy intake rates (NIR) of Zostera feeding Brent Geese were calculated as:

$$NIR=GIR_{afd}\times ME$$

(Prop & Deerenberg 1991).

CALCULATION OF DAILY ENERGY BALANCE AND MASS CHANGE II

The use of body mass to estimate DEE rely on the assumption that birds of a given body mass spend the same time on various activities such as feeding, roosting, flying etc. However, when comparing DEE and body mass increments of Zostera feeding brent geese with those from saltmarshes (based on Prop & Deerenberg 1991) a serious problem arise. Saltmarsh feeding Brent Geese fly eigth times as much as Zostera feeding geese (Clausen IV), and flying is by far the energetically most expensive activity (12.5×BMR in Black Ducks Anas rubripes in contrast to all other activities ranging from 1.4×BMR (resting) to 2.8×BMR (bathing); Wooley & Owen 1978).

A correction for this problem was approached by assuming that the DEE = 647×M$^{0.47}$ estimate of Boudewijn (1984) is represen-tative for a saltmarsh feeding Brent Goose. The DEE of a Zostera feeding brent goose was estimated as:

$$DEE=647\times M^{0.74}-RFC\ (kJ\cdot day^{-1})$$

where RFC is the reduced flying cost of a Zostera feeding Brent Goose, calculated as:

$$RFC=FC_{saltmarsh}-FC_{Zostera}$$

with $FC_{saltmarsh}$ and $FC_{Zostera}$ being the flight cost of saltmarsh and Zostera feeding Brent Geese respectively.The flight costs in the two habitats were calculated as:

$$FC_{habitat}=\frac{\%flyingtime_{habitat}\times daylength\times EFC}{100}$$

with 0.4% flying time on Zostera and 3.2% on saltmarshes (Clausen IV), and energetic flight costs (EFC)(J sec^{-1}) calculated as:

$$EFC=17.36\times M^{1.013}\times b_w^{-4.236}\times s_w^{1.926}$$

where M is the body mass (g)(starting with 1200 g on 10 April, and correcting for achieved body mass changes later in spring (as described above)); b_w is the wing-span in cm, and s_w is the total surface of both wings fully stretched in cm^2 (Masman & Klassen 1987). b_w was taken as 120.4 cm and s_w as 1251.5 cm^2 (after Ebbinge & Spaans 1992). A 1400 g Brent Goose would according to this formula use 2.1 kJ min^{-1}. By using a BMR estimate of a 1400 g Brent Goose of 393 kJ day^{-1} (307×M$^{0.734}$; M is body mass in kg, Aschoff & Pohl 1970) this may be compared to estimates of flight costs as multiples of BMRs, i.e. 12.5×BMR in Black Ducks (Wooley & Owen 1978), 14.1×BMR in short duration flights of Black Ducks (Berger et al. 1971), and 15.2×BMR in non-passerines (Hart & Berger 1972)), which would range from 3.4 to 4.1 kJ min^{-1} for a 1400 g Brent Goose. The use of Masman & Klassen's (1987) formula of energetic flight cost thus leads to a conservative estimate.

The calculations above does not include addition to DEE of costs of other activities replacing flying in the time budgets of Zostera feeding geese. A major part of these other activities were devoted to feeding (Clausen IV), which in fact would lead to a net surplus when contrasting intake of energy with energetic cost of feeding. Hence it was considered that the approximation by subtracting RFC alone would give a fair estimate of the difference.

Body mass changes, and changes in DEE as body mass increased, were calculated as described above, taking the reduced flight cost into account.

Results

EXPLOITATION PATTERNS OF ZOSTERA BEDS BY GRAZING BRENT GEESE

When the Brent Geese used a Zostera bed, they gradually grazed over the whole Zostera bed from one end to the other, and after having done this, they switched to feeding on an adjacent Zostera bed. The outcome of this exploitation pattern was that they made a rotational use of different Zostera beds, with most birds found in two or three beds on a single count, and dispersed to others on the following counts (Fig. 2).

PROTEIN CONTENTS, INTAKE RATES AND METABOLISABLE ENERGY OF ZOSTERA

Protein contents of Zostera in April and May were in the range 15-23% of organic matter, with a significant decline in the course of the spring of 1993 (Fig. 3), and significantly higher levels in (the late) springs 1991 and 1992 compared to (the early) springs 1990 and 1993 (Welch's approximate t-test, t=22.9, df=22.9, P=0.0003)(Fig. 3). Based on one sample date (early

June 1993) there was a significantly higher concentration of protein in the youngest leaves (Fig. 3).

Protein contents were signicantly lower in grazed (20.3%) compared to ungrazed (22.8%) leaves (Student's t-test, t=19.44, P<0.0001) in late May 1993 (Fig. 3).

Brent Geese that had fed on Zostera and went to roost defaecated at intervals of 5.16 minutes (n=26). Droppings weighed on average 1.11 g (dryweight)(n=24 samples). Gross intake rates of Zostera feeding Brent Geese were on average 0.22 g min^{-1} dryweight (range 0.17-0.27) equivalent to 0.16 g min^{-1} ashfree dryweights (range 0.12-0.20). Metabolisable energy of Zostera were on average 8.1 kJ g^{-1} ashfree dryweight (range 5.9-9.4). There was no clear sign of change in gross intake rates or metabolisable energy between/within springs (Fig. 4).

CELL WALLS AND SOLUBLE CONTENTS OF ZOSTERA

The apparent stability in metabolisable energy arose from relatively stable concentrations of solubles (proteins, lipids and soluble carbohydrates) as well as cell wall constituents (hemicellulose, cellulose and lignin) of Zostera (Fig. 5). The discrepancy between this finding, and the within season decline in protein contents in 1993 (Fig. 3) will be discussed below.

NET ENERGY INTAKE AND BODY MASS CHANGE

Net energy intake rates (NIR) averaged 1.35 kJ min^{-1} (range 0.73-1.89). Two curves of body mass increments per day for geese feeding solely on Zostera were calculated, one based on the $DEE=647 \times M^{0.47}$ estimate, and one taking the reduced flight cost of Zostera feeding Brent Geese into account. Both were based on the average values of ME and GIR (average NIR value), and gave a steady increase in weight increment per day, as a consequense of the constant ME, GIR and thus NIR in combination with increasing day length (Fig. 6). Body mass increments based on $DEE = 647 \times M^{0.47}$ were on average 1.5 g day^{-1} lower than those corrected for the reduced flying cost of Zostera feeding Brent Beese, resulting in estimated body masses of 1541 g and 1616 g, respectively, by the end of May (Fig. 6).

Discussion

ROTATIONAL USE OF ZOSTERA BEDS

Within a spring Brent Geese shifted between feeding on different Zostera beds. Such rotational use of feeding sites has been reported for Brent Geese feeding in saltmarsh mosaic areas (e.g. Drent & van Eerden 1980, Prins et al. 1980, Prop & Loonen 1989), and for Pink-footed Geese Anser brachyrhynchus grazing on saltmarshes and pastures (Lorenzen & Madsen 1985, Meire & Kuijken 1991)(allowing their food plants a period for regrowth before a new grazing event occurs). As the Brent Geese only consumed 13-32% of the Zostera net above-ground primary production (NAPP) in springs 1990, 1992, and 1993 from the most important Zostera bed (Clausen IV), in contrast to 65% consumption of the NAPP of Plantago in the mosaic areas (Prop & Loonen 1989), such a rotational use may seem unnecessary. However, it is known that the Brent Geese in spring primarily graze on the longest leaves, which in spring also are the youngest Zostera leaves (Clausen II). These have the highest nitrogen/protein contents (Pedersen & Borum 1993, Fig. 3). The finding that grazed Zostera have lower protein content than ungrazed Zostera is believed to be a result of this selectivity for young leaves. Hence the geese by rotation can continue to feed on the most nutritious leaves, instead of switching to older leaves, a cropping system similar to that used by green turtles Chelonia mydas grazing on the tropical seagrass Thalassia testudinum (Bjorndal 1980).

PROTEIN CONTENTS, INTAKE RATES AND METABOLISABLE ENERGY OF ZOSTERA

Protein content of Zostera declined in the course of the spring 1993, just as it does in Puccinellia, Festuca, Plantago and Triglochin (Prop & Deerenberg 1991), but the protein content of Zostera is consistently lower than in the four saltmarsh halophytes (cf. Prop & Deerenberg 1991). The declines in protein contents of the four halophytes generally occurred in connection with an increase in less digestible cell wall constituents (Prop & Deerenberg 1991), a trend also found in Juncus and Spartina (Buchsbaum & Valiela 1987). In Zostera, however, cell wall constituents as well as fat appear to be rather stable in concentration, whereas concentrations of soluble carbohydrates increase with the falling protein concentrations in the course of the spring and summer (Buchsbaum & Valiela 1987). The between year comparison of concentrations of solubles and cell wall constituents did not reveal this pattern of falling protein concentrations and rising soluble carbohydrates (Fig. 5), instead they appeared to be rather constant, leading to fairly constant metabolisable energies. Nevertheless, if soluble carbohydrates replace proteins, which both are easily digested, and have comparable energy contents, this would mean that Zostera in contrast to the saltmarsh plants does not show any significant decline in metabolisable energy in the course of the spring, and as the gross intake rates of the Brent Geese also appears to be constant, their net energy intake rate is constant. This is in contrast to Puccinellia and Festuca, which both have declining net energy intake rates; and Plantago and Triglochin, which have increasing net energy intake rates (Prop & Deerenberg 1991).

The gross intake rate of Zostera feeding Brent Geese in spring was found to be 0.16 g min^{-1} ashfree dry weight. Prop & Deerenberg (1991) found comparable GIR's of Puccinellia (increasing from 0.13 g min^{-1} in early April to 0.2 g min^{-1} in late May; lower scale in their figure erroneously presented as 0.1 instead of 0.2, J. Prop personal communication) and Festuca feeding geese (constant at 0.18 g min^{-1}); those of Plantago and Triglochin feeding geese were considerably higher (Plantago increasing from 0.4 g min^{-1} in late April to 0.6 g min^{-1} in late May, Triglochin increasing from 0.6 to 1.0 g min^{-1} over the same period).

The metabolisable energy content of Zostera was found to be constant at 8.1 kJ g^{-1}. This is higher than ME values of Plantago (7.5 kJ g^{-1} falling to 5.0 kJ g^{-1}), Festuca (7.0 kJ g^{-1} falling to 4.5 kJ g^{-1}), and Puccinellia (10 kJ g^{-1} but rapidly falling to 5.0 kJ g^{-1}), and in the range of Triglochin (9.0 kJ g^{-1} falling to 7.5 kJ g^{-1})(Prop & Deerenberg 1991).

BODY MASS INCREMENTS AND SPRING FATTENING ON ZOSTERA BEDS VS. SALTMARSHES

The daily body mass increments calculated from average values of GIR and ME of Zostera feeding Brent Geese and based on DEE = $647 \times M^{0.47}$ are higher than those of Brent Geese feeding on a pure Puccinellia diet on the saltmarshes, but lower than those feeding on a mixed diet of approximately 80% Puccinellia and 20% Plantago/Triglochin. Body mass increments corrected for the reduced flying cost of Zostera feeding Brent Beese are higher than those of Brent Geese feeding on either diets on the saltmarsh, except in mid May. The estimates of body mass achieved in the end of May by Zostera feeding Brent Geese are considerably higher than those of pure Puccinellia feeding geese, and, if one takes the reduced flying cost into account, similar to those feeding on mixed diets on the saltmarshes. Only a limited number of individuals have access to feeding on the rapidly depleted Plantago and Triglochin plants (Prop & Loonen 1989, Prop & Deerenberg 1991), therefore most Brent Geese will benefit from switching to Zostera feeding when water levels allow them to feed there, to improve spring fattening, and thereby increase their probability of breeding successfully in the subsequent season (Ebbinge 1989). This conclusion is especially valid in April, when the high GIR and high ME plants Triglochin and Plantago only occur in very low densities, and Brent Geese on the saltmarshes mainly feed on Puccinellia or Festuca. It is also in agreement with the observation that the Brent Geese in early spring utilise Zostera as soon as water levels permit them to do so (Clausen I).

The calculations of the body mass increments also show that the balance between feeding on Zostera and on the saltmarshes in May may be turned upside down, when increasing amounts of Plantago and Triglochin are available to Brent Geese feeding there. This is in agreement with the observation that the Brent Geese in late spring do not display the same preference for utilising Zostera even though water levels permit them to do so (Clausen I).

PROTEIN INTAKE ON ZOSTERA

An additional reason for using the saltmarshes in late spring may be that Brent Geese, in addition to building up an energy reserve in the form of fat (fuel for the non-stop flight to the breeding grounds) also have to build up a protein reserve (allocated to flight muscles, and egg laying by females), and consequently have to optimise both their energy and protein intake.

Buchsbaum & Valiela (1987) also found a high preference for Zostera by feeding geese, and pointed out, that Zostera in contrast to saltmarsh halophytes is very much like cereal grains, with a high energy content (high in soluble carbohydrates) but low in protein and mineral contents.

With the decline of protein content in late May 1993, Zostera approaches what is believed to be the lower threshold for optimisation of protein intake, i.e. a concentration of 15% (Prop & Deerenberg 1991). Hence, Brent Geese in May may switch between the two habitats to optimise their protein intake by feeding on saltmarsh halophytes. As the energetically most favourable halophytes Plantago and Triglochin become rapidly depleted during each grazing visit (Prop & Loonen 1989, Prop & Deerenberg 1991), the geese can optise their energy intake by feeding on Zostera instead of Puccinellia. This is in agreement with studies of grain feeding geese, i.e. MacLandress and Raveling (1981), who found that Canada Geese Branta canadensis that primarily fed on corn Zea mays in spring supplemented their protein intake by feeding on Poa pratensis, and Madsen (1985) who compared the energetics of grain and pasture feeding Pink-footed Geese in early spring. He found, that the best energy budget was obtained from feeding on grain, but suggested that the Pink-footed Geese, by doing so, accumulated too little protein reserves and would have to supplement these later in spring by pasture feeding.

In conclusion, the Brent Geese around Agerø can expect in most years to achieve a better accumulation of fat reserves by feeding on the Zostera beds. However, as the Zostera may be regularly unavailable because of high water levels, and it may have an unfavourable low content of proteins, the saltmarshes also play a significant role in the accumulation of body reserves of the geese in spring, as an alternative feeding habitat.

Acknowledgements
I would like to express my sincere thanks to Jan Drachmann and Morten J. Hansen who made the bulk of goose counts in 1992 and 1993, respectively; also to Jan Drachmann and Susanne Mark who mapped the Zostera beds around Agerø and Morten J. Hansen for scoring dropping rates of Zostera feeding Brent Geese. Jouke Prop, Tony Fox and Jesper Madsen reviewed a draft of the manuscript. Also thanks to the Danish Research Academy and the World Wildlife Fund - Denmark for financial support.

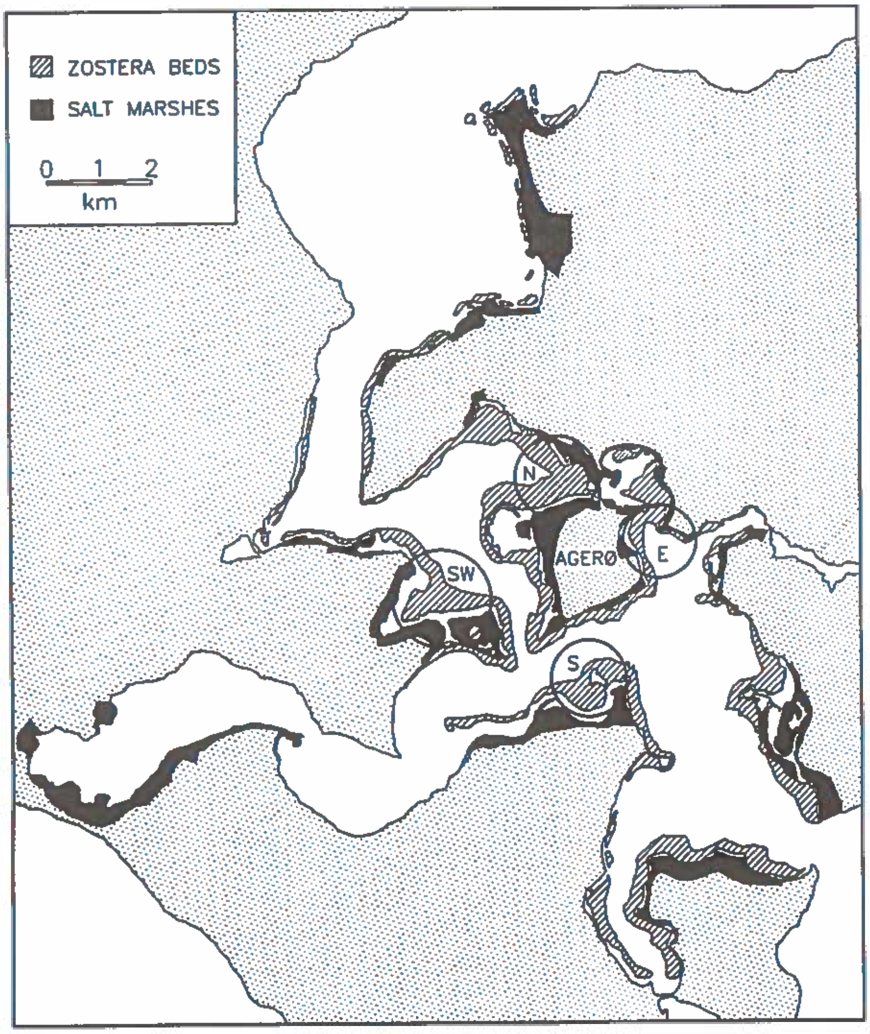

Fig. 1. The study area used by Brent Geese around Agerø in the western Limfjord, Northwest Denmark, showing saltmarshes (black) and Zostera beds (hatched). Encircled are the four most important Zostera beds north, southwest, south and east of Agerø.

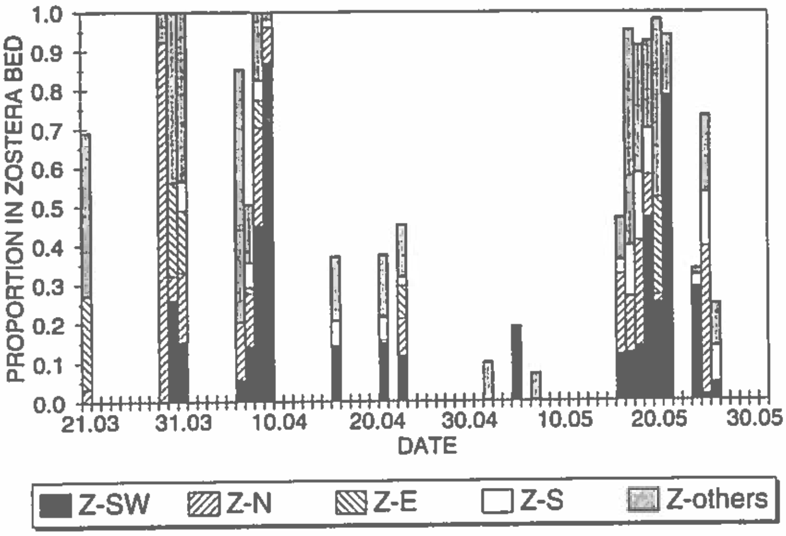

Fig. 2. The proportional use of the four main and other Zostera beds by Brent Geese around Agerø, spring 1992. SW, N, E, and S gives the location of the beds around Agerø (see Fig. 1). The Brent Geese were either not counted, or some used terrestrial feeding areas on days with a sum of proportions of less than 1.

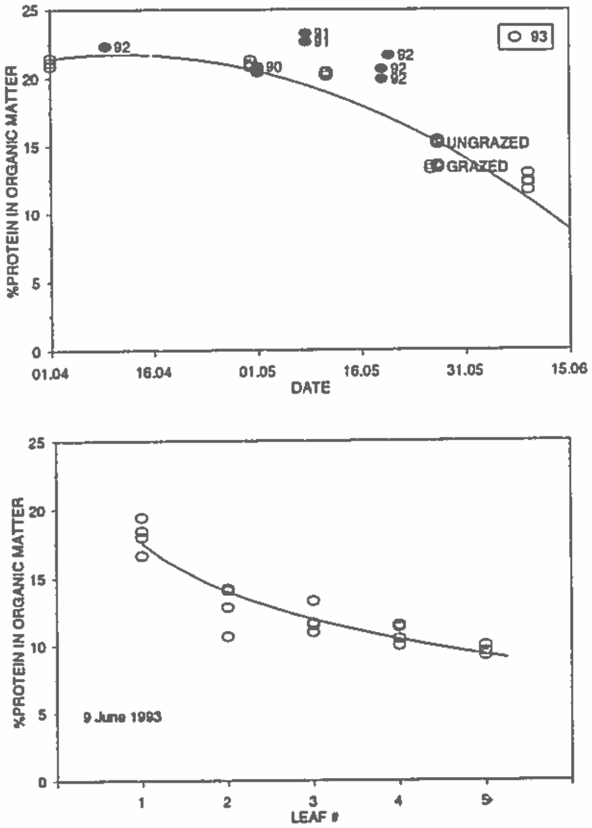

Fig. 3. Protein content of samples of Zostera leaves (from vegetative shoots), springs 1990-93. The upper graph gives content in samples including all leaves (all grazed except the samples marked ungrazed from late May 1993), with a curve fitted to the 1993 data (quadratic regression; r=-0.86, n=26, P<0.001). The lower graph gives content in leaves sorted by age (quadratic regression; r=-0.88, n=20, P<0.001).

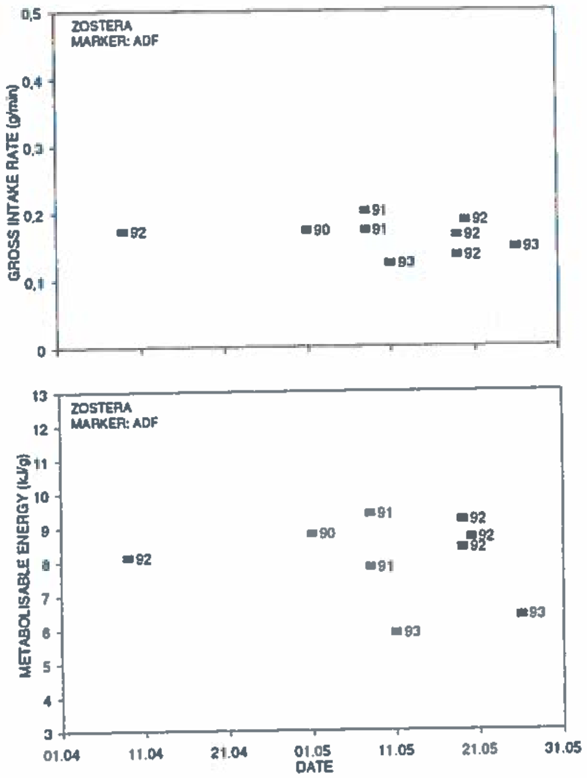

Fig. 4. Gross intake rates (g dryweight min^{-1}) and metabolisable energies (kJ g^{-1} dryweight) of Zostera, based on samples of Zostera leaves and droppings with ADF as indigestible marker, springs 1990-93.

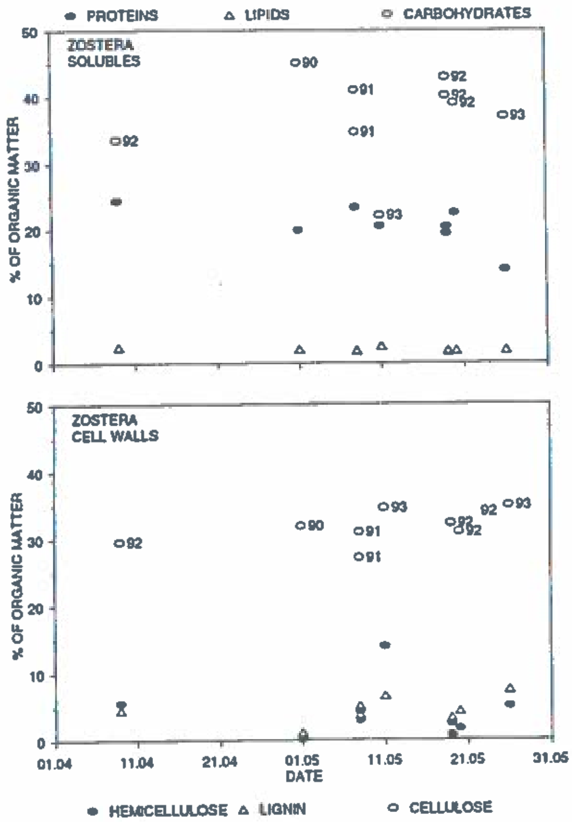

Fig. 5. Contents of soluble carbohydrates, lipids, proteins, hemicellulose, cellulose and lignin of the Zostera samples, on which the calculations of GIR and ME were based.

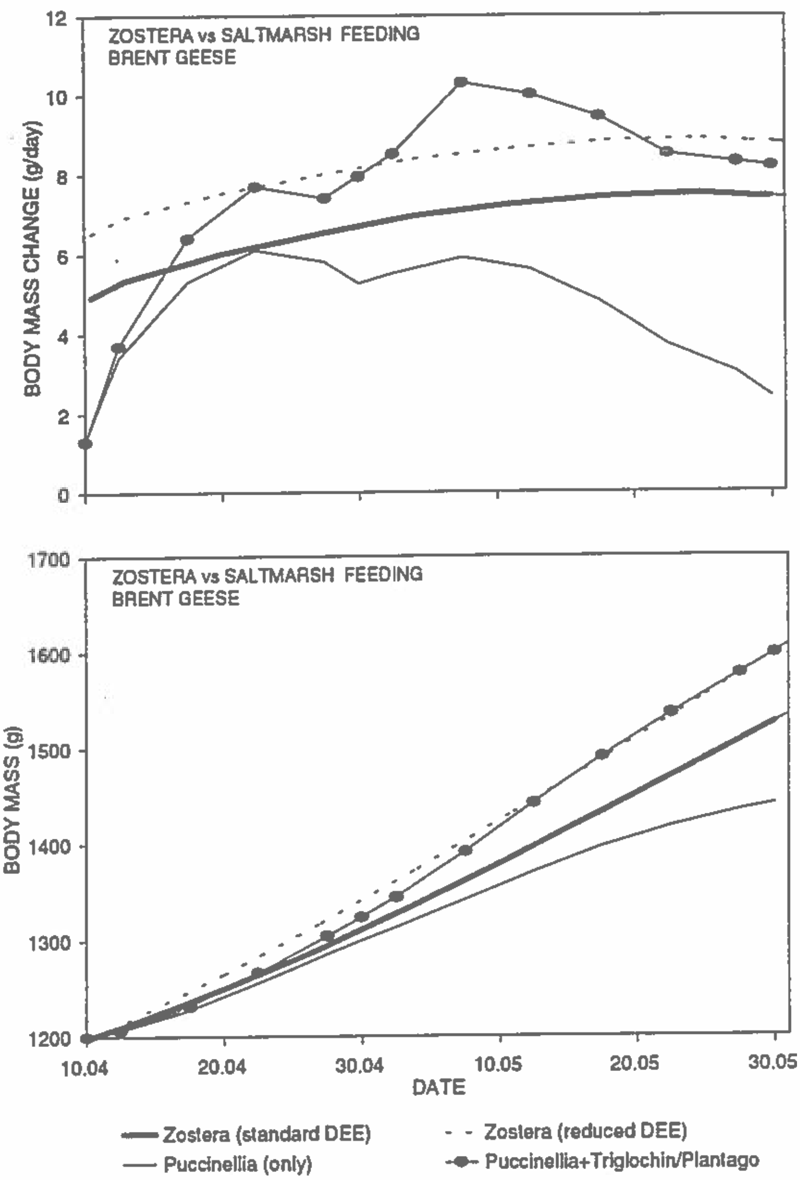

Fig. 6. Estimated body mass changes per day (upper) and cumulative body mass (lower) of Brent Geese feeding on a pure Zostera diet throughout spring (this study), and of Brent Geese feeding on a pure Puccinellia diet and on a mixed Puccinellia and Plantago/Triglochin diet on saltmarshes (based on Prop & Deerenberg 1991). Two estimates of mass changes of Zostera feeding geese is given, one based on a standard DEE estimate of DEE = $647\times M^{0.47}$ (after Boudewijn 1984, Prop & Deerenberg 1991), and one based on a reduced DEE, corrected for the reduced flying cost of Zostera feeding geese (this study).

