with bost wishes from P.

SPECIAL PAPERS IN PALAEONTOLOGY · 43

Benthic palaeoecology of the late Jurassic Kimmeridge Clay of England



THE PALAEONTOLOGICAL ASSOCIATION

BENTHIC PALAEOECOLOGY OF THE LATE JURASSIC KIMMERIDGE CLAY OF ENGLAND

BY

PAUL B. WIGNALL

with 50 text-figures

THE PALAEONTOLOGICAL ASSOCIATION LONDON

	CONTENTS	w.

A

	page	
Abstract	5	
INTRODUCTION	5	
Study Area	5	
Prerequisites for Palaeoecological Study	7	
Sedimentology	7	
Biostratigraphy	7	
Taxonomy	8	
Autecology	11	
Pseudoplanktonic forms	13	
Preservation in the Kimmeridge Clay	13	
DIVERSITY CONTROLS IN LEVEL-BOTTOM MARINE COMMUNITIES	14	
Community Palaeoecology	15	
Definitions	15	
The validity of community palaeoecology	16	
Analytical methods	16	
Gamma ray spectrometry	17	
Materials and results	17	
Lower Kimmeridge Clay Aerobic Associations	17	
A1 Corbulomima suprajurensis: Isocyprina implicata Association	17	
A2 Nanogyra nana: Deltoideum delta Association	22	
A3 Nanogyra nana: Quenstedtia laevigata Association	22	
A4 Procerithium multiplicatum: Lingula ovalis Association	27	
A5 Isocyprina minuscula: I. implicata Association	28	
A6 Thracia depressa: Nicaniella extensa Association	28	
A7 Prodentalium calvertensis: Grammatodon keyserlingii		
Association	30	
A8 Nicaniella extensa: Corbulomima suprajurensis Association	30	
A9 Nucinella birkelundi: Nanogyra virgula Association	32	
A10 Protocardia morinica: Lingula ovalis Association	32	^
A11 Protocardia morinica: Nanogyra virgula Association	33	
Dysaerobic Associations	33	
A/E1 Corbulomima suprajurensis: Grammatodon longipunctata		
Association	33	
El Protocardia morinica: Oyster Association	34	
E2 Protocardia morinica: Isocyprina minuscula Association	35	
E3 Protocardia morinica: Quadrinervus ornatus Association	39	

CONTENTS

E4 Liostrea multiformis: Pseudorhytidopilus latissima Association	39
E5 Protocardia morinica: Nicaniella extensa Association	40
E6 Isocyprina minuscula: Pseudorhytidopilus latissima	
Association	41
E7 Lingula ovalis: Protocardia morinica Association	41
E8 Pseudorhytidopilus latissima: Quadrinervus ornatus	
Association	41
E9 Pseudorhytidopilus latissima: Protocardia morinica	
Association	41
Upper Kimmeridge Clay Aerobic Associations	42
B1 Liostrea multiformis: Parainoceramus cramei Association	42
B2 Mesosaccella cypris: Corbulomima suprajurensis Association	43
B3 Trautscholdia phillis: Corbulomima suprajurensis Association	44
B4 Nicaniella cuneata: Mesomiltha concinna Association	45
B5 Liostrea expansa: Oxytoma inequivalve Association	45
LATERAL BIOFACIES VARIATIONS IN THE KIMMERIDGIAN OF ENGLAND	47
Dorset	47
Central Wiltshire	48
A12 Grammatodon keyserlingii: Gervillella aviculoides	
Association	49
The Weald	50
E10 Lingula ovalis: Nicaniella extensa Association	51
E11 Lingula ovalis: Liostrea multiformis Association	52
E12 Lingula ovalis: Musculus autissiodorensis Association	52
The Swindon region	52
A13 Tetraserpula dollfussi: Corbulomima suprajurensis	50
Association	55
A14 Corbulomima suprajurensis: Neocrassina ovata Association	55
Als Scaphopod: Thracia depressa Association	20
B6 Procerithium multiplicatum: Corbulomima suprajurensis	57
Association	59
B7 Cycloserpula intestinalis: Nanogyra nana Association	50
Eastern England E12 Ruchig maggingis: Lightrag multiformis Association	60
E15 Buchia mosquensis. Liostrea mailijormis Association	00
DISCUSSION	61
Substrates of the Kimmeridge Clay	61
Oxygen deficient environments of the Kimmeridge Clay	63
True communities in the Kimmeridge Clay?	65
Summary of the depositional history of the Kimmeridge Clay of	
England	65
Comparison with Callovian and Upper Jurassic associations	67
ACKNOWLEDGEMENTS	69
REFERENCES	69

ABSTRACT. Analysis of the fossil content of 700 samples from the Kimmeridge Clay, from both outcrops and boreholes, have led to the identification of nearly 55,000 specimens of benthos. These data have been combined with detailed sedimentological logging and a gamma ray spectrometry survey of the type locality at Kimmeridge Bay to provide a detailed depositional history.

The Kimmeridge Clay is readily divisible into three distinctive sequences. The lower sequence is developed as a widespread mudstone facies containing diverse benthic associations dominated, for the most part, by infaunal bivalves; only in the basal condensed beds are epifaunal forms common. The high diversity and relatively low values of organic carbon and authigenic uranium indicate normal benthic oxygen levels. The central sequence of the Kimmeridge Clay is marked by rhythmic alternations of organic-rich shales and mudstones. A marked decrease in diversity and a change of faunal composition to opportunistic forms indicates a drastic reduction of benthic oxygen levels coincident with the facies change. The principal controls on faunal distribution, other than low oxygen levels, were the substrate and the dispersal rate of the organisms. The last factor was of primary importance in an environment subject to wide fluctuations of benthic conditions; brief oxygenation events could only be exploited by the most rapidly colonizing organisms. Contrary to reports from other black shale formations, stunting of the benthic fauna was not observed in the dysaerobic biofacies. Indeed, some exceptionally large individuals from such facies appear to have grown rapidly as a physiological response to low oxygen. The upper sequence of the Kimmeridge Clay is marked by a return to normally oxygenated conditions similar to those of the lowest sequence although epifaunal forms are more important, probably reflecting a firmer substrate at this level.

Lateral facies changes are relatively minor in the lower part of the Kimmeridge Clay but towards the middle part of the formation (in the *autissiodorensis* Zone) facies variability becomes more distinct. Around the fringes of the London Platform a series of sandy formations are developed containing similar benthic associations to those found in the underlying Corallian beds.

INTRODUCTION

The Kimmeridge Clay is the penultimate formation of the onshore British Jurassic succession. Over a century of research has been intensified during the last few decades with the realization that the partly coeval Kimmeridge Clay Formation of the North Sea is the principal petroleum source rock of this region. Consequently most attention has been focused upon the character and origin of the organic-rich central part of the formation. However, many styles of mudrock deposition are represented in the Kimmeridge Clay, ranging from normal aerobic mudstone biofacies to predominantly anaerobic, organic-rich shale biofacies. It is the aim of this study to investigate the processes leading to the deposition of this range of facies types principally using a palaeoecological approach. However, whereas many palaeoecological studies have rather divorced themselves from other approaches to environmental interpretation, in this study an interdisciplinary approach is used, combining data from both geochemistry and sedimentology. The location of the benthic associations are related to logs of specific sections in order to aid any independent evaluation of the data presented here.

Prior to the present study, no detailed investigation has been undertaken on the Kimmeridge Clay as a whole. Only the basal-most beds have been investigated in detail (Brookfield 1973b; Fürsich 1977) whilst the palaeoecology of the overlying organic-rich strata has been the subject of preliminary study (Morris 1980; Myers and Wignall 1987; Wignall and Myers 1988; Oschmann 1988). These observations provide only a glimpse of the range of palaeoecological inferences to be had from the Kimmeridge Clay and, in some cases, they are considered to be misleading. The calcareous and silty mudstones which form the top of the Kimmeridge Clay have received virtually no attention with the exception of the study by Oates (1974), on a temporary inland exposure, and the early work of Blake (1875).

STUDY AREA

The type locality of the Kimmeridge Clay at Kimmeridge Bay only exposes the succession from the mid-*eudoxus* Zone to the top of the formation, albeit in a magnificent series of cliff exposures. Thus, in order to analyse a complete sequence through the entire Kimmeridge Clay, a composite section was compiled from scattered outcrops throughout southern England (text-fig. 1). At present the



TABLE 1 (cont.)

Species	Mode of life	. •
BRACHIOPODA (5 species) Torquirhynchia inconstans (J. Sowerby, 1821) Rhynchonella subvariabilis Davidson, 1852 Discinisca sp. 1 D. sp. 2 Lingula ovalis J. Sowerby, 1813	FES PES PES PES SIS	
CRUSTACEA (13 species) Mecochirus cf. minimus Hee, 1924 M. cf. peytoni Woodward, 1876 M. spp. Protaxius isochela (Woodward, 1876) ?Palaeopagurus sp. Zeugmatolepas reticulata (Blake, 1875) Z. costata Withers, 1928 Z. concinna (Morris, 1845) Z. fragilis Withers, 1928 Archaeolepas royeri (de Loriol, 1872) ?Calantica (Scillaelepas) ovalis Withers, 1928	IC IC IC MID EC CES CES CES CES CES CES	
ECHINODERMATA (5 species) Rhabdocidaris spinulosa (Roemer, 1836) indeterminate diademitid Balanocrinus subteres (Munster, 1831) Pentasteria (Pentasteria) cf. longispina Hess, 1968 unidentified ophiuroid	EHD EHD ESC EC ES	
BRYOZOA (3 species) Ropalonaria? arachne (Fischer, 1866) Hyporosopora sp. 'Berenicea' sp.	FB CES CES	
ANNELIDA (8 species) Cycloserpula subcrispa Parsch, 1952 C. gordialis (Schlotheim, 1820) C. intestinalis (Phillips, 1829) Dorsoserpula runcinata (J. Sowerby, 1829) D. delphinula (Goldfuss, 1831) Tetraserpula tetragona (J. de C. Sowerby, 1829) T. dollfussi (de Loriol, 1874) Hexaserpula sexangularis (Munster, 1831)	FES CNS FES CES FES FES FES FES	
OTHERS (3 species) Talpina ramosa Hagenow, 1840 (phoronid) Protulophila gestroi Roverto, 1901 (hydroid) Rhaxella sp. (sponge)	SB SB ES	

Bivalvia. The bivalves are the most common group represented in the Kimmeridge Clay both in terms of number of species and number of individuals. Only Blake (1875) has considered the bivalve fauna in its entirety, although many of the species were not illustrated. The bivalves of the Lower Kimmeridgian of the Westbury pit have recently been monographed (Clausen and Wignall, in press). The most significant taxonomic changes to arise from this study are the renaming of two of the most common species. Thus '*Lucina' minuscula* Blake, 1875 is a species of *Isocyprina* whilst *Nicaniella supracorallina* (d'Orbigny, 1850) is included in the synonomy of *N. extensa* (Phillips, 1829).

base of the formation is only seen in the degraded exposures at Black Head, near Osmington Mills (Cox and Gallois p. 6, 1981). Slightly higher beds are seen in a short section at Wyke Regis, Weymouth (Grid ref. SY 6695 7634). The overlying succession of the *mutabilis* and lower *eudoxus* Zones is poorly exposed on the Dorset coast but, conveniently, it is well seen in the Portland Cement works pit at Westbury in south Wiltshire (text-fig. 1). This pit was first documented by Birkelund *et al.* (1983) when they were also able to examine the sediments of the underlying *cymodoce* Zone. Subsequently this lower part of the succession has become obscured but new exposures at the top of the pit have now revealed strata almost up to the lowest level seen at Kimmeridge Bay (text-fig. 1).

PREREQUISITES FOR PALAEOECOLOGICAL STUDY

Fursich (1977) noted that a knowledge of the sedimentology, biostratigraphy, taxonomy and autecology were essential prerequisites for synecological study of the type undertaken here. To these requirements may be added a knowledge of the diagenesis and its control on the preservation of the fauna. Also important, particularly in the analysis of black shale faunas, is the ability to distinguish pseudoplanktonic from benthic forms. These aspects of the Kimmeridge Clay are reviewed and discussed below.

Sedimentology

The sedimentology of the Kimmeridge Clay has been discussed by Aigner (1980) and Wignall (1989). This has revealed the importance of storms in affecting a moderately shallow, broad epeiric sea. Storm mixing of the water column is considered to have been the principal mechanism of oxygen supply to the bottom waters.

Biostratigraphy

The currently used ammonite zonation scheme for the Kimmeridge Clay is discussed in Cope (1980). The detailed zonation of the Lower Kimmeridge Clay is not yet fully established (Birkelund *et al.* 1983), whilst the eight zones of the Upper Kimmeridge Clay have only been recently defined by Cope (1967, 1978). It should be noted that, throughout this study, the Upper Kimmeridge Clay of England is considered to have been deposited during the Upper Kimmeridgian although to many non-British geologists this time interval is considered to be the Lower Volgian or Lower Tithonian.

Cox and Gallois (1981) considered the biozones of the Lower Kimmeridge Clay to be chronozones as they are defined at the Black Head type section where they can be related to an isochronous event stratigraphy. The Upper Kimmeridge Clay zones, as originally defined, are biozones; however, Cope (1980) related the ammonite distributions to a measured section at Kimmeridge Bay. Many, if not all, of the beds in this sequence can be traced over a large part of England (Wignall 1988) and they therefore provide time lines with which to define the chronozones. Thus all the Kimmeridge Clay zones are here used as chronozones.

Due to the great lateral persistence of many beds of the Kimmeridge Clay, it is possible to achieve correlation on a much finer scale than the zonal level. In this study, bed numbers have been assigned to the smallest definable and correlatable beds by subdividing the bed numbering scheme of Gallois and Cox (1974, 1976) and Gallois (in prep.). Other numbering schemes have been applied to the Kimmeridge Clay (e.g. Blake 1875) but the Gallois and Cox scheme is the only one to apply to the whole formation.

TEXT-FIG. 1. Locality map showing outcrop and subcrop distributions of the Kimmeridge Clay Formation in England with an inset map illustrating the principal coastal localities in central and eastern Dorset. Inset, top left, shows the ammonite zones, a facies log and the range of strata covered in the four localities to provide a composite log.

Gastropoda. Gastropods are fairly common throughout the Kimmeridge Clay and, in a few assemblages, they are the dominant forms. However, they are woefully understudied. In many cases it has only been possible to assign forms tentatively to genera. The more common species are to be the subject of a separate study (Wignall in prep.). Some of the most significant forms are *Semisolarium hallami* Wignall MS., a heavily ornamented trochid, and *Pseudorhytidopilus latissima* (J. Sowerby, 1816) a patellid. The latter species has previously been assigned to the inarticulate brachiopod genus *Discinisca* (e.g. Blake 1875), but its calcareous, non-phosphatic shell and a number of morphological features indicate its affinities with the gastropods (Wignall in prep.). This conclusion has important consequences as other faunas containing *Discinisca* and the related form *Orbiculoidea* have been frequently recorded from black shales; they may in fact be gastropods.

Crustacea. Several dozen complete specimens of malacostracans, preserved in their original chitinophosphatic shell material, were discovered in the Kimmeridge Clay during the present study. Most specimens of this largely unknown fauna belong to the family Mecochiridae, although examples of the Anomura and the Paguroidea also occur. The only previous description of Kimmeridge Clay crustaceans was by Woodward (1875) on the fauna from boreholes in the Weald.

Cirripedes are the other major class of crustacean to occur in the Kimmeridge Clay (Table 1). Withers (1928) described Kimmeridgian cirripedes, mostly from Scottish localities; many of these species are also present in southern England.

.Autecology

Autecology is the study of the ecology of individual organisms, and roughly equates to the term, mode of life. This may be derived from three independent forms of analysis.

(i) Taxonomic uniformitarianism. This approach assumes that the mode of life of fossil species is similar to that of living organisms. This is only truly reliable when utilized on a broad scale; for example, the assumption that protobranch bivalves have always been deposit feeders. The method is inapplicable for major groups, such as the ammonites, which have become extinct.

(ii) Functional morphology. In many instances the fossilized hard parts of an organism are directly controlled by the mode of life. This is particularly so for bivalves but appears to be less so for gastropods.

(iii) Environmental distribution. As most marine organisms are fossilized close to the area in which they lived, their containing sediments can provide evidence of their environmental preferences. Similarly the range of facies in which an organism occurs can indicate the degree of eurytopy of the species.

There is always some degree of uncertainty in determining the autecology of fossil taxa as modes of life are to some extent controlled by environmental and biological factors (Tevesz and McCall 1979; Cadée 1984). Also, some species change their mode of life, often seasonally, as different conditions occur (e.g. Perron 1978).

The autecology of all Kimmeridge Clay benthic species is summarized in Table 1; the more equivocal or interesting species are discussed below.

Bivalvia. The autecology of the bivalves is probably one of the best understood of any major marine **mvertebrate** group, primarily due to the large number of extant forms and the work that has been **done** on them (Stanley 1970, 1972, 1975). Upper Jurassic taxa have been discussed in some detail **by** Hallam (1976), Duff (1978), Fürsich (1980, 1982) and Fürsich and Oschmann (1986). The mode **of life** of most Kimmeridge Clay bivalves is discussed in Clausen and Wignall (in press).

Gastropods. Autecological investigations of gastropods are problematical due to the apparent lack of relationship between shell morphology and mode of life. This is further complicated by the varying mode of life of some gastropods. For example, the Recent aporrhaid, *Aporrhais*, is an mfaunal form, deriving food from suspension and from the surface of the sediment (Yonge 1937); bowever, it can also be an epifaunal deposit feeder, depending upon the season (Perron 1978). As a generalization, a diverse or abundant gastropod fauna probably indicates the presence of benthic algae, as many gastropods are herbivores or detritivores.

Taxonomy

A total of 125 benthic species was recorded from the Kimmeridge Clay of southern England during the present study (Table 1). Their taxonomy is discussed below.

TABLE 1. Macrobenthic species recorded from the composite section of the Kimmeridge Clay of southern England (cf. text-fig. 1). Modes of life given in the right hand column are as follows: CES, cemented epifaunal suspension feeder; CNS, suspension feeder, cemented in nests; DIS, deep infaunal suspension feeder; DISB, deep infaunal species with symbiotic bacteria; EBS, epifaunal, byssally attached suspension feeder; EC, epifaunal carnivore; EHD, epifaunal herbivore and/or detritivore; ES, epifaunal suspension feeder; ESC, epifaunal suspension feeder attached by cirri; FES, free-lying epifaunal suspension feeder; MC, microcarnivore; MDIS, moderately deep infaunal suspension feeder; MID, mobile infaunal deposit feeder; PES, pedically attached epifaunal filter feeder; SB, suspension feeder; SISB, shallow infaunal suspension feeder; SISB, shallow infaunal nestling suspension feeder; SNS, semi-infaunal suspension feeder.

Species	Mode of life
BIVALVIA (66 species)	
Nuculoma obliquata (Blake, 1875)	MID
Palaeonucula menkii (Roemer, 1836)	MID
Dacromya venusta (Sauvage, 1871)	MID
Mesosaccella cypris (d'Orbigny, 1850)	MID
Solemya cf. woodwardiana Leckenby, 1859	DISB
Nucinella birkelundi Clausen and Wignall, in press	MID
Grammatodon (Grammatodon) longipunctata (Blake, 1875)	SIS
G. (G.) concinnus (Phillips, 1829)	SINS or SIS
G. (Cosmetodon) keyserlingii (d'Orbigny, 1850)	EBS
Barbatia cavata (de Loriol, 1875)	EBS
Hiatella (Pseudoaxicava) foetida (Cox, 1929)	EBS
Modiolus (Modiolus) bipartitus J. Sowerby, 1818	SNS
Musculus (Musculus) autissiodorensis (Cotteau, 1855)	SNS
M. (M.) fischerianus (d'Orbigny, 1845)	SNS
Pinna (Pinna) lanceolata J. Sowerby, 1821	SNS
Aguilerella sp.	EBS
Gervillella aviculoides (J. Sowerby, 1814)	SNS
Aulacomyella aff. farquaharsoni Cox, 1935	EBS
Parainoceramus cramei Clausen and Wignall, in press	EBS
Oxytoma (Oxytoma) inequivalve (J. Sowerby, 1819)	EBS
Entolium (Entolium) corneolum (Young and Bird, 1828)	FES
E. (E.) orbiculare (J. Sowerby, 1817)	FES
Camptonectes (Camptonectes) auritus (Schlotheim, 1813)	EBS
Radulopecten strictus (Munster, 1836)	EBS
Buchia mosquensis (von Buch, 1844)	EBS
Pseudolimea multicostata (Fürsich, 1982)	EBS
Placunopsis radiata (Phillips, 1829)	CES
Deltoideum delta (Smith, 1817)	CES or FES
Lopha (Actinostreon) gregarea (J. Sowerby, 1816)	CNS
Liostrea multiformis (Koch, 1837)	CES or FES
L. expansa (J. Sowerby, 1819)	CES
Nanogyra nana (J. Sowerby, 1822)	CNS and CES and FES
N. virgula (Deshaves, 1831)	CES and FES
Ctenostreon probiscideum (J. Sowerby, 1820)	CES and FES
Plicatula sp.	CES
Anomia suprajurensis Buvignier, 1852	CES
Trigonia (Trigonia) papillata Agassiz, 1840	SIS

Kimmeridge Clay gastropods are generally small, the only exceptions being *Pseudorhytidopilus* latissima which can approach 4 cm in diameter. The presence of this limpet-like form implies firm, if not hard, substrates. Two species of aporrhaid, *Dicroloma trifida* and *Quadrinervus ornatus*, develop a flared digitate margin late in ontogeny, indicating adaptation to soft substrates.

