
7. Macro-invertebrate Fauna in the Intertidal Mudflats

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Poole Harbour is a Special Protection Area (SPA) because of its importance to breeding and wintering waders and wildfowl. English Nature commissioned the Centre for Ecology and Hydrology to survey the intertidal food resources of these birds. Macro-invertebrate populations were sampled at 80 stations across the harbour. *Cirratulus filiformis* and *Tubificoides benedini* were by far the most numerically abundant species. *Nereis virens* and *Cirratulus filiformis* were the most abundant species in terms of biomass. Variation in the numerical or biomass density of macro-invertebrates across the harbour does not explain the birds' distribution. In terms of numerical densities, the macro-invertebrate community in Poole Harbour is similar to that on the Exe estuary. In terms of biomass, however, Poole Harbour is dominated by worms, whereas the Exe estuary is dominated by molluscs. A review of historical surveys of macro-invertebrates in Poole Harbour indicates that change rather than stability is the norm.

Introduction

Poole Harbour supports populations of waders and wildfowl that are of local, national and, in some cases, international importance (Pickess and Underhill-Day, 2002). In recognition of this, the harbour has been designated under national and international legislation. English Nature is required under European Union regulations to ensure that the interest features of the harbour, as a Special Protection Area (SPA), are maintained in "favourable condition". Accordingly, English Nature commissioned the Centre for Ecology and Hydrology to survey the macro-invertebrate abundance and biomass in the intertidal sediments of Poole Harbour. This will serve as a baseline against which to compare future surveys to detect any significant change in prey abundance and hence the "favourable condition" of the interest features of the harbour.

Methods

Survey plan

A 500 m x 500 m grid, based on the Ordnance Survey grid, superimposed on a map of the harbour, resulted in 80 intersections falling between Mean High Water and Mean Low Water. These sampling stations were spread evenly across the intertidal areas of Poole Harbour to which birds regularly gain access.

Field methods

The survey was conducted during September and October 2002. Sampling stations were visited either at low water on spring tides (on foot or by hovercraft) or at high water on neap tides (by boat). Three sampling methods were employed at each sampling station.

- (i) A single 10.6 cm diameter x 30 cm deep sediment core was removed with a steel pipe. Each core was sieved through a 0.5 mm nylon mesh. Sieve contents were fixed in 4% formalin and, after a number of days, were washed in freshwater and preserved in IMS.
- (ii) A randomly chosen area of 0.25 m² was 'dredged' using a hand-net with a mesh-size of 2 mm. The larger, near-surface dwelling organisms were collected. These samples were frozen.
- (iii) A randomly assigned 1 m² area of the mud surface was inspected and the numbers of *Arenicola marina* casts counted.

For each of the key species, a number of additional individuals spanning the range of sizes present in the harbour were collected. Single live specimens were placed in individual plastic bags and frozen.

Sample processing

Benthic invertebrates

All macro-invertebrates in each core and net sample were counted and identified to the lowest necessary level of taxonomic detail (i.e. species level for all except small worms). The length of all individuals of the key species was measured.

The numerical densities were derived from the core samples for all species except *Carcinus maenas*, *Crangon crangon*, *Tapes philippinarum*, *Crepidula fornicata*, *Macoma balthica*, all *Littorina* spp., *Gibbula umbilicalis* and *Hinia reticulata*. The numerical densities of these species were derived from the netted samples. The overall numerical density of *Cerastoderma edule* at each sampling station was calculated by combining estimates of the density of individuals <6 mm from the core and of individuals >6 mm from the net sample.

Biomass-length relationships

For each species (excepting small worms), each specimen was defrosted, measured and then processed according to standard laboratory procedures to yield its biomass in terms of ash-free dry mass (AFDM). In the case of molluscs that are typically opened by birds to remove the flesh, i.e. bivalves, only the flesh of each individual was processed. In the case of molluscs and crustaceans that are typically eaten whole by birds, e.g. *Hydrobia* spp. and *Carcinus maenas*, each animal was processed intact.

Calculation of biomass densities

For each species, the raw data relating the AFDM of an individual to its length were transformed (\log_e) and a linear regression model fitted to the data. Species-specific regression equations were used to predict the AFDM of an individual within each millimetre size class across the full size range for that species. For each species, the numerical density of individuals within each millimetre size class at each station was multiplied by the relevant predicted value of AFDM to yield the biomass density of that size class at that station. Biomass densities were summed across size classes to yield the total biomass density of a species at each station.

In the case of *Arenicola marina*, for which only the density of casts was assessed, the biomass density at each station was calculated by multiplication of cast density by the average AFDM of all the individuals processed to derive the AFDM-length relationship for that species.

In the case of many of the small tube-dwelling worms, and other small worms, that were not assigned to size classes, the biomass density at a station was calculated by multiplying the numerical density by the average AFDM of a small worm that was derived from ashing 100 such small worms *en masse*.

Biomass densities were derived for all species whose average numerical density across the harbour exceeded 2 individuals m^{-2} .

The effects of invertebrate distribution on bird distribution

Each sampling station was allocated to the appropriate Wetland Bird Survey (WeBS) count sector (Map 3 of Pickess and Underhill-Day, 2002) and the average overall numerical and biomass density of macro-invertebrates was calculated for each. The bird count data presented in Pickess and Underhill-Day (2002, p. 141) was re-worked excluding waterfowl. For each WeBS count sector, the sum of the harbour-wide percentages of the eight wader species (plus Shelduck) held by that sector was calculated and then expressed as a percentage of 900, i.e. the harbour-wide, across species sum of these percentages. These figures were regressed against the area of mud exposed at low water on Spring tides within each sector (see Pickess and Underhill-Day, 2002, pp. 6–7). The extent to which variation in the numerical or biomass density of invertebrates between sectors explained the residual variation in bird usage was explored.

