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Animal abundance and food availability in coastal lagoons and intertidal marine sediments

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The relationships between the standing stocks of deposit-feeding benthic invertebrates and benthic chlorophyll-*a*, phaeopigment and total combustible organic matter were investigated at a series of coastal lagoons and in the type of intertidal soft-sediment sites from which the lagoons originated. Across all the sites, in Norfolk, UK, an inverse relationship occurred between (a) the amounts of chlorophyll-*a* and of other potential food materials and (b) the degree of coverage by water. The biomass of consumers also decreased with increased water coverage, so that the lagoons supported less biomass than the adjacent high-level intertidal sites. Further, the deposit-feeder biomass supported by unit food decreased with extent of water coverage.

There was no evidence of any relationship between deposit-feeder and food biomass within any single site, in spite of the study period being selected to be that in which there was maximum likelihood of competition for microphytobenthic food. Whilst chlorophyll concentrations may set the maximum achievable level of consumer biomass at these sites, including in the deeper lagoons setting very low potential maximum population densities, the seasonal abundance patterns of the deposit feeders appear to be determined by other factor(s).

INTRODUCTION

Whether populations of coastal deposit-feeders are usually structured from the top downwards by epibenthic and other predators or from the bottom upwards by resource limitation, especially food, is contentious. Levinton (1972) argued that deposit-feeders ought to be limited by competition for resources, and intraspecific competition has indeed since been demonstrated in some of the most characteristic soft-sediment species, e.g. those of *Hydrobia* (Levinton & Bianchi, 1981; López-Figueroa & Niell, 1987; Morrisey, 1987), *Corophium* (Wilson, 1989) and *Macoma* (Ólafsson, 1986). Interspecific competition has also been shown between *Corophium* spp. (Jensen & Kristensen, 1990) and between *Hydrobia* spp. (Fenchel & Kofoed, 1976; Barnes & Gandolfi, 1998); and interspecific interference is widespread (e.g. Flach, 1996). Nevertheless, several studies have concluded that the overall abundance of intertidal and non-tidal, soft-sediment deposit feeders is not limited by competition, but is likely generally to be determined by, for example, recruitment limitation (Ólafsson et al., 1994), the dynamic nature of their sedimentary and hydrographic environment (Snelgrove & Butman, 1994; Hall, 1994), and by epibenthic and intra-sediment predation (see Wilson, 1989 and reviews by Peterson, 1979; Reise, 1985; Wilson, 1991; Barnes, 1994a and Gosselin & Qian, 1997). To date, however, most information has been derived from highly specific studies of single species at single sites, and the general argument has remained at the theoretical level set by Levinton (1972) and Beukema (1976). No field study has directly investigated whether a range of populations is actually held at or near the carrying capacity of their habitats.

A potentially useful system to investigate in this context is the coastal lagoon vs intertidal marine contrast, in that intuitively it would seem likely that the microphytobenthic food of deposit-feeders would be less abundant under permanently submerged lagoonal conditions. Further, population densities of the mudsnails, *Hydrobia*, and other deposit-feeding species that dominate these systems are consistently lower in coastal lagoons than on adjacent intertidal expanses of equivalent sediment. Maximum British lagoonal densities of *Hydrobia ulvae* (Pennant), for example, are $<5000\,\mathrm{ind\,m^{-2}}$ whilst maximum adjacent intertidal ones may exceed $75{,}000\,\mathrm{ind\,m^{-2}}$ (Barnes, 1990), and lagoonal densities of *H. neglecta* Muus are $<10{,}000\,\mathrm{ind\,m^{-2}}$ whilst the only known intertidal population of this species attains $>50{,}000\,\mathrm{ind\,m^{-2}}$ (Barnes, 1993, 1996). The same effect can be seen in European densities of the lagoonal *H. ventrosa* (Montagu) and *H. minoricensis* (Paladilhe) vs those of intertidal *Hydrobia* populations (Muus, 1967; Asmus & Asmus, 1985; Bachelet & Yacine-Kassab, 1987; Barnes, 1994b; Drake & Arias, 1995). One tenable hypothesis is that this phenomenon is related to the differing carrying capacities of the two types of habitat in terms of the diatoms on which *Hydrobia* feeds (Lopez & Levinton, 1978; Jensen & Siegismund, 1980; Asmus & Asmus, 1985; Forbes & Lopez, 1989a), and therefore to resource limitation.

This paper examines the differential abundance of *Hydrobia* and associated deposit feeders in lagoons and intertidally, and the relationship of consumer abundance to food stocks, by surveying these over the critical half-year period when resource limitation and therefore competition are most likely.

Table 1. *Mean quantities (in g* m^{-2} *±SE) of chlorophyll-*a*, phaeopigment, total combustible organic matter (p.o.m.),* Hydrobia *plus other chlorophyll-feeders, and total deposit-feeders at the various sites from July 1998 to January 1999.*

