THE FEEDING ECOLOGY AND PHYSIOLOGY OF THE SCALLOPS *PECTEN MAXIMUS* (L.) AND *AEQUIPECTEN OPERCULARIS* (L.) IN THE NORTH IRISH SEA

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by

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For my Dad, Jane & Simon

Thank you

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The feeding ecology and physiology of the scallops *Pecten maximus* (L.) and *Aequipecten opercularis* (L.) in the North Irish Sea

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ABSTRACT

This thesis investigates the feeding of the scallops *Pecten maximus* and *Aequipecten opercularis*, with special emphasis on examining what is actually available to them in the benthic boundary layer. The effect of algal concentration and flow rate on clearance rate (which was estimated using an indirect method) and particle size selection (calculated as Jacob's electivity index, D) was examined by monitoring the decline in particle numbers using a Coulter Counter Multisizer. The same techniques were also used in experiments to evaluate the effect of sediment on the feeding behaviour and physiology during both short and long-term exposures. These experiments additionally evaluated apparent absorption efficiency (i.e., measured using biodeposits rather than faeces), chlorophyll digestion efficiency and chlorophyll selection efficiency. The long-term experiment also calculated the scope for growth, which required the additional estimation of oxygen consumption and ammonia excretion rates.

The water in the benthic boundary layer was well mixed, with resuspended benthic diatom species present to at least one metre above the seabed. A distinct assemblage of benthic diatom species was resuspended in the water column throughout the year, which comprised the major dietary items of *P. maximus* and *A. opercularis*. Planktonic diatom species were only present in the benthic boundary layer in significant numbers during the Spring and early Summer. These ephemeral species were present in the gut contents of *P. maximus* and *A. opercularis* during those periods. Cluster analysis showed that the diatom assemblages in the gut contents of *P. maximus* were less closely associated with any of the sampled dietary sources than those of *A. opercularis*. This suggests that *P. maximus* exhibits greater selection with regard to which species are ingested, or that *P. maximus* feeds from a different source of food, which was not adequately sampled. Either of these are intuitively possible; that is, *P. maximus* recesses into the seabed sediment and is likely to receive a different, lower quality, diet than *A. opercularis*, which sits upon the sediment. Receiving a lower quality diet may also influence the degree of selectivity shown by the two species.

When the benthic diatom species are resuspended, they are present as part of a complex mixture which also includes bacteria, mineral particles and refractory organic material. This resuspended sediment has an important influence on the feeding behaviour and physiology of *P. maximus* and *A. opercularis*. Short-term exposures to low concentrations of sediment in the diet increased the clearance rates of both species, with a concomitant increase in absorption rate. At higher sediment concentrations, however, clearance rates and absorption rates were reduced. The pattern of response shown by both species was similar, but *P. maximus* was more adversely affected. *P. maximus* was more efficient at sorting particles prior to ingestion when algal concentrations were low. However, at high algal concentrations, *A. opercularis* was more efficient. In long-term sediment exposure experiments both species maintained positive scope for growths, which were at least as good, and often better, than those attained for pure algal diets. However, the oxygen consumption rates measured were low which suggests that the animals were nutritionally stressed. This is supported by the generally low oxygen to nitrogen ratios recorded. *P. maximus* exhibited a greater elevation in ammonia excretion, suggesting a greater sensitivity to sediment in the diet. Greater sensitivity to sediment in the diet may be a contributory factor determining the relative distribution of the two species. *P. maximus* and *A. opercularis* exhibit a more flexible feeding behaviour than was previously appreciated, involving the alteration of clearance rates and pseudofaeces production.

CHAPTER 1. GENERAL INTRODUCTION

The class Bivalvia constitutes a major group of subtidal benthic organisms which are widespread globally (Purchon, 1968; Yonge & Thompson, 1976; Morton, 1979). Within the bivalves, the family Pectinidae are important both commercially and with regard to their numbers and biomass present in coastal and nearshore communities (Brand, 1991). A large proportion of bivalves are suspension feeders which utilize suspended particulate matter in the benthic turbidity zone (B.T.Z.) (Griffiths & Griffiths, 1987). Their rôle as primary consumers provides an important trophic link between the primary producers (whether planktonic or benthic in origin) and the rest of the benthos and demersal food chains (e.g., Nagabhushanam, 1959; Armstrong, 1979; Patterson, 1983). In order to elucidate the importance of this rôle in benthic ecology a detailed knowledge of the feeding capabilities and the source of the diet is required.

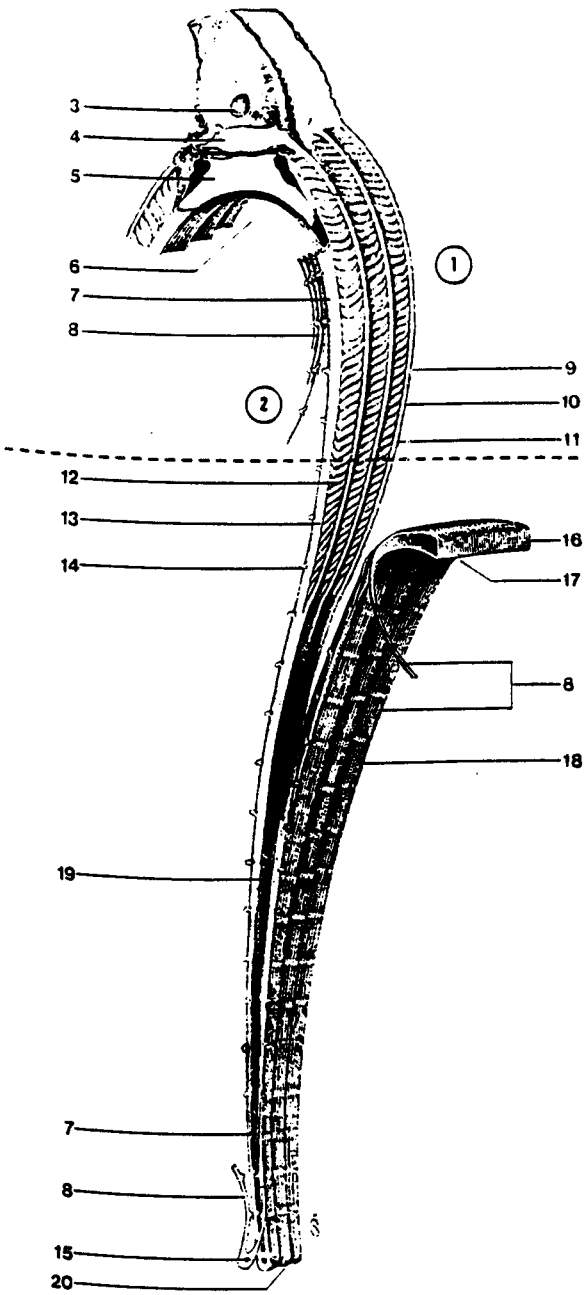
Members of the bivalve family Pectinidae (commonly known as pectinids) are known to feed on sedimenting phytoplankton (Christensen & Kanneworff, 1985, 1986) and suspended benthic diatoms (Hunt, 1925; Vernet, 1977; Shumway *et al.*, 1987), and therefore presumably resuspended detritus (Kirby-Smith, 1976; Cranford & Grant, 1990). The importance of each dietary source, and whether reliance alters seasonally is unclear, but it is known that the seston varies in quality and quantity both seasonally and over shorter time scales (Rhoads *et al.*, 1984; Berg & Newell, 1986, 1989; Wilson-Ormond *et al.*, 1993). Many pectinids are commercially important both in traditional fisheries and aquaculture (see Shumway, 1991). Therefore a greater understanding of their feeding ecophysiologies would aid management.

This thesis describes and compares the diets and feeding ecophysiologies of two commercially important North Irish Sea pectinids *Pecten maximus* (Linnaeus, 1758) and *Aequipecten opercularis* (Linnaeus, 1758), which overlap in their broadscale distributions. Locally, they may occur in single or mixed species grounds, but *P. maximus* does not tend to inhabit areas where the sediment is composed of a high proportion of fine material. In the rest of this introductory chapter the bivalve feeding organ - the ctenidium or gill - is outlined, as much recent work has been done on the structure and function of the gill. The feeding mechanism itself is then reviewed, particularly the current controversy concerning the biomechanics of feeding. Environmental factors affecting feeding and ingestion rates are then discussed. Responses to long-term exposure to resuspended material are then considered because of the importance of this factor in the benthic boundary layer. Finally, methodological approaches and problems in measuring bivalve clearance rates and particle size selection are reviewed as they are central to the whole thesis. This review then sets the scene for the aims of the thesis which are outlined at the end of this introduction.

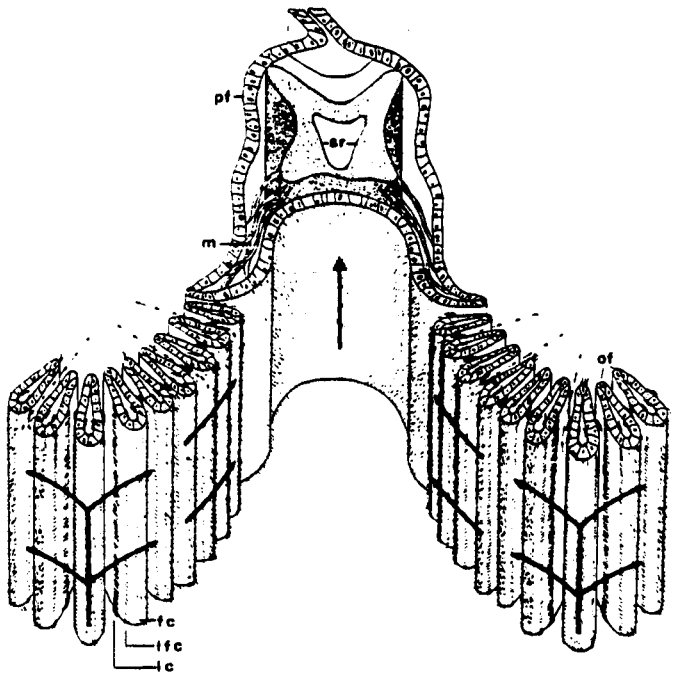
THE BIVALVE GILL

General descriptions of the anatomy of the bivalve ctenidium have been reviewed in Morton (1983), and more recently in Jørgensen (1990a; 1990b).

Bivalves have two ctenidia, one either side of the foot. Each ctenidium consists of a series of 'W' shaped filaments, which form two lobes or demibranchs, suspended in the mantle cavity. The ascending arms of the inner demibranchs are connected to either the other ctenidium or to the gonad, by ciliary junctions. The ascending arms of the outer demibranch



Macro-anatomy of the gill of *Placopecten magellanicus*. 1 - suprabranchial chamber, 2 - infrabranchial chamber, 3 - branchial nerve, 4 - afferent branchial vessel, 5 - efferent branchial vessel, 6 - gill arch, 7 - lateral wall of principal filament, 8 - ordinary filaments, 9 - descending branch of principal filament, 10 - dorsal respiratory expansion, 11 - afferent vessel, 12 - interconnecting vessel, 13 - efferent vessel in principal filament, 14 - ciliated spur, 15 - ciliated disc, 16 - dorsal bend, 17 - ciliated tract, 18 - ascending filaments, 19 - interlamellar junction, 20 - ventral bend. Ventral extremity is shown in a semi-contracted state. Reprinted from Beninger et al. (1988) with permission of Springer-Verlag.



Stereodiagram of the relaxed scallop gill as viewed from the frontal surface. Dorsal respiratory expansion and ciliated spurs not shown. Large arrows indicate dominant current flow; small arrows indicate progressive escape of water and smallest particles through interfilamentar spaces. cs, ciliated spurs; fc, frontal cilia; m, muscle fibres; of, ordinary filament; pf, principal filament; sr, supporting rods.

Fig. 1.1 The macroanatomy of the gill of *Placopecten magellanicus* (taken from Beninger *et al.*, 1988) and a schematic diagram of a scallop gill (taken from Beninger, 1991).

are connected to the mantle by ciliary junctions. The ciliary junctions can be broken and reformed. The two ctenidia therefore more or less effectively separate the bivalve into two chambers: the infrabranchial or inhalant chamber, and the suprabranchial or exhalant chamber (Beninger, 1991). The pectinid bivalve gill (see Fig. 1.1) has recently been described in detail by Beninger (1991) and Beninger & Le Pennec (1991). One important feature of the pectinid gill that should be noted is that it is plicate (folded in such a way that it resembles curtains hanging from a pole (Beninger, 1991)) and heterorhabdic (consisting of functionally and anatomically distinct filaments) (Morton, 1983).

The gill filaments have different types of ciliary tracts: on the surface facing the infrabranchial (inhalant) chamber there are frontal cilia which may be present in two forms, fine or coarse. Atkins (1937a; 1937b, summarized by Owen, 1978) described the median coarse tracts as being less active than the more laterally positioned fine tracts, and were only stimulated by the presence of coarse or heavy particles. The coarse tracts move particles ventrally to the gill margin, where they merge with other coarse tracts outside the food groove. Fine tracts move small particles dorsally to the food grooves; the fine tracts effectively constitute acceptance tracts (Morton, 1983).

The sides of the filaments are covered with tracts of lateral cilia, which have always been considered to generate the feeding and ventilation current. Recently it has been shown that abfrontal cilia in *Mytilus edulis* (L.) contribute to the creation of the water flow (Jones *et al.*, 1990), and may account for as much as 47% of the power of the bivalve 'pump'. These authors also frequently observed that the lateral cilia were inactive. They suggested that the lateral cilia may only operate to overcome the increased

resistance to water flow that occurs when the latero-frontal cirri are extended when the animal is filtering particles from the water.

Between the lateral cilia and the frontal cilia are the latero-frontal cirri. The latero-frontal cirri consist of bundles of several cilia, which project as side branches at various intervals along the cirrus. The latero-frontal cirri of adjacent filaments overlap slightly (Moore, 1971; Owen, 1974b; Silvester & Sleigh, 1984; Jones *et al.*, 1992) to span the gaps (ostia) between filaments. The side branches from adjacent cirri also overlap slightly, so that the cirri from adjacent filaments form a sieve-like structure. The latero-frontal cirri beat metachronally, which is described in Silvester & Sleigh (1984). The effective stroke of the cirrus is slow and directed towards the frontal cilia (uncovering the ostium); the recovery stroke is faster and is followed by a resting phase, when the cirrus lies across the ostium.

Each cirrus is approximately half a cycle out of phase with its neighbour, therefore the ostium should be covered by at least half of the cirri for much of the time. However, there will be short periods when the ostium will be uncovered, and it has been suggested that the duration of this uncovered phase may be controlled to adjust particle retention in response to changes in ambient food concentration (Dral, 1967; Jørgensen, 1976).

The tracts of latero-frontal cirri differ between families. Some have compound eu-latero-frontal cirri with pro-latero-frontal cirri flanking them frontally. This pattern is found in the commonly studied species *Mytilus edulis* (Owen, 1974b). In contrast, pectinids only have a single row of micro-latero-frontal cilia either side of frontal cilia (Owen & McCrae, 1976; Owen, 1978; Richards, pers. comm.).

At the oral end of each ctenidium are a pair of labial palps which have often been implicated in the pre-ingestive selection of particles. The inner surfaces of the labial palps are folded and have complex tracts of cilia (Morton, 1983; Newell & Jordan, 1983; Jørgensen, 1990a). Allen (1958) distinguished between acceptance tracts that run along the ridges of the folds towards the mouth, and rejection tracts which run in the troughs. Resorting tracts were described along the aboral sides of the folds. There is still much confusion as to the actual mechanism of particle selection.

THE FEEDING MECHANISM

Much argument surrounds this topic. Two main schools of thought have arisen. The first headed by C.B. Jørgensen maintains that the main forces involved in particle capture are hydromechanical in nature (e.g., Owen, 1978; Jørgensen, 1981b, 1982, 1990a). The second group argue that mucociliary mechanisms are involved in bivalve feeding (e.g. Silvester & Sleigh, 1984; Silvester, 1988; Jones *et al.*, 1990; Beninger, 1991), with hydromechanic influences also playing a part.

Dral (1967) and Foster-Smith (1975b) postulated a mucociliary feeding mechanism. This involved direct capture of the particles by the latero-frontal cilia, and then transfer to the frontal cilia where they are trapped in mucus. Jørgensen (1981b; 1982) proposed a hydromechanical explanation for particle capture. This mechanism is based on viscous shear forces acting on suspended particles in a region of complex flow patterns that arise at the entrance to the interfilamental spaces (Jørgensen, 1981b). He believes that the complex hydromechanical shear forces are created and modulated by the frontal and latero-frontal cilia groups to control particle retention.

All suspension feeding was thought to be characterized by low Reynolds numbers (R_e, the ratio of inertial forces to viscous forces, see Vogel, 1981). These are typically much less than one, which means that particle motion is dominated by viscous forces and that inertial forces are negligible (Rubenstein & Koehl, 1977; La Barbera, 1984; Jørgensen, 1990a). Jørgensen therefore thinks that it is unlikely that inertial forces would impinge large particles on to the surface of the gill. However, a review of the literature by Shimeta & Jumars (1991) has shown that the belief that all flow is creeping ($R_e \ll 1$) at the level of the individual filter element is a misconception, and that double figure Reynolds numbers can occur.

A further argument used by Jørgensen (1981b) against the gill acting as a sieve, was that he did not consider that the pressure head created by the lateral cilia would be high enough to force the water through the laterofrontal cilia if they were acting as a mechanical filter (Jørgensen, 1981b). Using the work of Foster-Smith (1976), he argued that the recorded pressure drop as the water moved through the gill, was only one tenth of that which would occur if the gill were acting as a sieve (Jørgensen, 1981b; La Barbera, 1984). Several authors believe that the cilia do create sufficient power to force the water through the interfilamanetal canals. For example, Silvester & Sleigh (1984) calculated that a little more than half of the pressure generated by the lateral cilia would be required to force the water through the gill. The remainder of the power would be utilized to circulate the water in and out of the siphons. They also concluded that the hydromechanic shear forces which are generated where different currents meet, would be insufficient to contribute significantly to particle capture. However, it was thought that shear forces may provide a means of retaining particles in the frontal current, without the aid of mucus (Owen, 1978; Jones *et al.*, 1990; Ward *et al.*, 1991), since it was recognized that not

all particle transport occurred in mucus. The traditional mucociliary interpretation could not explain that anomaly. Beninger *et al.* (1993) have shown, however, that particle transport always occurs in mucus, although the mucus may have a very low viscosity and be moved by hydromechanical means.

Rubenstein & Koehl (1977) believe that the basic concept of mesh filtration of Wallengren (1905; cited in Dral, 1967), when expanded to include hydromechanic principles appropriate to the morphology of aquatic organisms, provides the basic theory to explain the mechanics of filter-feeding. Direct interception of particles is thought to be the most common method of particle capture amongst marine suspension feeders, with inertial impaction, gravitational deposition, diffusion (motile) particle deposition and electrostatic attraction playing smaller rôles (Rubenstein & Koehl, 1977; Silvester & Sleigh, 1984; Shimeta & Jumars, 1991).

Jørgensen (1990a) states that direct ciliary capture and enrobement in mucous does occasionally occur, but that this is not the usual mechanism, and only occurs at high particle concentrations (Jørgensen, 1981a). He also considers that many earlier studies that reported the trapping and transport of particles in mucus, and the presence of mucus-bound particles in the stomach, were a direct result of the mutilation of the bivalves. One argument that Jørgensen (1990a) used against the use of mucus in normal feeding processes involved cut pieces of bivalve gill. The piece of gill would retain and move captured flagellate (i.e., motile) cells along its length, but when the cells reached the cut edge of the gill they immediately moved away unhindered; that is, they were not bound in mucus (Jørgensen, 1976, 1990a).

