SCIENTIA MARINA 72(2)
June 2008, 265-278, Barcelona (Spain)
ISSN: 0214-8358

Spatial and temporal characteristics of benthic invertebrate communities at Culbin Sands lagoon, Moray Firth, NE Scotland, and impacts of the disturbance of cockle harvesting

VANDA MARIYAM MENDONÇA [1,2,3], DAVID GEORGE RAFFAELLI [4], PETER BOYLE [5] and STEVE HOSKINS [5]

[1] Marine Science and Fisheries Centre, Ministry of Fisheries, P. O. Box 467, Muscat 113, Oman.
[2] Centre of Marine Sciences (CCMAR / CIMAR), University of Algarve, Gambelas Campus, 8000 Faro, Portugal.
[3] P. O. Box 3013, Seeb 111, Oman. E-mail: drvandamendonca@yahoo.com
[4] Department of Environment, University of York, YO 105DD, UK.
[5] Department of Zoology, University of Aberdeen, AB24 2TZ, UK.

SUMMARY: In the present study, Culbin Sands lagoon, a protected site in NE Scotland, was surveyed every 2 to 4 weeks during a three-year period (1994-1996) to study benthic invertebrate communities. Beds of *Mytilus edulis* covered 18000 m^2. 53 macroinfaunal species were identified outside these areas. The most conspicuous were: the lugworm *Arenicola marina* (mean up to 55 casts m^{-2}); and bivalves *Cerastoderma edule* (mean up to 158 ind. m^{-2}) and *Macoma balthica* (mean up to 79 ind. m^{-2}) after settlement. The standing stock ranged from 20 to 32 g AFDW m^{-2} yr^{-1} respectively from more exposed to more sheltered areas. Most species showed a clear recruitment peak in autumn, but others (e.g. *Capitella capitata*, and Spionidae) displayed several peaks in a year. Communities were also compared between the sampling sites before and after an incidental disturbance caused by cockle *Cerastoderma edule* harvesting, which took place in June 1995. One site showed –0.7% variation in the total standing stock, but +22% for smaller-cockles, as larger filter-feeding cockles were removed therefore enhancing their own larval settlement. Polychaete Spionidae populations also increased after larger cockles were removed. The polychaete *Arenicola marina* population returned to its normal activities just after the dramatic disturbance of the sediment.

Keywords: benthic invertebrates, *Arenicola marina*, *Cerastoderma edule*, Spionidae, Culbin Sands, recruitment, cockle harvesting.

RESUMEN: CARACTERÍSTICAS ESPACIALES Y TEMPORALES DE LAS COMUNIDADES DE INVERTEBRADOS BENTÓNICOS EN LA LAGUNA DE CULBIN SANDS, MORAY FIRTH, NE DE ESCOCIA, E IMPACTO DE LAS PERTURBACIONES DEBIDAS A LA RECOLECCIÓN DE BERBERECHOS. – En el presente estudio se muestreó la laguna Culbic Sand, un lugar protegido del NE de Escocia, cada 2-4 días, durante un periodo de 3 años (1994-1996), con objeto de estudiar las comunidades de invertebrados bentónicos. *Mytilus edulis* cubrió 18000 m^2. Además se identificaron 53 especies de la macroinfauna. La más conspicua fue *Arenicola marina* (media de hasta 55 ind. m^{-2}) y los bivalvos *Cerastoderma edule* (media de hasta 158 ind. m^{-2}) y *Macoma balthica* (media de hasta 79 ind. m^{-2}) después del asentamiento. El peso seco sin cenizas de la población permanente en áreas expuestas y protegidas fue de 20-32 g m^{-2} yr^{-1}, respectivamente. Muchas especies mostraron un pico de reclutamiento claro en otoño, pero otras (e.g. *Capitella capitata* y Spionidae) mostraron varios picos a lo largo del año. Se compararon también las comunidades, entre puntos de muestreo, con anterioridad y posterioridad a una perturbación incidental de recolección del berberecho *Cerastoderma edule* (Junio de 1995). Uno de los lugares mostró –0.7% de variación del total de la población permanente, y +22% para los berberechos menores, ya que los grandes filtradores fueron eliminados, aumentando con ello el asentamiento larvario. Las poblaciones de Polychaete Spionidae también se expandieron tras la eliminación de los grandes berberechos. Las poblaciones del poliqueto *Arenicola marina* volvieron a sus actividades normales inmediatamente después de la dramática perturbación del sedimento.

Palabras clave: invertebrados bentónicos, *Arenicola marina*, *Cerastoderma edule*, Spionidae, Culbin Sands, reclutamiento, recolección de berberecho.

INTRODUCTION

In intertidal areas, polychaetes, oligochaetes, molluscs and crustaceans are the most represented benthic macrofauna in sediments, and provide the main food source for many epibenthic predators (such as shrimps, crabs and fish; e.g. Raffaelli *et al*., 1989). These areas are also known to be nursery areas for many fish species (e.g. Modin and Pihl, 1996), and provide feeding grounds for several bird species (e.g. Piersma *et al*., 2003*;* van Gils, 2006a, 2006b). On sandy beaches in the NE Atlantic, polychaetes and oligochaetes are the most numerous. Among the most common polychaete species are *Arenicola marina, Nereis diversicolor, Capitella capitata, Fabricia sabella*; the most common oligochaete is *Tubificoides benedinii*. However, in terms of biomass, bivalve species *Mytilus edulis, Cerastoderama edule* and *Macoma balthica* are usually the most represented (e.g. Kamermans, 1994), although the polychaete *Arenicola marina* may dominate some flats (e.g. Asmus, 1987; Mendonça, 1997). Gastropod species *Hydrobia ulvae* and *Littorina* spp. may also reach high densities in the sediment, and be very important for many bird and fish species (e.g. van Gils, 2006a). Amphipod (especially *Gammarus* spp., *Corophium* spp. and *Bathyporeia* spp., which are also epibenthic species), isopods (e.g. *Eurydice pulchra*) and decapod (especially *Carcinus maenas*) crustaceans are also common in sediments, and constitute an important source of energy for many predators (e.g. Bonsdorff *et al.,* 1995).

The reproductive processes of invertebrates are highly dependent on temperature, thus the abundance of individuals of a given species will vary according to the time of year. As stated by Guillou *et al.* (1992), although temperature values may influence the reproductive cycle itself, in an ecological context (because there are intra- and interspecific interactions), other factors may be of equal if not more importance. In other words, early maturation is influenced by temperature, which affects the reproductive cycle, but recruitment probably depends more on biotic factors. Shallow coastal waters are also known to be more productive than the surrounding deeper waters, as inorganic and organic nutrients are often in much higher supply and they experience higher temperatures in summer. Therefore, shallow water environments provide suitable conditions for the recruitment of many species.

Finally, disturbances may also determine species survival, although many species have developed adaptive mechanisms to overcome stressing environmental conditions. The distribution and abundance of invertebrate species is closely associated with sediment properties and tidal height. With decreasing exposure and increasing stability, species richness, abundance, and total biomass increase to reach a maximum on sheltered shores (e.g. Raffaelli and Hawkins, 1996). The most obvious change occurs along the gradient from exposed to sheltered habitats, by the progressive addition of species and the loss of those unable to tolerate the fine-particles in mudflats (Allen and Moore, 1987). Mobile and robust forms, such as cirolanid isopods (e.g. *Eurydice pulchra*) and polychaetes such as *Ophelia rathkei*, characterise the more exposed beaches, as other groups are unable to survive in these highly unstable habitats.

In the present study, the benthic macrofauna (>500 μm) of Culbin Sands lagoon, a protected area in the Moray Firth, NE Scotland, was surveyed at several sites within the lagoon every 2 to 4 weeks for three years (1994-1994), in order to investigate species diversity and abundance (both in terms of numbers and standing stock), and seasonal variations. However, 1.5 years after the start of our sampling programme, an unprecedented and unexpected cockle harvesting event took place, which dramatically disturbed the sediment as it was conducted using tractors with mechanical rakes in some areas, and by boats using a suction dredge in other areas. Therefore, there was an opportunity to compare annual biomass fluctuations "before" and "after" the disturbance.

METHODS

The study area: Culbin Sands lagoon

Culbin Sands lagoon, in NE Scotland, is a 3-km-long and 1-km-wide coastal wetland, separated from the Moray Firth by two sandy peninsulas that form the Culbin Bar. The area is macro-tidal, and during low tide only the main gully is permanently submersed, although during high tide, almost the entire lagoon is covered by seawater. The seaward dune (Lady Culbin), the lagoon (with 1.5 ha of intertidal flats), and the adjacent planted forest (28 ha on the landward side) are part of a protected area, notified in July 1973 and re-notified as a Special Site of Scientific Interest (SSSI) under the Wildlife and Countryside Act of 1981. The area became a SSSI because of its exceptional geological interest due to the scale (as part of the largest sand dune system in Britain), complexity and diversity of its coastal geomorphology. It is undergoing a gradual westward migration of up to 1 m yr^{-1} (Smith, 1986).