	Chlorophyll	Phaeopigment	p.o.m.	*Hydrobia*, etc.	All deposit feeders
LAGOONS					
Broadwater					
July	0.37 ±0.04	0.26 ±0.04	464 ±42	1.87 ±0.82	6.88 ±6.54
August	0.28 ±0.02	0.12 ±0.01	277 ±09	0.70 ±0.38	8.27 ±7.65
September	0.23 ±0.03	0.25 ±0.02	398 ±43	1.16 ±0.37	15.24 ±18.63
October	0.19 ±0.01	0.36 ±0.04	575 ±37	0.89 ±0.35	14.33 ±17.74
November	0.11 ±0.01	0.43 ±0.06	892 ±47	0.82 ±0.23	9.40 ±14.95
December	0.18 ±0.02	0.41 ±0.05	842 ±86	1.13 ±0.51	10.04 ±9.98
Holkham Salts Hole					
July	0.05 ±0.01	0.12 ±0.01	272 ±19 0	0.22 ±0.18	0.60 ±0.43
August	0.04 ±0.01	0.08 ±0.01	136 ±14	0	0.69 ±0.15
September	0.05 ±0.01	0.10 ±0.01	214 ±19	0	2.71 ±0.54
October	0.05 ±0.01	0.12 ±0.01	230 ±21	0	1.48 ±0.34
November	0.05 ±0.00	0.14 ±0.01	178 ±11	0	2.53 ±0.94
December	0.05 ±0.01	0.17 ±0.01	222 ±16	0	3.19 ±0.83
January				0	1.37 ±0.39
Salthouse Broad					
August	0.11 ±0.01	0.13 ±0.01	294 ±24	16.82 ±2.2	17.31 ±2.22
September	0.07 ±0.01	0.11 ±0.01	311 ±34	10.03 ±0.97	10.09 ±0.94
October	0.06 ± 0.01	0.11 ±0.01	251 ±24	11.83 ±0.84	12.40 ±0.91
November	0.06 ±0.01	0.16 ±0.01	256 ±41	14.42 ±2.73	14.46 ±2.74
December	0.08 ±0.01	0.14 ±0.01	249 ±18	15.01 ±1.16	16.00 ±1.17
January				12.64 ±1.35	12.80 ±1.37
INTERTIDAL STATIONS					
Cocklebight					
July	0.14 ±0.01	0.15 ±0.02	538 ±59	24.23 ±2.47	24.38 ±2.43
August	0.12 ±0.01	0.12 ±0.02	385 ±53	20.80 ±2.05	20.96 ±2.04
September	0.05 ±0.00	0.22 ±0.01	715 ±50	21.53 ±1.24	21.30 ±1.20
October	0.07 ±0.01	0.13 ±0.01	391 ±69	19.66 ±0.64	20.10 ±0.58
November	0.06 ±0.01	0.12 ±0.01	268 ±27	20.58 ±4.56	21.35 ±4.55
December	0.08 ±0.01	0.14 ±0.01	270 ±08	20.01 ±1.61	24.24 ±1.66
January				21.72 ±0.48	22.08 ±0.50
Anchor					
July	0.14 ±0.01	0.19 ±0.01	849 ±81	32.83 ±3.96	32.95 ±3.93
August	0.13 ±0.01	0.24 ±0.03	464 ±30	26.73 ±3.20	28.91 ±3.58
September	0.04 ±0.01	0.13 ±0.01	475 ±28	22.04 ±3.47	22.79 ±3.43
October	0.05 ±0.01	0.18 ±0.01	297 ±48	18.78 ±4.06	19.67 ±3.94
November	0.06 ±0.01	0.15 ±0.01	252 ±27	24.61 ±4.12	25.50 ±4.21
December	0.09 ±0.01	0.16 ±0.01	357 ±28	34.98 ±3.26	35.00 ±3.26
January				33.57 ±2.85	34.22 ±2.96
Hut Gap					
July	0.22 ±0.02	0.17 ±0.02	266 ±08		
August	0.27 ±0.01	0.15 ±0.02	598 ±19		
September	0.19 ±0.02	0.17 ±0.01	337 ±19		
October	0.19 ±0.02	0.17 ±0.02	412 ±70		
November	0.15 ±0.01	0.18 ±0.02	184 ±18		
December	0.16 ±0.01	0.18 ±0.01	273 ±26		

METHODS

Sampling was carried out at three lagoonal and two intertidal-marine sites situated along a 35 km stretch of the north Norfolk coast: the lagoons of Broadwater (0°33′25″E 52°58′26″N; salinity during the sampling period 14–21 psu), Holkham Salts Hole (0°48′32″ 52°58′11″N; salinity 24–26 psu) and Salthouse Broad (1°04′57″E 52°57′35″N; salinity 22–30 psu); and intertidal sites on the nearby Scolt Head Island (Cocklebight, 0°40′48″E 52°59′05″N; and in front of Anchor Marsh, 0°40′46″E 52°59′10″N). The opportunity was also taken to sample the chlorophyll content of a third site on the island (Hut Gap Creek, 0°41′31″E 52°59′10″N): this is a creek bed that is normally exposed to the air but is submerged by the highest of spring tides. Before enclosure within the last 250 years, all three lagoonal sites were originally intertidal marine areas equivalent to, and at the same tidal height as, those sampled on Scolt Head (Hunt, 1971; Barnes, 1999a). Now they are isolated from direct contact with the sea and are non-tidal; the specific sampling stations being permanently submerged beneath

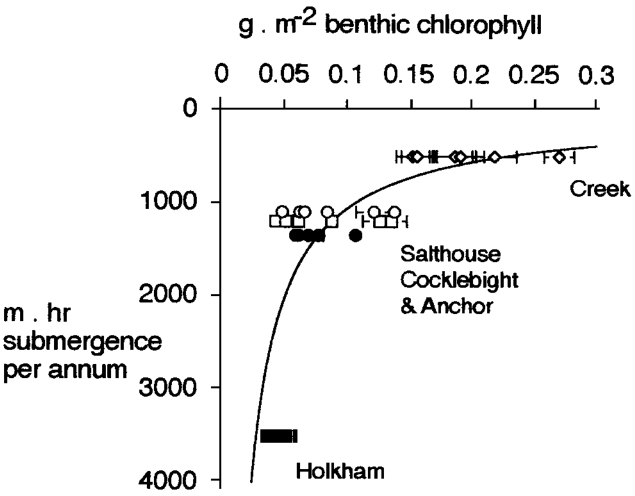

Figure 1. The relationship between biomass of benthic chlorophyll-*a* and degree of submergence (m depth×h of coverage by the depths concerned) in two lagoonal and three intertidal marine sites in Norfolk. Bars are 2 SE of the mean.