Ward *et al.* (1991) have made an *in vivo* study of the bivalve gill using an endoscope, which caused an extremely low level of disturbance, if any. Their work supports a mucociliary feeding mechanism. Further credence has been given to the mucociliary theory by Jones *et al.* (1990, 1992), who have remeasured the water pressures involved in the bivalve pump and have found that the water flows created would be powerful enough to force through the "sticky" laterofrontal cilia. Jørgensen had not considered, in his work, that cilia groups other than the lateral could add to the power of the pump. It was suggested as early as 1912 that abfrontal cilia helped in producing the main current (Orton, 1912, cited in Jones *et al.*, 1990). In *Mytilus edulis* the abfrontal cilia may contribute as much as 47% of the power of the pump (Jones *et al.*, 1990). Jørgensen (1981b) also did not believe that the mesh created by the latero-frontal cirri would be adequate to act as a sieve and to produce the published retention efficiencies. Jones *et al.* (1992) measured the interfilamental canals and laterofrontal cilia lengths using a scanning electron microscope (S.E.M.), and concluded that there would be an overlap of cilia from either side of the interfilamental canal; they could act as a mechanical filter.

Both groups of workers acknowledge that the gills of pectinids are anatomically different from the bivalves on which most of the work has been performed (commonly mytilids). *Pecten maximus*, for example, has no abfrontal cilia, and the latero-frontal cilia are very sparse and regressed (S.E.M. study, Owen Richards, pers. comm.). This would have implications for particle retention ability and the pumping forces generated (Owen, 1974b; Jørgensen, 1976; Owen & McCrae, 1976). Owen (1978) suggested that in *Chlamys varia* the form of the plicae, the 'U' shape of the principal filament and the dorsally directed flow of water created by the frontal ciliated tracts, all combine to form a region of low pressure

which tends to attract particles into the gutters formed by the principal filaments. He stressed that the particles are transported dorsally in suspension. Beninger *et al.* (1988) agreed with Owen's (1978) description of water current movements, but stated that particles were trapped by the cilia and mucus on the infrabranchial surfaces of the gill (Beninger, 1991). At high particle concentrations, typical of the benthic boundary layer, there is a reduction in the degree of plication due to contraction of the lateral walls of the principle filament (Beninger & Le Pennec, 1991), and the collection of particles by water currents can no longer occur. Direct ciliary action then acts to capture particles, combined with mucus secretion and entrapment, and particles are moved anteriorly.

Further work using an endoscope has shown that the principal and ordinary filaments of the gill of *Placopecten magellanicus* are functionally distinct: the principal filaments are used for feeding processes, whereas the ordinary filaments are used for cleaning the gill of excess material (Beninger *et al.*, 1992, 1993). Material in the ventral tracts is moved ventrally in high viscosity (mechanically stable) mucus, whereas material in the dorsal tracts is moved dorsally in low viscosity mucus in a 'slurry'. The material in the mucus slurry in the dorsal tracts moves faster than that in the ventral tracts (Ward *et al.*, 1993a). Mucus secretion occurs in the principal filaments (Beninger *et al.*, 1993), not in the dorsal ciliated tracts as proposed in Beninger *et al.* (1988). The mucus masses in the ventral tract are usually rejected as pseudofaeces (Ward *et al.*, 1993a). Beninger *et al.* (1992) summarized four methods that were observed to control the volume of ingested material: 1, the ejection of particle masses from the principal filament onto the ordinary filaments and then to the ventral rejection tracts; 2, intermittent cessation of the anterior flow in the dorsal ciliated (acceptance) tracts; 3, detachment of the dorsal bends from

the mantle to create a shunt (by-pass) of water (Wildish *et al.*, 1987, also recorded in *Mytilus edulis* in Beninger *et al.*, 1993) which will not only decrease clearance rates but also remove accumulations of particle rich slurry; and 4, short-term stoppages or reductions in the input of material from the principal filaments to the dorsal tract. At all particle concentrations the particles are transported in mucus (Beninger *et al.*, 1992).

In contrast to *Placopecten magellanicus*, particles are transported in *Mytilus edulis*, *Crassostrea virginica* and *Mya arenaria* in mucus strings in the ventral food groove, even at low food concentrations (Ward *et al.*, 1993a). Material was never found to be in suspension in the ventral food groove (Ward *et al.*, 1993a), as would occur if the hydromechanical theory were correct. In the dorsal ciliated tract the particles were carried in a low viscosity mucus slurry. Beninger *et al.* (1993) and Ward *et al.* (1993a) strongly support the idea that mucus is involved in the transport of particles on the frontal surface of the gill under normal feeding conditions. Ward *et al.* (1993a) concluded that mucociliary and hydromechanic mechanisms are not mutually exclusive, and that they occur simultaneously at different sites on the gill. Jørgensen (1993) did not consider that the work of Ward *et al.* (1993a) justifies concluding that mucus plays a rôle in normal feeding situations, since he found that the particles in stomach samples from *Mytilus edulis* were in a freely suspended state. Ward *et al.* (1993b) countered that particles had been shown to be ingested in mucus by five bivalve species (Beninger *et al.*, 1991), and that particles being freely suspended does not necessarily mean that mucus is absent. The transport of particles in the dorsal tracts of scallops and oysters occurs by hydromechanical means, but the particles are in a mucous medium.

Beninger *et al.* (1991) have confirmed that mucus is ingested with the food in five bivalve species (*Pecten maximus, Placopecten magellanicus, Chlamys varia, Mytilus edulis* and *Crassostrea virginica*). In *Crassostrea virginica* the mucus strings in the ventral groove are transported to the palps, where the mucus viscosity is reduced, and the particles are dispersed (Ward *et al.*, 1993b). The viscosity of the mucus may be altered by the mechanical action of the labial palps (Newell & Jordan, 1983), but selection probably takes place in the presence of mucus (Beninger *et al.*, 1993).

Pectinids are known to be inefficient at retaining small size classes of particles, 100% particle retention occurs at a size of 5-7μm (Palmer & Williams, 1980; Cranford & Grant, 1990), compared to, for example, *Mytilus edulis* which occurs at approximately 4μm (Møhlenberg & Riisgård, 1978). Jørgensen *et al.* (1984) suggested that pectinids have a higher size threshold for 100% particle retention due to the reduced latero-frontal cirri.

ENVIRONMENTAL FACTORS AFFECTING FEEDING

Flow rate

The rate of water flow affects bivalves in several fundamental ways; the most obvious of which are the transport of food and oxygen-rich water to the bivalve, and the removal of waste products. The effect of flow rate on the transport of food will be considered here. Flow rate controls feeding in two direct ways. Firstly, in conjunction with particle concentration, flow rate will control the particle flux; the number of particles per unit time impinging on the bivalve. The second consideration involves the physical inhibition of the feeding mechanism by high flow rates, for example, the ability of the cilia to move against the current, and the

creation of a pressure head (differential) which is too great for the cilial pump to act against.

The flow of water across the seabed also directly affects the supply of food to the benthos: the friction created by the movement of water over the seabed creates vertical fluxes of particles (Wildish & Kristmanson, 1984; Frechette & Bourget, 1985a; Wildish & Kristmanson, 1985; Frechette *et al.*, 1989; Frechette *et al.*, 1992; Wildish & Kristmanson, 1992), which are an important source of food for benthic fauna (Grant *et al.*, 1986a). Grant *et al.* (1986b) reported that 0.12-0.15 mg of chlorophyll *a* was resuspended per square metre every hour, illustrating the importance of this flux of material. The turbulent transfer of particles from the water above the benthic boundary layer is also enhanced by increased flow rates (Nowell & Jumars, 1984; Shimeta & Jumars, 1991; Wright *et al.*, 1992).

The water that moves over large beds of mytilid bivalves becomes depleted of seston (Wildish & Kristmanson, 1979; Wildish & Kristmanson, 1984; Frechette & Bourget, 1985b; Wildish & Kristmanson, 1985; Frechette & Lefaivre, 1990; Muschenheim & Newell, 1992), and the ambient flow rate has been shown to be a critical factor controlling growth and the population size (Wildish, 1977; Wildish & Peer, 1983; Wildish *et al.*, 1987). This is largely due to the effects of flow on vertical and horizontal transport of particles (Nowell & Jumars, 1984). The productivity of the horse mussel *Modiolus modiolus* in the Bay of Fundy was found to be positively correlated with ambient velocity, except at very high flow rates when zero productivity rates occurred (Wildish & Peer, 1983). The population response to flow rate has been shown to be very different from the individual response (Wildish & Kristmanson, 1992):

individual feeding was inhibited at much lower flow rates than would be predicted from the population data.

Scallop beds are generally not dense enough that large scale seston depletion would occur, but the ambient flow rates will affect the quantity and quality of available food. Physical inhibition of feeding and growth may also occur, as has been demonstrated in *Placopecten magellanicus* (Wildish *et al.*, 1987, 1992), *Argopecten irradians* (Kirby-Smith, 1972; Cahalan *et al.*, 1989; Eckman *et al.*, 1989) and *Mytilus edulis* (Wildish & Miyares, 1990) at flow rates between 3 and 10 cm per second. The results of Wildish *et al.* (1992) suggests that there is homeorheostatic control of feeding in *Placopecten magellanicus*, since the inhibition of feeding by high flow rate was increasingly delayed at higher food concentrations. The reduction of feeding was hypothesized to be the result of either the inhalant opening and valves shutting due to the creation of unfavourable pressure differentials between the inhalant and exhalant openings, or to some form of gill by-pass shunting mechanism (Wildish *et al.*, 1987; Beninger *et al.*, 1993). Recently, it has been shown that seston uptake rates of *Placopecten magellanicus* are reduced at high flow rates mainly by valve and mantle closure, which occurs to reduce the external pressure differences between the inhalant and exhalant openings. Concomitantly, the volumetric pumping and seston uptake rates are reduced (Wildish & Saulnier, in press 1993, cited in Wildish & Kristmanson 1992).

Particle concentration

The effect of particle concentration on feeding has been reviewed by Winter (1978), Bayne & Newell (1983), Griffiths & Griffiths (1987), and Bricelj & Shumway (1991).

As previously mentioned, the food concentration interacts with the flow velocity to control the particle flux. Cahalan *et al.* (1989) demonstrated that growth of *Argopecten irradians* was more dependent on food concentration, rather than the flow rate or particle flux. Wildish & Kristmanson (1992) have suggested that populations respond to seston flux, whereas individuals respond to the concentration and flow rate independently.

The effect of concentration on clearance rate and retention efficiency has been studied by many authors using many different species, and, perhaps more importantly, many different diets. Many of the studies performed used pure algal diets (e.g., Thompson & Bayne, 1974; Hildreth & Mallet, 1980; Riisgård & Randløv, 1981; Sprung & Rose, 1988; Riisgård, 1991), and although the trend now is to use natural assemblages of particles, they gave valuable initial insight into features of the feeding response. The variety of experimental methods and conditions used renders interspecific, and even intraspecific, comparisons very difficult to make. However, the feeding response does follow a general pattern: feeding is initiated above a low threshold concentration, after which clearance rates rapidly increase to a maximum. Few studies use particle concentrations which are low enough to detect this early phase of feeding (Winter, 1978; Hughes, 1980), but Griffiths (1980a) found that clearance rates of the mussel *Choromytilus meridionalis* declined to a plateau at approximately 0.35 cells μl^{-1}. Griffiths & King (1979) found that clearance rates increased rapidly above 1-2 cell μl^{-1}.

Above the concentration at which maximum clearance rates are attained, clearance rates gradually decrease with increasing concentration (Griffiths & Griffiths, 1987). The rate of decline varies between species, depending

upon the extent of pseudofaeces production (Foster-Smith, 1975b). Optimal ingestion rates can be maintained by three different ways: reduction of clearance rates, increased pseudofaecal production, or intermittent pumping. Pectinids have been shown to control ingestion rates by altering the pumping rate (Palmer & Williams, 1980; Kuenstner, 1988, working with *Argopecten irradians*), whereas *Mytilus edulis* maintains high clearance rates and regulates pseudofaeces production (Thompson & Bayne, 1974; Foster-Smith, 1975a, 1976). *Cerastoderma edule* was also originally thought to maintain ingestion rates by altering clearance rates (Foster-Smith, 1975a), but more recently this species has been shown to utilize pseudofaecal production to a greater extent than was previously realized (Iglesias *et al.*, 1992). *Mercenaria mercenaria* also controls ingestion primarily by altering the clearance rates (Bricelj & Malouf, 1984), as does the freshwater mussel *Dreissena polymorpha* (Sprung & Rose, 1988). The African infaunal estuarine bivalve *Solen cylindraceus* is an example of a bivalve which reduces the time spent filtering as the concentration of natural seston increases (de Villiers & Hodgson, 1993). It also exhibits the more common mechanisms of clearance rate reduction and alteration of pseudofaecal production, the relative importance of each depending on the seston concentration.

Further difficulties arise when comparing various authors' work due to the way in which the diet was expressed, which is usually in terms of the number of cells per millilitre. At the same concentrations, large algae will provide a greater ration than smaller algae (Griffiths & Griffiths, 1987). Expressing diets in terms of weight per ml, or volume per ml is more satisfactory. However it is now acknowledged that some measure of the diet quality (usually the organic matter content), should be included in the

diet descriptor (Bayne *et al.*, 1987, 1989; Navarro & Iglesias, 1992; Navarro *et al.*, 1992; Iglesias *et al.*, 1992).

Clearance rate and body weight

The weight exponent relating clearance rate to body weight for pectinid bivalves has been shown to vary between 0.58 and 0.94, with weight-standardized clearance rates (for a 1g animal) varying between 0.145 and 31 l h^{-1} (see Bricelj & Shumway, 1991, their tables 1 and 2). Most of the values recorded, except the value (0.94) recorded for *Chlamys hastata* by Meyhöfer (1985), fell within the range of those for bivalves reviewed by Winter (1978) and Bayne & Newell (1983). Clearance rates increase with increasing body weight, but weight-specific clearance rates (l h^{-1} g^{-1} dry body weight) decrease with increasing size.

In studies where a range of bivalve species have been examined by the same author, pectinid species have been shown to have high clearance rates or pumping rates when compared to other species of similar dry body weight. Meyhöfer (1985) found that *Chlamys hastata* had higher pumping rates than animals of comparable size of the infaunal species *Clinocardium nuttallii*, *Macoma nasuta*, and the intertidal epifaunal species *Mytilus californianus*. Likewise, Møhlenberg & Riisgård (1979) found that *Pecten furtivus* and *Aequipecten opercularis* had higher clearance rates than similarly sized animals of eleven other species, including *Mytilus edulis*, *Modiolus modiolus*, *Arctica islandica*, *Cardium edule*, and *Mya arenaria*. In contrast, an exception is the work of Riisgård (1988) who recorded clearance rates for *Argopecten irradians* which equalled those of the Atlantic ribbed mussel *Geukensia demissa*, but which were lower than those of *Crassostrea virginica*.

Retention efficiencies

Pectinids retain particles smaller than 7 μm less efficiently than other bivalve species (Table 1.1). Below the 7 μm threshold, the pattern of retention efficiency varies for different pectinid species, for example, Vahl (1972a; 1973) found that 50% particle retention efficiency occurred at 5 μm in *Aequipecten opercularis* but at 2 μm in *Chlamys islandica*. Most other bivalve species attain 100% particle retention at a particle size of 4 μm (Vahl, 1972b; Møhlenberg & Riisgård, 1978; Riisgård, 1988). Note that this does not mean that 100% of the particles are retained: it is usual to express retention efficiency relative to the most efficiently retained particle size class (see methodological section).

Table 1.1 The particle sizes (μm) at which 50% and 100% relative retention efficiencies occur in various pectinid species. Iso - *Isochrysis galbana* Mono - *Monoisochrysis lutherii* Tetra - *Tetraselmis suecica* Crypto - *Cryptomonas* sp. Dun - *Dunaliella marina.*

Species	Algal diet	50%	100%	Author
C.opercularis	Iso, Mono	5	7	Vahl 1972a
C.islandica	Natural	2	5	Vahl 1973
P.septemradius	Mono, Tetra &	4.5	5.5	Møhlenberg & Riisgård
P.opercularis	Dun	3	6.5	1978
A.irradians	Iso, Crypto	3	5	Riisgård 1988
P. magellanicus	Various	2.5	8.5	Cranford & Grant 1990

The effect of concentration and flow rate on retention efficiency is not fully understood. *Argopecten irradians concentricus* retains small particles (<3 μm) significantly more efficiently at high particle concentrations (6 mg wet weight l^{-1}), than at low concentrations (0.9 mg wet weight l^{-1}), which was attributed to the increased mucus production at higher concentrations (Palmer & Williams, 1980).

FACTORS AFFECTING INGESTION RATE

The quantity and quality of food

The quantity and quality of the food will interact to determine the response of the animal to the diet. It is therefore desirable to employ a descriptor of the diet that incorporates some measure of the quality as well as the quantity (Bayne *et al.*, 1987, 1989; Bayne, 1992; Navarro & Iglesias, 1992; Iglesias *et al.*, 1992; Navarro *et al.*, 1992). Particulate organic matter (P.O.M.) per mm^3 has been suggested by these authors, since the ultimate constraint on feeding is a volumetric one - gut volume.

Pseudofaecal production

The relative importance of the different mechanisms controlling ingestion rate will alter depending on both the diet quantity and quality (Navarro & Iglesias, 1992; Navarro *et al.*, 1992; de Villiers & Hodgson, 1993). In coastal waters with strong currents or water movement, a large proportion of the suspended material encountered by bivalves is likely to be of benthic origin. The resuspended material contains a variety of particles such as detritus, bacteria, diatoms and mineral particles (Zeitzschel, 1970; Parmenter *et al.*, 1983; Cranford & Grant, 1990), not all of which will have nutritional value. The ability to selectively ingest particles, which until the work of Kiørboe *et al.* (1980) was not thought to occur (Bernard, 1974; Foster-Smith, 1975c), counteracts the 'dilution' of P.O.M. by particulate inorganic matter (P.I.M.) (Widdows *et al.*, 1979). In *Mytilus edulis* the efficiency with which algae were ingested relative to the silt in the diet increased with increasing silt concentration (Kiørboe *et al.*, 1980). Conversely, in *Mercenaria mercenaria*, the percentage of algae lost in the pseudofaeces increased with increasing sediment concentration, but

only to a maximum of 18%, which suggests that sorting is efficient (Bricelj & Malouf, 1984). Kiørboe & Møhlenberg (1981) demonstrated pre-ingestive particle selection in ten species of bivalve, by comparing pseudofaecal chlorophyll to that in the available diet. Interestingly, Kiørboe & Møhlenberg (1981) showed that *Mytilus edulis* from two areas differing in ambient turbidity, showed different degrees of selection efficiency. *Aequipecten opercularis* was the fifth most efficient feeder, with a selection efficiency of 5.4, within an experimental range of 2.3-15.8. *Argopecten irradians* rejected only 25-35% of the algal cells filtered (Kuenstner, 1988) when offered bloom concentrations of 0.55-1.46 x 10^6 cells ml^{-1} (2.4-6.4 mg l^{-1}). The approximate threshold concentrations of pseudofaecal production seems to be lower when a pure algal diet is used (Table 1.2).

To illustrate the variability of estimates of the threshold concentration for pseudofaeces production within a species, *Mytilus edulis* has been shown by different studies to initiate production at <2mg l^{-1} (Tsuchiya, 1980) and at 5 mg l^{-1} (Widdows *et al.*, 1979), when fed natural seston (see Griffiths & Griffiths, 1987, their table 1). The mussels *Aulacomya ater* (Griffiths & King, 1979) and *Choromytilus meridionalis* (Griffiths, 1980a) both had much higher threshold values (>6 and 5.6-6.7mg l^{-1} respectively).

