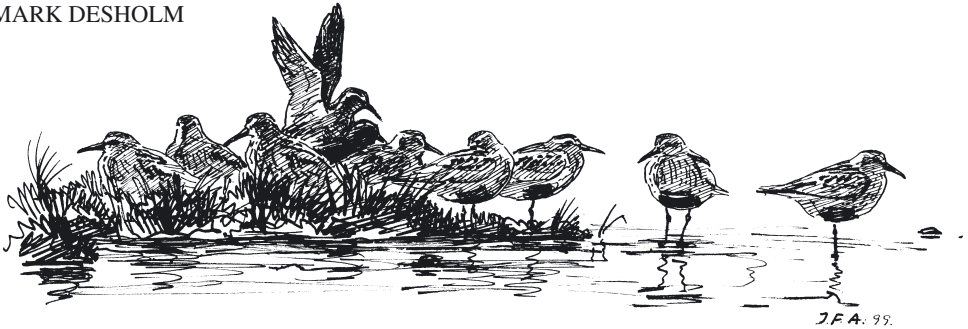# The relationship between the number of staging Dunlins *Calidris alpina* and the abundance of their benthic prey: the effect of severe winters

MARK DESHOLM

(Med et dansk resumé: Sammenhængen mellem antallet af rastende Almindelige Ryler og tætheden af deres byttedyr på Tipperne: effekten af hårde vintre)

Introduction

Studies on the relationship between shorebirds and their benthic prey organisms have been widely performed (Bengtson & Svensson 1968, Wolff 1969, Goss-Custard 1970, 1977b, Schneider & Harrington 1981, Wilson 1990, Colwell & Landrum 1993, Piersma et al. 1994, Meire 1996, and references therein), but unfortunately most papers deal with spatial variation in density only, neglecting the temporal aspect. However, a ten-year study on Oystercatchers *Haematopus ostralegus* showed that bird density in December was determined by the between years abundance of harvestable prey (Zwarts et al. 1996).

The present work arose from an attempt to identify factors influencing the number of staging Dunlins *Calidris alpina* during spring and autumn migration. What happens from year to year at the same staging area if e.g. the winter climate is highly variable? Near-extinctions of the populations of the amphipod *Corophium volutator* and the ragworm *Nereis diversicolor* (syn. *Hediste diversicolor*) have been reported after severe winters (Curtis & Smyth 1982). Such events are likely to influence the presence of Dunlins that commonly feed on these invertebrates (Meltofte 1987). Accordingly, it is asked whether the presence of staging Dunlins during spring and fall migration is correlated with the availability of prey organisms between years.

To answer these questions, data from ten years of weather recordings and from the wader and infaunal invertebrate monitoring at Tipperne, Denmark, were analysed. Additionally, an infaunal sampling program was executed between April and November 1996 after a severe winter, enabling a mapping of the process of recolonization of prey organisms.

Study area and methods

The study was performed at the scientific reserve Tipperne (55°53'N, 08°14'E), in the southern part of Ringkøbing Fjord, Western Jutland, Denmark (Fig. 1). The area is composed of reed swamps and meadows surrounded by mudflats and is exposed to non-tidal brackish (5-15‰) water. The mudflats at Tipperne are considered an important staging area for shorebirds both during spring and autumn migration (Meltofte 1987, Desholm 1998), and is known to support an appreciable population of invertebrates (Petersen 1981). Sediments of the area range from fine sand to clay.

Mean temperatures recorded at c. 600 national weather stations dispersed all over Denmark were obtained from Rosenørn & Lindhart (1996).

Since 1972 a standardized counting schedule has been followed at the Tipperne reserve, where birds present are recorded at least once in each international 5-day period. From these data the
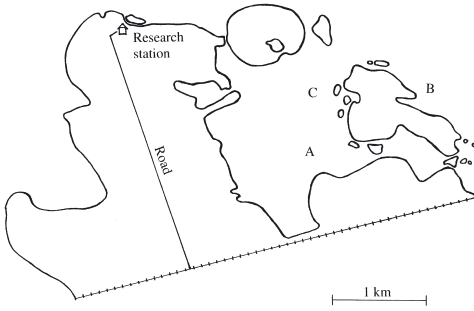
Fig. 1. Map showing the Tipperne reserve, the location of the research station, and the three invertebrate sampling sites (A and B: 1987-1996; C: recolonization monitoring during 1996).
Kort over Tipperreservatet med feltstationen og prøvestationerne for bunddyr angivet (A og B: bunddyrsmonitering 1987-96; C: prøvetagningssted for rekoloniseringsdata 1996).

number of bird-days between two counts was calculated as the average number of Dunlins observed during two counts multiplied by the number of days between them. Bird-days were then summed to obtain the total number of bird-days during spring (15 February - 4 June) and autumn (15 June - 1 December).