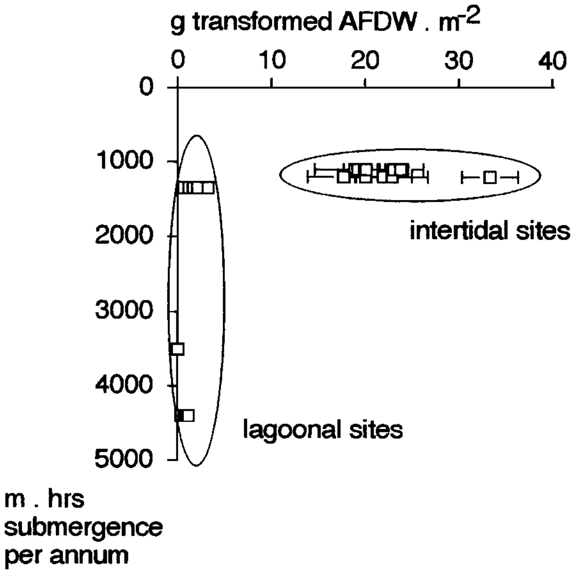

Figure 2. The relationship between biomass of the gastropod *Hydrobia* and degree of submergence (m depth x h of coverage by the depths concerned) in lagoonal vs intertidal marine sites in Norfolk. Bars are 2 SE of the mean.

some 0.4–0.5 m (Broadwater and Holkham Salts Hole) or 0.1–0.2 m (Salthouse Broad) of water that issues out of the salt water table within the isolating shingle barriers.

For ease of comparison with the intertidal stations, regions sampled in the lagoons were open areas of soft sediment, i.e. bare of submerged macrophytes such as *Ruppia* and *Chaetomorpha*. Sampling was carried out at each site within a belt of some 30×1 m monthly from July 1998 to January 1999 (inclusive) to assess the abundance of deposit-feeding animals and, from July to December 1998 (inclusive), to assess the available food, i.e. sedimentary chlorophyll-*a*, phaeopigment and total organic matter. The period from July to December represents the symmetrical second half of the local period of microphytobenthic productivity, and covers the period when productivity declines from its June/July peak to its November–February minimum (Leach, 1970; Cadée & Hegeman, 1974; Joint, 1978).

On each occasion and at each site, a minimum of six replicate cores of 26.4 cm^2 cross sectional area were taken to a depth of 10 cm, were sieved gently through 0.5-mm mesh, and then either the wet weights (after removal of surface water) or, in the case of the mudsnail *Hydrobia*, the shell heights (to the nearest 0.04 mm as determined via microscope eyepiece micrometer) of the retained deposit-feeding species were measured. Wet weights were converted to ash-free dry weights (AFDW) using the relationships given by Ricciardi & Bourget (1998) and shell heights of *Hydrobia* were similarly converted to

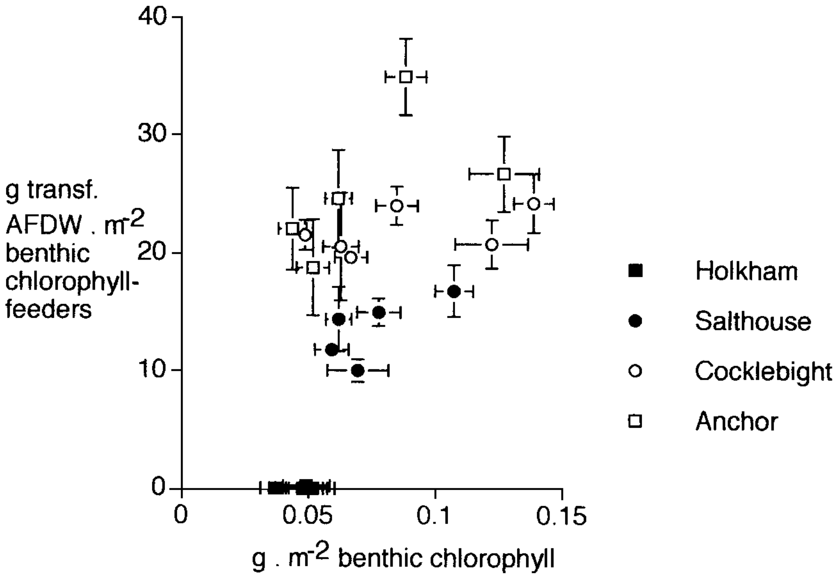

Figure 3. The overall relationship between the biomass of benthic chlorophyll-*a* and that of feeders on the microphytobenthos in two lagoonal and two intertidal marine sites in Norfolk. Bars are 2 SE of the mean.