Paper IV

Choosing between feeding on Zostera and saltmarsh: Factors affecting habitat use by Brent Geese in spring.

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Summary

This study examines factors contributing to differences in habitat use by Brent Geese Branta bernicla in a spring staging area where they feed on saltmarshes, Zostera marina beds, and new sown spring barley fields. Five years of study revealed significant between-year differences in the proportional use of the three main habitats, as well as three sub-habitats within the saltmarshes. Zostera beds may be favoured over the other habitats for several reasons. In a previous study it was found that energetic intake when feeding on Zostera is usually better than that attained from feeding on saltmarsh halophytes. This study shows, in addition, that Zostera beds generally have a higher production than the Puccinellia maritima saltmarsh zone, and that the Brent Geese react less to disturbance, and fly less when feeding on Zostera beds compared to saltmarshes, and thereby expend less energy on an energetically costly activity. However, large between-year variations in water level conditions limit the number of days the Brent Geese can utilise Zostera. Hence, saltmarshes act as important alternative feeding habitats for the Brent Geese, particularly in years with lower Zostera production (probably due to lower winter survival of Zostera shoots). New-sown barley fields were only used by Brent Geese in periods with low saltmarsh productivity and restricted accessibility of Zostera due to high water levels.

Keywords: Branta bernicla, eelgrass, saltmarsh, time budgets, primary production, weather, water levels.

Introduction

Dark-bellied Brent Geese Branta bernicla bernicla wintering in Western Europe have traditionally used three coastal habitats, namely Zostera spp. beds, Enteromorpha beds and saltmarshes (e.g. Mörzer Bruyns & Tanis 1955, Ranwell & Downing 1959). However, since the 1970s an increasing proportion of Brent Geese wintering in Britain and the Netherlands have utilised inland pastures and agricultural fields in mid-winter (especially winter wheat Triticum aestivum and in recent years oil-seed rape Brassica napus; e.g. Ebbinge et al. 1981, Tubbs & Tubbs 1982, Round 1982, McKay et al. 1993). This switch to inland feeding is partly explained by depletion of food resources in areas of intertidal Zostera and Enteromorpha beds (Charman 1979, Tubbs & Tubbs 1983, Madsen 1988, Summers 1990), although the reduced use of saltmarshes in mid-winter is not yet fully understood.

In spring Brent Geese again switch to feeding in the coastal zone, particularly on saltmarshes, probably reflecting reduced food availability in Zostera and Enteromorpha beds over winter (Tubbs & Tubbs 1983, Summers 1990), as it appears that submerged Zostera spp. and mixed Ruppia spp./Potamogeton spp. are preferred over saltmarshes in spring, when available to the Brent Geese (e.g. Madsen 1985a, Clausen I, III, Clausen & Percival V). Although many Brent Geese in Britain and in the Dutch-German-Danish Wadden Sea primarily use saltmarshes in spring (Charman & Macey 1978, Ebbinge et al. 1981, Summers & Critchley 1990), some use pastures managed for Brent Geese and even more switch to pastures during cold spring periods in the Netherlands (Ebbinge 1992). Brent Geese have recently started to use pastures in the Danish Wadden Sea (Madsen et al. 1990) and in the German Wadden Sea (Prokosch 1991) too.

Within the saltmarshes, they particularly use three different vegetation zones, i.e. areas dominated by Puccinellia maritima, areas dominated by Festuca rubra, and mosaic areas with a mixture of Puccinellia, Festuca, and the halophytes Plantago maritima, Triglochin maritima, Aster tripolium and Spergularia spp.. The timing of use of these three zones are primarily regulated by spring weather conditions (Madsen 1989, Prop & Deerenberg 1991).

This paper assesses factors influencing Brent Goose habitat choice in spring, when in addition to feeding on saltmarshes, they also have access to submerged perennial Zostera marina beds and new sown spring barley Hordeum vulgare fields.

Study area and methods

The study was conducted in the springs, of 1989-93. The Brent Geese studied come from the Svalbard breeding population of Light-bellied Brent Geese Branta bernicla hrota, of which 50-75% used the study area around Agerø, in the western Limfjord, Denmark (Fig. 1) throughout spring in recent years (Madsen et al. in press). Staging geese in the area roost communally northwest of the island of Agerø, and disperse to feed on submerged Zostera beds, saltmarshes, and (rarely) spring barley fields during the day.

The geese use an area including a total of 12.0 km^2 of Zostera beds and 7.5 km^2 of saltmarshes (Fig. 1; Drachmann et al. 1993, and P. Clausen unpublished data). The most important Zostera feeding area for Brent Geese lies southwest of Agerø, and the most important saltmarsh feeding site is situated on northwest Agerø (Jørgensen et al. 1994)(Fig. 1). These two sites were chosen for study of time budgets, vegetation sampling, and dropping counts (on saltmarshes).

The vegetation of the saltmarshes is dominated by Puccinellia maritima (lower marsh), and Juncus gerardi and Festuca rubra (higher marsh). Locally abundant supplies of halophytes such as Plantago maritima, Aster tripolium, Spergularia media, and Triglochin maritima are found in mosaic areas, with Juncus and the halophytes growing in tussocks and Puccinellia in between. 89% of the saltmarsh area is grazed by cattle (Clausen & Percival V), and may be considered of high quality for feeding Brent Geese (cf. Ebbinge 1992).

WEATHER CONDITIONS

Daily observations of weather (mean temperature, hours of bright sunshine and precipitation) were obtained from three nearby meteorological stations (Fig. 1).

Based on mean temperatures the T-200 date was used as an indix of the relative start of growth on the saltmarshes (Madsen 1989); T-200 is the date on which sum of daily mean (positive) temperatures, summed from 1 January, exceeds 200°C.

An estimate of the solar radiation available for plant photosynthesis was calculated from the daily hours of sunshine using a modified Ångström formula (Rietveld 1978):

$$R_g = R_a \times (a + b \times (\frac{n}{N}))$$

where R_g is the solar radiation (kW/m^2), R_a is the Angot value, n is recorded hours of sunshine, N is the astronomical daylength, and a and b are constants. Calculations of R_a and N were based on Olesen (1990), and the constants a and b were taken from Mikkelsen (1990).

WATER LEVELS, SALTMARSH FLOODINGS, AND ZOSTERA FEEDING

The tidal amplitude in the western Limfjord is on average 21 cm, but changes in wind direction, wind speed, and atmospheric pressure induce large changes in water level (Clausen I). Alternations in water level have two potential effects on habitat use by the Brent Geese: high water levels renders the Zostera beds inaccessible to feeding Brent Geese (Clausen I), and very high water levels flood the saltmarshes.

Estimates of average daily water levels (ADWL; measured relative to DNN, 'Danish Ordnance Datum') were obtained from Lemvig Harbour (September 1988 to September 1992) and Thisted Harbour (September 1991 to May 1993). Water levels at Lemvig and Thisted are highly significantly correlated, and thus both reflect water levels found around Agerø (see Clausen I, where a full analysis of water level in relation to geese is given).

An aerial photograph taken on 11 April 1982 showed that the lower Puccinellia zone of the northwest Agerø saltmarshes was flooded on that date. The whole saltmarsh was flooded on 25 March 1990 (personal observations). ADWL on these dates were 52.5 cm DNN and 85 cm DNN, respectively. The minimum number of flood days in all five seasons were thus estimated by the sum of days with ADWLs between 52.5 cm and 85 cm DNN (lower saltmarsh (only) flooded) and above 85 cm (whole saltmarsh flooded), and maximum number of days without floodings as the sum of days with ADWLs less than 52.5 cm.

Brent Goose only fed on Zostera beds when water levels were sufficiently shallow, and switched to feeding on land at a certain water level, termed c_2 (see a full analysis in Clausen (I)). Consequently the use of Zostera beds in spring could be influenced by differences in ADWL on count days, but as the Brent Geese switched between feeding on the fjord and on land at significantly different water levels in the five springs (Clausen I), a correction was made for this by scoring the number of count days with ADWL below c_2 (from Clausen I) as 'fjord feeding days' and the number of count days with ADWL above c_2 as 'land feeding days' for each period (periods defined below).

To test whether water levels on count days were representative of water levels over the whole period, the proportional number of days with ADWL below c_2 (on count days) were compared with the proportional number of days with ADWL below c_2 (all days). The test revealed that the proportion of count days with water levels below c_2 were significantly correlated with the proportion of all days with water levels below c_2 (Spearman rank correlation, $r_S=0.74$, n=8, $P<0.05$). Hence water levels on count days may be considered as representative for water levels in the whole period.

MAPPINGS OF GEESE AND VEGETATION

In all years except 1991 three to six weekly counts were made of all Brent Geese in the study area from the last week of March until the end of May, in 1991 one to four weekly counts were made. A full count of the area was usually made with telescope from eight observation posts in less than three hours. Positions of flocks and numbers of geese were drawn on field maps (scale 1:25,000).

To determine goose preferences of saltmarsh habitats, the saltmarshes were mapped at the end of May 1990. Saltmarshes were divided into three sub--habitats, i.e. Puccinellia dominated areas (more than 2/3 of Puccinellia zone), Juncus/Festuca dominated areas (more than 2/3 of Juncus/Festuca zone), and mosaic areas (intermediate). Mapping was achieved by walking through the whole area and drawing the information collected directly into field maps. The saltmarsh habitat use by the geese were quantified by subimposing the goose count maps over the saltmarsh habitat map.

For all counts the Brent Goose flocks feeding on Zostera were summed. Flocks of Brent Geese feeding on land were divided into those feeding in Puccinellia, mosaic, and Juncus/Festuca saltmarsh areas, and spring barley fields, and summed for each habitat. The differential use of the five habitats for each spring was calculated as the sum of observed individuals in each habitat.

Throughout this paper, two subjectively chosen periods are used, i.e. early spring (21 March - 25 April) and late spring (26 April - 31 May).

TIME BUDGETS

When feeding on saltmarshes around Agerø Brent Geese are highly mobile and move between different saltmarshes throughout the day, with small or large flocks coming to and from any site under continuous observation. Hence compilation of a time budget based on a single 'flock' from dawn to dusk is impossible. Time budget bouts of one to eleven hours of continuous observation were made on Zostera as well as saltmarsh-feeding Brent Geese from mid April to mid May 1990 to 1993, spread throughout the day. Time budgets were made by instant scans of the observed flock every 15 minutes (Altmann 1974), dividing the flock into indivials engaged in: feeding, roosting, preening, walking, swimming, flying, drinking, alertness, and birds engaged in aggressive encounters. In addition, disturbances, the source of disturbance and the reaction by the geese (proportion of flock flying up) were recorded for each 15 minute period.

GOOSE USE, STANDING CROP AND NAPP OF SALTMARSHES

The timing and intensity of goose use of northwestern Agerø saltmarshes was studied by counting goose droppings along a transect of permanent circular plots (2 m radius) centrally marked by small wooden pegs in 1989, 1990 and 1993. The plots were placed at 10 m intervals in a mosaic sward. The percentage coverage of Puccinellia zone and Juncus/Festuca zone, respectively, was estimated to the nearest 5% in each plot. In 1990 and 1993 droppings were counted and removed at every two weeks from the end of March to late May. Weekly counts were made in 1989 so counts from every other week that year were summed. This methodological change is considered of minor importance, because individual faeces are recognisable for at least 3-4 weeks, even after heavy rainfall (J. Madsen, unpublished data), and saltmarshes were not flooded during the sample period (results below).

Standing crop in the Puccinellia zone along the transect was measured on three occasions in 1989 and 1993, and twice in 1990. On each occasion, grass turves were sampled randomly, in 1989 and 1990 three-four each sized 0.07 m^2, and in 1993 six sized 0.02 m^2. In the laboratory vegetation was clipped to the soil surface, washed, and living material sorted into plant species. In 1993, dead above-ground plant material was also sorted and removed. Samples were dried at 80°C for 24 hours, cooled in an exicator and weighed.

The net above-ground primary production (NAPP) along the grazed transect was estimated by the amount of vegetation sampled, and the amount consumed by the geese:

$$NAPP = x_f - x_i + C$$

where x_i is the biomass (live+dead) present at the start of the season, x_f is the biomass (live+dead) remaining after the departure of the geese, and C is the forage consumed (Cargill & Jefferies 1984). Dead biomass in 1989 and 1990 was estimated on the assumption that the ratio of dead:live material was similar to that found in 1993. C was calculated from the cumulative number of droppings in sampled plots and the retention rates of the food plants after gut passage. Retention rates of Puccinellia was taken as 25% in April and 32% in May (after Madsen 1989). Calculations were based on dryweights of fresh droppings collected along the transect, dried at 80°C for 24 hours, cooled in an exicator and weighed.

GOOSE USE, STANDING CROP AND NAPP OF ZOSTERA BEDS

Zostera was sampled in a grazed study area in the Zostera bed Southwest of Agerø (Fig. 1) on two occasions in 1992 and three in 1993 during early April to late May. Samples were taken by placing a 0.1 m^2 square steel frame on the bottom; Zostera plants growing inside the frame but flattened when placing the frame were gently pulled inside, and plants growing outside were likewise pulled out. A square of Zostera turf was cut along the inside of the frame, and the whole turf removed to the surface in a sieve (1 mm mesh). All samples were sieved in saltwater, and the resulting material collected in plastic bags. In the laboratory samples were sorted into vegetative shoots, flowering shoots, rhizomes, and dead material. All fractions were dried to constant weight at 70°C in an oven and weighed.

Additional data on Zostera biomass was obtained from the same area from spring 1990, collected during a study of population dynamics of Zostera marina (Olesen 1993, Olesen & Sand-Jensen 1994a, 1994b).

For each count the number of Brent Geese feeding within the sampled Zostera bed were extracted, and the number of goosedays used there was calculated. The number of goosedays between two counts was calculated as the average number of geese observed at the two counts multiplied by the number of days between them; the calculated goosedays were then summed to give the total number of goosedays (G) used over the entire period.

The total area of the sampled Zostera bed is 845,800 m^2 (Drachmann et al. 1993), although only part of this is available to feeding Brent Geese. Brent Geese can only reach 40 cm below surface when feeding (a water level found in the sample area when a water level equivalent to -20.8 cm DNN 'Danish Ordnance Datum' occurs, Clausen I), and all Zostera in spring becomes unavailable to feeding Brent Geese when the water level rises by an average of 22 cm (1.2 cm DNN)(Clausen I). Since water level rarely falls below -30 cm DNN (Clausen I), only Zostera found at water depths of approximately 0-70 cm is usually available to feeding brent geese. Since 7 of 34 plots sampled plots in a 100x300 meter grid within the Zostera bed occurred in this water depth range (0-70 cm, corrected for deviations from 'normal' i.e. 0 cm DNN; J. Drachmann, S. Mark & P. Clausen, unpublished data), the Zostera area available to feeding brent geese, Z_a, was estimated as:

$$Z_a = 7/34 \times 845{,}000 \text{ m}^2 = 174{,}100 \text{ m}^2.$$

The consumption of Zostera m^{-2} was calculated as:

$$C = G/Z_a \times GIR_d \times D \times P_f$$

where G and Z_a are as defined above, GIR_d is the intake rate for Brent Geese feeding on Zostera (0.22 g dryweight min^{-1}; from Clausen III), D is the average day length (min day^{-1}), and P_f is the proportion of the day length used for feeding by Brent Geese (0.784, from time budgets; see below).

Estimates of NAPP in the grazed Zostera bed were calculated by an approximate method based on Cargill & Jefferies (1984):

$$NAPP = x_f - x_i + C$$

where x_i is the vegetative and flowering shoot biomass present in early spring, x_f is that present in late spring (after departure of the geese), and C is the amount consumed by the geese as defined above.

This approximation of NAPP does not include changes in dead above-ground biomass, and will probably give an underestimate. Dead biomass was excluded, because very many leaves are lost by wave action or shedding (a natural habit of Zostera by which loading of epiphytes are reduced; Sand-Jensen 1977) which may float around and decompose elsewhere in the Zostera bed, accumulate and decompose in deeper parts of the Limfjord, or wash onto surrounding beaches to decompose there. Consequently changes in dead biomass within the sample area might represent Zostera produced elsewhere, and introduce an inexpedient error in the NAPP estimate. Acknowledging this limitation of the calculations, the outcoming NAPP estimates will be termed residual net above-ground primary production rNAPP.

Results

WEATHER CONDITIONS

All five springs followed very mild winters, with monthly average temperatures more than 2°C above normal in January-March of all years (except February 1991). Monthly average temperatures in April 1990, May 1992 and May 1993 were more than 1°C above normal, and May 1991 less than 1°C below normal (Table 1). These differences in temperatures resulted in highly different cumulative temperatures, with T-200 ranging from 6 February (1989) to 25 March (1991)(Fig. 2), equating to a 47 day difference in onset of growth on the saltmarshes between the warmest and coldest study year.

Solar radiation was similar in all years deviating less than 25% from normal in most months (Table 1). The cumulative solar radiation curves were consequently quite similar, adding up to between 87.9 and 96.4 kW/m^2 (Fig. 2).

Precipitation was highly variable in the five years, both in timing and amount; all years experienced cumulative rainfall at or above normal, 1990 had extremely heavy rainfalls in February, and 1992 through March-April, whereas 1989, 1991 and 1993 were drier years compared to 1990 and 1992 (Table 1, Fig. 2).

WATER LEVELS, SALTMARSH FLOODINGS, AND ZOSTERA FEEDING

Water levels fluctuated greatly in all five winters and springs, ranging from -80 cm to 200 cm respectively, and ADWL ranged from -76 cm to 167 cm during 1 September - 31 May, 1988-93 (Fig. 3).

Saltmarshes flooded regularly during westerly storms from September until March, whereas no flooding occurred during April and May. In autumn and early winter (1 September - 31 December) there were no significant differences between the number of days with unflooded saltmarsh, lower saltmarsh (only) flooded, and whole saltmarsh flooded, in the five years (χ^2=13.24, df=8, P>0.10), whereas a significant difference was found for the late winter and spring period (1 January-31 May)(χ^2=47.47, df=8, P<0.001)(Table 2). Between year comparisons showed a significantly higher number of days with flooding of the higher saltmarsh in 1990 and 1993, compared to 1989, 1991 and 1992; and significant differences in number of days with flooding of the lower saltmarsh (Table 2). Due to ambiguous results with overlapping similarities between years, flooding of the lower saltmarsh can only approximately be ranked with 1992 lowest, followed by 1991, 1989, and 1993, and 1990 highest (Table 2).

A significant correlation between habitat use and water level was found in eight spring periods, and c_2 values estimated (Clausen I, Table 4). The proportion of count days with water levels below and above c_2, respectively, was highly significantly different in these eight periods (χ^2=17.60, df=7, P<0.025), i.e. significant differences between these periods in Zostera use may reflect the differences in water levels.

GOOSE NUMBERS AND DIFFERENTIAL HABITAT USE

The Agerø area was used by 2,200 to 3,100 Brent Geese throughout the spring staging period, 1989-93 (Table 3). The number of geese found in the area within a single spring was fairly constant (Clausen 1991 and unpublished).

The Brent Geese showed highly significant differences in their use of the three main habitats, Zostera beds, saltmarshes and spring barley fields in early and late springs all years (pairwise comparisons between all years/periods by χ^2 tests, all $\chi^2 \geq 214.15$, P<0.001)(Table 3). The predominant use of saltmarshes in the early springs of 1989 and 1993, contrast an almost even use of Zostera beds and saltmarshes in the other years. In late springs the predominant use of saltmarshes in 1989 and 1990, and to some extent 1993, contrast the more even use of Zostera beds and saltmarshes in 1991 and 1992. The relatively high use of barley fields in spring 1991 was unusual.

The proportional use by Brent Geese of the three habitats within the saltmarshes was highly significantly different in early and late spring in all years (All $\chi^2 \geq 173.11$, P<0.001), with a proportionally low use of Puccinellia zone saltmarsh in early spring 1990, high use of Juncus/Festuca zone in early and late spring 1991, and high use of mosaic areas in early spring 1990, and late spring 1989 and 1990 (Table 3).

The proportional use of Zostera beds was significantly correlated with the proportion of count days with water levels below c_2 (on which the Brent Geese could be expected to feed on the fjord), as predicted from the water level in the Limfjord (Spearman rank correlation, r_S=0.81, n=8, P<0.05)(Fig. 4).

TIME BUDGETS

A total of 216 scans were made on flocks feeding on saltmarshes, and 105 scans on Zostera beds. Flocks under observation on saltmarshes were significantly more variable in size and smaller than those observed on Zostera beds, with mean flock sizes of 694 (±S.D. 503) on saltmarshes and 811 (±S.D. 327) on Zostera beds ($F_{215,104}$=2.36, P<0.001; Welch's approximate t-test, t=-2.49, df=293.1, P=0.0132).

Comparison of time budgets of saltmarsh- and Zostera-feeding Brent Geese revealed no significant difference between the two habitats in the proportion of time spent in the two main activities, feeding and roosting, which together represented 93.2% and 97.2% of the time used in saltmarshes and Zostera beds respectively (Table 4). However, Brent Geese feeding on saltmarshes spent significantly more time flying, walking, alert, and drinking, whereas there were no significant differences in time spent on swimming, preening, and aggression in the two habitats (Table 4).

There was no significant difference between the disturbance rate in the two habitats, i.e. 0.56 disturbances per hour in both. However, Brent Geese feeding on the saltmarshes reacted more strongly when disturbed, with 84.5% of the flock flying up on saltmarshes compared to 60.4% on Zostera beds (Student's t-test of arcsin transformed proportions, $t=2.58$, $df=43$, $P=0.0132$). The most important disturbance source in both habitats were Grey Herons Ardea cinerea that flew to and from their feeding areas from a nearby heronry (63.3% of disturbances caused by Grey Herons in saltmarshes, 40.0% in Zostera beds; χ^2 test with Yates correction for continuity of proportions of Grey Heron disturbances vs. other disturbances in the two habitats, $\chi^2=1.36$, $df=1$, $P>0.1$). Other sources of disturbance were Goshawks Accipiter gentilis, farmers, and foxes Vulpes vulpes (on saltmarshes), fishermen (on Zostera beds), and aircraft (both habitats). When disturbed by Grey Herons, 82.7% of Brent Geese feeding on saltmarshes flew up in contrast to 46.2% of Zostera feeding geese ($t=2.70$, $P=0.0126$).

GOOSE USE, STANDING CROP AND NAPP OF PUCCINELLIA

Brent Goose use assessed by cumulative goose dropping densities on the saltmarsh along the transect on northwest Agerø was significantly different between 1989, 1990 and 1993, with highest utilisation in 1989 and lowest in 1990 (Fig. 5). As some pegs disappered between seasons, some circles were not exactly identical along the transect, but the observed difference in goose utilisation was not influenced by a difference in Puccinellia:Juncus/Festuca ratio, as the transect was dominated by Puccinellia all years, but also comprised considerable amounts of Juncus/Festuca (i.e. on average 62.9 % Puccinellia in 1989, 53.2 % in 1990, and 62.2% in 1993, but no significant differences between years; one-way ANOVA (arcsin transformed proportions), $F_{2,47}=0.74$, $P=0.4813$).

Live above-ground Puccinellia biomass on sample dates were highly significantly different (ANOVA, $F_{7,25}=17.65$, $P<0.0001$) (Fig. 5), with a significant increase in Puccinellia biomass during spring 1989 (ANOVA, $F_{2,6}=8.50$, $P=0.0178$) and spring 1993 ($F_{2,15}=17.22$, $P<0.0001$), whereas no increase was detected in spring 1990 ($F_{1,4}=0.02$, $P=0.8893$)(Fig. 5). The development in Puccinellia apparently was significantly lower in 1990 compared to 1989 and 1993, whereas no significant difference were found between 1989 and 1993.

The higher Brent Goose use of the Puccinellia marsh in 1989, combined with the similarity of above-ground biomass in 1989 and 1993, suggest that NAPP in the Puccinellia zone was slightly higher in 1989 than in 1993 (Table 5). The NAPP in 1990 may have been less than 25% of that found in 1989 and 1993 (Table 5).

GOOSE USE, STANDING CROP, AND RNAPP OF ZOSTERA BEDS

Vegetative Zostera shoot biomass on sample dates were highly significantly different (ANOVA, $F_{7,66}=12.85$, $P<0.001$)(Fig. 6). There was a significant increase in vegetative Zostera biomass during all springs (1990 ANOVA, $F_{2,51}=13.23$, $P<0.002$; 1992 $F_{1,6}=58.88$, $P<0.001$; 1993 $F_{2,9}=25.65$, $P<0.001$).

The general increase in the number of Brent Geese that use the Zostera beds around Agerø has resulted in increasing Zostera biomass being grazed by Brent Geese in spring. Although there was less biomass in 1993 than 1990, some of the difference is caused by the grazing Brent Geese. Nevertheless, rNAPP in 1993 was apparently only about 50% of that in 1992, with 1990 intermediate (Table 6).

Discussion

ANNUAL VARIATIONS IN HABITAT USE OF THE BRENT GEESE

This study found large within- and between-year variations in Brent Goose habitat use around Agerø.

Use of Zostera beds as feeding habitat was significantly correlated with the proportion of count days on which the Brent Geese could be expected to feed on Zostera, as predicted from the water level, suggesting that the Brent Geese will feed on the fjord as soon as water levels permit them to do so. Hence Zostera should be considered the preferred habitat in spring, because if the Brent Geese preferred the saltmarshes or barley fields there would be no reason to switch to the Zostera beds when the water level fell. This conclusion holds for the early spring period of all years, and late spring 1991, with very strong correlations found between water level in the Limfjord and habitat use of the Brent Geese (Clausen I). The situation in late spring is more complicated, with no correlation between water level and habitat use in late springs 1989-90, and with less clear correlations in late springs 1992-93 (Clausen I). A possible explanation for this difference between early and late springs is given in detail by Clausen (III).

Water levels on count days were representive of water levels for the whole period, so observed differences in the proportional use of Zostera beds (ranging from 27% to 58% in early springs) may be considered as genuine between-year variations, i.e. water level fluctuations relative to switch water levels in some years give the Brent Geese high access to feeding on Zostera, in other years low access.

Spring barley fields around Agerø were used when Zostera was unavailable due to high water levels, and saltmarsh growth was poor due to low temperatures, as in spring 1991. Brent Geese probably derive high energetic intake rates from grain feeding in newly sown barley fields (cf. Madsen 1985), but appear very nervous when doing so and are frequently disturbed by the farmers, avoiding feeding in the fields in most years.