During the years 1987-1996 (except autumn 1995), the infaunal invertebrates on the mudflats have been monitored once each spring (between 15 March and 1 April) and autumn (between 15 September and 1 October) at two stations (A and B; Fig. 1) situated in the core area for foraging shorebirds in general and for Dunlins in particular (Petersen 1977, Meltofte 1987, own unpubl. data). The invertebrates were sampled by a corer (10 cm diameter) to a depth of 20 cm. Five sediment cores were taken at each of the two stations within an area of 5×5 m, and sieved through a 600 µm mesh. The invertebrates were sorted to species, counted, and oven dried at 100°C for 24 hours before dry mass determination.

An additional station (C) was placed north of station A (Fig. 1). Here three sediment cores were taken on 15 April, 17 May, 18 June, 15 July, 6 and 28 August, 17 September, 7 October, and 16 November 1996. The samples were sieved through a 500 µm mesh, and retained animals were preserved in 4% buffered formalin for later analysis in the laboratory. The invertebrates were sorted to species, counted, and measured using an eyepiece micrometer mounted on a binocular microscope. For generation of size-frequency histograms, different biometric mesurements were used. The length of *C. volutator* was measured from the tip

of the rostrum to the end of the telson, the width of *N. diversicolor* and *Tubificoides benedii* was measured at segment number 10, and the maximum diameter of the operculum was measured on the gastropods *Hydrobia ventrosa* and *Potamopyrgus jenkinsi*. These abundant invertebrates are all well known prey species for Dunlins (Evans et al. 1979, Petersen 1981, Worrall 1984, Durell & Kelly 1990). All other invertebrates occurred in numbers at least one order of magnitude lower than these species and are not treated in this study. The measurements used are all assumed to correlate with the size of the respective organisms (Boates & Smith 1979, Pienkowski et al. 1984). Finally, the invertebrates were oven dried at 100°C for 24 hours for dry mass determination.

In order to assess the reproductive stage of the *T. benedii* the number of cocoons in the sediment was recorded for each sample.

Statistical analyses were carried out using SPSS for Windows (Norusis 1993). Spearman Rank Correlation Coefficients and their P-values were calculated to test for apparent correlations between variables. Before one-way analysis of variance (ANOVA) was used to test for temporal differences in the density of a species between sampling periods, homogeneity of variances was verified using Levene's test (0.05 level of significance). In cases where homogeneity could not be verified, the non-parametric Kruskal-Wallis test was applied. The Tukey q-test was used for multiple comparisons between sampling dates, and the Mann-Whitney U-test was applied when comparing means from non-parametric data.

Results
Relationship between Dunlins, prey and winter severity
Two severe winters occurred during the study period (1986/87 and 1995/96), showing an overall mean temperature in Denmark for January-March of -1.1°C and -1.7°C, respectively. The overall mean temperature for the same period during the other winters (1987/88 – 1994/95) was 3.1°C (range 1.8°C - 4.7°C).

When analysed on a temporal scale (1987-1996), the mean winter (January-March) temperature could explain most of the variation in the biomass (g/m²) of infaunal invertebrates during spring on the mudflats at Tipperne (Spearman Rank, r_s=0.67, P=0.033).

The overall biomass of infaunal prey during the springs of 1987-1996 could explain most of the

variation in abundance of Dunlins (Spearman Rank, r_S=0.72, P=0.019, Fig. 2). Most of the variation in Dunlin abundance was attributable to variation in the abundance of *N. diversicolor* (Spearman Rank, r_S=0.78, P=0.008) (Table 1). In contrast, no relationship between the abundance of Dunlins and the overall biomass of prey organisms was observed for the autumns (Spearman Rank, r_S=0.15, P=0.70) (Fig. 2), nor did any single group of invertebrates show a significant correlation with the abundance of Dunlins during fall migration (all P>0.24) (Table 1).

The mean biomass of infaunal prey was significantly higher in autumns (13.2 g/m²) than in springs (7.1 g/m²) (Mann-Whitney Test, U=16.0, P=0.017).

Recolonization by invertebrates
Corophium volutator. The overall density of *C. volutator* changed significantly during 1996 (one-

way ANOVA, $F_{8,18}$=34.97, P<0.001). A population of *C. volutator* with a unimodal size distribution (2-7 mm) recolonized the mudflats between 17 May and 18 June (Fig. 3, Fig. 4a). The density of individuals did not change significantly between 18 June and 15 July (Tukey q-test, P=1.0), but the size distribution moved to the right and became asymmetric. On 6 August, a significant increase in density to more than 100 000 individuals/m² was recorded (Tukey q-test, P<0.001, Fig. 3), with 80% of the population being smaller than 2 mm (Fig. 4a). The mean density during the rest of the year did not vary (Tukey q-test, P>0.81), although the size distribution again became unimodal.