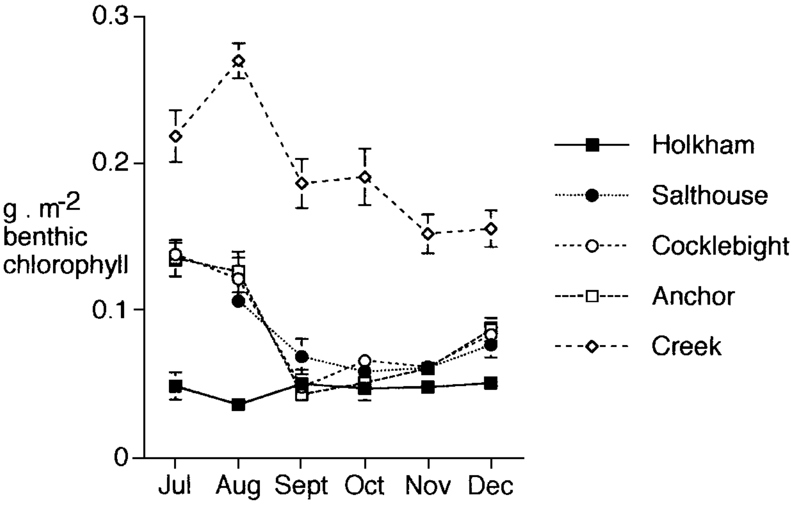

Figure 4. Changes in the biomass of benthic chlorophyll-*a* in two lagoonal and three intertidal marine sites in Norfolk during the period July to December 1998. Bars are 2 SE of the mean.

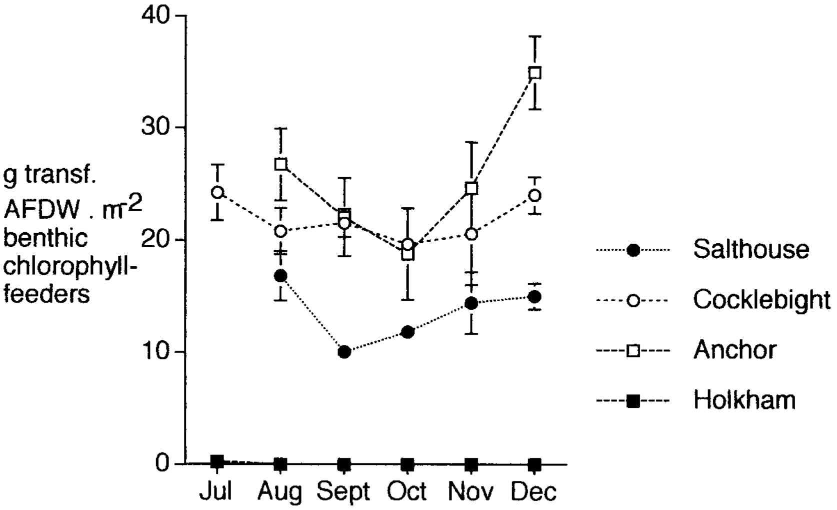

Figure 5. Changes in the biomass of feeders on the micro-phytobenthos in two lagoonal and two intertidal marine sites in Norfolk during the period July 1998 to January 1999. Bars are 2 SE of the mean.

AFDW using the equations given by Siegismund (1982) and Bachelet & Yacine-Kassab (1987). All individual weights (in mg AFDW) were transformed to (mg AFDW)$^{0.75}$ before being summed, since metabolic rate scales as mass$^{0.75}$ and metabolic rate per unit mass is a better indicator of required food consumption than is biomass (Schmidt-Nielsen, 1984). All biomasses of animals stated below are these transformed values. True total biomasses approximate 75% of transformed values.

Of the benthic animals encountered (Appendix 1), *Hediste diversicolor* (Müller) was assumed not to be a deposit-feeder, because this feeding mode figures only half way down the preference hierarchy of this species (Pashley, 1985), and neither were the predatory or suspension-feeding *Nematostella vectensis* Stephenson, nemertines, phyllodocid and sabellid polychaetes, *Carcinus maenas* (L.), *Retusa obtusa* (Montagu) and cockles (*Cerastoderma* spp.). Pelagic or epibenthic animals (mysids, prawns and the isopod *Idotea chelipes* (Pallas)) accidentally retained by the lagoonal coring procedure were also discounted. Hydrobiids, *Corophium* spp., *Abra tenuis* (Montagu) and *Pygospio elegans* (Claparède), were scored as chlorophyll-feeders (after information in Muus, 1967; Lopez & Levinton, 1978; Coles, 1979; Jensen & Siegismund, 1980; Cammen, 1989; Forbes & Lopez, 1989a; etc.), whilst chironomid and tipulid larvae, tubificid oligochaetes, and the rarer capitellid, orbiniid and ampharetid polychaetes and *Scolelepis* spp. were included as 'other deposit-feeders'.

At the same time as the faunal samples, 20 replicate cores of 1.77 cm^2 cross sectional area and depth of 15 mm were taken from the same immediate area for absorption spectrophotometric determination of surface chlorophyll-*a* and phaeopigment by the acetone-extraction methodology recommended by Wolff (1987) and Greiser & Faubel (1988), together with a minimum further five similar cores for determination of total contained organic matter by incineration in a muffle furnace, for 24 h at 475°C to avoid decomposition of carbonates (Greiser & Faubel, 1988). All samples for chlorophyll determination were taken during mid morning low tides, without other allowance for potential