Previously published studies on Culbin Sands protectorate were mostly related to the unstable characteristics of its sand dune, which made it a hazardous area. On several occasions it covered the existing human settlements overnight. Therefore, since the 19^{th} century, the members of the neighbouring surviving villages have kept their distance. As a consequence, apart from planting the stabilizing forest and the poles erected on the tidal flats during World War II as glider defence to prevent vessels landing, the area has not been subjected to any other anthropogenic impacts. The isolation of the area for a century (perhaps more) has provided an opportunity for wildlife populations to prosper in an undisturbed environment, and it is currently a site of interest for its biodiversity, both in aquatic and terrestrial habitats.

As part of our extensive studies conducted at Culbin Sands lagoon, the impacts of overwintering teleost fish and of shorebirds on the benthic invertebrate communities have been described by Mendonça *et al.* (2007a, 2007b). In the present study, we looked in detail at the benthic invertebrate community itself, and analysed the impact of the cockle harvesting event, which took place within the protected area in June 1995. In order to avoid this event happening again, access to the area is now restricted by a gated road, and permission from the authorities is required for both visitors and researchers alike.

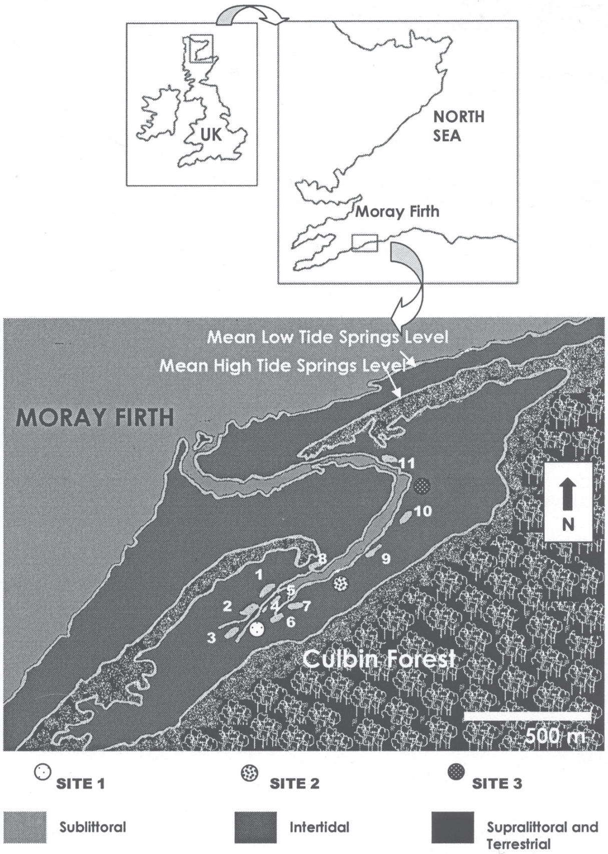
Spatial and temporal characteristics of benthic communities

In the present study, the area covered by musselbeds *Mytilus edulis* was estimated partially by direct mapping using a Global Positioning System (GPS) MIDAS II mobile receiver (MIDAS II, 1993) in the field, which registered continuous information on the co-ordinates of the perimeter of each musselbed. This information was complemented by an aerial photograph taken in July 1994 (scale 1:1500; source: PhotoAir, provided by the Scottish Natural Heritage in Elgin, Scotland), as there were rarely sufficient satellites (at least five).

In order to study the invertebrate macrofauna in sediments outside musselbeds, a pilot survey conducted in February 1994, at several sites, showed that only three sampling sites should be selected for a sampling programme, as these would most likely differ in their hydrodynamic regime, although they were all reached by seawater between 3.5 and 4 h after the low tide. Recorded median particle sizes were up to 120 μm for Sites 1 and 3, and 130-140 μm for Site 2; silt contents of 0-5% were recorded for all three sites (Mendonça, 1997). The pilot survey also showed that six cores (100 cm^2 area; taken to a sediment depth of 15 cm) provided as much information as ten cores on the abundance of most species, with 5% error. The minimum number of cores to be collected was investigated every six months, in order to check whether the amount of samples was still enough, which it was.

Following results from the pilot survey, samples were collected monthly during winter and every 2 weeks in summer, from May 1994 to August 1996, from within a randomly placed 1 m^2 quadrat at low tide. Sediment samples were sieved over a 500 μm mesh and preserved in alcohol (70%). As larger species could not be effectively sampled by this method (e.g. Holme and McIntyre, 1984), lugworm *Arenicola marina* densities were estimated by counting the number of casts in 10 quadrats of 0.5 m x 0.5 m randomly placed at each of the sites. Lugworms were sampled only in winter (February 1994 and February 1995) and summer (July 1994 and August 1996). *Semibalanus* spp. were attached to dead shells and were especially abundant on the poles erected during World War II, more specifically at the levels reached by the high tide. These species were not sampled in this study.

Data on invertebrate abundance in core samples were used to conduct the following multivariate analyses (e.g. KCS, 2001): The Shannon Diversity Index, H ($H = -\sum p_i \ln p_i$), i ranges from 1 to S, with S being the total number of species in the community (or richness). For each species, the proportion of individuals or biomass that contributes to the total in the samples is p_i for the i^{th} species); The Pielou Evenness Component of the Diversity: $E = H/\log_2 S$; and DECORANA within each site over time, and between the three sampled sites over time. Abundance of individuals *Arenicola marina* in quadrats was compared between winter and summer at the three sites and between seasons and sites by TWO-WAY ANOVA (e.g. Sokal and Rohlf, 1984).



MUSSELBED #	AREA (m^2)	MUSSELBED #	AREA (m^2)
1	2000	7	1250
2	5700	8	600
3	250	9	400
4	1500	10	1050
5	3550	11	700
6	1050	TOTAL	18050

Fig. 1. – Culbin Sands, Moray Firth, NE Scotland, with the location of the three sampled sites (1-3) and the musselebeds of *Mytilus edulis* indicated.

Standing stock of benthic communities, before and after the cockle harvesting event

Standing stock or mean available biomass in sediments (g AFDW m^{-2} yr^{-1}; AFDW = ash free dry weight) was estimated for each species based on the mean numbers of individuals (ind. m^{-2}, extrapolated from ind. $core^{-1}$), and the mean individual AFDW (obtained from the mean individual dry weight, DW, of 30 individuals per size class, when size class separation was possible). Bivalve *Cerastoderma edule* individuals were separated into five size classes (500-1000, 1000-1500, 1500-2000, 2000-3000, and >3000 μm). For other species, as most individuals were of a similar size, only two size classes were considered (500-1000 and >1000 μm). The shell-

Table 1. – Species checklist for benthic invertebrate macrofauna at Culbin Sands lagoon, NE Scotland, found in this and previous studies (1 = Recorded; 0 = Not recorded)

		Previous estudies (*)	This study
Foraminiferans	Unidentified	0	1
Nematodes	Unidentified	1	1
Nemerteans	Unidentified	1	1
Polychaetes	*Arenicola marina*	1	1
	Capitella capitata	1	1
	Chaetozone setosa	1	1
	Cirratulus cirratus	1	1
	Eteone longa	1	1
	Fabricia sabella	1	1
	Harmthoe sp.	0	1
	Heteromastus filiformis	0	1
	Malacoceros sp.	1	0
	Nereis diversicolor	1	1
	Nereis virens	0	1
	Nepthys hombergii	1	1
	Nepthys sp.	0	1
	Notomastus sp.	0	1
	Ophelia rathkei	1	1
	Ophelia cluthensis	1	0
	Orbinia sp.	0	1
	Phyllodoce mucosa	1	1
	Polydora ciliata	1	1
	Pygospio elegans	1	1
	Scolelepis squamata	1	1
	Scoloplos armiger	1	1
	Sphaerodoridium minutum	0	1
	Spiophanes bombix	1	1
	Travisia forbesi	1	1
Oligochaetes	*Tubificoides benedini*	1	1
	Unidentified	1	1
Sipunculids	*Priapulus* sp.	1	1
Crustaceans	*Semibalanus* sp.	1	1
	Bathyporeia pilosa	1	1
	Bathyporeia sarsi	0	1
	Corophium arenaria	1	1
	Corophium volutator	1	1
	Eurydice pulchra	1	1
	Gammarus duebeni	1	0
	Gammarus sp.	0	1
	Talitrus saltator	1	1
Insects	Chironomid larvae	0	1
	Staphilinidae	1	1
	Limnophilus sp.	1	0
	Unidentified larvae	0	1
Chitons	*Lepidochitona cinereus*	0	1
	Tonicella marmoreal	0	1
Gastropods	*Hydrobia ulvae*	1	1
	Littorina littoreia	1	1
	Littorina sp.	1	1
	Patella vulgata	1	1
	Retusa obtusa	1	1
Bivalves	*Cerastoderma edule*	1	1
	Macoma balthica	1	1
	Mya arenaria	1	1
	Mytilus edulis	1	1
	Tellina tenuis	1	1
Ascideans	*Molgula* sp.	0	1
TOTAL spp.		42	53

(*) Review of unpublished reports available for the site (Mendonça, 1997).

free dry weight (SFDW) was estimated for species with a shell (bivalves and gastropods). Gastropods (mostly *Hydrobia ulvae*) were not easily dissected from the shell because of their small size, but flesh dry weight (FDW) was estimated as 27% of DW, following studies in the area conducted by Raffaelli and Boyle (1986). All material was dried for 24 h at 70°C to constant weight, in an incinerator, and AFDW was derived from DW using standard conversion factors estimated for these species in NW Europe (Rumohr *et al.*, 1987). Biomass values were converted into Joules, using conversion factors (Cummins and Wuycheck, 1971; Ankar and Elmgreen, 1976; Rumohr *et al.,* 1987; Brey *et al.,* 1988), and could also be converted into other units according to McNeill and Lawton (1970) as 1 cal = 4.187 J; 12 kcal = 1 gC.