ANNUAL VARIATIONS IN GOOSE USE OF SALTMARSH ZONES AND SALTMARSH PRODUCTION

The lower saltmarsh zone and Puccinellia maritima have often been reported as the prime feeding habitat and food item, respectively, for saltmarsh feeding Brent Geese (e.g. Madsen 1989, Prop & Deerenberg 1991, Olff et al. 1992). Therefore the relatively low use of the Puccinellia zone by Brent Geese in early springs 1990 and 1991 may be considered as unusual. The low use may be explained by low standing biomass and low NAPP of the Puccinellia sward. Madsen (1989) and Prop & Deerenberg (1991) explained similar seasonal variations in Puccinellia production and Brent Goose use in terms of differences in spring weather conditions. Reduced use of the Puccinellia zone and higher use of the Festuca zone occurred in cold springs, which would explain the low use of the Puccinellia zone and high use of the Juncus/Festuca zone in early spring 1991, and the high use of the Juncus/Festuca zone in late spring 1991, the coldest spring studied. But it fails to explain the low use of the Puccinellia zone in early spring 1990 which contrasts the high use in 1989, as these years had the warmest springs. Two lines of evidence may explain this inconsistency. Saltmarshes were flooded much more in late winter 1990 than in 1989, and precipitation was much higher in late winter of 1990 than in any other of the years studied. Armstrong et al. (1985) showed that summer floodings and heavy rainfall caused depression 'redox' potentials of Puccinellia saltmarsh soils, and suggested that autumn and winter flooding and rainfall might induce more permanent low redox potentials (i.e. reducing, anoxic soils). Howes et al. (1981) found that waterlogging and reduced soils inhibited Spartina alterniflora growth, and Armstrong et al. (1985) proposed this would be even more pronounced in Puccinellia, with its lower capacity to aerate soil around the roots with oxygen taken from the atmosphere, and thus compensate for the anoxia of the soils, as compared to Spartina. Hence it is suggested that increased flooding and rain on Agerø saltmarshes in late winter 1990 prolonged the period of waterlogging on the lower saltmarsh and depressed production. Later spring growth may have been hampered by the very high temperatures and insolation in April 1990, which dehydrated lower saltmarshes, and consequently increased soil salinity. Increasing salinities reduce growth rates of many halophytic monocots, such as Puccinellia (Rozema 1991).

The greater use of mosaic areas early spring 1990, and in late spring 1989 and 1990, compared to other years, may result from the earlier and warmer springs of 1989 and 1990, because the halophytes Triglochin, Plantago, Aster and Spergularia start growing slightly later than the graminoids Puccinellia, Juncus and Festuca. No field data were collected on densities of Triglochin, Aster, Spergularia and Plantago, but it was my impression from field work on the saltmarshes, that especially 1990 was characterised by an early growth of the four halophytes in the mosaic areas, in contrast to the cold spring 1991, when only very few plants of these species could be found in the same areas even in mid May.

ANNUAL VARIATIONS IN ZOSTERA PRODUCTION

It appears that 1993 had a lower Zostera production than 1992, with 1990 intermediate. This may result from differences in winter survival of Zostera shoots, as shoot densities in the three years can be ranked likewise, i.e. 748 ± 123 shoots m^2 (Mean ± SE, n=4) in 1993, 1125 ± 123 (n=4) in 1992 (P. Clausen, unpublished data), and c. 825 ± 85 shoots m^2 (n=18) in 1990 (Olesen & Sand-Jensen 1994a). Nevertheless, between-year variations in Zostera rNAPP were smaller than those of NAPP in the Puccinellia zone. This may be explained by a difference in the most important growth regulating factor in the two habitats. Variation in radiation explained 75% of the variation in growth rates of Zostera marina (Sand-Jensen & Borum 1983), whereas temperature is the most important growth regulator in terrestrial plants (Larcher 1980), and between-year variation in radiation was much less than variation in temperature.

TIME BUDGETS IN SALTMARSHES AND ON ZOSTERA BEDS

The Brent Geese used significantly more time flying, walking, alert and drinking when feeding in saltmarshes compared to Zostera beds. Predation risks are less on Zostera, because predators (foxes and Goshawks) found around Agerø could not successfully attack feeding Brent Geese on water. Hence, Brent Geese spend less time alert on the Zostera beds, also because flocks feeding on Zostera are larger (cf. Inglis & Lazarus 1981). When disturbed, fewer birds react on Zostera probably due to the greater safety provided from feeding on water. However, saltmarsh-feeding Brent Geese spent eight times longer flying than those feeding on Zostera, and differences in reactions to disturbance can only account for less than a twofold increase. Brent Geese feeding on saltmarshes throughout the day make many small flights between different saltmarsh vegetation zones, between saltmarsh sites, over fences, and to and from drinking sites in small ponds on the saltmarshes. Zostera feeding Brent Geese usually makes two daily flights, from the roost to the Zostera bed in the morning and back in the evening, and occasionally a single flight between two Zostera beds during the day. Apart from these movements, the Zostera feeding Brent Geese tend to gradually graze over the whole Zostera bed from one end to the other, without flying. They do not spend time on drinking, probably because the Zostera ingested provides them with enough water, as Zostera contains on average 84% water (n=10)(Clausen III), whereas Puccinellia only contains 69% (Prop & Deerenberg 1991).

CHOOSING BETWEEN ZOSTERA BEDS AND SALTMARSHES

There are several good reasons for the Brent Geese to feed on Zostera as soon as it is available. (i) intake rates and metabolisable energy contents of Zostera are usually higher than on the saltmarshes (Clausen III). (ii) they fly less due to the greater safety of feeding on water and differences in exploitation pattern of the two habitats. They thereby save energy, as flight is by far the most costly activity (i.e. 12.5×BMR in contrast to the other time budgetted activities ranging from 1.4 to 2.3×BMR; Wooley & Owen 1978)(see Clausen III). (iii) Zostera productivity is higher than in saltmarshes. rNAPP estimates for the spring period for the Zostera bed southwest of Agerø were on average twice those found in the Puccinellia zone on northwest Agerø. This is in agreement with annual production estimates of above-ground biomass in Danish Zostera beds ranging from 654 g m^{-2} to 1670 g m^{-2} (n=9; Sand-Jensen 1975, Wium-Andersen & Borum 1984, Pedersen & Borum 1993, Olesen & Sand-Jensen 1994a) compared to annual above-ground production of Festuca rubra, Puccinellia maritima, Juncus gerardi, Triglochin maritima and Plantago maritima in Dutch saltmarshes ranging from 70 g m^{-2} to 992 g m^{-2} (n=9; Bakker et al. 1993).

Intake rates of Brent Geese in the different habitats are dependent on growth form, size, production, and available biomass of their food plants, and in the case of Zostera feeding, water level. The Brent Geese throughout their staging period face daily changes in water level and weather conditions, which may favor feeding in either the Zostera beds or on the saltmarshes, and in different habitats within the saltmarshes (Prop & Deerenberg 1991). On a given day, the available biomass on the saltmarshes may be considered as constant, whereas that available in the Zostera bed fluctuate with the water level. An illustration of this situation is provided from the two years, where biomass development and NAPP were monitored in both the Zostera bed and in the Puccinellia zone. In 1990 growth in the Puccinellia zone was very poor, and the Brent Geese grazed 97% of NAPP. In 1993 growth was higher, with NAPP being at least 3-4 times that found in 1990, and the geese only grazed 20% of NAPP. In the Zostera bed the opposite situation occurred, with better growth in 1990 (NAPP being 1.4 times that found in 1993). The response from the geese to this difference was that in early spring 1990 the geese switched to feeding on Zostera at a significantly higher water level (7.9 cm DNN) than in early spring 1993 (-9.6 cm DNN)(Clausen I).

The annual variations in productivity in the two habitats, as well as in fluctuations in water level, are highly dependent on weather conditions, and thereby affect habitat use of the Brent Geese. In some years, saltmarshes may be a very important alternative to the Zostera beds for the feeding Brent Geese, in other years they are less important. Nevertheless, when these two alternative feeding habitats are available, I propose that the Brent Geese in most years will have a much better chance of achieving good condition in late spring. This may in fact be one very good reason behind the general belief that Brent Goose populations were much higher in last century and the start of this century (e.g. Salomonsen 1958), before the eelgrass 'wasting disease' almost wiped out Zostera marina in Western Europe (e.g. Rasmussen 1977), simply because when only having the saltmarshes as feeding habitat in spring, some years have less favourable spring fattening conditions (Prop & Deerenberg 1991), and thereby may lead to failed breedings (Ebbinge 1989).

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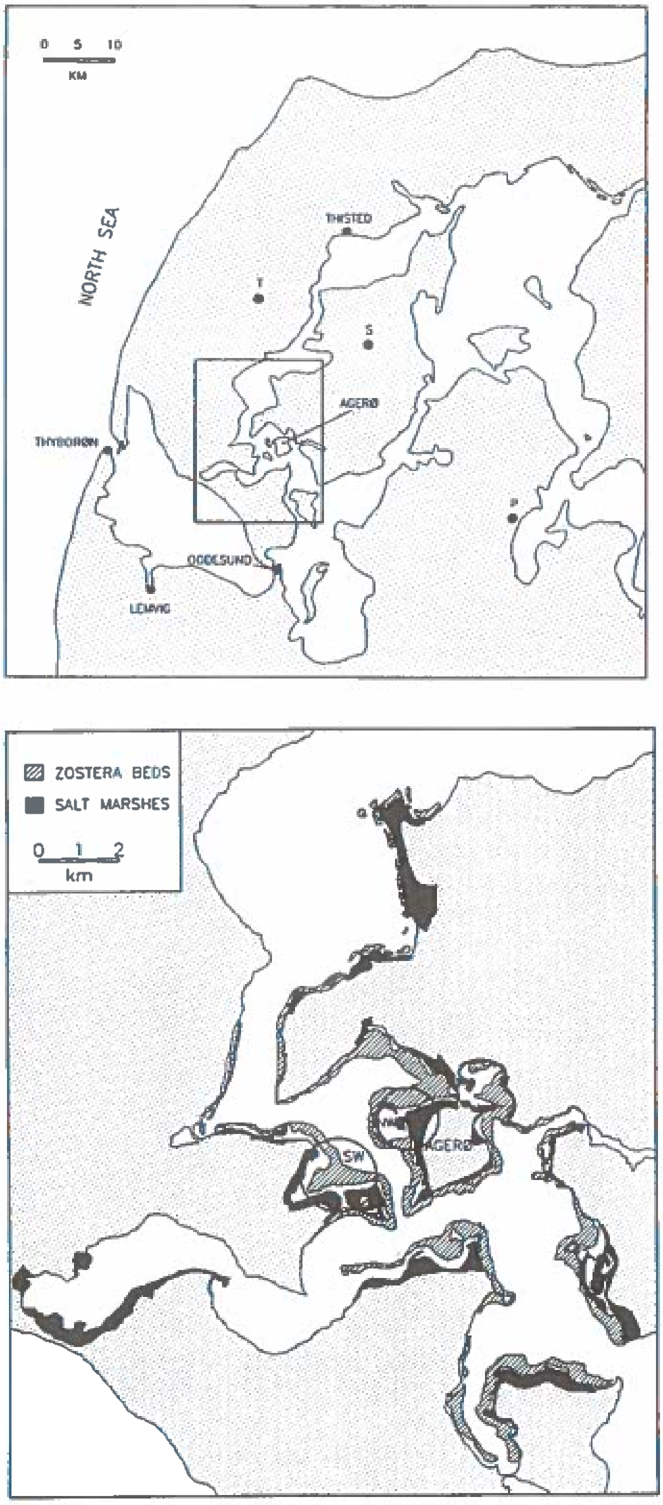


Fig. 1. The study area around Agerø in the western Limfjord, northwest Denmark. The upper large scale map with dots indicating Thyborøn (the opening of the fjord to the North Sea), Lemvig and Thisted (from which water level measurements were obtained), and the three meterological stations (from which measurements of temperature (T), sunhours (S), and precipitation (P) were obtained). The lower detailed map shows the area used by Brent Geese roosting at Agerø, with saltmarshes (black) and Zostera beds (hatch). Encircled are the most important Zostera bed southwest of Agerø, and the most important saltmarsh area on northwest Agerø.

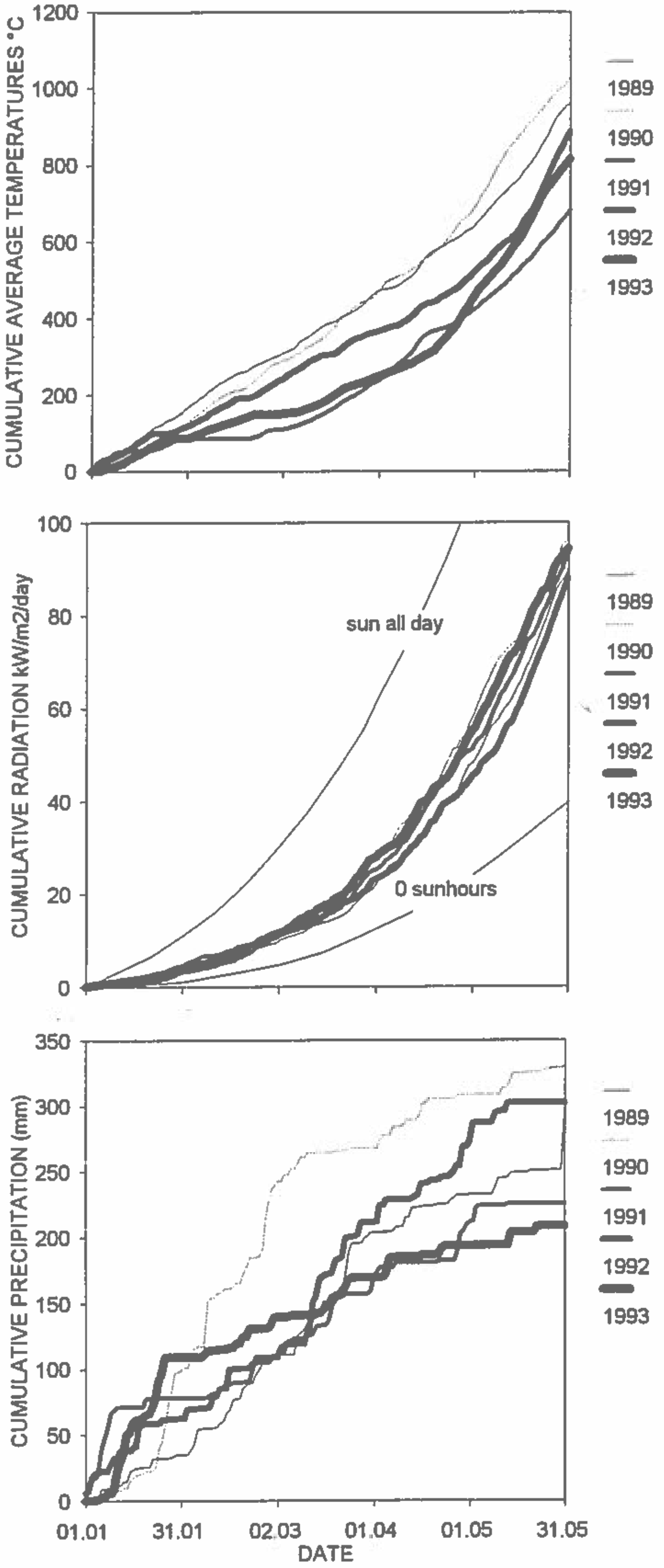


Fig. 2. Cumulative curves of average positive temperatures, radiation and precipitation, springs 1989-93, around Agerø. The two additional curves in the radiation figures gives minimum and maximum radiation curves, based on the assumptions of no sun all days and sun from sunrise to sunset all days.

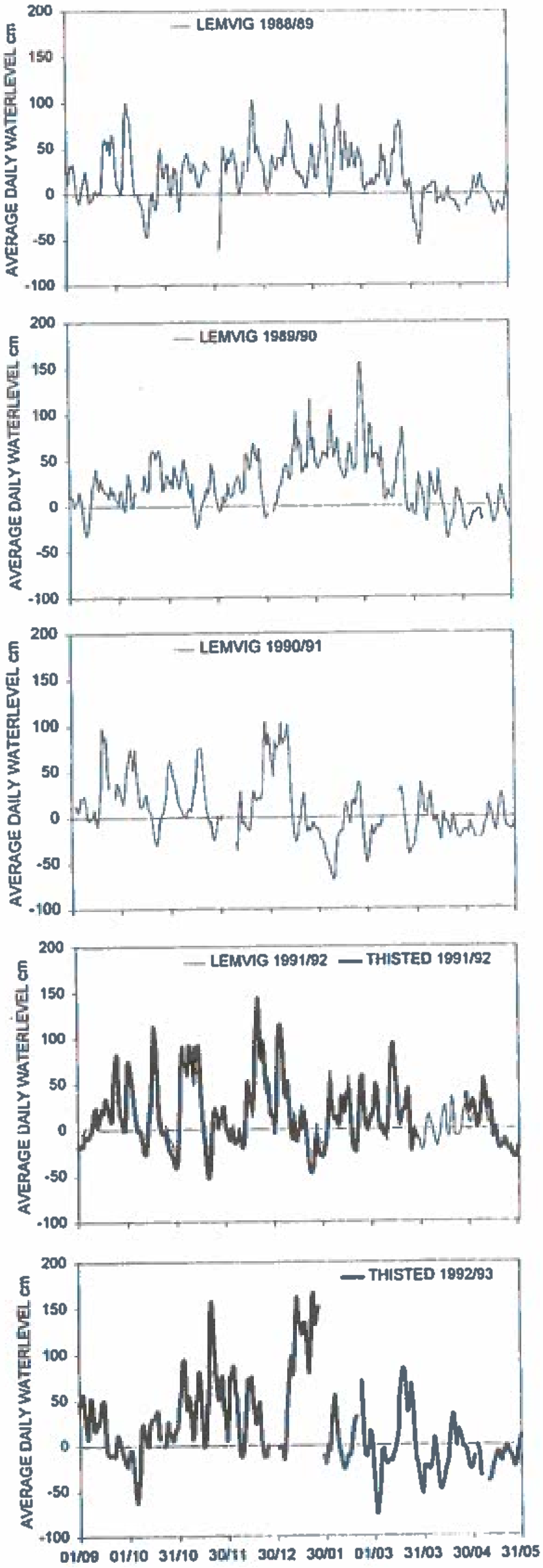


Fig. 3. Water level fluctuations in the Western Limfjord September through May, 1988/89-1992/93.

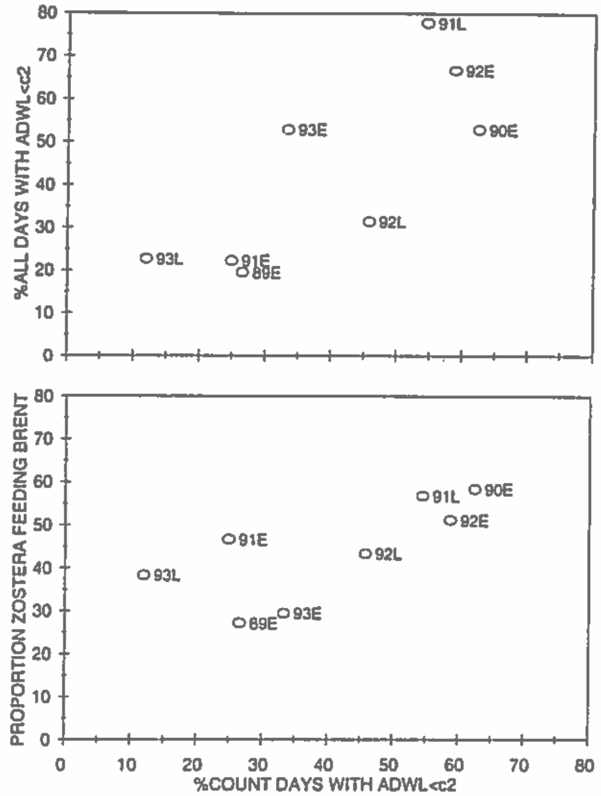


Fig. 4. Relationships between the proportion of count days with average daily water levels below the 'switch' water level c_2 (i.e. predicting that the Brent Geese should feed on the fjord), and (upper) the proportion of all days with average daily water levels below c_2, and (lower) the proportion of Brent Geese actually observed feeding on Zostera. Numerals and letters gives the year and period (E=early, L=late) respectively.

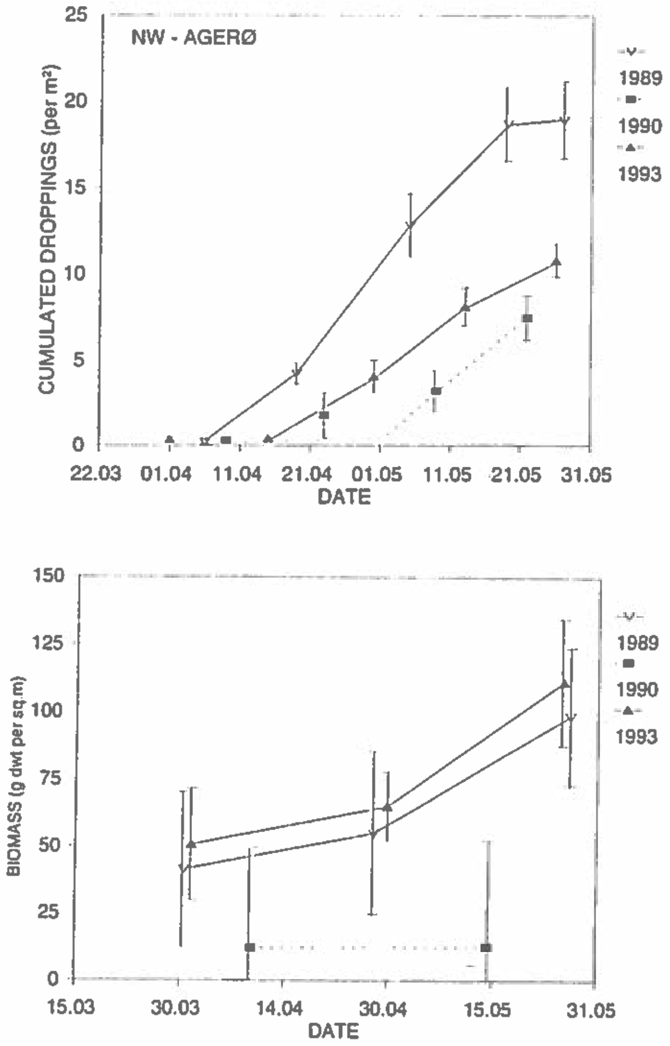


Fig. 5. Cumulative goose droppings and Puccinellia biomass on the northwest Agerø saltmarsh, springs 1989, 1990 and 1993. The curves give average values ± 95% confidence intervals.

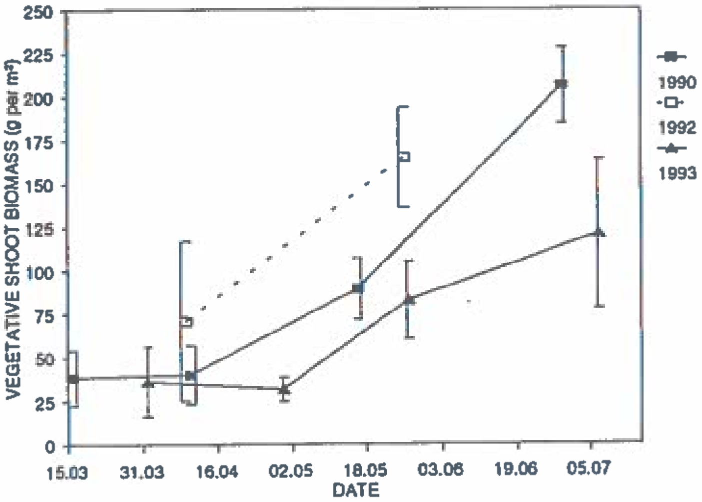


Fig. 6. The development in Zostera biomass in the Zostera bed southwest of Agerø, springs 1990, 1992 and 1993. The curves give average values ± SE.

Table 1. Summary of weather conditions around Agerø January-May, 1989-93, based on measurements from three nearby meterological stations (Fig. 1). Normal values are average values of data for 1971-90 (radiation) and 1931-60 (temperature and precipitation)(Danish Meterological Institute).

	Month	Year					Normal
		1989	1990	1991	1992	1993	
Temperature (°C)	January	5.4	4.0	2.5	3.4	2.7	0.2
	February	4.9	5.6	-1.4	3.9	2.0	-0.2
	March	5.4	5.8	4.0	4.1	3.1	1.8
	April	5.5	7.2	6.1	5.1	6.8	6.0
	May	10.5	11.1	8.5	12.0	11.8	10.7
Radiation (kW/m²/day)	January	0.10	0.10	0.15	0.13	0.12	0.10
	February	0.23	0.25	0.25	0.23	0.27	0.26
	March	0.37	0.55	0.44	0.39	0.53	0.49
	April	0.89	0.97	0.86	0.72	0.88	0.88
	May	1.36	1.29	1.38	1.40	1.30	1.21
Precipitation (mm/month)	January	35	99	78	62	109	61
	February	74	138	31	46	26	39
	March	95	31	50	103	35	34
	April	29	41	50	58	24	39
	May	70	22	17	33	15	35

Table 2. Estimates of the maximum number of days without floodings and minimum number of days with flooding of the Agerø saltmarshes 1 September - 31 May, 1988/89-1992/93. For each season flooding was separated into the periods prior to and after 1 January. These were further divided into days with flooding of the whole saltmarsh and those with floodings of the lower saltmarsh (only).

Season		1 September- 31 December			1 January - 31 May		
		Unflooded	Whole saltmarsh flooded	Lower saltmarsh flooded (only)	Unflooded	Whole saltmarsh flooded	Lower saltmarsh flooded (only)
1988/90	Lemvig	103	3	11	129	2	17
1989/90	Lemvig	108	0	11	112	12	26
1990/91	Lemvig	92	4	16	132	3	8
1991/92	Lemvig	91	4	19	143	3	5
1992/93	Thisted	87	6	20	114	16	12

Table 3. Habitat use by Brent Geese within the Agerø area in early and late springs, 1989-93. "Geese staging" gives an approximate number of geese which stayed in the area throughout each spring. "Geese counted" represents the sum of individuals with known habitat use for each period. Their proportional habitat use, as well as the proportional sub-habitat use of those using saltmarshes are tabulated for each period.

		Year				
		1989	1990	1991	1992	1993
Geese staging in spring		2,200	2,200	2,600	3,100	2,600
Early spring	(21 March-25 April)					
Switch water level (c_2)(cm)[1]		-10.65	7.92	-15.80	3.89	-9.62
Geese counted		25,289	24,722	12,259	45,944	43,973
Proportional habitat use	*Zostera* beds	27.1	58.3	46.6	51.1	29.4
	Saltmarshes	72.5	41.7	47.7	48.9	70.6
	Spring barley fields	0.4	0	5.7	0	0
Proportional saltmarsh sub-habitat use						
	Puccinellia	53.0	20.4	34.1	50.2	45.1
	Mosaic	16.3	46.9	19.7	15.8	21.5
	Juncus/Festuca	30.6	32.7	46.2	34.0	33.4
Late spring	(26 April-31 May)					
Switch water level (c_2)(cm)		-	-	0.82	-11.34	-28.15
Geese counted		22,218	16,765	15,823	75,186	105,980
Proportional habitat use	*Zostera* beds	16.0	14.8	56.7	43.3	38.3
	Saltmarshes	84.0	85.2	36.6	55.5	61.7
	Spring barley fields	0	0	6.7	1.2	0
Proportional saltmarsh sub-habitat use						
	Puccinellia	44.7	46.7	51.8	63.8	53.6
	Mosaic	44.6	34.9	10.9	11.8	18.5
	Juncus/Festuca	10.7	18.3	37.3	24.4	27.9

[1] c_2 values were taken from Clausen (I). There was no relationship between water level and habitat use in late spring 1989 and 1990.