Table 1.2 The approximate pseudofaecal threshold level in pectinid species

Author	Species	Diet	Threshold	
			mg l^{-1}	Nos. ml^{-1}
Kiørboe & Møhlenberg, 1981	*A. opercularis*	Silt & *Phaeodactylum*	20-30mg	
MacDonald & Thompson, 1986	*P. magellanicus*	Natural seston	NONE at 5-10mg	
Kuenstner, 1988	*A.irradians*	*Aureococcus*	2.4-6.4 mg	0.55-1.46x10^6

Absorption efficiency

In bivalves the absorption efficiency is often positively related to the diet quality (mg P.O.M. l^{-1}, or mg P.O.M. mm^{-3}) (Bayne *et al.*, 1987, 1989; Navarro *et al.*, 1991; Bayne, 1992; Navarro & Iglesias, 1992; Iglesias *et al.*, 1992; Navarro *et al.*, 1992). Some authors have reported it to be inversely related to ration, although quality was not necessarily measured (Foster-Smith, 1975a; Griffiths & King, 1979; Griffiths, 1980b; Møhlenberg & Kiørboe, 1981; Bricelj & Malouf, 1984; Hawkins & Bayne, 1984).

The absorption efficiency is controlled by two main features of digestion: the digestive investment (the enzymes produced, energy lost with the faeces) and the gut passage time (for references see Bayne, 1992; Navarro & Iglesias, 1992; Chapter 4). At a constant rate of ingestion the gut passage time may additionally be altered by changes in gut capacity (volume). In the above examples, where absorption efficiency is inversely related to ration, absorption efficiency is probably changing as gut passage time alters. As ingestion increases, the throughput of material through the gut increases with a concurrent decrease in absorption efficiency, since the time available for absorption of organic material and the reabsorption of mucus, digestive enzymes and undigested material from intracellular digestion (Hawkins & Bayne, 1984, 1985; Hawkins *et al.*, 1990) will decrease. Maintaining ingestion rates but increasing the gut capacity will result in a greater residency time per unit of material ingested, and therefore an increase in absorption efficiency.

Most of the above studies used the faeces to calculate absorption efficiency. If pseudofaeces are produced at the same time, however, the principles upon which the Conover (1966) method was developed are violated; that

is, that no pre-ingestive selection occurs (Bricelj & Malouf, 1984; Widdows, 1985a). Iglesias *et al.* (1992) showed that apparent absorption efficiencies were usually smaller than, or equal to, the true absorption efficiencies, depending upon whether pseudofaeces were produced. The largest observed difference occurred when the cockles (*Cerastoderma edule*) were fed 5.79 $mm^3\ l^{-1}$ of pure silt, when apparent absorption efficiencies were 0.286 and true absorption efficiencies were 0.517. Generally, apparent absorption efficiencies deviated the most from true values when the cockles were fed lower quality diets, understandably, since more pseudofaeces are produced.

RESPONSE TO LONG-TERM EXPOSURE TO RESUSPENDED SEDIMENT

Over a two week period the acclimation response of *Mytilus edulis* to long-term exposure to silt in the diet included the adaptation of the absorption efficiencies from negative values to as high as 50-60%, increased ingestion rates, and a possible increase in gut capacity (Bayne *et al.*, 1987). Cranford & Grant (1990) recorded an erratic response in the net (true) absorption efficiency of *Placopecten magellanicus* on exposure to various algal and detrital diets. When fed resuspended sediment, the absorption efficiency declined from an initial value of 40% on day 0, to negative values in the second and third weeks. In the fourth week the absorption efficiency was again positive (approximately 10%), but was negative in the fifth week, after which the absorption efficiency increased to approximately 10%, and remained positive until the end of the experimental period (eight weeks). Grant & Cranford (1989) found that diets of resuspended sediment and aged or fresh kelp did not support tissue growth in *Placopecten magellanicus*, and the condition index declined over the eight week experimental period.

During the exposure of the soft-shell clam *Mya arenaria* to resuspended sediment for 35 days, oxygen consumption declined and ammonia excretion rate increased (the resultant oxygen to nitrogen ratios decreased from 27 to 14). The clams showed no change in body weight during the experimental period (Grant & Thorpe, 1991). The oxygen consumption rate of the cockle *Cerastoderma edule* also declined significantly over a ten day acclimation period, with a concomitant increase in scope for growth when fed all but one diet (Navarro *et al.*, 1992). Other acclimation responses included, at medium particle concentrations, slightly decreased clearance rates, and slightly increased absorption efficiencies. This response combined to produce no overall change in absorption rate. At low and high particle concentrations very little change in clearance rate or absorption efficiency occurred. If all three diets are considered together, there were significant changes in clearance rates, but not in absorption efficiencies, after ten days of acclimation. The acclimation of oxygen consumption, clearance rates and absorption efficiency differed between particle concentrations.

The surf clam, *Spisula solidissima* also showed a variable acclimation response to clay in the diet, that depended on clay concentration (Robinson *et al.*, 1984). After 21 days of feeding on diets containing 100 and 500 mg of clay per litre, the amount of chlorophyll ingested and the digestion efficiency increased. The animals were unable to acclimate to 1000mg l^{-1} of clay in the diet.

The growth rate of *Mercenaria mercenaria* was unaffected by resuspended sediment concentrations up to 25 mg l^{-1}, but the growth rates and the condition of the clams were reduced at 44 mg l^{-1} (Bricelj *et al.*, 1984). Conversely, suspended sediment in the diet has been shown to increase

the growth rates of *Mytilus edulis* (Winter, 1975; Kiørboe *et al.*, 1981) and *Spisula subtruncata* (Møhlenberg & Kiørboe, 1981).

In addition to utilizing resuspended sediments, some bivalves can also maintain a positive net energy balance when fed macroalgal or vascular plant detritus. The bay scallop *Argopecten irradians* was found to grow slowly, but continually, when fed fresh detritus derived from the vascular plant *Spartina alterniflora* (Kirby-Smith, 1976). The growth rate was approximately a third of that obtained using phytoplankton cultured from natural populations. No growth occurred when the diet consisted of *Spartina alterniflora* aged for six months. Kirby-Smith (1976) considered that the differences in growth rates between scallops fed different diets were best explained by differences in food quality rather than quantity. The ratio of carbon to nitrogen (and presumably the protein content) did not appear to be a good indicator of the nutritional value of a food for scallops.

Stuart (1982) found that the scope for growth of the ribbed mussel *Aulacomya ater* increased with increasing ration when fed kelp detritus. Negative scope for growth values occurred at the lowest rations used (0, 0.5mg l^{-1}, and 1.0mg l^{-1}) for the two smallest size classes of animals tested. The bacterial microflora on the surface of the resuspended sediment or detritus is also an important source of food (Stuart *et al.*, 1982a, 1982b; Levinton, 1989; Rice & Rhoads, 1989). Stuart *et al.* (1982a) found that 67-70% of bacterial cultures isolated from kelp were absorbed by *Aulacomya ater*. Bacteria are only likely to be an energetically significant source of nutrition to bivalves that live in or near kelp beds, eutrophic estuaries or marshes (Wright *et al.*, 1982; Langdon & Newell, 1990), and will be less important in open ocean areas. Lucas *et al.* (1987) estimated that *Mytilus*

edulis from estuaries and coastal sites would primarily utilize phytoplankton as a food source, but free-living bacteria would also contribute to the carbon and nitrogen budgets, to a greater extent in estuarine populations. The bivalves *Donax serra* and *Mactra lilacea* do not utilize available bacterioplankton efficiently, due to their poor retention of particles below 1.4 μm (Matthews *et al.*, 1989). Bacteria may play a more significant rôle in providing the nitrogen, rather than the carbon, required by suspension feeders (Newell & Field, 1983; Seiderer *et al.*, 1984; Stuart & Klumpp, 1984; Seiderer & Newell, 1985).

Oxygen consumption and ammonia excretion rates

Rates of oxygen consumption have been evaluated for several pectinid species (Bricelj & Shumway, 1991 their tables 3 and 5). Values determined have varied between 0.182 (Vahl, 1972a for *A. opercularis*) and 0.425 ml O_2 g^{-1} h^{-1} (Bricelj, 1987 for *Argopecten irradians irradians*). Depressed rates of oxygen consumption due to nutritive stress have been observed in *Mytilus edulis* (Bayne, 1973b), and in *Placopecten magellanicus* (Grant & Cranford, 1991). Few experiments that have measured ammonia excretion rates in pectinids have been published. Barber & Blake (1985) studying *Argopecten irradians concentricus* recorded values that varied seasonally between 72 and 140 μg N g^{-1} dry body weight h^{-1} (5.1-10.0 μM N g^{-1} dry body weight h^{-1}).

The ratio of atomic equivalents of oxygen respired to nitrogen excreted (the O:N ratio) is a good 'whole-animal' indicator of stress and nutritional condition (Bayne & Thompson, 1970; Bayne, 1973a, 1975; Widdows, 1985a). The O:N ratio has a theoretical minimum of 9.3 (Mayzaud, 1973; Bayne, 1973a), but this value was calculated using mammalian protein and

therefore may not be strictly applicable to planktonic proteins (Mayzaud, 1973). Values may go below the theoretical minimum if the ammonia nitrogen is utilized in any other synthetic pathway, or if the amino acid carbon skeletons are not completely oxidized (Bayne, 1975). Barber & Blake (1985) recorded seasonal O:N ratios that varied between about 7 and 22. Other studies on pectinids have included that of Volckaert (1988), who found that starved *Placopecten magellanicus* juveniles fed on algae had O:N ratios of 31.2, whereas starved individuals had values of 12.7. Thermally stressed *Placopecten magellanicus* had O:N ratios of 8.9 (Grant & Cranford, in preparation, cited in Grant & Cranford, 1991). In *Mytilus edulis* O:N ratios of above 50 indicate a healthy mussel, values below 30 generally indicates a stressed animal (Widdows, 1985a). Bayne (1973a) recorded O:N ratios in *Mytilus edulis* greater than 300.

METHODOLOGICAL COMMENTS

Estimation of clearance rates

Clearance rates are frequently measured using flow-through feeding chambers, an indirect method which avoids any problems associated with the build-up of metabolites. Direct and indirect methods are compared in several reviews (Owen, 1974a; Bayne *et al.*, 1976a; Hildreth, 1976; Winter, 1978; Famme *et al.*, 1986). Direct methods involve the isolation and measurement of the exhalant water flow. Dyes are sometimes added to the inhalant water to aid identification of the exhalant stream. The disadvantages of direct methods are that the isolation of the exhalant water stream (e.g. using rubber aprons, partitions, surgery or at the very least immobilization of the animal) often disturbs the animals. Either back-pressure or siphoning may occur, which will result in the underestimation and overestimation of the pumping rate respectively

(Hildreth, 1976; Møhlenberg & Riisgård, 1979; Famme *et al.*, 1986). The use of thermister flow meters may overcome this problem (Harris, 1990) but they are difficult to calibrate and use quantitatively. Direct methods measure the pumping or ventilation rate; that is, the actual volume of water passing through the animal. Indirect methods measure the removal of particles from suspension in static or flow-through systems. Indirect methods estimate pumping rates indirectly as filtration or clearance rates. Filtration rates are defined as the volume of water cleared of particles per unit time (usually litres per hour) and therefore are only equal to pumping rates if 100% retention of particles occurs. The major disadvantage of indirect methods is that the assumptions on which they are based are not always fulfilled, most importantly that the pumping rate remains constant throughout the experiment and that a constant percentage of particles is filtered (Coughlan, 1969; Winter, 1978). However, the animals are usually much less disturbed than when used in direct methods.

It is important when using indirect methods that water in the feeding chamber does not recirculate; water that has passed through the animal once must not be reprocessed. If re-circulation occurs then the results will be under-estimates of the true clearance rates (Hildreth & Crisp, 1976; Riisgård, 1977). The feeding chambers used in any experiment to estimate clearance rate must be designed to minimize re-circulation of water within them. Feeding chamber geometry can be checked for the occurrence of re-circulation by observing the course of dyes or milk added at the inflow (Crisp, 1956; Vahl, 1972a) or by assessing the deviation from the line of equality when recording the relationship between flow and clearance rate (Riisgård, 1977). If, at low flow rates, the clearance rates deviate significantly from the equality line then the feeding chambers are not

suitable for the animals under study, either all the water entering the chamber is not available to the animal, or re-circulation is occurring.

The flow rate of water is also important - if it is too slow re-circulation will occur. Minimum flow rates to use can be determined by plotting clearance rate against flow rate and determining when the resultant line departs from the equality line (Riisgård, 1977). This indicates the minimum flow rate to use in order to avoid re-circulation in that particular flow-through set-up.

The equation used to calculate clearance rate depends upon whether a concentration gradient develops within the chamber, which will depend upon whether the chamber is stirred throughout the experiment. If it is stirred, the concentration of particles around the animal will be similar to that at the outflow and equation (1) is used:

$$\text{Clearance rate} = F \times ((Ci - Co)/Co) \qquad 1$$

where F is flow rate ($l\ h^{-1}$), Ci and Co are the particle concentrations at the inflow and outflow respectively (Hildreth & Crisp, 1976). If the chamber is not stirred a concentration gradient develops and the equation below should be used (e.g. Thompson & Bayne, 1972; Bayne *et al.*, 1976a, 1976b):

$$\text{Clearance rate} = F \times ((Ci - Co)/Ci) \qquad 2$$

Indirect methods usually yield higher results than direct methods (Hildreth, 1976; Famme *et al.*, 1986), probably because of the disadvantages of the direct method mentioned earlier (i.e., mechanical disturbance, back-pressure and siphoning effects).

Estimation of retention efficiency

The ability to retain particles of different sizes is usually expressed as the retention efficiency (3) or the relative retention efficiency (4):

$$\text{retention efficiency} = 1 - Co/Ci \qquad 3$$

$$\text{relative retention efficiency} = \frac{(1 - Co / Ci)}{\text{max. retention efficiency}} \qquad 4$$

where Ci and Co are the concentrations of particles of size x in the inflow and outflow water respectively.

The maximum retention efficiency is usually found at particle sizes of 8 μm or greater. Retention efficiency and relative retention efficiency are both independent of the concentrations of other particles in the food. Some authors (e.g., Bayne *et al.*, 1976b; Wilson, 1980; Lopez & Cheng, 1982; Harris, 1990) have also used Jacobs' electivity index (D) to investigate the selection of different particle sizes. Jacobs (1974) altered Ivlev's original electivity index E (Ivlev, 1961), because E altered with not only the degree of selection of a food type but also with the relative abundance of a food type in the environment. Therefore if the change in selection of a particular food type or size with changing overall concentration of that food is required, Ivlev's index would be meaningless. Jacobs altered Ivlev's index so that numerically it is independent of relative abundance, but is dependent on the proportional concentration of particles of a certain food type or size in the environment (the available ration) and the ingested ration.

$$D = \frac{r - p}{r + p - 2rp} \qquad 5$$

where r is the proportion of particles of size x in the ingested ration and p is the proportion of particles of size x in the available ration.

r and p have been defined by some workers who have used Jacob's electivity index as being the concentration of particles of size x in the inflow minus the outflow, and that in the inflow respectively (Bayne *et al.*, 1976b; Wilson, 1980; Harris, 1990). However, this is incorrect, for the formula should be based on proportions.

Use of the Coulter Counter

Many experiments estimate clearance rates and selection of particles by measuring the depletion of algal suspensions using a Coulter Counter or a Coulter Counter Multisizer. Whilst the Coulter Counter and the Coulter Counter Multisizer are very convenient analysis tools, several problems with their use do occur.

An experiment comparing retention efficiencies, calculated using the Coulter Counter, with those based on direct bacterial counts showed that Coulter Counters overestimate retention efficiencies of small particles of 2 μm and less (Jørgensen *et al.*, 1984). This has been attributed to interference by conductive colloidal particles in sea water and electrical noise at the lower limit of resolution of the particle counter (Jørgensen *et al.*, 1984).

Coulter Counters measure the equivalent spherical diameters (E.S.Ds) of particles rather than their actual dimensions. When a particle passes through the tube aperture of the Coulter Counter, it disturbs the electronic field that occurs at the aperture (Sheldon & Parsons, 1967). The level of disturbance caused by the particle is related to that caused by a sphere of diameter x. The particle is then given an E.S.D. of that sphere. To keep the E.S.Ds as close to the actual dimensions of particles used in feeding

experiments as possible it is desirable to use algal species that are spherical, or nearly so.

AIMS

The overall aim of this study was to establish what the pectinid species *Pecten maximus* and *Aequipecten opercularis* feed on, the origin of the diet, and the effect of suspended bottom material on the feeding behaviour. The potential contribution of this flux of bottom material to the energy balance of *P. maximus* and *A. opercularis* was also considered.

Chapter 2 investigates the effect of concentration of food and flow rate on the amount of material filtered, and the particles sizes removed from suspension. The aim of this chapter was to determine which sizes of naturally occurring particles the pectinids are able to utilize, and the quantity of suspended material that is filtered. This information was obtained using pure algal diets, which although less desirable than using more natural particle assemblages, gave results which are more comparable to other work.

In Chapter 3 the diatoms present in the gut contents of the pectinids were used as biological markers to assess the origin of the diet. Diatoms were used as they are not digested rapidly due to their silicon frustules. The aims of this chapter were to determine if there was any difference in the origin of the diets of *P. maximus* and *A. opercularis*, and whether reliance on a particular dietary source changed seasonally. A further aim was to determine the actual amount and quality of food available to *P. maximus* and *A. opercularis* seasonally, by sampling the sediment and the water in the benthic boundary layer, immediately above the seabed.

Chapter 4 aimed to determine how the presence of sediment in the diet would affect the short-term feeding behaviour, and whether *P. maximus* and *A. opercularis* regulate ingestion by pre-ingestive selection and pseudofaecal production. A long-term exposure experiment was carried out to determine whether the two species could maintain a net positive energy balance when feeding on sediment. The physiological approach used was one which integrates the overall response to the exposure to sediment, particularly the scope for growth and the oxygen to nitrogen ratio. A further consideration was whether there were any physiological and behavioural differences between *P. maximus* and *A. opercularis* which may influence their distributions on different sediment (seabed) types.

Finally, in the general discussion select topics are considered. The methodological difficulties encountered are reviewed initially, after which the feeding behaviours and physiologies of *P. maximus* and *A. opercularis* are compared and contrasted. Hydrographic features, and their possible influence on the supply of food to the benthic community, are then considered, with special reference to the Irish Sea. Lastly, rate limiting features of the bivalve feeding and digestive system are discussed with regard to their overall influence on ingestion rate, and suggestions for further work are made.

CHAPTER 2. THE EFFECT OF FLOW RATE AND PARTICLE CONCENTRATION ON CLEARANCE RATE AND PARTICLE SELECTION

INTRODUCTION

The feeding physiology of pectinids has been studied with regard to the effect of particle concentration on clearance rate (Møhlenberg & Riisgård, 1979; Palmer, 1980; Meyhöfer, 1985; Kuenstner, 1988; Riisgård, 1988; Cahalan *et al.*, 1989) and particle retention efficiency (Palmer & Williams, 1980; Barillé *et al.*, 1993). Cahalan *et al.* (1989) studied the interactive effect of flow and concentration on the feeding and growth of *Argopecten irradians*, but most studies only alter one variable at a time. The feeding and growth of pectinids has been shown to be affected by flow rate (Kirby-Smith, 1972; Wildish *et al.*, 1987; Eckman *et al.*, 1989; Wildish *et al.*, 1992; Wildish & Saulnier, 1992), but the effect of flow on particle retention has not been established. Most work on bivalve feeding responses has been performed on mytilid species (see reviews by Winter, 1978; Bayne & Newell, 1983; Griffiths & Griffiths, 1987). Pectinids generally have high clearance rates in comparison to other bivalve species (Møhlenberg & Riisgård, 1979; Riisgård, 1988), but retain small particle size classes poorly (Vahl, 1972a, 1973; Møhlenberg & Riisgård, 1978; Palmer & Williams, 1980; Riisgård, 1988).