Combining the size distribution and the density estimates gives the density (individuals/m²) of potential amphipod prey (individuals ≥4 mm in length, see discussion): 854 on 18 June, 4412 on 15 July, 5154 on 6 August, 11 561 on 28 August, 14 472 on 17 September, 17 967 on 7 October, and 11 175 on 16 November 1996.

The biomass of *C. volutator* (all individuals combined) also changed significantly during 1996 (Fig. 3; one-way ANOVA, $F_{8,18}$=32.84, P<0.001), the first significant increase being between 18 June and 15 July (Tukey q-test, P=0.006). The peak biomass of 4.07 g/m² (SD=0.78) on 6 August, coinciding with the appearance of juveniles, represents a highly significant increase (Tukey q-test, P<0.001). The biomass had dropped to 2.71 g/m² (SD=0.60) on 28 August (Tukey q-test, P=0.032) and stayed at this level during the remaining fall migration period (Tukey q-test, P>0.44, range 1.90-3.07 g/m²).

Nereis diversicolor. The density of *N. diversicolor* also changed significantly during 1996 (one-way ANOVA, $F_{8,18}$=8.62, P<0.001). It was absent from the April and May samples, but was recorded in densities between 1400 and 3225 individuals/m² from 18 June onwards, with no significant changes between sampling events (Tukey q-test, P>0.064, Fig. 3). The first-appearing individuals on 18 June all belonged to the smaller size classes (<1.5 mm in width, Fig. 4b). No obvious change in the shape of their size distribution was detected during autumn, but the individuals became gradually larger with time.

The biomass of *H. diversicolor* also showed significant changes (one-way ANOVA, $F_{8,18}$=19.88, P<0.001). From 18 June onwards a steady increase was observed, reaching a peak of 20.4 g/m² (SD=5.3) on 7 October. On 16 November, the biomass had decreased to 10.7 g/m² (SD=2.6, Tukey q-test, P<0.007, Fig. 3).
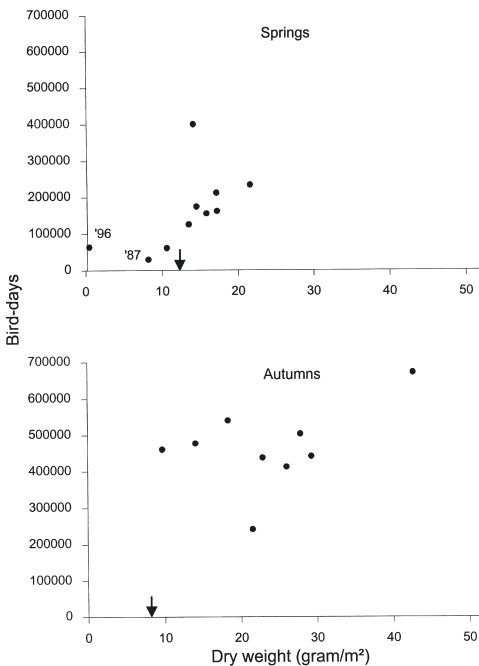
Fig. 2. The relationsship between the mean biomass of invertebrates and the number of bird-days for the years 1987-1996. The two springs following severe winters are marked by the corresponding year. Arrows indicate threshold densities (see text).
Sammenhængen mellem invertebratbiomassen og antallet af fugledage forår og efterår i årene 1987-96. De to forår, der efterfulgte hårde vintre, er markeret med årstal. Grænseværdierne (se teksten) er markeret med pile.

Table 1. The monitoring data for Dunlins and invertebrates for the years 1987-1996. Bird-days are calculated for 110 and 170 days in spring and autumn, respectively. Mean abundance of invertebrates is given as gram dry weight m^{-2}. N.d.: *Nereis diversicolor*; C.v.: *Corophium volutator*; T.b.: *Tubificoides benedii*; Gast: the gastropods *Potomopyrgus jenkinsi* and *Hydrobia ventrosa*. r$_S$ and P values relate to Spearman Rank statistics between bird-days and invertebrate density.
Moniteringsdata for Almindelige Ryler og invertebrater for årene 1987-96. Gennemsnitstætheden af invertebrater er givet som gram tørvægt pr m². Antal fugledage er beregnet for perioder på henholdsvis 110 og 170 dage forår og efterår. N.d.: Nereis diversicolor; C.v.: Corophium volutator; T.b.: Tubificoides benedii; Gast: dyndsneglene Potomopyrgus jenkinsi og Hydrobia ventrosa. r$_S$- og P-værdier relaterer til Spearman Rang statistik mellem antal fugledage og bunddyrstætheden.