Table 4. Proportion of time spent in different activities by Brent Geese feeding on Zostera beds and saltmarshes, respectively (from timebudgets).

Activity	Saltmarsh feeding	Zostera feeding	t[1]	Probability[1]
Feeding	76.5	78.4	-1.38	P=0.17
Roosting	16.7	18.8	-0.71	P=0.48
Flying	3.2	0.4	2.76	P=0.0062
Walking[2]	0.5	0		
Alert	1.8	0.05	13.75	P<0.001
Drinking[2]	0.3	0		
Swimming	0.3	1.7	-0.69	P=0.49
Preening	0.5	0.1	1.71	P=0.09
Agression	0.1	0.02	1.87	P=0.06

[1]Tests and probabilities are t-tests based on arcsin transformed proportions (Student's t for equal variances, Welch's approximate t for unequal variances). [2]Non-testable due the fact that all observations in Zostera beds had 0 geese walking and drinking respectively.

Table 5. Estimates of net above-ground primary production (NAPP) in the Northwest Agerø Puccinellia saltmarsh zone springs 1989, 1990, 1993, based on estimates of goose consumption and biomasses early and late in spring. Values of live and dead biomasses and consumption are means (± SE in brackets).

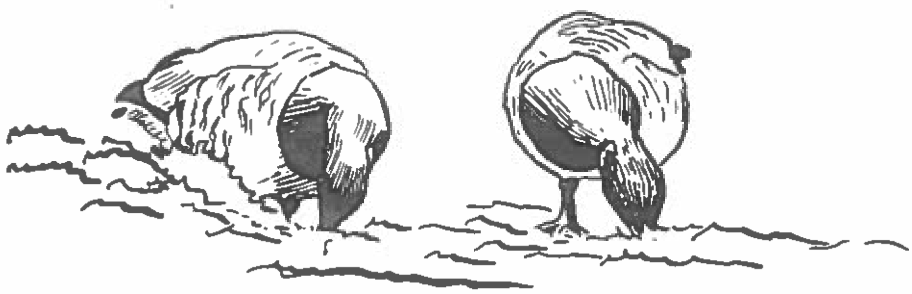
Year	Period	Live biomass (start) g m^{-2} x_i	Live biomass (end) g m^{-2} x_f	Dead biomass (start) g m^{-2} x_i	Dead biomass (end) g m^{-2} x_f	Increment in biomass (live+dead) g m^{-2} $x_f - x_i$	Consumption by brent geese g m^{-2} C	NAPP g m^{-2} $x_f - x_i + C$
1989	31 March - 27 May	41.4 (32.4-50.5)	98.6 (90.6-106.6)	6.1[2]	8.2[2]	59.3	26.7 (25.1-28.2)	85.9
1990	10 April - 15 May[1]	11.9 (10.8-13.0)	12.5 (9.6-15.5)	1.6[2]	1.2[2]	0.3	10.8 (9.5-12.0)	11.1
1993	1 April - 26 May	50.7 (42.6-58.8)	111.2 (102.1-120.3)	7.4 (6.3-8.5)	9.2 (8.7-9.7)	62.3	15.3 (14.4-16.2)	77.7

[1]Consumption based on the period 10 April - 22 May 1990. [2]Dead biomass in 1989-90 was estimated on the assumption that the live:dead ratio in these years were similar to that found in 1993.

Table 6. Estimates of residual net above-ground primary production (rNAPP) in the Zostera marina bed southwest of Agerø springs 1990, 1992, 1993, based on estimates of goose consumption and live biomasses (vegetative and flowering shoots) early and late in spring. Live biomass values are means (± SE in brackets).

Year	Period	Birddays used in the Zostera bed	Vegetative biomass (start) g m^{-2} x_i	Vegetative biomass (end) g m^{-2} x_f	Flowering biomass (start) g m^{-2} x_i	Flowering biomass (end) g m^{-2} x_f	Increment in biomass (vegetative +flowering) g m^{-2} $x_f - x_i$	Consumption by brent geese g m^{-2} C	rNAPP g m^{-2} $x_f - x_i + C$
1990	1 April-27 May[1]	16356	39.5	118.5	0	15.0	94.0	14.3	108.3
			(31.7-47.3)	(109.7-127.3)		(6.2-23.8)			
1992	9 April-26 May	23123	34.5	165.0	0	9.9	140.38	21.0	125.0
			(20.1-48.9)	(156.0-174.1)		(7.2-12.6)			
1993	1 April-27 May	26892	36.3	82.8	0	5.1	51.61	23.8	75.4
			(29.9-42.6)	(75.8-89.8)		(2.8-7.3)			

[1] Biomass on 1 April was estimated by interpolation between samples from 15 March and 10 April, and on 27 May between samples from 16 May and 29 June, 1990.



Paper V

Changes in distribution and habitat use of Svalbard Light-bellied Brent Geese *Branta bernicla hrota*, 1980-92.

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Summary

The Svalbard breeding population of light-bellied brent geese which winters in Denmark and at Lindisfarne, England, changed phenology, distribution, and habitat use within all six areas used during the 1980s, and colonised two new areas during the late 1980s. The major causes of the changes appear to have been (1) reduction or even disappearance of Zostera beds in four of the traditionally used areas, especially those used in autumn and winter, (2) cessation of cattle grazing and hay cutting of saltmarshes in the formerly most important spring staging area. In addition, (3) the remaining beds of Zostera apparently have been depleted more rapidly in autumn and winter partly as a result of increased goose use. These changes led to increased use of other areas, and the establishment of two new sites of international importance for this brent goose population. It is argued that the changes may have had a negative effect on the winter survival of the geese, and thereby the population development in the 1980s. The implications of the new patterns of dispersal are discussed in relation to future management of the areas which the brent geese use. Recommendations includes the establishment of a hunting free reserve at Lindisfarne, increased management of saltmarshes throughout their range and preparation of an international conservation plan.

Key words: Brent geese, habitat loss, Zostera, eutrophication, saltmarsh, management.

Introduction

The vulnerable Svalbard breeding population of light-bellied brent geese Branta bernicla hrota winters in Denmark and at Lindisfarne in Northeast England; throughout the 1960s and 1970s Zostera beds and saltmarshes were the only habitats which the brent geese used (Fog 1967, 1972; Jepsen 1967, 1984; Madsen 1984, 1986). Madsen (1984, 1986, 1987) who, based on observations in 1980-83, described the development, distribution and habitat choice of the population, argued that eutrophication and saltmarsh reclamation might have had a negative impact on the population development since the 1960s.

Eutrophication can influence the growth of Zostera and other submerged macrophytes; this is because increased levels of nutrients often induce heavy colonisation by epiphytic algae growing on the plants and severe growth of phytoplankton populations in the water above the plants. Both the epiphytes and phytoplankton reduce the light available for the macrophytes and thereby their growth, and the macrophytes may disappear in severely eutrophicated areas (Borum et al. 1990; Sand-Jensen & Borum 1991; Valiela et al. 1992).

Saltmarshes are present in all areas used by the brent geese (Madsen 1986, this study), but they are only of value for the geese when the sward is kept low by appropriate grazing pressure (e.g. Summers & Critchley 1990). The low sward is maintained by sheep or cattle grazing or mowing (e.g. Cadwalldr & Morley 1973). If unmanaged, the saltmarsh vegetation grows tall, large amounts of dead plant material accumulates (Bakker 1978; Lorenzen & Madsen 1985), and food plants favoured by the brent geese (e.g. Puccinellia maritima, Plantago maritima and Triglochin maritima; Boudewijn 1984) are replaced by other plants such as Halimione portulacoides and Artemisia maritima (Jensen 1984) or in the very brackish Danish fjords, reed Phragmites australis (Jepsen 1984).

Studies were conducted in Denmark and at Lindisfarne in 1988-92 which aimed at improving knowledge about the habitat use and feeding ecology of the light-bellied brent geese. As a result, it would be possible to explore whether problems associated with eutrophication and/or saltmarsh management might be causing a reduction in the birds' food supplies at critical periods through winter, effectively acting as a bottle-neck to the population and limiting its development.

In a previous paper we reviewed the population development and changes in winter site use by the light-bellied brent geese during 1980-92 (Madsen et al. in press). In this paper we: review evidence for changes in habitat availability within the eight principal wintering areas for the light-bellied brent geese, and how the geese responded the observed changes. The changes in habitat availability are discussed in relation to eutrophication, saltmarsh management, and carrying capacities of the sites used; and the present goose use of areas are used in an attempt to explain why the geese changed their use of the different areas. Finally proposals for improved management of the population are put forward.

Materials and methods

STUDY POPULATION AND AREAS

The Svalbard breeding population of light-bellied brent geese has been censused regularly since the 1960s (Fog 1967, 1972; Madsen 1984, 1987; Madsen et al. in press), and has, compared to the Siberian dark-bellied brent goose Branta b. bernicla population, shown a less pronounced increase in numbers following the shooting ban in Denmark in 1972; i.e. the dark-bellied population has increased five-fold (Madsen 1987), whereas the light-bellied population has at most tripled since 1972 (Madsen et al. in press).

Traditionally light-bellied brent goose population made a successional use of six traditional sites (Fig. 1). The Danish Wadden Sea was used in autumn, followed by Mariager and Randers fjords in winter, switching to Lindisfarne during cold winters; in late winter the birds moved to Nissum Bredning, and from here split between Nissum Fjord and Agerø, the two spring roosts (Madsen 1984). During the 1980s this migration pattern was changed. Although the brent geese still used the same overall pattern, their phenology changed in most sites. Lindisfarne became a regular autumn and winter site (irrespective of winter conditions), and two additional sites in Denmark were used (Madsen et al. in press). The changes in phenology are described in detail by Madsen et al. (in press); in summary: compared to 1980-83 the staging period of the brent geese in the Wadden Sea was one-two months shorter in 1988-92 and consequently, the majority of the brent geese arrived one-two months earlier at Mariager-Randers Fjords. At the other end of the staging period at Mariager-Randers Fjords, a few hundred brent geese departed in December (peak occurrence period in 1980-83) to Agerø, Nissum Bredning and the two new sites: Nibe Bredning and the Northern Kattegat coast. The rest departed in February, one-two months earlier than in 1980-83. At Lindisfarne, a similar pattern emerged, i.e. arrival occurred in early September and departure in February in 1988-92, one month earlier than in 1980-83; peak numbers occurred in December in 1988-92, one month earlier than in 1980-83. In Northwest Jutland the change has been most obvious around Agerø. In 1980-83 Agerø was only used in spring; now it is used from November throughout the winter and spring until the departure for the breeding areas in late May. Data from the mid 1980s are intermediate, suggesting that the changes have been gradual rather than abrupt.

GOOSE COUNTS, DISTRIBUTION, AND HABITAT USE

Detailed counts of light-bellied brent geese were made on at least a monthly basis throughout 1980-92 at the five most important Danish staging areas and at Lindisfarne (for details, see Madsen et al. in press). In addition to counting the geese, observers in Denmark carefully mapped all flocks of geese on maps (scale 1:25,000), and took detailed notes on habitat choice and disturbances caused by humans. Two new sites used by light-bellied brent geese in the late 1980s had been counted regularly by local observers throughout 1980-92 (Northern Kattegat coast), and as part of a research programme carried out by the National Environmental Research Institute in 1985-93 (Nibe Bredning; Madsen et al. 1992a, 1992b).

The use of areas and habitats is expressed as the sum of observed flocks or as the number of birddays. The number of birddays between two counts is calculated as the average number of birds observed at the two counts multiplied by the number of days between counts; the calculated and counted birddays is then summed over the season for each area or habitat.

FOOD SUPPLIES AND FEEDING PERFORMANCE

Light-bellied brent geese staging in Denmark usually feed on submerged macrophytes and saltmarsh halophytes (Clausen 1991); in the Danish Wadden Sea and at Lindisfarne they mainly feed on intertidal Zostera spp. and Enteromorpha spp. (Clausen & Fischer 1994; S. Percival, W.J. Sutherland & P.R. Evans, unpublished data). Monitoring of submerged macrophyte stands is carried out irregularly by the Danish County Councils in most of the areas used by light-bellied brent geese in Denmark. The method applied is usually a combination of aerial photographs and field observations. The latter are made either from boat or by wading along permanent transects, where abundance and depth ranges of individual plant species are recorded. The eutrophication status of the areas are evaluated by the presence/absence of eutrophication indications such as high nutrient levels, high concentrations of phytoplankton or epiphytic algae on rooted macrophytes in the surveyed areas, and algae blooms of *Ulva lactuca*, *Enteromorpha* spp., *Cladophora* spp. and other filamentous algae. Occasionally detailed mappings of the distribution of *Zostera* and *Ruppia* species have been made.

As gaps remained in our knowledge about distribution of submerged and intertidal macrophytes in some areas, we also mapped macrophyte distribution in the Wadden Sea (Clausen & Fischer 1994), in Mariager-Randers Fjords (Clausen 1990), around Agerø (Drachmann *et al.* 1993), and at Lindisfarne (S. Percival, W.J. Sutherland & P.R. Evans, unpublished data). It must be noted that the available historical record of macrophyte distribution in the areas the brent geese use is of varying quality, and that we therefore only can make rough comparisons for some areas, whereas firmer conclusions can be drawn in other areas.

Madsen (1988) showed that declines in *Zostera* supplies on intertidal mudflats in the Wadden Sea had several effects on the feeding behaviour of dark-bellied brent geese; when *Zostera* supplies dropped, feedings bouts (measured as the time of uninterrupted feeding with the head below the level of the shoulder), pace rates (time it took a feeding bird to take 10 steps), and dropping rates (number of droppings per hour) all declined too. He also found that percentage *Zostera* cover of the mudflat surface (assessed by visual observation), gave a reasonable estimate of available biomass. In the Wadden Sea and at Lindisfarne we therefore used some of these parameters as indicators of available food densities. In the Wadden Sea plant cover was scored and feeding bout lengths measured at some of the primary feeding areas for light-bellied brent geese; at Lindisfarne plant cover, pace rates and dropping rates were scored, the latter by use of the method of Bédard & Gauthier (1986), and plant cover was calibrated to biomass by sampling *Zostera* in areas where the percentage cover was also assessed by eye, the samples were sorted into above- and below-ground materials of *Zostera* spp. and *Enteromorpha* spp. thalli, dried to constant weight at 60°C, and weighed.

Data on the present grazing and mowing status of all saltmarshes within the areas were collected by subjectively scoring the marshes to three levels of quality: a) *well managed:* grazing and/or mowing giving a short sward, less than five cm high throughout; b) *poorly managed:* some grazing and/or mowing, but with uneven intensity resulting in tall vegetation over large parts of the saltmarsh; c) *unmanaged:* potentially useful for the geese if managed, *i.e.* *Puccinellia* or *Juncus/Festuca* marsh. The area of individual saltmarshes was measured from maps (scale 1:25,000). Unmanaged *Halimione* and *Spartina* marshes, of little relevance for the geese as foraging sites, were omitted from the analysis.

ESTIMATION OF CARRYING CAPACITIES OF SALTMARSHES

In the spring fattening period, a time which is of crucial importance for the breeding success of the geese (Ebbinge 1989), Ebbinge (1992) found that carrying capacities of grazed and ungrazed saltmarshes were 30 and 10 brent geese per hectare respectively. We estimated carrying capacities of Danish saltmarshes used by brent geese in spring as 30 geese per ha of well managed saltmarshes, 10 geese on poorly managed saltmarshes, and 0 geese on unmanaged saltmarshes. The figures used here are slightly more conservative than those Ebbinge (1992) obtained, because most of the unmanaged saltmarshes in Northwest Jutland rapidly deteriorate, and are abandoned by the geese, due to the growth of reed. In contrast, the saltmarshes along the more saline Wadden Sea have a much slower succession rate, partly caused by the grazing geese, and hence deterioration rate (Olff 1992).

Results

DANISH WADDEN SEA

Although the northern part of the Danish Wadden Sea was considered as an important staging area for the population by Salomonsen (1958), Fog (1967, 1972), and Madsen (1984, 1987), there were no regular counts of larger flocks made before 1986 (Clausen & Fischer 1994). It has now been confirmed that light-bellied brent geese stage primarily in the northern Danish Wadden Sea (Clausen & Fischer 1994). That study found that during low tide brent geese feed on intertidal mudflats, where *Zostera marina* and *Z. noltii* are the main food items eaten. At high tide, the geese fly to roosts where no food is available. In 1986 and 1987 observations were restricted to areas surrounding the island Fanø, and most of the light-bellied brent geese feeding in this area roosted communally at Keldsand, south east of Fanø (Fig. 2). In 1988 observations were made from mainland Jutland as well, and the majority of the 1400 brent geese staging in the area then fed near Fanø and along the mainland coast east of the island

Manø, and roosted at Keldsand. In 1989, this system broke up, when no roosting flocks were observed at Keldsand until 15 September, despite the fact that there were 2600 light-bellied brent geese in the area. Instead several other feeding areas and highwater roosts were used, all along the mainland coast (Fig. 2). Light-bellied brent goose use of intertidal feeding areas in the vicinity of Fanø declined from 58,800 goosedays in 1986-87 to 24,750 goosedays in 1988-89 (both figures are an average of two autumns).

Data on changes in food availability in the Danish Wadden Sea are scarce, but very few Zostera beds occur in the area (Fig. 3). Furthermore, concurrent data from three important feeding sites for light-bellied brent geese indicate that the densities of food plants in the area are poor at present (Clausen & Fischer 1994). Thus, low densities of Zostera were found during visits to the mudflats of Søjord, Klyngvese Sand, and Råhede in September 1989; at Søjord the leaf cover was estimated to 15.3% for Z. marina and 0.7% for Z. noltii (means for 15 plots along a transect). At Klyngvese Sand it was found that feeding bout lengths of light-bellied brent geese which fed on Z. noltii were comparable with those of dark-bellied brent geese feeding at food densities of around 10-20% leaf cover of Z. noltii (taken from Madsen 1988), and similar results were found in Z. marina feeding light-bellied brent geese at Råhede and Søjord (Clausen & Fischer 1994). Approximately 40% of the brent geese at Råhede were observed paddling, i.e. trampling in sediment submerged under 5-10 cm of water, thereby loosening whole Zostera plants from the sediment; Madsen (1988) showed, that this behaviour increased in importance as Zostera cover decreased, and a level of 40% brent geese paddling in a flock was only observed at very low Zostera cover (0-20%). The feeding bout observations were conducted in the period 6-17 September 1989. They suggest that low leaf coverage (equivalent to 10-20% recorded by Madsen 1988), were present in mid September 1989 in the areas used by the light-bellied brent geese (Clausen & Fischer 1994).

MARIAGER AND RANDERS FJORDS

When staging in Mariager-Randers Fjords the brent geese primarily feed on submerged macrophytes (Clausen 1991). The earlier arrival in autumn and a slight increase in numbers of geese using the area have caused an increase in total goose use, despite the fact that the geese leave the area earlier (Madsen et al. in press). In 1980-83 151,700 goosedays (average of three seasons; Madsen 1986) and in 1988-90 249,000 goosedays (average of two seasons) were spent in the area. The principal feeding areas in both fjords were restricted to the outermost parts of the fjords during 1980-85, now they are found some kilometres inside the fjords (Fig. 4). Furthermore, the brent geese have taken to foraging on saltmarshes in winter (Fig. 4); in 1980-85 the geese fed on the fjords throughout the staging period, in the winter 1987/88 the first flocks of brent geese were observed feeding on saltmarshes, and in 1988-90 11.5% of goosedays were spent on saltmarshes; most of the saltmarsh feeding occurs in winter (Clausen 1991; Jørgensen et al. 1994).

There is evidence from Mariager Fjord that Z. marina stands in the outer end of the fjord have disappeared in the 1980s (Fig. 5), whereas its status in the inner parts is seemingly unchanged (Jørgensen 1980; Nordjyllands Amt 1988a; Clausen 1990). Mariager Fjord is the most important of the two fjords for the brent geese and has increased in importance during the 1980s (Fig. 4), so Randers Fjord is only now used in mid- and especially late winter. This is probably explained by generally low densities of Ruppia, Zostera and Ulva found in Randers Fjord at present (Clausen 1990). About half of the saltmarshes in the area are poorly managed or unmanaged (Table 1).

NIBE BREDNING AND THE NORTHERN KATTEGAT COAST

In the winters 1989/90 through 1991/92 up to 600 light-bellied brent geese were observed in two new sites, Nibe Bredning and the Northern Kattegat coast (Fig. 1)(Madsen et al. in press). In both these areas very few light-bellied brent geese had been observed before (Madsen et al. 1992a; P. Clausen, unpublished data), and the new occurrence is believed to be a true establishment of new sites, rather than an accidental discovery of already established sites. In both areas the brent geese primarily feeds on Zostera (Madsen et al. 1992b, B. Laubek, pers.comm.), and also on Ruppia and saltmarshes along the Northern Kattegat coast (B. Laubek, pers. comm.).

LINDISFARNE

Lindisfarne was recognised as the major light-bellied brent goose site in England in the 1950s (Salomonsen 1958), but no detailed research on the feeding ecology, habitat use and distribution of the geese within the area was made before 1989-92. However, the distributions of brent geese and wigeon Anas penelope were mapped in 1973/74 (Fig. 6, Boorman & Ranwell 1977), and Zostera data have recently been collected by the second author. A comparison of these records with the situation in 1989-92 (Fig. 6) reveals that almost all Zostera on Holy Islands Sands disappeared, resulting in a 20% decrease in Zostera area from 9.5 km^2 in 1973/74 to 7.6 km^2 in 1989-92. As a result, there are two major effects of the disappearance of the Holy Islands Sands Zostera beds: (1) the brent geese have switched to feeding on Zostera on Fenham Flats, and (2) brent geese and wigeon now feed in the same areas to a higher extent than previously (Fig. 6). In addition to these changes in use of Lindisfarne by light-bellied brent geese and wigeon, dark-bellied brent geese have also started to use the area. Previously only very few dark-bellied brent geese were seen among the light-bellied brent geese, with annual peak counts ranging from 5 to 39 geese in 1973-88 (NCC counts), but in 1988-92 annual peaks ranged from 352 to 453 geese. As with Mariager-Randers Fjords, the earlier arrival in autumn and increase in brent geese numbers caused an increase in total goose use, despite the earlier departure of geese from the area. In 1980-83 77,200 goosedays (average of three seasons) and in 1989-92 250,600 goosedays (average of three seasons) were spent in the area; of the latter 9.8% to 20.5% were spent by dark-bellied brent geese. One effect of this increased use of the area by brent geese is that the Zostera supplies are significantly grazed down from 21.1 g/m^2 in September to 5.6 g/m^2 in February (Fig. 7), and consequently the feeding performance of the brent geese declined during winter, i.e. pace rates declined significantly from 92.0 (seconds per 20 steps) in September to 34.2 in February (Fig. 7). Measurements of dropping rates suggest a decline too, as they fell from 18.2 droppings per hour in October to 9.8 February (Z=1.43, P=0.0771, method Bédard & Gauthier 1986).

NISSUM BREDNING

The importance of Nissum Bredning as a staging area for the light-bellied brent geese increased during the 1980s. In 1980-87 brent geese only used the area in late winter, i.e. February and March. In the mild winters from 1988/89 to 1991/92 light-bellied brent geese arrived even earlier at Nissum Bredning each year, and a few hundred geese were found throughout the period November to May; numbers still peaked in February-March, but large flocks tended to stay longer in the area than previously. As a consequence, the number of goosedays spent in the area increased from 7,000 in 1980-83 (average of three seasons, Madsen 1986) to 13,900 in 1988/89, and thereafter increased annually to 55,300 goosedays by 1991/92. In 1988-92 a major change in use of habitats occurred; i.e. in 1988/89 77%, 1989/90 86%, 1990/91 26%, and 1991/92 21% of goosedays were used feeding on saltmarshes in the area, the remaining goosedays were spent on Z. marina beds in the Limfjord. The few saltmarshes in the area are well managed, and Zostera are abundant (Table 1).

NISSUM FJORD

Since Nissum Fjord was described by Salomonsen (1957) as an important area for light-bellied brent geese, several authors have dealt with the use of the fjord by brent geese (Jepsen 1967, 1984; Fog 1967, 1972; Madsen 1984, 1986; Christensen 1987). Throughout the 1960s it was believed that the whole population was found here in spring (Fog 1972, 1979). Since the early 1980s the number of brent geese staging in the area has decreased, to a present level of 800 geese in spring (Madsen et al. in press). Formerly the brent geese fed primarily on submerged Z. marina in the fjord throughout spring, and only used saltmarshes occasionally during high water levels (Salomonsen 1957; Jepsen 1967). A drastic decline in the distribution of Z. marina, from 11 km^2 in 1966-76 to zero in 1988 (Fig. 8), caused the brent geese to feed primarily on saltmarshes, especially on Holmen and Kromanden (Fig. 9), and pastures were also used (Madsen 1984, 1986, Christensen 1987) (Table 2). Two sites, Klægodde and Fjandø, almost unused by the brent geese in 1984-85, became quite important for the brent geese in 1989-92 (Fig. 9). A site was established at Klægodde in 1989 where pink-footed geese Anser brachyrhynchos are baited with barley Hordeum vulgare grains on a pasture from mid April to early May. The light-bellied brent geese started to use this site immediately, and also used newly sown barley fields more than before (Table 2). The island of Fjandø is made of low sand dunes, and only a small part of the vegetation is saltmarsh, the rest is typical sand dune swards, an unusual brent habitat.

Almost half (46%) of the saltmarsh area along the west coast of Nissum Fjord was reclaimed for agriculture in the 1960s and 1970s, thereby reducing the saltmarsh area from 4.1 km^2 in 1958 to 2.2 km^2 in 1981 (measured from 1:25,000 maps from the Geodaetical Institute, Copenhagen); Jepsen (1967, pers. comm.) only recorded two minor reclamations in 1965, and no additional reclamations were made from 1981 to 1992 (comparing the 1981 map and own field data), so almost all reclamations were made in the period 1966-80. The remaining saltmarshes were intensively grazed by cattle or mown for hay in the 1960s, but this practice ceased in several areas in the late 1970s and early 1980s (Jepsen 1984; Madsen 1984), and the marshes are now growing tall vegetation and reed beds are developing (Jepsen 1984; Christensen 1987). From 1985 to 1992 only minor changes in management practice occurred, comparing our 1992 data with those of Ringkjøbing Amt (1985b). Only 30% of the saltmarshes are managed today, and their carrying capacity was estimated at 1947 geese in 1992 (Table 1).

AGERØ AREA

In 1973 the first small flocks of light-bellied brent geese were observed feeding in spring on saltmarshes on the island Agerø. Since then the number of brent geese in the area has risen annually to 3,100 geese in April-May 1992. The number of goosedays spent in the area rose from 52,600 in 1980-83 (average of three seasons; Madsen 1986) to 183,600 in 1988/89, remained at 164,100 in 1989/90 and 177,300 in 1990/91, and increased to 284,100 in 1991/92. When spring staging in the area 1980-83 brent geese only fed on saltmarshes (Madsen 1984, 1986), but in 1989-92 41% (range 22-55%) of goosedays used in the area in spring were spent feeding on Zostera beds, and 1.8% (range 0-6.3%) on spring barley fields. Until the mid 1980s brent geese were confined to areas in the immediate vicinity of Agerø, but since then more remote saltmarshes and Zostera beds have been used, the most recent being 12 km from Agerø. The large use of Zostera in recent years was seemingly not related to limitation of resources found on the saltmarshes, at least not in 1989, when brent geese grazed only half of the Puccinellia maritima available in an experimental plot (Clausen 1991). Densities of Zostera increased considerably and new areas were colonized by Zostera around Agerø from 1988 to 1992 (Drachmann et al. 1993)(Fig. 10). Saltmarshes in the area are well managed, most of them grazed by cattle, and their carrying capacity was estimated at 18,900 geese in 1992 (Table 1).