Work on European pectinid species has concentrated on the retention efficiencies of *Chlamys islandica* (Vahl, 1973) and *A. opercularis* (Vahl, 1972a, 1980a; Møhlenberg & Riisgård, 1978), and the effect of particle concentration on the feeding and growth of *A. opercularis* (McLusky, 1973; Richardson *et al.*, 1984). Wallace & Reinsnes (1985) and Wilson (1987) also

studied the effects of various environmental parameters on the growth of *Chlamys islandica* and *A. opercularis* respectively.

In the Irish Sea *P. maximus* and *A. opercularis* overlap in their broadscale distributions, but may occur locally in mixed or single species grounds. *P. maximus* live in shallow recesses in the seabed whereas *A. opercularis* sit upon it. *P. maximus* do not generally inhabit areas where the sediment is composed of a high proportion of fine material. The behavioural and ecological differences between the species may result in them exploiting the seston within the benthic boundary layer differently. This chapter examines the effect of flow and particle concentration on the clearance rate and particle size selection of *P. maximus* and *A. opercularis*. Clearance rates and particle size selection were estimated by monitoring changes in particle concentration using a Coulter Counter Multisizer. Clearance rates were measured using flow-through feeding chambers, a frequently used indirect method which avoids any problems with the build-up of metabolites (see Chapter 1 for review). A pure algal diet was used, which although less desirable than using natural seston, is more comparable with other previous work.

The specific aims were to determine whether the two species exhibited any differences in clearance rates and particle selection efficiency, and the effect that altering particle concentration and water flow rate would have on these responses.

MATERIALS AND METHODS

Algal culture

Master cultures of *Rhinomonas reticulata* (strain no. CCAP 995/2) *Isochrysis galbana* (strain no. unknown) and *Monoisochrysis lutherii* (strain no. unknown) were obtained from the Culture Collection of Algae and Protozoa, Dunstaffnage Marine Research Laboratory, Oban. Master-cultures were kept under natural light conditions and at seasonal room temperature (10-20°C). The algal species were batch cultured in Erhlenmeyer flasks using Walne's media (Appendix 1). Aseptic techniques were used to inoculate 500 ml or 1 litre starter cultures from the master-cultures. The seawater was filtered to 0.2µm and autoclaved in the flasks (20 minutes at 15lb/sq. in.). Cotton wool plugs were used to prevent contaminants from entering the flasks.

The flasks were vigorously aerated with polymer wool filtered air under constant illumination (7.5 µmol photons m^{-2} sec^{-1}) at 15°C (Dickey-Collas, 1991). After 4-5 days the starter cultures were used to inoculate a succession of larger flasks to a maximum of 20l. When possible the algae was cropped in its exponential stage of growth (4-7 days after inoculation). However, due to variable demands upon the algae, this was not always possible. When a single flask of each species was being cultured the algal cell numbers were monitored using a Multisizer Coulter Counter with a 70 µm orifice tube.

Use of the Coulter Counter Multisizer

Whilst the Coulter Counter is a very convenient tool for estimating clearance rates and particle size selection, it has some limitations which

should be recognised (see Chapter 1 for review). I discovered a further problem specifically relating to the Coulter Counter Multisizer, which does not appear to have been previously recognised: the sampling stand counts particles faster than the Multisizer can channelize them. The percentage of particles counted that are channelized changes with sample particle concentration. It was found that there was a linear relationship between the number channelized and the particle concentration.

$$N = -3314.6 + 1.3542\Sigma_{max} \qquad r^2 = 0.980 \qquad n=60 \qquad 1$$

This relationship was calculated using various combinations of sea water, *Rhinomonas reticulata* and sediment.

The actual number of particles in channel i counted by the sampling stand is therefore

$$Ni \times (\underline{N}/\Sigma_{max}) \qquad 2$$

where Σ_{max} is the total number of particles channelized (i.e., Σ when the cursors are furthest apart), $\underline{N}$ is the total number of particles counted by the sampling stand, and Ni is the number of particles in channel i.

It was therefore necessary to correct the data obtained in these experiments. Fortunately the relationship between $\underline{N}$ and Σ_{max} was a strong one. $\underline{N}$ was calculated from Σ_{max} using equation (1), and all the channel data multiplied by equation (2). Below a concentration of 10,000 particles ml^{-1} virtually 100% channelization occurred and no correction was necessary.

This problem was not discovered until after the practical work had been completed, when it had been thought that $\underline{N}$ need not be recorded (the Coulter Counter manual defines Σ as 'Σ represents the total number of particles counted between the cursor limits'). If all the sample concentrations for the feeding experiments were the same then no correction would be required, however, particle concentrations varied widely and the action of bivalve feeding itself reduced concentrations to much lower than the control levels. Thus very different percentages of the particles counted by the sampling stand would be channelized which would have important repercussions in the calculation of clearance rate, retention efficiency and Jacob's electivity index, D.

Clearance rates and retention efficiency

Juvenile *P. maximus* and *A. opercularis* were collected from pearl nets on a long line system in Bay Fine, Isle of Man. The animals were maintained in the laboratory in a constant temperature room at 12 ± 2°C for a minimum of one week before use. The animals were fed on the naturally occurring particles in the seawater (which was coarsely filtered through a sand filter) supplemented by three algal species: *Rhinomonas reticulata, Isochrysis galbana* and *Monoisochrysis lutherii.*

For experimental purposes the animals were placed in 1l plastic feeding chambers supplied with seawater from a mixing chamber. The inlet tubes were directed towards the bottom of the chambers, to break the force of the flow. In order to help prevent re-circulation of water within the feeding chamber (which would under-estimate the clearance rate, Hildreth & Crisp, 1976; Riisgård, 1977) a baffle was placed across the surface of the water. Re-circulation of water was assessed by introducing milk into the inflowing

water with a pipette, and proved to be negligible. A peristaltic pump was used to deliver various diets at a constant rate to the mixing chamber. Vigorous aeration ensured an homogenous distribution of the diet within the mixing chamber and hence to the feeding chambers. Experimental animals were placed in the feeding chambers the evening prior to the start of the experiment. This helped to reduce mechanical disturbance of the pectinids.

The effect of flow rate on feeding and retention efficiency

Three animals of each species were placed in individual feeding chambers. A seventh chamber (containing an empty shell modelled to the shape of a feeding pectinid) acted as a control. The animals were fed on the naturally occurring particles in the seawater system plus the alga *Rhinomonas reticulata* at a concentration of 8 cells μl^{-1}, a concentration which has resulted in maximum clearance rates with other bivalves (Harris, 1990). The mean temperature of the constant temperature room during the experiment was 7.5°C (± 1.0 SD).

Animals were left for at least forty minutes to equilibriate to experimental conditions. Clearance rates were measured at flow rates between 0.3 and 30.5 l h^{-1} . Eight repeat measurements were made at 3, 12 and 24 l h^{-1} to assess the effect of flow rate on particle retention efficiency as well as on clearance rate. Duplicate timed water samples were made at each repeated measurement to record the flow rate.

The effect of algal concentration on clearance rate and retention efficiency

The flow of water through the feeding chamber was kept above 200 ml $minute^{-1}$ so that clearance rate would be independent of flow. Six animals

were used in the apparatus at any one time, six animals from each of two size groups of each species were tested. Two further chambers (containing empty shells of the appropriate species modelled like feeding pectinids) acted as controls.

The animals were fed on naturally occurring particles in the sea water system supplemented with equal ratios by number of *Rhinomonas*, *Isochrysis* and *Monoisochrysis*. These algal species were chosen because of their near spherical shapes, so that the Coulter Counter would record their sizes as accurately as possible. The species chosen provided a range of particle sizes from 3 to 10 μm.

Animals were left to equilibriate to the algal concentration for at least forty minutes. Four repeat measurements of clearance rate were made at approximately 5, 9, 13, 15, 17, 21 and 23 cells μl^{-1}. Algal concentrations actually varied between 0.7 and 30.5 cells μl^{-1}. Eight repeat measurements of clearance rate and retention efficiency were made at 2, 7, 11, 19 and 25 cells μl^{-1}. Duplicate timed samples of the outflow water were taken at each repeat measurement to record flow rate.

A Coulter Counter Multisizer was used to determine the concentrations of particles in the samples, and the numbers of particles in each of 32 size classes from 1.4 to 34.4 μm were recorded. For the flow rate experiments five counts of 0.5 mls were made, from which it was decided that further samples need only be counted in triplicate. Therefore, for further experiments three 0.5 ml counts were made. In all experiments a 70 μm aperture tube was used.

Clearance rates

Clearance rates were calculated using equation (3):

$$\text{Clearance rate } (l\ h^{-1}) = F\ (Ci\text{-}Co/Ci) \qquad 3$$

where F is the flow rate ($l\ h^{-1}$), Ci is the concentration of particles in the inflowing water (particles ml^{-1}) and Co is the concentration of particles in the outflowing water (particles ml^{-1}).

Retention efficiencies

The electivity indices of *A. opercularis* and *P. maximus* for different particle size classes were calculated using equation (4), produced by Ivlev (1961) and modified by Jacobs (1974):

$$D = \frac{r - p}{r + p - 2rp} \qquad 4$$

The electivity index was considered to be more useful than the retention efficiency since D takes into account the selection of a particle size class relative to what is available in the whole ration.

At the end of all the experiments the heights, lengths and dry weights of the animals used were determined. Heights and lengths were measured to the nearest mm using vernier calipers. Dry weights were recorded to the nearest 0.01g after drying the animal bodies at 103°C for 24 hours.

Statistical analysis

The statistical analysis of electivity indices, including Jacobs', is considered to be unacceptable (Lopez & Cheng, 1982). The electivity index was therefore analysed indirectly; it was used to indicate at which particle size classes greatest selection was occurring, and then those size classes were analysed. A second method of analysis was also attempted, a comparison of the relative extent of positive and negative particle selection over the whole size range was made by summing the values of D for each size class.

The data were checked for normality using 'Nscores' (a Minitab approximation of the powerful Shapiro-Wilk normality test) and for homogeneity (homoscedascicity) of variances by examining the fitted values and residuals graphically after an initial analysis of variance, or by using the F_{max} test (Sokal & Rohlf, 1981). If the data were not normal and/or the variances were not homogenous the data were transformed. The data were often initially coded by adding one, two or three, to remove values less than one (Sokal & Rohlf, 1981). Analysis of covariance (ANCOVA) was used to standardize the results to allow for initial variations in factors such as body weight or control particle concentration, which may significantly affect the results.

Bonferroni Least Significant Difference tests (Morrison, 1976) were used to find where significant differences occurred between the different levels within a factor which was found to be significant by ANOVA or ANCOVA. The Bonferroni L.S.D. test is an *a priori* test whose statistical significance is adjusted to allow for the total number of comparisons being made between levels of a significant factor. This is to reduce the probability of committing a Type I error (rejecting a hypothesis when it is in fact correct), since the

probability of committing a Type I error increases rapidly with the number of comparisons being made (Zar, 1984). This "experimentwise error rate" (Morrison, 1976; Zar, 1984) was set at a probability level of 0.05.

Flow rate experiment

An analysis of covariance was performed on the weight-standardized clearance rates (l h^{-1} g^{-1} dry body weight), using the control particle concentration as the covariate. The data were transformed by adding one to the data (to remove values less than one) and then applying a Box-Cox transformation ($Y=(Y^{\lambda}-1)/\lambda$, Sokal & Rohlf, 1981) with λ optimized at -0.5. The particle size class at which maximum selection occurred and the sum of values of D were analysed by ANCOVA, using body weight and control particle concentration as covariates. Bonferroni's Least Significant Differences (L.S.Ds) were then calculated if a factor proved to be significant. The summed values of D were transformed by adding two and then applying a Box-Cox transformation with λ optimized at 0.1.

Concentration experiment

An analysis of variance was carried out on weight-standardized clearance rates. The weight-standardized clearance rates were transformed using the logarithm of Y+1. The particle size class at which maximum selection occurred (transformed by $Y^{2)}$ and the sum of values of D (transformed using the Box-Cox transformation with λ optimized at 0.1, on data coded by adding three) were analysed by ANCOVA, using body weight as a covariate. Bonferroni's L.S.Ds were calculated if a factor proved to be significant.

RESULTS

The effect of flow rate on clearance rate

At low flow rates clearance rates for *P. maximus* and *A. opercularis* are strongly dependent on flow rate and do not deviate markedly from the filtration rate = flow rate line (Fig. 2.1). At flow rates above 8-10 l h^{-1} (133-166 ml min^{-1}) clearance rate shows great variability, but usually reaches a plateau and is independent of flow rate. This indicates that no re-circulation of exhaled water is occurring, therefore flow rates greater than 8 l h^{-1} were used in all further experiments. At high flow rates the range of clearance rates recorded also increased. Figure 2.2 shows mean clearance rate at flow rates of 3, 12 and 24 l h^{-1} for each animal. Clearance rate increases with increasing flow rate. When calculated as weight-standardized clearance rates (l h^{-1} g^{-1} dry body weight) the smallest animals have the highest weight-standardized clearance rates, however one *Pecten* (dry body weight 1.23g) has low readings (Fig. 2.3).

Analysis of covariance on Box-Cox transformed data (λ=-0.5) (Table 2.1) confirmed that flow significantly affects weight-standardized clearance rate ($F_{0.05}$, 2, 205 = 50.50, $P < 0.001$). Bonferroni's Least Significant Difference tests showed that clearance rates at 3 l h^{-1} were significantly smaller than those at 12 and 24 l h^{-1}, but that clearance rates at 12 l h^{-1} did not differ from those at 24 l h^{-1}. Clearance rates differed significantly between species ($F_{0.05}$, 1, 205 = 37.97, $P < 0.001$), with *P. maximus* exhibiting lower clearance rates.

Table 2.1 Analysis of covariance comparing the effect of flow rate on the transformed (Box-Cox transformation λ= -0.5 on Y+1) weight-standardized clearance rates of *A. opercularis* and *P. maximus*, using the control concentration as a covariate. Pairwise comparisons of levels within factors which were significant were made by calculating Bonferroni's Least Significant Differences (using an experimentwise error rate (EER) of 0.05). * and ** indicate significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	MS	$F_{0.05}$	P	
Covariate (control concentration)	1	0.283	0.014	0.014	0.44	0.508	
Flow rate	2	3.214	3.193	1.560	50.50	< 0.001	**
Species	1	1.202	1.200	1.200	37.97	< 0.001	**
Flow & species	2	0.035	0.035	0.018	0.56	0.572	
Error	205	6.480	6.480	0.032			
Total	211	11.214					

Bonferroni Least Significant Differences. S and NS signify statistically significant (at P = 0.05) and non-significant differences respectively, between the indicated levels of the factor being tested. 3, 12 and 24 represent flow rates in l h^{-1}

Comparison	N1	N2	MS Error	Critical F	L.S.D.	Significance
			Flow rates			
3 vs. 12	71	70	0.032	5.83	0.072	S
3 vs. 24	71	71	0.032	5.83	0.072	S
12 vs. 24	70	71	0.032	5.83	0.072	NS

The effect of flow rate on particle size selection

Jacobs' electivity index D was plotted against particle size for each individual of the two species at each flow rate (Fig. 2.4). There was much variation between individuals but generally, with increasing flow rate, D peaked at a larger size class and the peak was higher. Analysis of covariance on the coded (Y+2) and transformed (Box-Cox transformation with λ=0.1) summed values of D (Table 2.2) showed that selection was significantly greater in *P. maximus* than *A. opercularis* ($F_{0.05}$, 1, 133 = 4.19, P = 0.043) and was significantly affected by flow rate ($F_{0.05}$, 2, 133 = 10.01, P <

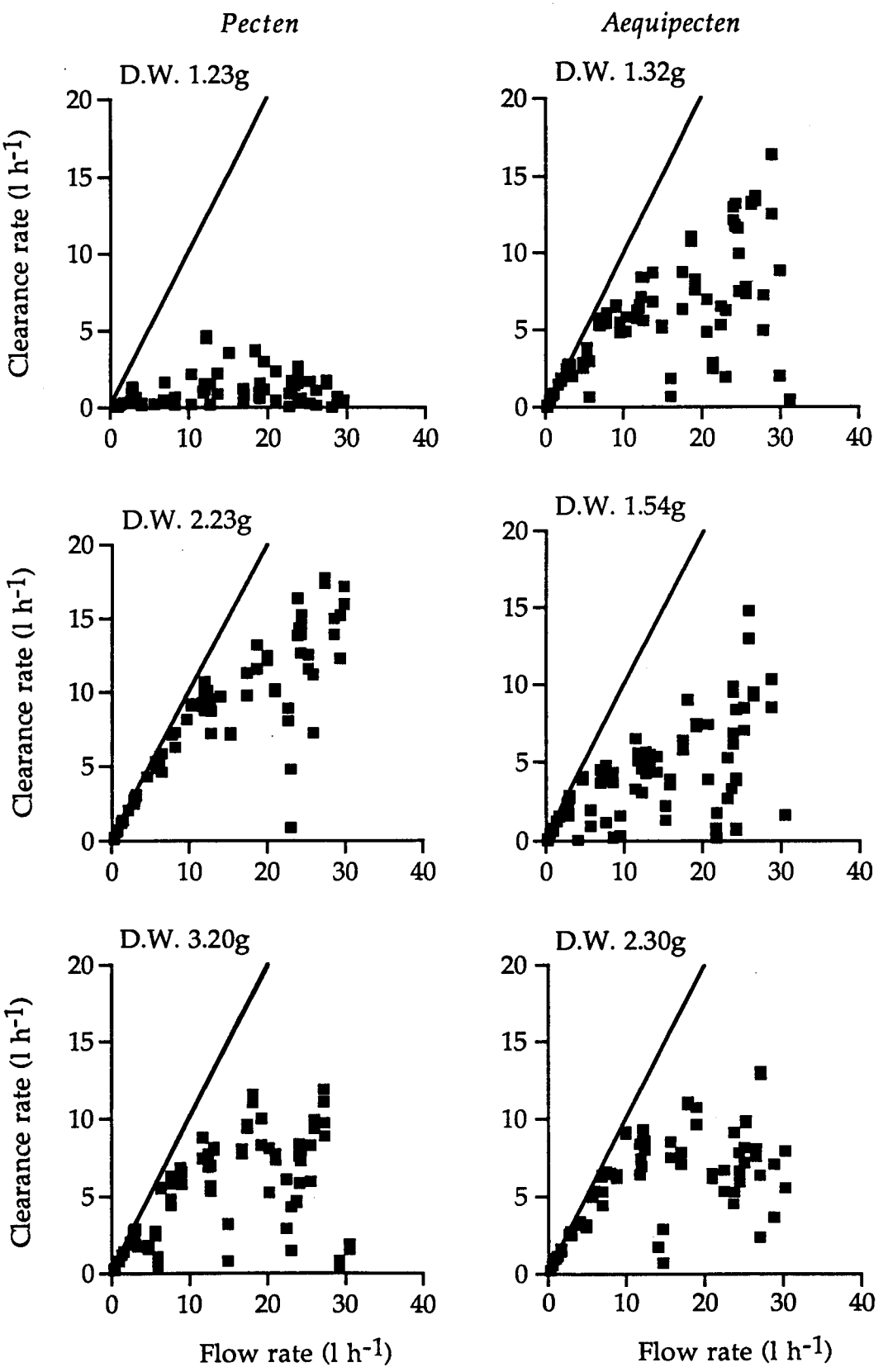


Fig. 2.1 The effect of flow rate on clearance rate of individual *P. maximus* and *A. opercularis* of differing dry body weight (D.W.). Each point represents a single instantaneous determination. Also shown is the line where clearance rate equals flow rate.