For each of the most conspicuous species and in particular for the different size classes of cockles *Cerastoderma edule,* variations (%) in annual mean biomass before (May 1994 to May 1995, or 1994/95) and after (June 1995 to August 1996, or 1995/96) the harvesting event were investigated.

RESULTS

Spatial and temporal characteristics of benthic communities

A total of 11 musselbeds of *Mytilus edulis* were registered at Culbin Sands lagoon, covering an area of 18050 m^2 (Fig. 1), and 53 macrobenthic species (11 spp. more than previously recorded in the area) were identified in sediments outside the musselbeds (Table 1). The most conspicuous species were the lugworm *Arenicola marina* (mean up to 55 casts m^{-2}), and bivalve species: *Cerastoderma edule* (mean number up to 158 ind. m^{-2}) and *Macoma balthica* (mean number up to 79 ind. m^{-2}), with older bivalves occurring at Site 3 (Table 2). Chitons *Lepidochitona cinereus* and *Tonicella marmoreal*, the limpet *Patella* sp. and ascideans *Molgula* sp.were only found close to musselbeds and attached to shells.

TABLE 2. – Mean number of individuals per area per annum (ind. m^{-2}) in 1994-1995 and 1995-1996 at the three sampled sites at Culbin Sands, Moray Firth, Scotland, and respective biomass (g AFDW m^{-2} yr^{-1} and kJ m^{-2} yr^{-1}), outside musselbed areas (not sampled: musselbeds and *Semibalanus* sp. population on poles left by World War II; species with an abundance <2 ind. m^{-2} at all sites were not listed).

Benthic macrofauna		Abundance (ind. m^{-2})					
			1994/95			1995/96	
Site		1	2	3	1	2	3
Nematodes		1710	388	684	3210	342	342
Nemerteans		300	80	250	350	75	280
Polychaetes	*Arenicola marina*	55	53	54	50	50	52
	Capitella capitata	289	26	236	500	131	218
	Fabricia sabella	9	4	52	4	13	5
	Nereis diversicolor	5	5	13	4	4	6
	Nephtys hombergii	0	5	15	0	5	10
	Ophelia rathkei	0	25	30	0	5	10
	Phyllodoce mucosa	66	52	66	53	13	50
	Polydora ciliata	13	13	1	4	4	13
	Pygospio elegans	26	26	52	105	131	79
	Scoloplos armiger	54	30	13	53	4	26
	Travisia forbesi	3	3	4	4	4	4
Oligochaetes	*Tubificoides benedini*	3000	421	1342	2315	263	315
Crustaceans	*Bathyporeia pilosa*	5	210	131	6	157	13
	Corophium volutator	5	0	0	10	0	0
	Eurydice pulchra	0	0	5	0	0	4
Insect larvae	Chironomidae	290	13	150	13	3	26
Gastropods	*Hydrobia ulvae*	10	0	0	6	0	0
	Littorina littorea	13	10	10	13	6	6
	Retusa obtusa	15	5	10	13	5	6
Bivalves	*Cerastoderma edule*						
	500-1000 µm	43	36	30	35	27	56
	1000-1500	32	22	80	35	27	56
	1500-2000	15	10	24	18	5	30
	2000-3000	10	8	17	8	2	25
	>3000 µm	5	3	7	2	0.2	4
	Macoma balthica	79	26	52	53	26	52
	Mya arenaria	3	0	0	2	0	0
	Tellina tenuis	13	5	5	13	5	6
TOTAL (ind. m^{-2})		6173	1559	3583	7046	1403	183
TOTAL (g AFDW m^{-2})		30.64	25.03	32.01	23.52	20.50	24.29
TOTAL (kJ m^{-2})		702	576	740	541	472	559

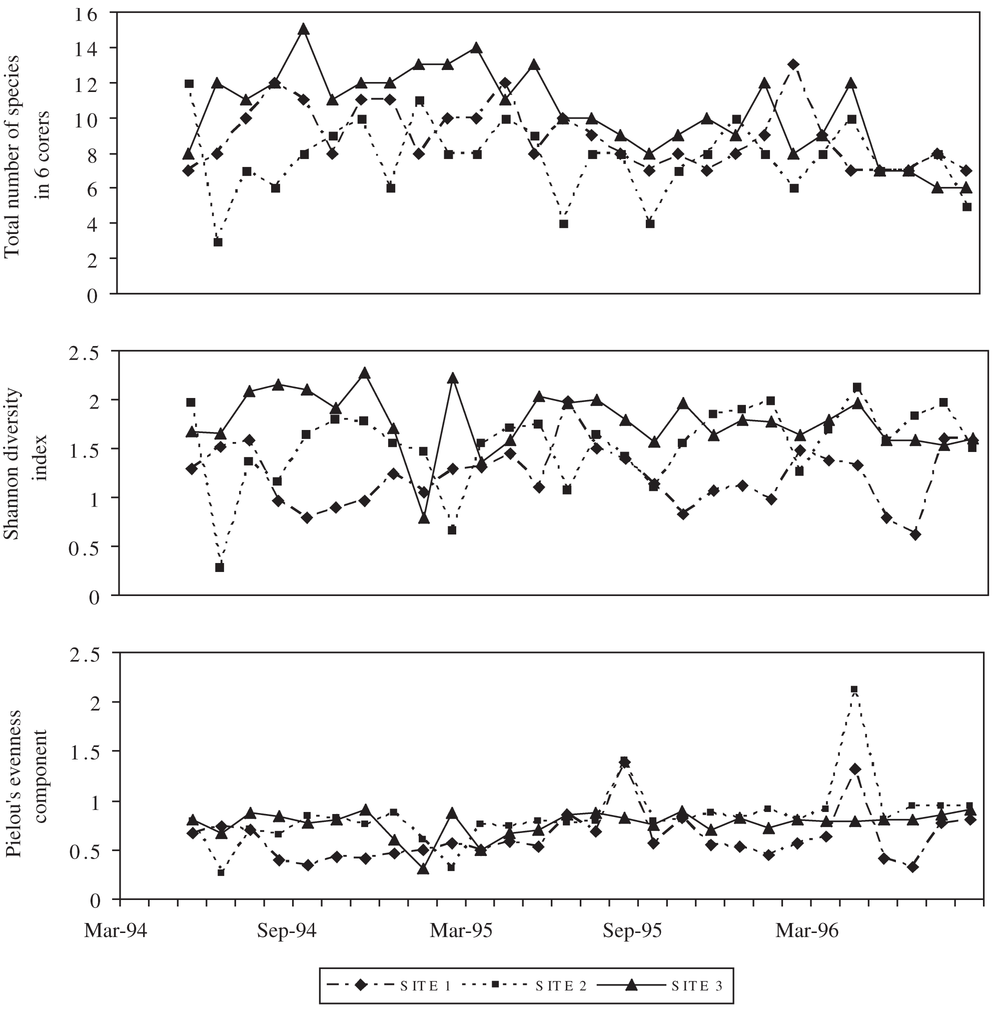


FIG. 2. – Comparison of diversity indices at three sampled sites during 1994-1996 for benthic macrofauna at Culbin Sands lagoon, NE Scotland.