Scaphopoda. The Recent scaphopod Dentalium conspicuum consumes forams (Dinamani 1964), and the close correlation between fossils scaphopods and forams (Duff 1975) suggests that they too were microcarnivores. Scaphopods are relatively common in the Kimmeridge Clay although they decline rapidly in abundance in the more organic-rich facies, suggesting an intolerance of lowered oxygen levels.

Cephalopoda

Ammonites. Probably the least understood aspect of Mesozoic marine palaeoecology is the trophic group and mode of life of the ammonites. Many authors have suggested that ammonites were epibenthic (e.g. Lehmann 1981), possibly belonging to trophic groups occupied by present day gastropods. The main evidence available for interpreting their mode of life comes from analysis of their taphonomy and environmental distribution.

In the Kimmeridge Clay Aigner (1980) inferred that mass mortalities of ammonites occurred due to the anoxic overturn of the bottom waters, thus implying that the ammonites lived in close proximity to the sea floor. This deduction principally applies to Lower Kimmeridgian ammonites, particularly *Sutneria*, which are commonly found covering bedding planes. Size-frequency analysis of these horizons shows a full range of sizes suggesting a mass mortality of the whole population, in support of Aigner's (1980) claim.

In contrast, the Upper Kimmeridge ammonites tend to be independent of lithology and occur more sporadically in the sediments. Only in sediments interpreted to have been deposited in severely oxygen-deficient environments does ammonite abundance show a marked decline. This suggests that Upper Kimmeridgian ammonites lived some distance above the sediment and that they were unaffected by the majority of benthic perturbations.

Kimmeridgian ammonites do not have a widespread distribution as they tend to occur in discrete geographic areas and facies types. For example, they are virtually absent from the coeval marginal marine sediments of the Boulonnais with the exception of a few (drifted?) individuals. This implies that they lived below the surface waters and were not subject to the significant post-mortem drifting that affects near-surface dwelling cephalopods (Collins and Minton 1967). A similar conclusion was reached by Batt (1989) for many Cretaceous ammonites. As suggested above, ammonites of the Upper Kimmeridge Clay do not appear to have been affected by benthic conditions and so it must be assumed that they lived at some intermediate depth in the water column.

Aspidoceras is one of the few Kimmeridgian ammonites to have a widespread facies distribution; it occurs in the offshore mudstones of southern England and the nearshore sediments of the Boulonnais. It may therefore have inhabited surface waters thus giving it the potential to be preserved in a wide range of facies. However, it also possessed heavily calcified aptychi which may have been used as a 'shovel' for disturbing benthic organisms (Lehmann 1981), indicating an epibenthic mode of life. It is possible that Aspidoceras was an extremely eurytopic ammonite able to survive in a wide range of benthic conditions.

Coleoids. The only belemnites in the Lower Kimmeridgian of England occur in the basal baylei Zone where Pachyteuthis explanata (Phillips, 1869) and Cylindroteuthis sp. juv. occur in moderate numbers. Above this horizon belemnites are absent from England and from the contemporary nearshore sediments of the Boulonnais. There is no obvious reason for this disappearance as belemnites remained abundant in the Boreal and Tethyan realms to the north and south of this region throughout the Kimmeridgian (Doyle 1987).

Other coleoids in the Kimmeridge Clay include Belemnoteuthis antiqua Pearce, and rarer specimens of the vampire squid Trachyteuthis which are principally found in organic-rich shales.

 TABLE 1 (cont.)

Species	Mode of life
Myophorella clavellata (Parkinson, 1811)	SIS
Mesomiltha concinna (Damon, 1860)	DISB
Neocrassina (Neocrassina) ovata (Smith, 1816)	SIS
Nicaniella (Nicaniella) extensa (Phillips, 1829)	SIS .
N. (N.) cuneata (J. Sowerby, 1816)	SIS
N. (N.) desoriana (Cotteau, 1855)	SIS
Trautscholdia phillis (d'Orbigny, 1850)	SIS
indeterminate crassatellacean	SIS
Protocardia (Protocardia) morinica (J. de C. Sowerby, 1829)	SIS
Quenstedtia laevigata (Phillips, 1829)	SNS
Corbicellopsis unioides (de Loriol, 1875)	DIS
Anisocardia isocardioides (Blake and Hudleston, 1877)	SIS
Isocyprina (Isocyprina) roederi Arkell, 1932	SIS
I. (Venericyprina) argillacea Casey, 1952	SIS
I. (V.) implicata (de Loriol, 1875)	MDIS
I. (V.) pellucida Casey, 1952	SIS
I. (V.) nordgreni Clausen and Wignall, in press	SIS
I. (V.) minuscula (Blake, 1875)	SIS
Eocallista pulchella (de Loriol, 1875)	SIS
Corbulomima suprajurensis (d'Orbigny, 1850)	SISB
C. westburvensis Clausen and Wignall, in press	SISB
Pholadomva (Pholadomva) hemicardia Roemer, 1836	DIS
$P_{\rm c}(P_{\rm c})$ aeaualis J. de C. Sowerby, 1827	DIS
Gonioma (Goniomva) literata (J. Sowerby, 1819)	DIS
Wyonholas multicostata (Agassiz, 1842)	DIS
M. sp. nov.	DIS
Pleuromya uniformis (J. Sowerby, 1813)	DIS
Plectomya sp	DIS
Thracia (Thracia) depressa (J. de C. Sowerby, 1823)	DIS
GASTROPODA (16 species)	
Pseudorhytidopilus latissima (J. Sowerby, 1817)	EHD
Dicroloma trifida (Philips, 1829)	SFID and/or EHD
Quadrinervus ornatus (Buvignier, 1852)	SFID and/or EHD
indeterminate cerithiacean	EHD
Procerithium multiplicatum (Blake, 1875)	EHD
P. (Rhabdocolnus) auchenense (de Loriol, 1874)	EHD
P cf. struckmani	EHD
Oonia sp	EHD
Acteoning sp	EHD
Semisolarium hallami Wignall MS	EHD
Calliomphalus sp	EHD
Ampulling sp	EHD
Neritoma sp.	FHD
Clabularia sp.	MC
Acteoning (Striggtooning) sp	FHD
Piettein sn	EHD
E SELECE SU.	
SCAPHOPODA (6 species)	•
Prodentalium calvertensis Palmer, 1975	MC
Prodentalium sp.	MC
Plagioglypta spp.	MC
Episophon sp.	MC

This probably reflects a taphonomic bias due to the quieter depositional conditions of the shales (Hewitt and Wignall 1988).

Echinodermata. The abundance and diversity of echinoderms in the Kimmeridge Clay generally mirrors the distribution of organic-rich facies, reflecting an intolerance of lowered oxygen levels. The exception is the ophiuroids which are locally prolific in a number of organic-rich beds from the *elegans* to *wheatleyensis* Zones. This probably represents opportunistic colonization during temporarily amenable conditions. Complete specimens of ophiuroids also occur in an organic-rich shale in the *pectinatus* Zone (Ensom and Etches 1987).

Holothurians are common in the conditions of low oxygen experienced in Recent upwelling zones (Rhoads and Morse 1971), and Aigner (1980) has recorded them from the Kimmeridge Clay. However, extensive SEM study of all Kimmeridgian lithologies failed to find any holothurian spicules, nor were their distinctive 'clothes-line' faecal pellets (Edwards 1985) observed. It would appear that holothurians were rare or absent from the Kimmeridge Clay depositional environment.

Crustacea. Crustaceans are common in the oxygen minimum zone off California (e.g. Mullins et al. 1985). However, they are rare in the organic-rich facies of the Kimmeridge Clay and reach the peak of their abundance in the organic-poor marly mudstones of the *pallasioides* Zone. On taphonomic grounds alone, crustaceans would be expected to be most common in the organic-rich facies where occasional episodic burial and the absence of bioturbation would have provided optimum conditions for preservation (Brett and Baird 1986). Presumably their absence from such facies reflects a genuine intolerance of low oxygen levels.

Functional morphology of the Kimmeridge Clay taxa suggests that the majority were infaunal forms, whilst the elongate first periopods of a number of *Mecochirus* species indicates that they were carnivores (Förster 1971).

Pseudoplanktonic forms

In the present study the term hypoxic is used to describe environmental conditions that are thought to have been oxygen-deficient whilst the term dysaerobic is used to describe biofacies formed under such conditions. Black shales are commonly regarded as the products of deposition beneath hypoxic or anoxic bottom waters. Thus the apparent presence of abundant benthic fossils in such facies has proved puzzling. In some cases the apparent benthos is thought to have been attached to floating objects (Seilacher 1982). Criteria used to distinguish between these drifting pseudoplanktonic species and benthic species have been discussed in Wignall and Simms (in press).

As floating attachment sites are rare, pseudoplanktonic forms will never be abundant. Therefore, the description of supposedly abundant pseudoplankton is unlikely to be true (e.g. Kammer *et al.* 1986, p. 111). In the Kimmeridge Clay some of the likely pseudoplanktonic forms include rare individuals of *Buchia mosquensis* and *Oxytoma inequivalve* which occur scattered at a number of kevels in the Kimmeridge Clay. Elsewhere these species appear to have been part of the true benthos as they are too abundant to have been derived from low density pseudoplanktonic populations. This ability to vary between a benthic and a pseudoplanktonic existence is probably common to many attached sessile forms and it may be responsible for many conflicting palaeoecological interpretations.

Preservation in the Kimmeridge Clay

In general, all the calcareous fauna in the Kimmeridge Clay has been preserved with little alteration, although some specimens have been reduced to thin calcite films. This is somewhat surprising considering the wide range of depositional conditions and contrasts markedly with the range of preservational types in the Oxford Clay (Hudson and Palframan 1969). The commonest diagenetic change in the Kimmeridge Clay is the replacement of aragonite by secondary calcite (A. Williams, pers. comm.). The good state of preservation is probably a reflection of a high sedimentation rate combined with frequent, episodic burial by storm-generated mud turbidites (Wignall 1989).

Pyrite replacement of shells is rare and is species-specific. The plates of *Saccocoma* are always pyritized, although this is rarely the case for other echinoderms. *Liostrea multiformis* is the commonest bivalve to show pyrite replacement, whilst it occurs less frequently in *Buchia* and *Parainoceramus*.

DIVERSITY CONTROLS IN LEVEL-BOTTOM MARINE COMMUNITIES

One of the simplest measurements of diversity is species richness, S, which simply records the number of species present in a sample. Often it is desirable to know the relative proportions of the species and a number of indices are available to measure this. One of the most frequently used is the Shannon-Wiener index, H, defined by the equation:

$$H=-\sum_{i=1}^{S}Pi\ln Pi,$$

where Pi is the proportion of the *i*th species. This index has the advantage that it is relatively samplesize independent. For example during this study, an initial sample from bed 36c of the *elegans* Zone contained 114 specimens belonging to 7 species, and the *H* value was 1.14. A larger sample was then counted from the same horizon and this was found to contain a further 506 specimens. The species richness increased to 10 whilst *H* remained relatively unchanged at 1.06. Equitability is another useful measure in ecology. This considers the relative proportion of species in a sample irrespective of the number of species.

Sanders' (1968) rarefaction curves have been used in a number of palaeoecological studies to measure diversity (e.g. Duff 1975; Fürsich 1977). However, the method is mathematically inaccurate (Hurleburt 1971) and the large number of constraints necessary for its application render it virtually useless (Tipper 1979). Ecologists no longer use this method and palaeoecologists should follow suit.

Factors controlling diversity have been the subject of considerable debate over many decades. The influential paper by Sanders (1968) was based on observations of the deep sea where he noted that the faunas were of low density but extremely high diversity. He therefore proposed that in highly stable environments more time is available for niche subdivision and so, over evolutionary time, a higher diversity arises by increased specialization. From this model, termed the stability-time hypothesis, two end members arise:

(a) biologically accommodated communities which are subject to rare disturbance; they consist of specialized, equilibrium species (K strategists) which are resource limited.

(b) physically-controlled communities which are subjected to frequent disturbances and consist of unspecialized opportunistic species (r strategists) exhibiting rapid population growth rates.

More recent ecological studies suggest that the stability-time hypothesis is an over-simplification as only one feeding type predominates in many communities (Woodin and Jackson 1979). Depositfeeding bivalves in particular inhibit many other benthic species by producing a thixotropic surface layer of faecal pellets which is easily suspended (Rhoads and Young 1970). More recent work on deep sea faunas has shown that Sanders' original assumption of stability in this environment may be incorrect. Disturbance occurs in the form of low density turbidity currents (Gross *et al.* 1988) and rapid burial by bioturbation (Smith *et al.* 1986), whilst the supply of food, far from being stable, shows distinct seasonal fluctuations reflecting summer phytoplankton blooms high in the water column. Thus some deep sea benthic species have adopted an opportunistic life strategy (Gage and Tyler 1985).

An alternative hypothesis for diversity controls was suggested by Huston (1979) based upon quantitative modelling. He proposed that the two principal controls on diversity are growth rates and disturbance frequency (text-fig. 2). In contrast to Sanders, Huston suggested that long periods of interspecific competition caused a reduction in diversity as the most successful species, usually Kstrategists, eventually dominate. The attainment of competitive equilibrium depends upon the growth rates of these species compared to the remainder of the fauna. A second factor which may prevent this domination is the occurrence of disturbances, such as sudden changes in salinity or



TEXT-FIG. 2. Huston's (1979) model of diversity controls showing the importance of growth rates and disturbance frequency. Equal diversity contours are greatest in the central region and decrease outwards.

oxygen levels or sudden burial beneath a sediment layer, which tends to set the succession to lower **levels**. Under low levels of disturbance the competitive dominants will flourish and diversity will be **low** whilst very high levels of disturbance will also lead to low diversity as only a few opportunistic species will be able to colonize during the brief intervals between the disturbance events. Highest **diversity** occurs at some intermediate value which is equivalent to the mean generation time. This **allows** the optimum number of species to colonize before competition becomes important. Huston's **elegantly** simple model has yet to be applied to palaeoecology.

COMMUNITY PALAEOECOLOGY

Definitions

Communities are defined as recurring groups of species exhibiting some degree of integration commonly caused by competitive interaction. Both the Sanders and the Huston model predict that a succession of species is caused by this interaction. Therefore, communities must be considered to be in a state of dynamic disequilibrium. If integration is high then the spatial and temporal boundaries of the community must be sharp as the loss of only a few species will cause a major structural change. Rapid lateral changes need not necessarily imply a steep environmental gradient. If integration is weak then communities may appear as a mosaic of individual species in which boundaries are arbitrarily defined. It is in situations like this that the utility of rigid community definitions can be questioned as they represent man-made artefacts rather than natural divisions.

Communities are classified using three criteria:

(i) species composition;

(ii) structural attributes such as the dominance-diversity value and the proportion of trophic and guild types. Trophic composition refers to the feeding levels whilst guild types, also called life stes (Walker and Bambach 1974), refer to the utilization of ecospace. Structural attributes of communities appear more stable than species groupings alone (Heatwole and Levins 1972) and so they may be more applicable to study in the time scale available in palaeoecology. Trophic and guild types have been pictorially represented in the trophic group triangles of Scott (1976) and the bar charts of Fürsich (1977);

(iii) physical environmental controls.

Ancient communities are not directly analogous to present day ones due to significant information loss during preservation. Therefore, Fürsich (1977) called the ancient examples associations, a terminology that is used here. Subdivisions of associations were called subsets by Fürsich and Werner (1986) but the term subassociation is preferred here.

The validity of community palaeoecology

'The application of the community concept in paleoenvironmental reconstruction has been on a very meagre theoretical foundation' (Dodd and Stanton 1981, p. 385). In fact this foundation is based on the community paradigm (Hoffman 1979, 1982) which assumes that recurrent species groupings represent a distinct level of biotic organization due to their high degree of integration. Hoffman is sceptical that such integration is sufficient to cause coevolution or to lead to community stability. In shallow marine ecosystems the interactions between species may take the form of predation (e.g. Peterson 1979; Woodin 1983) either of adult forms or of larvae (e.g. Thorson 1966; Woodin 1976). More subtle forms of interaction include the disturbance of sessile forms by more mobile species (Peterson and Andre 1980).

Hoffman (1979, 1982) has recommended the abandonment of the community approach in palaeoecology, particularly the quasitaxonomic approach used by Fürsich (1977) and in this study. His main objection is that wholly unpredictable biases are caused by soft body loss and time averaging. The main argument that can be brought against Hoffmans' pessimistic appraisal of community palaeoecology is that many of the biases are likely to be constant within a given macrohabitat. Thus, it is perfectly valid to consider community changes within a given facies type in the fossil record. Comparison between ancient and modern communities is obviously fraught with more difficulties but in most palaeoecological studies such comparisons are not, and should not be, the object of the study. In summary, it is better to study the changes in the data which are preserved than to bemoan that which has been lost.

Analytical methods

Samples were taken every metre or more frequently if lithological changes occurred on a finer scale. An average of 0.02 m^3 of material was analyzed per sample, although this was exceeded if the fossils occurred in low density. All elements of the fauna were counted and notes were made on the taphonomic and palaeoecological information. This included the state of preservation, the degree of articulation, the orientation and distribution of the fauna in the sediment, and the degree of fragmentation. Only the identifiable fragmented fauna was included in the faunal count; fine shell hash was excluded from the analysis.

In order to evaluate the benthic associations the raw data was converted to give percentages of benthic species after the removal of all the pelagic forms (ammonites, *Saccocoma*) and all the rare specimens interpreted to have been pseudoplanktonic. The abundance of species with multi-element skeletons, such as echinoderms and cirripedes, was difficult to quantify as the elements were commonly very small and easily overlooked. Only when samples were broken down and disaggregated, as part of a separate meiofaunal analysis (Wignall 1988), were they frequently encountered. A semi-arbitrary value of three elements per individual was assigned to echinoderms and two for cirripedes. Three palaeoecological information indices were then evaluated from the converted data set: the fragmentation index, the species richness and the dominance-diversity index (see above).

Benthic associations were evaluated by ranking the species and grouping samples with similar speciesabundance distributions. The associations are characterized by their trophic nuclei, defined as the dominant species which make up 80% of the fauna (Neyman 1967), and the area they occupy on trophic-guild group triangles (Scott 1976), which should be reasonably small. A semi-quantitive estimate of the biomass can be obtained if the widths of the bars in trophic nuclei diagrams are proportional to the maximum dimensions of the species (Duff 1975). This is approximately true if the species are roughly equidimensional but more linear forms, such as serpulids, are more accurately measured by their aperture width. In a number of cases samples were found to contain very similar species lists but in widely differing proportions – these were grouped as subassociations of the same association. The subassociations invariably plotted in the same field of the trophicguild group triangles indicating their close affinity.

A limited number of samples from the Upper Kimmeridgian were analyzed using Q-mode cluster analysis to check independently the validity of the associations derived from the simple ranking technique outlined

above. The results from the cluster analysis were in very close agreement, indicating that the associations have been defined with some degree of objectivity. Oschmann (1988) also used cluster analysis to identify Upper Kummeridge Clay benthic associations which led him to recognise two of the benthic associations found during the present study. The failure to discover the remaining associations is probably due to his limited number of samples; only 18 samples were taken in 260 m of strata whilst 259 samples were analyzed in the same section for this study.

Gamma ray spectrometry

Gamma ray spectrometry has been shown to be a useful tool in environmental interpretation of oxygendeficient marine mudrocks (Myers and Wignall 1987). Uranium becomes enriched during prolonged periods of bottom water anoxia and so the evaluation of this enrichment provides a useful criterion with which to assess independently palaeoecological inferences. Therefore, for the purposes of this study, a Geometrics 410A portable gamma ray spectrometer was used to measure potassium, thorium and uranium levels in the Lower Kimmeridge Clay and the topmost Kimmeridge Clay. Values from the intervening sediments were obtained from Myers (1987). Complete coverage of every bed was not possible due to the need for continuous wave-cut platform exposure. Levels of authigenic uranium were calculated using the technique discussed in Myers and Wignall (1987).

Materials and results

Samples were obtained from the composite section (Black Head to Weymouth to Westbury to Kimmeridge Bay, see text-fig. 1), in order to obtain a virtually complete vertical section. A total of 466 samples containing \$7,800 specimens were analyzed. These were divided into 26 associations of which 2 associations were divided into a further 7 subassociations. The associations fall into two groups:

(i) Aerobic mudstone associations. A total of 15 such associations (A1-A15) were recorded from the Lower Kimmeridge Clay, whilst a further 7 (B1-B7) came from the Upper Kimmeridge Clay. Samples from these associations generally have a dominance-diversity value exceeding 1.5. One association found in the *missiodorensis* Zone appeared to be transitional between the aerobic and dysaerobic associations, this was abelled A/E1.