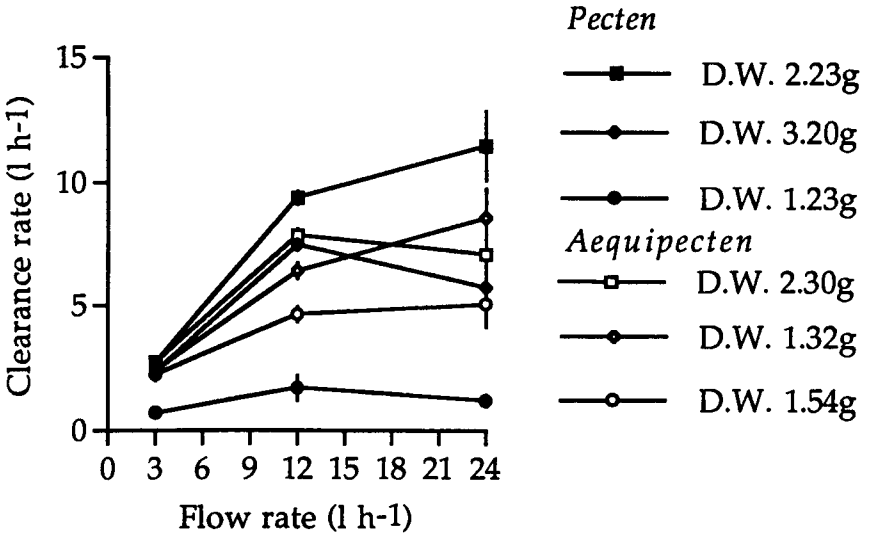


Fig. 2.2 The effect of flow rate on clearance rate of individual *P. maximus* and *A. opercularis* of differing dry body weight (D.W.). Each point represents the mean of 10-13 determinations. Standard errors are plotted where large enough.

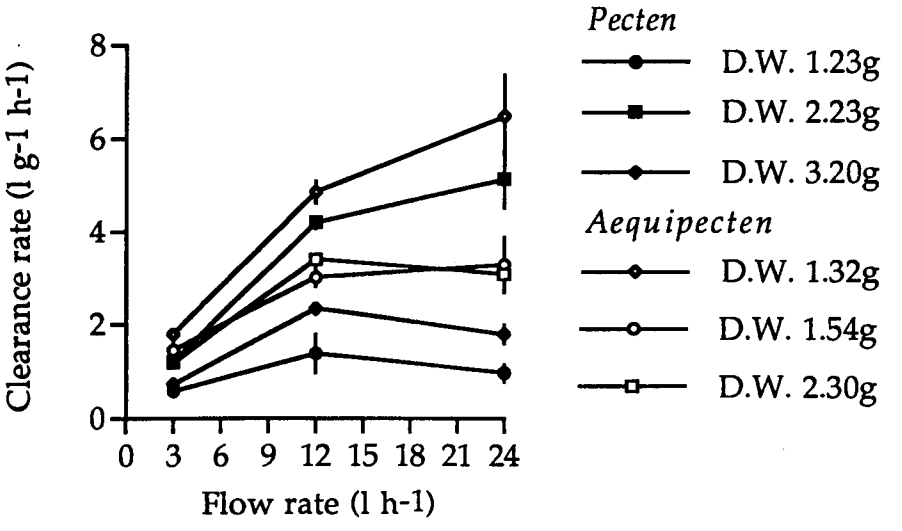


Fig. 2.3 The effect of flow rate on weight-standardized clearance rates of individual *P. maximus* and *A. opercularis* of differing dry body weight (D.W.). Each point represents the mean of 10-13 determinations. Standard errors are plotted where large enough.

0.001). Further analysis using Bonferroni's Least Significant Difference tests showed that selection at 3 l $h^{-1}$was not significantly different from that at 12 l h^{-1}, but that selection at 24 l h^{-1} was significantly greater than that at 3 l h^{-1} and 12 l h^{-1} (that is, 3 = 12 < 24).

Table 2.2 Analysis of covariance on the summed values of Jacobs' electivity index D (coded by adding two and then transformed using the Box-Cox transformation with λ=0.1) , comparing the effects of flow rate on the particle selection of *P. maximus* and *A. opercularis*, using animal body weight as a covariate. Individual comparisons of levels within factors which were significant were made by calculating Bonferroni's Least Significant Differences (using an experimentwise error rate (EER) of 0.05). * and ** indicate significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	MS	$F_{0.05}$	P	
Covariate (weight)	1	3.692	2.143	2.143	9.17	0.003	**
Covariate (control concentration)	1	0.813	0.346	0.346	1.48	0.226	
Species	1	0.974	0.980	0.980	4.19	0.043	*
Flow rate	2	4.715	4.682	2.341	10.01	< 0.001	**
Species & flow	2	0.102	0.102	0.051	0.22	0.804	
Error	133	31.091	31.091	0.234			
Total	140	41.386					

Bonferroni Least Significant Differences. S and NS signify statistically significant (at P = 0.05) and non-significant differences respectively, between the indicated levels of the factor being tested. 3, 12 and 24 represent flow rates in l h^{-1}

Comparison	N1	N2	MS Error	Critical F	L.S.D.	Significance
			Flow rates			
3 vs. 12	48	46	0.234	5.88	0.24	NS
3 vs. 24	48	47	0.234	5.88	0.24	S
12 vs. 24	46	47	0.234	5.88	0.24	S

Analysis of covariance on the particle sizes at which maximum values of D occurred (Table 2.3) showed that flow significantly affected size class selection ($F_{0.05}$, 2, 134 = 5.03, P = 0.008), Bonferroni's L.S.Ds showed that

selection at 3 l h^{-1} and 12 l h^{-1} were significantly different (that is, 3 < 12 = 24).

Table 2.3 Analysis of covariance analysing the effect of flow rate on the particle size class most selected by *A. opercularis* and *P. maximus*, using animal dry weight and control concentration as covariates. Individual comparisons of levels within factors which were significant were made by calculating Bonferroni's Least Significant Differences (using an experimentwise error rate (EER) of 0.05). * and ** indicate significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	MS	$F_{0.05}$	P	
Covariate (weight)	1	0.571	0.225	0.225	0.06	0.805	
Covariate (control concentration)	1	16.169	16.810	16.810	4.59	0.034	*
Flow rate	2	36.836	36.827	18.414	5.03	0.008	**
Species	1	0.007	0.006	0.006	0.00	0.967	
Flow & species	2	0.295	0.295	0.148	0.04	0.961	
Error	133	486.775	486.775	3.660			
Total	140	540.652					

Bonferroni Least Significant Differences. S and NS signify statistically significant (at P = 0.05) and non-significant differences respectively, between the indicated levels of the factor being tested. 3, 12 and 24 represent flow rates in l h^{-1}

Comparison	N1	N2	MS Error	Critical F	L.S.D.	Significance
			Flow rates			
3 vs. 12	48	46	3.66	5.88	0.04	S
3 vs. 24	48	47	3.66	5.88	0.04	NS
12 vs. 24	46	47	3.66	5.88	0.04	NS

The effect of algal cell concentration on clearance rate

Clearance rates varied both within and between species. Fig. 2.5 shows the clearance rates of the three animals of each size class within each experiment plotted together. The results obtained were very variable but three patterns of feeding seemed to occur: a dome-shaped response, a gradual increase with increasing concentration, often reaching a plateau, or

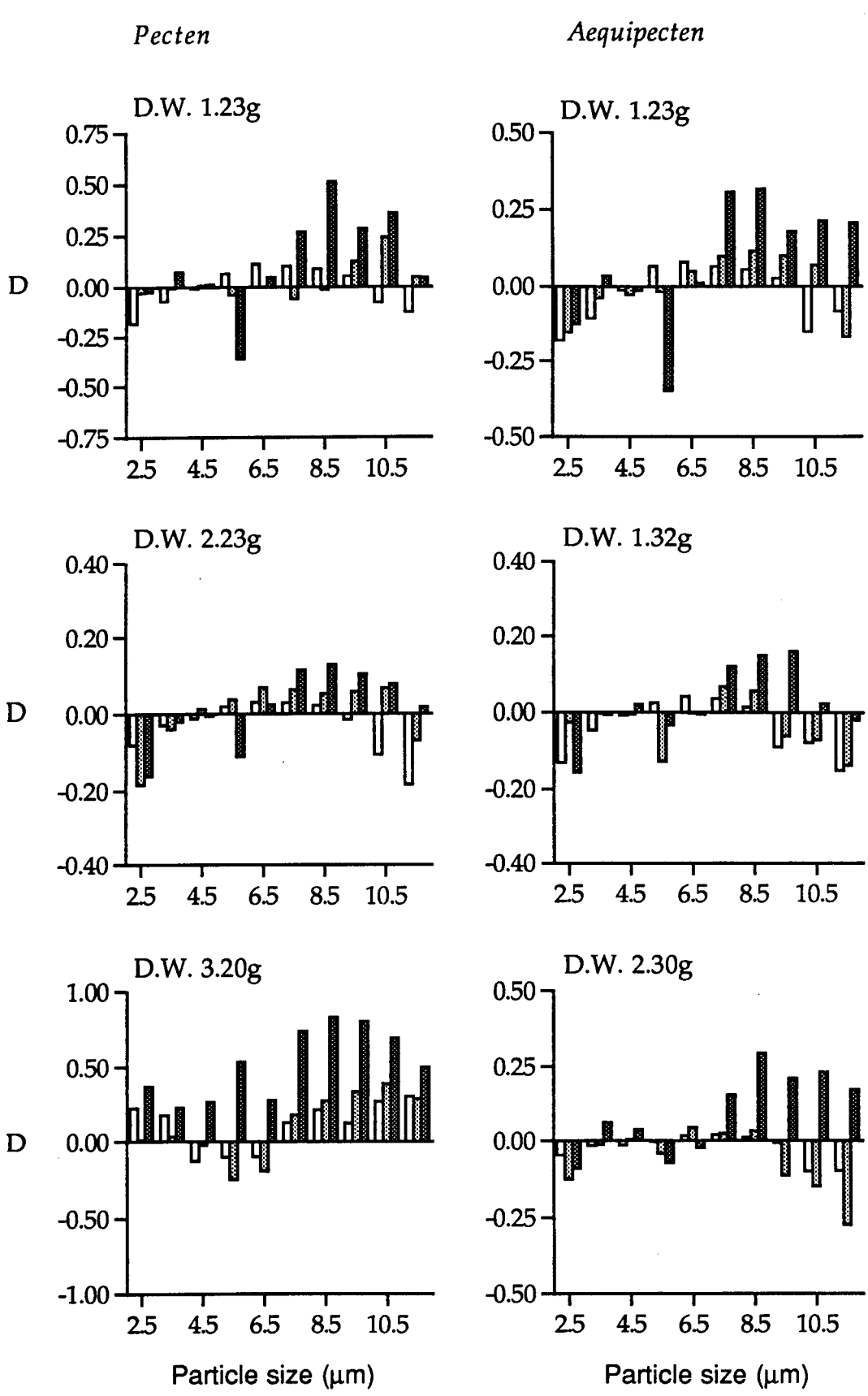


Fig. 2.4 The effect of flow rate on the particle selection (D) of P. maximus and A.opercularis of differing dry body weight (D.W.). Each point represents the mean of eight determinations. Note different scales for D. Symbols represent:

□ 3 l h -1 ▒ 12 l h-1 ■ 24 l h-1

a decline from low to high concentrations. Dome-shaped responses occurred more often in the smaller individuals, whereas a gradual increase was more evident in larger individuals.

When weight-standardized clearance rates were plotted against concentration, smaller animals consistently had higher clearance rates than larger animals (Fig. 2.6). An analysis of variance on the logarithm of (Y+1) showed that species (*P. maximus* > *A. opercularis*, $F_{0.05}$, 1, 1314 = 164.09, $P < 0.001$), size of animal (small > large, $F_{0.05}$, 1, 1314 = 1060.43, $P < 0.001$) and particle concentration ($F_{0.05}$, 11, 1314 = 7.87, $P < 0.001$) all significantly affected weight-standardized clearance rates (Table 2.4). A nested factor (experiment number within species) also proved to be significant ($F_{0.05}$, 2, 1314 = 180.90, $P < 0.001$). Bonferroni's Least Significant Difference tests showed that experiment number within species was significantly different for both species.

The ANOVA interaction terms showed that the pattern in weight-standardized clearance rates between size groups within each species was different between species ($F_{0.05}$, 1, 1314 = 180.04, $P < 0.001$). The effect of algal cell concentration on weight-standardized clearance rates was also different within each size group ($F_{0.05}$, 11, 1314 = 3.72, $P < 0.001$) and within each size group within each species ($F_{0.05}$, 11, 1314 = 4.91, $P < 0.001$).

The number of Bonferroni comparisons possible to make within the various interaction terms between concentration, animal size and species categories was too large to be calculated readily (up to 55 in some categories). A complete pairwise examination of all the levels within a significant factor was not necessary since not all of these combinations were of interest. Therefore, comparisons were only made at concentrations of 2,

7, 11, 19 and 25 cells μl^{-1}, and at 25 cells μl^{-1} for the three-way interaction term. Weight-standardized clearance rates were also significantly smaller at 2 than at 7, 11, 19 and 25 cells μl^{-1}, and smaller at 7 than at 25 cells μl^{-1}. Weight-standardized clearance rates were significantly different between size groups at every concentration. At 25 cells μl^{-1} the weight-standardized clearance rates were different between every species and size group combination, except between large *P. maximus* and large *A. opercularis* (that is, PS>AS>PL=AL, for codes see Table 2.4) .

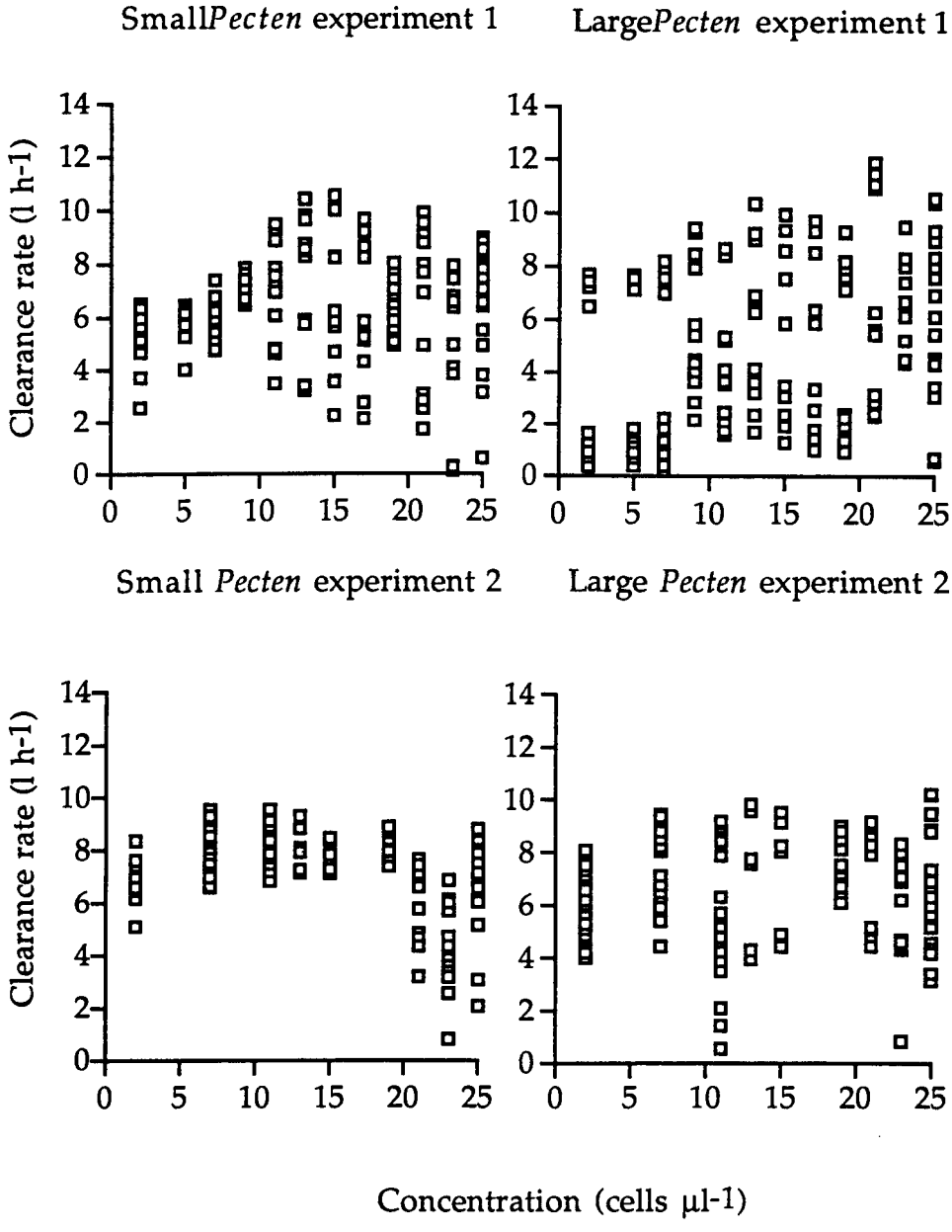


Fig. 2.5 The effect of algal cell concentration on the clearance rates of *P. maximus* and *A. opercularis*. Each graph shows the clearance rates of the three individuals in each size group within each experiment. Each point represents a single determination.