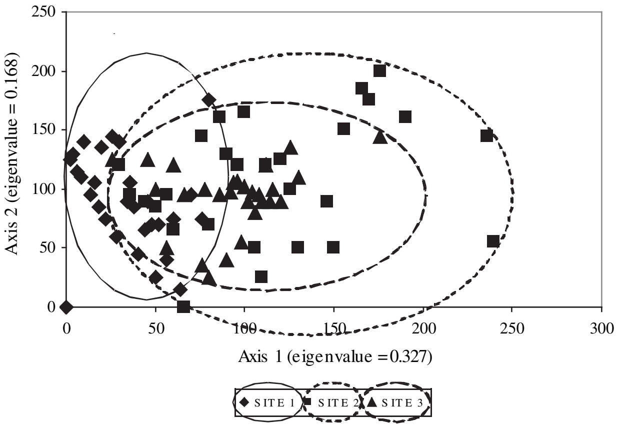


FIG. 3. – Comparison of the three sampled sites during 1994-1996 for benthic macrofauna at Culbin Sands lagoon, NE Scotland (test: DECORANA, only values along the two main eigenvalues were plotted).

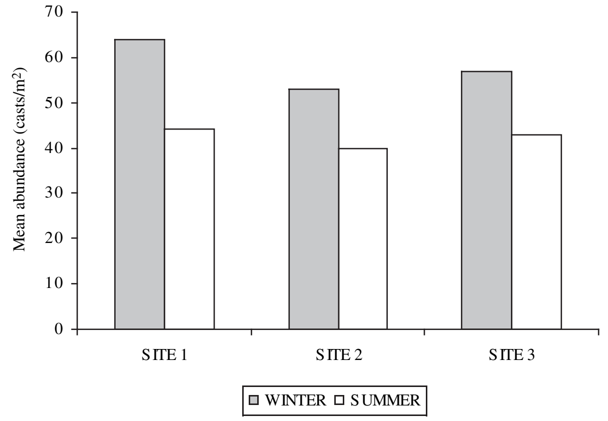


FIG. 4. – Mean abundance of lugworms *Arenicola marina* at Culbin Sands lagoon, NE Scotland, in winter and summer, at the three sampled sites ($P<0.01$ between seasons in 1995, and between seasons and sites in 1996; test: TWO-WAY-ANOVA).

In general, macroinvertebrates were more abundant at Sites 1 and 3, which also had more species, larger diversity indices and respective evenness components (Fig. 2). In fact, DECORANA results showed that the more sheltered sites (1 and 3) presented less variation (along the axis of higher eigenvalue) than the most exposed site (Site 2) (Fig. 3).

The mean abundance of *Arenicola marina* (casts

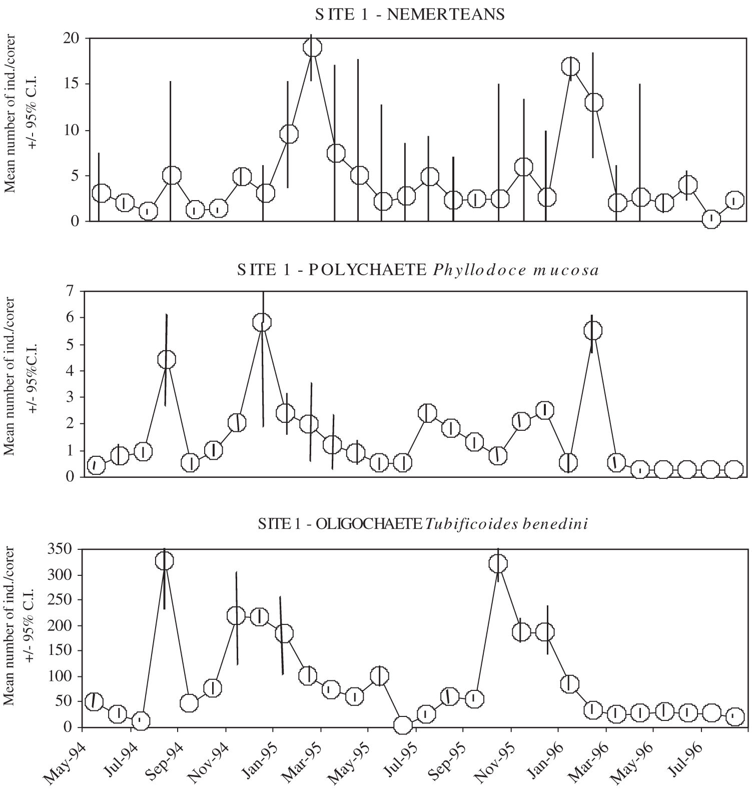


FIG. 5. – Mean abundance of some of the most conspicuous species at Site 1, Culbin Sands lagoon, NE Scotland during 1994-1996 (confidence intervals, C.I., when not fully represented, can be obtained from the symmetrical value).

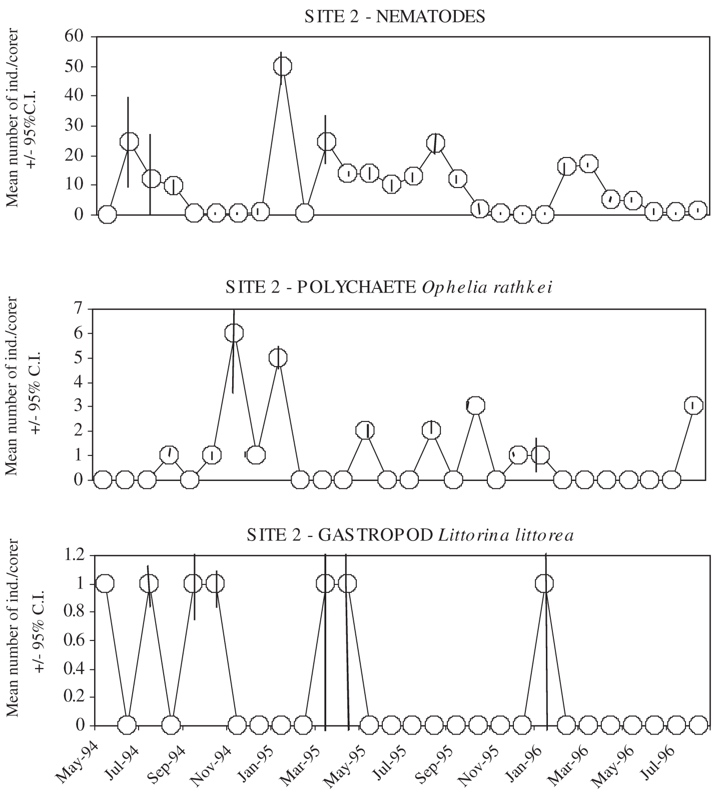


FIG. 6. – Mean abundance of some of the most conspicuous species at Site 2, Culbin Sands lagoon, NE Scotland during 1994-1996 (confidence intervals, C.I., when not fully represented, can be obtained from the symmetrical value).

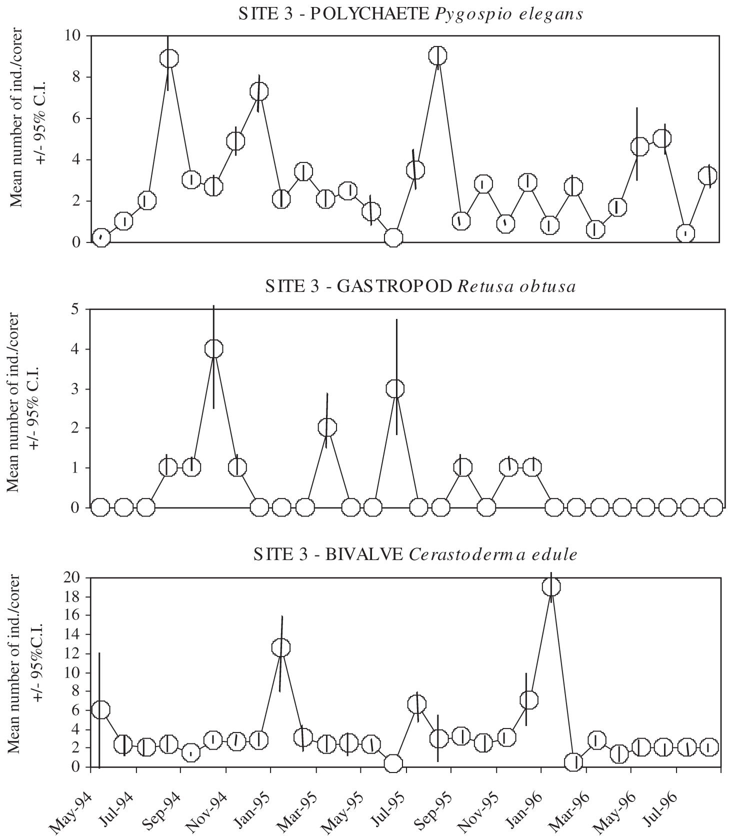


FIG. 7. – Mean abundance of some of the most conspicuous species at Site 3, Culbin Sands lagoon, NE Scotland during 1994-1996 (confidence intervals, C.I., when not fully represented, can be obtained from the symmetrical value).

m^{-2}) at Culbin Sands lagoon, NE Scotland, in winter was significantly higher than in summer at all sites (P<0.01 between seasons in 1995, and between seasons and sites in 1996; TWO-WAY-ANOVA; Fig. 4). However, the mean abundance of other benthic macrofaunal species did not always present seasonal variations or they were not synchronised. For instance: Nemerteans peaked in winter, as well as the cockle *Cerastoderma edule* after the recruitment in autumn; Oligochaetes and the gastropod *Retusa obtusa* peaked in summer; Nematodes did not show any clear peak; whilst the polychaete species (e.g. *Phyllodoce mucosa, Pygospio elegans* and *Ophelia rathkei*) had several peaks in the year (Figs. 5-7). In fact, DECORANA showed little evidence of a strong seasonal cycle in abundance in sediments at the three sites, with more variation in summer at Site 1, and less variation in summer at sites 2 and 3 (Fig. 8).