(ii) Dysaerobic mudstone and shale associations. Seven examples of oxygen-restricted associations were found in the central part of the Kimmeridge Clay, labelled E1–E7. Authigenic uranium values of the associated **red**iments typically exceed 2 ppm whilst the dominance-diversity index H is less than 1.5.

The data are presented as a series of trophic nuclei diagrams illustrating the autecology of the constituent ara, and as a series of trophic-guild triangles. The occurrences of these associations, along with the palaeocological indices of dominance-diversity, species richness and the fragmentation index and the authigenic uranium data, are illustrated in a series of logs (text-figs 3-11) from the composite section shown a text-figure 1. Examples of an aerobic and a dysaerobic benthic association data table are given in Table 2. The complete data set is in Wignall (1988), and has been deposited with the British Library, Boston Spa, Yorkshire, UK, as Supplementary Publication No. SUP 14038 (33 pages). Large representative samples of the farme have been deposited at the British Museum (Natural History), London, and the British Geological Survey, Keyworth.

LOWER KIMMERIDGE CLAY AEROBIC ASSOCIATIONS

The associations are discussed in the order of their first appearance.

- Corbulomima suprajurensis: Isocyprina implicata Association
- samples, 1255 specimens, 43 species, 21% average fragmentation, H = 1.60)

An association with a simple trophic structure dominated by infaunal filter feeding bivalves (text-

ix 12) of which 11% were deep burrowers. Deposit feeding bivalves form up to 20% of some ties (text-fig. 13). This is an exceptionally long-ranging association as it occurs in the topmost

• the lower *mutabilis* Zone (text-fig. 3) and in bed group 44 of the *hudlestoni* Zone (text-figs. 8-9),

Brookfield (1978) discussed the depositional conditions of the Ringstead Waxy Clay and



TEXT-FIG. 3. Logs of the lithologies and palaeoecological information indices for the basal Kimmeridge Clay at Black Head (left) and the lower *mutabilis* Zone at Weymouth (right); a short gap spanning the *cymodoce*: *mutabilis* Zonal boundary separates the two sections. The bed numbers are from Gallois and Cox (1976); in later logs this scheme is subdivided to provide higher resolution correlation. The key also applies to all subsequent logs. Localities are shown in text-figure 1.



TEXT-FIG. 4. Lithological and palaeoecological logs of the *mutabilis-eudoxus* Zone interval seen in the Westbury Pit, Wiltshire. Key as for text-figure 3. Plots of authigenic uranium values are also shown, these are calculated from data gathered by a portable gamma ray spectrometer in the field.



TEXT-FIG. 5. Log of the upper *eudoxus* to mid-*autissiodorensis* Zones at Hobarrow Bay, approximately 1 km to the west of Kimmeridge Bay. A short stratigraphic gap separates the base of this section from the top of the Westbury section (text-fig. 4). Authigenic uranium values are derived from gamma ray spectrometry data. Symbols and key as for text-figure 3.



TEXT-FIG. 6. Log from the mid-autissiodorensis to the lower elegans Zones of Kimmeridge Bay. Key as for text-figure 3.



TEXT-FIG. 7. Log of the lower *elegans* to lower *wheatleyensis* Zones measured between Kimmeridge Bay and Clavells Hard. Key as for text-figure 3.



TEXT-FIG. 8. Log of the lower *wheatleyensis* to mid-*hudlestoni* Zones measured to the east of Clavells Hard. Key as for text-figure 3.



TEXT-FIG. 9. Log of the mid-hudlestoni to lower pectinatus Zones measured to the east of Clavells Hard. Key as for text-figure 3.



TEXT-FIG. 10. Log of the lower *pectinatus* to lower *pallasioides* Zones at Egmont Bight, 1 km to the west of Chapmans Pool. Authigenic uranium values were not measured above bed 50a due to lack of suitable wavecut platform exposures. Key as for text-figure 3.



TEXT-FIG. 11. Log of the lower *pallasioides* to lower *rotunda* Zones measured between Egmont Bight and Chapmans Pool. Key as for text-figure 3.

suggested that the substrate was very soft, although occasional 'firming' episodes allowed echinoid and oyster colonization. This interpretation is supported by the predominance of infaunal forms in the ecological structure and may account for low values of diversity.

A2 Nanogyra nana: Deltoideum delta Association

(4 samples, 485 specimens, 41 species, 34% average fragmentation, H = 1.77)

The structure of this association is again simple (text-fig. 13) and consists mostly of large, sessile, epifaunal forms, principally oysters and serpulids (text-fig. 14). Infaunal species do not account for more than 20% in any sample (text-fig. 13). The association is restricted to the lower *baylei* Zone and the Ringstead Coral Bed (Brookfield 1978), where it occurs in sandy mudstones with common reworked phosphatic nodules. Species richness correlates inversely with the fragmentation index (text-fig. 3), possibly indicating the loss of some species due to mechanical destruction.

The reworked nodules and the high fragmentation index suggests prolonged reworking and condensation. Sediment influx must have been rare as most species were fixosessile and would have been unable to exhume themselves. *Torquirhynchia inconstans* is restricted to this association from the basal beds of the Kimmeridge Clay. Brookfield (1973a) has suggested that the asymmetric commissure of this brachiopod indicates adaptation to a tidal regime, although it is probably only safe to infer that benthic currents were of varying direction without any tidal connotations (see also Fürsich and Palmer (1984) for an alternative interpretation of the functional morphology of this brachiopod).

A3 Nanogyra nana: Quenstedtia laevigata Association

(3 samples, 528 specimens, 29 species, 21 % average fragmentation, H = 2.42)

A high diversity association with a heterogenous trophic nucleus of similiar taxonomic composition to A2 (text-fig. 15) and an ecological structure with roughly equal proportions of infaunal and

TABLE 2. Data table for aerobic association A6 and dysaerobic association E3

Ъ

	(*		Abundance	Presence	
		Trophic nucleus position	(%)	(%)	
		Bivalvia			
	1	Thracia depressa	19.2	100	
	2	Nicaniella extensa	15.0	100	
	3	Grammatodon longipunctata	9.9	100	
	4	Palaeonucula menkii	9.0	100	
	5	Nucinella birkelundi	6.4	100	
	6	Corbulomima supraiurensis	4.3	83	
	7	Nanogyra virgula	4.3	83	
	8	Mesomiltha concinna	3.0	100	
	10	Liostrea multiformis	2.6	100	
	11	Isocvprina minuscula	2.5	100	
		Corbulomima westburyensis	2.4	67	
		Isocyprina pellucida	2.4	50	
		Grammatodon concinnus	2.1	33	
		Grammatodon keyserlingii	2.1	100	
		Isocyprina implicata	1.7	50	
		Entolium corneolum	1.7	83	· ·
		Neocrassina ovata	1.5	83	·········
		indet. crassatellacean	1.2	50	
		Protocardia morinica	0.7	33	
		Isocyprina roederi	0.2	33	
		Deltoideum delta	0.2	33	
		Entolium corneolum	0.2	33	
		Myopholas cf. multicostata	0.2	17	
		Camptonectes auritus	0.4	67	
		Trigonia papillata	0.3	33	
		Pinna lanceolata	0.3	33	× .
		Radulopecten strictus	0.2	17	
		Pleuromya uniformis	0.5	33	
		Placunopsis radiata	0.1	17	
		Gervillella aviculoides	0.1	17	
ъ		Quenstedtia laevigata	0.1	17	
		GASTROPODA			
		Procerithium multiplicatum	2.2	33	
		Acteonina sp.	0.8	17	
		Ampullina sp.	0.3	17	
		Dicroloma trifida	0.2	17	
		Quadrinervus ornatus	0.2	17	
	•	Drodontalium en	1.5	33	
		Frodentatium sp.	15	55	
		Brachiopoda			
		Rhynchonella sp.	0.2	33	
	9	Lingula ovalis	2.6	83	•
		Echinodermata			
		Rhabdocidaris spinulosa	0.2	33	
		-			
		OTHERS	- ·	07	
		Laipina ramosa	1	85	A

\$

TABLE 2 (cont.)

· •		Abundance	Presence		
•	Trophic nucleus position	(%)	(%)		
	BIVALVIA				
	1 Protocardia morinica	39.5	100		
	3 Corbulomima supraiurensis	8.1	67		
	4 Liostrea multiformis	5.4	67		
	Isocyprina minuscula	• 3.3	53		
	Parainoceramus cramei	1.9	40		
1	Nanogyra virgula	1.2	20		
	Buchia mosauensis	0.8	27		
	indet. crassatellacean	0.5	20		
	Grammatodon longipunctata	0.4	7		
	Corbicellopsis unioides	0.3	13		-
	Mesomiltha concinna	0.2	7		
	Entolium orbiculare	0.1	13		
	Camptonectes auritus	0.1	7		
	Grammatodon keyserlingii	0.1	7		
	GASTROPODA				
	2 Quadrinervus ornatus	27.1	100		
	2 Quuurmervus ornarus Pseudorhytidonilus latissima	271	33		
	Procerithium struckmani	0.7	12		
	Clobularia sp	0.7	13		
	Diovoloma trifda	1.0	13	•	
	indet eerithiseeen	1.0	7		
	indet. centmacean	0.1	1		
	Scaphopoda				
	Plagioglypta sp. 1	1.2	27		
	Brachiopoda				
×	Lingula ovalis	3.3	47		
	Discinisca sp. 2	0.6	7		
	Echinodermata				
·	diademitid	0.3	7		
	ophiuroid	0.1	7		
	Balanocrinus subteres	0.1	7		
	CRINTACEA				
.'	Maaaahirus so	1.2	12		
ч. С	Zaugmatolonga roticulata	0.2	13		
	Zeugmaioiepas reliculaia	03	13		
	Anahaaalan aa navani	0.3	12		
	Archaeolepas royeri Zauzmatolonga fragilia	0.1	13		
	Leugmatolepas jragilis	0.1	. /		
	Serpulidae	\$			
	Cycloserpula sp.	0.5	13		
	Tetraserpula dollfussi	0.1	7		

epifaunal suspension feeding bivalves. Herbivores and deposit feeders form up to 30% of the total in some samples (text-fig. 13). The association is restricted to the calcareous clays of the upper *baylei* Zone (text-fig. 3) where pavements of *Deltoideum delta* are prominent.

The high diversity indicates normal marine conditions. Mud sedimentation was greater than in



TEXT-FIG. 12. Trophic nucleus of A1, the Corbulomima suprajurensis: Isocyprina implicata association from organic-poor, calcareous mudstones. Key: 1, Corbulomima suprajurensis; 2, Isocyprina implicata; 3, Thracia depressa; 4, Palaenucula menkii; 5; Liostrea multiformis; 6, Protocardia morinica; 7, Isocyprina roederi; 8, Grammatodon keyserlingii.



TEXT-FIG. 13. Trophic-guild triangles for the aerobic associations of the Lower Kimmeridge Clay. Key: ES, epifaunal suspension feeders; IS, infaunal suspension feeders; DF, deposit feeders.



TEXT-FIG. 14. Trophic nucleus of A2, the Nanogyra nana: Deltoideum delta association from the condensed beds of the basal Kimmeridge Clay. Key: 1, Nanogyra nana; 2, Deltoideum delta; 3, Cycloserpula intestinalis; 4, Dorsoserpula runcinata; 5, Cycloserpula gordialis; 6, Corbulomima suprajurensis; 7, Liostrea multiformis.



TEXT-FIG. 15. Trophic nucleus of A3, the Nanogyra nana: Quenstediia laevigata association from the less condensed beds of the basal Kimmeridge Clay. Key: 1, Nanogyra nana; 2, Quenstediia laevigata; 3, Grammatodon longipunctata; 4, Deltoideum delta; 5, Corbulomima suprajurensis; 6, Procerithium multiplicatum; 7, Isocyprina minuscula; 8, ophiuroid; 9, Thracia depressa; 10, Dorsoserpula runcinata.

the underlying association, although the horizons of *Deltoideum* probably indicate firm substrate conditions. The occurrence of 10% gastropods and more than 4% echinoids suggests, although it does not prove, the presence of benthic algae and thus relatively shallow conditions in the photic zone. This tentative conclusion is supported by the presence of echinoid algal grazing marks on some *Deltoideum* valves.

A4 Procerithium multiplicatum: Lingula ovalis Association

(3 samples, 375 specimens, 26 species, 20% average fragmentation, H = 2.09)

A moderately high diversity association (H = 2.1) with a trophic structure dominated by roughly equal proportions of infaunal suspension feeders and deposit feeders/herbivores (text-fig. 13). It ranges from the upper *cymodoce* Zone to the lower *mutabilis* Zone in medium grey calcareous clays (text-fig. 3).

As with association A3, the abundant herbivores probably indicate the presence of benthic algae and thus deposition in the photic zone. Unlike the earlier A3 association however, sessile epifauna is virtually absent, apart from *Liostrea* (text-fig. 16), suggesting that the substrates were soft and inhibited most epifauna. This may be partially due to the presence of 6% deposit feeding bivalves which would have have produced a pelleted, thixotropic surface layer (Rhoads and Young 1970). Such conditions may have been particularly inimical for deep infauna as this guild group is poorly represented in this association, although both these trophic-guild groups are represented in association A1.



TEXT-FIG. 16. Trophic nucleus of A4, the Procerithium multiplicatum: Lingula ovalis association from the calcareous and silty mudstones of the upper cymodoce and lower mutabilis Zones. Key: 1. Procerithium multiplicatum; 2, Lingula ovalis; 3, Corbulomima suprajurensis; 4, diademitid echinoid; 5, Palaeonucula menkii; 6, Isocyprina implicata; 7, Liostrea multiformis; 8, Neocrassina ovata; 9, Anisocardia isocardioides.

A5 Isocyprina minuscula: I. implicata Association

(1 sample, 109 specimens, 10 species, 22% average fragmentation, H = 1.76)

This unusual low diversity association was only found in one sample from an horizon in the midmutabilis Zone of Westbury (text-fig. 4). By strict definition it is therefore not a true association as it does not recur at other horizons. However, it is included here as the unique composition of the single sample bears no comparison to other Kimmeridge Clay associations. The trophic structure is dominated by shallow infaunal, filter feeding species of *Isocyprina* (text-fig. 17). The pointed anterior margin and moderately elongate outline of *I. implicata* implies that it was relatively better at burrowing than the other species, although it has an entire pallial line suggesting that it did not possess large siphons.



TEXT-FIG. 17. Trophic nucleus of A5, the Isocyprina minuscula: Isocyprina implicata association from the midmutabilis Zone. Key: 1, Isocyprina minuscula; 2, Isocyprina implicata; 3, Isocyprina pellucida; 4, Quenstedtia laevigata.

The predominance of one feeding type is clearly not in accord with any niche-partitioning hypothesis (Sanders 1968), although soft-bodied deposit feeders may have been present. Competition between the bivalves could have been slightly lessened by some size-selectivity during filter feeding (Peterson and Andre 1980). Filter feeders are typically opportunists due to the fluctuating nature of their food source and consequently they tend to have widely overlapping niches (Levinton 1972). The occurrence of a simple trophic structure in this association may therefore indicate a fluctuating, disturbed environment. This is further supported by the low diversity value. The nature of the disturbance is, however, unclear.

A6 Thracia depressa: Nicaniella extensa Association

(6 samples, 1123 specimens, 41 species, 36% average fragmentation, H = 2.57)

A high diversity association found in calcareous mudstones, with large septaria, in the upper *mutabilis* Zone at Westbury. It alternates with association A8 (text-fig. 4). The average fragmentation index is very high at 36%. The deep infaunal forms, *Mesomiltha* and *Thracia* form 25% of the fauna (text-fig. 18) whilst mobile deposit feeders, *Palaeonucula* and *Nucinella*, form up



TEXT-FIG. 18. Trophic nuclei of associations A6, the Thracia depressa: Nicaniella extensa association and of A9, the Nucinella birkelundi: Nanogyra virgula association from organic-poor mudstones at Westbury. Key: 1, Thracia depressa; 2, Nicaniella extensa; 3, Grammatodon longipunctata; 4, Palaeonucula menkii; 5, Nucinella birkelundi; 6, Corbulomima suprajurensis; 7, Nanogyra virgula; 8, Mesomiltha concinna; 9, Lingula ovalis; 10, Liostrea multiformis; 11, Isocyprina minuscula; 12, Protocardia morinica; 13, Tetraserpula dollfussi.

to a third of the total in some samples (text-fig. 13). In contrast, sessile epifaunal forms, of which *Nanogyra virgula* is the most common, form only a few percent of the total (Table 2).

The deep infauna indicate that benthic oxygen levels were very high and not restricting whilst the high fragmentation indicates either the occurrence of a shell crushing predator or slow sedimentation rates allowing prolonged periods of exposure to such biomechanical processes. Benthic currents were not sufficiently prolonged to winnow the sediments as the mudstones are not especially shelly. The rarity of sessile epifaunal forms suggests that the sediments were soft, which again may be due to the presence of deposit feeding bivalves. However, infaunal filter feeding bivalves do not appear to have been inhibited by the presence of the deposit feeders. The reason for this may be elucidated from some studies of recent faunas. Most interspecific competition between deposit feeders and infaunal suspension feeders occurs at the adult-larval level; of particular importance is the consumption of newly-settled planktotrophic larvae of filter feeders by deposit feeders (Woodin 1976; Peterson 1979). But, if environmental disturbances occasionally wipe out the deposit feeders then the filter feeders are able to establish themselves before the more slowly dispersing deposit feeders can recolonize. Predation on deposit feeders' larvae by filter feeders may be less important, due to the large size of their larvae (Jablonski and Lutz 1983). Interactions undoubtedly occur between epifaunal suspension feeders' larvae and adult deposit feeders as well, but the presence of a pelleted surface sediment will inhibit the former throughout their growth as they will be constantly at risk of foundering.

A7 Prodentalium calvertensis: Grammatodon keyserlingii Association (2 samples, 617 specimens, 39 species, 23% average fragmentation, H = 2.60)

An exceptionally diverse assemblage with five marine classes in the trophic nucleus (text-fig. 19). Typical Kimmeridge Clay opportunists, such as *Protocardia morinica*, are absent, but many other forms, which are rare elsewhere, occur in this association; these include *Dacromya venusta*, *Lopha gregarea* and the asteroid *Pentasteria* cf. *longispina*. The range of the association at Westbury (text-fig. 4), includes the Pentacrinus bed (Gallois and Cox 1976; Birkelund et al. 1983) named after the crinoid, *Balanocrinus subteres*, which is also common at this horizon.

The high diversity of this association and the rarity of opportunists indicates a stable environment. However, infrequent perturbations presumably affected the fauna as low diversities, caused by prolonged competition, do not occur (Huston 1979; text-fig. 2). Alternatively, the diversity could be due to time-averaging and condensation although this might be expected to have produced shellier sediments than those in which this association occurs.



TEXT-FIG. 19. Trophic nucleus of A7, the Prodentalium calvertensis: Grammatodon keyserlingii association from silty mudstones of the mid-mutabilis Zone which include the Pentacrinus bed of Gallois and Cox (1976). Key: 1, Prodentalium calvertensis; 2, Grammatodon keyserlingii; 3, Cycloserpula gordialis; 4, Palaeonucula menkii; 5, ophiuroid; 6, Corbulomima suprajurensis; 7, Thracia depressa; 8, Isocyprina argillacea; 9, Acteonina sp.; 10, Pleuromya uniformis.

A8 Nicaniella extensa: Corbulomima suprajurensis Association

(12 samples, 3176 specimens, 36 species, 29% average fragmentation, H = 1.69)

A low diversity association found in the upper *mutabilis* and lower *eudoxus* Zones at Westbury (textfig. 4). *Nicaniella extensa* constitutes nearly half of the total fauna (text-fig. 20) and it forms the Supracorallina shell bed, bed 22 of the *mutabilis* Zone (Gallois and Cox 1976). At Westbury a similar shell bed also occurs in the base of bed 26 of the lower *eudoxus* Zone. Algal borings of shells are



TEXT-FIG. 20. Trophic nuclei of associations A8, the Nicaniella extensa: Corbulomima suprajurensis association from mudstones of the upper mutabilis Zone, and of A11, the Protocardia morinica: Nanogyra virgula association from mudstones of the lower eudoxus Zone at Westbury. Key: 1, Nicaniella extensa; 2, Corbulomima suprajurensis; 3, Palaeonucula menkii; 4, Grammatodon longipunctata; 5, Quadrinervus ornatus; 6, Nucinella birkelundi; 7, Nanogyra virgula; 8, Protocardia morinica; 9, Tetraserpula dollfussi; 10, Isocyprina minuscula; 11, Liostrea multiformis.

common in the shell beds but encrusting and epifaunal forms are not important, forming only 6% of the total. Specimens of *Nicaniella* in bed 28a lose their coarse comarginal ornament and become smooth with only growth line ornament developed.