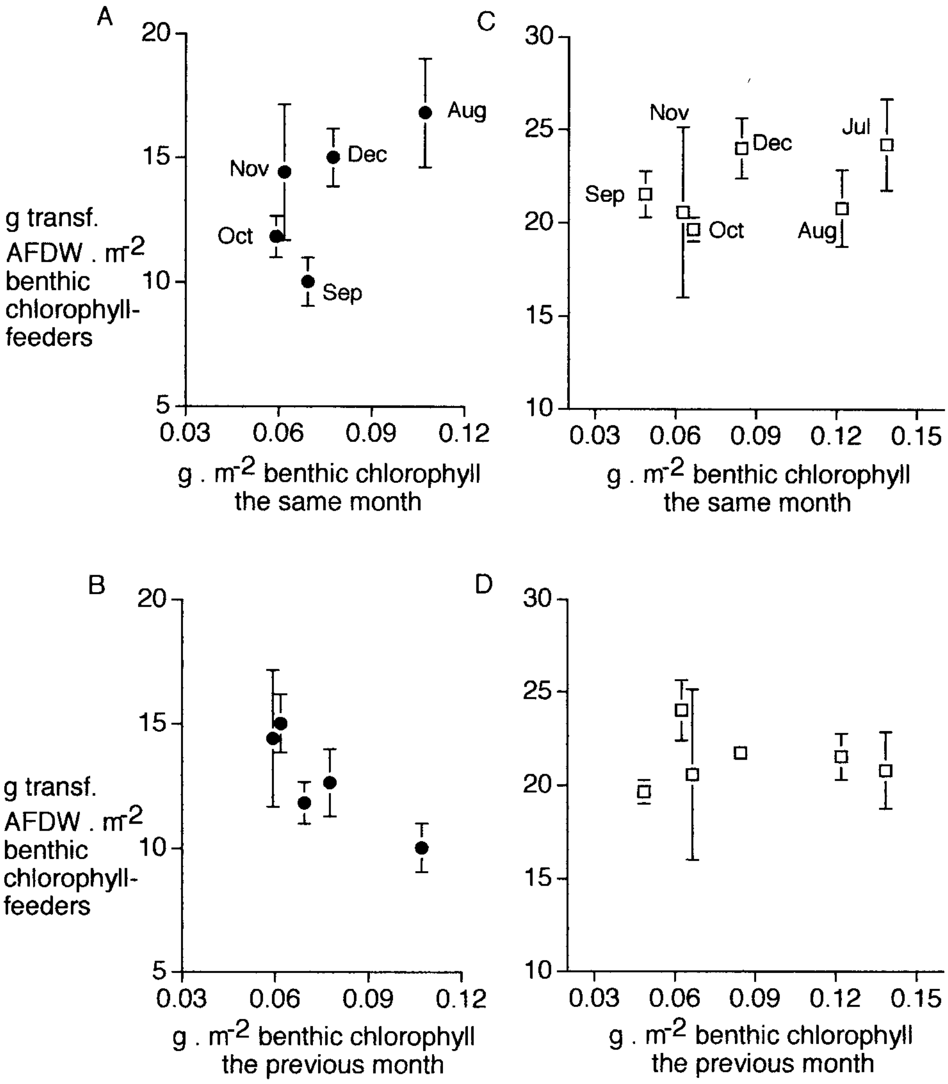

Figure 6. The specific relationship between the biomass of benthic chlorophyll-*a* and that of feeders on the micro-phytobenthos in the Salthouse Broad lagoon (A & B) and in the Cocklebight intertidal site (C & D). In A and C, consumer biomass is plotted against the chlorophyll-*a* values recorded at the same time; in B and D, it is plotted against the chlorophyll-*a* levels of the previous month. Bars are 2 SE of the mean.

vertical migration within the sediment. Annual water coverage was calculated directly for the lagoons, and was estimated for the intertidal sites from their heights on the beach and the local tide curves.

Relationships between chlorophyll-*a*, phaeopigment, etc. and other variables were tested by correlation and regression analyses. Correlation coefficients were subjected to Fisher's *r* to *Z* transformation, and the regression *F* was derived from the sum of squares and mean squares as in ANOVA.

RESULTS

Nature of the fauna

The deposit-feeding fauna of the various lagoons was dominated by the following animals, with their average percentage of the total biomass given parenthetically: Holkham Salts Hole, *Tubificoides pseudogaster* (Dahl) and other tubificids (64%); Broadwater, chironomid larvae (88%); and Salthouse Broad, *Abra tenuis*, *Corophium volutator* (Pallas) and *Hydrobia ventrosa* (43%, 36% and 15%, respectively). The intertidal sites were all dominated by *Hydrobia ulvae* (with an average of 91% of the total biomass). The intertidal animal biomasses ranged from 16 to 28 g AFDW m^{-2} (untransformed) and were therefore all average by world mudflat standards (Piersma et al., 1993).

Almost throughout the entire period of study, the water body of Broadwater supported a dense 'pea-soup' bloom of phytoplankton, with Secchi disc depths of the order of 15 cm, suggesting (after Moss, 1998) a photic zone of some 25 cm (maximum 40 cm). Since this depth is less than that of the lagoon bed, it was therefore assumed that the apparent measured benthic chlorophyll, which was at 0.23 g m^{-2} (average) five times higher than in Holkham Salts Hole and three times that in the shallow Salthouse Broad, was not produced *in situ* but had sedimented out of the water column. It supported less than 1.2 gAFDW m^{-2} of chlorophyll-feeding hydrobiids, and Broadwater is mostly excluded from the results presented below.