Year	Springs					Autumns				
	Bird-days	N.d.	C.v.	T.b.	Gast	Bird-days	N.d.	C.v.	T.b.	Gast
1987	29762	2.26	4.54	0.74	0.64	460816	4.09	4.72	0.94	0.00
1988	60957	4.32	5.89	0.04	0.35	241424	15.16	4.79	0.58	1.06
1989	155191	7.09	6.40	0.87	1.48	437513	14.56	2.46	0.65	5.29
1990	161968	9.82	2.98	0.98	3.45	477053	8.67	0.86	0.62	3.95
1991	125124	10.84	1.33	0.94	0.40	540153	10.33	2.89	0.56	4.60
1992	233854	16.84	4.27	0.50	0.03	441513	21.57	2.25	1.09	4.46
1993	174422	11.63	1.95	0.52	0.42	411968	19.12	3.77	1.14	2.07
1994	211895	15.62	1.11	0.38	0.05	503392	19.99	6.24	0.34	1.37
1995	400502	10.43	2.07	0.93	0.75	-	-	-	-	-
1996	64001	0.00	0.03	0.42	0.00	671334	20.43	2.42	2.48	17.50
r$_S$		0.78	-0.22	0.15	0.06		0.03	-0.23	-0.08	0.43
P		0.01	0.53	0.68	0.88		0.93	0.55	0.83	0.24

Tubificoides benedii. This species was present in all 1996-samples with densities varying between 5941 and 24360 individuals/m^2 (one-way ANOVA, $F_{8,18}$=4.79, P=0.003, Fig. 3). The density increased significantly from 11204 individuals/m^2 on 17 September to 24360 individuals/m^2 on 16 November (Tukey q-test, P<0.031), although no significant changes were observed between successive sampling events (Tukey q-test, P>0.29). From April to July at least 50% of the population consisted of larger individuals (width >0.36 mm), but from August onwards the distribution was skewed towards younger individuals (Fig. 4c).

A high cocoon density was recorded from 18 June to 6 August and from 7 October to 16 November (mean egg density 22460 m^{-2} and 16509 m^{-2}, respectively), with no significant changes between sampling events within each of these two periods (Tukey q-test, P>0.13) (Fig. 3).

No significant changes in dry weight per m^2 of *T. benedii* was found (Kruskal-Wallis test, KW=13.0, df=8, P=0.11). The biomass ranged between 0.99 and 2.54 g/m^2 during the entire year (Fig. 3).

Gastropods. The presence of gastropods was characterised by a low abundance in spring and summer samples (169-1018 individuals/m^2), and a slightly higher density during autumn (1740-4541 individuals/m^2) (Fig.3). No significant change in density between successive sampling events was recorded (Tukey q-test, P>0.07).

Interpretation of the size distribution must be done with care due to the low sample

size, especially during the first four sampling events. However, from 6 August onwards a small displacement towards larger individuals was recognisable (Fig. 4d).

The dry weight per m^2 of gastropods showed no significant temporal changes (one-way ANOVA, $F_{8,18}=2.48$, $P>0.052$), but peaked at 2.02 g/m^2 on 17 September (Fig. 3).

Discussion

The present study indicates that in springs following severe winters the densities of prey are below a threshold density (c. 12 g/m^2), at which the number of staging Dunlins at Tipperne are suppressed (Fig. 2). The fluctuating prey abundance around this threshold density results in a positive correlation during the springs between the number of staging Dunlins and the density of their benthic prey. During cold springs it may be energetically disadvantageous to feed at Tipperne if the invertebrate density fall below the threshold level (as descried by Evans et al. 1979), which may result in a relatively high turnover of staging Dunlins. In turn, this will result in a low maximum number of Dunlins and eventually in a low number of bird-days.

Moreover, variation in spring densities of Dunlins was positively correlated with the density of a single invertebrate species, *Nereis diversicolor* (Table 1), the same species found to correlate with Dunlins also at a spatial scale (Wolff 1969). It is therefore suggested that ragworms constitute the main prey for staging Dunlins at Tipperne during spring, in general agreement with previous reports showing *N. diversicolor* to be an important prey organism for Dunlins (Bengtson & Svensson 1968, Petersen 1981, Worrall 1984, Buchanan et al. 1985).