Results

Species presence and distribution

Sixty-one kinds of macro-invertebrates were identified (Table 1). Species-richness was fairly even around the harbour, although the upper Wareham Channel and the bays on its north-east side were the least rich areas (Figure 1). The numerical density of macro-invertebrates was, however, high in the upper reaches of the Wareham channel and several other sheltered areas (Figure 2). The biomass density of macro-invertebrates was quite patchy around the harbour (Figure 3). Some of the quiet backwaters on the southern shore (Middlebere Lake, Wych Lake and Brands Bay) were poor in this respect. Hotspots of biomass density occurred around the harbour, with the greatest concentration being around Baiter and Parkstone Bay (Figure 3).

Only a very few species occurred throughout the harbour, the most cosmopolitan being *Tubificoides benedini* and *Cerastoderma edule*. *Cirratulus filiformis*, the most numerous species, was absent from the harbour's more seaward bays as was *Hediste diversicolor*. *Hediste diversicolor* was replaced at the seaward end of the harbour by *Nereis virens*. *Arenicola marina* was particularly abundant immediately adjacent to the harbour mouth. *Cyathura carinata*, one of the most abundant crustaceans, was restricted to sheltered mudflats far from the harbour mouth. In contrast, *Abra tenuis*, the most abundant bivalve mollusc, was distributed throughout the harbour, being absent only from those areas immediately opposite the harbour mouth and around the bays on the north-east shore of the harbour. *Hydrobia* spp. were the third most abundant species overall and were widely distributed but especially abundant in Lytchett Bay. Detail on the distribution of the species in Poole Harbour is available in Thomas *et al.* (2004).

Numerical and biomass densities

The average harbour-wide numerical and biomass densities of macro-invertebrates are presented in Table 1. Only two species (*Cirratulus filiformis* and *Tubificoides benedini*) occurred at average densities of over 1000 individuals m⁻². When the species were ranked according to their average biomass density, several of the rarer but larger molluscs (*Mya arenaria*, *Cerastoderma edule*, *Tapes philippinarum* and *Scrobicularia plana*) became considerably more important. Nonetheless, three of the four top-ranked species in terms of biomass are worms (Tables 1 and 3).

Comparison between Poole Harbour and the Exe estuary

The macro-invertebrates of the Exe estuary were surveyed in autumn 2001 (Durell *et al.* 2005). Here, 59 kinds of invertebrates were identified (Table 2). The top three species in terms of numerical density were the same as in Poole Harbour (Tables 1–3). When the species were ranked according to their average biomass density, several mollusc species became markedly more important. In contrast to Poole Harbour, however, three of the four top-ranked species in terms of biomass, were bivalve molluscs, the mussel *Mytilus edulis* being by far the most dominant species (Tables 2 and 3).

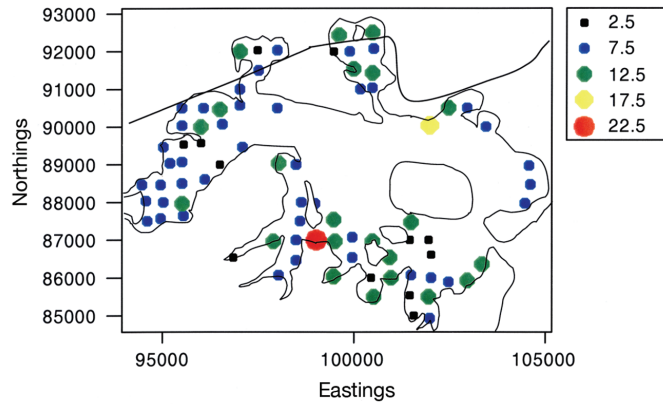


Figure 1 An illustrative sketch of Poole Harbour showing the location of the 80 sampling stations and the number of species of macro-invertebrate found at each. In this figure, as in Figures 2 and 3, the values in the key denote the mid-points of bands into which stations have been grouped. (i.e. in this case 2.5 = 1–5 spp., 7.5 = 5–10, 12.5 = 10–15, 17.5 = 15–20, 22.5 = 20–25).

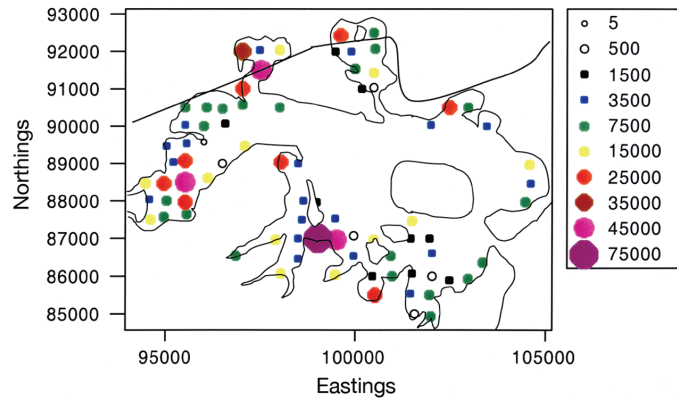


Figure 2 The overall numerical density ($n\ m^{-2}$) of all macro-invertebrates at each of the 80 sampling stations.