Discussion

REASONS BEHIND THE CHANGES IN DISTRIBUTION AND HABITAT USE

The Danish Wadden Sea

Birds are well known to be able to search for, find, and use patches of abundant food supplies (e.g. Kamil et al., 1987). In agreement with this Madsen (1988) described how dark-bellied brent geese, when undisturbed, selected those areas where leaf cover of Z. noltii was highest. Therefore we argue that light-bellied brent geese will feed in the best foraging sites within those parts of the Danish Wadden Sea which they traditionally have used. The feeding performance of light-bellied brent geese in mid September 1989 in three of the most used sites was comparable to that observed in dark-bellied brent geese, feeding on Z. noltii at 10-20% of leaf cover (Clausen & Fischer 1994). This suggest that the Zostera beds were depleted to 10-20% of coverage by mid September. Madsen (1988) recorded 80% coverage in September and depletion to 10-20% coverage in November. Van Eerden (1984) showed that threshold densities in food supplies are found, below which feeding no longer is profitable for the birds, and Charman (1979) found a threshold leaf cover of around 15% for Z. noltii feeding dark-bellied brent geese. Madsen (1988) agreed with this threshold cover, and argued that depletion of food supplies to this threshold caused the birds to change habitat or leave the area. Therefore we explain the earlier departure of light-bellied brent geese from the Wadden Sea in the late 1980s by an earlier depletion of the food supplies within the staging area. This earlier depletion of the food supplies is not caused by exploitative food competition from increasing numbers of the two other important herbivorous waterfowl using the same areas, viz. dark-bellied brent geese and wigeon. On the contrary, the dark-bellied brent geese have shown an even more drastic decline in their use of the area, as have the wigeon (Clausen & Fischer 1994). The declines in use of the area by dark-bellied brent geese and wigeon were not caused by a general decrease in their total population sizes (Madsen et al. 1990; Madsen 1992); instead it appears that it was caused by declines in Zostera biomass within the area, i.e. Zostera is disappearing from areas east of Fanø, where it formerly occurred (Fig. 3) and peak densities of Zostera in summer have diminished within areas where it is still found. Two reasons behind the observed decline may be a recent increase in eutrophication levels in the northern part of the Danish Wadden Sea and deposition of sludge dredged from Esbjerg Harbour in the area east of Fanø (Clausen & Fischer 1994).

Mariager and Randers Fjords

The overall change in foraging areas used by brent geese in Mariager Fjord in the 1980s (Fig. 4) is apparently caused by a decline of Zostera in the outermost end of the fjord (Fig. 5). The reason behind this decline remains uncertain. There is no evidence of eutrophication in the outer part of the fjord (Nordjyllands Amt 1988a; Clausen 1990), but some former Zostera areas are now covered with silty sediments, less suitable for Zostera growth. The establishment of the Overgaard barrage in the early 1960s changed the width of the opening of the fjord to the sea from 2 km to 400 m, and this may have caused sand deposition in the outer part of the fjord, and thus the Zostera decline (Clausen 1990).

The earlier departure from Mariager-Randers Fjords in the late 1980s may have been related to depletion of food supplies in the fjords. This is indicated by the pre-dominant use of saltmarshes as foraging sites by the brent geese late in season. Similar shifts from fjord to terrestrial habitats have been explained by depletion of Zostera and algae resources by Charman (1979) and Tubbs & Tubbs (1982). In 1989/90 brent geese, coots Fulica atra and mute swans Cygnus olor all fed in the areas with the highest densities of food plants early in the season, but the coots and mute swans remained for longer in these areas. In contrast, although the brent geese initially fed in areas of high food densities they later switched to forage in areas where very low densities occurred (Clausen 1991). Recent studies in autumns 1992 and 1993 (P. Clausen & H. Ettrup, unpublished data) confirmed that *Zostera* supplies are indeed depleted during autumn, and that this partly may be caused by exploitative food competition between brent geese, coots and mute swans. The brent geese are first affected by this competition, because the coots (by diving) and the mute swans (because of their longer necks) can feed at greater depths than the brent geese (i.e. the food resources is depleted first for the brent geese). To avoid the competition the brent geese disperse to fjord areas with low densities of food, switch to saltmarshes, or leave the area. Thus, it appears that the carrying capacity of the fjord areas for the brent geese has been reached.

Lindisfarne

At Lindisfarne there is only minor evidence of eutrophication, and the main reason behind the decline of *Zostera* on Holy Islands Sands is believed to be the establishment of the Holy Island causeway in 1958, which have lead to changes in sedimentation processes, and caused a change from muddy to sandy substrate on Holy Islands Sands. The development in *Zostera* biomass, pace rate and dropping rate measurements (Fig. 7) are all comparable to those found by Madsen (1988), and indicates that the *Zostera* supplies in February are depleted to threshold levels. A similar conclusion is reached with a modelling approach by S. Percival, W.J. Sutherland & P.R. Evans (unpublished data). Therefore the brent geese should leave the area or switch habitats (Madsen 1988), and indeed they do, as they migrate to the spring staging areas in Denmark.

The recent increase in use of Lindisfarne by dark-bellied brent geese may be seen as an effect of the steady increase of their population in Great Britain, and particularly at the sites nearest to Lindisfarne, *i.e.* the Wash and the North Norfolk coast (Owen *et al.* 1986, Kirby & Cranswick 1993). If they continue to increase in numbers, this may lead to increased competion for food supplies between the brent geese and wigeon.

Nibe Bredning, the Northern Kattegat coast and Nissum Bredning

The recent use of Nibe Bredning, the northern Kattegat coast and Nissum Bredning as well as Agerø in late autumn and winter may be seen as a choice made by many of the geese formerly staging in Mariager and Randers Fjords. By migrating away instead of switching to the saltmarshes, they can continue to feed on submerged *Zostera*, as they do in the four areas mentioned, and thereby probably derive more efficient net energetic gains (cf. Drent *et al.* 1978/79).

Nissum Fjord

The changes in habitat availability and the response by the geese at Nissum Fjord are summarised in Fig. 11. While staging in Nissum Fjord, the light-bellied brent geese traditionally fed on *Zostera* beds, and on saltmarshes during high water levels in spring (Salomonsen 1957; Jepsen 1967). The decline of *Zostera* in the fjord (Fig. 8) was caused by severe eutrophication (Ringkjøbing Amt 1985a, 1988). The species disappeared almost totally during 1988, when the sluice in a few months was closed for repair, and the salinity in the fjord as a consequence fell below 6-8‰, considered as the lower salinity tolerance limit for *Zostera marina* (Ringkjøbing Amt 1993). Since 1990 *Zostera* reestablished and in summer 1991 covered 3.0 km^2 (Ringkjøbing Amt 1993). The vast majority of the reestablished *Zostera* bed is, however, found at water depths greater than 1 m, and is therefore of reduced value for the geese.

The decline in *Zostera* has gradually reduced the foraging opportunities in the area since 1976, which have been further reduced by reclamation of saltmarshes for agricultural purposes in the late 1960s and 1970s, and the cessation of both cattle grazing and mowing of other saltmarshes over the same period. However, although the data collected at Nissum Fjord can not be analysed statistically, due to most mappings of *Zostera* and saltmarsh availability being made in years without simultaneous goose studies, it is obvious that the saltmarsh reclamations *per se* did not affect the brent geese in the 1960s and 1970s. The brent geese continued to feed on *Zostera* (Fig. 11), and it was only after the decline of *Zostera* the saltmarsh feeding has been important (Fig. 11), and probably declined in recent years because of poor management. This has prompted some brent geese to forage on pastures, sand dunes and newly sown cereal fields in spring (Table 2). The use of sand dune vegetation on Fjandø as forage for brent geese is very unusual, but the whole island is grazed by sheep, maintaining a low sward which may attract the geese. Fjandø is also the most important breeding island for gulls *Larus* spp. in Nissum Fjord, with more than 10,000 breeding pairs in total (Christensen 1987); faeces from gulls are known to increase nitrogen levels and hence the nutritious quality for geese feeding on the plants growing near the colonies (Bazely *et al.* 1991). The recent use of newly sown cereal fields and the baiting site could also reflect a high energetic profitability of these sites; Madsen (1985) showed that pink-footed geese could reduce their daily feeding activities from 80% of the daylight hours on pastures to 54% on newly sown barley fields, because of the high energetic profit from grain feeding. Other brent geese were prompted to leave the area and search for new foraging areas, resulting in the successful establishment of the Agerø spring haunt. In spite of the reduction of quality of Nissum Fjord for spring staging brent geese, the carrying capacity of the saltmarshes still appears beyond that used by the geese (Table 1), but it must be noted that the peak number of 2700 brent geese recorded in spring 1976 (Madsen et al. in press) could not be maintained in the fjord by saltmarsh feeding alone, given the present management practice.

Agerø area

There are indications of a positive development in Zostera stands throughout the Limfjord in the late 1980s and early 1990s, and especially around Agerø (Limfjordsovervågningen 1992b; Drachmann et al. 1993). Three factors or a combination of these may have caused this development (reviewed in Drachmann et al. 1993): large investments in waste water cleaning plants in the 1970s and 1980s have led to a reduction in the eutrophication of the Limfjord; a series of extraordinary mild winters 1987-92 have allowed the Zostera to grow throughout the year, and there have been no diebacks due to bottom freezing in mid-winter; the prohibition of blue mussel Mytilus edulis fishery around Agerø in 1987 stopped the negative impact which the fishery was believed to have had on Zostera growth in the Limfjord. Whatever factor led to the reestablishment of Zostera in the Limfjord, the historical literature (Salomonsen 1957; Jepsen 1967) and the present habitat use of brent geese around Agerø suggest that the 'optimal' spring feeding strategy for the light-bellied brent geese is to combine the two habitats, Zostera beds and saltmarshes. This is because the brent geese feed on the Zostera beds at low water levels, and switch to saltmarshes during high water levels (Clausen 1991); the use of the Zostera gives the geese an on average better energical intake than feeding on the saltmarshes, but the saltmarshes acts as an important alternative feeding habitat, when Zostera becomes unavailable during high water levels (Clausen I). Only two of the three areas used at present in spring by the light-bellied brent geese offers suitable conditions, i.e. Nissum Bredning and especially the area around Agerø, where large areas of well managed saltmarshes and large Zostera beds are found (Table 1). In this connection it is worth noting that the sudden increase in the numbers of light-bellied brent geese using the Agerø area from 1987 to 1992 (Madsen et al. in press) coincided with the extinction of Zostera in Nissum Fjord (Fig. 8), and the increase in densities of Zostera around Agerø (Fig. 10).

IMPACTS OF CHANGES ON POPULATION DEVELOPMENT

Geese are birds of tradition, and it evident from long-term studies of dark-bellied brent geese that they use the same feeding sites year after year (StJoseph 1979; Prokosch 1984; Ebbinge & StJoseph 1992). In Greenland white-fronted geese Anser albifrons flavirostris tradition is so pronounced that the geese use not only the same sites, but the same corner of the same field from year to year (Wilson et al. 1991). There is also evidence from arctic breeding grounds of lesser snow geese Chen caerulescens that habitat choice is determined by tradition (Cooke & Abraham 1980). In situations with predictable food supplies, traditional migration routes and wintering sites used by adult geese and goslings following their parents is an evolutionary stable strategy, in contrast to opportunistic geese which may risk early food depletion and dispersal to areas without food. This could lower winter survival or reduce spring fattening, thus reducing their reproductive output. However, in periods with rapid changes in food resources, a more exploratory strategy may be favoured over use of traditional sites and habitats.

It is evident that from the late 1950s through to the early 1980s, the light-bellied brent geese have been using the same sites within the same areas, at the same times of the year (Salomonsen 1957, 1958; Jepsen 1967; Fog 1967, 1972, 1979; Madsen 1984, 1986, 1987). The only major changes in this period were the abandoning of Nissum Fjord as an (irregular) autumn site, and the gradual depletion of saltmarshes in the same area, the latter change of minor importance then, because the brent geese in that period primarily fed on Zostera in spring (Madsen 1984; Jepsen 1984; Christensen 1987). Although the relatively low reproductive output of the light-bellied brent geese (Madsen 1987; Madsen et al. in press) must be an important contributing factor behind the less pronounced development of the light-bellied brent goose population since the shooting ban in 1972, it is suggested that the recent changes within the wintering sites also may have had a negative impact, as tradition may have further hampered population development. It appears that the brent geese in the 1980s have suffered from decreasing Zostera resources in the main autumn and winter sites, i.e. the Wadden Sea and Mariager-Randers Fjords. The winter period is critical to geese, because they only crop plants that grew in the previous summer and autumn, and Owen et al. (1992) showed that the well documented declines in body mass of geese in mid-winter are caused by a failure to meet energetic demands from available food resources. The light-bellied brent geese are now apparently depleting intertidal and submerged Zostera stands in the Wadden Sea, Mariager-Randers Fjords, and at Lindisfarne just prior to departure. One reason behind the frequently observed juvenile mortality during winter (Madsen et al. in press) may be that geese following a more traditional wintering strategy leave these areas in poor condition, and may suffer enhanced mortality during the flights over the North Sea and cross country. The recent colonisation of the Agerø area, Nibe Bredning and the northern Kattegat coast, the use of Lindisfarne as a wintering site, even in mild winters, and the habitat shifts at Nissum Fjord suggest, that an exploratory segment of the population have succeeded in finding new wintering strategies which may enhance survival. As a consequence, the population has located new areas for winter feeding and spring fattening, and it appears that the carrying capacities for the spring fattening areas far exceed the present goose use (Table 1).

PROPOSALS FOR FUTURE MANAGEMENT

The future now seems more promising for this goose population given the present dispersal pattern, as long as the brent geese have the opportunity to breed successfully in Svalbard. However, the fact that the brent geese staging in autumn at Lindisfarne now utilise Zostera supplies to threshold levels in winter, implies that if the whole population should migrate over there (e.g. as a result of a severe Danish winter), they would encounter food limitation, since there are few saltmarshes found in the area (Table 1). There are no alternative Zostera (Perring & Walters 1977; Owen et al. 1986) or saltmarsh areas near Lindisfarne (own observations) which the geese could move on to, so they would either have to switch to pastures on Holy Island or agricultural fields in Northumberland, and thereby cause local conflicts with farmers. At present only very few individuals do this.

The changes in autumn phenology and distribution have other implications for management; formerly the brent geese were only disturbed by hunters in the Wadden Sea and Mariager-Randers Fjords, as most geese arrived at Lindisfarne after the wigeon hunters had left. Now brent geese are found in all areas except Nissum Fjord when intensive hunting takes place. In Denmark a major change in legislation in 1993 will impose one or more shooting-free areas in all EEC Special Bird Protection Areas, and if the recommendations of the National Environmental Research Institute (Madsen et al. 1992b; Madsen & Pihl 1993) are followed, all light-bellied brent goose sites in Denmark will give the geese very good protection from hunting disturbance. However, at Lindisfarne the changes in distribution patterns of the brent geese and wigeon in recent years (Fig. 6) has meant that brent geese frequently are disturbed by hunters.

CONCLUSIONS

The Svalbard light-bellied brent goose population has within the last 10-15 years suffered as a result of eutrophication, changes in saltmarsh management and saltmarsh reclamations, and probably also changes in sedimentation processes, following constructions of the Overgaard barrage and the Holy Islands causeway. The geese have responded to the changes in their environment by finding new feeding areas, and changing habitats and phenology, which may enhance their chances of future survival. However, the quality of most of their feeding areas could be increased by managing saltmarshes, and this could increase winter survival. It is recommended that a refuge area without hunting should be established at Lindisfarne, management of saltmarshes along the flyway should be improved, and an international conservation plan for this vulnerable population be made.

Acknowledgements

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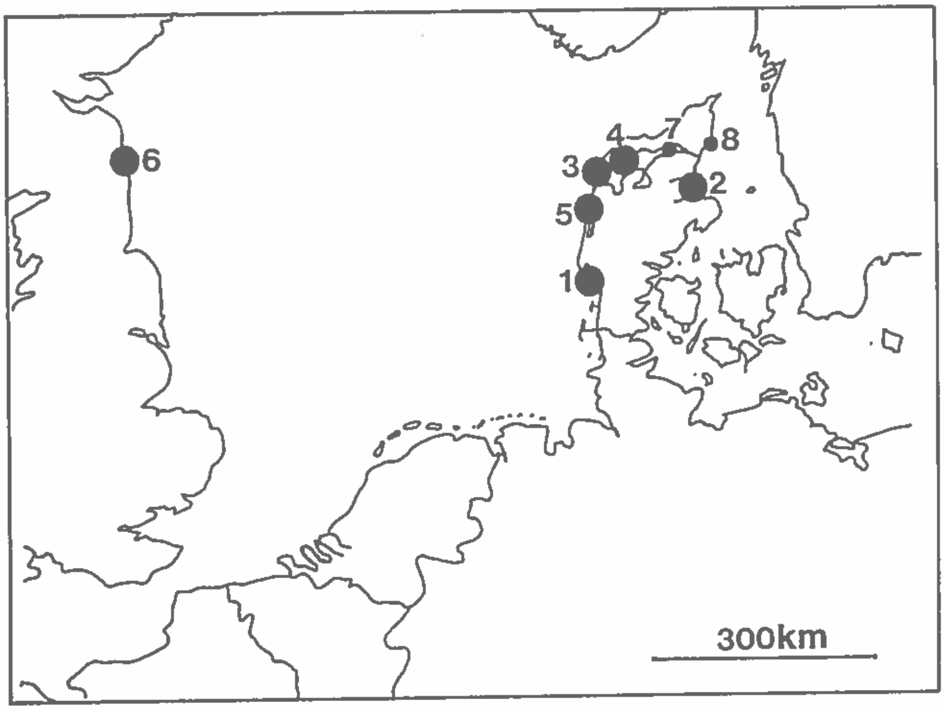

Fig. 1. Map showing the position of the six sites used regularly by light-bellied brent geese within the last two decades, i.e. 1) the Danish Wadden Sea, 2) Mariager & Randers Fjords, 3) Nissum Bredning, 4) the Agerø area, 5) Nissum Fjord and 6) Lindisfarne, as well as two new sites taken in use in the late 1980s, 7) Nibe Bredning and 8) the Northern Kattegat coast.

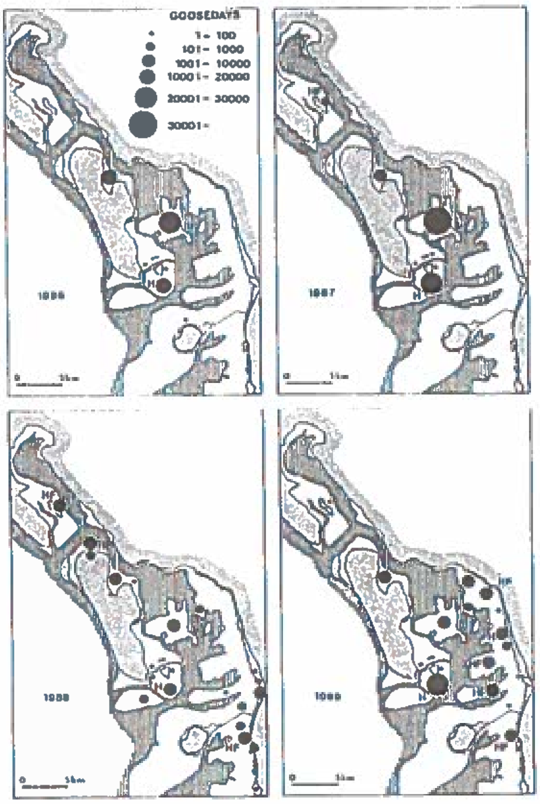

Fig. 2. Autumn distribution of light-bellied brent geese in the Danish Wadden Sea, 1986-1989. The dots indicate numbers of goosedays spent in the period 1 September - 31 December. H= areas used as high tide roosts only, HF= areas used both as high tide roosts and low tide feeding areas. The remaining sites are used as low tide feeding areas only. (For legends concerning hatched and dotted areas, and the position of sites mentioned in the text refer to Fig. 3).

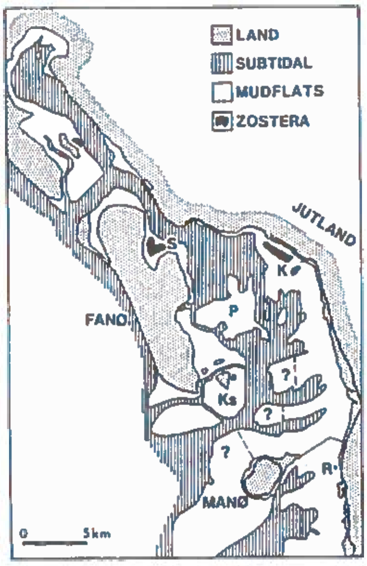

Fig. 3. The distribution of <u>Zostera</u> spp. in the northern part of the Danish Wadden Sea, 1988-89. In the black areas the coverage locally exceeded 10-20%. ? denotes unchecked areas; P = Pendersand, an important feeding site for light-bellied brent geese in 1986-87, where Zostera occurred formerly but not in 1989; Ks = Keldsand, the main roost site until 1989; S = Søjord, K = Klyngvese Sand and R = Råhede, the three important feeding areas in September 1989, where observations on feeding bouts were made (based on Clausen & Fischer 1994).

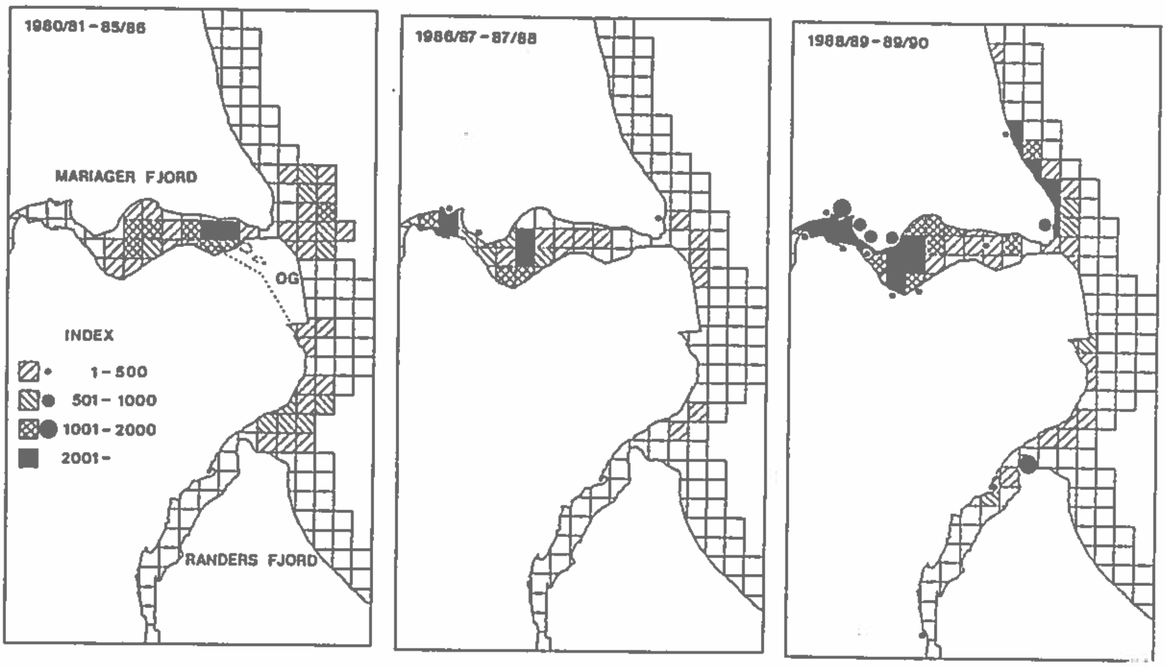

Fig. 4. The distribution of light-bellied brent geese in Mariager-Randers Fjords, 1980-90. The importance of different feeding areas is given as an index (the sum of all observed flocks). Foraging on the fjord is given in a 1x1 km^2 grid, on land as dots, respectively. On the fjordareas an area correction was applied to incomplete quadrats (from Jørgensen et al. 1994). OG indicates the Overgaard barrage, and the stipled lines the former coastline and two islets.

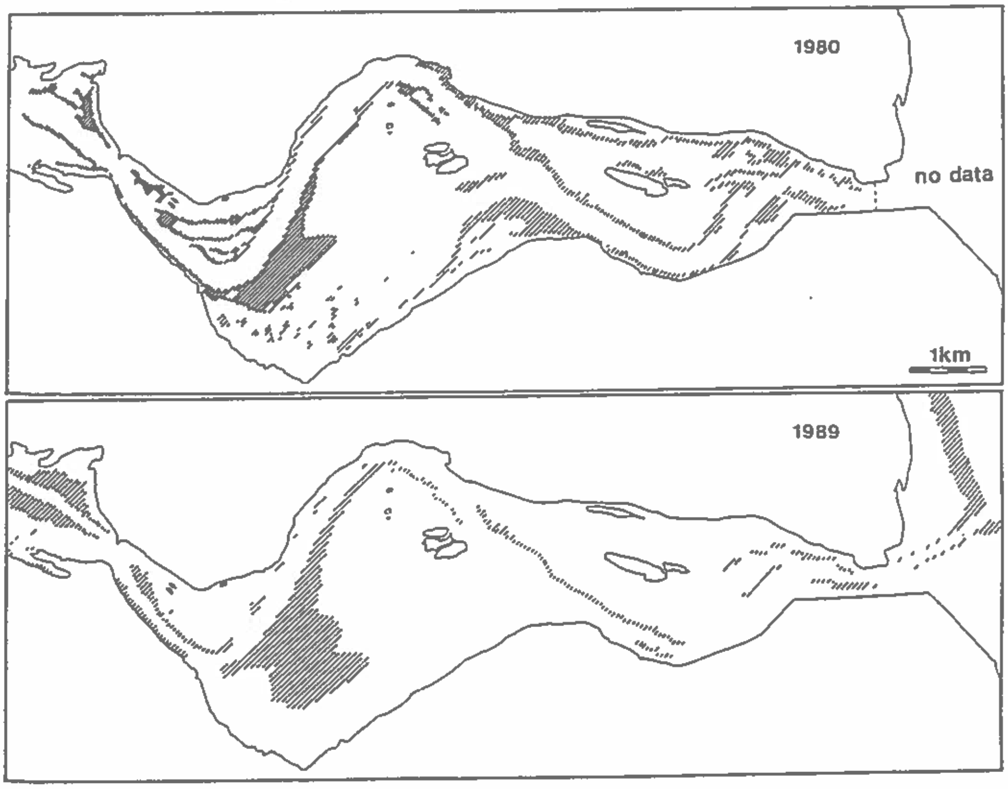

Fig. 5. The overall distribution of Zostera marina in the outermost end of Mariager Fjord, 1980 and 1989 (based on Jørgensen 1980; Clausen 1990).