The low prey densities in springs following severe winters can be ascribed directly to winter mortality, as a significant positive correlation between prey abundance and mean winter temperature was recorded. Hence, as previously pointed out by Meltofte (1987), the occurrence of Dunlins at Tipperne during spring seems indirectly determined by the severity of the previous winter.

The lack of a significant relationship between birds and prey density during autumn suggests that the density of benthic prey always exceed a threshold density ($\leq$8 g/m^2, Fig. 2) above which the abundance of Dunlins is unaffected. Hence, in autumn the birds' rate of feeding and fat deposition
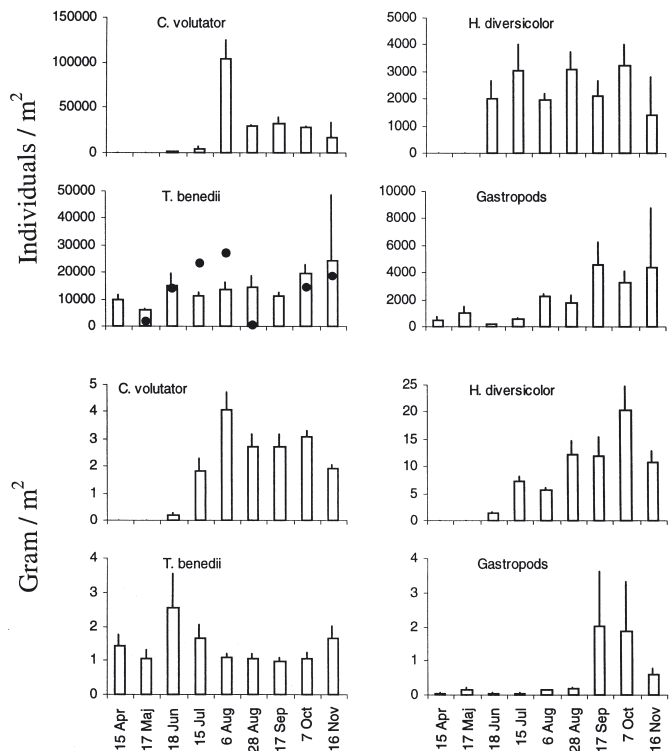

Fig. 3. Mean density and mean dry weigth per m^2 (+ SD) of invertebrates during 1996 at the Tipperne reserve. Dots denote eggs from *T. benedii* (data are lacking for April and September).
Gennemsnitlig tæthed og biomasse i tørvægt pr m^2 (+ SD) af invertebrater gennem året 1996 på Tipperne. Fyldte cirkler angiver tætheden af æg fra T. benedii *(data mangler for april og september).*
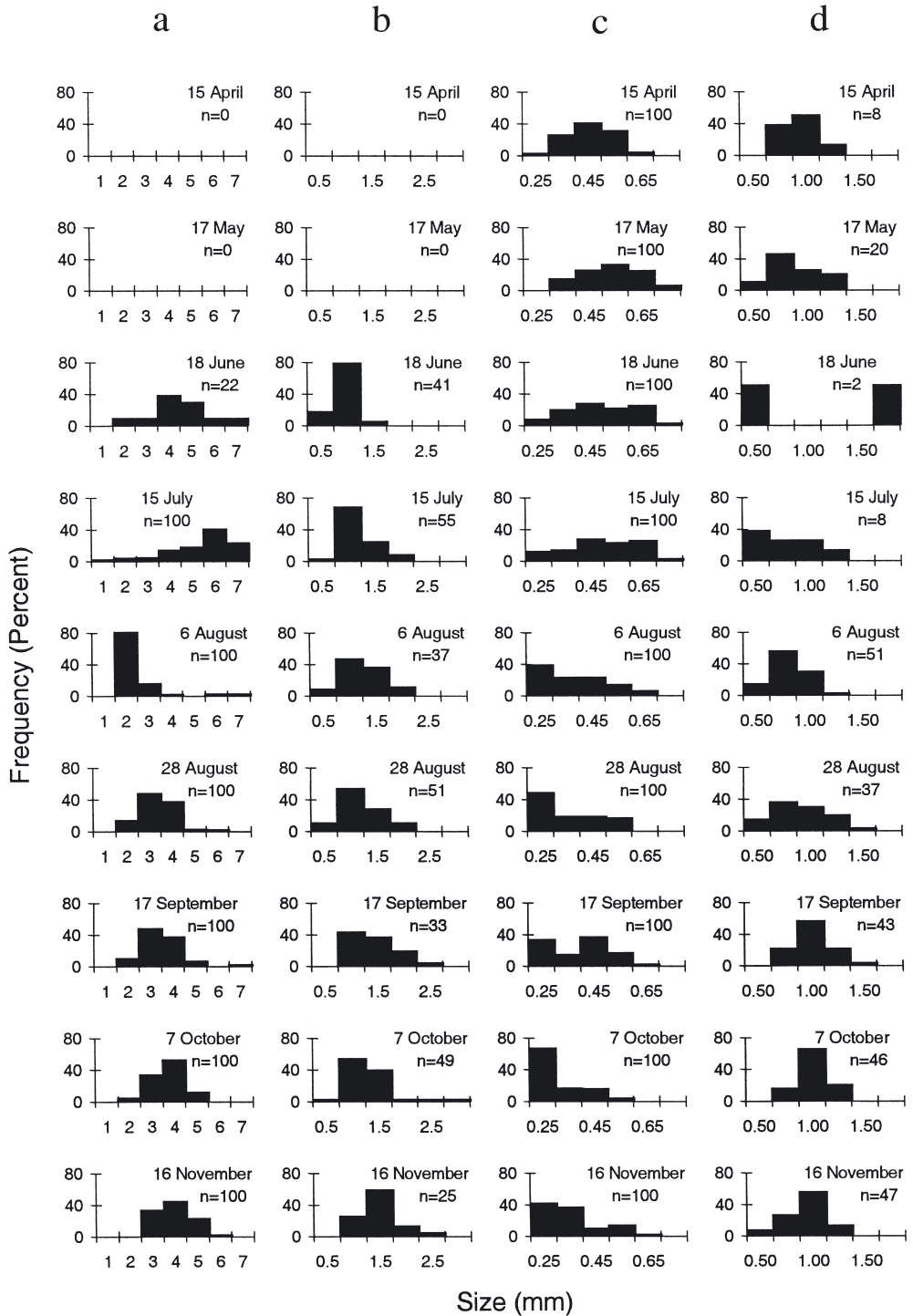
Frequency (Percent)