The shelliness of the sediments indicates winnowing and/or low sedimentation rates, whilst the rarity of epifauna suggests a soft sediment. This apparent contradiction in the data may be attributable to turbid bottom waters. Thus, whilst the net sedimentation rate of mud may have been low, the permanent presence of soupy sediments would have been sufficient to deter epifaunal forms and would account for the low levels of diversity. The smooth *Nicaniella* are suggestive of a reduction in salinity as many present-day molluscs lose their ornament in brackish waters (Remane 1971). This is not substantiated by the rest of the fauna however, for the diversity actually increases at this horizon. The cause of the morphological change therefore remains a mystery.

Co-occurring in the same sediments with association A8 are horizons of abundant, large Aulacomyella aff. farquharsoni. Their valves are often articulated although they are usually opened

out. Despite increasing the shelliness of the sediments, the posidoniids are not encrusted and they do not cause any change in the composition of the benthos at the horizons in which they occur. This apparent independence from the remainder of the benthos was also noted by Duff (1975) for Oxfordian posidoniids; it led him to remove them from his benthic association analyses and the same procedure is followed here. The mode of life of *Aulacomyella* is not clear; they are too abundant to have been pseudoplanktonic and yet they do not appear to reflect normal benthic conditions. Their swarm abundance at discrete horizons suggests that they were colonizing transiently favourable benthic conditions, conditions that were inimical to other benthic forms.

A9 Nucinella birkelundi: Nanogyra virgula Association

(9 samples, 1814 specimens, 33 species, 30% average fragmentation, H = 2.08)

A relatively diverse association with a wide range of trophic and guild types in the trophic nucleus (text-fig. 18). Both deposit feeders and shallow infaunal suspension feeders are well represented (text-fig. 13). Deep infauna is the rarest group, constituting only 2.6% of the total. The association occurs in the upper *mutablis* and lower *eudoxus* Zones at Westbury, interbedded with association A8 (text-fig. 4).

The increased abundance of sessile epifaunal species, compared to A8, indicates a considerably firmer substrate. Thus the presence of deposit feeding *Nucinella* does not appear to have inhibited the epifauna to the same extent as the deposit feeding protobranchs.

A10 Protocardia morinica: Lingula ovalis Association

(15 samples, 3218 specimens, 53 species, 23% average fragmentation, H = 2.17)

P. morinica dominates this association forming nearly a quarter of the total fauna (text-fig. 21). The remainder of the fauna occurs in slowly decreasing proportions and thus exhibits a high equitability. Filter feeding bivalves are dominant, although up to 60% herbivores and deposit feeders may occur in some samples (text-fig. 13) mainly due to local abundances of *Procerithium*. The association occurs in mudstones and two thin organic-rich shales in bed group 28 of the lower *eudoxus* Zone at Westbury (text-fig. 4).

Many species in this association are the oxygen-tolerant forms found in the organic-rich sediments higher in the Kimmeridge Clay succession. This factor, together with the occurrence in



TEXT-FIG. 21. Trophic nucleus of A10, the Protocardia morinica: Lingula ovalis association from thin, moderately organic-rich shales and mudstones of the lower eudoxus Zone at Westbury. Key: 1, Protocardia morinica; 2, Quadrinervus ornatus; 3, Lingula ovalis; 4, Isocyprina minuscula; 5, Corbulomima suprajurensis; 6, Liostrea multiformis; 7, Cycloserpula subcrispa; 8, Cycloserpula gordialis; 9, Procerithium multiplicatum; 10, Grammatodon longipunctata; 11, Corbulomima westburyensis; 12, Parainoceramus cramei.

bed group 28, suggests that slightly lowered oxygen levels may have been a structuring factor in this association. The first influence of lowered oxygen is therefore reflected by a change in taxonomic composition and ecological structure prior to any reduction in diversity and equitability. Authigenic uranium values are not notably enriched in the sediments in which A9 occurs (text-fig. 4).

All Protocardia morinica: Nanogyra virgula Association

(10 samples, 3580 specimens, 48 species, 21% average fragmentation, H = 2.24)

A high diversity association dominated by infaunal and epifaunal filter feeding bivalves (text-fig. 20). It ranges through 8 m of mudstone in the lower *eudoxus* Zone at Westbury (text-fig. 4). Deposit feeders form only 8% of the total, whilst deep infauna is even rarer at 1.4%. The sediments locally become very shelly due to the abundance of valves of *N. virgula*; sessile epifauna, such as *Tetraserpula*, increase in importance at such horizons. Algal-bored shells are also common in the shell beds.

Both N. virgula and T. dollfussi possess very small attachment scars suggesting that they were free-lying for much of their life. N. virgula was probably able to recline on fairly soft sobstrates (Fürsich and Oschmann 1986), but the long thin tests of T. dollfussi could only have reclined on firm substrates. The epifaunal content of this association therefore indicates muddy firmground conditions whilst the shell abundance attests to low sedimentation rates. Thus the N. virgula shell beds have a different origin to the N. extensa shell beds which are attributed to slow sedimentation in turbid conditions. Most members of the trophic nucleus of association A11 are the euryoxic forms (text-fig. 20) which abound in true dysaerobic biofacies. Consequently, as with association A10, benthic oxygen levels may have been slightly lowered. The algal borings indicate that the depositional environment lay within the photic zone.

The first major organic-rich shales appear in bed group 31 of the mid-*eudoxus* Zone at Westbury (text-fig. 4). This is reflected by a dramatic decrease in the species richness and diversity of the benthic fauna and an increase in the authigenic uranium content of the sediments. The taxonomic composition of associations A10 and A11 indicate that benthic oxygen levels may have been modestly lowered prior to this event. The dysaerobic associations are discussed below.

DYSAEROBIC ASSOCIATIONS

Shelly benthic fossils are found in virtually every horizon of the Kimmeridge Clay despite the occurrence of some exceptionally organic-rich shale beds. Perhaps the only exceptions are three finely laminated coccolith limestones from the *pectinatus* Zone (text-figs 9 and 10). However, even in these beds a few bioturbated horizons can be found, indicating that benthic colonization occurred in every bed of the Kimmeridge Clay during some of their depositional time.

A/E1 Corbulomima suprajurensis: Grammatodon longipunctata Association (13 samples, 759 specimens, 39 species, 22% average fragmentation, H = 1.80)

This is an association transitional between aerobic and dysaerobic associations. Thus the large total of species recalls the aerobic associations whilst the paucity of species in the trophic nucleus is typical of the dysaerobic associations. The trophic nucleus is dominated by filter feeding bivalves; deep infaunal forms are absent (text-fig. 22), whilst the diversity is moderately high. The fauna occurs well distributed in silty mudstones associated with organic-rich shales, particularly in the *autissiodorensis* Zone (text-figs 5 and 6). The appearance of this association in the midst of organic-rich strata, with relatively more impoverished faunas, indicates an improvement in benthic oxygenation over a period of perhaps several thousand years. Authigenic uranium values are notably low in the same strata.



TEXT-FIG. 22. Trophic nucleus of A/E1, the transitional aerobic: dysaerobic Corbulomima suprajurensis: Grammatodon longipunctata association from metre-thick mudstone beds interbedded with organic-rich shales in the autissiodorensis Zone. Key: 1, Corbulomima suprajurensis; 2, Grammatodon longipunctata; 3, Liostrea multiformis; 4, Isocyprina minuscula; 5, Plagioglypta sp. 1; 6, Protocardia morinica; 7, Mesosaccella cypris.

El Protocardia morinica: Oyster Association

(25 samples, 1594 specimens, 22 species, 23% average fragmentation, H = 1.02)

An association dominated by *P. morinica* with lesser numbers of oysters and *C. suprajurensis* (textfig. 23); other species are very rare. The fauna is abundant on some bedding planes and absent on others. *Nanogyra virgula* is the dominant oyster in the mid-*eudoxus* Zone but above this level slightly lower diversity samples contain *Liostrea multiformis* in the free-lying epifaunal niche. The association ranges up to bed group 45 of the upper *hudlestoni* Zone (text-fig. 9). Both subassociations are found in organic-rich shales and mudstones; the shales are notably enriched in authigenic uranium.

The abundance of organic matter and authigenic uranium in the sediments indicates prolonged periods of benthic anoxia (Wignall and Myers 1988). The occurrence of the fauna at discrete horizons is suggestive of transient colonization by opportunists during brief oxygenation events (Myers and Wignall 1987). This appears to be the pattern for most organic-rich shale faunas in the Kimmeridge Clay. The associated mudstones normally contain a fauna throughout their thickness, albeit impoverished. Periods of benthic colonization were probably more prolonged in the mudstones, although the taxonomic composition is commonly the same as for the interbedded shales. Stable conditions of low oxygen can lead to a high diversity (e.g. Arntz et al. 1976) but this is not observed in the Kimmeridge Clay. Therefore, some environmental instability presumably occurred during deposition of the mudrocks to cause the low diversity. In many modern seas a summer thermocline develops in the water column which inhibits oxygen renewal to the bottom waters. Sometimes oxygen is totally absent for a period of months with disastrous effects for most marine life. Bivalves appear to be the best adapted group to survive such conditions (e.g. Dries and Theede 1974; Kitching et al. 1976; Pearson and Rosenberg 1978). The Kimmeridge Clay mudstones were probably deposited beneath a seasonally-stratified water column in which benthic oxygen levels may have been very low or totally anoxic in the summer, a conclusion also reached by Oschmann (1988). The organic-rich shales were probably deposited beneath a more permanently



TEXT-FIG. 23. Trophic nuclei of dysaerobic associations E1, the Protocardia morinica: oyster association, E3, the Protocardia morinica: Quadrinervus ornatus association and of E7, the Lingula ovalis: Protocardia morinica association. E1 is subdivided into E1a, the Protocardia morinica: Nanogyra virgula subassociation and E1b, the Protocardia morinica: Liostrea multiformis subassociation. All the associations are derived from organic-rich shales and mudstones from the central part of the Kimmeridge Clay Formation at Kimmeridge Bay. Key: 1, Protocardia morinica; 2, Nanogyra virgula; 3, Corbulomima suprajurensis; 4, Liostrea multiformis; 5, Quadrinervus ornatus; 6, Lingula ovalis.

stratified water column in which anoxic bottom water conditions were only occasionally improved during brief oxygenation events (Wignall 1989).

E2 Protocardia morinica: Isocyprina minuscula Association

(206 samples, 16,423 specimens, 42 species, 22% average fragmentation, H = 0.99)

This is the most common associations in the Kimmeridge Clay. It ranges throughout much of the upper *eudoxus* to *hudlestoni* Zones (text-figs 5–8). The association is dominated by three species of infaunal filter feeding bivalves to the virtual exclusion of any other trophic-guild group (text-fig. 24). Of the seven possible combinations of the three species only five occur (text-fig. 25); of these the *Protocardia morinica*: *Carbulomima suprajurensis* and *Protocardia morinica*: *Isocyprina minuscula* subassociations are the most common. Oschmann (1988) identified three of these subassociations, although he considered them to be of association rank. Only one or two species is dominant in any one sample and, in the organic-rich shale shell pavements, only one species is dominant on each bedding plane. The shell pavements are common in subassociations E2b–e but in subassociation E2a P. morinica valves are much rarer and scattered throughout, although they are often of a large size, being up to 35 mm in height compared to the normal size of less than 20 mm in the aerobic associations. Rare specimens of *C. suprajurensis* in E2a are also substantially larger than those found in other associations. E2a occurs in some of the most organic rich beds of the Kimmeridge Clay and it also bounds some of the rare beds of the Kimmeridge Clay which are totally devoid of



TEXT-FIG. 24. Trophic-guild triangles for the dysaerobic associations of the Kimmeridge Clay. Key: ES, epifaunal suspension feeders; IS, infaunal suspension feeders; HDF, herbivores and deposit feeders.

benthos (e.g. bed group 39 of the *scitulus* Zone, text-fig. 7). Values of authigenic uranium can be up to 13 ppm in the same horizons.

All three bivalve species are also common in some of the aerobic associations indicating a wide facies tolerance. This eurytopy, combined with their swarm abundances in this association, is typical of opportunistic forms (Levington 1970). Their ability rapidly to colonize an area could have been of greater ecological importance than their ability to survive low oxygen values (Pearson and Rosenberg 1978).

An analysis of growth rates, using growth line spacing, was facilitated by the generally excellent state of preservation (text-fig. 26). Individuals of *C. suprajurensis* and *I. minuscula* showed widely varying rates but neither demonstrated any consistent, facies-related pattern. By way of contrast, *P. morinica* showed consistently higher growth rates in organic-rich shales than in normally oxygenated mudstones (text-fig. 27), indicating an apparent preference for lowered oxygen levels. This may reflect a reduction in competition (e.g. Peterson and Andre 1980), or a preference for hypoxic conditions. Small individuals generally have a higher weight specific oxygen consumption (Bayne 1971); it is therefore advantageous to grow to a large size in oxygen deficient environments. Thus the large specimens of *P. morinica* from subassociation E2a may be exhibiting rapid growth rates as a physiological response to low oxygen levels.

The population dynamics of the shell pavements have been discussed in Wignall (1989). Sizefrequency histograms are commonly bimodal or even trimodal. This may reflect a few separate colonization events, as is the case for populations of *Macoma balthica* in the oxygen-deficient Baltic (Andersin *et al.* 1978). Alternatively, the peaks may represent sudden, short-term increases in


TEXT-FIG. 25. Trophic nuclei of the five subassociations of E2, the Protocardia morinica: Isocyprina minuscula association. E2a, Protocardia morinica subassociation; E2b, Corbulomima suprajurensis: Isocyprina minuscula subassociation; E2c, Corbulomima suprajurensis: Protocardia morinica subassociation; E2d, Isocyprina minuscula: Protocardia morinica subassociation; and E2e, Isocyprina minuscula subassociation. Key: 1, Protocardia morinica; 2, Isocyprina minuscula; 3, Corbulomima suprajurensis.

mortality rates during transient environmental deterioration. Implicit in both interpretations is the occurrence of a highly fluctuating benthic environment. Mortality in such organic-rich sediments could have been caused by anoxic interstitial waters rising into the bottom waters. This would drive infaunal bivalves to the sediment surface where they subsequently perish. This can be caused by an increase in bottom water temperature and a concomitant increase in microbial activity which leads to the rapid consumption of oxygen (Jørgensen 1977). Fluctuations in benthic temperatures may account for the dominance of only one bivalve species on any one bedding plane. All three species were clearly euryoxic and lowered oxygen levels are unlikely to account for the absence of *Protocardia* from *Corbulomima*-dominated bedding planes for example. Benthic temperatures during spawning or benthic recruitment may have been important.

The Protocardia subassociation represents the most transient, oxygen-restricted conditions; the diversity index H is 0.3, the lowest for any Kimmeridge Clay association. The Isocyprina



TEXT-FIG. 26. Right valve of *Protocardia morinica* from an organic-rich shale of the lower scitulus Zone near Kimmeridge Bay, illustrating clearly developed growth striae. × 2.5.



TEXT-FIG. 27. Growth rates of *Protocardia morinica* from dysaerobic associations in organic-rich shales of the *elegans* Zone and aerobic associations in mudstones of the *mutabilis* Zone. Growth rates are consistently higher in the organic-rich shales.

subassociation represents only slightly improved conditions. Subassociation E2b is the most diverse (H = 1.3) and represents the most inhabitable benthic conditions indicated by this association.

E3 Protocardia morinica: Quadrinervus ornatus Association

(15 samples, 1082 specimens, 33 species, 21 % average fragmentation, H = 1.55)

This is one of the most diverse of the dysaerobic associations, with a variety of trophic feeding groups represented (text-fig. 24). The association occurs in mudstones of the upper *eudoxus* Zone (text-fig. 5) and the *hudlestoni* Zone (text-figs 8 and 9) where authigenic uranium values do not exceed 2 ppm. The fauna is distributed throughout the sediment and includes several species of *Mecochirus* (Table 2).

The moderate diversity of this association suggests upper hypoxic conditions although this conclusion is rather surprising as the constituent species are all highly euryoxic. The distinction between the ecology of the association and of the individual species may indicate an emergent property not apparent at the species level.

E4 Liostrea multiformis: Pseudorhytidopilus latissima Association

(17 samples, 771 specimens, 24% average fragmentation, H = 1.08)

An association with roughly equal proportions of filter feeding bivalves and a gastropod, which was probably herbivorous (text-fig. 28). It occurs sporadically from the mid-*autissiodorensis* to the mid-



TEXT-FIG. 28. Trophic nuclei of associations E4, the Liostrea multiformis: Pseudorhytidopilus latissima association, E5, the Protocardia morinica: Nicaniella extensa association, E6, the Isocyprina minuscula: Pseudorhytidopilus latissima association and of E8, the Pseudorhytidopilus latissima: Quadrinervus ornatus association. All from the organic-rich shales and mudstones of the Upper Kimmeridge Clay. Key: 1, Liostrea multiformis; 2, Pseudorhytidopilus latissima; 3, Protocardia morinica; 4, Isocyprina minuscula; 5, Nicaniella extensa; 6, Semisolarium hallami; 7, Quadrinervus ornatus; 8, Chondrites. The relative abundance of Chondrites cannot be quantified, although it is consistently present in association E8.

pectinatus Zones (text-figs 5 and 10), most commonly on discrete bedding planes in organic-rich shales. Beneath the Washing Ledge Stone Band of the *autissiodorensis* Zone (text-fig. 5), association E4 occurs in three organic-rich shales containing bedding planes covered in the ammonite Nannocardioceras.

Nannocardioceras has not been included in the benthic faunal analysis, but its distribution within the sediment suggests that it was probably a nektobenthic form living close to the substrate (see discussion above, p. 12), where it may have interacted with the true benthos. *P. latissima* is one of the few species to occur in dysaerobic but not in aerobic associations. This suggests that it was specifically adapted to low oxygen environments in contrast to the majority of non-specialized opportunistic species in the dysaerobic associations. It may have browsed on bacterial mats which are known from other dysaerobic environments (Williams 1984). Such mats may be formed from non-photosynthetic bacteria and their presence need not constrain the depositional environment to within the photic zone.

E5 Protocardia morinica: Nicaniella extensa Association

(19 samples, 2652 specimens, 24 species, 21% average fragmentation, H = 1.30)

A moderately diverse association found in the organic-rich shales of the lower scitulus and lower hudlestoni Zones (text-figs 7 and 8), where it alternates with subassociation E2d. Authigenic uranium values typically approach 3 ppm in these sediments. The trophic composition exhibits a wide range of variation due to fluctuating abundances of Semisolarium hallami Wignall MS; however, epifaunal filter feeders are always rare (text-figs 24 and 28). The association contains a high proportion of characteristic species which are not found in other dysaerobic associations; these include N. extensa, S. hallami and small specimens of Mesomiltha concinna. Rare deep burrowing forms also occur (text-fig. 29).

S. hallami may have fed on bacterial mats and the presence of this gastropod suggests that the substrate was fairly firm as this thick-shelled form has no obvious adaptations to life on a soft substrate. This association appears to have been previously identified by Oschmann (1988) as his N. extensa association, although he failed to recognise the characteristic Semisolarium and



TEXT-FIG. 29. Bedding plane accumulation from association E5 from the lower scitulus Zone near Kimmeridge Bay, showing an articulated specimen of *Plectomya* surrounded by many smaller specimens of *Semisolarium* hallami. Most of the broken valves are of *Isocyprina minuscula*. × 1.5.

Mesomiltha. However, he only took five samples and both of these genera vary greatly in abundance from sample to sample.

E6 Isocyprina minuscula: Pseudorhytidopilus latissima *Association* (9 samples, 430 specimens, 7 species, 10% average fragmentation, H = 0.64)

A low diversity association dominated by two trophic-guild types which, like E4, are infaunal filter feeders and epifaunal herbivores (text-fig. 28). It ranges from the upper *wheatleyensis* to the lower *hudlestoni* Zones (text-fig. 8) and has the distinction of occurring in some of the most organic-rich shales in the geological record – the Bubbicum and the Blackstone beds; beds 42c and d respectively in text-figure 8. As is typical for the organic-rich shales the benthos is restricted to discrete bedding planes but the average fragmentation index is the lowest value for any Kimmeridge Clay association.

The palaeocological evidence indicates episodic colonization under hypoxic conditions, as with most other dysaerobic associations. The exceptionally low fragmentation values may reflect the low residence time at the sediment surface thus reducing the amount of time available for biomechanical fragmentation to occur. The presence of any benthos at all, in sediments which contain up to 50% organic carbon, is enigmatic as the rate of bacterial consumption of oxygen during the brief oxygenation events would have been enormous.

E7 Lingula ovalis: Protocardia morinica Association

(15 samples, 322 specimens, 12 species, 18% average fragmentation, H = 0.88)

Suspension feeders constitute the only preserved trophic group of this association (text-figs 23 and 24). It occurs in thick beds of calcareous blocky mudstones in the upper *hudlestoni* and the lower *pectinatus* Zones (text-fig. 9). The associated values of authigenic uranium are extremely variable, ranging from 0 to 5 ppm. Absolute abundance is extremely low: an average of 21 specimens per sample was found compared to an overall average of 103 specimens per sample for all the Kimmeridge Clay samples. Sedimentation rates do not appear to have been high for fish scale abundance, used as an index of sedimentation rate, is not unusually low.