Between-site comparisons

Across all the sites, excluding Broadwater but including Hut Gap Creek, chlorophyll-*a* levels declined with amount of coverage by water, as estimated by metres depth multiplied by hours of submergence by those depths ($r=-0.63$; $Z=-3.78$; $P=0.0002$; Regression $F=9.3$; $P=0.0001$) (Figure 1), as did total combustible matter ($r=-0.40$; $Z=-2.13$; $P=0.03$; Regression $F=4.2$; $P=0.01$) and phaeopigment ($r=-0.44$; $Z=-2.41$; $P=0.02$; Regression $F=2.9$; $P=0.04$). The biomass of both assumed chlorophyll-feeding species ($r=-0.61$; $Z=-3.526$; $P=0.004$; Regression $F=66.4$; $P<0.0001$) and all deposit feeders ($r=0.57$; $Z=-3.269$; $P=0.001$; Regression $F=61.3$; $P<0.0001$) did likewise (Table 1). The biomass of hydrobiid molluscs was throughout the study period lower under the permanently submerged conditions of the non-tidal lagoons than it was intertidally (Figure 2), with a maximum lagoonal density of 17,000 ind m^{-2} and a minimum intertidal one of 30,000 (maximum 110,000) ind m^{-2}.

Across these sites, there was a significant relationship between values of chlorophyll-*a* and the supported biomass of both chlorophyll feeders ($r=0.57$; $Z=2.83$; $P=0.005$; Regression $F=9.7$; $P=0.005$) (Figure 3) and all deposit-feeding species ($r=0.57$; $Z=2.85$; $P=0.004$; Regression $F=9.9$; $P=0.005$). The biomass of consumers was less related to the quantity of chlorophyll-*a* available the previous month ($r=0.46$; $Z=2.20$; P=0.03; Regression $F=5.55.7$; $P=0.03$). It is evident, however, that the lagoons support lower concentrations of benthic chlorophyll-*a* and lesser biomasses of deposit feeders than do the adjacent high-level intertidal zones, such as Cocklebight and Anchor, from which type of habitat they originated. It was also evident that there was no overlap in the ratio of detritus-feeder to chlorophyll-*a* + phaeopigment biomass between the intertidal sites and the lagoons, being high intertidally (minimum of 78:1 and an average of 104:1) and much lower lagoonally (maximum of 74:1), averaging 68:1 at Salthouse Broad, 21:1 at Broadwater and 11:1 at Holkham. This is another clear relationship with degree of water coverage ($r=-0.89$; $Z=-6.15$; $P<0.0001$; Regression $F=50$; $P<0.0001$).

The surface layers of the sediments of all sites were rich in organic matter, with an average of 340 g m^{-2}, those of the intertidal zone visibly containing salt-marsh debris and those of the lagoons material deriving from adjacent beds of *Ruppia* and/or *Chaetomorpha*. Although the ratio of total organic matter to chlorophyll carbon (assuming a carbon to chlorophyll ratio of 50:1) was effectively the same in the lagoons and the intertidal zone (lagoons 82:1, SE 4; intertidal 89:1, SE 16) (Mann–Whitney $U=51$; $P=0.78$), the intertidal sites were considerably more variable, with ranges of: lagoonal 55:1 to 110:1; intertidal 24:1 to 294:1.

Within site comparisons

The quantity of benthic chlorophyll-*a* was relatively constant in Holkham Salts Hole. In Salthouse Broad and the two main intertidal sites, however, it more or less followed the expected pattern of seasonal productivity, being high in July and August and declining thereafter, although in all three it rose again unexpectedly in December (Figure 4). Chlorophyll-feeder biomass at those three sites also reached a minimum in September/October and rose in November and/or December to a level almost as high or even higher than summer values (Figure 5). Unit standing stock of chlorophyll then supported least chlorophyll feeder biomass during July/August (or at Salthouse in September), and most intertidally in September and, lagoonally, in November. Nevertheless, within each site, there were no significant relationships between the biomass of chlorophyll feeders or that of all deposit feeders and either chlorophyll-*a* or chlorophyll-*a* + phaeopigment, either when analysed as contemporaneous comparisons (for all correlations $P>0.2$) or when the fauna was compared with the phaeopigment and/or chlorophyll-*a* present the previous month (for all correlations $P>0.5$), except in respect of the Salthouse Broad lagoon in which the relationship between chlorophyll-*a* and the consumers one month later was significant but negative ($r=-0.89$; $Z=-2.03$; $P=0.04$) (see Figure 6), and of the intertidal Cocklebight site with regard to chlorophyll-*a* + phaeopigment and all deposit-feeders one month later which approached significance and was also negative ($r=-0.75$; $Z=-1.66$; $P=0.09$). Nor were any significant positive relationships found between consumers and total combustible matter (for all correlations $P>0.15$), although a negative relationship was present between total combustible matter and the abundance of consumers one month later at Cocklebight ($r=-0.85$; $Z=-2.19$; $P=0.03$; Regression $F=10.7$; $P=0.03$).

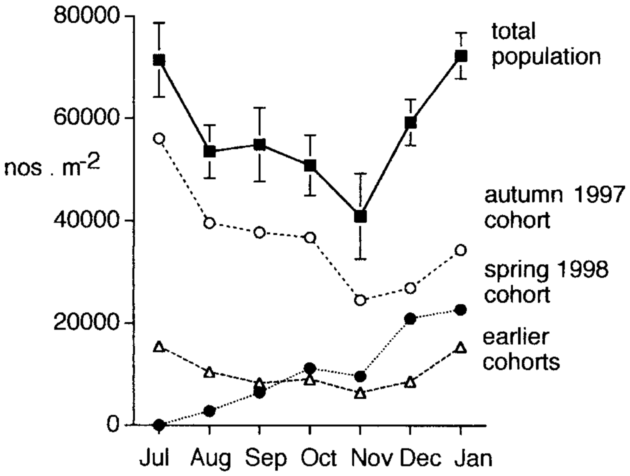

Figure 7. Variation in the population density of the gastropod *Hydrobia ulvae* in the Norfolk intertidal mudflat sites over the study period, with the contributions to the total of the component cohorts. Average data of the Cocklebight and Anchor sites; bars being 2 SE of the mean. Note the apparent December/January increase in the autumn 1997 and earlier cohorts as a result of movement.