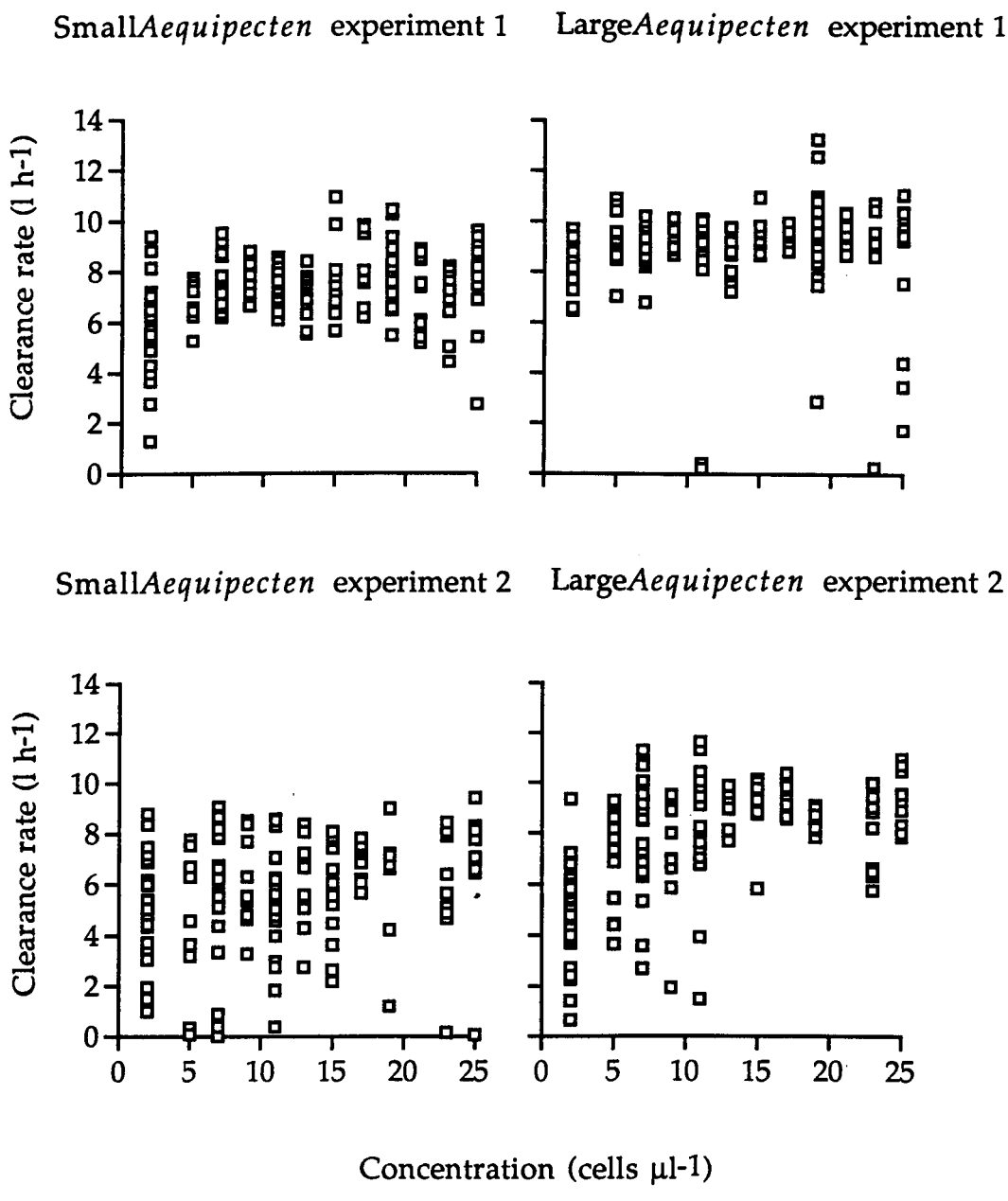


Fig. 2.5 continued. The effect of algal cell concentration on the clearance rates of *P. maximus* and *A. opercularis*. Each graph shows the clearance rates of the three individuals in each size group within each experiment. Each point represents a single determination.

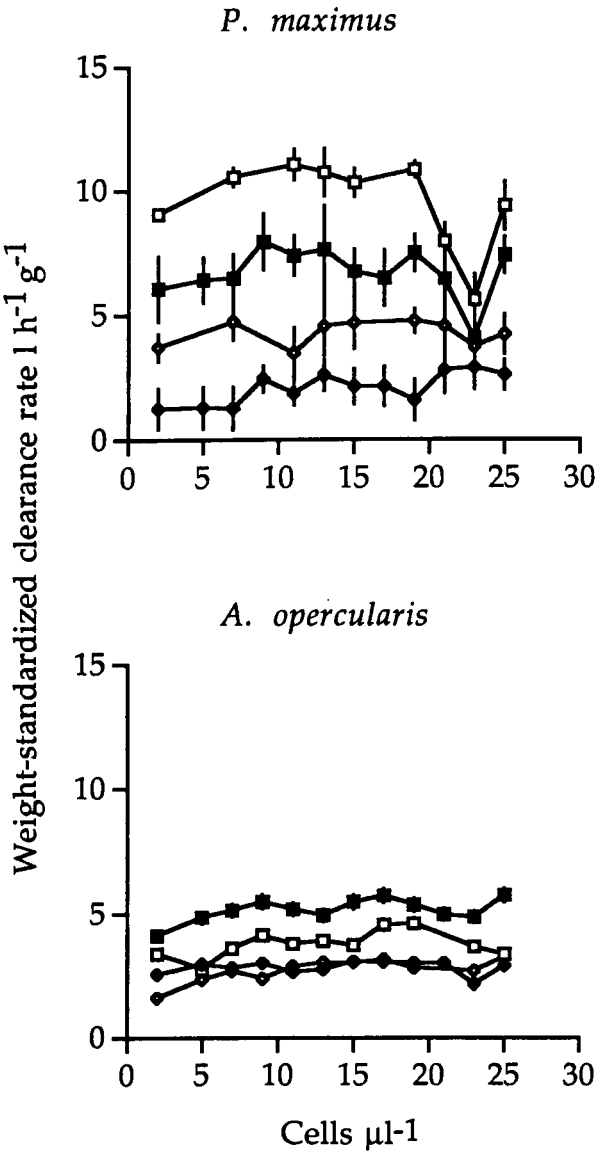


Fig 2.6 The effect of cell concentration on the weight-standardized clearance rates of *P. maximus* and *A. opercularis*. Each point represents the mean of six to eight determinations on each of three animals (± standard errors where large enough to be plotted).

Small (experiment 1) Large (experiment 1)

Small (experiment 2) Large (experiment 2)

Table 2.4 Analysis of variance comparing the effects of particle concentration, animal size, and experiment number on the transformed (logarithm of Y+1) weight-standardized clearance rates of *A. opercularis* and *P. maximus*. Individual comparisons of levels within factors which were significant were made by calculating Bonferroni's Least Significant Differences (using an experimentwise error rate (EER) of 0.05). * and ** indicate significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	MS	$F_{0.05}$	P	
Species	1	3.208	3.087	3.087	164.09	< 0.001	**
Experiment	2	7.443	6.806	3.403	180.90	< 0.001	**
Animal size	1	23.409	19.949	19.949	1060.43	< 0.001	**
Concentration	11	1.741	1.628	0.148	7.87	< 0.001	**
Species & animal size	1	4.147	3.387	3.387	180.04	< 0.001	**
Species & concentration	11	0.309	0.315	0.029	1.52	0.117	
Animal size & concentration	11	0.852	0.770	0.070	3.72	< 0.001	**
Species & animal size & concentration	11	1.017	1.017	0.092	4.91	< 0.001	**
Error	1314	24.719	24.719	0.019			
Total	1363	66.844					

Bonferroni Least Significant Differences. S and NS signify statistically significant (at P = 0.05) and non-significant differences respectively, between the indicated levels of the factor being tested. P represents *P. maximus*, A *A. opercularis*, L large and S small.

Comparison	N1	N2	MS Error	Critical F	L.S.D.	Significance
Experiment number within species						
P expt 1 vs. expt 2	356	275	0.019	5.02	0.02	S
A expt 1 vs. expt 2	397	336	0.019	5.02	0.03	S
Concentration (cells μl^{-1})						
2 vs. 7	162	190	0.019	7.88	0.04	S
2 vs. 11	162	165	0.019	7.88	0.04	S
2 vs. 19	162	145	0.019	7.88	0.04	S
2 vs. 25	162	164	0.019	7.88	0.04	S
7 vs. 11	190	165	0.019	7.88	0.04	NS
7 vs. 19	190	145	0.019	7.88	0.04	NS
7 vs. 25	190	164	0.019	7.88	0.04	S
11 vs. 19	165	145	0.019	7.88	0.04	NS
11 vs. 25	165	164	0.019	7.88	0.04	NS
19 vs. 25	145	164	0.019	7.88	0.04	NS
Animal size & concentration (cells μl^{-1})						
2 L vs. S	80	82	0.019	6.63	0.06	S
7 L vs. S	94	96	0.019	6.63	0.05	S
11 L vs. S	83	82	0.019	6.63	0.05	S
19 L vs. S	70	75	0.019	6.63	0.06	S
25 L vs. S	81	83	0.019	6.63	0.06	S
Species & size group at 25 cells μl^{-1}						
25 PS vs. PL	48	47	0.019	6.96	0.07	S
25 PS vs. AS	48	33	0.019	6.96	0.08	S
25 PS vs. AL	48	36	0.019	6.96	0.08	S
25 PL vs. AS	47	33	0.019	6.96	0.08	S
25 PL vs. AL	47	36	0.019	6.96	0.08	NS
25 AS vs. AL	33	36	0.019	6.96	0.09	S

The effect of concentration on size selection of particles

Values of D for *P. maximus* were consistently higher than for *A. opercularis* (Fig. 2.7). Large *P. maximus* also usually selected particles to a greater extent than small *P. maximus*, but the different sizes of *A. opercularis* showed no consistent pattern. Values of D peaked at concentrations of 11 cells μl^{-1} and 2 cells μl^{-1} for *P. maximus* and *A. opercularis* respectively, thereafter declining slowly. D became positive at smaller size classes for *A. opercularis* than for *P. maximus*, but at higher size classes (especially at higher concentrations) D became negative, whereas values of D for *P. maximus* remained positive.

Analysis of variance on the Box-Cox transformed (λ=0.1 on data coded by adding three) summed values of D showed that *P. maximus* exhibited greater selection than *A. opercularis* ($F_{0.05}$, 1, 844 = 6.96, P = 0.009). Particle concentration ($F_{0.05}$, 4, 980 = 5.36, P < 0.001), and experiment number ($F_{0.05}$, 2, 844, = 46.31, P < 0.001) all affected selection significantly (Table 2.5), as did animal size ($F_{0.05}$, 1, 844 = 14.01, P < 0.001), where small animals exhibited less selection than large animals. Bonferroni's Least Significance Difference tests showed that selection at 2 cells μl^{-1} was greater than that at 7 μl^{-1}, and selection at 7 was less than that at 11, but all other combinations of comparisons were not significant. Concentration affected selection within species differently ($F_{0.05}$, 4, 844 = 3.84, P = 0.004). Bonferroni Least Significance Difference tests showed that *P. maximus* exhibited significantly greater selection than *A. opercularis* at concentrations of 7, 11, 19, and 25 cells μl^{-1}, the same pattern occurred at 2 cells μl^{-1}, but the difference was not significant. The experiments within both species also differed significantly.

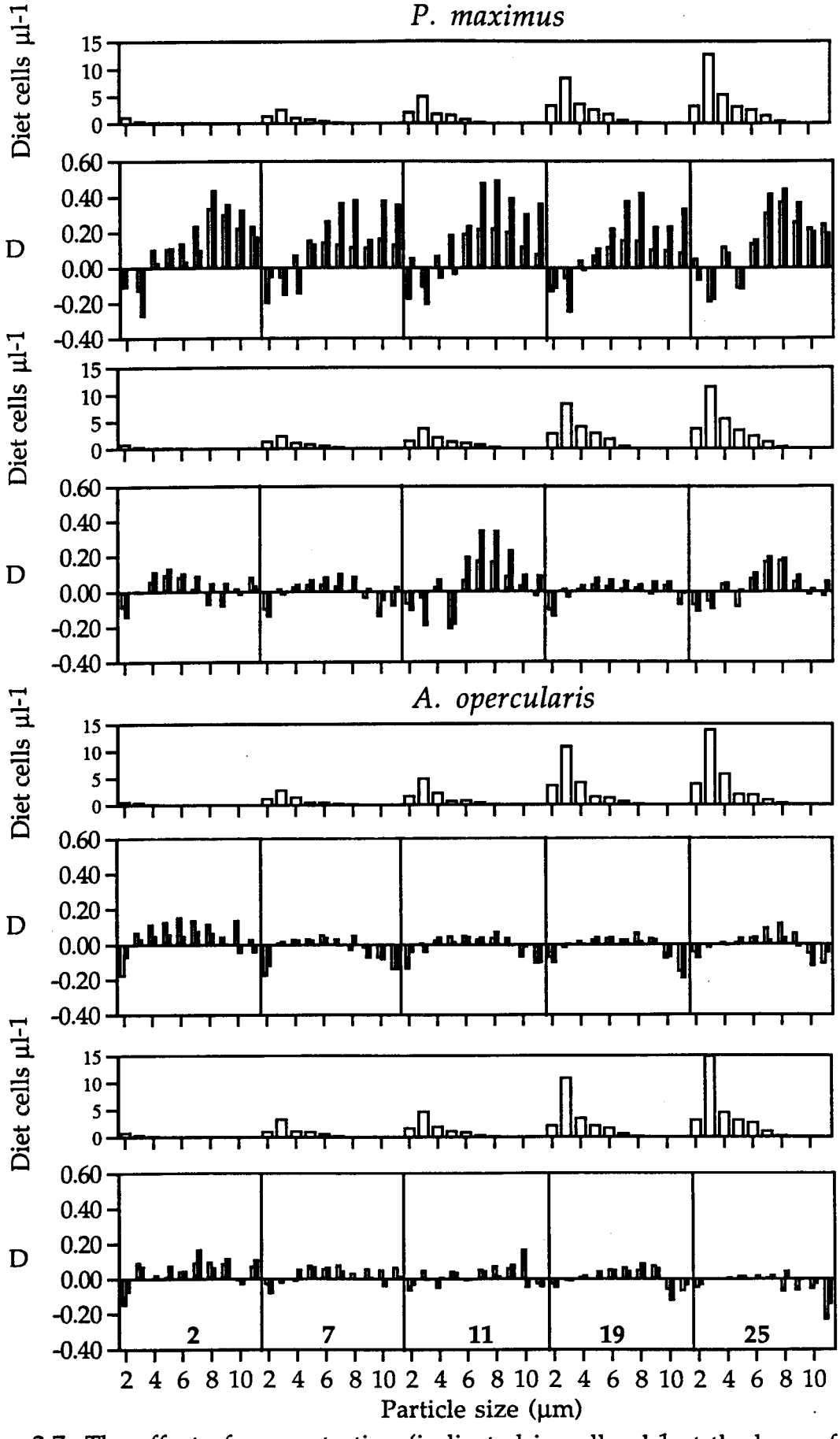


Fig. 2.7 The effect of concentration (indicated in cells µl-1 at the base of the bottom histogram) on particle selection (D) in *P. maximus* and *A. opercularis* of two different size classes. Each bar is the mean of six to eight determinations on each of six animals. The particle size spectra of the experimental diets are plotted above the histograms of D, where each bar is the mean of sixteen determinations. ☐ Small ■ Large

Analysis of covariance on the particle size classes where D was maximum (transformed by squaring) showed that particle concentration affected selection differently within each species ($F_{0.05}$, 4, 845 = 2.50, P = 0.041). No significant combinations for the species and concentration interaction term could be found although the analysis of covariance term was significant.

Table 2.5 Analysis of covariance on the summed values of Jacobs' electivity index D (coded by adding three and transformed by Box-Cox transformation with λ=0.1), comparing the effects of particle concentration, animal size, and experiment number on the particle selection of *P. maximus* and *A. opercularis*, using animal body weight as a covariate. Individual comparisons of levels within factors which were significant were made by calculating Bonferroni's Least Significant Differences (using an experimentwise error rate (EER) of 0.05). * and ** indicate significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	MS	$F_{0.05}$	P	
covariate (weight)	1	1.093	0.714	0.714	10.48	0.001	**
species	1	8.146	0.474	0.474	6.96	0.009	**
experiment	2	5.555	6.311	3.155	46.31	< 0.001	**
concentration	4	1.530	1.462	0.366	5.36	< 0.001	**
animal size	1	1.492	0.954	0.955	14.01	< 0.001	**
species & concentration	4	1.023	1.047	0.262	3.84	0.004	**
species & size	1	0.162	0.150	0.150	2.20	0.139	
concentration & size	4	0.335	0.351	0.088	1.29	0.273	
species & concentration & size	4	0.134	0.134	0.033	0.49	0.743	
Error	844	57.501	57.501	0.068			
Total	866	76.971					

Bonferroni Least Significant Differences. S and NS signify statistically significant (at P = 0.05) and non-significant differences respectively, between the indicated levels of the factor being tested. P represents *P. maximus*, A *A. opercularis*.

Comparison	N1	N2	MS Error	Critical F	L.S.D.	Significance
Experiment number within species						
P 1 vs. 2	238	203	0.068	5.02	0.06	S
A 1 vs. 2	238	189	0.068	5.02	0.06	S
Concentration (cells μl^{-1})						
2 vs. 7	182	189	0.068	7.88	0.08	S
2 vs. 11	182	188	0.068	7.88	0.08	NS
2 vs. 19	182	145	0.068	7.88	0.08	NS
2 vs. 25	182	163	0.068	7.88	0.08	NS
7 vs. 11	189	188	0.068	7.88	0.08	S
7 vs. 19	189	145	0.068	7.88	0.08	NS
7 vs. 25	189	163	0.068	7.88	0.08	NS
11 vs. 19	188	145	0.068	7.88	0.08	NS
11 vs. 25	188	163	0.068	7.88	0.08	NS
19 vs. 25	145	163	0.068	7.88	0.08	NS
Species & concentration (cells μl^{-1})						
2 P vs. A	84	99	0.068	6.63	0.10	NS
7 P vs. A	95	94	0.068	6.63	0.10	S
11 P vs. A	95	93	0.068	6.63	0.10	S
19 P vs. A	72	73	0.068	6.63	0.11	S
25 P vs. A	95	68	0.068	6.63	0.11	S

Table 2.6. Analysis of covariance on the particle sizes at which maximum selection occurred (transformed by squaring), comparing the effects of particle concentration, animal size, and experiment number on the particle selection of *P. maximus* and *A. opercularis*. Individual comparisons of levels within factors which were significant were made by calculating Bonferroni's Least Significant Differences (using an experimentwise error rate (EER) of 0.05). * and ** indicate significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	MS	$F_{0.05}$	P	
Covariate (Weight)	1	1715.5	74.9	74.9	0.08	0.779	
Species	1	223.3	573.1	573.1	0.60	0.438	
Experiment	2	10267.9	5386.8	2693.4	2.83	0.059	
Concentration	4	5769.4	5251.3	1312.8	1.38	0.238	
Animal size	1	154.3	598.6	598.6	0.63	0.428	
Species & concentration	4	9531.3	9499.1	2374.8	2.50	0.041	*
Species & animal size	1	923.9	1059.4	1059.4	1.11	0.291	
Concentration & animal size	4	1552.4	1482.6	370.7	0.39	0.816	
Species & concentration & animal size	4	4165.6	4165.6	1041.4	1.1	0.357	
Error	845	802959.8	802959.8	950.2			
Total	867	837263.4					

Bonferroni Least Significant Differences. S and NS signify statistically significant (at P = 0.05) and non-significant differences respectively, between the indicated levels of the factor being tested. P represents *P. maximus*, A *A. opercularis*.

Comparison	N1	N2	MS Error	Critical F	L.S.D.	Significance
			Species & concentration (cells μl^{-1})			
2 P vs. A	84	99	950.2	6.63	11.77	NS
7 P vs. A	95	94	950.2	6.63	11.54	NS
11 P vs. A	95	93	950.2	6.63	11.58	NS
19 P vs. A	72	73	950.2	6.63	13.18	NS
25 P vs. A	95	68	950.2	6.63	12.61	NS

DISCUSSION

The effect of flow rate on clearance rate

The relationship between clearance rate and flow rate has been studied by several authors. Walne (1972) found a positive relationship between flow and clearance rate in five species of bivalves, but this was later invalidated because he used an inappropriate clearance rate formula, which did not actually measure clearance rate. Hildreth (1976) and Hildreth & Crisp (1976) pointed this out, maintaining that no relationship between flow and clearance rate existed in Walne's data and any that had been shown was an artefact created by the use of the equation F(Ci-Co)/Ci rather than F(Ci-Co/Ca), where Ca is the concentration of particles around the bivalve. The first equation does not actually measure filtration rate, but the rate of particle uptake. The results will underestimate the actual filtration rates by Co/Ci, an error which will be more pronounced at low flow rates because the dilution of the inflowing water will be more important. Above a critical flow rate the error becomes insignificant, and clearance rates will approximate filtration rates (Hildreth & Crisp, 1976; Riisgård, 1977).