The population dynamics of this association were clearly fundamentally different to the other associations discussed above. Although the fauna consists of oxygen-tolerant opportunists, they do not occur in the swarm abundances typical of the other dysaerobic associations.

E8 Pseudorhytidopilus latissima: Quadrinervus ornatus Association

(10 samples, 1989 specimens, 22 species, 26% average fragmentation, H = 0.93)

An unusual association dominated by gastropods (text-fig. 28) with infaunal bivalves only forming 8% of the fauna (text-fig. 24). It ranges through 10 m of sediment in the mid-*pectinatus* Zone (text-fig. 10) characterized by abundant fish scales and common *Chondrites* traces. Density is very high with an average of 199 specimens per sample. Authigenic uranium values reach the high figure of 10 ppm in some of the shales containing E8 (e.g. bed 49g, text-fig. 10).

The abundant gastropods in this association may have eaten a bacterial mat or even benthic algae. Virtually the entire fauna lived on the sediment surface and the substrate was presumably very firm. The high density of the fish scales and the benthic fauna probably indicates a slow sedimentation rate, a factor which undoubtedly controlled the nature of the sediment. The exceptional levels of authigenic uranium enrichment are probably also party attributable to low sedimentation rates (Myers and Wignall 1987).

E9 Pseudorhytidopilus latissima: Protocardia morinica Association

(6 samples, 1073 specimens, 16 species, 24% average fragmentation, H = 1.58)

This is the most diverse of the dysaerobic associations with a fauna dominated by epifaunal forms (text-fig. 24), with the exception of the ubiquitous *P. morinica* (text-fig. 30). It is found in the mudstones and paper shales of the *pectinatus* and *pallasioides* Zones (text-figs 10 and 11). In the



TEXT-FIG. 30. Trophic nucleus of E9, the Pseudorhytidopilus latissima: Protocardia morinica association from mudstones and paper shales of the pectinatus and pallasiodes Zones. Key: 1, Pseudorhytidopilus latissima; 2, Protocardia morinica; 3, Tetraserpula dollfussi; 4, Parainoceramus cramei.

latter lithology bedding planes are frequently covered in bivalve prodissoconchs displaying a few growth lines.

The high diversity indicates only moderate levels of oxygen restriction. The bacterial mats may have stabilized the sediment and facilitated the colonization of the epifaunal forms, although conditions were commonly inimical to bivalve settlement as many spat-falls appear to have died only a few days after settlement.

UPPER KIMMERIDGE CLAY AEROBIC ASSOCIATIONS

Aerobic associations first reappear briefly in the mid-*hudlestoni* Zone (text-figs 8 and 9) although it is not until one zone higher, in the mid-*pectinatus* Zone, that they again become important (text-fig. 10). The transition is less clear cut than in the Lower Kimmeridge Clay and dysaerobic and aerobic associations alternate with one another up to the base of the penultimate zone, the *rotunda* Zone (text-figs 10 and 11).

B1 Liostrea multiformis: Parainoceramus cramei Association

(14 samples, 1122 specimens, 36 species, 26% average fragmentation, H = 1.76)

The trophic-guild composition of this association is dominated by fixosessile and free-lying species (text-fig. 31). Three species of epibyssate bivalves are common, as is the crinoid *Balanocrinus* subteres (text-fig. 31). Diversity is low and deep infaunal species form only 1% of the total. The association first appears in calcareous mudstones of bed 49d and again in thin shales of the



TEXT-FIG. 31. Trophic-guild triangles for Upper Kimmeridge Clay aerobic associations. Key: ES, epifaunal suspension feeders; IDF, herbivores and deposit feeders.

pallasioides Zone. The shales are relatively organic-poor (total organic carbon values are less than 5%), although they have a papery fissility.

The dominance of epifauna is unlike any association from the Lower Kimmeridge Clay with the exception of the Nanogyra shell beds of association A11. L. multiformis may have replaced Nanogyra virgula, which became extinct in the basal hudlestoni Zone, as the dominant free-lying bivalve in the Upper Kimmeridgian (both these species were cemented during their earliest growth stages, but for the majority of their ontogeny they were unattached). The abundance of epifauna in association B1 suggests firm substrates which may also have inhibited the deep infauna. The low diversity values and the association's occurrence in paper shales suggests that benthic oxygen levels were moderately low. The absence of wave-cut platforms at the appropriate level makes it impossible to measure the authigenic uranium values and thus to assess independently this latter assertion.

B2 Mesosaccella cypris: Corbulomima suprajurensis Association

(22 samples, 1545 specimens, 31 species, 28% average fragmentation, H = 1.91)

A moderately diverse association with roughly equal proportions of infaunal filter feeding bivalves and deposit feeding protobranchs (text-fig. 32); epifaunal forms, mostly *Liostrea*, can form up to a quarter of some samples (text-fig. 31). The association is common in the calcareous mudstones of the *pallasioides* and *rotunda* Zones (text-fig. 11).

Again this association is unlike any other from the Lower Kimmeridge Clay, although it does resemble some Oxford Clay examples (Duff 1975). The presence of abundant protobranchs would have caused a thixotropic surface layer likely to inhibit free-lying suspension feeders (Rhoads and Young 1970). However, epifaunal forms do occur in this association suggesting that the substrate was not always inhibiting. Association B2 is undoubtedly time-averaged with the benthic populations fluctuating from epifauna-dominated to infauna-dominated. Like all other Upper Kimmeridge Clay aerobic associations the diversity index of B2 is relatively low compared to the Lower Kimmeridge associations. Kilenyi (1978) has noted a similar diversity decline amongst ostracode populations culminating in the highly impoverished assemblages in the overlying Portlandian. Benthic oxygen levels do not appear to have been restrictive in these organic-poor



TEXT-FIG. 32. Trophic nuclei of associations B1, the Liostrea multiformis: Parainoceramus cramei association from marly mudstones of the mid-pectinatus Zone, and of B2, the Mesosaccella cypris: Corbulomima suprajurensis association from similar lithologies in the upper pectinatus and pallasioides Zones. Key: 1, Liostrea multiformis; 2, Parainoceramus cramei; 3, Pseudolimea multicostata; 4, Protocardia morinica; 5, Corbulomima suprajurensis; 6, Buchia mosquensis; 7, Balanocrinus subteres; 8, Grammatodon longipunctata; 9, Mesosaccella cypris; 10, Palaeonucula menkii; 11, diademitid echinoid.

sediments of the topmost Kimmeridge Clay and they are probably not responsible for the lowered diversity. The presence of stenohaline forms, such as echinoderms, indicates that salinity variations were also not a contributory factor. General environmental stresses were presumably higher at this time in the Upper Jurassic but their nature is unclear.

B3 Trautscholdia phillis: Corbulomima suprajurensis Association

(7 samples, 706 specimens, 40 species, 38% average fragmentation, H = 1.89)

A rare association from calcareous mudstones and paper shales of the upper *pallasioides* Zone (text-fig. 11), exhibiting unusually high fragmentation values. Infaunal and epifaunal filter feeders dominate in roughly equal proportions (text-fig. 33), whilst deposit feeding bivalves form only 0.2% of the total.

The taxonomic composition is similar to association A8, although the proportion of epifauna is higher, suggesting a firmer substrate. Low sedimentation rates may have allowed more time for biomechanical breakage to occur. This is probably responsible for the high levels of fragmentation.



TEXT-FIG. 33. Trophic nucleus of B3, the Trautscholdia phillis: Corbulomima suprajurensis association from calcareous mudstones and fissile shales of the upper pallasioides Zone near Chapmans Pool. Key: 1, Liostrea multiformis; 2, Protocardia morinica; 3, Trautscholdia phillis; 4, Corbulomima suprajurensis; 5, Grammatodon longipunctata; 6, Balanocrinus subteres; 7, Pseudolimea multicostata; 8, Isocyprina minuscula; 9, Plagioglypta sp. 1; 10, Plagioglypta sp. 2.

It is noteworthy that the astartids *T. phillis* and *Nicaniella cuneata* were both locally abundant during the upper *pallasioides* Zone and yet they never co-occur, suggesting that interspecific competition was occurring between these two bivalves.

B4 Nicaniella cuneata: Mesomiltha concinna Association

(6 samples, 439 specimens, 32 species, 29% average fragmentation, H = 2.10)

An unusual association with a wide range of trophic and guild types in the trophic nucleus (textfig. 34). Solemya is a rare but characteristic bivalve not found elsewhere in the Kimmeridge Clay. The association ranges through a few metres of strata between the topmost pallasioides Zone and basal rotunda Zone at Chapmans Pool (text-fig. 11). Measurements of growth line spacing in P. morinica from the highest horizon showed that growth rates in this bed were higher than for any other horizon in the Kimmeridge Clay; this may explain the occurrence of exceptionally large individuals in the basal bed of the rotunda Zone.

Modern-day lucinids, Solemya and some scaphopods are all thought to possess sulphideoxidizing bacteria (Reid and Brand 1986). Therefore, the co-occurrence of representatives of these groups in association B4 suggests that conditions were highly favourable for sulphide-oxidising symbiosis during the latest *pallasioides* Zone. However, as in most associations in the Kimmeridge Clay, suspension feeders constitute over half of the fauna (text-fig. 31).

B5 Liostrea expansa: Oxytoma inequivalve Association

(6 samples, 614 specimens, 35 species, 34% average fragmentation, H = 2.00)

The topmost beds of the Kimmeridge Clay, the Rhynchonella Marls and Hounstout Marls, are poorly exposed at present. However, examination of the limited outcrops and fallen blocks in Chapmans Pool (text-fig. 1) reveals the diverse association shown in text-figure 35. In comparison with other Kimmeridge Clay associations, B5 contains an unusual abundance of non-molluscan forms such as articulate brachiopods (3.6%), crustaceans (3.5%) and echinoderms (11.9%). Thin sections of the siltstones and muddy sandstones in which this fauna is contained reveals common spicules of the sponge *Rhaxella* which may have been an important element of the fauna.



TEXT-FIG. 34. Trophic nucleus of B4, the Nicaniella cuneata: Mesomiltha concinna association from the topmost pallasioides Zone at Chapmans Pool. Key: 1, Protocardia morinica; 2, Liostrea multiformis; 3, Nicaniella cuneata; 4, Mesomiltha concinna; 5, Procerithium multiplicatum; 6, Plagioglypta sp.; 7, Mesosaccella cypris; 8, Isocyprina minuscula; 9, indeterminate crassatellacean; 10, Camptonectes auritus; 11, diademitid echinoid; 12, Quadrinervus ornatus; 13, hypothetical benthic alga.



TEXT-FIG. 35. Trophic nucleus of B5, the Liostrea expansa: Oxytoma inequivalve association from the topmost silty and sandy sediments of the Kimmeridge Clay at Chapmans Pool. Key: 1, Liostrea expansa; 2, Oxytoma inequivalve; 3, Camptonectes auritus; 4, diademitid echinoid; 5, Prodentalium sp.; 6, Mesosaccella cypris; 7, Grammatodon longipunctata; 8, Balanocrinus subteres; 9, Protocardia morinica; 10, Plagioglypta sp. 1; 11, Rhynchonella subvariabilis; 12, Isocyprina implicata; 13 Palaeonucula menkii; 14, Rhabdocidaris spinulosa; 15, Rhaxella (relative abundance has not been determined).

Sedimentary structures include megaripple lamination partially obliterated by *Rhizocorallium* and *Planolites* burrows.

Cope (1978) has suggested that sedimentation rates were high in these highest beds, based on bed thicknesses, although periods of reduced sedimentation are said to be reflected by concentrations of ammonites. The abundance of sessile epifauna in this association (text-fig. 31) suggests that substrates were firm, supporting Cope's second contention. The abundant *O. inequivalve* may have attached themselves to sponges, as may *Balanocrinus* and *Rhynchonella* (text-fig. 35).

LATERAL BIOFACIES VARIATIONS IN THE KIMMERIDGIAN OF ENGLAND

In the preceding sections it has been possible to document the changing environmental conditions in a composite vertical section of the Kimmeridge Clay from southern England. However, the Kimmeridge Clay is the most laterally extensive of all the British Jurassic formations (Hallam and Sellwood 1976) and no survey of depositional conditions would be complete without examining the lateral facies variations. During most of the early Kimmeridgian mudrock deposition appears to have extended throughout the outcrop, although with substantial lateral variations in thickness caused by active extensional faulting during deposition (Chadwick 1986). The main stable areas and subsiding basins are shown in text-figure 36. In the late Kimmeridgian depositional gradients appear to have become more pronounced and coarser grained facies were developed particularly on stable areas such as the London Platform.

Lateral variations were investigated in some small and temporary outcrops, whilst a number of boreholes drilled by the British Geological Survey have provided ample data for regions with no present day outcrop.

Dorset

The Kimmeridge Bay outcrops, discussed above, were deposited on the northern flank of the Central Channel Basin. Further west, along the Dorset coast at Ringstead Bay (text-fig. 1), a series of weathered exposures illustrates a highly condensed sequence lying on the Purbeck-Isle of Wight fault system (Cox and Gallois 1981). The condensation is achieved by a general thinning of the beds without the development of any major hiatuses; thus the section is as complete as that seen at Kimmeridge Bay, although markedly different facies are developed in the lowest zones.

During the cymodoce Zone a limonitic-oolitic sandstone, the Abbotsbury Ironstone, developed on the Purbeck-Isle of Wight fault system in the most westerly outcrops of Dorset (text-fig. 1). The benthic associations of the ironstone are unusual as they are dominated by articulate brachiopods, *Nanogyra nana*, pectinids, serpulids and sponges (Brookfield 1973c); this assemblage is reminiscent of the *Liostrea expansa: Oxytoma inequivalve* association from the topmost beds of the Kimmeridge Clay at Chapmans Pool.

Facies variability is less pronounced in the higher zones of the Kimmeridge Clay in Dorset probably due to a general deepening of the sea which ultimately led to the widespread deposition of organic-rich facies. A short section in such facies in bed group 34 of the *autissiodorensis* Zone was examined at Ringstead Bay where the sediments are three times thinner than the equivalent strata at Kimmeridge Bay. The benthic associations were found to be identical at both outcrops with subassociation E2c occurring at this horizon. Benthic conditions appear to have varied little from the rapidly subsiding basins to the slowly subsiding swells in the offshore areas; a conclusion also supported by sedimentological analysis (Wignall 1989).

It was possible to examine lateral variations from higher in the Kimmeridge Clay sequence due to the occurrence of a temporary exposure of the *pallasioides*: rotunda Zone boundary on the east side of the Isle of Portland (text-fig. 1), in February 1986. The succession was only slightly thinner than that seen at Chapmans Pool and essentially the same vertical section occurs, except for the loss of the highest organic-rich shale in bed 55b at Portland. Further evidence for slightly higher oxygen levels at Portland was provided by the benthic associations. The sub-dysaerobic association A/E1 in bed 54b at Chapmans Pool was replaced by the fully aerobic association B3 at Portland.



TEXT-FIG. 36. Stable platforms and depositional basins in England during the Kimmeridgian.

Presumably the Chapmans Pool area was slightly deeper and therefore slightly more oxygen restricted than in the Portland area during the late Kimmeridgian.

Central Wiltshire

The Westbury sequence, discussed above (p. 28), lies to the north side of the Vale of Pewsey basin (text-fig. 36). Only the *mutabilis-eudoxus* Zone sequence is exposed at this pit, although it appears

to preserve identical facies to the poorer exposures at Black Head on the Dorset coast (text-fig. 1). In February 1988 a temporary exposure at Pearce's Pit, Calne (Grid ref. SU 018 712) revealed the following 5.5 m section of bed group 18 of the *mutabilis* Zone, overlain by the Lower Greensand (Aptian):

Lower Greensand	8 m,	
Fullers Earth	0.1 m	34
Pyrite-cemented sands with pebbles and wood at the base.		
Rhizocorallium piped into the underlying bed	0·05–0·01 m [·]	
erosion surface		
Mudstone was abundant Nicaniella at the top	1·25 m	- sabitiv
Septarian nodule horizon	0·5 m	HILLOY
Mudstone with common <i>Rhabdocidaris</i> spines 0.9 m from the top	1·25 m	
Shell plaster, mostly of Gervillella aviculoides	0·05 m	
Mudstone	1·25 m	

This section enabled the localized biofacies variations to be investigated, as Calne lies 22 km to the north east of Westbury (text-fig. 1). The same associations, A6 and A8, occurred at the same levels as Westbury. However, on one bedding plane 4.5 m below the unconformity, the prolific assemblage of A12 was discovered.

A12 Grammatodon keyserlingii: Gervillella aviculoides Association (2 samples, 78 specimens, 15 species, H = 1.84)

This unusual association contains over 75% endobyassate bivalves whilst suspension feeders in general constitute 97% of the fauna (text-fig. 37). Sporadic Gervillella also occur at the same



TEXT-FIG. 37. Trophic nucleus of A12, the Grammatodon keyserlingii: Gervillella aviculoides association trom the mutabilis Zone near Calne, in Wiltshire. Key: 1, Grammatodon keyserlingii; 2, Gervillella aviculoides; 3, Pinna lanceolata; 4, Isocyprina implicata.

horizon at Westbury (Birkelund *et al.* 1983), although in fewer numbers. The occurrence of this association from Calne, only a short distance from Westbury, indicates a small-scale environmental heterogeneity that is not apparent from the lithology alone.

The Weald

The thickest Kimmeridge Clay succession is preserved in the Weald Basin (Sellwood *et al.* 1986). Data were obtained from the Warlingham borehole from the northern margin of the basin (Callomon and Cope 1971). Detailed logging of sections of this borehole showed that virtually all the organic-rich shales on the Dorset coast can be traced to Warlingham although they are all considerably attenuated (Wignall 1988).



TEXT-FIG. 38. Log of the mid-hudlestoni to lower pectinatus Zones in the Warlingham borehole, showing the distribution of the benthic associations illustrated in text-figure 39.

Palaeoecological information is rarely derived from boreholes although they can provide ample data (e.g. Pederson 1986). The upper *wheatleyensis* to upper *pectinatus* Zone sediments of the Warlingham borehole were analysed for this study. Samples at any one horizon are necessarily small with the result that meaningful numbers can only be obtained over a significant vertical section, normally spanning several metres. This contrasts with samples obtained in the field which, in this study, generally encompass less than 0.1 m of vertical section.

The benthic associations from the *wheatleyensis* Zone at Warlingham are the same as those from Kimmeridge Bay, although the mid-dysaerobic association E5 is more common and lower dysaerobic associations are rarer. Diversity values appear higher for the Warlingham assemblages, but it is not possible to make direct comparisons due to the different nature of the samples. Slightly higher benthic oxygen levels can probably be inferred for the Warlingham facies.

From the mid-hudlestoni Zone upwards, three associations, E10 to E12, dominate the succession (text-fig. 38).

E10 Lingula ovalis: Nicaniella extensa Association

(123 specimens, 12 species, 34% average fragmentation, H = 1.76)

This association is similar to association E2 from Kimmeridge Bay with both *Protocardia morinica* and *Isocyprina minuscula* dominating the fauna. However, it is distinguished by the co-occurrence of common L. ovalis and N. extensa (text-fig. 39).



TEXT-FIG. 39. Trophic nuclei of associations E10, the Lingula ovalis: Nicaniella extensa association, E11, the Lingula ovalis: Liostrea multiformis association and of E12, the Lingula ovalis: Musculus autissiodorensis association from the Warlingham borehole. Key: 1, Protocardia morinica; 2, Isocyprina minuscula; 3, Lingula ovalis; 4, Nicaniella extensa; 5, Liostrea multiformis; 6, Camptonectes auritus; 7, Oxytoma inequivalve; 8, Musculus autissiodorensis; 9, Quadrinervus ornatus.

E11 Lingula ovalis: Liostrea multiformis Association (136 specimens, 11 species, 28% average fragmentation, H = 1.78)

This association is unusual for the paucity of the normally ubiquitous bivalves P. morinica and I. minuscula which together form only 1.4% of the total. Instead the association contains Camptonectes auritus and Oxytoma inequivalve (text-fig. 39), two epibyssate bivalves which are rare at Kimmeridge Bay.

E12 Lingula ovalis: Musculus autissiodorensis Association (494 specimens, 14 species, 26% average fragmentation, H = 1.74)

This is one of the few Kimmeridge Clay associations to show well developed niche partitioning (text-fig. 39), but this is probably only fortuitous. *M. autissiodorensis*, the second ranking species, is not known from Kimmeridge Bay, although it is common in contemporaneous mudstones of northern France (Oschmann 1988).