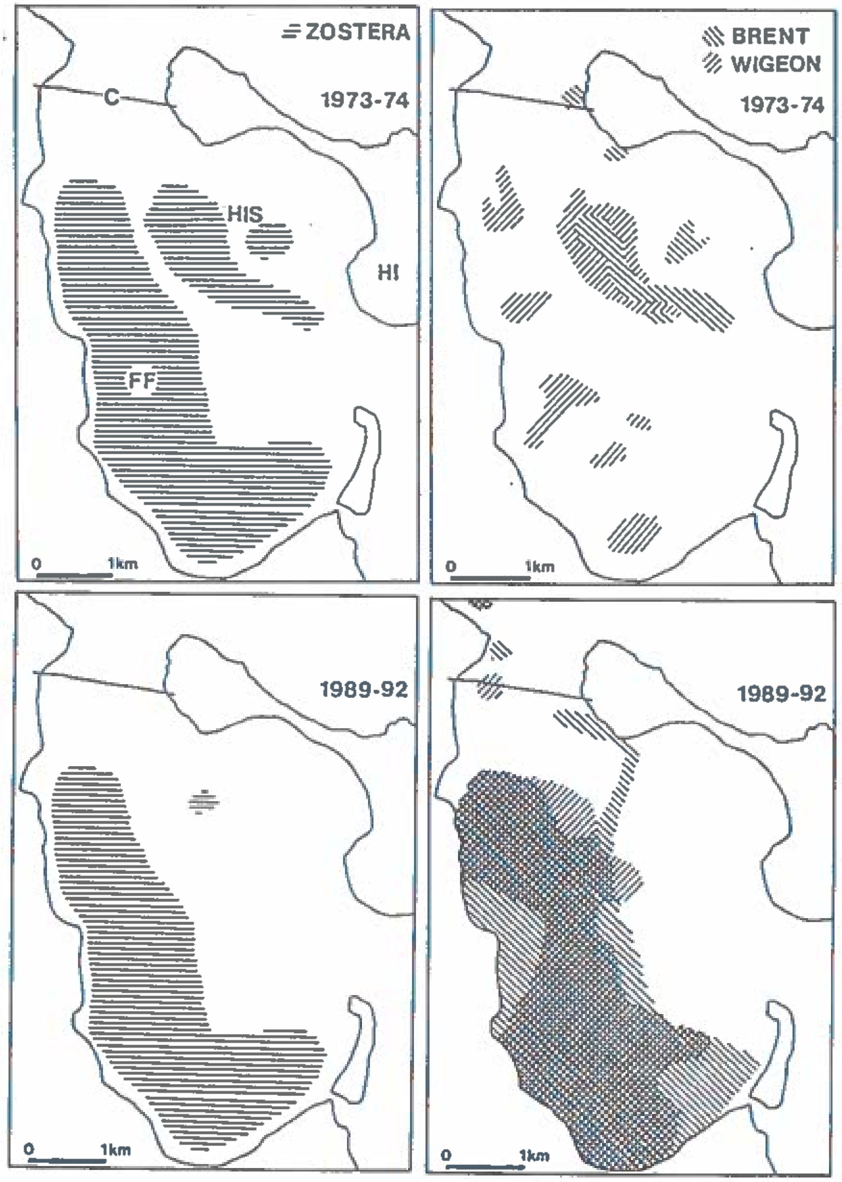

Fig. 6. The overall distribution of Zostera spp., and feeding areas for light-bellied brent geese and wigeon at Lindisfarne in 1973-74 (above) and 1989-92 (below). HIS = Holy Islands Sands, FF = Fenham Flats, HI = Holy Island, C = the Causeway (based on Boorman & Ranwell 1977; Percival, unpubl.).

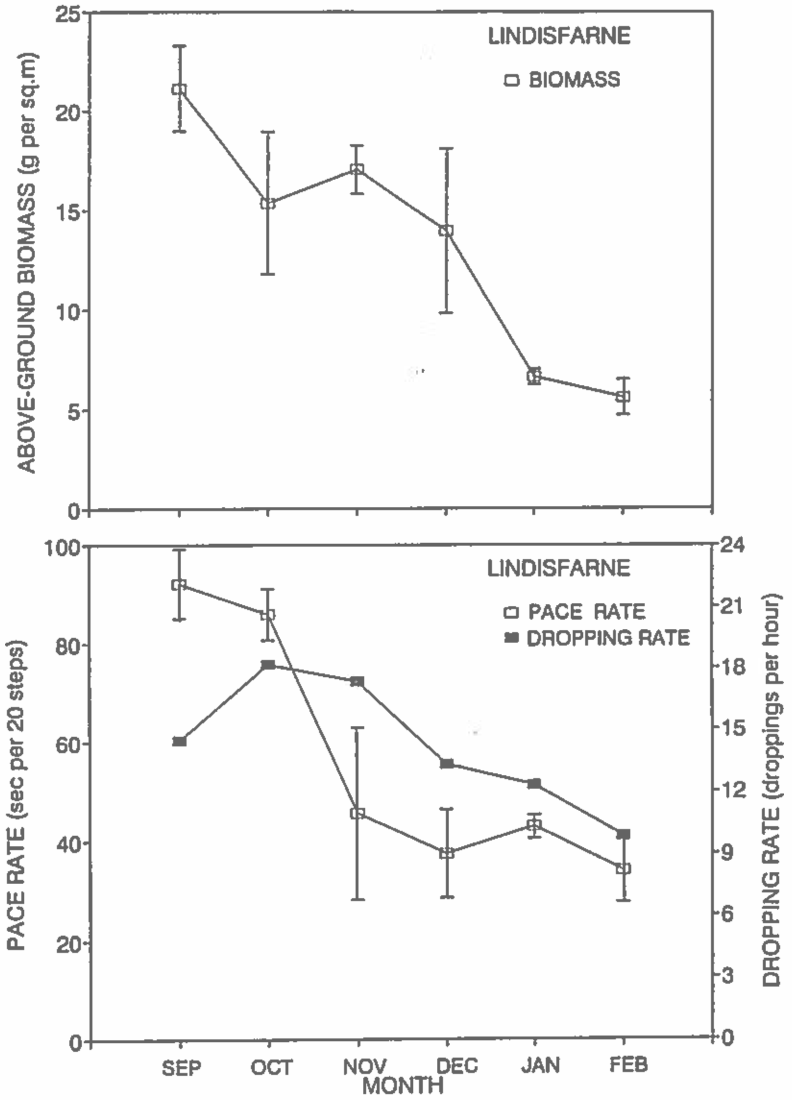

Fig. 7. Development in biomass of Zostera in plots where dropping and pace rates were measured on feeding flocks of brent geese (above), and in pace and dropping rates (below), Lindisfarne 1989-92. The curves for biomass and pace rates shows the development in average values ± 95% confidence limits (vertical bars).

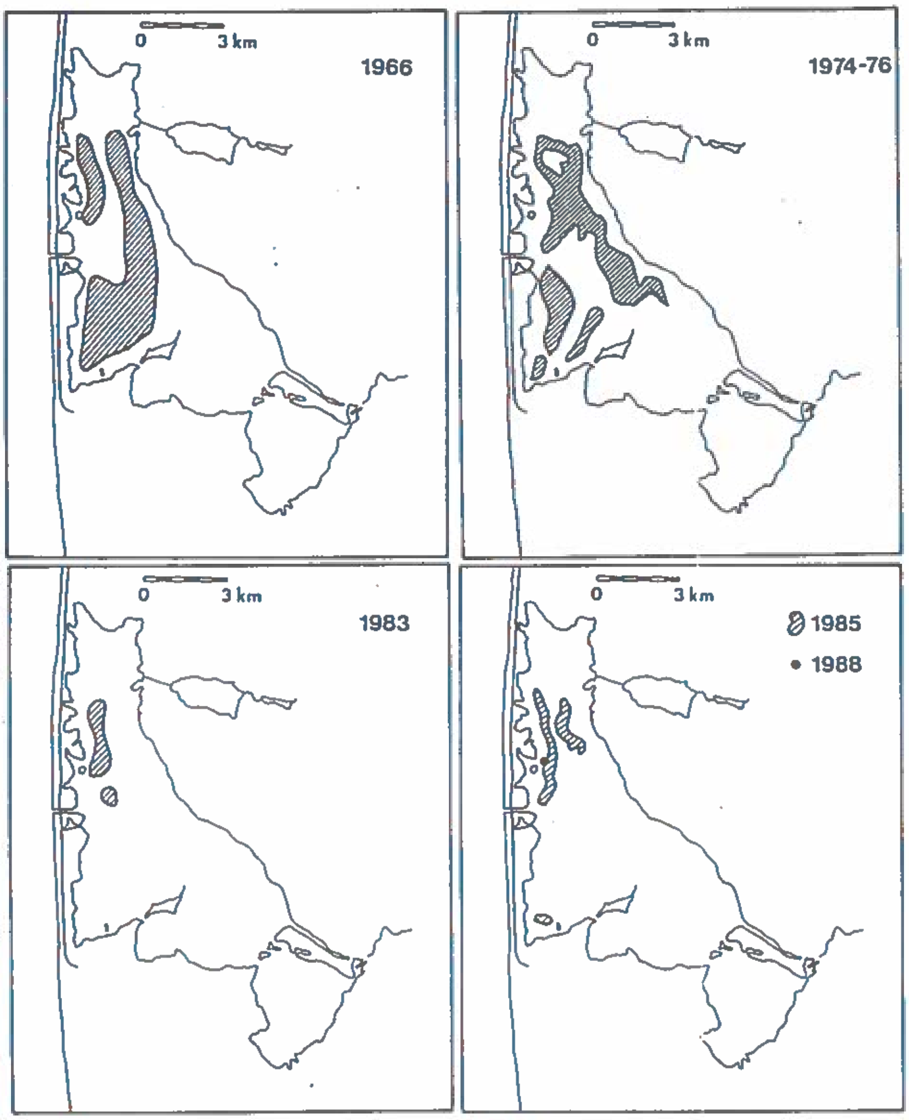

Fig. 8. The overall distribution of Zostera marina in Nissum Fjord, 1966-1988. In 1988 a single shoot was found at the site depicted by a dot (based on Jepsen 1967, 1984; Rasmussen 1976; Ringkjøbing Amt 1985a, 1988).

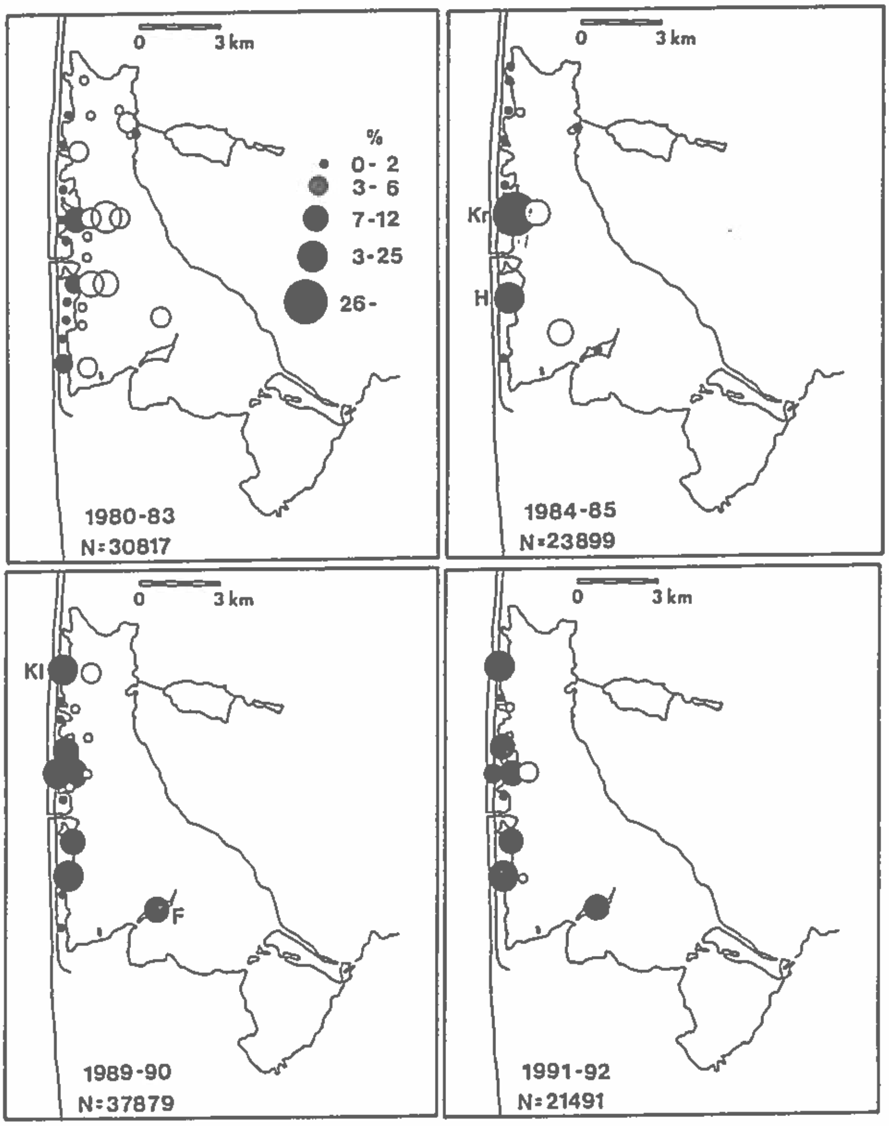

Fig. 9. The distribution of feeding flocks of light-bellied brent geese in Nissum Fjord, 1980-92. The circles gives the percentage distribution of all individuals recorded (=N) in the period January - May; closed circles = feeding on land, open circles = on the fjord. Kr = Kromanden, H = Holmen, Kl = Klægodde (baiting site) and F = Fjandø.

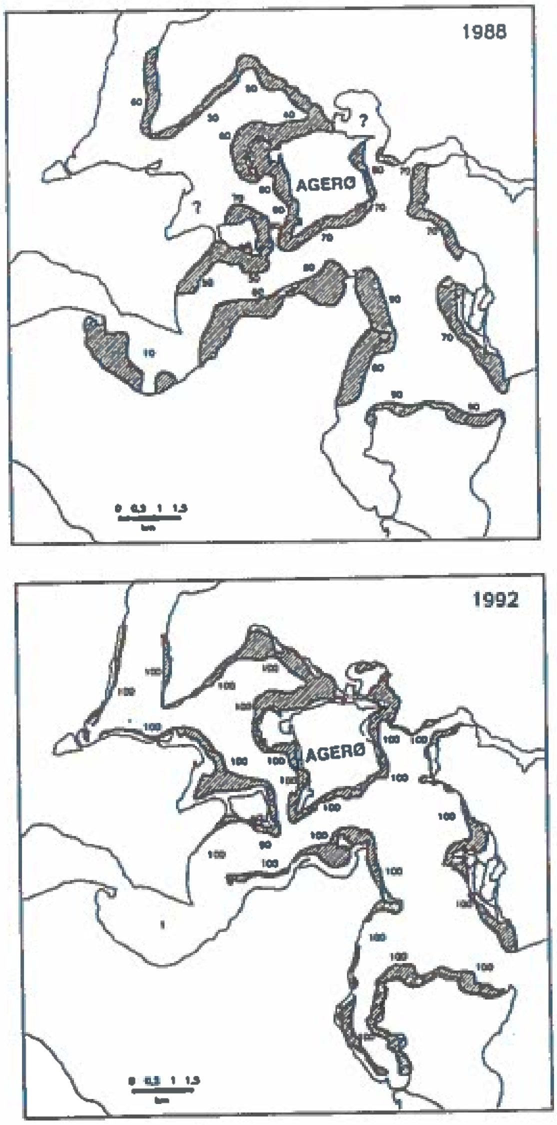

Fig. 10. The overall distribution and bottom covers of Zostera marina around Agerø, 1988 and 1992. The hatched areas gives the distribution and the figures denotes maximum bottom covers of Zostera in specific areas. ? denotes two areas where some Zostera beds probably were overlooked in the 1988 survey; the map for 1992 was drawn from aerial photographs with support from a field survey, whereas the 1988 map only is based on field survey, hence the 1992 mapping is considered more accurate (based on Limfjordskomitéen 1989; Drachmann et al. 1993).

Erratum

Two tables concerning paper V (Changes in distribution and habitat use of Svalbard Light-bellied Brent Geese *Branta bernicla hrota*, 1980-92) accidentally fell out when the final lay-out of my PhD thesis was made.

Table 1. Areas of saltmarshes and submerged/intertidal Zostera, Ruppia, green algae Ulva/Enteromorpha beds within the eight staging areas used by light-bellied brent geese in 1980-92.

The area and management status of saltmarshes (based on own data and Nordjyllands Amt (1988b, 1991)), and their estimated carrying capacity and present use by brent geese for the sites used in spring is tabulated; the saltmarsh area in the Wadden Sea was not calculated, due to the insignificant use of saltmarshes in this area (Clausen & Fischer, 1994).

Zostera, Ruppia, and algae data summarised from Limfjordskomitéen, 1987; Ringkjøbing Amt, 1993; Clausen, 1990; Madsen et al., 1992a; B. Laubek, pers.comm.; Percival, unpubl.; Limfjordsovervågningen, 1992; Clausen & Fischer, 1994. + in Zostera/Ruppia scores indicates presence of these habitats, but the exact area unknown or negligible.

Area	Zostera	Ruppia	Green algae	Saltmarsh	Management status 1992			Carrying capacity spring 1992	Peak count spring 1992
					Well managed	Poorly managed	Un-managed		
	km^2	km^2	km^2	km^2	%	%	%	geese	geese
Danish Wadden Sea	5.0	0.0	+						
Mariager-Randers Fjords	4.3	4.8	1.3	3.2	49.6	13.8	36.6		
Northern Kattegat coast	+	+	+	4.2	≈ 30.0	≈ 20.0	≈ 50.0		
Nibe Bredning	45.0	+	+	5.3	≈ 48.0	≈ 33.0	≈ 9.0		
Lindisfarne	7.7	+	+	0.4	0.0	0.0	100.0		
Nissum Bredning	7.0		+	0.9	91.3	0.0	8.7	2,492	200
Nissum Fjord	0.0	+	+	2.2	29.1	0.8	70.0	1,947	800
Agerø area	11.3			7.5	81.4	7.5	11.1	18,928	3,100

Table 2. Habitat utilisation of light-bellied brent geese staging at Nissum Fjord, March-May, 1980-92 in years with intensive counting activities; the figures give the percentage distribution of observed individuals; the total number of geese for which the habitat use were known is given in the lower line. Data for 1984-85 are taken from Christensen (1987) who did not distinguish between saltmarsh and pasture. * indicates years which are highly significantly different from previous year (χ^2 tests, all $P<0.001$; saltmarsh and pasture pooled for comparisons with 1984-85).

Habitat	1980	1981*	1982*	1983*	1984*	1985*	1989*	1990*	1991*	1992*
Fjord = Zostera	100.0	59.1	55.3	0.0	28.0	1.0	3.9	12.5	0.0	3.8
Saltmarsh	0.0	36.3	42.0	81.1	72.0	98.0	35.5	60.5	63.2	32.2
Pasture	0.0	4.6	2.7	18.9			8.9	5.6	3.8	12.8
New sown barley field	0.0	0.0	0.03	0.0	0.0	1.0	10.8	2.7	16.5	0.2
Baiting site (established 1989)							23.0	9.3	9.6	27.4
Sanddune	0.0	0.0	0.0	0.0	0.0	0.0	17.8	9.4	6.8	17.6
Geese counted	7,500	15,100	7,313	4,038	14,924	8,975	16,033	12,803	8,657	11,654

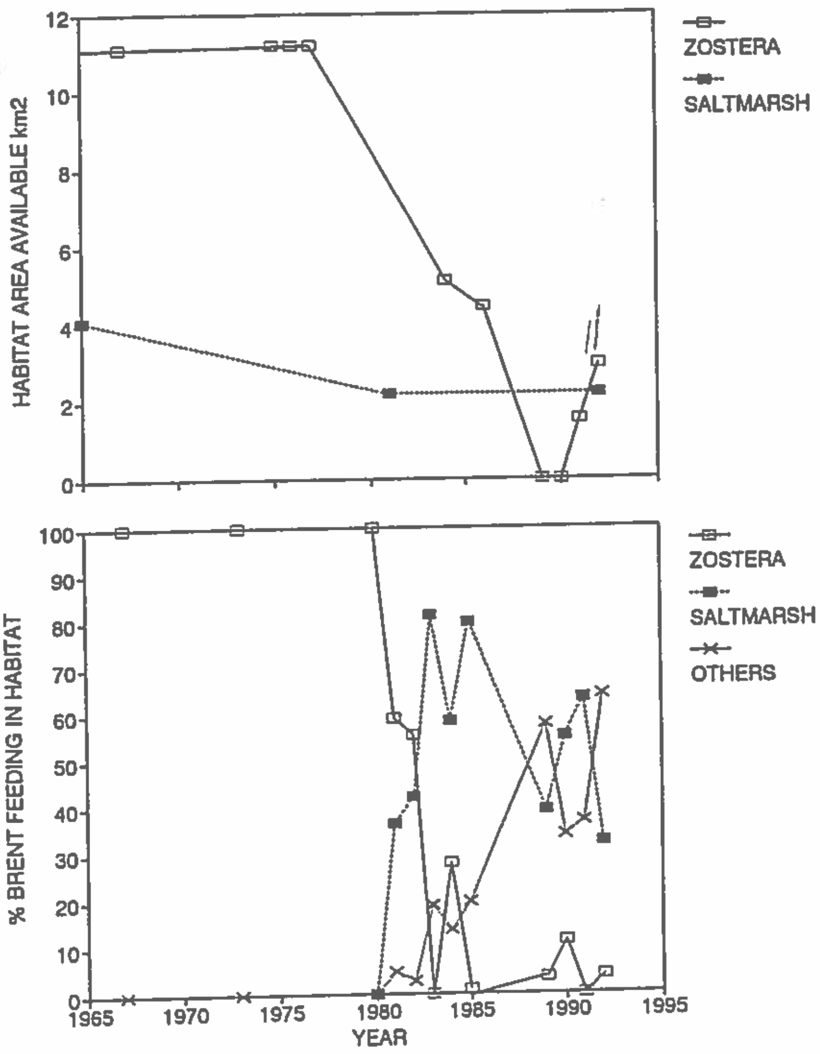

Fig. 11. Summary figure of changes in natural habitats available (above) and the proportional use of these and other habitats by light-bellied brent geese (below) at Nissum Fjord, 1965-92. The areas of Zostera beds was based on Jepsen (1967, 1984); Rasmussen (1976); Ringkjøbing Amt (1985a, 1988, 1993); and those of saltmarshes on maps from the Geodaetical Institute, Copenhagen. The habitat use by brent geese was based on Jepsen (1967, 1979), Christensen (1987) and Table 2. Christensen (1987) did not distinguish between saltmarsh and pasture: when drawing the figure it was assumed that the ratio between saltmarsh/pasture feeding brent geese in 1984-85 was equal to that found in 1983.

Paper VI

An annual budget of eelgrass Zostera marina consumption by herbivorous waterfowl in a shallow Danish estuary

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Summary

Grazing by waterfowl on submerged Zostera marina populations has generally been considered of minor importance for Zostera growth and decomposition, as previous estimates of annual consumption rates were below 4% of annual Zostera production. In this paper we report on a study in a shallow Danish eutrophic estuary. Waterfowl consumption was estimated on basis of waterfowl counts, daily energy expenditure estimates, and metabolisable energy values of Zostera marina, Zostera productivity on basis of biomass sampled. We estimate that waterfowl grazed 12% (range 8-21%) of Zostera produced per year. The high proportion consumed may be explained by three factors; the eutrophication level in the estuary is high, probably leading to low Zostera productivity; herbivore bird density may be high in the estuary; and as access to feeding on Zostera in submerged populations are limited by water depth, a relatively shallow estuary, such as the study site, will allow a higher consumption rate.

Key words: Zostera marina, seagrass, waterfowl, Fulica atra, Cygnus olor, grazing, annual consumption estimate.

Introduction

Studies of goose grazing on the above-ground parts of plants in the upper tidal zone, i.e. on saltmarshes, have demonstrated that the birds consumed considerable amounts of plant material. For example lesser snow geese Anser caerulescens consumed 80% of the net above-ground primary production (NAPP) of Puccinellia phryganodes and Carex subspatacea in summer (Cargill & Jefferies 1984); and dark-bellied brent geese Branta bernicla bernicla consumed 65% of NAPP of Plantago maritima (Prop & Loonen 1989), and 85-87% of NAPP of Puccinellia maritima (Madsen 1989) in spring.

Exclosure studies of waterfowl grazing on Zostera beds in intertidal mudflats in autumn showed that grazing by brent geese and dabbling ducks Anas spp. increased the rate of loss of above-ground plant parts in Zostera noltii beds (Jacobs et al. 1981, Tubbs & Tubbs 1983, Madsen 1988), and in Zostera marina beds (Tubbs & Tubbs 1983, Maheo & Denis 1987). Jacobs et al. (1981) and Madsen (1988) also found that brent geese took a large part of the rhizomes of Zostera noltii by trampling and digging in the sediment. Jacobs et al. (1981) estimated that waterfowl grazed 51% of the maximum biomass and 26% of the annual Zostera noltii production, and Madsen (1988) estimated consumption of 66-91% of the maximum biomass equivalent to 33-45% of the total annual production of Zostera noltii (estimates from both studies dealing with above- and below-ground biomasses). Similar values were found in a recent study of grazing the impact of black brant Branta bernicla nigricans and dabbling ducks on the introduced Zostera japonica on the west coast of Canada, i.e. a consumption equivalent to 50% of the maximum above-ground biomass and 43% of the below-ground biomass (Baldwin & Lovvorn 1994).

Studies of grazing by waterfowl in brackish or marine submerged seagrass communities are much more ambiguous. Exclosure studies in a multi-species community in a brackish Danish estuary by Kiørboe (1980) failed to find an impact of grazing on biomass in grazed plots compared to ungrazed plots. In the same study area Jensen (1986), however, found that grazing reduced the biomass in Potamogeton pectinatus, Zannichellia palustris, and Chara aspera, but not of Ruppia maritima and Tolypella nidifica.

Both authors estimated that the birds consumed 29% (range 15-60%) of the estimated total annual macrophyte production, i.e. they took a major part of above-ground plant materials which would have disappeared anyway due to winter storm action and natural die-back. Verhoeven (1980) likewise estimated 25% consumption of the annual production of Ruppia cirrhosa by coot Fulica atra in a brachish pond. In contrast bird grazing on submerged Zostera marina populations has been considered unimportant; it only constituted 3-4% of the annual eelgrass production in both Chesapeake Bay (Thayer et al. 1984) and the saline lagoon Lake Grevelingen (Nienhuis & Groenendijk 1986).

Here we report on the significance of waterfowl grazing on Zostera marina in a shallow Danish estuary. We discuss factors affecting the proportion of annual seagrass production consumed by waterfowl.

Materials and methods

STUDY AREA

The study was carried out in a small (8.34 km^2) eutrophic estuary, Kertinge Nor/Kerteminde Fjord, situated on the east coast of Funen, Denmark (Fig. 1). The estuary is composed of the inner wide and generally shallow Kertinge Nor (< 3 m deep), and the outer deeper and narrow Kerteminde Fjord (generally 2 to 7.7 m deep). Kertinge Nor sediments were covered by a dense macrophyte vegetation of low species diversity. Zostera marina was the dominant rooted macrophyte between 0.5 and 3 meters (area: 3.4 km^2), Ruppia cirrhosa and R. maritima dominated areas in the shallow zone from c. 0.2 to 0.5 meters depth (0.39 km^2)(Fig. 1)(Larsen et al. 1994). Rooted macrophytes were absent from the inner sheltered parts of the Nor. Filamentous macroalgae, mainly Chaetomorpha linum and Cladophora sericea, occurred throughout the Nor with highest biomass in inner sheltered areas (Larsen et al. 1994). In Kerteminde Fjord macrophyte densities are generally very low, flowering plants have virtually disappeared from 1987 to 1990 (0.3 km^2 of Zostera marina and 0.1 km^2 of Ruppia spp. remaining in the inner part)(Fig. 1), and now only filamentous, red and brown algae are found throughout the fjord (Larsen et al. 1994).