a   b   c   d

Fig. 4. Size-frequency histograms of a) *C. volutator*, length; b) *N. diversicolor*, width of segment No. 10; c) *T. benedii*, width of segment No. 10; d) gastropods, maximum length of operculum. 15 April – 16 November 1996. *Størrelsesfordeling for a)* C. volutator, *længde; b)* N. diversicolor, *bredde af kropssegment nr 10; c)* T. benedii, *bredde af kropssegment nr 10; d) dyndsnegle, maximumlængde af operculum. 15. april til 16. november 1996.*

may not be constrained by the abundance of prey. At the higher prey densities found during autumn compared to spring, Dunlin densities seem to reach a plateau level. This phenomenon is also demonstrated for wintering Oystercatchers on a spatial scale (Sutherland 1982, Meire 1996). The difference in threshold density between spring and autumn may result from a seasonal difference in food requirements among the staging Dunlins, with relative high requirements during the northward migration.

An additional factor working against a correlation of Dunlin numbers and the density of their main prey *N. diversicolor* is the relatively low accessibility (increasing burrow depth) of the latter towards the end of the season (Zwarts & Esselink 1989). Furthermore, the poor correlation between Dunlin numbers and prey biomass could, to some extent, be a result of an unknown rate of predation during the autumns. In contrast to the springs, the autumn sampling took place late in the migration period, allowing Dunlins and other waders to harvest a significant part of the prey biomass before the data were collected. However, the effect of sampling date on the data was probably minor sice the relative rate of predation apparently is rather low at Tipperne from June to February (Petersen 1981).

As described by Desholm (1998), the water level at Tipperne is highly influenced by wind conditions, so that the mudflats are exposed during southerly winds and flooded during northerly winds. One might expect the water level – and hence the number of staging Dunlins – to be highly variable during the autumn migration period, due to the often variable weather. Actually, however, the number of days where the mudflats were exposed to Dunlins varied little during autumn (mean 142, range 123-151, SD 9.0; 1986-1995).

Recolonization

The severe winter of 1995/96 was disastrous to the population of benthic invertebrates at Tipperne, resulting in an almost complete disappearance of all species except *T. benedii*. They did, however, quickly recolonize the area during the subsequent spring and summer.

Corophium volutator is widespread and often very abundant in marine sediments of northern Europe and north-eastern North America. It does not migrate offshore during the winter months (Holmstöm & Morgan 1983) and will in shallow waters be exposed to low temperatures and ice (mechanical disturbance, oxygen depletion) during severe winters. Since it has no larval stage

(Hughes 1988), the recolonization of disturbed areas has to rely on pelagic dispersal of immature or adult individuals, an activity known to be associated with flood tides (Essink et al. 1989, Stearns & Dardeau 1990). By active vertical migration *C. volutator* expose itself to tidal or wind-stowage currents, thereby obtaining a passive drift.