Byssate bivalves are present in significant numbers in both associations E11 and E12, whilst this is a rare life strategy in the Kimmeridge Bay samples. It is possible that some of the epibyssate taxa from Warlingham were attached to benthic algae. None of the associations E10 to E12 occur in the thin organic-rich shales of Warlingham, whereas the Kimmeridge Bay associations are only known from these thin shales at Warlingham (text-fig. 38). Clearly higher levels of benthic oxygen at Warlingham favoured the development of a number of different associations to those found at Kimmeridge Bay. Only during the short intervals of organic-rich shale deposition were benthic oxygen levels sufficiently similar to those of Kimmeridge Bay for the development of the same associations. The basal *pectinatus* Zone appears to have been one of the last intervals when such shales were common to both localities.

The Swindon region

The Kimmeridge Clay thins markedly across the London Platform and, in the Upper Kimmeridgian, a heterolithic facies sequence is developed. Exposures in brick pits were fairly extensive in the Swindon and Oxford region during the last century, and records from these localities now provide most of the available information on the area (e.g. Chatwin and Pringle 1922; Arkell 1947).

Relatively little is known of the Lower Kimmeridge Clay although the *baylei* to *eudoxus* Zones appear to be developed in a thin mudrock facies (Cope 1980). Mudstones and shales of the *eudoxus* Zone are unconformably overlain by the laterally extensive Wheatley Nodule Clays of the upper *wheatleyensis* Zone (text-fig. 40). In turn, the clays are unconformably overlain by the Shotover Fine Sands in the west of the region, although they may be absent at Thame in the east (text-fig. 40). The precise age of the Fine Sands is uncertain. Cope (1978, p. 530) thought that they may belong to the early *pectinatus* Zone (although he failed to illustrate them in Cope, 1980, fig. 14). The Fine Sands are succeeded by the Shotover Grit Sands, of known *pectinatus* Zone age (Cope 1978, 1980). The Lower Lydite Bed, a condensed phosphatic conglomerate, separates the Grit Sands from the overlying Hartwell Clay of the upper *pallasioides* Zone (Cope 1980).

In the east of the region, around Wheatley and Brill, the upper Hartwell Clay appears to pass laterally into the Thame Sand (the Wheatley Sand of some authors, see Cope, 1978). Ballance (1963) mapped the distribution of this elongate sand body and showed it to have a north-west to southeast orientation. The sand was suggested to have accumulated in an erosive channel (Ballance 1963, fig. 2), but it appears to pass laterally into the Hartwell Clay (Casey 1967) and the elongate sand body may represent a marine sand bar. It is perhaps noteworthy that the pre-Aptian faults and folds also have a NW-SE trend (Arkell 1947, fig. 23), suggesting a tectonic control for the orientation of the Thame Sand.

The study of the Kimmeridge sediments in the region has been greatly aided by the drilling of the Swindon borehole (Grid ref. SU 1413 8349) by the British Geological Survey for the Oil Shale Project (Gallois 1978). The virtually complete sequence has been logged and the fauna analyzed (text-fig. 41).



TEXT-FIG. 40. Correlation of the Upper Kimmeridgian formations formerly exposed in the area around Swindon and Oxford, described in Arkell (1947).

A13 Tetraserpula dollfussi: Corbulomima suprajurensis Association (139 specimens, 20 species, 29% average fragmentation, H = 2.31)

The basal *baylei* Zone sediments contain this diverse bivalve-serpulid dominated association (textfig. 42). It contains a similar species assemblage to the *Nanogyra nana*: *Deltoideum delta* association from the same horizon on the Dorset coast (see above, p. 17). However, infaunal bivalves are not important in A13 suggesting softer substrates. This is further indicated by the presence of the softsediment association A1 from higher in the *baylei* Zone at Swindon (text-fig. 41).

The Swindon sediments are slightly less condensed and more muddy than the offshore sediments of Dorset. This difference is accentuated in the *cymodoce* Zone which is 10 m thick at Swindon (text-fig 41) as opposed to 5 m at Black Head (Cox and Gallois 1981). The more proximal Swindon sediments contain a higher proportion of silty and sandy horizons.

A14 Corbulomima suprajurensis: Neocrassina ovata Association (243 specimens, 18 species, 24% average fragmentation, H = 2.34)

This association occurs at three levels in the topmost cymodoce and lower mutabilis Zones at Swindon where it is found in mudstones and slightly organic-rich shales (text-fig. 41). Like many





TEXT-FIG. 41. Log of the Kimmeridgian from the Swindon borehole. Bed numbers are those devised by Gallois and Cox (1976) for the Kimmeridge Clay Formation of eastern England. Above bed 33 the change to more arenaceous sediments makes the numbering scheme inapplicable.

of the mudstone associations from Westbury, shallow infaunal filter feeding bivalves dominate the association (text-fig. 43). However, deep infaunal forms constitute 6.8%, whilst deposit feeders, mostly *Nucinella birkelundi*, make up 12.8% of the total.

Association A14 occurs at the same level as associations A1 and A4 at Wyke Regis, Dorset (textfig. 3) where organic-rich shales are better developed. Above this level, from the mid-*mutabilis* to the mid-*eudoxus* Zones, the same sequence of benthic associations and facies types is developed at Swindon, Westbury, and Black Head, and the beds of Gallois and Cox (1976) can be easily correlated. Thus, whilst lateral facies changes existed during the lower part of the Kimmeridge Clay, the mid-Lower Kimmeridge Clay illustrates an extraordinarily uniform depositional environment across a wide area. This was brought to a halt in the upper *eudoxus* Zone when siltstones and



TEXT-FIG. 42. Trophic nucleus of A13, the Tetraserpula dollfussi: Corbulomima suprajurensis association from the baylei and cymodoce Zones of Swindon (text-fig. 41). Key: 1, Tetraserpula dollfussi; 2, Corbulomima suprajurensis; 3, Dorsoserpula runcinata; 4, Thracia depressa; 5, Deltoideum delta; 6, Pinna lanceolata.

mudstones began to accumulate at Swindon (text-fig. 41) whilst organic-rich shales continued to form offshore.

A15 Scaphopod: Thracia depressa Association

(100 specimens, 18 species, 19% average fragmentation, H = 2.65)

This association, from the *autissiodorensis* Zone of Swindon, is characterized by an indeterminate scaphopod, deep infaunal bivalves and *Myophorella voltzii* (text-fig. 43). Dominance-diversity, species richness and equitability are all high, indicating amenable conditions. Benthic oxygen levels are likely to have been normal.

The upper part of the Lower Kimmeridge Clay is not present to the east of Swindon (text-fig. 40), suggesting that the Swindon sediments may have been deposited close to an ancient shoreline. Evidence for the presence of a mid-Kimmeridgian island in this region comes from the discovery of *Camptosaurus* (Hulke 1880) at the base of the Wheatley Nodule Clays at Cumnor (text-fig. 40). Clearly depositional palaeoslopes had steepened in the late Lower Kimmeridgian for organic-rich shales were forming in the offshore basins whilst dinosaurs roamed the land around Oxford.

The Lower: Upper Kimmeridge Clay boundary is an erosive unconformity marked by phosphatic nodules (text-fig. 40). Association E5 occurs in muddy sandstones and siltstones of the basal 2 m above this boundary (text-fig. 41), suggesting the occurrence of dysaerobic conditions. The succeeding 20 m of sediment are a heterolithic mixture of mudstones, siltstones and muddy sandstones with pervasive bioturbation. This sequence was probably formerly exposed in Hill's brickyard, Swindon (Chatwin and Pringle 1922). It is difficult to date the sediments beyond a general lower Upper Kimmeridgian age. The calcareous mudstone between 40.5 m and 43 m (textfig. 41) may correlate with the Wheatley Nodule Clays (text-fig. 40). The shelly fauna, which is



TEXT-FIG. 43. Trophic nuclei of A14, the Corbulomima suprajurensis: Neocrassina ovata association (from the mudstones of the mutabilis Zone) and of A15, the scaphopod: Thracia depressa association (from the siltstones of the autissiodorensis Zone) at Swindon. Key: 1, Indeterminate scaphopod; 2, Thracia depressa; 3, Myophorella voltzii; 4, Grammatodon longipunctata; 5, Camptonectes auritus; 6, Protocardia morinica; 7, Liostrea multiformis; 8, Nicaniella extensa; 9, Entolium orbiculare; 10, Pleuromya uniformis; 11, Corbulomima suprajurensis; 12, Neocrassina ovata; 13, Isocyprina argillacea; 14, Nucinella birkelundi.

diverse throughout, belongs to associations B2, B4 and B6. The first two are known from higher horizons on the Dorset coast, whilst association B6 is unique to Swindon.

B6 Procerithium multiplicatum: Corbulomima suprajurensis *Association* (172 specimens, 19 species, 6% average fragmentation, H = 2.31)

A diverse range of trophic-guild types is present in the trophic nucleus of this association (text-fig. 44), although P. multiplicatum is the only common epifaunal form. The fragmentation index is exceptionally low. The bivalves of this association are uniformly distributed throughout the sediment, whilst P. multiplicatum shows more patchy abundance. The local concentrations of gastropods may have gathered around vegetated areas of the sea floor. The abundance of deep infaunal forms suggests that oxygen levels were normal, whilst the rarity of sessile epifauna may indicate unstable surface sediments.

The succeeding Shotover Fine Sands reach 25 m in thickness at Swindon, although only a short section was cored in the BGS borehole due to their uncemented nature. This contains abundant



TEXT-FIG. 44. Trophic nucleus of B6, the Procerithium multiplicatum: Corbulomima suprajurensis association from the silts and sands of the lower part of the Upper Kimmeridgian of Swindon. Key: 1, Procerithium multiplicatum; 2, Corbulomima suprajurensis; 3, Pleuromya uniformis; 4, Thracia depressa; 5, Protocardia morinica; 6, Nicaniella cuneata; 7, hypothetical benthic alga.

traces of *Rhizocorallium*, *Teichichnus* and possibly *Ophiomorpha* in a glauconitic sand with occasional wave ripples. It thus differs from the outcrops to the east, around Oxford, where it is reported to be a muddy sand (Arkell 1947). The short section of the overlying Shotover Grit Sand, cored at Swindon (text-fig. 41), is distinct from the Fine Sands in being coarser and more shelly. Pebbles of chert are common and shells are concentrated at the base of erosive horizons. Thin section analysis revealed that echinoid fragments are fairly common and that some grains have oolitic coatings. The Grit Sands are well-cemented by poikilotopic calcite (the core may have passed through one of the 'Giant's Marbles' concretions described and illustrated by Arkell 1947). The abundant fauna belongs to association B7.

B7 Cycloserpula intestinalis: Nanogyra nana Association (146 specimens, 13 species, 11% average fragmentation, H = 1.78)

Cemented epifaunal forms dominate this association although infaunal bivalves are also important (text-fig. 45). Free-lying epifaunal forms, which are normally the dominant epifaunal guild type in Kimmeridge Clay associations, are rare. This may reflect unstable, shifting substrate conditions for the Shotover Grit Sands.

The succeeding Hartwell Clay was not recovered in the Swindon core, although Oates (1974) has described a section from a temporary exposure at Aylesbury. Benthic conditions were highly favourable as a diverse fauna occurs, including bivalves, such as *Hartwellia* and *Arcomytilus*, which have not been recorded from elsewhere in the Kimmeridge Clay during this study. The proportion of epifaunal forms fluctuates markedly suggesting varying substrates (Oates 1974). No younger Kimmeridgian sediments are known from the region.



TEXT-FIG. 45. Trophic nucleus of B7, the Cycloserpula intestinalis: Nanogyra nana association from the Shotover Grit Sands, an Upper Kimmeridgian glauconitic sandstone, of Swindon. Key: 1, Cycloserpula intestinalis; 2, Nanogyra nana; 3, Myophorella voltzii; 4, Camptonectes auritus; 5, Nicaniella cuneata.

Eastern England

The Kimmeridge Clay north of the London Platform accumulated in two main depocentres, separated by the Market Weighton High. The East Midland Shelf occurs to the south of this high and the poorly-known Cleveland Basin occurs to the north (text-fig. 36). Only limited exposures occur on the East Midland Shelf, but a series of boreholes for the British Geological Survey Oil Shale Project (Gallois 1978) and the Wash Water Storage Scheme (Gallois 1979) have provided plentiful information (e.g. Gallois and Cox 1974, 1976; Wilkinson 1983).

The baylei and cymodoce Zones are developed in a condensed facies similar to southern England. The fauna is also similar although some different associations may be present as forms such as *Dicroloma*, which are never abundant in southern England, are frequently recorded (Gallois and Cox 1976). From the mid-mutabilis to the mid-euxodus Zones the same series of beds present in southern England are developed, with familiar horizons such as the Pentacrinus Bed and the Supracorallina Bed occurring throughout the region (Gallois and Cox 1976), although organic-rich shales appear at an earlier horizon. However, in the autissiodorensis and subsequent Zones the shales become thinner than their Dorset correlatives. Faunal lists include the usual Kimmeridge Clay forms, such as *Protocardia morinica* and *Isocyprina minuscula* (Gallois and Cox 1974, 1976), but the dysaerobic associations from Warlingham may also be present as *Musculus autissiodorensis* and

Camptonectes auritus are frequently mentioned. This is not unexpected as the depositional setting of the two areas is closely similar; both occur a similar distance away from the London Platform (text-fig. 36).

Further north on the East Midlands Shelf, the succession in Lincolnshire and Humberside has been described from boreholes (Richardson 1979; Bradshaw and Penney 1982). The major difference from the Wash area occurs in the *cymodoce* and basal *mutabilis* Zones. The former zone is exceptionally thick, reaching over 30 m, and organic-rich shales are developed at their lowest level in the Kimmeridge Clay. In *mutabilis* Zone times the Elsham Sandstone appears to have been shed off the southern flank of the Market Weighton High (Kent and Casey 1963; Richardson 1979). Faunal lists from this region are limited, although Bradshaw and Penny (1982, p. 130) state that the more major organic-rich shales are virtually devoid of benthos, a unique absence in the Kimmeridge Clay. If this is the case then the north Lincolnshire Kimmeridge Clay was deposited in some of the most oxygen-deficient, presumably deepest water conditions of any onshore outcrops in England.

The most northerly Kimmeridge Clay outcrops of England occur in the Vale of Pickering and on the coast at Filey Bay (text-fig. 1). Cope (1974) described two inland pits which are still available for examination. The lowest horizons are seen in the Green Lane Pit where alternating rhythms of organic-rich shales and mudstones of the *eudoxus* Zone contain abundant *Amoeboceras*. The only benthos consists of a few scattered specimens of *Protocardia* and *Liostrea*. It would appear that anoxic bottom waters were present for considerable periods of time suggesting fairly deep waters. Subsidence rates were also high as the reported thickness of the *eudoxus* Zone in this area is nearly 80 m (Cox *et al.* 1987); one of the thickest values for any Kimmeridge Clay zone in England.

A small outcrop in the upper *wheatleyensis* Zone was examined in Filey Bay in March 1988. This showed the following section:

Boulder clay	
Organic-rich shale	0∙08 m
Mudstone	0·32 m
Very organic-rich shale	0·10 m
Mudstone	0·35 m
Septarian nodules in mudstone	0·10 m
Mudstone with small blebs of cream-coloured phosphate 0.1 m from the to	p 1.00 m

The fauna was dominated by *Isocyprina minuscula* with lesser numbers of *Lingula* and *Liostrea*; small belemnites were not uncommon.

Lower *pectinatus* Zone shales and mudstones are seen in the Golden Hill Pit in the Vale of Pickering where association E13 occurs.

E13 Buchia mosquensis: Liostrea multiformis Association

(5 samples, 4 species, 43 specimens, 9% average fragmentation, H = 1.13)

Both the composition and abundance of this association differs greatly from equivalent organic-rich shale associations of southern England. Thus, the normally ubiquitious *Protocardia morinica* and *Corbulomima suprajurensis* do not occur, whilst a number of forms typical of more northern waters, such as belemnites and *B. mosquensis*, are dominant although they rarely reach high densities in the sediment (text-fig. 46).

It would appear that a divide existed between the Boreal and Sub-boreal provinces in the Upper Kimmeridgian along the line of the Market Weighton High. This divide was effective in prohibiting the northward migration of sub-boreal forms, whilst Boreal forms were able to spread progressively southwards during this time. For example, *B. mosquensis* first appears in south Dorset in the *hudlestoni* Zone, although it is not abundant until the *pallasioides* Zone. The southward progress of the Boreal belemnite *Pachyteuthis* was more gradual; it is first recorded on the London Platform in the lower *pectinatus* Zone but it did not reach south Dorset until the upper *pallasioides* Zone.

The causes of the faunal provinciality have been discussed in detail (e.g. Hallam 1972; Fürsich



TEXT-FIG. 46. Trophic nucleus of E13, the Buchia mosquensis: Liostrea multiformis association from the Upper Kimmeridge Clay of the Golden Hill Pit, Vale of Pickering. Key: 1, Buchia mosquensis; 2, Liostrea multiformis; 3, Lingula ovalis.

and Sykes 1977) and it has been suggested that the degree of environmental stability and heterogeneity appears to have been important. The evidence from the Kimmeridge Clay examples is enigmatic; the widespread organic-rich shale facies crosses the faunal divide between the two provinces and yet it does not appear to have been a control of the provincialism.

DISCUSSION

Substrates of the Kimmeridge Clay

From the foregoing documentation of the Kimmeridge Clay associations it is clear that there is a major change in their characteristics in the mid-part of the Upper Kimmeridge Clay. This appears to be partly attributable to a fundamental change in sediment type.

Substrate consistency is an important environmental factor and it is one of the few that can be directly investigated in the geological record. Soft substrates in particular are often invoked as a major control of faunal distribution (e.g. Kauffman *et al.* 1977). In general, higher sedimentation rates in muddy environments lead to soft sediments whilst slower rates lead to firmer substrates (Hattin 1986; Elder 1987). The Kimmeridge Clay appears to have been deposited rapidly compared to the underlying Oxford Clay. (Hallam and Sellwood 1976), due primarily to an increase in subsidence rate (Penn *et al.* 1986). However, the evidence from the associations discussed above indicates considerable variation on this theme.

For much of the Kimmeridge Clay the benthic associations are dominated by infaunal forms suggesting the presence of soft substrates (Oschmann 1988). Evidence for soft sediments in the *elegans* Zone, in particular, comes from the occurrence of rare, horizontally-aligned mosaics of non-



TEXT-FIG. 47. Armoured (terebelloid?) worm tube from an organic-rich shale of the *elegans* Zone at Kimmeridge Bay, formed of variably sized fragments of tessellated *Protocardia morinica* valves. Tubes reach up to 150 mm in length. × 1.2

overlapping shell fragments (text-fig. 47). These were probably originally constructed by terebelloid worms to prevent their burrow from collapsing.

From the middle of the *pectinatus* Zone, Upper Kimmeridge Clay associations generally contain a much higher proportion of epifauna than the associations from beneath this level, suggesting firmer sediments. Particularly important is the occurrence of *Tetraserpula dollfussi* in association E9, which was free-lying throughout most of its ontogeny, and the epibyssate bivalves of associations B1 and B3 which had a relatively small contact area with the substrate. All of these taxa would have foundered into soft muds and their presence indicates firm substrate conditions. Also present in associations B2 and B4 is the epibyssate bivalve *Hiatella foetida* which is closely similar to related modern day hardground-dwelling species (Kelly 1980). In contrast Oschmann (1988) considered all Kimmeridge Clay substrates to be soft, primarily due to limited sampling which led him to the erroneous belief that epifaunal forms are rare. Only association B2 contains a significant proportion of infauna in the upper part of the Upper Kimmeridge Clay, but this is probably attributable to the presence of protobranchs; it need not imply higher sedimentation rates than other Upper Kimmeridge Clay associations.

The abundance in sediments of pelagic elements of the fauna, such as fish and marine reptiles, is partly a function of sedimentation rates. Thus, horizons with abundant fish scales are probably due to slow rates of sedimentation. Ammonite abundance is more directly controlled by benthic conditions as many genera were probably nektobenthic. In the Kimmeridge Clay fish bones and scales are most common in organic-rich shales, particularly those of the *pectinatus* to *pallasioides* Zone interval. Marine reptiles also tend to be more common in these higher zones (Taylor and Benton 1985): both are suggestive of a decrease of sedimentation rate in the upper part of the Upper Kimmeridge Clay.

Geochemical evidence can also provide an independent measure of sedimentation rate. Precompactional nodules formed in the sulphate reduction zone require considerable periods of time for their formation (Brett and Baird 1986; Elder 1987). Conversely more rapid burial rates can remove significant amounts of unreacted organic matter and iron to the underlying methanogenic

zone where ferroan carbonates and dolomites can form by microbial fermentation (Loh *et al.* 1986). In the Kimmeridge Clay both dolostones and carbonate nodules occur, but it is significant that they are never found in the same horizon. The highest dolostones occur in the early *pectinatus* Zone whilst carbonate nodules appear in the late *pectinatus* Zone. The transition from infaunal-dominated to epifaunal-dominated associations occurs at approximately the same level and indicates a major change in sedimentation regimes at this time.