In my experiments, the clearance rates closely approximated filtration rates at flow rates above 8-10 l h^{-1}; that is, the clearance rates become independent of flow rate. Below that critical flow rate both *P. maximus* and *A. opercularis* can reduce particle concentrations to insignificant levels, and the clearance rates approach the flow rates. Similar results were obtained for other species by Riisgård (1977). At flow rates above 10 l h^{-1} the results for both *P. maximus* and *A. opercularis* become erratic. This could be due to the animals pumping intermittently, as seen in most subtidal species of bivalve, but which was not seen to occur in *A. opercularis* (Brand & Taylor, 1974) or the animals may be physiologically

stressed by the high flow rate (Taghon & Greene, 1992). The animals may react to increasing particle flux (particles encountered per unit time) in a manner similar to when exposed to increasing particle concentrations. In *Argopecten* reduced shell gape, retracted mantle tentacles and increased numbers of shell adductions have been observed (Palmer & Williams, 1980). Shell adductions would resuspend particles and give artificially low clearance rates. It is therefore difficult to determine whether clearance rates are reduced at high flows or whether low recorded clearance rates are due to particle resuspension by the animals. No behavioural changes of the animals were observed, although observations were difficult to make in the dimly lit constant temperature room without disturbing the animals. It is unlikely, however, that adductions would occur often enough and consistently between animals to produce the response shown by many of the animals.

One of the three *P. maximus* (number 1, dry body weight 1.23g) had consistently low clearance rates, which peaked at approximately 12 l h^{-1}. This could be due to the intrinsic variability of physiological responses, or it could be that the chamber geometry was inappropriate for the size of animal used; either all the water entering the chamber was unavailable to the scallop or water was being re-circulated. *A. opercularis* of similar dimensions (*A. opercularis* numbers 1 and 2) did not exhibit such low clearance rates which suggests that chamber geometry was not the problem, although *A. opercularis* is shaped differently from *P. maximus*. A further alternative is that smaller *P. maximus* are more sensitive to increased flow velocities. This has been suggested on theoretic grounds by Eckman *et al.* (1989), using hydrodynamic scaling and physiological principles. However, available evidence at that time (Kirby-Smith, 1972; Wildish *et al.*, 1987; Cahalan *et al.*, 1989; Eckman *et al.*, 1989) suggested that the opposite

occurred: adults seemed to be more sensitive to flow velocity (growth inhibition occurred at 3-5 cm s^{-1} in adult *Argopecten irradians concentricus* (Kirby-Smith, 1972) and at >9-18 cm s^{-1} in juveniles (Eckman *et al.*, 1989). The suggestion that adults were more sensitive to flow rate was made by comparing separate experiments by different authors. Wildish & Saulnier (1992) have since shown that growth rates of juvenile *Placopecten magellanicus* were more readily inhibited by increasing flow velocity than adults.

It is unlikely that the small range of animal sizes used in my experiment would show any size-related trends between flow rate and clearance rate, (the sizes used were not chosen in order to elucidate any such relationship) and no size-related trends were evident. At 24 l h^{-1} clearance rates declined or reached a plateau, relative to clearance rates at 12 l h^{-1}, in four of the six animals (Figs 2.1 and 2.2). In the remaining two animals the rate of increase of clearance rate with flow declined. The relationship between clearance rate and body size is well documented (e.g., Bayne *et al.*, 1976a; Winter, 1978; Griffiths & Griffiths, 1987; Bricelj & Shumway, 1991) clearance rates increase with increasing body weight. Weight-standardized clearance rates, like most physiological indices, are greater for smaller animals and this general trend was apparent.

Contrary to the results of Hildreth & Crisp (1976), experiments with *Placopecten magellanicus* (Wildish *et al.*, 1987, 1992) and *Mytilus edulis* (Wildish & Miyares, 1990) showed that filtration rate and seston uptake rate are affected by flow velocity. Wildish *et al.* (1992) found that both seston uptake rate (μm Chl *a* consumed per gram wet weight per hour) and clearance rate were reverse ramp functions of velocity. In other words, the relationship is positive over a narrow range of flow rates, reaching a

maximum and then declining as flow increases further (Grizzle *et al.*, 1992). Wildish *et al.* (1992) suggested that their results implied a homeorheostatic control of feeding in the giant scallop, which involved the recognition of cell density, as well as ambient velocities around the scallop. Their results showed that there is an interactive effect between velocity and cell concentration: the velocity above which clearance rates rapidly declined increased with increasing algal concentration up to 10^4 cells ml^{-1}. At 10^5 cells ml^{-1} the relationship became a simple negative linear one. At 10^4 cells ml^{-1} uptake rates plateaued between approximately 10-32 cm s^{-1} after which uptake rates declined. In my study, clearance rates of *P. maximus* and *A. opercularis* fed 8 cells μl^{-1} tended to reach a plateau or decline after velocities of 12-15 l h^{-1} (approximately five to seven cm s^{-1}). This is confirmed by the Bonferroni L.S.D. results (Table 2.1) which show that clearance rates at $3 \neq 12 = 24$ l h^{-1}.

Several studies have shown experimentally that growth is inhibited by high flow rates in a range of bivalve species: in *Placopecten magellanicus* (Wildish *et al.*, 1987, 1992), *Argopecten irradians* (Kirby-Smith, 1972; Cahalan *et al.*, 1989; Eckman *et al.*, 1989) and *Mytilus edulis* (Wildish & Miyares, 1990) at flow rates between 3 and 10 cm s^{-1}, and it has been suggested that feeding responses to velocity are the probable mechanisms (Wildish *et al.*, 1987). Wildish *et al.* (1987) hypothesized that the growth inhibition of the giant scallop *Placopecten magellanicus* was due to a direct physical effect of flow velocity on feeding rate: when the ambient seawater pressure at the inhalant opening exceeds that at the exhalant opening, by an amount greater than the pressure head developed by the ciliary pump, the scallop responds by reducing or stopping filtering. Eckman *et al.* (1989) used hydrodynamic scaling arguments to suggest that juveniles should be more sensitive to increasing flow velocities than adults if the pressure

differential hypothesis of Wildish *et al.* (1987) was correct. They then suggested that the hypothesis may not be correct because the growth of the adult bay scallops (*A. irradians*) used by Kirby-Smith (1972), was more sensitive to flow than the juveniles that they used in their study. Comparing results obtained under such different conditions obviously cannot be regarded as conclusive, and Wildish & Saulnier (1992) have shown that the growth of juvenile *Placopecten magellanicus* is more sensitive to increased flow velocity than adults.

Reduced filtration may be achieved by physically restricting the inflow of water by mantle or valve closure (equivalent to the changes made to siphon aperture size in order to control water inflow in *Mytilus edulis* described by Foster-Smith (1976)) or by shunting the water between the inner demibranchs (a by-pass mechanism demonstrated in *Mytilus edulis* by Famme & Kofoed (1983) and Famme *et al.* (1986)). Physical interference of the filtering mechanism may also occur (Kirby-Smith, 1972; Jørgensen *et al.*, 1986; Wildish *et al.*, 1987; Wildish & Miyares, 1990; Taghon & Greene, 1992). Any of these mechanisms would reduce filtration. It is possible, however, that pumping rate remains unaffected by flow velocity and that gill by-pass mechanisms occur which reduce the filtration efficiency (Wildish & Miyares, 1990). Wildish & Saulnier (1993, in press in Wildish & Kristmanson, 1992) have presented results which suggest that seston uptake rates in *Placopecten magellanicus* are reduced by valve and mantle closure.

The responses of individual or small groups of animals to flow rate in the laboratory are difficult to extrapolate to that of a population, because of the unnatural hydrodynamic conditions encountered in feeding chambers and, to a lesser extent, in flumes. Single animals in feeding chambers would

probably not experience seston depletion, which has been shown to occur over beds of *Mytilus edulis* and *Modiolus modiolus* (Wildish & Kristmanson, 1984; Frechette & Bourget, 1985a, 1985b). The particle concentrations used are often unnaturally high, which is important as it is known that algal concentration affects the flow velocity and clearance rate relationship (Wildish *et al.*, 1992). It is also very likely that seston quality would complicate the response further.

The 'ramp' and negative (declining) sections of the response curve are thought to occur at much higher velocities in field populations (Wildish & Kristmanson, 1992). Wildish & Peer (1983) showed that *Modiolus modiolus* production was correlated positively with flow, and had not begun to decline even at velocities of 65 cm s^{-1} (six data points were removed from the data set however, where at high velocities zero production had occurred, Wildish & Kristmanson, 1992). The supply of seston to the depleted benthic boundary layer (the depleted layer has been recorded to be at least 10cm deep in flume studies by Wildish & Kristmanson (1984) and Butman *et al.* (in prep., cited in Frechette *et al.*, 1992) and in field studies by Frechette *et al.*, (1989)) is controlled by turbulent transfer processes (Wildish & Kristmanson, 1979, 1992; Wildish & Peer, 1983; Frechette *et al.*, 1989, 1992) which are velocity dependent. Increasing flow velocity increases seston supply and consequently feeding and production rate (Wildish & Kristmanson, 1979). Wilson (1987) found that growth of *P. maximus* and *Ostrea edulis* in suspended culture, after accounting for other variables between the sites, was greatest where flow velocities were highest (approximately 30 cm s^{-1}). This was probably due to the increased particle flux experienced at the high flow site. Cahalan *et al.* (1989) showed however, that the growth of *Argopecten irradians* was

correlated more strongly to absolute particle concentration and flow velocity than to particle flux.

It is not known how behavioural and morphological differences between the two species may affect their feeding: *P. maximus* recess into the sediment in a shallow pit, from which they do not readily move (Hartnoll, 1967; Mathers, 1976) whereas *A. opercularis* remain above the surface and are generally considered to be more mobile. The relationship between height above the seabed and flow velocity is logarithmic (Nowell & Jumars, 1984; Wildish & Kristmanson, 1984; Frechette *et al.*, 1992; Wright *et al.*, 1992) and it is feasible that the two species encounter different flow regimes, both with regard to turbulence and flow velocity. The boundary layer is usually turbulent except for a few centimetres (Wildish & Kristmanson, 1979), in the lowermost region of this viscous sublayer vertical motion of particles occurs only by molecular diffusion (Nowell & Jumars, 1984) and shear stresses remain constant. Immediately above the viscous sublayer flow is turbulent with high rates of mixing and diffusion, and shear stresses decrease with distance from the seabed. As flow rates increase and bottom roughness increases the viscous sublayer decreases in depth, and may disappear altogether (Nowell & Jumars, 1984). This pattern is complicated further in flows over continental shelf and shallow subtidal seabeds as the oscillations within the water column (caused by surface or internal waves) create a boundary layer within the boundary layer caused by the water body movement (Nowell & Jumars, 1984).

The recess pits of *P. maximus* undoubtedly also influence the flow velocity of the water moving over them; the water slowing down and shear stresses falling, so that sedimentation of particles is enhanced and residence time of suspended particles increases (Nowell & Jumars, 1984). This is presumably

beneficial to *P. maximus*, assuming that flow velocities remain high enough that seston depletion does not occur and waste materials are removed. Accumulated detritus can be observed in the recess pits of *P. maximus* (pers. obs.). Grant *et al.* (1993) have observed that once *Placopecten magellanicus* are recessed, the flow across the seabed acts to recess them further. Various troughs and crests of sediment are formed around the recessed animal (Grant *et al.*, 1993), emphasising that the recesses do alter flow patterns on the seabed. *A. opercularis* would probably experience higher shear stresses and more turbulent flows than *P. maximus* (laminar flow is generally restricted to approximately one centimetre from the bed, if it exists at all (Nowell & Jumars, 1984)), but the importance of this is uncertain. Eckman *et al.* (1989) showed that within the velocity range of 1.7-3.9 cm s^{-1} *Argopecten irradians concentricus* was unaffected by whether flow was laminar (Reynolds number R_e 450), laminar with regular eddies in the wakes of scallops (R_e 600) or turbulent (R_e 840). Grizzle *et al.* (1992), however, hypothesized that differences in feeding height between oysters (*Crassostrea virginica*) and hard clams (*Mercenaria mercenaria*) could be important because of potential differences in hydrodynamic sorting of suspended particles and differences in shear stresses (Muschenheim, 1987a).

The effect of flow rate on particle selection

The ration filtered by the animals does not change much between 12 and 24 l h^{-1} (ingestion levels would follow the patterns in Fig 2.3), but the selection exhibited increases significantly.

No work has been carried out specifically to determine the effect of flow rate on particle selection in bivalves. The retention ability of the bivalve

may be altered by the physical effects of flow on the feeding mechanisms and apparatus, or selection may be affected by the changing particle flux and energetic demands of increasing flow rate (flow-related stress and feeding against increased drag forces). A combination of these factors will probably determine the effect of flow on retention efficiency, which will be confounded by differences in diet quality.

High flow rates have been shown to inhibit feeding activity (Kirby-Smith, 1972; Jørgensen *et al.*, 1986; Wildish *et al.*, 1987; Wildish & Miyares, 1990). If the ability of the laterofrontal cirri to move freely is being affected and the angle of beat changed, then a similar effect on retention efficiency may occur to that when serotonin is added to the bivalve. Jørgensen *et al.* (1986; 1988) found that adding serotonin to *Mytilus edulis* (which reduces the angle of beat of the laterofrontal cirri) strongly reduced the retention efficiency of small particles (< 6 μm) but had much less effect on 14 μm particles. Very high concentrations of serotonin also reduced the retention efficiency of large particles (Jørgensen *et al.*, 1988). In my experiment on *P. maximus* and *A. opercularis* the size class of particle most selected increased from 3 l h^{-1} to 12 l h^{-1}, and then declined slightly at 24 l h^{-1}. There was no general increase in 'leakiness' to small particles as described by Jørgensen *et al.* (1986) for *Mytilus edulis*, indeed the pattern below 6.5 μm was erratic, which may have been due, in part, to the confounding effect of the mechanical limitations of the pectinid gill to capturing small particles (e.g., Bricelj & Shumway, 1991). Above 6.5 μm however, increasing flow did increase particle selection. At 10.5 μm and larger, particle selection was often negative at flow rates of 3 l h^{-1}, but became positive (or less negative) at higher flow rates.

Rubenstein & Koehl (1977) hypothesized that direct interception of particles was probably the most common method of particle capture among marine suspension feeders, but predicted that inertial impaction would be important for organisms feeding at high velocities on large or dense prey. Increasing flow velocity will increase the rate of capture by inertial impaction (the particles will be moving faster and therefore impact forces will be greater (Rubenstein & Koehl, 1977; La Barbera, 1984)) and possibly by direct interception (La Barbera, 1984). With increasing particle size the ability of a filter to capture by direct interception, inertial impaction and gravitational deposition increases. As velocity increases, the combined action of these mechanisms serves to decrease the size of the particle size class retained the least (Rubenstein & Koehl, 1977). It is therefore possible that the larger particles, when moving faster in higher velocity flows, would be intercepted more readily by both direct interception and inertial impaction. Shimeta & Jumars (1991) however, predict that the retention of particles will decrease with increasing particle size and with increasing velocity. Certainly the retention of a particle is decided by the balance between the forces of drag and particle inertia (McFadden, 1986; Okamura, 1987). Shimeta & Jumars (1991) conclude that 'available data are insufficient to demonstrate or to rule out the occurrence of a shift between encounter mechanisms for a single particle type under natural variations in velocity'.

It is also possible that pumping rates remain constant when flow rates are increased but that clearance rates are reduced by shunt mechanisms allowing water to by-pass the gill (Wildish & Miyares, 1990). Famme & Kofoed (1983) and Famme *et al.* (1986) showed that water was shunted, unfiltered, between the inner demibranchs of *Mytilus edulis*, even at flow rates of 400-500 mls h^{-1}, but that the particle concentration of the water by-

passing the gills was still reduced. They suggested that hydromechanical mechanisms were acting to remove the particles from the shunt water flow. Presumably, if water shunting increases non-linearly with increasing flow rate (after the bivalve pump has reached its maximum capacity) then particle selection may be altered if the mechanisms of removal are different from those acting on water passing through the gill.

It is energetically more expensive to move the latero-frontal cirri and other cilia against high flow velocities (because of increased drag forces (McFadden, 1986; Taghon & Greene, 1992)). This may result in the animals optimally selecting larger, energetically more beneficial particle sizes. Willows (1992) predicts that at high energy investment rates only high quality particles will be ingested. This may also relate to the energetic benefits of ingesting larger particles, when particle quality remains constant. Okamura (1987) found that the bryozoan *Bugula stolonifera* switched particle size preference to larger particles when subjected to increased flow rates. The larger species *B.neritina* did not exhibit the same pattern, however: the particle size captured decreased. Okamura hypothesized that *B.stolonifera* was altering its feeding behaviour; changing from ciliary current feeding to tentacular capture. Tentacular capture may be energetically more expensive and so only be utilized when there are high concentrations of large particles available per unit time (i.e., high flux rates). Okamura also suggested that particle concentrations and flow rates may need to be higher to elicit the same response in *B. neritina.*

It is again difficult to differentiate between the effects of increased flow velocity and the indirect effect of increased particle flux, although Cahalan *et al.* (1989) found that the growth of *Argopecten irradians* was less sensitive to food flux than to the algal concentration and flow rate. The

same response may occur with regard to retention efficiency. The covariate 'control concentration' was a significant variable affecting the size class most selected, which suggests that particle flux may have played some rôle in the response. It did not significantly affect the extent of selection, however (Table 2.2).

The covariate 'body weight' had the reverse effect: it significantly affected the extent of selection but not the size class most selected. This may possibly be explained by theoretical hydrodynamic scaling arguments (Eckman *et al.*, 1989), which predicted that juveniles would be more sensitive to flow rate than adults. This was found to occur with regard to the growth of *Placopecten magellanicus* (Wildish & Saulnier, 1992).

P. maximus exhibited selection to a greater degree than *A. opercularis*, but the size classes preferentially selected did not differ between the two species. The difference in the degree of selection exhibited could be due to differences in the shell geometry affecting water flow around and through the animal or the fact that the average weight of the *P. maximus* was greater than the *A. opercularis* (but see Fig. 2.7, which again shows differences between the two species).

The effect of particle concentration on clearance rate

There have been many different experimental studies relating the effect of particle concentration on clearance rate (see reviews by Winter, 1978, Griffiths & Griffiths, 1987, and Bricelj & Shumway, 1991, for pectinids). The results seem very conflicting, but Griffiths & Griffiths (1987) considered that they can be reconciled by the differences in experimental diet sizes and concentrations used. They found that most of the authors

who found increasing clearance rates with increasing concentration were working with low concentrations of particles or the food was introduced to animals held in clean seawater (e.g., Griffiths & King, 1979; Griffiths, 1980a). Those who worked at low to intermediate concentrations (< 10 mg l^{-1}) found no effect of concentration, while those that worked with concentrations greater than 10 mg l^{-1} recorded declining clearance rates. Feeding is usually initiated at some low threshold value, after which clearance rates increase to a maximum and then decline (Lehman, 1976; Winter, 1978). When food availability is low the feeding rate is constrained by the energetic costs of feeding (Willows, 1992).