In the non-tidal shallow waters at Tipperne, *C. volutator* from deeper waters just outside the Tipperne peninsula may use wind induced currents to reoccupy the disturbed shallow water areas. In 1996, this recolonization took place between 17 May and 18 June by individuals from all size groups (>2 mm, unimodal size distribution). On 6 August a new cohort appeared, probably representing the offspring of the recolonizing individuals, which resulted in a peak biomass of 4.07 g/m^2. However, more than 90% of this population consisted of juveniles (<3 mm in length) which are of doubtful value as prey for Dunlins. Semipalmated Sandpipers *Calidris pusilla* (bill length 15-22 mm) is known to feed selectively on *Corophium* greater than 4 mm in length (Peer et al. 1986). Applying this limit also to foraging Dunlins (bill length 27-34 mm for *C.a. alpina*, Prater et al. 1977) showed that only c. 25% of the fall biomass of *C. volutator* consisted of individuals large enough to be prey for Dunlins. *C. volutators* will nevertheless be an important prey organism from mid-summer onwards, with densities of individuals larger than 4 mm ranging from 4412-17967 individuals/m^2. This means that both local post-breeding Baltic Dunlins *C. a. schinzii* and, later in the autumn, staging Northern Dunlins *C. a. alpina* may benefit from *C. volutator*. The increasing number of larger individuals appearing during the autumn is due to growing juveniles (see Fig. 4a).

Nereis diversicolor is a major prey item for estuarine wader species throughout its range on the intertidal mudflats along the coast of Europe and NW Africa (Zwarts & Esselink 1989). In 1996 it recolonized the mudflats at Tipperne during the same period as *C. volutator* (between 17 May and 18 June), but the immigrating population consisted of small individuals only. In the following months no new arrivals appeared, and the density stayed unchanged for the rest of the year. Hence, the observed increase in biomass (Fig. 3) was due to the growth of individual animals (Fig. 4b). The effect of predation by waders was not visible in the data, probably due to the relatively low rate of predation at Tipperne from June to February (Petersen 1981). During 1996, the period of peak predation rate (from March to May, Petersen 1981)

coincided with the period of minimum prey abundance. As autumn prey for Dunlins, *N. diversicolor* was the most abundant species in terms of biomass, ranging from 5.7 to 20.3 g/m^2.

H. diversicolor is probably an energetically superior prey item for Dunlins regardless of size, compared to the other invertebrate species at Tipperne (at least individuals down to 0.5 mg dry weight, see Goss-Custard 1977a).

Tubificoides benedii is a common marine and brackish oligochaete in British, Baltic, and Danish waters (Muus 1967, Timm 1970, Hunter & Arthur 1978). It is known to tolerate the low oxygen levels of sulphidic sediments for prolonged periods (Hunter & Arthur 1978, Giere et al. 1988). This may explain why it was the only invertebrate species to survive the long periods of ice cover at Tipperne during the severe winter of 1995/96. The two-peaked temporal distribution of cocoon density, together with the skewed size distribution from 6 August onwards, indicate a significant recruitment during the autumn. In the Thames Estuary *T. benedii* is reported as having one main breeding period from April to August (Hunter & Arthur 1978), occurring earlier and being more narrow than the breeding period observed in this study. The biomass at Tipperne stayed unchanged within the range of 1.0 - 2.5 g/m^2 through the study period. Different authors disagree about the significance of *T. benedii* as a prey organism for Dunlins. In the Wash in East England small tubificid oligochaetes were reported to be the major prey item for Dunlins (Kelsey & Hassall 1989), whereas Evans (1987) considered *T. benedii* as too small for Dunlins to prey upon. Whether or not the species is important for Dunlins, it constituted the only abundant, potential infaunal invertebrate prey during the early spring migration period at Tipperne in 1996.

Gastropods. Mudsnails were present at the start of the study period in mid-April and may have recolonized the shallow water well before the two other immigrating species, or simply survived the winter. Mudsnails are known to migrate with the water currents fixed to the surface by the surface tension (Vader 1964). The relative low abundance of this invertebrate group, both with regard to density and biomass, makes it a subordinate prey item for Dunlins at Tipperne.

Conclusion

In springs following severe winters at Tipperne, the densities of benthic prey are below a threshold level, resulting in a positive correlated Dunlin/prey relationship. During such springs, recolonization and reproduction by the invertebrates results in a slow but steady increase in population densities, reaching values well above an autumn threshold level for Dunlins before the start of the fall migration. Hence, no Dunlin/prey correlation will be apparent in autumn.