Standing stock of benthic communities, before and after the cockle harvesting event

An overall standing stock of benthic macrofauna, outside musselbeds, for Culbin Sands lagoon, was estimated to be 26 g AFDW m^{-2} yr^{-1}, which is equivalent to 500 kJ m^{-2} yr^{-1}. Standing biomass was higher at more sheltered sites (Sites 1 and 3) than at the more exposed site (2) (Table 2). The biggest contributors were polychaetes (lugworms *Arenicola marina* contributed 95% of the total polychaete standing stock) and bivalves (cockles *Cerastoderma edule* contributed 85% of the bivalve standing stock) (Fig. 9).

Although some species showed a clear negative reaction to the disturbance caused by the harvesting event of June 1995, others, such as the polychaete *Arenicola marina*, seemed to cope well (including at Site 2), as they were observed returning to their activity just a few hours after the disturbing harvesting event. However, nemerteans, the Spionidae polychaetes *Polydora ciliata, Pygospio elegans* and *Scoloplos armiger*, the cosmopolitan polychaete *Capitella capitata,* and the small sized bivalve *Tellina tenuis* increased their abundance after the disturbance of the harvesting event (Fig. 10). Differences in abundances of several species, including cockles, between Sites 1 and 3 may have been due to the fact that Site 3 still had higher amounts of larger cockles

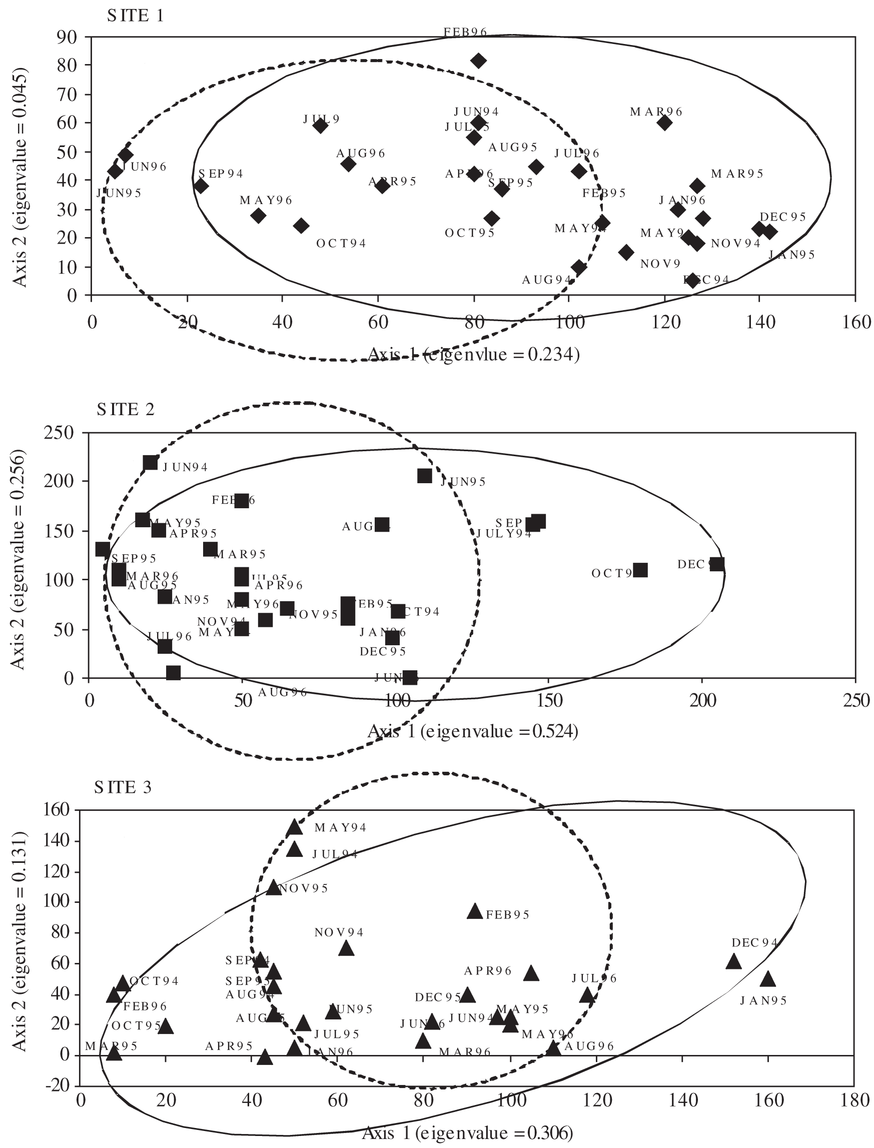


FIG. 8. – Comparison of benthic invertebrate macrofauna in summer (----) and winter (—) at the three sampled sites, during 1994-1996, at Culbin Sands lagoon, NE Scotland (test: DECORANA, only values along the two main eigenvalues were plotted).

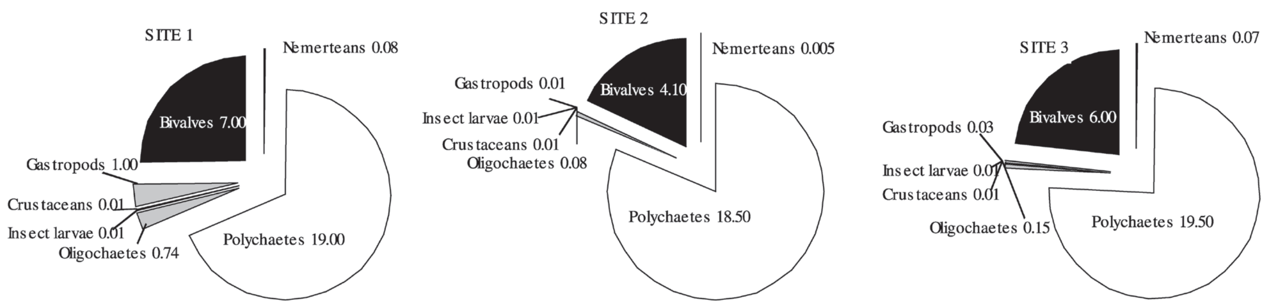


FIG. 9. – Standing stock of benthic invertebrates (in biomass, g AFDW m^{-2} yr^{-1}), outside musselbed areas, at Culbin Sands lagoon, NE Scotland, during 1994-1996: *Arenicola marina* contributed to 95% of the total polychaete stock, and *Cerastoderma edule* contributed to 85% of the total bivalve stock.

(Fig. 11) and therefore higher filtration rates, which affect the recruitment not only of bivalve species, but also of other species and of suspended particles in the water column. The removal of larger filter feeders probably contributed to the increase in biomass of smaller-sized bivalves in the following year,