The population of *H. ulvae* dominating the deposit-feeding biomass of the larger Cocklebight region (the Cocklebight and Anchor stations) increased considerably from October 1998 to January 1999. This, however, was not solely due to the continued recruitment of small mudsnails that was first encountered in the sampled population in August, but was also a result of movement of individuals from older cohorts into the general area (Figure 7).

DISCUSSION

The effect of the permanent water mass in coastal lagoons will be to reduce light intensities at the sediment surface and this is reflected in lower concentrations of benthic chlorophyll-*a* than in the intertidal zone, although, as in Broadwater, there can be an input of chlorophyll to the benthos in the form of fall-out from the water column. The same effect of light limitation has been noted on individual mudflats. At mid-tide level in those of the Lynher Estuary in south-western England, for example, the 'rate of [benthic] photosynthesis decreased rapidly as the mudflat was submerged and was not detectable . . . only 30 min after flooding' (Joint, 1978). In the sites investigated here this is correlated with a lesser biomass of benthic deposit feeders in the lagoons. The reduction is not pro rata, however, in that lagoonal biomasses are small in relation to unit standing stock of chlorophyll-*a*. This is in spite of the fact that, being situated at about high water neap tide level, consumers living in the intertidal sites sampled can devote considerably less than half the time feeding that can be achieved by the lagoonal species. It can be concluded that the productivity of the lagoonal benthic microflora is disproportionately small.

Hydrobiid populations in small coastal lagoons are known often to be short-lived and/or to fluctuate between two or more dominant species (Barnes, 1991, 1994b), and this study has produced further evidence of this. As suggested by earlier studies, the biomass of hydrobiids was throughout this study period lower in the non-tidal lagoons than intertidally, the maximum lagoonal density being 17,000 ind m^{-2}. In the recent past, *Hydrobia* densities at Broadwater and Holkham Salts Hole have been higher, though not exceeding 30,000 ind m^{-2}. The Salts Hole supported a population of up to 4000 *H. ulvae* m^{-2} ten years ago (Barnes, 1988, 1990) that now appears to be extinct, and that of *H. ventrosa* in Broadwater (Barnes, 1994b) has, perhaps in conjunction with the shading effects of the phytoplankton bloom, currently declined to <1000 ind m^{-2}. This continues the trend reported earlier for Broadwater which saw a reduction from nearly 30,000 ind m^{-2} in early 1992 down to 10,000 ind m^{-2} in late 1993 (Barnes, 1994b). Despite the salinity being >14 psu, the hydrobiid population there was during the study period dominated by the relatively freshwater *Potamopyrgus antipodarum* (Gray). Hitherto, such population declines and species replacements have been attributed to the action of predation, competition and periodically adverse climate (Fenchel, 1975; Lassen & Kristensen, 1978; Hylleberg & Siegismund, 1987; Planas & Mora, 1987; Barnes, 1994a, 1999b; Barnes & Gandolfi, 1998). The results presented here suggest that the very low benthic chlorophyll-*a* levels characterizing such systems may also set such low ceilings to maximum population density as to render local extinction statistically likely. It is notable in this context that the feeding rate of *Hydrobia* appears to be constant regardless of the chlorophyll-*a* content of the sediment, although it does remain longer in areas rich in chlorophyll by reducing its speed of movement (Forbes & Lopez, 1986), and it would therefore be ill-equipped to compensate for low food concentrations.

Notwithstanding the general relationship seen between deposit feeding biomass and chlorophyll-*a* concentrations across the range of habitats, however, there is no evidence within any of the individual sites that consumers are at and held to the carrying capacity of their habitat in respect of chlorophyll-*a* in that no (positive) relationships between deposit-feeder and chlorophyll-*a* biomass were found. This is in spite of the study period being the one during which microphytobenthic productivity and chlorophyll biomass are declining from their mid-summer peak (Leach, 1970; Cadée & Hegeman, 1974; Joint, 1978) whilst at the same time hydrobiid and other deposit feeder numbers are being boosted by the influx of new, fast-growing recruits (Barnes, 1994b and the results above) with, presumably, large food requirements. Peak consumer biomasses in the late summer or early autumn have been recorded for several equivalent north-west European lagoons and estuaries (e.g. Muus, 1967; Joint, 1978). Forbes & Lopez (1989a,b) have also concluded that one population of the mudsnail *Hydrobia* was held below its carrying capacity, although Levinton & Lopez (1977) considered that some *Hydrobia* populations may be at the carrying capacity of their habitats, but one set not by food *per se* but by the breakdown rate of their faecal pellets into re-ingestible materials (see also Forbes & Lopez, 1986). No evidence for pelletization of the sediments was forthcoming from this study.

Although standing stock is what is immediately available to consumers, they are obviously really dependent on productivity and hence arguments based on biomass data must be treated with caution. If the benthic position here is comparable with the local seasonal pattern of phytoplankton and dependent herbivore biomass (Steele, 1974), then one would expect to see deposit-feeder biomass mirror than of benthic chlorophyll with a time lag of some weeks. Such is certainly the case in the River Lynher (Joint, 1978), where the benthic heterotrophs reach their maximum some three months after the major peak in chlorophyll-*a*, although their August peak there does coincide with a secondary peak in chlorophyll-*a* biomass. No such relationship was evident at these sites, and indeed in Salthouse Broad the low point in deposit-feeder biomass occurred in September, one month before that of the chlorophyll began. It must be said, however, that if the time lag is very long, this study would not have detected its action.