The infauna at Tipperne appears to be unstable but persists through time, being dominated by opportunistic species which regularly recolonize the area. This benthic community constitutes a reliable food source for Dunlins during autumn migration, but not necessarily during spring migration.

Resumé

Sammenhængen mellem antallet af rastende Almindelige Ryler og tætheden af deres byttedyr på Tipperne: effekten af hårde vintre

Dette arbejde er udført i et forsøg på at forstå de basale mekanismer, der påvirker antallet af rastende Almindelige Ryler på Tippernes vadeflader. Hvad sker der fra år til år på den samme rasteplads, når f.eks. vintervejret er yderst variabelt? Næsten total udryddelse af vadefuglenes byttedyr er flere gange rapporteret efter isvintre, og sådanne hændelser vil sandsynligvis påvirke tilstedeværelsen af Almindelige Ryler. Meltofte påviste allerede i 1987 en sammenhæng mellem isvintre og lave forårstal af både Almindelig Ryle og Lille Kobbersneppe på Tipperne. Mere præcist stiller artiklen spørgsmålet: Er tilstedeværelsen af rastende Almindelige Ryler under forårs- og efterårstrækket korreleret med tilgængeligheden af byttedyr.

For at besvare dette blev vejrdata og moniteringsdata for byttedyrstætheder og antal ryler på Tipperne analyseret for årene 1986-96 (ti sæsoner). Ydermere blev der udført et intensivt prøvetagningsprogram fra april til november 1996 for at kortlægge bunddyrenes rekolonisering efter en relativt hård isvinter. For yderligere informationer omkring naturreservatet Tipperne og de rastende vadefuglebestande, se Meltofte (1987).

Resultaterne viste en signifikant positiv sammenhæng mellem mængden af almindelige bunddyr (specielt børsteormen *Nereis diversicolor*) og de Almindelige Ryler (antal fugledage) om foråret. Om efteråret var der

Photo: Erik Thomsen.

ingen signifikant korrelation mellem antallet af fugle og deres byttedyr, hverken samlet eller for bestemte arter af bunddyr.

De lave byttedyrstætheder i forår efter hårde isvintre (1986/87 og 1995/96) kan tilskrives vinterdødeligheden, idet der blev fundet en signifikant positiv korrelation mellem mængde af bunddyr og gennemsnitlig vinter-temperatur. Resultaterne tyder derfor på, at vinterens hårdhed indirekte bestemmer tilstedeværelsen af Almin-delige Ryler på Tipperne om foråret, men ikke om efter-året. Grænseværdien for hvornår mængden af byttedyr udgør en tilstrækkelig stor føderessource for de Almin-delige Ryler, så sidstnævnte ikke reguleres af førstnævn-te, er større om foråret (ca 12 g/m^2) end om efteråret (ca 8 g/m^2), formentlig pga. et større energibehov hos ryler-ne om foråret end om efteråret. Denne forskel og væks-ten i bunddyrfaunaen forår og sommer gjorde, at fugle-nes tilstedeværelse ikke var reguleret af mængden af byttedyr i noget efterår gennem den tiårige projektperio-de. Selv i de efterår, der fulgte efter isvintre, var bund-dyrsfaunaen reetableret i en sådan grad, at de Alminde-lige Ryler aldrig havde dårlige fødesøgningsmuligheder. I modsætning hertil ligger Tippernes brugbarhed som forårsrasteplads en del under det acceptable efter hårde vintre, hvilket afstedkommer et lavt antal fugledage.

Isvinteren 1995/96 udslettede næsten alle invertebra-ter på Tippernes mudderflader, bortset fra børsteormen *Tubificoides benedii*, som er kendt for at kunne tolerere meget lave iltkoncentrationer. De to andre væsentlige byttedyr for de Almindelige Ryler var børsteormen *Nereis diversicolor* og slikkrebsen *Corophium volutator*, som begge udviste et højt rekoloniseringspotentiale og derfor var at finde i relativt høje tætheder, da rylernes efterårstræk satte ind. De to arter rekoloniserede mudder-fladerne på Tipperne mellem 17. maj og 18. juni 1996, og er sikkert indvandret fra de dybere vande uden for Tipperhalvøen vha. vindstuvningsstrømme. Hos slik-

krebsen indvandrede dyr af meget forskellige aldre og størrelser, mens det kun var små individer af børsteorme, der indtog mudderfladerne på Tipperne.

Så selv om infaunaen på Tipperne virker ustabil, består den gennem tiden. Faunaen er domineret af opportunistiske arter, der er i stand til at kolonisere områ-det år efter år, og kan derfor karakteriseres som en påli-delig fødekilde for Almindelig Ryle under efterårstræk-ket, men ikke nødvendigvis under forårstrækket.

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