House (1985) has suggested a technique for measuring absolute sedimentation rates based on his assumption that Milankovitch-type changes in global climate are responsible for the Kimmeridge Clay rhythms. Whilst this may be true it is difficult, if not impossible, to say which type of Milankovitch cyclicity was the cause. The only absolute measure of time, upon which House's hypothesis is based, is the approximation that Jurassic ammonite zones represent 1 Ma of time. It is clear that the zones of the Kimmeridge Clay deviate significantly from this average. For example, much of the *pectinatus* Zone sediments appear to have been fairly slowly deposited, based on the palaeoecological and geochemical criteria and yet it is one of the thickest zones in the Kimmeridge Bay succession, being nearly twice as thick as the more rapidly deposited *elegans* Zone sediments. Thus, the derivation of absolute times of deposition for individual beds, based on ammonite zone duration, is not recommended.

Oxygen deficient environments of the Kimmeridge Clay

The fissile, organic-rich shales of the Kimmeridge Clay generally contain fish scales and ammonites scattered throughout, whilst benthic species tend to be confined to discrete, but common, horizons. As discussed above (p. 34), this probably represents the response of rapidly colonizing opportunists to brief, oxygenated intervals. A viable modern analogue of these depositional conditions comes from comparison with sewage polluted modern-day shelf seas. The benthic oxygen levels in such environments fluctuate over a period from weeks to years. Dispersal rate is a fundamental control of the faunal composition (Pearson and Rosenberg 1978) with the most rapid colonizers, such as the polychaete Capitella capitata, dominating most assemblages. Tolerance to low oxygen levels may only be of secondary importance because C. capitata is less able to withstand low oxygen levels than many other polychaetes (Reish 1970). Bivalves are slightly less rapid colonizers than the capitellids but once they are established they appear more resistant to subsequent oxygen restriction than other groups (e.g. Kitching et al. 1976). Many benthic species are able to survive short periods of anoxia by using anaerobic metabolic pathways and their own stored products (Herreid 1980), for which bivalves are particularly well adapted due to their ability to close themselves off from the outside environment. Anaerobic pathways are easier to accomplish in colder temperatures (Theede 1973), and this may account for the greater resistance of high latitude forms to low oxygen levels (Oertzen and Schlungbaum 1972; Rosenberg 1977).

Shell pavements of benthic species in black shales fall into the shelly laminite category of Hallam (1987) and the exaerobic biofacies of Savrda and Bottjer (1987). The latter authors defined this biofacies as containing bedding plane accumulations of epibenthic species in laminated or fissile organic-rich shales lacking evidence of bioturbation (Savrda *et al.* in press). Clearly this definition would have required modification to accommodate the Kimmeridge Clay examples for many associations are dominated by shallow infaunal species.

In the original definition of their biofacies Savrda and Bottjer (1987) suggested that exaerobic faunas, of which the majority are bivalves, may be specialized chemosymbionts living on the boundary between anoxic and hypoxic conditions. Chemosymbiosis was suggested to be achieved by the farming of sulphide oxidising bacteria on the gills of the bivalves – a mode of life that has recently been discovered in a variety of taxa. In particular the bivalve families Solemyidae, Lucinidae and Thyasiridae and some scaphopods and archaeogastropods have all been reported to have sulphide oxidizing bacteria (Felbeck 1983; de Burgh and Singla 1984; Reid and Brand 1986). A number of these groups occur in association B4, although the high diversity argues against oxygen restricted conditions for this example. Indeed most of the modern chemosymbionts come from environments with normal benthic oxygen levels. The exception is then provided by the faunas

associated with the rather specialized conditions of deep sea vents, although even here the surrounding ocean waters are well oxygenated. Chemosymbionts have yet to be found in more 'normal' oxygen restricted environments, such as sewage polluted seas and the California borderlands, and it is unlikely that they were ever important in ancient black shale environments.

The changes in the nature and composition of the fauna along the gradient of benthic oxygen levels represented in the Kimmeridge Clay is illustrated in text-figure 48. Deep infaunal species, which form over 10% of the total in some high diversity aerobic associations, are absent in dysaerobic biofacies. Also, taxa which probably possessed chemosymbiotic bacteria, such as the lucinid *Mesomiltha concinna*, reach their peak abundance in the aerobic associations (text-fig. 48).



- DECREASING O2 / INCREASING FREQUENCY OF ANOXIC CONDITIONS

TEXT-FIG. 48. Summary of the trends in faunal distribution in the Kimmeridge Clay under a decreasing oxygen gradient. Individuals size refers to the maximum size attained for a given species.

The majority of species in the dysaerobic biofacies are eurytopic opportunists, also found in many of the aerobic associations, although they appear to have reached considerably larger sizes under hypoxic conditions. This appears to be attributable to faster growth rates (e.g. text-fig. 27). The most significant forms to occur in dysaerobic, but not aerobic, associations are several species of gastropod. These may have exploited bacterial mats unique to low oxygen environments.

The proportion of filter feeding bivalves increases in the dysaerobic biofacies, mainly due to the loss of the deposit feeding trophic group. Oschmann (1988, p. 56) has suggested that: 'This is due to anoxic conditions in the substrate.' However, many Kimmeridge Clay filter feeding bivalves are infaunal and they were clearly not inhibited by anoxia in the substrate. Infaunal bivalves derive their oxygen from the bottom waters immediately overlying the substrate (Ankar and Jansson 1973; Theede 1973). Oschmann (1985) had earlier suggested that the absence of deposit feeding protobranchs from the organic-rich strata of the Kimmeridge Clay was due to their poor dispersal

rate; this is considered to be a far more likely alternative considering the abundant evidence for environmental instability (e.g. Wignall 1989). Indeed the faunal gradient in text-figure 48 can probably also be viewed as a gradient in frequency and duration of oxygenation events (Wignall in press). Temperature fluctuations may also have been important in controlling the recruitment (see discussion of association E2 for example).

Morris (1980) has also proposed a classification scheme for black shale biofacies, which includes the Kimmeridge Clay amongst its examples. Morris considered that his lowest oxygen level bituminous shale biofacies should be characterized by epifaunal bivalves (this therefore equates with the later exaerobic biofacies concept of Savrda and Bottjer 1987). He reasons that under conditions of low oxygen levels bivalves will not be able to survive within the sediment. This is contradicted by many modern examples (Wignall in press), and by the Kimmeridge Clay examples. Morris substantiates his assertion with a plot of bivalve feeding groups for *wheatleyensis* Zone sediments of Kimmeridge Bay (Morris 1980, table 4). However, his data are grossly inaccurate because his two epifaunal bivalves, *Liostrea* and *Nanogyra virgula*, do not occur in anything like the abundances he claims. Indeed *N. virgula* is on the point of extinction at this level.

True communities in the Kimmeridge Clay?

It has not been the aim of this research to analyse the validity of the community paradigm, but a cursory examination of the Kimmeridge Clay benthic associations illustrates a few interesting features. A number of associations appear to show different properties from their constituent species, E3 in particular is restricted to upper hypoxic conditions whilst the component species also occur in lower hypoxic conditions. The majority of associations have sharp boundaries suggesting some degree of integration, although this could also indicate sharp environmental gradients. Association diversity appears to increase with increasing stress, a trend that is the opposite for the species themselves. For example, aerobic association A11 breaks down to give the dysaerobic associations E1, E2 and E3. This may be a true emergent property in the sense of Salt (1979), but a more plausible interpretation of this pattern is that the community structure is broken down into its constituent species under high stress. In essence, increasing stress causes a loss of community cohesion as interacting K strategists are replaced by non-competing r strategists.

Summary of the depositional history of the Kimmeridge Clay of England

The depositional history is readily divisible into five time periods characterized by the nature and distribution of the biofacies.

(i) baylei – lower mutabilis Zones. The basal sediments of the Kimmeridge Clay were deposited over a wide area but they illustrate major lateral facies variations. This is probably a reflection of a generally shallow depth of deposition. The baylei Zone consists of condensed mudrocks with erosive-based phosphatic pebble beds and the characteristic oyster *Deltoideum*. In the muddy sediments fringing the London Platform *Myophorella* and *Corbulomima* are dominant. From the *cymodoce* to the lower *mutabilis* Zones distinct localized facies types are developed; these include the Abbotsbury Ironstone of south Dorset and the Elsham Sandstone of Lincolnshire. The earliest organic-rich shales to form in the Kimmeridge Clay are found on the East Midlands Shelf where rapid subsidence presumably created a locally deep area.

(ii) Mid-mutabilis – mid-eudoxus Zones. This sequence is characterized by the development of uniform conditions over virtually the entire Kimmeridge Clay outcrop. All the individual beds, numbered by Cox and Gallois (1981), can be traced over 300 km across swells and basins suggesting very low depositional gradients. It is probable that the London Platform was drowned at this time as there is little hint of any marginal facies in this region. Intra-Cretaceous erosion has since removed more positive evidence. The synchronous development of organic-rich shales in bed group 31 of the eudoxus Zone may represent a transgressive pulse of some importance during this interval.

(*iii*) Upper *eudoxus* – mid-*wheatleyensis* Zones. In the upper *eudoxus* Zone renewed differentiation between the swells and the basins, probably caused by tectonic activity, resulted in major changes in basin configuration. In the offshore basinal areas, such as south Dorset, thick sequences of rhythmic organic-rich shales and mudstones accumulated. Low diversity populations of opportunists, such as *Corbulomima* and *Protocardia*, colonized during brief oxygenation events. The sediments were generally fairly soft and excluded most epifaunal forms. Similar conditions were developed on the East Midlands Shelf although from the *autissiodorensis* Zone upwards water depths appear to have become shallower than those of Dorset. This is suggested by the lower proportion of organic-rich shales and the occurrence of genera, such as *Thracia* and *Nicaniella*, indicative of higher oxygen levels (text-fig. 49). Further north, in the Cleveland Basin, very deep conditions appear to have occurred as benthic species are virtually absent from the organic-rich shales indicating permanently anaerobic bottom conditions.



TEXT-FIG. 49. Biofacies relationships across southern and eastern England during the interval spanning the upper *eudoxus* to mid-*wheatleyensis* Zones.

The two main regions of organic-rich shale deposition were separated by the London Platform. Previously a condensed but complete sequence of mudstones had developed in this area but in this Kimmeridgian interval a series of shallow, heterolithic facies containing large bivalves, such as *Myophorella* and *Pleuromya*, are found in the Swindon area. Further to the east a large hiatus occurs in the section. The dinosaur bones on the base of the unconformity indicates the presence of land in this area (text-fig. 49).

(*iv*) Upper *wheatleyensis* – Upper *pectinatus* Zones. During this interval sediments were again deposited on and around the margins of the London Platform in a series of hiatus-bounded thin sequences of sandy and muddy sediments. The Wheatley Nodule Clays are particulary extensive and show little sign of lateral facies variations suggesting that the entire London Platform was again drowned. The overlying Shotover Fine and Grit Sands are a shallower water facies. The presence of abundant free-lying serpulids in the sands indicate stable substrates. The substantial lateral



TEXT-FIG. 50. Biofacies relationships during the lower *pectinatus* Zone. The London Platform was probably completely transgressed at this time and covered in a relatively condensed, glauconitic facies.

thickness changes of the sands (text-fig. 40) may indicate deposition in elongate sand bars (text-fig. 50).

Organic-rich, dysaerobic biofacies continued to form in the offshore areas with the last great episode occurring in the early *pectinatus* Zone. Lateral biofacies variations were more marked than previously, possibly reflecting a steeper depositional gradient. Byssate bivalves, such as *Musculus* and *Camptonectes*, along with *Lingula*, are typical of the near-shore muddy environments (text-fig. 50) as found in the Weald and Wash areas. The more offshore mudstones found at Kimmeridge Bay contain *Pseudorhytidopilus* along with the omnipresent *Protocardia*. Epifaunal forms are more common at this level suggesting that substrates were firmer and, by implication, sedimentation rates were slower than they had been before the mid-*pectinatus* Zone. Depositional conditions in the northerly Cleveland basin were probably similar to the Dorset section although *Buchia* was the dominant bivalve genus.

(v) Upper *pectinatus Zone* – end Kimmeridgian. The topmost sequence of the Kimmeridge Clay illustrates a gradual shallowing of the depositional environment with the area of organic-rich shale deposition becoming progressively more restricted to the centres of the offshore basins. Organic-rich shales are last seen in the mid-*pectinatus* Zone at Warlingham, whilst they persisted to the basal *rotunda* zone in south Dorset. On the London Platform, the Hartwell Clay represents the last pulse of mudrock deposition in this area. North of the Platform the top Kimmeridgian sediments have been removed by erosion.

The faunas of the latest Kimmeridgian are diverse and indicate well oxygenated shallow marine conditions. They are, however, less diverse than equivalent sediments from the Lower Kimmeridge Clay, a pattern that is also observed for the microfauna (Kilenyi 1978). This trend, along with the southward migration of Boreal forms at this time, requires further study.

Comparison with Callovian and Upper Jurassic associations

The nature of community change over a period of millions of years is only poorly understood and changes within microhabitats are only known on a broad scale. It would appear that communities

from high stress environments show the greatest longevity (Kammer *et al.* 1986), although it is not clear if this merely reflects the greater longevity of the opportunistic species which populate these environments.

Upper Jurassic communities have been documented from a wide range of facies types in NW Europe.

England. The onset of Oxford Clay deposition heralded a prolonged period of mudrock deposition in England which reached its greatest extent in the mid-*eudoxus* Zone and persisted to the end-Kimmeridgian. The palaeoecology of the Lower Oxford Clay has been studied in detail by Duff (1975). Many of his biofacies are reminiscent of the Upper Kimmeridge aerobic associations, suggesting similar environmental conditions of slow sedimentation rates and the upper levels of hypoxia. Association B2 of the Kimmeridge Clay is similar structurally, and at the generic level, to the foraminifera-rich bituminous shale and the *Grammatodon* shell bed biofacies of Duff (1975), although *Procerithium* and pendent bivalves are much more abundant in all the Oxford Clay assemblages.

The associations of the Middle and Upper Oxford Clay are recorded in the semi-quantitative data of Hudson and Palframan (1969). The fauna of some beds of the Spinosum Clays is dominated by abundant deposit feeders and *Astarte*, with few epifaunal forms. This appears to be equivalent to the *Nicaniella extensa*: Corbulomima suprajurensis association from the Lower Kimmeridge Clay. The Mariae Clays of the Upper Oxford Clay contain associations dominated by *Dicroloma* and *Pinna*; no equivalent is known from the Kimmeridge Clay.

The development of the succeeding Corallian facies introduced shallow-water carbonatedominated deposition to much of England (Fürsich 1977). The contained faunas have much in common with the associations from the heterolithic facies of the Upper Kimmeridgian developed on the margins of the London Platform. The *Myophorella clavellata* association of the Corallian is very similar at the generic level to association B7 from the Shotover Grit Sands, whilst the *Corbulomima* association is similar to association B6 from the Kimmeridgian of Swindon. The *Pinna* association, from the Corallian Sandsfoot Grit, is similar to association A12 from Calne as both contain 75% endobyssate bivalves.

The carbonate facies of the Portlandian, which succeeded the Kimmeridge Clay, contain associations which are dominated by deep infaunal forms, such as *Pleuromya* and *Plectomya*, and trigoniids (Oschmann 1988) – an assemblage which bears little comparison with those from the Kimmeridge Clay.

Scotland. Upper Jurassic benthic associations in Scotland have been described by Sykes (1975). Organic-rich shales are known from the Callovian to Oxfordian interval and their faunas provide interesting comparisons with the Kimmeridge Clay examples. The Brora Shale contains high density assemblages of *Protocardia* and *Trautscholdia* which are probably identical, at the generic level, to some of the Kimmeridge Clay dysaerobic associations. The faunas of the Flodigarry Shale more closely resemble the Lower Oxford Clay associations as deposit feeders and pendent bivalves are recorded.

Portugal. The benthic associations of the Upper Jurassic of Portugal have been described in detail (Werner 1985; Fürsich and Werner 1986). Although the depositional environments were generally shallow with lowered salinities, a number of associations are similar at the generic level to the associations of the Kimmeridge Clay. The endobenthic associations of the euhaline to brachyhaline prodelta muds are particularly familiar. The *Mesosaccella dammariensis*: *Corbulomima suprajurensis* association contains the same first three genera of the trophic nucleus as Kimmeridge Clay association B2. *M. dammariensis* is closely related, and may be conspecific, with the Kimmeridge Clay *M. cypris*. Similarly, the *Thracia depressa*: *C. suprajurensis* association resembles A1, the *Nicaniella* sp. nov.: *Protocardia peraltensis* association resembles A8, and the *Protocardia intexta*: *C. suprajurensis* association resembles E2c. The common factors controlling these spatially and

environmentally separated associations were probably soft substrates and a moderately high disturbance frequency. In the Portuguese examples this latter factor probably took the form of salinity fluctuations, whilst in the Kimmeridge examples the fluctuations were of benthic oxygen levels. Therefore, dispersal rate was probably an important factor in controlling the composition of these associations.

Greenland. A range of marine facies was deposited in north east Greenland from the Upper Bathonian to the mid-Volgian (Fürsich 1984*a*, *b*). The Grakloft Member of the mid-Lower Kimmeridgian is a black, laminated, silty shale with occasional opportunistic bivalve associations. These include the *Buchia* sp. association which is comparable to association E13 from the Cleveland Basin. A number of associations are also reminiscent of aerobic associations from the Kimmeridge Clay. The *Grammatodon keyserlingii* association is similar to association A12 as both are dominated by endobyssate bivalves and the *Astarte praeveneris maimechaensis* association is similar to association A8.

Boucot (1978), in an analysis of community longevity, noted that level-bottom communities like those discussed here generally exhibit a stability and longevity over a period of tens of millions of years. The general conclusion to be drawn from the survey above is that the associations which are widespread spatially also tend to show the greatest longevity. For instance very similar associations to the *Nicaniella extensa*: *Corbulomima suprajurensis* association, A8, of the Lower Kimmeridge Clay are also found in coeval sediments of Greenland and Portugal, whilst generically and structurally similar associations can be traced back through the Middle and Lower Oxford Clays. This pattern mimics that of opportunistic species which are also long-ranging and widespread, although the communities themselves are not necessarily composed of opportunists. It is at the generic and structural level of the community that the greatest stability is exhibited. An apparent exception to this pattern is provided by the pendent bivalve associations, of which the *Aulacomyella* assemblages provide an example from the Kimmeridge Clay. These are widespread spatially but they are also very short-lived.

Acknowledgements. This research formed part of a PhD project at Birmingham University, funded by the NERC and the British Museum (Natural History), supervised by Tony Hallam and Noel Morris, to whom I give my thanks. I also thank Keith Myers for supplying a gamma ray spectrometer, John Hudson and an anonymous reviewer for reading an early draft of the manuscript, and Karen Wignall for typing. I am grateful to Beris Cox for providing some of her unpublished data on the boreholes of eastern England and to the staff of the Portland Cement Company at Westbury for allowing access to their pit on numerous occasions.

REFERENCES

- AIGNER, T. 1980. Biofabrics and stratinomy of the Lower Kimmeridge Clay (U. Jurassic, Dorset, England). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 159, 324-338.
- ANDERSIN, A. B., LASSIG, J., PARKKONEN, L. and SANDLER, H. 1978. The decline of the macrofauna in the deeper parts of the Baltic proper. *Kieler Meersforscherung Sonderheft*, 4, 23–52.
- ANKAR, S. and JANSSON, B.-O. 1973. Effects of an unusual natural temperature increase on a Baltic soft bottom community. *Marine Biology*, 18, 9–18.

ARKELL, W. J. 1947. The geology of Oxford. Clarendon Press, Oxford, vi+267 pp.

ARNTZ, W. E., BRUNSWIG, D. and SARNTHEIN, M. 1976. Zonierung von Mollusken und Schill in Rinnensystem der Kieler Bucht (Westliche Ostsee). Senckenbergiana Maritima, 8, 189–269.

BALLANCE, P. F. 1963. The beds between the Kimmeridge and Gault Clays in the Thame-Aylesbury neighbourhood. *Proceedings of the Geologists' Association*, 74, 393-418.

BATT, R. J. 1989. Ammonite shell morphotype distributions in the Western Interior Greenhorn Sea and some paleoecological implications. *Palaios*, **4**, 32–42.

BAYNE, B. L. 1971. Oxygen consumption by three species of lamellibranch molluscs in declining ambient tension. Comparative biochemistry and physiology 40A, 955–970.

BIRKELUND, T., CALLOMON, J. H., CLAUSEN, C. K., NOHR-HANSEN, H. and SALINAS, I. 1983. The Lower Kimmeridge Clay at Westbury, Wiltshire, England. *Proceedings of the Geologists' Association*, 94, 289–309.

BLAKE, J. F. 1875. On the Kimmeridge Clay of England. Quarterly Journal of the Geological Society of London, 31, 196-233.

BOUCOT, A. J. 1978. Community evolution and rates of cladogenesis. Evolutionary Biology, 11, 545-655.

BRADSHAW, M. J. and PENNEY, S. R. 1982. A cored Jurassic sequence from north Lincolnshire, England: stratigraphy, facies analysis and regional context. *Geological Magazine*, **119**, 113–134.