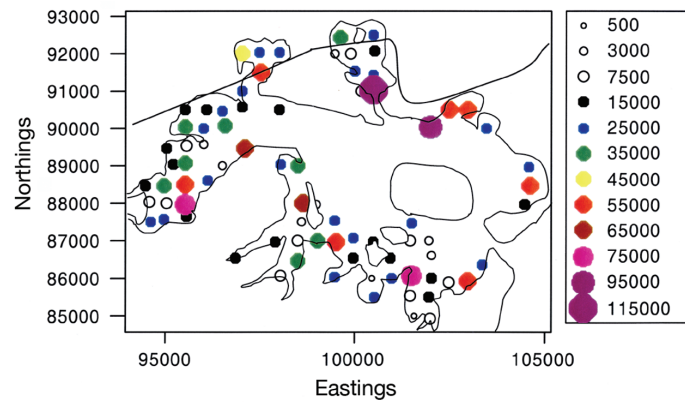


Figure 3 The overall biomass density ($mg\ ash\text{-free}\ dry\ mass\ m^{-2}$) of macro-invertebrates at each of the 80 sampling stations.

Table 1 The harbour-wide average numerical density of all 'species' of macro-invertebrate (in rank order) and the average biomass density of those macro-invertebrates whose numerical density exceeded 2 m⁻² in Poole Harbour (also in rank order)

Species	Average number m ⁻²	Species	Average mg ash- free dry mass m ⁻²
<i>Cirratulus filiformis</i>	3819.6	<i>Nereis virens</i>	4567
<i>Tubificoides benedini</i>	1818.5	<i>Cirratulus filiformis</i>	4545
<i>Hydrobia</i> spp.	756.3	<i>Hediste diversicolor</i>	2453
<i>Microdeutopus gryllotalpa</i>	635.9	<i>Mya arenaria</i>	2323
<i>Hediste diversicolor</i>	614.7	<i>Tubificoides benedini</i>	2164
<i>Malacoceros fuliginosus</i>	422.0	<i>Cerastoderma edule</i>	2155
<i>Corophium volutator</i>	373.9	<i>Arenicola marina</i>	1176
<i>Cyathura carinata</i>	355.5	<i>Tapes philippinarum</i>	1155
<i>Gammarus locusta</i>	277.6	<i>Scrobicularia plana</i>	1093
<i>Scoloplos armiger</i>	263.4	<i>Nephtys hombergii</i>	552
<i>Abra tenuis</i>	254.9	<i>Littorina</i> spp.	537
<i>Spionid</i> spp.	151.5	<i>Malacoceros fuliginosus</i>	502
Anemones (unident)	114.7	<i>Hydrobia</i> spp.	449
<i>Capitella capitata</i>	113.3	<i>Scoloplos armiger</i>	313
<i>Nereis virens</i>	80.7	<i>Abra tenuis</i>	301
<i>Eteone longa</i>	60.9	<i>Cyathura carinata</i>	252
Chironomid larvae	51.0	<i>Carcinus maenas</i>	213
<i>Nephtys hombergii</i>	46.7	<i>Spionid</i> spp.	180
<i>Urothoe poseidonis</i>	42.5	<i>Corophium volutator</i>	148
<i>Neomysis integer</i>	35.4	<i>Capitella capitata</i>	135
<i>Ampharete grubei</i>	34.0	<i>Eteone longa</i>	72
<i>Cerastoderma edule</i>	30.2	<i>Neomysis integer</i>	54
<i>Polycirrus caliendrum</i>	29.7	<i>Microdeutopus gryllotalpa</i>	48
<i>Corophium arenarium</i>	28.3	<i>Ampharete grubei</i>	40
<i>Scolecopsis foliosa</i>	19.8	<i>Gammarus locusta</i>	39
<i>Mesopodopsis slabberi</i>	15.6	<i>Polycirrus caliendrum</i>	35
Nemerteans	12.7	<i>Scolecopsis foliosa</i>	24
<i>Scolecopsis squamata</i>	11.3	<i>Corophium arenarium</i>	20
<i>Pygospio elegans</i>	11.3	<i>Mesopodopsis slabberi</i>	16
<i>Anaitides mucosa</i>	9.9	Nemerteans	15
<i>Cirriformia tentaculata</i>	9.9	<i>Praunus flexuosus</i>	15
<i>Heteromastus filiformis</i>	9.9	<i>Scolecopsis squamata</i>	13
Nematodes	9.9	<i>Pygospio elegans</i>	13
<i>Praunus flexuosus</i>	9.9	<i>Anaitides mucosa</i>	12
<i>Mya arenaria</i>	9.9	<i>Cirriformia tentaculata</i>	12
<i>Scrobicularia plana</i>	8.5	<i>Heteromastus filiformis</i>	12
<i>Gammaropsis palmata</i>	7.1	Nematodes	12
<i>Tapes philippinarum</i>	4.6	<i>Urothoe poseidonis</i>	7
<i>Idotea neglecta</i>	4.2	<i>Palaemon longirostris</i>	5
<i>Idotea pelagica</i>	4.2	<i>Bathyporeia sarsi</i>	3
Chironomid pupae	4.2	<i>Idotea neglecta</i>	2
<i>Littorina</i> spp.	4.0	<i>Harmothoe</i> spp.	2
<i>Arenicola marina</i>	3.3	<i>Glycera tridactyla</i>	2
<i>Bathyporeia sarsi</i>	2.8		
<i>Palaemon longirostris</i>	2.8		
<i>Carcinus maenas</i>	2.1		

Table 1 cont.