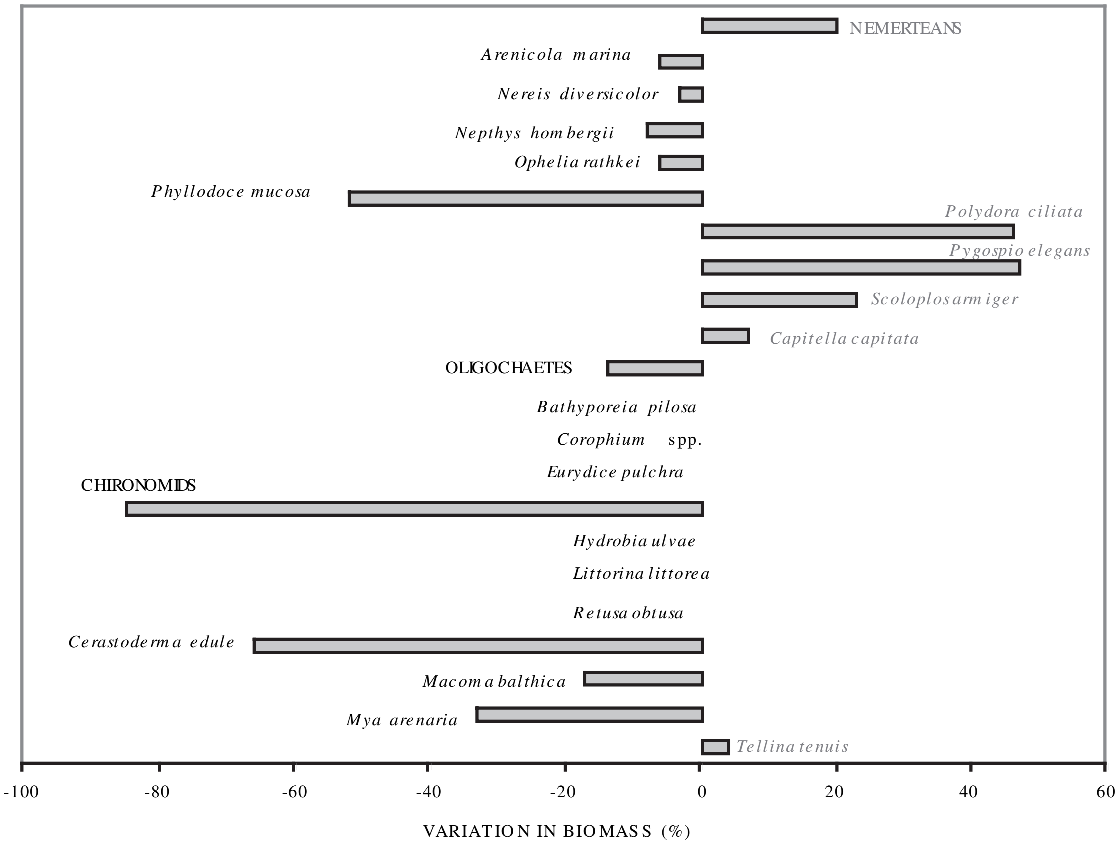


FIG. 10. – Variation in standing stock (biomass) of invertebrates (benthic and small epibenthic amphipods), "before" and "after" the cockle harvesting, which occurred in June 1995.

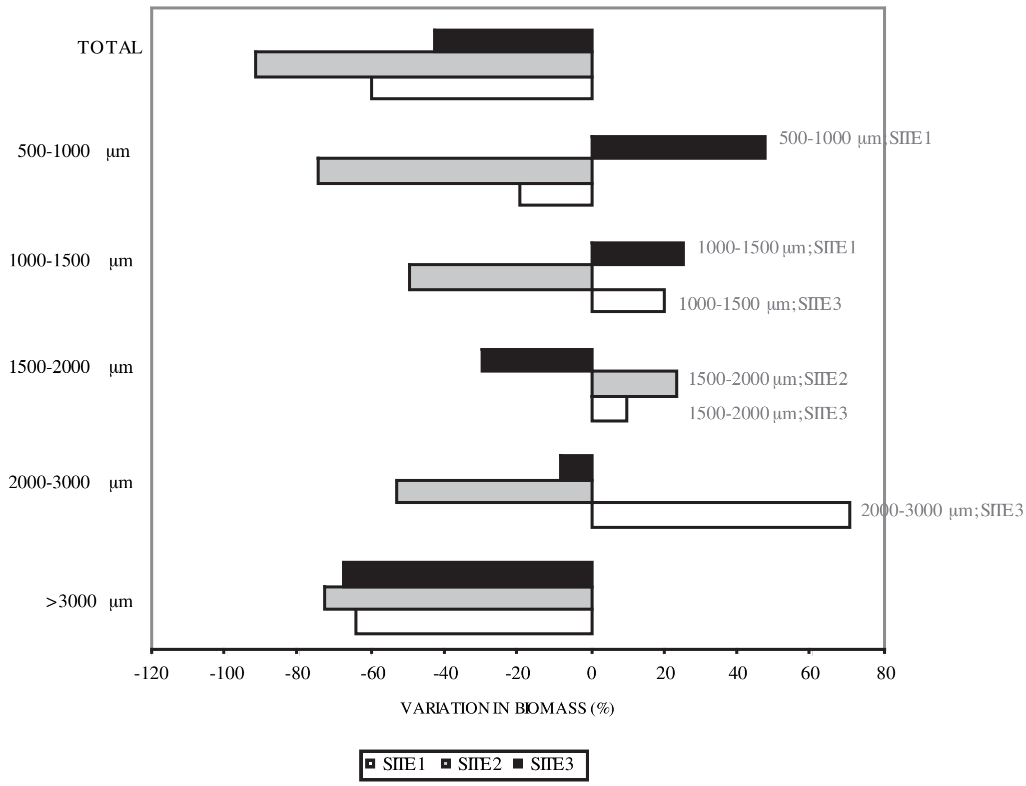


FIG. 11. – Variation in standing stock (biomass) of cockles *Cerastoderma edule* according to size class, "before" and "after" the cockle harvesting, which occurred in June 1995.

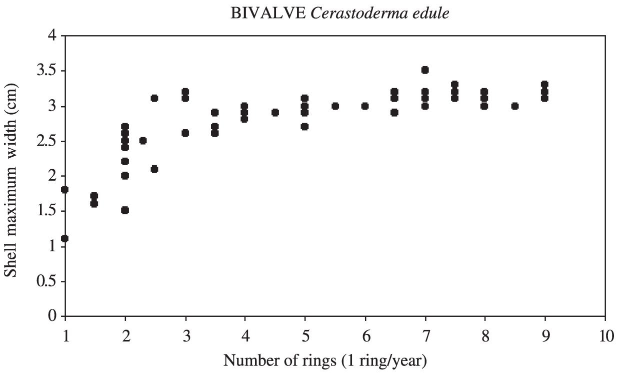


FIG. 12. – Age of cockles at Culbin Sands lagoon, from a pooled sample of 90 ind. from all sampled sites.

as before the cockle harvesting, some *Cerastoderma edule* individuals were at least 9 years old (Fig. 12).

DISCUSSION

Spatial and temporal characteristics of benthic communities

The presence of several musselbeds of *Mytilus edulis* in such a small area at Culbin Sands lagoon may have negative effects on the settlement of larvae of many species, including on cockle *Cerastoderma edule* beds, which lie at high levels on the shore. Studies by Kamermans (1994) showed that cockles have reduced shell increments, lower body weight and poor condition when inside musselbeds compared with outside. This is probably due to the effects of mussels on the particle concentration in the water column (Ertman and Jumars, 1988). However, re-suspension of the sediment by bivalve activity disorientates species such as the small epibenthic amphipod *Corophium* spp. (Flach and Debrwin, 1994) and probably other amphipods such as *Bathyporeia* spp., which then become easy prey for larger epibenthic predators (Mendonça *et al.,* 2007a).

Outside musselbeds, the most numerous infaunal taxa were nematodes, polychaetes, oligochaetes and bivalves; and the list of species found for Culbin Sands lagoon was in fact not very different from that presented by Raffaelli and Boyle (1986) for Nigg Bay, a nearby area, also in the Moray Firth. However, with the exception of the nemerteans, species abundance was generally lower at Culbin Sands lagoon than at other sites in the Moray Firth. This was probably due to differences in sediment characteristics. For instance, the silt content of Nigg Bay may be higher than 20%, whereas it rarely reaches that value at Culbin Sands (Mendonça, 1997). Nemerteans occur under stones, in sand, mud, rock, amongst turf algae, and other populations of sedentary organisms (Hayward and Ryland, 1990); thus, the presence of dense musselbeds may explain between-site differences in the numbers of nemerteans within the Moray Firth. Most species found at Culbin Sands were also found in the Ythan estuary, NE Scotland, just outside the Moray Firth area. This is a muddier coastal ecosystem, but it has about 15 more species than Culbin. However, Ythan has been more extensively studied for at least 30 years (Milne and Dunnet, 1972; Chambers and Milne, 1975), and further studies on the musselbeds at Culbin could lead to a longer species checklist. Interestingly, most species found at Culbin Sands were also found in the Gullmar Fjord, Sweden (Evans, 1982), which is an area with sediment characteristics closer to those at Culbin Sands although with harsher winter conditions than at Culbin.

Crustaceans and gastropods were the least abundant taxa at Culbin Sands lagoon, with the amphipod *Bathyporeia* spp. being the most common epibenthic crustacean species, and *Eurydice pulchra* the most common benthic crustacean species, which reflects the highly unstable sediment characteristics of Culbin Sands lagoon. The small epibenthic crustaceans *Bathyporeia* spp. have seasonal migration into the water column (Persson, 1982), so that abundance estimates based on core sampling may lead to underestimated densities. Other species that were also probably underestimated were nematodes, the gastropod *Littorina* spp. and chironomid larvae. Nematodes are meiofaunal organisms, and the numbers presented here only refer to those individuals retained in the 500 μm sieve, so that most individuals probably passed through the mesh. *Littorina* spp. were found in lower numbers in the core samples, but were observed at higher densities in the musselbeds, or associated with mussel clumps, where samples were not taken. However, it is probable that abundance of many species is higher in areas covered by musselbeds, mussel clumps and those associated with macrophytes or other biogenic structures (e.g. Cardoso *et al.,* 2004a, 2004b), despite limitations imposed by the larvae-retaining filter-feeding communities. Persson (1982) has also shown that abundance and biomass of invertebrates is higher in vegetated substrates. Drifting algae may also enhance higher invertebrate abundance; however, if algal mats are very abundant, they may increase anoxia and have the opposite effect.