BRETT, C. E. and BAIRD, G. C. 1986. Comparative taphonomy: a key to paleo-environmental interpretation based on fossil preservation. *Palaios*, 1, 207–227.

BROOKFIELD, M. E. 1973 a. The life and death of *Torquirhychia inconstans* (Brachiopoda, Upper Jurassic) in England. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 13, 241–259.

— 1973b. Palaeogeography of the Upper Oxfordian and Lower Kimmeridgian (Jurassic) in Britain. Palaeogeography, Palaeoclimatology, Palaeoecology, 14, 137–167.

— 1978. The lithostratigraphy of the Upper Oxfordian and Lower Kimmeridgian beds of south Dorset. *Proceedings of the Geologists' Association*, **89**, 1–32.

CADÉE, G. H. 1984. 'Opportunistic feeding,' a series pitfall in trophic structure analysis of (paleo)faunas. Lethaia, 17, 289-292.

CALLOMON, J. H. and COPE, J. C. W. 1971. The stratigraphy and ammonite succession of the Oxford and Kimmeridge Clays in the Warlingham borehole. *Bulletin of the Geological Survey of Great Britain*, 36, 147–176.

CASEY, R. 1967. The position of the Middle Volgian in the English Jurassic. Proceedings of the Geological Society of London, 1640, 128-133.

- CHATWIN, C. P. and PRINGLE, J. 1922. The zones of the Kimmeridge and Portland rocks at Swindon. Summary of the Progress of the Geological Survey, 1921, 162–168.
- CLAUSEN, C. K. and WIGNALL, P. B. In press. Early Kimmeridgian bivalves of southern England. Mesozoic Research, 2/3.
- COLLINS, D. H. and MINTON, P. 1967. Siphuncular tube of Nautilus. Nature, 216, 916–917.
- COPE, J. C. W. 1967. The palaeontology and stratigraphy of the lower part of the Upper Kimmeridge Clay of Dorset. Bulletin of the British Museum (Natural History) (Geology), 15, 1-79.

— 1980. Kimmeridgian correlation chart. 76–84. In COPE, J. C. W., DUFF, K. L., PARSONS, C. F., TORRENS, H. S., WIMBLEDON, W. A. and WRIGHT, J. K. (eds.). A correlation of Jurassic rocks in the British Isles. Part 2: Middle and Upper Jurassic, Special Report of the Geological Society of London, 15, 109 pp.

- COX, B. M. and GALLOIS, R. W. 1981. The stratigraphy of the Kimmeridge Clay of the Dorset type area and its correlation with some other Kimmeridgian sequences. *Report of the Institute of Geological Sciences*, **80/4**, 44 pp.
- --- LOTT, G. K., THOMAS, J. E. and WILKINSON, I. P. 1987. Upper Jurassic stratigraphy of four shallow cored boreholes in the UK sector of the southern North Sea. *Proceedings of the Yorkshire Geological Society*, 46, 97–110.
- DE BURGH, M. E. and SINGLA, C. L. 1984. Bacterial colonization and endocytosis on the gill of a new limpet species from a hydrothermal vent. *Marine Biology*, 84, 1–6.
- DINAMANI, P. 1964. Feeding in Dentalium conspicuum. Proceedings of the Malacological Society of London, 36, 1–5.
- DODD, J. R. and STANTON, R. J. 1981. Paleoecology, concepts and applications. Wiley Interscience, New York, 559 pp.
- DOYLE, P. 1987. Lower Jurassic Lower Cretaceous belemnite biogeography and the development of the Mesozoic Boreal realm. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, **61**, 237–254.
- DRIES, R.R. and THEEDE, H. 1974. Sauerstoffmangelresistenz mariner Bodenvertebraten aus der westliche Ostsee. Marine Biology, 25, 327–333.
- DUFF, K. L. 1975. Palaeoecology of a bituminous shale: the Lower Oxford Clay of central England. *Palaeontology*, 18, 443-482.
 - 1978. Bivalvia from the English Lower Oxford Clay (Middle Jurassic). *Palaeontographical Society*, *Monograph*, 137 pp.

CHADWICK, R. A. 1986. Extension tectonics in the Wessex Basin, southern England. Journal of the Geological Society of London, 143, 465–488.

- EDWARDS, B. D. 1985. Bioturbation in a dysaerobic, bathyal basin: California borderland. 309-332. In CURRAN, H. A. (ed.). Biogenic structures: their use in interpreting depositional environments. Society of Economic Paleontologists and Mineralogists, Special Publication, 35, 347 pp.
- ELDER, W. P. 1987. The paleoecology of the Cenomanian-Turonian (Cretaceous) stage boundary extinctions at Black Mesa, Arizona. *Palaios*, **2**, 24-40.
- ENSOM, P. C. and ETCHES, S. M. 1987. Ophiuroids from the Kimmeridge Clay, pectinatus zone, Freshwater Steps, Dorset. Proceedings of the Dorset Natural History and Archaeological Society, 108, 205.
- FELBECK, H. 1983. Sulfide oxidation and carbon fixation by the gutless clam *Solemya reidi*: an animal: bacteria symbiosis. *Journal of Comparative Physiology*, **152**, 3–11.
- FÖRSTER, R. 1971. Die Mecochiridae, eine spezialisierte Familie der mesozoischen Glypheoidea (Crustacea, Decapoda). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 137, 396–421.
- FÜRSICH, F. T. 1977. Corallian (Upper Jurassic) marine benthic associations from England and Normandy. *Palaeontology*, **20**, 337–385.
- ----- 1980. Preserved life position of some Jurassic bivalves. *Paläontologische Zeitschrift*, 54, 289-300.
- 1984*a*. Benthic macroinvertebrate associations from the Boreal Upper Jurassic (Milne Land; East Greenland). Bulletin Gronlands Geologiske Undersogelse, 149, 72 pp.
- and OSCHMANN, W. 1986. Storm shell beds of *Nanogyra* in the Upper Jurassic of France. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **60**, 65–74.
- and PALMER, T. J. 1984. Commissural asymmetry in brachiopods. Lethaia, 17, 251-266.
- and SYKES, R. M. 1977. Palaeobiogeography of the European Boreal Realm during Oxfordian (Upper Jurassic) times: a quantitative approach. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **155**, 137–161.
- and WERNER, W. 1986. Benthic associations and their environmental significance in the Lusitanian Basin (Upper Jurassic, Portugal). *Neues Jahrbuch für Geologie und Paläontologie*, *Abhandlungen*, **172**, 271–329.
- GAGE, J. D. and TYLER, P. A. 1985. Growth and recruitment of the deep-sea urchin *Echinus affinis*. Marine Biology, 90, 41-53.
- GALLOIS, R. W. 1978. A pilot study of oil shale occurrences in the Kimmeridge Clay. Report of the Institute of Geological Sciences, 78/13, 26 pp.
- 1979. Geochemical investigation for the Wash Water Storage Scheme. Report of the Institute of Geological Sciences, 78/19, 74 pp.
- and COX, B. M. 1974. Stratigraphy of the Upper Kimmeridge Clay of the Wash area. Bulletin of the Geological Survey of Great Britain, 47, 1–28.
- ---- and ---- 1976. The stratigraphy of the Lower Kimmeridge Clay of eastern England. Proceedings of the Yorkshire Geological Society, 41, 13-26.
- GROSS, T. F., WILLIAMS, A. J. and NOWELL, A. R. M. 1988. A deep-sea sediment transport storm. *Nature*, 331, 518-521.
- HALLAM, A. 1972. Diversity and density characteristics of Pliensbachian-Toarcian molluscan and brachiopod faunas of the North Atlantic. *Lethaia*, **5**, 389–412.
- ------ 1976. Stratigraphic distribution and ecology of European Jurassic bivalves. Lethaia, 9, 245–259.
- and SELLWOOD, B. W. 1976. Middle Mesozoic sedimentation in relation to tectonics in the British area. *Journal of Geology*, 84, 301-324.
- HATTIN, D. E. 1986. Carbonate substrates of the Late Cretaceous Sea, Central Great Plains and Southern Rocky Mountains. *Palaios*, 1, 347–367.
- HEATWOLE, H. and LEVINS, R. 1972. Trophic stability and faunal change during recolonization. *Ecology*, **53**, 531–534.
- HERREID, C. F. 1980. Hypoxia in invertebrates. Comparative Biochemistry and Physiology, 67A, 311-320.
- HEWITT, R. A. and WIGNALL, P. B. 1988. Structure and phylogenetic significance of *Trachyteuthis* (Coleoidea) from the Kimmeridge Clay of England. *Proceedings of the Yorkshire Geological Society*, **47**, 149–153.
- HOFFMAN, A. 1979. Community paleoecology as an epiphenomenal science. Paleobiology, 5, 357-379.
- —— 1982. Community evolution and stratigraphy. Newsletters in Stratigraphy, 11, 32–36.
- HOUSE, M. R. 1985. A new approach to an absolute time scale from measurements of orbital cycles and sedimentary microrhythms. *Nature*, **316**, 721–725.

HUDSON, J. D. and PALFRAMAN, D. 1969. The ecology and preservation of the Oxford Clay fauna at Woodham, Buckinghamshire. *Quarterly Journal of the Geological Society of London*, **124**, 387–418.

HULKE, J. W. 1880. Iguanodon prestwichii from the Kimmeridge Clay. Quarterly Journal of the Geological Society of London, 36, 433-456.

HURLEBURT, S. H. 1971. The nonconcept of species diversity. Ecology, 52, 577-586.

HUSTON, M. 1979. A general hypothesis of species diversity. Ecology, 113, 81-101.

JABLONSKI, D. and LUTZ, R. A. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews*, 58, 21-89.

- JØRGENSEN, B. B. 1977. The sulphur cycle of a coastal marine sediment (Limfjord, Denmark). Limnology and Oceanography, 22, 814-832.
- KAMMER, T. W., BRETT, C. E., BOARDMAN, D. R. and MAPES, R. H. 1986. Ecologic stability of the dysaerobic biofacies during the Late Paleozoic. Lethaia, 19, 109–121.
- KAUFFMAN, E. G., HATTIN, D. E. and POWELL, J. D. 1977. Stratigraphic, paleontologic and paleoenvironmental analysis of the Upper Cretaceous rocks of Cimmaron County, north-western Oklahoma. *Memoir of the Geological Society of America*, 149, 150 pp.

KELLY, S. R. A. 1980. Hiatella – a Jurassic bivalve squatter? Palaeontology, 23, 769-781.

- KENT, P.E. and CASEY, R. 1963. A Kimmeridge sandstone in Lincolnshire. Proceedings of the Geological Society of London, 1606, 57-62.
- KILENYI, T. 1978. The Jurassic part 3 Callovian to Portlandian. 259–298. In BATE, R. H. and ROBINSON, G. (eds.). A stratigraphical index of British Ostracoda. Geological Journal, Special Issue, 8, 538 pp.
- KITCHING, J. S., EBLING, F. J., GAMBLE, J. C., HOARE, R., MCLEOD, A. A. Q. R. and NORTON, T. A. 1976. The ecology of Lough Ine. XIX Seasonal change in the western trough. *Journal of Animal Ecology*, **45**, 731–758.

LEHMANN, U. 1981. The ammonites: their life and their world. Cambridge University Press, Cambridge, 246 pp. LEVINTON, J. S. 1970. The paleoecological significance of opportunistic species. Lethaia, 3, 69–78.

- LOH, H., MAUL, B., PRAUSS, M. and RIEGAL, W. 1986. Primary production, maceral formation and carbonate species in the Posidonia shale of NW Germany. 397–421. In DEGENS, E. T. et al. (eds.). Biogeochemistry of black shales. Hamburg University, 422 pp.
- MORRIS, K. A. 1980. Comparison of major sequences of organic-rich mud deposition in the British Jurassic. Journal of the Geological Society of London, 137, 157-70.
- MULLINS, H. T., THOMPSON, K., MCDOUGALL, K. and VERCOUTERE, T. L. 1985. Oxygen-minimum zone edge effects: Evidence from the central California coastal upwelling system. *Geology*, **13**, 491–494.

MYERS, K. J. 1987. Onshore-outcrop gamma-ray spectrometry as a tool in sedimentological studies. Unpublished PhD Thesis, University of London.

- and WIGNALL, P. B. 1987. Understanding Jurassic organic-rich mudrocks new concepts using gamma ray spectrometry and palaeoecology: examples from the Kimmeridge Clay of Dorset and the Jet Rock of Yorkshire. 175–192. In LEGGET, J. K. and ZUFFA, G. G. (eds.). Marine clastic environments: concepts and case studies, Graham and Trotman, London, 232 pp.
- NEYMAN, A. A. 1967. Limits to the application of the trophic group concept in benthic studies. Oceanology, Academy of Science, 7, 149-155.
- OATES, M. J. 1974. The stratigraphy and paleoecology of the Hartwell Clay (Upper Kimmeridgian) of Aylesbury, Buckinghamshire. *Proceedings of the Geologists' Association*, **85**, 367-375.
- OERTZEN, J. A. VON and SCHLUNGBAUM, G. 1972. Experimentell-okologische Untersuchungen über O₂-Mangel und H₂S Resistenz an marinen Evertebraten der westlichen Ostsee. *Beiträge zur Meereskunde*, **29**, 79–91.
- OSCHMANN, W. 1985. Faziensentwicklung und Provinsialismus in Nordfrankreich und Südenengland zur Zeit des obersten Jura (Oberkimmeridge – Portland). Müncher Geowissenschaftliche Abhandlungen, 2, 102 pp, 9 pl.
 - 1988. Upper Kimmeridgian and Portlandian marine macrobenthic associations from southern England and northern France. *Facies*, **18**, 49–82.
- PEARSON, T. H. and ROSENBERG, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology, Annual Review, 16, 229–311.
- PEDERSEN, G. K. 1986. Changes in the bivalve assemblage of an early Jurassic mudstone sequence (the Fjerritslev Formation in the Gassum 1 well, Denmark). *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 53, 139–168.
- PENN, I. E., COX, B. M. and GALLOIS, R. W. 1986. Towards precision in stratigraphy: geophysical log of Upper
Jurassic (including Callovian) strata of the eastern England shelf. Journal of the Geological Society of London, 143, 381-410.

- PERRON, F.E. 1978. Seasonal burrowing behaviour and ecology of *Aporrhais occidentalis* (Gastropoda, Strombacea). *Biological Bulletin*, **154**, 463–471.
- PETERSON, C. H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. 233–264. In LIVINGSTON, R. J. (ed.). Ecological processes in coastal and marine systems, Plenum Press, New York.

— and ANDRE, S. M. 1980. An experimental analysis of interspecific competition among marine filter-feeders in a soft-sediment environment. *Ecology*, **61**, 129–139.

- REID, R. G. and BRAND, D. G. 1986. Sulfide-oxidising symbiosis in lucinaceans: implications for bivalve evolution. Veliger, 29, 3-24.
- REISH, D. J. 1970. Water Research, 4, 721-735.
- REMANE, A. 1971. Ecology of brackish waters. 1–120. In REMANE, A. and SCHLIEPER, C. (eds.). Biology of brackish waters. Binnengewässer, 25, 1–372.
- RHOADS, D. C. and MORSE, I. W. 1971. Evolutionary and ecologic significance of oxygen-deficient marine basins. *Lethaia*, 4, 413–428.
- and YOUNG, D. K. 1970. The influence of deposit feeding organisms on bottom-sediment stability and trophic structure. Journal of Marine Research, 28, 150–178.
- RICHARDSON, G. 1979. The Mesozoic stratigraphy of two boreholes near Worlaby, Humberside. Bulletin of the Geological Survey of Great Britain, 58, 26 pp.
- ROSENBERG, R. 1977. Benthic macrofaunal dynamics, production and dispersion in an oxygen-deficient estuary off west Sweden. Journal of Experimental Marine Biology and Ecology, 26, 107-133.
- SALT, G. W. 1979. A comment on the use of the term emergent properties. *American Naturalist*, **113**, 145–148. SANDERS, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist*, **102**, 243–282.
- SAVRDA, C. E. and BOTTJER, D. J. 1987. The exaerobic zone, a new oxygen-deficient marine biofacies. *Nature*, **327**, 54-56.
- —, and SEILACHER, A. In press. Redox-related benthic events. In RICKEN, W., EINSELE, G. and SEILACHER, A. (eds.). Cycles and events in stratigraphy. Springer-Verlag, Berlin.
- SCOTT, R. W. 1976. Trophic classification of benthic communities. 29–66. In SCOTT, R. W. and WEST, R. R. (eds.). Structure and classification of paleocommunities, Dowden, Hutchinson and Ross, Stroudsberg, 291 pp.
- SEILACHER, A. 1982. Ammonite shells as habitats in the Posidonia shales of Holzmaden floats or benthic islands? Neues Jahrbuch für Geologie und Paläontologie, Monatsheft, 1982, 98-114.
- SELLWOOD, B. W., SCOTT, J. and LUNN, G. 1986. Mesozoic basin evolution in southern England. Proceedings of the Geologists' Association, 97, 259–289.
- SMITH, C. R., JUMARS, P. A. and DE MASTER, D. J. 1986. In situ studies of megafaunal mounds indicate rapid sediment turnover and community response at the deep-sea floor. Nature, 323, 251-252.
- STANLEY, S. M. 1970. Relation of shell forms to life habits of the Bivalvia (Mollusca). Memoirs of the Geological Society of America, 125, 269 pp.

- SYKES, R. M. 1975. The stratigraphy of the Callovian and Oxfordian stages (Middle and Upper Jurassic) in northern Scotland. Scottish Journal of Geology, 11, 51–78.
- TAYLOR, M. A. and BENTON, M. J. 1985. Reptiles from the Upper Kimmeridge Clay (Kimmeridgian, Upper Jurassic) of the vicinity of Egmont Bight, Dorset. Proceedings of the Dorset Natural History and Archaeological Society, 107, 121-125.
- TEVESZ, M. J. S. and MCCALL, P. L. 1979. Evolution of substrate preference in bivalves (Mollusca). Journal of Paleontology, 53, 112-120.
- THEEDE, H. 1973. Comparative studies on the influence of oxygen deficiency and hydrogen sulphide on marine invertebrates. *Netherlands Journal of Sea Research*, 7, 244–252.
- THORSON, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Netherlands Journal of Sea Research, 3, 267–293.
- TIPPER, J. C. 1979. Rarefaction and rarefiction the use and abuse of a method in paleoecology. *Paleobiology*, 5, 423–434.
- WALKER, K. R. and BAMBACH, R. 1974. Feeding by benthic invertebrates: classification and terminology for paleoecological analysis. Lethaia, 7, 67–78.

- WERNER, W. 1985. Palökologische und biofazielle Analyse des Kimmeridge (Oberjura) von Consalação, Mittelportugal. Zitteliana, 13, 3-109.
- WIGNALL, P. B. 1988. The palaeoecology and sedimentology of the Kimmeridgian of England and northern France. Unpublished PhD Thesis, University of Birmingham.

— In press. Observations on the evolution and classification of dysaerobic communities. In MILLER, W. (ed.). Paleocommunity temporal dynamics: the long-term development of multispecies assemblies. Paleontological Society, Special Publication, 10.

— and MYERS, К. J. 1988. Interpreting benthic oxygen levels in mudrocks: a new approach. Geology, 16, 452–455.

— and simms, м. J. In press. Pseudoplankton. *Palaeontology*.

WILKINSON, I. P. 1983. Kimmeridge Clay ostracods of the North Wootton borehole, Norfolk, England. Journal of Micropalaeontology, 2, 17–29.

- WILLIAMS, L. A. 1984. Subtidal stromatolites in Monterey Formation and other organic-rich rocks as suggested contributors to petroleum formation. *Bulletin of the American Association of Petroleum Geologists*, **68**, 1879–1893.
- WITHERS, T. H. 1928. Catalogue of fossil Cirripedia in the Department of Geology. Vol. 1. Triassic and Jurassic. British Museum (Natural History), London, 131 pp.
- WOODIN, S. A. 1976. Adult-larval interactions in dense infaunal assemblages. Journal of Marine Research, 34, 25-41.
- ——1983. Biotic interactions in recent marine sedimentary environments. 3–38. In TEVESZ, M. J. S. and MCCALL, P. L. (eds.). Biotic interactions in recent and fossil benthic communities. Plenum Press, New York, 837 pp.
- ---- and JACKSON, J. B. C. 1979. Interphyletic competition among marine benthos. *American Zoologist*, 19, 1029–1043.
- WOODWARD, H. 1875. On some new macrurous Crustacea from the Kimmeridge Clay of the sub-Wealden borings, Sussex, and from the Boulogne-sur-Mer. Quarterly Journal of the Geological Society of London, 32, 47-50.
- YONGE, C. M. 1937. The biology of Aporrhais pespelicani (L.) and A. serresiana (Mich.). Journal of the Marine Biological Association of the UK, 21, 687-703.

Typescript received 16 December 1988 Revised typescript received 4 July 1989 PAUL B. WIGNALL, Department of Earth Sciences University of Leeds Leeds LS2 9JT

74

Printed in Great Britain at the University Printing House, Cambridge

ISBN 0 901702 42 0