Species	Average number m ⁻²	Species	Average mg ash- free dry mass m ⁻²
<i>Harmothoe</i> spp.	1.4		
<i>Glycera tridactyla</i>	1.4		
<i>Idotea balthica</i>	1.4		
<i>Talitrus saltator</i>	1.4		
<i>Palaemon serratus</i>	1.4		
<i>Macoma balthica</i>	1.4		
<i>Haminoea navicula</i>	1.4		
<i>Crangon crangon</i>	1.2		
<i>Crepidula fornicata</i>	0.9		
Ascidians (unident)	0.4		
<i>Gibbula umbilicalis</i>	0.4		
<i>Hinia reticulata</i>	0.2		
Mysidae spp.	0.1		

Table 2 The estuary-wide average numerical density (in rank order) and the average biomass density (also in rank order) of all 'species' of macro-invertebrate on the Exe estuary in autumn 2001

Species	Average number m ⁻²	Species	Average mg ash- free dry mass m ⁻²
<i>Hydrobia</i> spp.	2925.8	<i>Mytilus edulis</i>	21628
<i>Tubificoides benedeni</i>	2509.8	<i>Scrobicularia plana</i>	9993
<i>Cirratulid</i> spp.	2103.5	<i>Hediste diversicolor</i>	6911
<i>Spio</i> spp.	1632.5	<i>Cerastoderma edule</i>	3892
<i>Hediste diversicolor</i>	944.1	<i>Littorina</i> spp.	3724
<i>Pygospio elegans</i>	794.6	<i>Hydrobia</i> spp.	1760
<i>Heteromastus filiformis</i>	279.7	<i>Tubificoides benedeni</i>	863
<i>Cyathura carinata</i>	245.2	<i>Cirratulid</i> spp.	724
<i>Capitella capitata</i>	193.7	<i>Spio</i> spp.	562
<i>Scrobicularia plana</i>	151.1	<i>Nephtys hombergii</i>	457
<i>Ampharete acutifrons</i>	129.4	<i>Lanice conchilega</i>	432
<i>Cerastoderma edule</i>	118.2	<i>Carcinus maenus</i>	329
<i>Gammarus locusta</i>	112.1	<i>Crangon crangon</i>	316
<i>Corophium arenarium</i>	110.1	<i>Pygospio elegans</i>	273
<i>Tubifex</i> spp.	109.3	<i>Cyathura carinata</i>	246
<i>Corophium volutator</i>	94.8	<i>Corophium volutator</i>	110
<i>Malacoceros fuliginosus</i>	88.0	<i>Arenicola marina</i>	106
<i>Eteone longa</i>	85.2	<i>Heteromastus filiformis</i>	96
<i>Mytilus edulis</i>	72.7	<i>Capitella capitata</i>	67
<i>Littorina</i> spp.	69.9	<i>Malacoceros fuliginosus</i>	59
<i>Scolecopsis squamata</i>	49.0	<i>Gammarus locusta</i>	50
<i>Nephtys hombergii</i>	47.0	<i>Tubifex</i> spp.	38
<i>Crangon crangon</i>	44.2	<i>Ampharete acutifrons</i>	37
<i>Neomysis integer</i>	42.2	<i>Scolecopsis squamata</i>	33
Nematodes	39.8	<i>Eteone longa</i>	29
<i>Lanice conchilega</i>	29.3	<i>Corophium arenarium</i>	26

Table 2 cont.

Species	Average number m ⁻²	Species	Average mg ash- free dry mass m ⁻²
<i>Carcinus maenus</i>	26.5	<i>Anaitides mucosa</i>	24
<i>Bathyporeia sarsi</i>	20.9	<i>Ophelia bicornis</i>	23
<i>Urothoe poseidonis</i>	16.1	<i>Neomysis integer</i>	22
<i>Anaitides mucosa</i>	13.7	<i>Bathyporeia sarsi</i>	21
<i>Praunus flexuosus</i>	11.7	<i>Urothoe poseidonis</i>	8
Dipteran larva	9.6	<i>Scoloplos armiger</i>	3
<i>Angulus tenuis</i>	9.6		
Nemerteans	5.6		
<i>Sphaeroma serratum</i>	5.6		
<i>Mya arenaria</i>	5.6		
<i>Scoloplos armiger</i>	5.2		
<i>Ophelia bicornis</i>	5.2		
<i>Arenicola marina</i>	4.0		
<i>Bathyporeia pelagica</i>	3.2		
<i>Gibbula umbilicalis</i>	3.2		
<i>Macoma balthica</i>	3.2		
<i>Idotea pelagica</i>	2.8		
<i>Jaera albifrons</i>	2.8		
<i>Idotea chelipes</i>	2.4		
Chironomid larva	2.4		
<i>Glycera tridactyla</i>	2.0		
<i>Kefersteinia cirrata</i>	2.0		
<i>Tapes decussatus</i>	1.6		
<i>Melita palmata</i>	1.2		
<i>Eurydice pulchra</i>	1.2		
<i>Eteone viridis</i>	0.8		
<i>Euclymene lumbricoides</i>	0.8		
<i>Harmothoe</i> spp.	0.8		
<i>Tanaid</i> sp.	0.8		
<i>Crepidula fornicata</i>	0.8		
<i>Abra alba</i>	0.8		
<i>Lepidochitona cinereus</i>	0.8		
<i>Nematoneis unicornis</i>	0.8		

Source: Durell *et al.* (2005).