BIRD COUNTS AND BIRD DAYS USED

Herbivorous waterfowl were counted with telescopes from April 1991 to August 1992, at least every other week. Herbivorous waterfowl (obligate herbivores and omnivores) were distinguished from obligate carnivores based on food preferences described in Cramp & Simmons (1977, 1980). Species, position and number of individuals in each bird flock were recorded in field maps (scale 1:25,000), with notes distinguishing between feeding and roosting flocks.

Only two herbivorous waterfowl species were counted in significant numbers (subjectively defined as regular occurrence of >100 individuals), and were extracted for further analysis, namely mute swan Cygnus olor and coot.

The number of birddays used by mute swans and coot were calculated for three water depth intervals in the estuary, i.e. 0-1 m, 1-2 m and >2 m, and for birddays used on land (pastures, agricultural fields). The number of birddays used between two counts was calculated as the average number of birds observed at the two counts multiplied by the number of days between them; the calculated birddays were then summed to give the total number of birddays used over the entire period. Calculations were made for an annual budget, i.e. the period 1 August 1991 to 31 July 1992. As there were large between-year differences in Zostera growth and the size of the moulting mute swan population (see below), we also calculated mute swan days spent during the two summers, i.e. 1 June to 31 August 1991 and 1992.

FOOD CHOICE

It was very often possible to observe directly food items taken by birds at Kertinge Nor. Food choice by mute swans and coot was consequently studied by following individual birds with a KOWA TSN1 20-60×77 zoom telescope. Food choice observations were conducted every other month, by following a minimum of ten individuals of each species, and recording a minimum of five food items taken by each individual.

ENERGY EXPENDITURE AND CONSUMPTION OF ZOSTERA BY BIRDS

The daily energy expenditure (DEE) of mute swans and coot were estimated by two methods, based on body mass (M_b) of the birds, taken as 10 kg for mute swans (Andersen-Harild 1981) and 760 g for coot (Cramp & Simmons 1980).

Method 1: Drent et al. (1978/79) estimated DEE as 2.6×BMR (basal metabolic rate), BMR was calculated from body mass after Lasiewski & Dawson (1967): $\log \mathrm{BMR} = \log 78.3 + 0.723 \log M_b$ (BMR in kcal·day^{-1}; M_b in kg), which equals to $\mathrm{BMR} = 327.6 \times M_b^{0.723}$ kJ·day^{-1}.

Method 2: Walsberg (1983) estimated DEE directly from the body mass as: $\ln \mathrm{DEE} = \ln 12.84 + 0.61 \times \ln M_b$, which rearranged gives $\mathrm{DEE} = 12.84 \times M_b^{0.61}$ (kJ·day^{-1}, M_b in g).

Estimates from method 1 exceed those of method 2 when M_b>1200 g, but are slightly lower for M_b<1200 g. Estimates of DEE using both methods are therefore considered as maximum and minimum values of DEE, providing a range of DEE and thereby consumption (see below).

The daily energy expenditure was recalculated as daily Zostera consumption (ashfree dry weight, DCZ_{afd}) using the formula:

$$DCZ_{afd} = \frac{DEE(kJ \cdot day^{-1})}{ME_Z(kJ \cdot g^{-1} ashfree\ dryweight)}$$

where ME_Z is the metabolisable energy value of ingested Zostera marina. ME_Z for mute swan was set to 8.8 $kJ \cdot g^{-1}$ ashfree dry weight (J. Madsen, P. Clausen & A.D. Fox unpublished data), and to 8.1 $kJ \cdot g^{-1}$ ashfree dry weight for coot (the value from the more similar sized (1.6 kg) light-bellied brent goose Branta bernicla hrota; Clausen, III). DCZ_{afd} was converted to equivalent daily consumption of Zostera dry weight (DCZ_d) by multiplication with 1.33, as Zostera on average contained 25% ash (range 18% to 31% in 11 samples from March, April, May, June, July and October from three Danish study areas, P. Clausen unpublished data).

Annual consumption of Zostera dry weight was culculated by multiplying DCZ_d with the annual number of birddays used.

ZOSTERA BIOMASS AND PRODUCTION

Macrophytes were sampled by professional SCUBA-divers monthly during May to September 1991, and in February, May to August, and October 1992. In 1991 and 1992 vegetation was sampled at four stations situated along a north-south transect on the east coast of Kertinge Nor in the 1.0-1.5 m depth zone (Fig. 1). In 1992 vegetation biomass was sampled from four stations at 2.0-2.5 m depth (Fig. 1). Three samples were taken in each station by placing a circular ring (area 0.25 m^2) on the bottom, and harvesting the above-ground fraction of macrophytes within the ring. In the laboratory macrophytes were sorted into "flowering plants" (predominantly Zostera; other seagrasses constituted less than 1% in all samples, and are neglected in the following analysis), "filamentous algae", and "other macroalgae". The samples were oven dried to constant weight at 82°C.

Estimates of total above-ground biomass of Zostera in Kertinge Nor at each sampling event were derived by areal interpolation, assuming that each sampling station was representative of the depth range and section of the estuary they were found in, i.e. biomass values per unit area of samples from 1-1.5 m depth was multiplied by the area of the section with a depth of 0.5-1.5 m (acknowledging the fact that Zostera was not found inside the 0.5 m contour), and biomass of samples from 2-2.5 m depth was multiplied by the area of the section with 1.5-3 m depth.

The annual above-ground production of Zostera marina in Kertinge Nor was estimated by multiplying the maximum above-ground biomass of Zostera by 4, i.e. the average ratio of annual above-ground production:maximum above-ground biomass from four Danish studies of Zostera marina biomass development and production (Sand-Jensen 1975 ratio 4.0, Wium-Andersen & Borum 1984 5.9, Pedersen & Borum 1993 2.4, Olesen & Sand-Jensen 1994 3.7). The range of estimates was calculated by multiplication with the smallest and largest ratio.

Results

NUMBERS OF BIRDS, BIRDDAYS USED AND DISTRIBUTION OF BIRDS

A maximum of 261 mute swans and 5,600 coot were counted during 1 April 1991 to 31 August 1992. Highest numbers of both occurred during October to January, but mute swans numbers were more constant throughout the year, due to the presence of c. 100 moulting individuals in summer 1991 and c. 175 individuals in summer 1992 (Fig. 2).

During 1 August 1991 to 31 July 1992 mute swans spent 49,500 birddays in the estuary and 7,500 birddays on land (preferably winter wheat Triticum aestivum and winter barley Hordeum vulgare fields from mid February to mid June). Coot spent 701,700 birddays in the estuary and 400 on land (pastures, mid March to mid June). Of the birddays spent in the estuary, 94% of mute swan days and 98% of coot days were spent in Kertinge Nor, the remaining birddays in Kerteminde Fjord. In the estuary, 53% of the mute swans and 70% of the coot fed at water depths larger than 1 m, and most feeding in water less than than 1 m deep occurred in the summer period (Fig. 3).

FOOD CHOICE OF BIRDS FEEDING ON THE ESTUARY

Mute swans were obligate herbivores. They primarily fed on Zostera, and during the summer also on Ruppia and Cladophora sericea (Fig. 4). By multiplying the proportional use of food items per month by the number of swandays per month in the estuary, an estimated 40,150 swandays (81.1%) were spent feeding on Zostera during August 1991 to July 1992.

Moulting mute swans spent 8500 birddays in Kertinge Nor during summer (June-August) 1991, of these 6200 birddays (72.9%) were spent feeding on Zostera. In summer 1992 15,200 birddays were spent in the estuary, and 11,250 birddays (74.1%) on Zostera.

Coot were omnivores (Fig. 4). The animal part of their diet primarily consisted of Cardium edulis and Hydrobia spp., which were picked from filamentous algae brought to the surface by diving or up-ending. The vegetable part of their diet primarily consisted of Zostera during autumn and winter (when most birds were found there), and of Ruppia during the summer (Fig. 4). An estimated 384,450 coot days (55%) were spent feeding on animals and 315,250 coot days (45%) on plants, including 224,000 coot days (71%) feeding on Zostera.

ZOSTERA BIOMASS AND ANNUAL PRODUCTION ESTIMATES

Zostera above-ground biomass differed significantly between-years (samples from 1.0 to 1.5 m depth range from May to August, sampled both years; $F_{7,64}=10.06$, $P<0.0001$). There was a significant difference between-depths in biomass phenology (1992 data only; ANOVA $F_{3,61}=3.36$, $P=0.024$), but no significant difference in above-ground biomass ($F_{1,61}=0.11$, $P=0.74$). Biomass peaked in August 1991 and June 1992, respectively, in the 1.0 to 1.5 m depth range (Fig. 5), and in August-September 1992 in the 2.0 to 2.5 m depth range (Fig. 5). Peak biomass in 1991 (54.3 g m^{-2}) was more than twice that in 1992 (22.3 g m^{-2}) in the 1.0 to 1.5 m depth range.

Peak biomass per unit area converted to total biomass in Kertinge Nor in 1991 totalled 105.4 metric tonnes dryweight, equivalent to an estimated annual production of 421.6 tonnes dryweight (Table 1). In 1992 peak biomass totalled 79.5 tonnes dryweight, and annual production 318.0 tonnes (Table 1).

ZOSTERA CONSUMPTION BY WATERFOWL

Mute swan consumption of Zostera was estimated at 24.4 metric tonnes dryweight, and consumption by coot at 26.4 tonnes dryweight; Zostera consumption by waterfowl thus totalled 50.9 tonnes (Table 1).

As the majority of grazing took place over the autumn and winter 1991/92, the most appropriate Zostera production estimate to compare with is that from 1991. Thus, an estimated 12% (range 8% to 21%) of the annual production of Zostera was consumed by waterfowl during 1991/92 (Table 1). Assuming that comparable numbers of waterfowl spent the winter 1992/93 feeding on Zostera in the estuary, 16% (range 10% to 28%) of the annual production would have been consumed (Table 1).

The moulting mute swans consumed 3.8 tonnes dryweight during summer 1991, and 6.8 tonnes in 1992 (Table 2).

Discussion

ZOSTERA BIOMASS DEVELOPMENT AND PRODUCTION

The peak biomass values of Zostera marina in Kertinge Nor 1991 and 1992 was far less than those previously reported from Danish coastal waters, ranging from 151 to 710 g m^{-2} dryweight (Sand-Jensen 1975; Wium-Andersen & Borum 1984; Pedersen & Borum 1993; Olesen & Sand-Jensen 1994a; Clausen III; Madsen, Clausen & Fox VII), indeed Olesen and Sand-Jensen (1993) in their review only found two out of 40 studied temperate Zostera marina populations with peak above-ground biomass values below 100 g m^{-2} dryweight. The low biomass of Zostera may result from the very high level of eutrophication in the estuary, leading to high rates of production amongst filamentous algae and phytoplankton (Christensen et al. 1994, Larsen et al. 1994). High algal and phytoplankton production are known to occur at the expense of rooted submerged macrophytes, such as Zostera, due to shading and competition for nutrients (Sand-Jensen & Borum 1983, 1991).

The estuary was subject to a radical change in sewage discharges in 1990. Four sevage treatment plants surrounding the estuary discharged directly into the estuary, but from January 1990 these were channelled through pipelines to a new treatment plant and flushed into the Great Belt. This reduced annual nitrogen and phosphorus discharges into the estuary of 45% and 78%, respectively (Larsen et al. 1994). The change in sewage discharges in 1990 led to a highly unstable ecosystem, with large between-year differences in production of filamentous algae, phytoplankton, and phytoplankton grazers such as jellyfish Aurelia aurita and the ascidian Ciona intestinalis (Christensen et al. 1994, Larsen et al. 1994, Riisgård et al. 1994). Phytoplankton production was extremely high in summer 1992 compared to 1990 and 1991, which led to a reduction in Secchi depth from c. 2.5 to 1 meter (Larsen et al. 1994), i.e. causing high shading effects on macrophytes, and this is believed to be major cause for the between-year difference in Zostera biomass in the 1.0-1.5 m depth range.

The use of biomass values from the 2.0 to 2.5 meter depth range from 1992 in the estimate of the 1991 production in the deeper part may lead to an underestimation of Zostera produced in 1991, because of the lower productivity in 1992.

ANNUAL CONSUMPTION OF ZOSTERA BY WATERFOWL

Using BMR and DEE in relation to body mass of the waterfowl to estimate macrophyte consumption introduces considerable sources of error. We estimated daily consumption rates of mute swans ranging from 535 g to 682 g dryweight day^{-1} *Zostera*. Mathiasson (1973) feed captive moulting mute swans ad libitum and found they consumed an average of 3.66 kg fresh weight of *Zostera marina*, equating to 586 g dryweight day^{-1} (84% water in *Zostera* samples; Clausen III). Hence our estimates for daily *Zostera* consumption by mute swans seem reliable. Equivalent data for coot are not available, hence we can not evaluate the reliability of those estimated by us.

Waterfowl consumed an estimated 12% of the annual *Zostera marina* production in Kertinge Nor, with a range from a conservative estimate of 8% (high *Zostera* production and low consumption due to conservative DEE estimate) to a liberal estimate of 21% (*vice versa*). The heavily eutrophicated nature of the estuary suggests that *Zostera* production is low (Sand-Jensen & Borum 1991), *i.e.* the proportional consumption estimate is more likely to be above 12% than below. An annual consumption estimate of 12% is considerably higher that those previously published from submerged *Zostera marina* stands, with less than 4% consumed (Thayer *et al.* 1984, Nienhuis & Groenendijk 1986), and approaching estimates from *Ruppia* and/or *Potamogeton* dominated communities (15-50%, Kiørboe 1980, Verhoeven 1980, Jensen 1986, Mitchell 1989).

Obviously, if *Zostera* production is low and density of herbivorous waterfowl high, the proportion consumed will be high. To illustrate this we can compare the situation at Kertinge Nor with that of Nibe Bredning, one of the most important staging areas for waterfowl in Denmark, supporting one of the largest Danish *Zostera* beds (44.6 km^2). In Kertinge Nor 40,150 swandays and 224,000 cootdays were spent on the 3.4 km^2 *Zostera* bed, equivalent to 11,800 swandays km^{-2} and 65,800 cootdays km^{-2} of *Zostera* bed.

Madsen *et al.* (1992a, 1992b) conducted an intensive study of waterfowl use of Nibe Bredning in relation to establishment of huntingfree reserves, with intensive counts of waterfowl during 1985-91, with counts throughout the year in 1985-87, and in autumn/winter (the hunting season) in 1988-91. If we assume that bird utilisation in spring was unaffected by the introduced non-hunting scenario in autumn, *i.e.* birddays from springs 1985-87 could be combined with birddays from autumn in 1988-91, an annual waterfowl use in 1991 of 340,000 swandays (mute swans, whooper swan *Cygnus cycnus* and Bewick's swan *Cygnus colombianus bewickii*), c. 1,500,000 wigeon *Anas penelope*-days and c. 275,000 cootdays (Madsen *et al.* 1992a) can be estimated. If we assume that all swans and wigeon fed on *Zostera* (wigeon is an obligate herbivore, and similar sized to coot; Cramp & Simmons 1977), and 75% of coot fed on *Zostera* (*Zostera* in believed to be of higher importance to feeding coot in Nibe Bredning than in Kertinge Nor, J. Madsen personal communication), an estimated 7,600 swandays km^{-2} and 38,200 coot/wigeondays km^{-2} of *Zostera* bed were spent thers.

Thus, herbivorous waterfowl density in Kertinge Nor in comparison with Nibe Bredning appeared to at least a factor two higher than that found in 1991. Peak above-ground biomass of *Zostera marina* in Nibe Bredning in 1991 and 1992 ranged from 160 to 210 g m^{-2} (P. Clausen, unpublished data), suggesting a production at least three times higher than that found in Kertinge Nor. In combination these two figures suggest that waterfowl only may have consumed:

$$\frac{0.5\times(\textit{waterfowldensity})\times 12\%(\textit{consumption})}{3\times(\textit{Zosteraproduction})}=2\%$$

of the annual *Zostera* production in Nibe Bredning in 1991, and this would partly explain why exclosure experiments conducted in Nibe Bredning during 1991/92 failed to find evidence of grazing impact on *Zostera* (P. Clausen unpublished data).

Another important factor, in determining the proportion of *Zostera* production consumed, is water depth in the areas used by waterfowl. Kertinge Nor is relatively shallow and much *Zostera* expectedly can be consumed. Most herbivorous waterfowl feed by submerging their necks or up-ending, relatively few by diving (only coot and pochard *Aythya ferina* in western Europe, Cramp & Simmons 1977, 1980). Among non-diving waterfowl, swans reach c. 100 cm when up-ending (Madsen *et al*. VII), brent geese 40 cm (Clausen I), and wigeon even less due to their smaller size. Water depth thus limits access to feeding on *Zostera*, even though large amounts of detached *Zostera* will be available after autumn and winter storms, where it floats on the surface until washed onto beaches or falls to decompose in deeper water. This constraint on access to feeding on *Zostera* must have been one important parameter in determining the low proportion consumed in Lake Grevelingen (3.7% Nienhuis & Groenendijk 1986). There *Zostera* grew down to 4 m, and even though highest above-ground biomass occurred at depths of 1.0 to 1.5 m, an average plant length of 40-50 cm in this depth range (Nienhuis & de Bree 1980) would prevent all waterfowl except swans from exploting *Zostera*, and even for swans only half of the biomass would be available (see Clausen I). Most biomass below 1.5 m would be unavailable for all birds in Lake Grevelingen, as already pointed out by Jacobs *et al.* (1981). Water depth can also explain the generally higher proportional consumption in

Ruppia dominated seagrass communities, as these generally occur at lower depth than Zostera marina beds.

POSSIBLE INFLUENCE OF WATERFOWL ON ZOSTERA BIOMASS DEVELOPMENT

The majority of waterfowl grazing on *Zostera* took place over autumn and winter 1991/92, which is the period of lowest *Zostera* biomass (Fig. 5) and production (Wium-Andersen & Borum 1984, Pedersen & Borum 1993, Olesen & Sand-Jensen 1994). Grazing on the overwintering biomass will cause a reduced standing stock at the onset of the following growth season, and may thus cause a reduction in eelgrass biomass and production of the following year.

During the summer period of maximum *Zostera* biomass (Fig. 5) and production (Sand-Jensen 1975, Wium-Andersen & Borum 1984, Olesen og Sand-Jensen 1994), waterfowl density was low and consequently the relative impact of waterfowl grazing on eelgrass during summer was less than during winter.

We observed a difference in timing of peak biomass of Zostera between shallow areas (June) and deeper areas (August) of Kertinge Nor in 1992. Moulting mute swans are known to be able to partly graze down Zostera marina stands (Madsen et al. VII), and in 1992 there was an increased use of Kertinge Nor as a moulting site compared to 1991. Swans can reach most Zostera growing in the 1.0 to 1.5 depth range, but Zostera growing at 2.0 to 2.5 m depth is out of their reach. We suggest that grazing by the moulting mute swan population on the shallow water Zostera beds may have contributed to the difference in timing of peak biomass between shallow and deeper areas.

Acknowledgements

This study was made as a part of our two PhD studies, partly funded by the Danish Research Academy. The investigation in Kertinge Nor was conducted as part of the Danish environmental research programme 'Hav90' and financed by the Danish National Agency of Environmental Protection. Jesper Madsen and Peter Bondo Christensen acted as our respective supervisors. Tony Fox read the first draft of the manuscript. Divers from Bio/consult and the County Council of Funen took the vegetation samples, and Marlene Venø Jessen helped with sorting them out. Kurt Due Johansen made half of the bird counts. Without the effort invested by these people, the outcome of this paper would not have been the same, thanks to all!

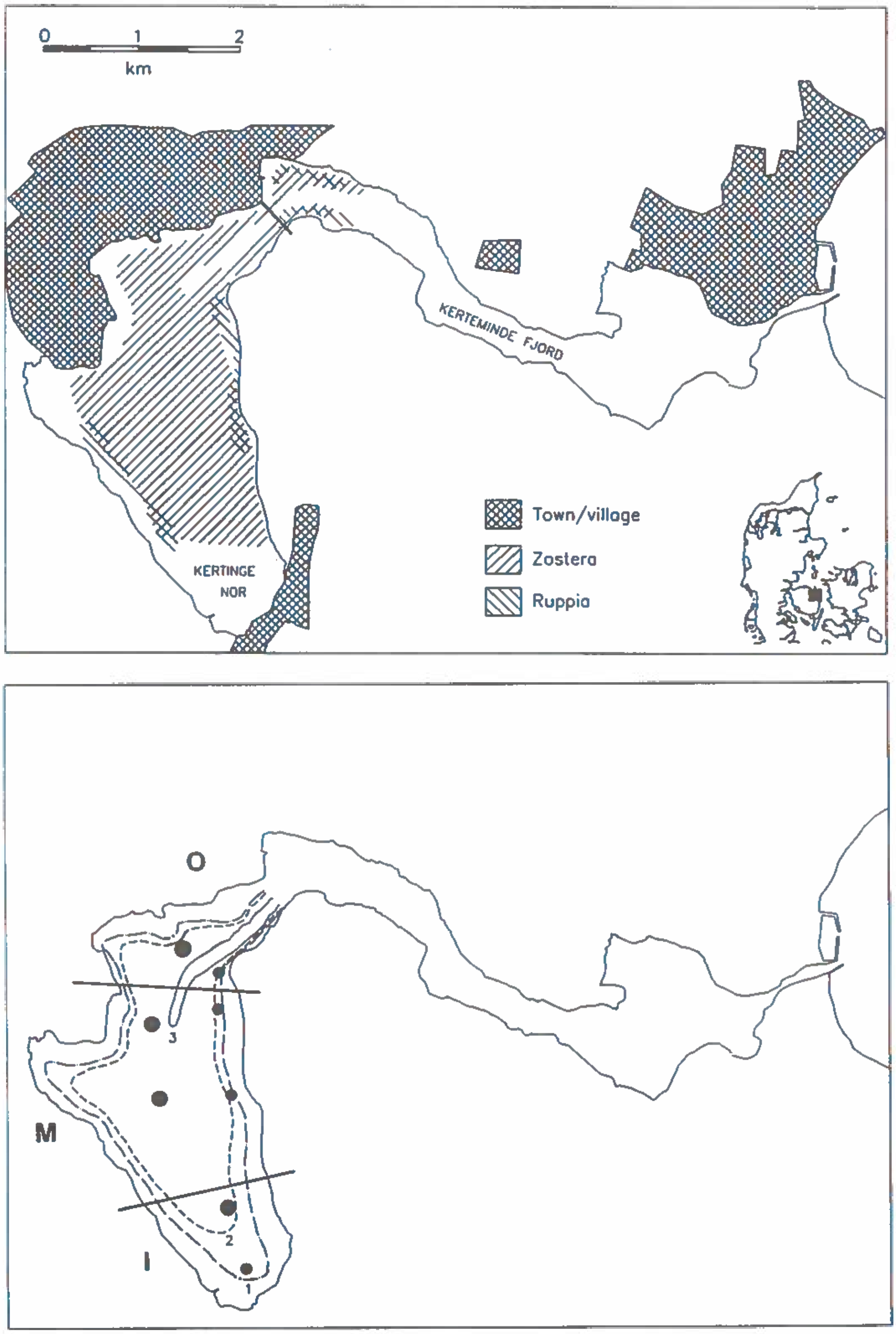

Fig. 1. The upper map gives Zostera marina and Ruppia spp. distribution in Kertinge Nor/Kerteminde Fjord estuary, with a map of Denmark inserted. The lower depicts stations used when sampling Zostera marina in Kertinge Nor; small dots refers to shallow (1.0-1.5 m depth) and large to deep (2.0-2.5 m depth) sample stations. Three sections in Kertinge Nor (I=inner, M=mid, O=outer) are separated by lines, and the 1, 2 and 3 meter depth contours indicated.

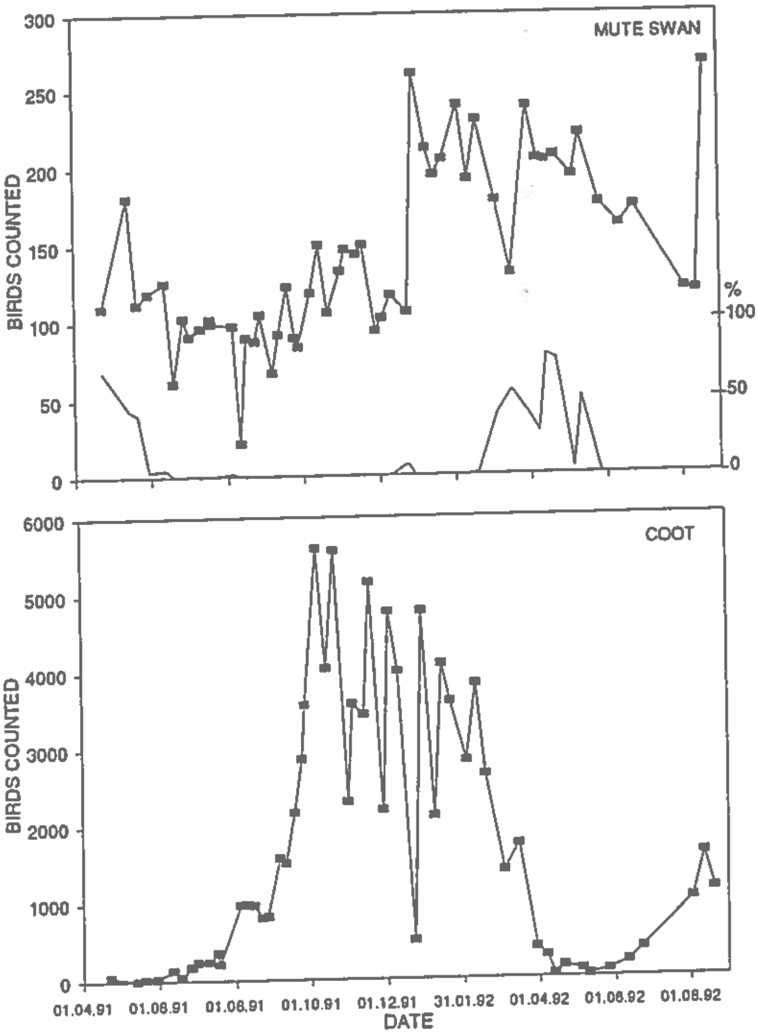

Fig. 2. Numbers of mute swans and coot counted in Kertinge Nor/Kerteminde Fjord estuary from April 1991 to August 1992. The thin line in the lower part of the mute swan diagram indicate the proportion of counted mute swans that fed on arable land adjacent to the estuary.