Chironomid larvae were found at very low abundances in the sediment samples sieved through the 500 μm sieve, but would have been found in much higher numbers if sampling had also been directed at meiofauna.

Lugworms *Arenicola marina* were also more abundant in winter than in summer, in agreement with other studies (e.g. Flach, 1992). This may be related to their pattern of recruitment, but it is probably due to depletion by predators in summer when epibenthic communities such as fish and shrimps are more abundant (Mendonça *et al.,* 2007a). Lugworms are known to have negative effects on the abundance of juveniles of other polychaetes such as *Nereis diversicolor, Nephtys hombergii, Heteromastus filiformis, Scoloplos armiger, Pygospio elegans* and *Capitella capitata*, and on bivalves *Mya arenaria, Cerastoderma edule* and *Macoma balthica*, because of their burrowing behaviour which causes high sediment resuspension that affects larval settlement (e.g. Lin and Hines, 1994; Flach and Debrwin, 1994).

Cockles at Culbin Sands also occurred in higher abundances than in the Gullmar Fjord, Sweden, where they can reach a monthly mean of 63 ind. m^{-2} (Evans, 1982). At Culbin Sands, the peak of abundance was after the major settlement, which occurred in late autumn to early winter in 1994-1995 and 1995-1996. Reproductive processes in bivalves are dependent on water temperatures, which lag behind air temperature so that autumn temperatures remain high. They are also dependent on the phytoplankton bloom. This means that the autumn months are the best time for bivalve recruitment at higher latitudes. In fact, Guillou (1994) has recorded similar findings in northern Brittany. However, the major settlement is not just related to temperature. According to Guillou *et al.* (1992), temperature has more influence on the reproductive cycle itself, but in an ecological context, other factors may be of equal if not more importance. In other words, early maturation is influenced by temperature, which affects the reproductive cycle, but recruitment probably depends more on biotic factors.

In summary, with the exception of the lugworm *Arenicola marina*, infaunal species were found in higher abundances in the Ythan estuary, than at Culbin Sands (Milne and Dunnet, 1972; Chambers and Milne, 1975), but again, more in conformity with results for the Gullmar Fjord, Sweden (Evans, 1982). For instance, in the Ythan estuary, *Macoma balthica* can reach 6 x 10^3 ind. m^{-2} (maximum at Culbin was 184 ind. m^{-2}), *Hydrobia ulvae* 120 x 10^3 ind. m^{-2} (the maximum at Culbin was 26 ind. m^{-2}, and the monthly mean in the Gullmar Fjord was up to 1130 ind. m^{-2}), and *Corophium* spp. 60 x 10^3 ind. m^{-2} (the maximum at Culbin was 25 ind. m^{-2} and the monthly mean in the Gullmar Fjord was up to 969 ind. m^{-2}). However, at Culbin Sands lagoon, sites with more stable sediment conditions were characterised by higher numbers of individuals, which is also consistent with several other authors (e.g. Hayward and Ryland, 1990). Diversity also generally declines on shores affected by low salinity (Raffaelli and Hawkins, 1996), but this is not likely to be the case at Culbin Sands, where there is no significant, direct freshwater input.

However, the absence of a clear temporal cyclical tendency is probably also due to the highly unstable sediment characteristics. The presence of species such as *Eurydice pulchra* and *Ophelia rathkei,* which are typically associated with these conditions (e.g. Raffaelli and Hawkins, 1996), evidences this. Although a moderate disturbance may enhance abundance and variability of individuals in a population, too much disturbance and stress make the shores devoid of species (Warwick and Clarke, 1993).

Standing stock of benthic communities, before and after the cockle harvesting event

The values of the standing stock estimated for Culbin Sands lagoon were also lower than those found in muddier areas, just outside the Moray Firth (e.g. Ythan Estuary, Scotland; Milne and Dunnet, 1972; Chambers and Milne, 1975), or in seagrass beds (e.g. Gullmarsvik, Sweeden; Moller and Rosenberg, 1982). They are nevertheless higher than those found in most sandy habitats in the North Sea, Baltic Sea and the Wadden Sea. In fact, the values encountered for Culbin Sands are more in conformity with values obtained for sandy sites in Gullmar Fjord in Sweden (Evans, 1982), which are areas with physical and sediment characteristics similar to Culbin Sands, although with harsher winter conditions. Higher values for muddier areas are probably fully explained by the more stable sediment characteristics, milder hydrodynamic conditions (with not as strong currents), and higher content of organic matter. Vegetated areas also promote sediment stability and provide a refuge for invertebrates to escape from predators.

Differences in standing stock, "before" and "after" the cockle harvesting event of June 1995, could have been due to natural variations as recorded in other studies (e.g. Beukema *et al.,* 1993); however, they are more likely to have been caused by the disturbance provoked by the cockle harvesting activities. In fact, many abiotic (e.g. wave action, sediment characteristics) and biotic factors (e.g. action of parasites and diseases) may affect the recruitment and settlement of invertebrate species. Interestingly, it seems that there were no negative effects caused by the disturbance on the cockle population itself. Cockles were in fact more abundant in number (because of successful recruitment and settlement) one year after harvesting than they were before, and in general their production also increased, especially at Site 1. Larger bivalves were mostly harvested, and this might have enhanced the survival of smaller individuals, as bivalves are filter-feeders. Larger bivalves have higher filtration rates and they may inhibit their own and other species´ larval settlement and the growth rate of smaller individuals (e.g. Bachelet *et al*., 1992).

Nevertheless, it seems that, especially at Site 2, the harvesting disturbance negatively affected other species. Harvesting by tractor clearly affected the topography of the shore, and tons of sediment were removed from harvesting areas and deposited many metres away. Cockles broken during the harvesting and left to decompose at the site would have contributed (at least temporarily) to anoxic conditions in the sediment. No sediment samples were collected for chemical or bacteriological analysis, but the effect was obvious from the smell affecting the whole area, even on windy days, at all sites. Although it may not apply to this case, the effects of hypoxia on invertebrate populations have been discussed by Diaz and Rosenberg (1995); these effects probably provoked a decrease in the annual production values, causing differences in annual standing stock.

In agreement with the results obtained in this study, previous studies also showed that removing cockles led to the proliferation of the Spionid polychaete *Pygospio elegans* (Desprez *et al.*, 1992) and the Capitellid polychaete *Capitella capitata* (Chesney and Tenore, 1985). In fact, the significance of biological and physical disturbances for structuring bottom communities, and the importance of moderate disturbances or stress (natural or from anthropogenic sources) in increasing variability, has been discussed by some authors (e.g. Brey, 1991; Warwick and Clarke, 1993). It has been concluded that if disturbance is not extreme, re-colonisation of sediments is a short-term process.

However, although the removal of larger cockles may enhance larval settlement in some species, it can negatively affect the bird populations feeding on tidal flats (e.g. van Gils, 2006a, 2006b). Therefore, it is not recommended to encourage cockle harvesting in a protected area such as Culbin Sands, where many shorebird species (Mendonça *et al.,* 2007b) depend on these resting and feeding grounds.

ACKNOWLEDGEMENTS

During this study, the first author was supported by the Ministry of Science, Technology and Higher Education of Portugal (PhD Research Fellowship Reference BD/CIÊNCIA/2593-IG, 25%co-financed by the European Union Social Fund). We are also grateful for the logistics provided by the University of Aberdeen, and the help of Mr. Robert Donaldson of the Bodiversity and Conservation Field Station. We gratefully appreciate the help provided by the concerned authorities to access the study site, especially Mr. David Law of the Scottish Natural Heritage / North East Region, Elgin, UK. Finally, we thank Prof. Mark Young and Prof. Martin Gorman, both of Aberdeen University, for their comments during the sampling stage and data treatment, which greatly improved our work.

REFERENCES

Allen, J.A. and J.J. Moore. – 1987. Invertebrate macrofauna as potential indicators of sandy beach instability. *Estuar. Coast. Shelf Sci.,* 24:109-125.

Ankar, S. and R. Elmgreen. – 1976. The benthic macro- and meiofauna of the Asko-Landsort area (northern Baltic proper). A stratified random sampling survey. *Contrib. Asko Lab.,* 11: 1-115.

Asmus, H. – 1987. Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. *Mar. Ecol. Prog. Ser.,* 39: 251-266.