Historical perspective

The macro-invertebrate populations of the intertidal flats of Poole Harbour have been surveyed several times (Table 4). In the early 1970s, the Nature Conservancy surveyed the entire harbour. In 1987, several independent studies combined to yield an extensive survey. *Scrobicularia plana* and *Macoma balthica* are considerably scarcer now than they have been over the last 30 years (Table 5). In contrast, other bivalves, notably *Cerastoderma edule* and in particular *Abra tenuis* have become more abundant. *Hydrobia* spp. are also more abundant now as are errant polychaetes. Sedentary polychaetes may also have increased since the 1970s. In contrast, *Corophium volutator* seems to be far less abundant now than it has been in the past, but increases in other crustaceans (*Microdeutopus gryllotalpa* and

Table 3 Summary of key statistics and characteristics of the intertidal macro-invertebrate communities in Poole Harbour and the Exe estuary

	Poole Harbour	Exe estuary	Species in common
Total 'species'	61	59	38
Molluscs	15	13	8
Polychaete worms	20	22	14
Crustaceans	20	17	11
Numerical density	<i>Cirratulus filiformis</i>	<i>Hydrobia</i> spp.	<i>Hydrobia</i> spp.
Top three species ($n\ m^{-2}$)	<i>Tubificoides benedini</i> <i>Hydrobia</i> spp.	<i>Tubificoides benedini</i> <i>Cirratulus filiformis</i>	<i>Tubificoides benedini</i> <i>Cirratulus filiformis</i>
N spp. $>1000\ m^{-2}$	2	4	<i>Tubificoides benedini</i> <i>Cirratulus filiformis</i>
N spp. $>100\ m^{-2}$ and $< 1000\ m^{-2}$	12	11	<i>Hediste diversicolor</i> <i>Cyathura carinata</i> <i>Gammarus locusta</i> <i>Capitella capitata</i>
N spp. $>10\ m^{-2}$ and $< 100\ m^{-2}$	15	16	<i>Eteone longa</i> <i>Nephtys hombergii</i> <i>Urothoe poseidonis</i> <i>Neomysis integer</i> <i>Scolecopsis squamata</i>
N spp. $< 10\ m^{-2}$	30	28	<i>Mya arenaria</i> <i>Idotea pelagica</i> Chironomids <i>Arenicola marina</i> <i>Harmothoe</i> spp. <i>Glycera tridactyla</i> <i>Macoma balthica</i> <i>Crepidula fornicata</i> <i>Gibbula umbilicalis</i>
Overall numerical density ($n\ m^{-2}$)	10603	13195	
Biomass density	<i>Nereis virens</i>	<i>Mytilus edulis</i>	<i>Hediste diversicolor</i>
Top species (mg AFDM m^{-2})	<i>Cirratulus filiformis</i> <i>Hediste diversicolor</i> <i>Mya arenaria</i>	<i>Scobicularia plana</i> <i>Hediste diversicolor</i> <i>Cerastoderma edule</i>	
Biomass density N spp. $> 1000\ mg\ AFDM\ m^{-2}$	9	6	<i>Hediste diversicolor</i> <i>Cerastoderma edule</i> <i>Scrobicularia plana</i>
Biomass density N spp. $> 100\ mg\ AFDM\ m^{-2}$ and $< 1000\ mg\ AFDM\ m^{-2}$	11	11	<i>Nephtys hombergii</i> <i>Cyathura carinata</i> <i>Carcinus maenas</i> Spionid sp. <i>Corophium volutator</i>
Overall biomass density (mg AFDM m^{-2})	25689	52862	
Dominant group in terms of biomass	Polychaete worms	Bivalve molluscs	

Source: Data for Exe estuary from Durell *et al.* (2005).

Table 4 Details of historical surveys of intertidal macro-invertebrates in Poole Harbour

Year	Location	Number of sampling stations	Numerical densities	Size classes	Source
1971	Various locations	8	yes	no	Arnold (1971)
1972	Whole harbour	189	yes	no	Anderson <i>et al.</i> (unpublished data)
1982–83	Parkstone Bay	75	yes	no	Harris (1983a)
1982–83	Holes Bay	?	?	?	Harris (1983b)
1985	Various locations	45	yes	no	Institute of Offshore Engineering (1986)
1987	Holes Bay	22	yes	no	Dyrynda (1989)
1987	Cleavel - Ower	41	yes	no	McGrorty <i>et al.</i> (1987)
1987	Whitley Lake, Brands Bay, Newton Bay, Keyworth	105	yes	(<i>Hediste</i> and <i>Nephtys</i> only)	Warwick <i>et al.</i> (1989)
1991	Holes Bay	31	yes	no	Environment Agency (unpublished report)
1991	Wych Lake and Channel	15	yes	no	Jensen <i>et al.</i> (1991)
1999	Arne Bay, Brands Bay, Newton Bay	36	yes	no	J. Gill (unpublished data)
2002	Whole harbour	80	yes	yes	This study
2002	Holes Bay	10	yes	yes	Caldow <i>et al.</i> (2003)

Cyathura carinata) have more than offset this. The overall number of macro-invertebrates has been relatively stable over the last 20 years but (subject to the effect of differing sieve mesh sizes) has increased since the 1970s. This is largely due to a marked increase in the numbers of sedentary polychaetes and other worms (e.g. oligochaetes).