Thus it appears that whilst consumer biomass does vary with chlorophyll levels across the range of habitats studied and to that extent food supplies may set a theoretical maximum level of consumer biomass, the precise abundances of the deposit-feeders are determined by some other factor(s), and the results from the sites studied do not contradict the hypothesis that this other factor may lie within intra-sediment, epibenthic and vertebrate predation. Predation has been much studied in the type of environment under investigation here (see, e.g. McArthur, 1998a,b,c; Van der Veer et al., 1998; and the reviews of Reise, 1985; Barnes, 1994a), and predators of deposit feeders are also an important element in the faunas of these Norfolk sites. The intertidal stations and Salthouse Broad support numerous shore-birds, and Broadwater and Holkham Salts Hole are frequented by wildfowl (Eve & Hibberd, undated). Gobies (*Pomatoschistus microps* (Krøyer)), eels (*Anguilla anguilla* (L.)), sticklebacks (*Gasterosteus aculeatus* L.) and prawns (*Palaemonetes varians*

(Leach)) have been commonly observed (e.g. Downie, 1996; Bamber, 1997; and Appendix). Benthic samples also yielded *Carcinus maenas*, *Retusa obtusa*, *Hediste diversicolor*, *Lineus ruber* (Müller), *Tetrastemma* spp. and, at Salthouse, the Red Data Book anemone *Nematostella vectensis* in densities of up to 950 ind m^{-2}. These are all species known to consume hydrobiids and other small benthic invertebrates (Reise, 1985; McArthur, 1998a,b,c; R.S.K. & C.J. de V., personal observations).

Predation, however, is not the only potential controlling process. Random factors are also likely to be involved, especially at the intertidal sites. It was evident that considerable movement of the dominant *Hydrobia ulvae* into (and possibly out of) the Cocklebight and Anchor sites was occurring. Large scale involuntary movement of *H. ulvae* at the mercy of flooding tides has previously been reported from this area (Barnes, 1998), as has passive floating from salt-marsh plants, etc. under equivalent circumstances (Barnes, 1981). Although not observed locally, drifting (*sensu* Armonies, 1994) may also occur as it does so across other southern North Sea flats (Armonies & Hartke, 1995; Jaklin & Günther, 1996). These could well serve to render any potential numerical relationship between consumers and their food in any precise local region transitory.

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Appendix 1. *Benthic fauna encountered in the core-tube samples. Note that this Appendix does not purport to be a fauna list for the areas concerned in that it is restricted to the precise stations sampled.*

LAGOONS

Species	Holkham Salts Hole	Broadwater	Salthouse Broad
Nematostella vectensis Stephenson	✓		
Tubificoides pseudogaster (Dahl)	✓	✓	✓
Other tubificids	✓	✓	
Pygospio elegans (Claparde)			✓
Scolecolepis spp.			✓
Hediste diversicolor (Müller)	✓	✓	✓
Arenicola marina (L.)	✓		
Tetrastemma sp.			✓
Hydrobia ventrosa (Montagu)		✓	✓
Potamopyrgus antipodarum (Gray)		✓	
Rissostomia membranacea (Adams)	✓		
Littorina saxatilis (Olivi)			✓
Abra tenuis (Montagu)			✓
Cerastoderma glaucum (Poiret)	✓		
Corophium volutator (Pallas)			✓
Idotea chelipes (Pallas)	✓	✓	✓
Paramysis nouveli Labat			✓
Praunus flexuosus (Müller)	✓		
Neomysis integer (Leach)	✓		
Palaemonetes varians (Leach)	✓	✓	✓
Conopeum seurati (Canu)	✓		✓
Chironomid larvae	✓	✓	✓

INTERTIDAL SITES

Species	Cocklebight	Anchor	Hut Marsh Creek
Tubificoides pseudogaster	✓	✓	✓
Tubificoides benedeni (Udekem)	✓	✓	✓
Pygospio elegans	✓	✓	✓
Scolecolepis spp.		✓	
Tharyx marioni (St Joseph)	✓	✓	
Scoloplos armiger (Müller)	✓	✓	
Hediste diversicolor	✓	✓	✓
Nephtys sp.			✓
Eteone longa (Fabricius)	✓	✓	✓
Phyllodoce sp.		✓	
Arenicola marina	✓	✓	
Capitella capitata (Fabricius)	✓	✓	
Notomastus latericeus M. Sars	✓		
Ampharete acutifrons Grube	✓	✓	
Lanice conchilega (Pallas)		✓	
Fabricia sabella (Ehrenberg)		✓	
Lineus ruber (Müller)	✓	✓	
Hydrobia ulvae (Pennant)	✓	✓	✓
Littorina saxatillus		✓	
Littorina littorea (L.)	✓	✓	
Retusa obtusa (Montagu)			✓
Cerastoderma edule (L.)	✓	✓	
Abra tenuis	✓	✓	
Macoma balthica (L.)		✓	
Scrobicularia plana (da Costa)	✓	✓	
Corophium volutator			✓
Lekanesphaera rugicauda (Leach)			✓
Crangon crangon (L.)	✓	✓	
Carcinus maenus (L.)			
Tipulid larvae	✓	✓	