Bachelet, G., M. Desprez, J.P. Ducrotoy, J. Guillou, P.J. Labourg., H. Ribarczk, P.G. Sauriau and M. Glemarec. – 1992. The role of intraspecific competition in regulating recruitment in the cockle *Cerastoderma edule* (L.). *Ann. Inst. Oceanogr.,* 68(1): 75-87.

Beukema, J.J., K. Essink, H. Michaelis and L. Zwarts. – 1993. Year to year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea - how predictable is this food source for birds. *Neth. J. Sea Res.,* 31(4): 319-330.

Bonsdorff, E., A. Norkko and E. Sandberg. – 1995. Structuring zoobenthos: the importance of predation, cropping and physical disturbance. *J. Exp. Mar. Biol. Ecol.,* 192: 125-144.

Brey, T. – 1991. The relative significance of biological and physical disturbance: an example from intertidal and subtidal sandy bottom communities. *Estuar. Coast. Shelf Sci.,* 33: 339-360.

Brey, T., H. Rumohr and S. Ankar. – 1988. Energy content of macrobenthic invertebrates: general conversion factors from weight to energy. *J. Exp. Mar. Biol. Ecol.,* 117: 271-278.
Cardoso, P.G., M.A. Pardal, A.I. Lillebo, S.M. Ferreira, D.G. Raffaelli and J.C. Marques. – 2004a. Dynamic changes in seagrass assemblages under euthrophication and implications for recovery. *J. Exp. Mar. Biol. Ecol.*, 302: 233-248.
Cardoso, P.G., M.A. Pardal, D.G. Raffaelli, A. Baeta and J.C. Marques. – 2004b. Macroinvertebrate response to different species of macroalgal mats and the role of disturbance history. *J. Exp. Mar. Biol. Ecol*., 308: 207-220.
Chambers, M.R. and H. Milne. – 1975. The production of *Macoma balthica* (L.) in the Ythan estuary. *Estuar. Coast. Shelf. Sci.,* 3: 443-455.
Chesney, E.J. and K. R. Tenore. – 1985. Effects of predation and disturbance on the population growth of the polychaete *Capitella capitata* (type 1). *Mar. Biol.,* 85: 77-82.
Cummins, K.W. and J.C. Wuycheck. – 1971. Calorific equivalents for investigations in ecological energetics. *Int. Ver. Theor. Angew. Limnol. Verh.,* 18: 1-158.
Desprez, M., H. Rybarczyb, J.G. Wilson, J.P. Ducrotoy, F. Sueur, R. Olivesi and B. El Kaim. – 1992. Biological impact of eutrophication in the Bay of Somme and the induction and impact of anoxia. *Neth. J. Sea Res.*, 30: 149-159.
Diaz, R.J. and R. Rosenberg. – 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of the benthic macrofauna. *Oceanogr. Mar. Biol. Annu. Rev.,* 33: 245-303.
Ertman, S.C. and P.A. Jumars. – 1988. Effects of bivalve siphonal currents on the settlement of inert particles and larvae. *J. Mar. Res.,* 46: 797-813.
Evans, S. – 1982. Production, predation and food niche segregation in a marine shallow soft bottom community. *Mar. Ecol. Prog. Ser.,* 10: 147-157.
Flach, E.C. – 1992. Disturbance of benthic infauna by sediment reworking of the *Arenicola marina. Neth. J. Sea Res.,* 30: 81-87.
Flach, E.C. and W. Debrwin. – 1994. Does the activity of cockles *Cersatoderma edule* and lugworms *Arenicola marina* make *Corophium volutator* more vulnerable to eoibenthic predators? *J. Exp. Mar. Biol. Ecol.,* 182(2): 265-285.
Guillou, J., G. Bachelet and M. Glemarec. – 1992. Effects of temperature fluctuations and recruitment in the cockle *Cerastoderma edule. Ann. Inst. Oceanogr.* 68(1): 65-74.
Guillou, J. – 1994. Post-larval and juvenile mortality in a population of the edible cockle *Cerastoderma edule* (L.) from northern Brittany. *Neth. J. Sea Res*., 33(1): 103-111.
Hayward, P.J. and J.S. Ryland. – 1990. *The marine fauna of British Isles and Northwest Europe.* Vol. I and II. Clarendon Press. Oxford, UK.
Holme, N.A. and A.D. McIntyre. – 1984. *Methods for the study of marine benthos.* Blackwell, Oxford.
Kamermans, P. – 1994. Similarity in food source and timing of feeding in deposit feeding and suspension feeding bivalves. *Mar. Ecol. Prog. Ser.,* 104(1-2): 278-285.
KCS. – 2001. *Multivariate statistical package, MVSP.* Version 3.1. User's Manual. Kovanch Computing Services (KCS), Wales.
Lin, J.D. and A.H. Hines. – 1994. Effects of suspended food availability on the feeding mode and burial depth of the Baltic clam *Macoma balthica*. *Oikos,* 69(1): 28-36.
McNeill, S. and J.H. Lawton. – 1970. Annual production and respiration in animal populations. *Nature*, 225: 472-474.
Mendonça, V.M. – 1997. *Predator-prey interactions in a sandy shore system in the Moray Firth, NE Scotland.* Ph. D. thesis*,* Univ. Aberdeen.
Mendonça, V.M., D.G. Raffaelli, P.R. Boyle and C. Emes. – 2007a. The ecological role of overwintering fish in the food web of the Culbin Sands lagoon ecosystem, NE Scotland: Identifying major trophic links and testing effects of fish *Pomatoschistus microps* (Pallas) on benthic invertebrates. *Sci. Mar.,* 71(4): 649-660.
Mendonça, V.M., D.G. Raffaelli and P.R. Boyle. – 2007b. Interactions between shorebirds and benthic invertebrates at Culbin Sands lagoon, NE Scotland: Effects of avian predation on their prey community density and structure. *Sci. Mar.,* 71(3): 579-591.
M.I.D.A.S. II. 1993. *Mapping Information Database and Acquisition System*. Mobile field receiver, version 2.1. Steanne Software Development Ltd, Cheshire.
Milne, H. and G.M. Dunnet. – 1972. Standing crop, productivity and trophic relations of the fauna of the Ythan estuary. In: R.S.K. Barnes. and J. Green (eds), *The estuarine environment,* pp. 88-106. Appl. Sc. Pub., England.
Modin, J. and L Pihl. – 1996. Small-scale distribution of juvenile plaice and flounder in relation to predatory shrimp in a shallow Swedish bay. *J. Fish Biol.,* 49(6): 1070-1085.
Moller, P. and R. Rosenberg. – 1982. Recruitment, abundance and production of *Mya arenaria* and *Cardium edule* in marine shallow waters, western Sweden. *Ophelia,* 22: 33-55.
Persson, L.E. – 1982. Temporal and spatial variation in coastal macrobenthic community structure, Hano Bay (Southern Baltic). *J. Exp. Mar. Biol. Ecol.,* 68: 277-293.
Piersma, T., A. Dekinga, J. A. van Gils, B. Achterkamp and G. H. Visser. – 2003. Cost-benefit analysis of mollusc-eating in a shorebird. I. Foraging and processing costs estimated by the doubly labelled water method. *J. Exp. Biol*., 206: 3361–3368.
Raffaelli, D.G. and P.R. Boyle. – 1986. The intertidal macrofauna of Nigg Bay. *Proc. R. Soc. Edinb*., 91B: 113-141.
Raffaelli, D., A. Conacher, H. MacLachlan and C. Emes. – 1989. The role of epibenthic crustacean predators in an estuarine food web. *Estuar. Coast. Shelf Sci.,* 28: 149-60.
Raffaelli, D.G. and S.J. Hawkins. – 1996. *Intertidal Ecology.* Chapman and Hall, London.
Rumohr, H., T. Brey and S. Ankar. – 1987. A compilation of biometric conversion factors for benthic invertebrates of the Baltic Sea. *Baltic Biol.,* 9: 1-56.
Smith, J.S. – 1986. The coast of the Moray Firth. *Proc. R. Soc. Edinb.,* 91B: 1-12.
Sokal, R.R. and F.J. Rohlf. – 1984. *Biometry*. 2nd. W. H. Freeman and Co, London.
van Gils, J.A., B. Spaans, A. Dekinga and T. Piersma. – 2006a. Foraging in a tidally structured environment by red knots (*Calidris canutus*): ideal, but not free. *Ecology,* 87: 1189–1202.
van Gils, J.A., T. Piersma, A. Dekinga, B. Spaans and C. Kraan. – 2006b. Shellfish dredging pushes a flexible avian top predator out of a marine protected area. *PLoS Biol.,* 4(12): 376.
Warwick, R.M. and K.R. Clarke. – 1993. Increased variability as a symptom of stress in marine communities. *J. Exp. Mar. Biol. Ecol.,* 122: 215-226.

Scient. ed.: J.D. Ros.
Received November 23, 2006. Accepted December 12, 2007.
Published online April 10, 2008.