Holes Bay has been surveyed in each of the last four decades. Within Holes Bay, very similar patterns to those seen across the harbour as a whole are apparent (Table 6). *Scrobicularia plana* and *Macoma balthica* have been virtually absent since the early 1970s. In contrast, *Cerastoderma edule* and particularly *Abra tenuis* have increased markedly over the same time. *Hydrobia* spp. are also much more abundant now than in the past. Both errant and sedentary polychaetes have fluctuated dramatically between decades, although not in synchrony. Consequently, the total density of all worms has been fairly similar in all decades except the 1980s. *Corophium volutator* abundance has also fluctuated widely. Other crustaceans seem to have increased since the 1980s, the numbers being dominated by Ostracoda and *Cyathura carinata* in the 1990s and by *C. carinata*, *Microdeutopus gryllotalpa* and *Gammarus locusta* in 2002. The total count of

Table 5 Comparison of the average numerical densities of key species and groups of macro-invertebrates on intertidal flats in Poole Harbour over the last 30 years

Year survey	Source		
	Anderson <i>et al.</i> (unpublished data)	Dyrynda (1989); McGrorty <i>et al.</i> (1987); Warwick <i>et al.</i> (1987)	Current study
	1972	1987	2002
<i>Scrobicularia plana</i>	53	239	8
<i>Macoma balthica</i>	42	10	1
Other bivalves	27	133	300
All bivalves	120	383	310
<i>Hydrobia</i> spp.	214	135	756
Errant polychaetes	376	478	814
Sedentary polychaetes	2023	6570	4909
Other worms	6	1884	1841
All worms	2398	8931	7564
<i>Corophium</i> spp.	1540	2882	374
Other crustaceans	56	177	1430
All crustaceans	1577	3059	1804
All	4309	12508	10434
Number of samples	189	168	80

all crustaceans has fluctuated widely. In spite of these fluctuations, the total invertebrate numbers have been fairly consistent over the four decades with the notable exception of the 1980s when numbers of all groups were much reduced.

Bird and invertebrate associations

When the WeBS count data were restricted to exclude waterfowl (except Shelduck) and to the 24 count sectors for which invertebrate data were available, there was a highly significant association between bird usage and the area of mud within a sector ($r^2 = 63.8\%$, d.f. = 23, $P < 0.001$) (Figure 4). Across the harbour there was a significant but imperfect correlation between the numerical and biomass density of invertebrates ($r = 0.32$, $n = 80$, $P < 0.01$) (Figure 5). The residual scatter around the birds vs area of mud regression line was not, however, associated with either the variation in the numerical ($P = 0.733$) or biomass ($P = 0.082$) density of macro-invertebrates between the sectors (Figure 6).

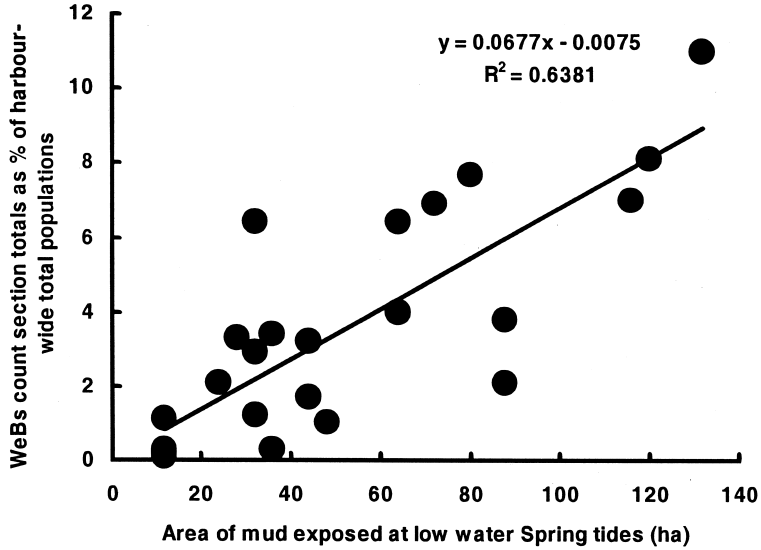


Figure 4 The relationship between the percentage of the harbour-wide populations of all waders and Shelduck within each of the WeBS count sectors at low water and the area of intertidal flats exposed within that sector at low water (data taken from Pickess and Underhill-Day, 2002).

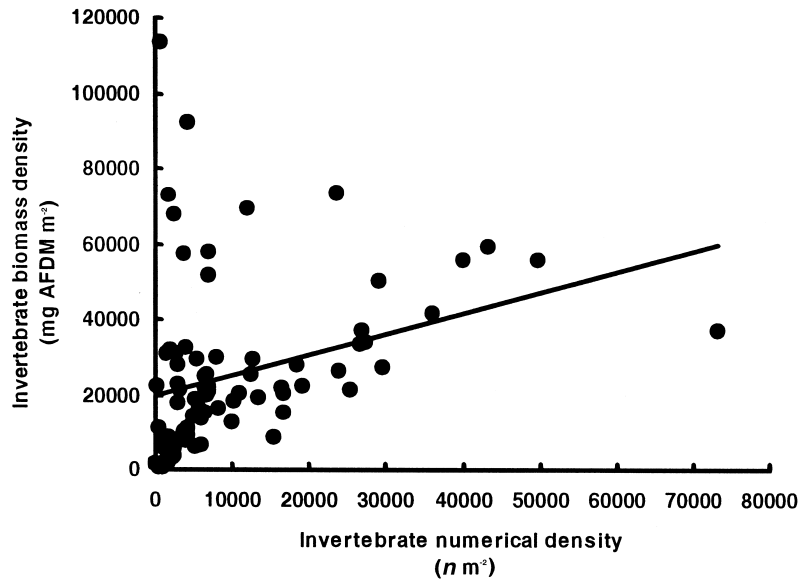


Figure 5 The relationship between the overall biomass density and overall numerical density of invertebrates at each sampling station. The solid line is the line of least squares best fit.