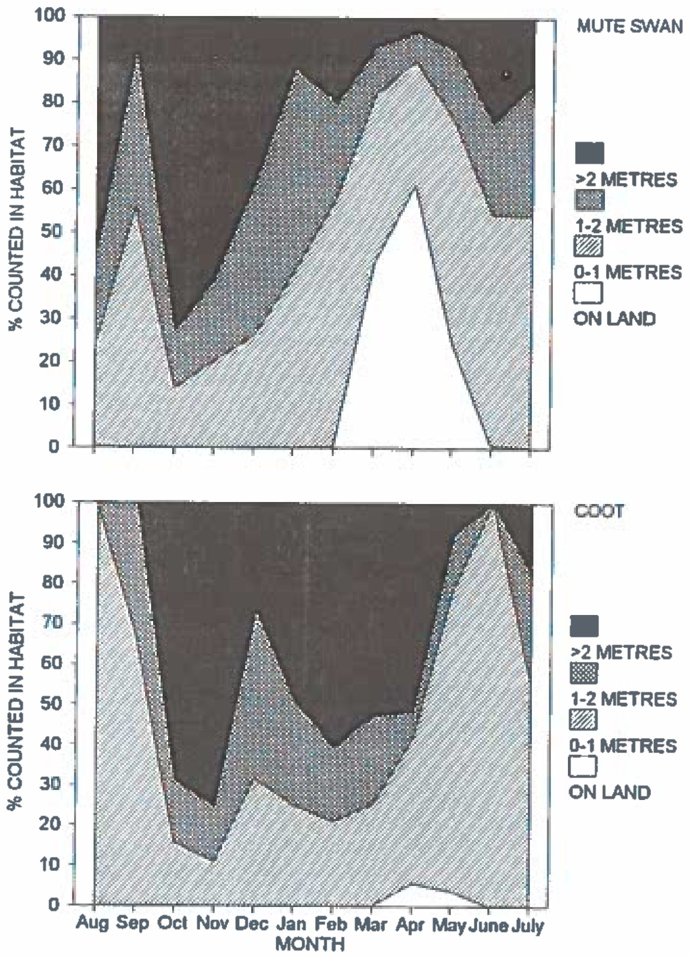

Fig. 3. Depth distribution of feeding mute swans and coot in Kertinge Nor/Kerteminde Fjord estuary from August 1991 to July 1992.

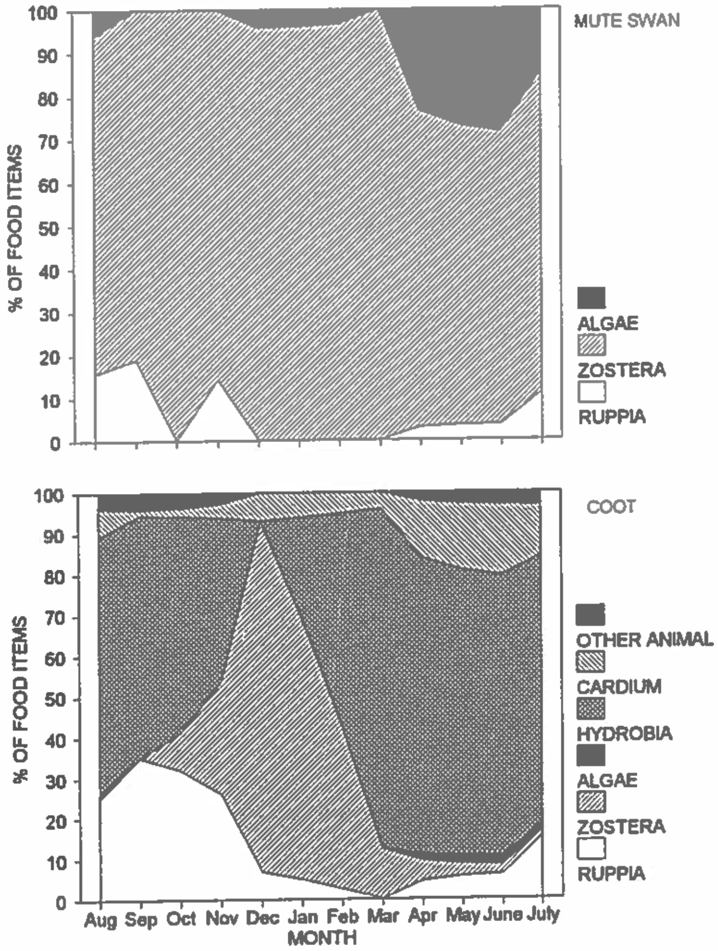

Fig. 4. Food choice of feeding mute swans and coot in Kertinge Nor/Kerteminde Fjord estuary from August 1991 to July 1992.

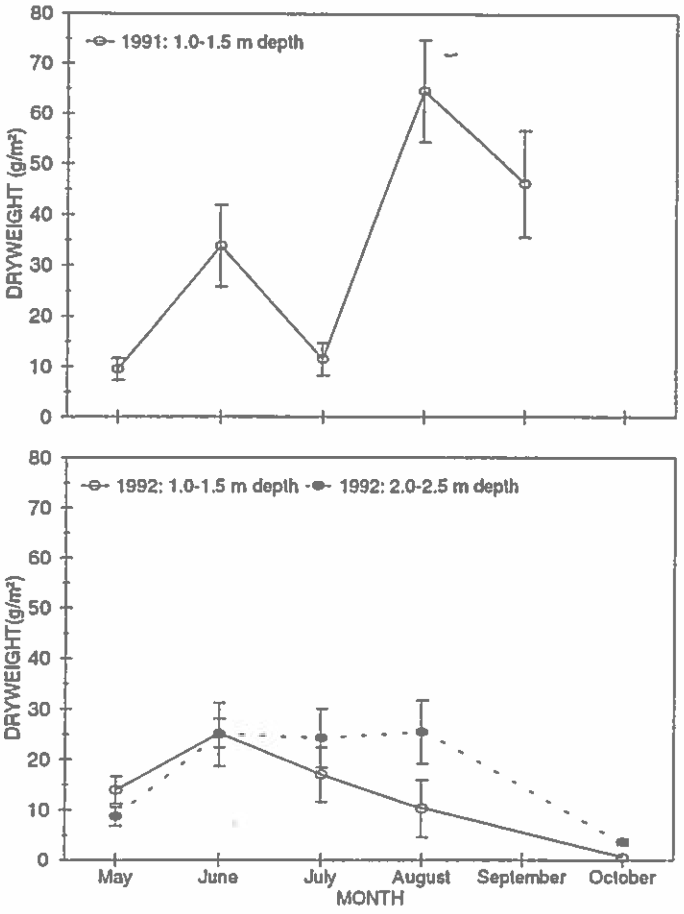

Fig. 5. Above-ground biomass development of Zostera marina in Kertinge Nor 1991-92, given as mean ± SE-bars.

An annual budget of Zostera consumption by waterfowl

Table 1. Estimates of annual Zostera production and consumption by waterfowl in Kertinge Nor estuary 1991-92.

Annual Zostera consumption by waterfowl (metric tonnes dryweight)	Maximum consumption estimate (method 1)	Minimum consumption estimate (method 2)	Mean consumption estimate
Mute swans: Daily energy expenditure (DEE)(kJ day^{-1})	4501	3536	
Daily consumption of Zostera (g dryweight)	682.0	535.8	
Birddays spent feeding on Zostera (days/year)	40153	40153	
Annual Zostera consumption by mute swans (tonnes)	27.4	21.5	24.4
Coot: Daily energy expenditure (DEE)(kJ day^{-1})	698	734	
Daily consumption of Zostera (g dryweight)	115.0	120.9	
Birddays spent feeding on Zostera (days/year)	224025	224025	
Annual Zostera consumption by coot (tonnes)	25.8	27.1	26.4
Total annual Zostera consumption by waterfowl	53.1	48.6	50.9
Zostera peak biomass and annual production (metric tonnes dryweight)	Minimum production estimate (2.4xpeak biomass)	Maximum production estimate (5.9xpeak biomass)	Average production estimate (4.0xpeak biomass)
1991 Peak biomass (105.4 tonnes)			
Annual production estimate (tonnes)	253.0	621.9	421.6
1992 Peak biomass (79.5 tonnes)			
Annual production estimate (tonnes)	190.8	469.1	318.8
Proportion of annual Zostera production consumed by waterfowl	Maximum estimate	Minimum estimate	Average estimate
1991	21%	8%	12%
1992	28%	10%	16%

Table 2. Estimates of Zostera consumption by moulting mute swans in Kertinge Nor estuary, June-August, 1991-92.

Zostera consumption by moulting mute swans (metric tonnes dryweight)	Maximum consumption estimate (method 1)	Minimum consumption estimate (method 2)	Mean consumption estimate
Mute swans: Daily energy expenditure (DEE)(kJ day^{-1})	4501	3536	
Daily consumption of Zostera (g dryweight)	682.0	535.8	
1991 Birddays spent feeding on Zostera (days/summer)	6192	6192	
Zostera consumption by mute swans (tonnes/summer)	4.2	3.3	3.8
1992 Birddays spent feeding on Zostera (days/summer)	11247	11247	
Zostera consumption by mute swans (tonnes/summer)	7.7	6.0	6.8

Paper VII

Base-line Investigations of Moulting Mute Swans on Saltholm, June-October 1993

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Udvidet resumé af rapport til Øresundskonsortiet 12 november 1993 (Madsen *et al.* 1993). Rapporten er ikke umiddelbart offentligt tilgængelig, men kan evt. fås ved henvendelse til Øresundskonsortiet / Extended abstract of the full report to the Sound Link Company, 12. November 1993 (Madsen *et al.* 1993). The report is not subject to public access, but may be obtained from the Sound Link Company.

Extended abstract

As part of the base-line bird studies related to the planned construction of a Fixed Link between Copenhagen and Malmö an investigation was carried out on the moulting Mute Swans *Cygnus olor* at Saltholm.

Mumbers and distribution of swans were assessed by monthly aerial counts in the entire Øresund region, weekly aerial photographic counts of the island of Saltholm and its associated inshore waters and ground counts of the Saltholm area. Mute Swans aggregated to moult flight feathers in the shallow inshore waters around Saltholm, with most birds arriving in late June. The majority of swans started to moult in early July, but some birds commenced moulting into August. The moult period lasted 6-7 weeks, so flightless swans occurred until late September. Peak numbers counted were 2,700 (July), but because of the turnover of birds it is estimated that between 3,400 and 3,500 swans moulted at Saltholm in 1993. Most birds left the island as soon as they regained powers of flight.

The swans feed exclusively on the submerged inshore vegetation. At water levels below 20-30 cm DNN they grazed predominantly the leaves of *Zostera marina*, but at deeper water levels the *Zostera* became unavailable and the swans moved closer to the coast exploiting primarily *Ruppia* and *Potamogeton* (Fig. 1 and 2).

In early July the moulting swans spent on average 45% of the daylight hours feeding; swimming, resting and preening took up the majority of the remaining time. During the night most swans were inactive. The moulting site around Saltholm is relatively little disturbed by human activities. Regular helicopter flights had little effects on time budgets and, even when disturbed by the close approach of fishing boats, the swans showed low level avoidance behaviour and quickly resumed their former activities.

Exclosure plots established in *Zostera* and *Ruppia-Potamogeton* communities showed that the moulting swans had a grazing impact on shoot lengths of *Zostera* (Fig. 3 and 4)(but not on biomass; Fig. 3) and above-ground biomass of *Ruppia-Potamogeton* (Fig. 5). A model was developed to assess the effects of water depths on the predicted availability and profitability of different food items. This model predicted that the swans should graze *Zostera* until water levels exceeded 30 cm DNN and then shift to *Ruppia-Potamogeton* (Fig. 6). Furthermore, as the season progressed, that the shift should take place at increasingly lower water levels (Fig. 7). The predictions fitted well with the observed patterns of swan feeding and distribution.

As the moulting period progressed, foraging activity declined and feeding swans up-ended increasingly to reach the *Zostera* vegetation. During the moulting period defaecation rates declined, as did the condition of swans (assessed by scoring abdominal profiles of individual birds at known stages of moult). Overall, these observations indicate that food became less available during moult. Until a full assessment of the between-year differences in water level dynamics in Øresund can be carried out, it is not possible to determine whether this situation would prevail in every moulting season.

Further analysis, integrating the precise foraging distribution of the swans to the distribution,

abundance and availability of their various food resources needs to be completed before a full evaluation can be made of their feeding ecology during moult.

Moulting Mute Swans use the shallow-waters around Saltholm because they provide a combination of low disturbance rates and abundant food resources. The swans graze a considerable part of the vegetation which is available to them and there are reasons to suggest that numbers are close to carrying capacity of the resources. Because of the expected effects of the release of plumes of disturbed sediment into the water column and the physical deposition of such suspended material as a consequence of the Fixed Link construction work, the food intake of swans may be affected as a result of modifications to their feeding resource. However, since the swans show relatively low levels of response to disturbance, it is suggested that regulated disruptive activities resulting from the construction work is less likely to severely affect the moulting aggregations than changes in feeding resources.

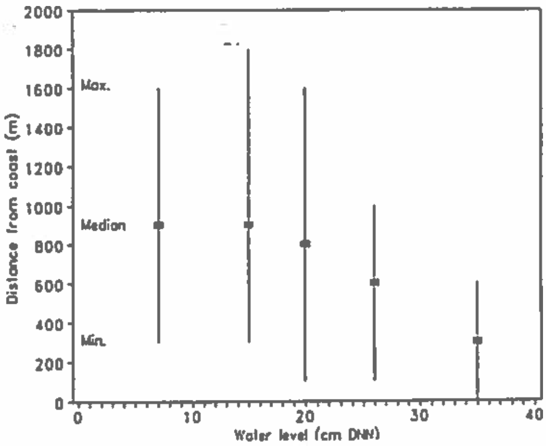

Fig. 1. Relationship between water levels and distribution of feeding flocks of moulting Mute Swans east of Saltholm, 7-9 July 1993. The median is the estimated median distance of the centres of the flocks, the maximum is the end of a flock farthest from land, and the minimum the end of a flock closest to land.

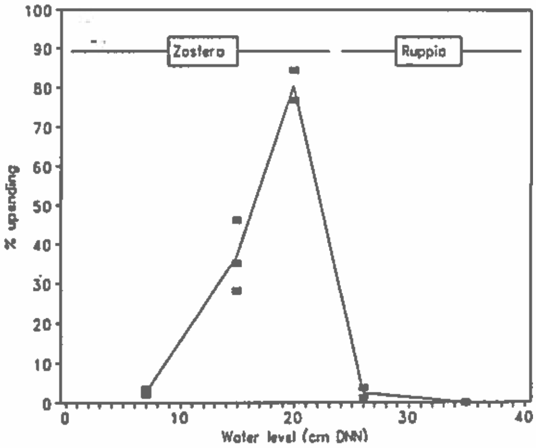

Fig. 2. Relationship between water levels and the relative use of upending as foraging mode by moulting Mute Swans, east of Saltholm, 7-9 July 1993. Above the graph is inserted within what range of water levels *Zostera* and *Ruppia-Potamogeton*, respectively are used.

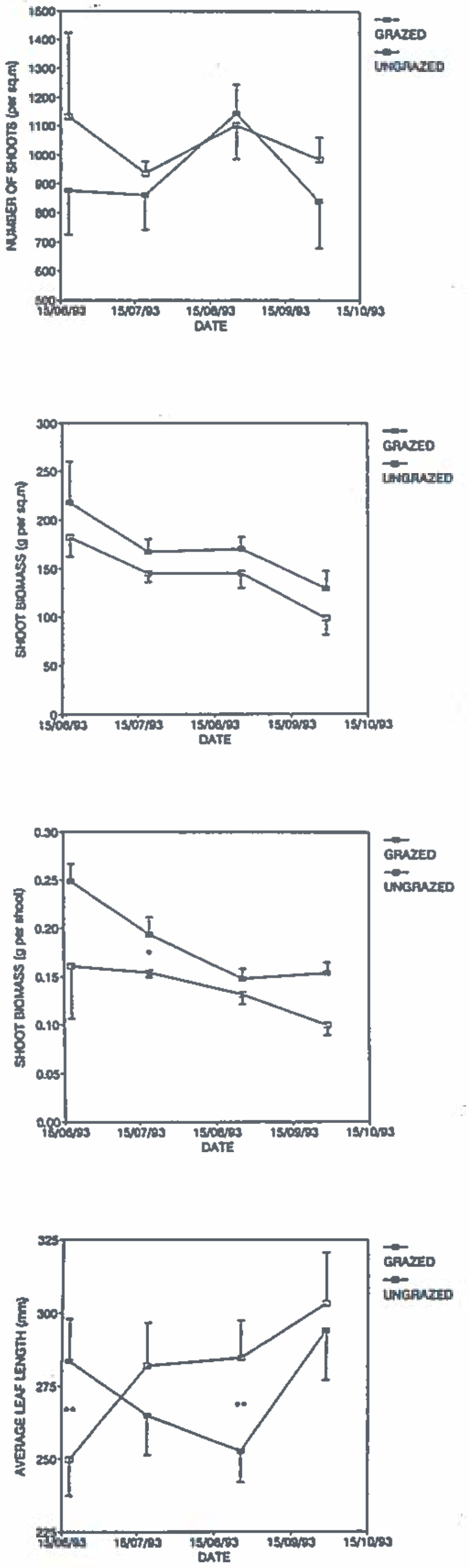

Fig. 3. Changes in the number of shoots, biomass per m^2, shoot biomass, and average leaf length of *Zostera marina* in grazed and ungrazed plots, June-September, 1993. The figure shows the development in average values, with bars giving SE (for the number of shoot and biomass values) and 95% confidence limits (for leaf length).

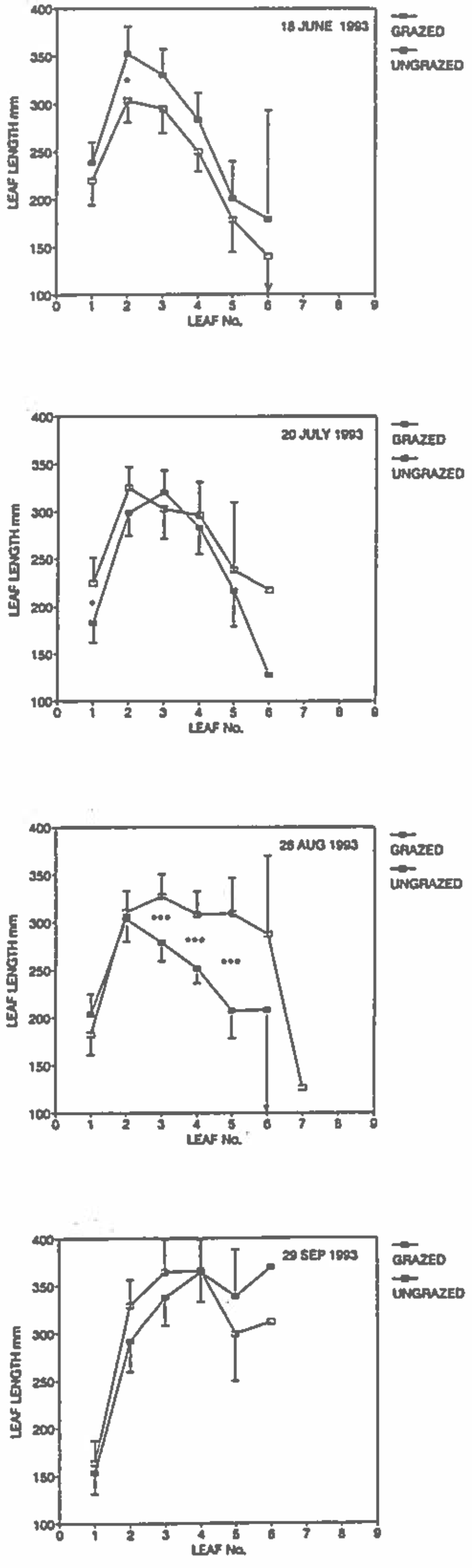

Fig. 4. Average leaf length of *Zostera* leaves of different age (the leaves were classified as leaf 1 = the youngest, leaf 2 = the second youngest leave and so on), June-September, 1993. The figure shows average values, with 95% confidence limit bars, for grazed and ungrazed plots. Significantly different means are marked by asteriks, * $P<0.05$, ** $p<0.01$, *** $P<0.001$ (Student's t-test for samples with equal variances, Welch's approximate t-test for samples with unequal variances).

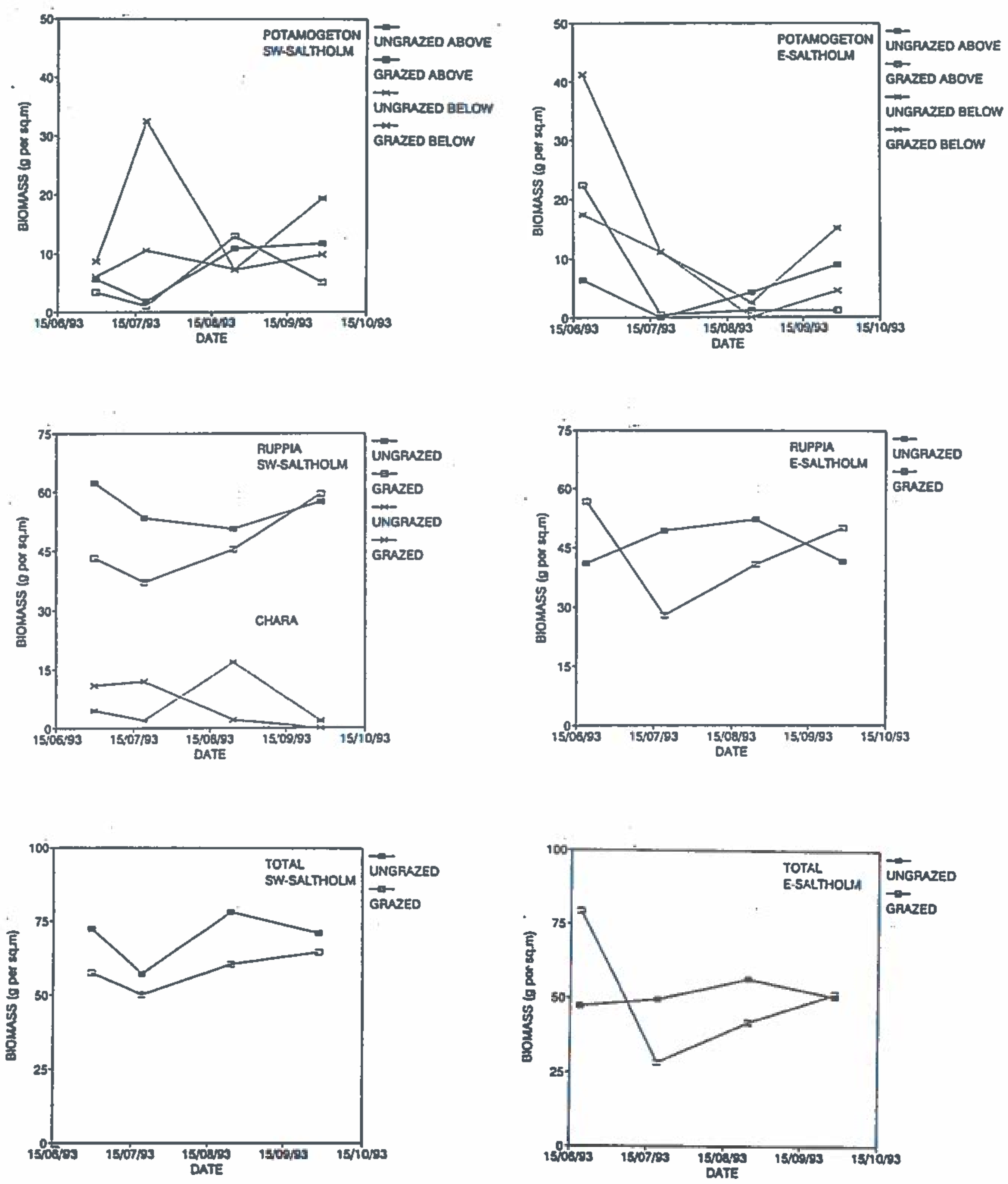

Fig. 5. Development of *Potamogeton*, *Ruppia*, *Chara*, and total biomass in grazed and ungrazed plots SW and E of Saltholm, June-September, 1993. The figures show the change in mean values.

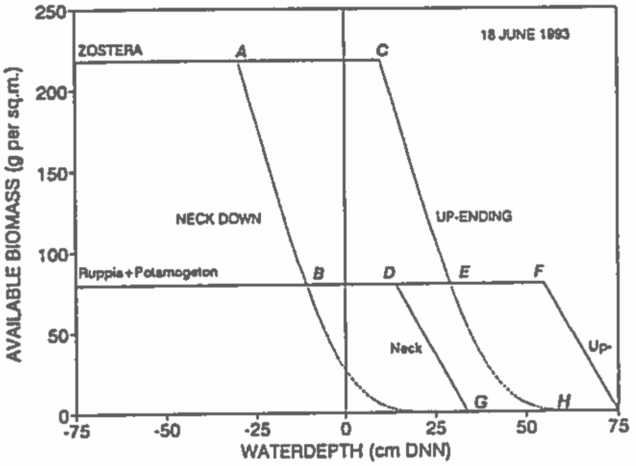

Fig. 6. A model used to estimate available biomass of *Zostera* and *Ruppia+Potamogeton* east of Saltholm, June 18 1993, in relation to the water level, in cm DNN. Availability curves are based on biomass samples in the grazed plots, and on the assumption that a Mute Swan reaches 100 cm below surface by up-ending, and 60 cm below by surmerging their neck ('neck down'). A and C are threshold points where the biomass of *Zostera* will gradually be reduced by increasing water levels for swans that feed by 'neck down' and up-ending, respectively; B and D likewise for *Ruppia-Potamogeton* feeding swans. B and E gives 'switch' points, where the swans should switch from feeding on *Zostera* to *Ruppia+Potamogeton*, if availability of biomass alone determines their switching. G gives the water level where no more food is available for swans that feed by 'neck down' in the *Ruppia+Potamogeton area*, H likewise for up-ending *Zostera* feeding swans.

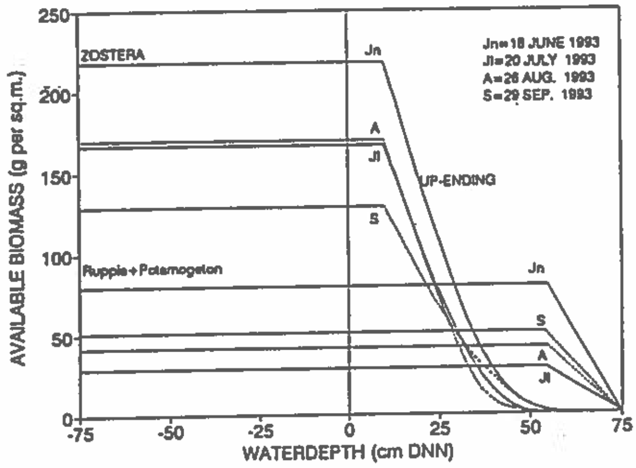

Fig. 7. Modelling of available biomasses of *Zostera* and *Ruppia+Potamogeton* to swans that feed by up-ending in relation to the water level, June-September 1993.

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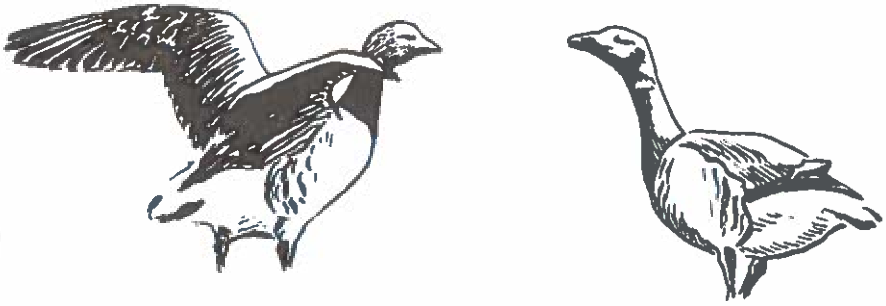

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