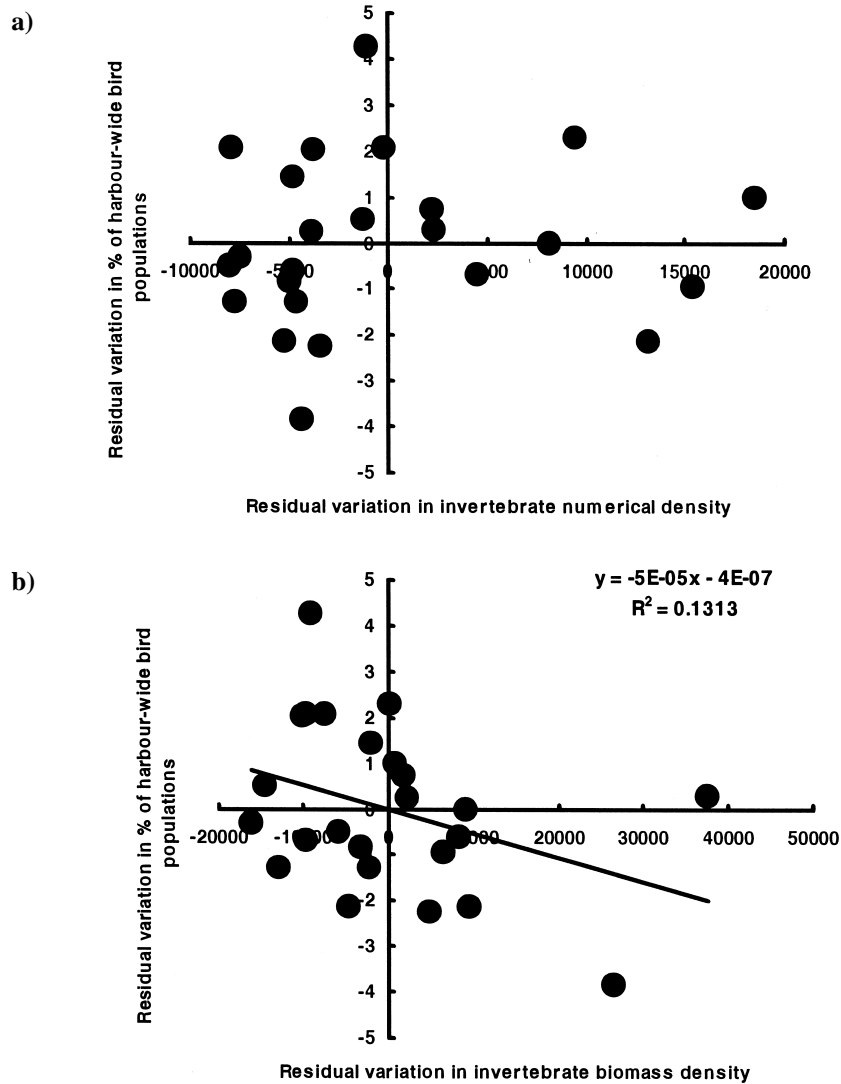


Figure 6 Plots of the residual variation in the percentage of the harbour-wide populations of all waders and Shelduck within each of the WeBS count sectors at low water that is not explained by the area of intertidal flats exposed within that sector at low water against: a) the residual variation in the macro-invertebrate numerical density ($n\ m^{-2}$) within a WeBS count sector that is also not explained by the area of intertidal flats exposed within that sector at low water; and b) the residual variation in the macro-invertebrate biomass density ($mg\ AFDM\ m^{-2}$) within a WeBS count sector that is not explained by the area of intertidal flats exposed within that sector at low water. These plots represent the relationships between the bird usage of a sector and its macro-invertebrate population, controlling for the partial effect of mudflat area on both.

Table 6 Comparison of the average numerical densities of key species and groups of macro-invertebrates on intertidal flats of Holes Bay, Poole Harbour over the last 30 years

Year survey	Source			
	Anderson <i>et al.</i> (unpublished data)	Dyrynda (1989)	Environment Agency (unpublished report)	Current study
	1972	1987	1991	2002
<i>Scrobicularia plana</i>	32	0	4	6
<i>Macoma balthica</i>	77	1	1	0
Other bivalves	43	4	780	294
All bivalves	146	5	785	300
<i>Hydrobia</i> spp.	31	0	253	1013
Errant polychaetes	619	123	2750	992
Sedentary polychaetes	5008	177	582	3491
Other worms	0	205	576	610
All worms	5627	506	3908	5093
<i>Corophium</i> spp.	2457	50	623	13
Other crustaceans	14	3	513	835
All crustaceans	2265	53	1135	848
All	8069	563	6081	7254
Number of samples	21	22	31	19

Discussion

The current macro-invertebrate community

The richness of the macro-invertebrate community is fairly uniform across the whole harbour. However, very few species were ubiquitous. Only *Tubificoides benedini* and *Cerastoderma edule* occur throughout the harbour. Amongst the other species, there is a wide range of distribution patterns. Some species are restricted to the areas furthest from the harbour mouth, e.g. *Cirratulus filiformis* and *Hediste diversicolor*, others to areas near the harbour mouth, e.g. *Arenicola marina*. Some species, e.g. *Cyathura carinata*, appear to favour the quietest backwaters. All of these species-specific distribution

patterns will reflect the tolerance of each species to environmental factors that vary across the harbour. As a consequence of the varying species-specific distributions, both the overall numerical density and the overall biomass density are highly variable around the harbour. However, these two parameters are not perfectly correlated. The locations with the greatest numerical densities are generally in the quieter backwaters (upper reaches of the Wareham Channel, Lytchett Bay, around Fitzworth Point). There are, however, numerous other areas where the biomass density is high. The poorest areas of the harbour in terms of both numerical and biomass density are Brands Bay, the low-level sandflats opposite the harbour mouth and the north shore of the upper Wareham Channel.

Birds and invertebrates

Although every WeBS count sector of the harbour supports several species of waders or waterfowl, only a few sectors support over 5% of their combined populations (Pickess and Underhill-Day, 2002). When the bird data are restricted to the eight species of wader plus Shelduck, there is a strong positive association between the extent of mud within a sector and the percentage of birds held by it. There is, however, considerable scatter around this relationship. Several areas are markedly under-used, e.g. Lytchett Bay, the south-eastern quarter of Holes Bay, Sandbanks and the eastern (outer) part of Brands Bay. In contrast, the western (inner) part of Brands Bay is over-used by the birds, as are the areas around Fitzworth, Wych Lake, Keysworth and Swineham. Such 'outliers' cannot be explained by either a shortage or an excess of food supplies. Three of the four most under-used sectors have relatively high invertebrate biomasses whereas all five of the most over-used sectors have relatively low invertebrate biomasses. Pickess and Underhill-Day (2002) speculated that human disturbance may be a factor driving birds' distribution in the harbour. Three of the under-used areas (Brands Bay (east), Sandbanks and the south-eastern quarter of Holes Bay) are all subject to heavy boat traffic. It is unclear at present why Lytchett Bay should be so under-utilized.

Further work will be required to identify the reasons underlying the variation around the bird usage vs area relationship. At the crudest level of analyses in which all birds and invertebrates are considered together, the food supply cannot explain the discrepancies. A more detailed analysis in which the distributions of individual bird species are analysed in relation to the abundance of only their preferred prey species may yield more powerful insights into this issue. However, the fact that all of the under-used sectors are not impoverished in terms of food, and all the over-used areas are not the best in terms of food supplies, raises a number of interesting issues.

The decision to survey the macro-invertebrates across the entire harbour is fully justified. The survey has revealed several areas that are currently under-exploited by the birds yet are not lacking in food. The harbour may be capable of supporting many more birds than at present. Birds displaced from currently favoured areas may be able to relocate to under-utilized parts of the harbour where there is as much or even more food

than where they currently feed. Conversely, perhaps human disturbance or other factors, e.g. green algal cover, restrict the usage of certain areas and hence the populations of birds that the harbour currently supports.

Poole Harbour 2002 survey in context

Comparison with the Exe estuary

Poole Harbour and the Exe estuary in Devon are remarkably similar in terms of:

- the total number of macro-invertebrate species identified
- the balance in species numbers between molluscs, polychaete worms and crustaceans
- the most numerically abundant species
- the frequency distribution of species numerical abundance
- the overall numerical density.

However, this similarity disappears when the biomass of the macro-invertebrates is considered. Worms dominate the biomass of Poole Harbour whereas bivalve molluscs dominate the biomass on the Exe estuary. Although the frequency distribution of species' biomass densities is similar, the numbers of species in common between the two sites in the biomass rank orders is much reduced. The Exe estuary is dominated by the large population of intertidal mussels *Mytilus edulis*. The net result is that the overall biomass of macro-invertebrates on the Exe is twice that in Poole Harbour.

This pronounced difference between the two sites is almost certainly due to their different physical characteristics. However, it is also possible that the dominance of mussels on the Exe is not entirely natural, most of the mussel beds having been created by man. A comparison of the bird populations in Poole Harbour and the Exe might reveal whether this major difference between the invertebrate communities is associated with differences in the wintering populations of birds.

Poole Harbour in the past

The intertidal macro-invertebrates of Poole Harbour have been surveyed many times in the past. However, sampling techniques (e.g. sieve mesh sizes) differ between surveys. Thus, the simple comparisons of historical and current data presented here must be treated with some caution. Subject to this caveat, comparison of the three extensive surveys and the four surveys of Holes Bay show that there have been pronounced changes between decades in the abundance of virtually every group of invertebrate. It is impossible to say whether these fluctuations in the invertebrate populations are entirely natural or a response to changed conditions brought about through man's activities in and around the harbour. However, it would seem that change, whatever its cause, is the norm rather than stability.

The future

Pickess and Underhill-Day (2002) demonstrated that of 19 key species of waders and waterfowl, the populations of 10 have increased recently, 5 have been stable and 4 (Shoveler, Oystercatcher, Redshank and Curlew) have declined. There are no explanations for these trends. Although populations of wintering migratory birds in Poole Harbour are determined to a large extent by events and conditions elsewhere, local events and conditions will influence the number of potential recruits that choose to settle and that can survive the winter in good condition. Thus, data local to Poole Harbour will be essential in understanding any continued changes in the population sizes of key bird species.

This survey has established a baseline of macro-invertebrate numerical abundance and biomass. The location of each sampling station has been recorded and each could be revisited to detect changes in prey abundance. Incidental observations indicate that *Mya arenaria* are more abundant in the harbour now than in 2002. The Manila Clam *Tapes philippinarum* is likely to continue its spread within the harbour. A repeat survey is likely to reveal changes. Attributing any such change to human activities will require quantitative data on the important environmental parameters that man's activities might alter, e.g. nutrient inputs, chemical pollution, frequency and intensity of fishing and shellfishing activity and intensity of boat traffic. For a complete analysis, quantitative data on other naturally varying environmental factors, e.g. salinity, sea water temperature and tidal exposure patterns, will also be needed. Understanding the causes of changes to the food supply will be essential in attempting to understand any future changes in the harbour's bird populations.

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