Work on pectinids has shown quite dramatic decreases in clearance rates with increasing concentration. Palmer (1980) found a 95% decrease in clearance rates of juvenile *A.irradians concentricus* with increasing concentrations of *Tetraselmis suecica* from 0.94-9.4 mg dry weight l^{-1} (1.23-12.3 μm^3 ml^{-1}). Kuenstner (1988, cited in Bricelj & Shumway, 1991) recorded an 85% decrease in clearance rates over a concentration range of 1.2-12 cells μl^{-1} (0.83-8.3 x 10^6 μm^3 ml^{-1}) in juvenile *A.irradians*. Cahalan *et al.* (1989) found that clearance rates decreased over the concentration range 7.5 to 68 cells μl^{-1} by approximately 56%. This is the general pattern described by most workers, however there is a threshold level below which clearance rate is very low resulting in a dome shaped response curve. Most experiments do not use particle concentrations low enough to detect the early phase of the response (Hughes, 1980). Richardson *et al.* (1984) found that maximum shell growth (and presumably feeding) of *A. opercularis* when fed *Tetraselmis suecica* occurred in the range 1-3.3 cells μl^{-1} (5.85-4.04 mg l^{-1}), *Tetraselmis* is a large alga however (from their measurements apparently $1.5x10^{-3}$ μg $cell^{-1}$, but this seems too large) and so the concentration at which maximum feeding occurred would probably be

lower than for other smaller algae (Griffiths & Griffiths, 1987; Harris, 1990). The diets in my study cover a wider range of diets, in terms of volume, numbers and weight than the study of Kuenstner (1988), and similar in terms of volume to Cahalan *et al.* (1989) (Table 2.8). The data (Fig. 2.5) however, do not exhibit the same decline as seen by those authors. In view of the comments by Griffiths & Griffiths (1987) it is surprising that such drastic reductions occurred, since the diet levels were probably below 10 mg l^{-1}. Most of the work they quoted, though, was performed on mussels and it is possible that pectinids show a different response.

Table 2.8 Diet characteristics used in experiments studying the effect of algal cell concentration on clearance rate in pectinids. This study used a mixed algal diet of *Rhinomonas reticulata, Isochrysis galbana* and *Monoisochrysis lutherii.*

Algal species	mg l^{-1}	μm^3 ml^{-1}	Number μl^{-1}	Author
Thalassiosira	0.94-9.4	$1.23\text{-}12.3 \times 10^6$	50-340	Palmer 1980
Thalassiosira	Not known	$0.83\text{-}8.3 \times 10^6$	1.2-12	Kuenstner 1988
Isochrysis	Not known	$0.25\text{-}2.28 \times 10^6$	7.5-68	Cahalan *et al.* 1989
Mixed (see above)	0.15-2.5	$0.08\text{-}2.2 \times 10^6$	2-28	This study

The results of my study showed that weight-standardized clearance rates of small *P. maximus* > small *A. opercularis* > large *P. maximus* = large *A. opercularis* (Table 2.4) and that several different types of response of clearance rate to concentration occurred. The results were variable between animals within a species and within a size group. This was probably largely due to the variations in weight between the animals, *P. maximus* especially seemed to show a size dependent pattern, changing from declining clearance rates to constant or plateau responses, to continual increases with increasing size and concentration. An important genetic contribution to

such physiological variability has been previously recognised: higher metabolic rates occur in more homozygous individuals due to reduced metabolic efficiencies (see references in Bayne, 1986). Small reductions in standard metabolic rate result in higher rates of net energy gain as well as higher feeding rates and higher optimal feeding rates (Bayne, 1986). The smaller the metabolic cost of pumping water the greater is the animals flexibility to increase its feeding rate at low concentrations and so reach its optimum feeding rate more rapidly (Willows, 1992). Larger animals have a lower metabolic rate per gram body weight than small individuals (and therefore presumably lower pumping costs), so it may be expected that they would have lower optimal feeding concentrations and be less sensitive to changes in cell concentration (Bayne, 1985). This was found in *Aulacomya ater* by Griffiths & King (1979).

Smaller animals would also have smaller gut volumes (Bayne, 1992) so it would be more likely that the concentrations used would elicit a reduction in clearance rates. This response was most evident in *P. maximus*, the species which included the smallest animals used in this experiment. The concentrations used were not low enough that all the animals exhibited very low clearance rates (except in some of the large animals). The Bonferroni results show that clearance rates at 2 cells μl^{-1} are significantly lower than clearance rates at any other concentration, and that clearance rates at 7 cells μl^{-1} were lower than at 25 cells μl^{-1} (Table 2.4), supporting the presence of a general plateau response of the animals.

The effect of animal size on the response pattern may also explain the differences between the results of my study and those of Palmer (1980), Kuenstner (1988) and Cahalan *et al.* (1989) working with *Argopecten irradians*, all the above studies used juvenile animals (37-47 mm shell

height, 0.5-1.29g dry weight, Palmer, 1980; 10-37 mm Richardson *et al.*, 1984; 3-10 mm shell height, Cahalan 1989). Although Palmer (1980) used animal sizes that overlapped at the upper end with those used in my study, he used such high concentrations of a large alga that the animals would be expected to exhibit such a dramatic response. The smallest *P. maximus* used in my experiment often showed the same response as the larger animals in Palmer (1980), but the early part of the theoretical feeding response curve was recorded using the diets in my study. Harris (1990) found that *Venus casina, Glycymeris glycymeris* and *Modiolus modiolus* all exhibited higher clearance rates when fed mixed algal diets rather than unialgal diets. The animals fed a mixed algal diet in my study may have maintained high clearance rates at concentrations that would otherwise have caused a declining response if unialgal diets had been used.

Møhlenberg & Riisgård (1979) found that filtration rates of *P. furtivus* and *P. (Aequipecten) opercularis* were consistently high and independent of food concentration over the range 0.02 to 0.30 mg dry weight organic matter l^{-1}. Cranford & Grant (1990), working on adult *Placopecten magellanicus* (105mm shell height), also found no relationship between clearance rate and concentration over a concentration range of 0.5-2.5 mg l^{-1}, although they were comparing different diets. The diet volumes used in this study were lower than those used in the other studies, Bayne (1992) showed that at diet volumes up to 1 μm^3 ml^{-1} the clearance rate response would be dome-shaped, but above that volume clearance rates would decrease. Griffiths (1980a) found constant clearance rates above 0.4 cells μl^{-1} in *Choromytilus meridionalis*. The results of the above mentioned authors working on pectinids, who found clearance rates to be independent of concentration, were probably not using low enough concentrations to elicit inhibited clearance rates. Small animals also have smaller gut volumes,

and so maximum clearance rates would occur at lower concentrations as maximum digestion capacity is reached earlier.

The factor actually controlling feeding rate is the volume of material ingested; how quickly the gut is filled and maximum digestion capacity achieved (Lehman, 1976; Hughes, 1980; Willows, 1992; Bayne, 1992; Navarro & Iglesias, 1992; Iglesias pers comm., 1992). Most authors, however, express diets in terms of numbers of cells per unit volume of water, whereas they are best expressed in terms of volume or, less preferentially, mg l^{-1}.

Differences between experiments within species may be due to a combination of factors: variations in diet quality (e.g., algal culture age, Griffiths, 1980a) or in the algal species ratio (which should have been 1:1:1 by number in my experiment) would elicit different responses. The different weights of the animals would also be important, as can be seen when the animals within an experiment were not well matched. The animals were matched by height into size classes expected to give similar body weights between species (*P. maximus* of 50-56 and 60-65mm and *A. opercularis* of 49-54 and 58-65mm). However, the dry weights of both species were still variable within a size class.

The effect of algal concentration on particle size selection

Why *P. maximus* show greater selection than *A. opercularis* (which was also found in the flow experiment) is uncertain. However, the particle size class at which maximum selection occurs is not significantly different between the species, which suggests that it is not due to different physical limitations of the gill causing differences in particle retention abilities. As

D is an index of selection rather than retention, differences in gill structure may still be a possible reason. The size above which effective particle retention occurs in pectinids is approximately 5-7 μm (see General Introduction Table 1.1). Below that, size retention efficiency patterns vary between species, but will presumably be influenced by the size and species of alga used as food.

A. opercularis have been shown to have greatest growth rates at between 1-3.3 cells μl^{-1} (Richardson *et al.*, 1984). Therefore at the lowest concentration used in this experiment (2 cells μl^{-1}) *A. opercularis* would probably obtain the greatest net energy gain and would presumably be able to expend more energy on selection than at higher concentrations.

The response may also be due, in part, to the species having adapted to different diets in the environment. *A. opercularis* may feed more on sedimenting phytoplankton (Christensen & Kanneworff, 1985) than *P. maximus*: this diet would be of quite high quality, so *A. opercularis* may not exhibit selection to as great an extent as *P. maximus*, which probably encounters more refractory particles of lower digestibility and energetic value than *A. opercularis*, as it lives recessed in the sediment. *P. maximus*, however, would not be expected to show selection under the experimental conditions of pure algal diets, unless the retention efficiency and selection of particles is not sufficiently 'plastic' to be switched off entirely. Acclimation to pure algal diets may result in lowered selection.

It is possible that *A. opercularis* have higher metabolic rates than *P. maximus* and their energy budgets do not allow as much flexibility to allow particle selection, which would presumably be energetically expensive. The Bonferroni results show that selection between the two species is

different at every concentration except at 2 cells μl^{-1}, which is the concentration at which *A. opercularis* exhibit the greatest selection.

The larger *P. maximus* also show more selection than the smaller animals but the pattern in *A. opercularis* is not as clear. Small *A. opercularis* exhibited greater selection at 2 cells μl^{-1} in experiment 1 but not in experiment 2. The selection exhibited by *A. opercularis* was generally more erratic, which may again indicate that *A. opercularis* do not exercise as much particle selection. Small *P. maximus* have higher metabolic rates per gram body weight than large individuals. Presumably feeding costs are higher, which results in reduced flexibility of the feeding response (Willows, 1992) and hence the energy budget of the smaller animals may be less able to spare energy for an energetically expensive response. The small *P. maximus* showed their greatest selection response at 25 cells μl^{-1}, at which concentration net energy gain may be high enough to allow selection to be energetically beneficial. Selection in bivalves will only occur above a threshold filtration cost (Willows, 1992), below which net energy gain would probably not be high enough to justify selection.

Palmer & Williams (1980), studying *Argopecten irradians*, found an increase in retention efficiency of 1.73-3.45 μm particles with increasing concentration of food. They attributed this to increased mucus secretion on the gill. My study did not show this response, though again D is a measure of selection, whereas relative retention efficiency simply relates the number of particles of a certain size class in the inhalant and exhalant water flows. Palmer & Williams (1980) also compared a wider range of diets in their study (0.88-6.08 mg l^{-1}) than in my study. Riisgård (1988) considered, due to the consistency between the results in his work and that of Møhlenberg & Riisgård (1978), that the bivalves they studied probably

did not change their retention efficiency in response to particle concentration. However, the retention efficiency of the Japanese oyster *Crassostrea gigas* does respond to increasing quantities of food, but not to changing quality (Barillé *et al.*, 1993). The Japanese oyster is less efficient at retaining particles with an E.S.D. of less than 8 μm when the seston concentration is increased (Barillé *et al.*, 1993), which is the opposite response to that found by Palmer & Williams (1980). This may again be a function of the concentrations, and qualities, of diet tested, Barillé *et al.*. (1993) used seston concentrations between 1.34 and 64.37 mg l^{-1} which incorporated silt. Perhaps most importantly, this response was evident in experiments using natural seawater, with no extra particles added (Barillé *et al.*, 1993). Stenton-Dozey & Brown (1992) showed that when the concentration of available food increased, the retention efficiency pattern exhibited by *Venerupis corrugatus* altered to maximally exploit the most abundant size class.

Over the range of diets used in my study, selection of particles > 10 μm often became negative at high concentrations, *A. opercularis* showing negative selection of these sizes at lower concentrations than *P. maximus*. This may reflect a preference for one of the species in the mixed algal diet. When a preferred food is at high enough concentrations the less-preferred food will be more strongly rejected (Lehman, 1976; De Mott, 1990). Thus it is possible that, in my study, *Rhinomonas* (the largest alga) was being selected against at high concentrations. Small *P. maximus* may need higher concentrations of preferred food to elicit the response because they have higher feeding costs.

The differences in feeding exhibited between the two species may infer adaptation to the different environments which they inhabit: since *P.*

maximus recesses it may receive a lower quality diet (Muschenheim, 1987a, 1987b), which would probably necessitate greater pre-ingestive selectivity. *P. maximus* would also typically encounter lower flow rates, and presumably particle flux, which may require that greater volumes of water are processed.

CONCLUSIONS

P. maximus and *A. opercularis* differed in their basic feeding physiologies. *P. maximus* had greater clearance rates than *A. opercularis*, except in the flow experiment due to one individual exhibiting very low clearance rates. The two species responded to increasing flow rates in the same manner: clearance rates increased with flow until approximately 10 l h^{-1}, after which clearance rates remained essentially constant.

P. maximus exhibited greater selection than *A. opercularis*. Both species selected to a greater extent at higher flow speeds, and the size class selected the most also increased. The amount of material cleared from suspension remained essentially constant between 12 and 24 l h^{-1}, but larger particles were being selected.

Within the two species the way that the maximally selected size class changed with particle concentration differed. Further analysis did not detect where the differences lay, but *P. maximus* selected a larger size class than *A. opercularis* at every concentration tested except at 11 cells μl^{-1}. Both species showed an erratic but gradual decline in the maximum size class selected.

CHAPTER 3. FOOD AVAILABILITY IN THE BENTHIC BOUNDARY LAYER AND ITS UTILIZATION BY *PECTEN MAXIMUS* AND *AEQUIPECTEN OPERCULARIS*.

INTRODUCTION

The flux of food from the water column to the benthos has always been recognised as being of great importance (e.g., Johnstone *et al.*, 1925; Graf *et al.*, 1982; Davies & Payne, 1984; Christensen & Kanneworff, 1985, 1986; Graf, 1987). The input of material from the sedimenting phytoplankton is likely to be utilized very quickly in the benthos (Graf *et al.*, 1982, 1983; Graf, 1987) leading to food limitation. Thus the maintenance of the benthic community must depend on an additional source of food. Petersen & Jensen (1911) suggested that this missing energetic link may be resuspended sediment. In most marine environments more energy is transferred from one trophic level to another via detrital algal material than by living algal material consumed directly by a grazer (see review by Mann, 1988). The influence of sediment resuspension is often underestimated in energy budgets (Oviatt & Nixon, 1975) but has been shown to have an important influence since it increases water column primary production and bacterial productivity (Wainright, 1987, 1990; Shaffer & Sullivan, 1988; Muschenheim *et al.*, 1989).

Resuspended sediment will be a complex mixture of mineral particles, refractory and labile organic matter, diatoms and bacteria (Zeitzschel, 1970; Parmenter *et al.*, 1983; Cranford & Grant, 1990). The effect that this mixture has on the growth of benthic organisms will vary between species and with the degree of sediment transport. Taghon & Greene (1992) found that the growth rates of two species of polychaetes, when feeding on

resuspended particulate matter, differed. Grant *et al.* (1990) found that the effect of resuspended sediment on the growth of *Ostrea edulis* depended on the extent of resuspension. At low levels of resuspension the growth of *O. edulis* was enhanced. In contrast, Frechette & Grant (1991) found no evidence of growth enhancement in *M. edulis*.

The availability of food within the benthic boundary layer (BBL, also called the benthic turbidity zone (BTZ) or the Ekman layer) has been the subject of much recent research (Wildish & Kristmanson, 1984, 1985; Frechette & Bourget, 1985b; Frechette *et al.*, 1989; Wildish & Miyares, 1990). This has focussed largely on the effect of dense beds of mussels or oysters on the concentration of food in the overlying water, and the consequent limitation to the growth of the whole population. Less work has been done on solitary bivalves such as pectinids. The work that has examined the food available to solitary bivalves was often studied for comparison with gut content analyses, such as those performed on *Argopecten irradians* (Davis & Marshall, 1961) and the Patagonian scallop *Chlamys tehuelchus* (Vernet, 1977). In European and British waters, Widdows *et al.* (1979) and Hummel (1985) examined seasonal changes in the food available to *Mytilus edulis* and *Macoma balthica* respectively. Petersen & Jensen (1911) concluded that, with regard to food availability, there were no 'sharp boundaries' between the diatoms that were pelagic and those that were benthic. In Northern Europe attention is now being focussed on the nutrient flux between mussel beds and the plankton (Asmus & Asmus, 1990, 1991, 1992; Prins & Smaal, 1990; Dame *et al.*, 1991; Smaal & Prins, 1992).

The overall purpose of this study was to explore the food availability and utilization of food in the benthic boundary layer of shallow, coarse

sediment bottoms with well mixed water typical of much of the Irish Sea. On these grounds scallops and queens are major filter feeders. Particular emphasis was placed on trying to unravel the rôles of fluxes from the plankton to the benthos and resuspension from the bottom. To explore the differences in the diet that occurred seasonally, several different parameters of diet quality and quantity were examined (chlorophyll, phaeopigment, total particulate matter, particulate organic matter and particulate inorganic matter). This is especially important since the most reliable way of expressing quality has not been definitely established.

P. maximus and *A. opercularis* also potentially receive different diets: *P. maximus* recesses into the sediment whereas *A. opercularis* sits upon it. Although the difference in feeding heights between the species is small (1-2 cms), the influence on the water flow and the particle availability may not be (Muschenheim, 1987a, 1987b; Levinton, 1989; Grizzle *et al.*, 1992). The possibility that the two species receive, and feed upon, different sources of food was therefore also explored.

The specific aims of my study were firstly to evaluate any seasonal changes in the food available in the water and sediment. It was found that a peak in chlorophyll was evident in early summer, but that chlorophyll levels remained above 4 $\mu g\ l^{-1}$ throughout the year. Secondly, by using diatoms as biological markers, to determine the main source of the diatoms in the diet of *P. maximus* and *A. opercularis*. This would enable the determination of whether the animals encounter, and use, resuspended sediment, and whether the reliance on any dietary source alters seasonally. On the basis of seasonal sampling, the months to be analysed were decided by assessing the chlorophyll and phaeopigment concentrations of the sediment and water, and choosing months that were either typical of a

season, or where peaks occurred. The months chosen were May 1991 (low pigment concentrations in the sediment and water), July 1991 (high concentrations in both), December 1992 (low concentrations in the water) and March 1992 (medium concentrations in both).

MATERIALS AND METHODS

Experimental site

Two cages (136 x 124 x 23 cm and 146 x 110 x 30) were constructed of Dexion and plastic coated chicken wire and placed beyond the Port Erin Breakwater, at a depth which varied between 14.8 and 19.2 m when diving. The cages were secured using tent pegs and concrete weights. This method of anchorage proved to be successful, although running repairs needed to be carried out as the sediment moved. In November 1991 one cage was replaced with one with dimensions of 146 x 102 x 27 cm, as storm damage proved too excessive for repairs to be undertaken. For ease of location the cages were attached by ropes to a central concrete weight and shot line.

Sampling methods

Pecten maximus and *Aequipecten opercularis* were dredged from commercial scallop grounds around the south of the Isle of Man by the R.V. Cuma and R.V. Roagan. The animals were held until required in a flow-through seawater system. They were fed on the naturally occurring particles in the seawater system, supplemented with several cultured unialgal species 2-4 times weekly.

Approximately once a month from April 1991 until May 1992 ten animals of each species were placed in each cage by SCUBA divers. Animals were chosen which were 7-8 cm in shell height. A minimum of four days later the animals were collected from the cages by divers. Water and sediment samples were taken at the same time. Two samples of water were taken from each of two heights above the seabed: 2 cm and 1 m. Three sediment samples were taken from within each of the two cages.

Large Durapipe water samplers (5 l) were attached to the central concrete weight, to counteract the increase in buoyancy which occurred during the sampling procedure. A tap at the top of the water sampler was closed and the water sampler filled with air from a compressed air cylinder, via an aperture at the base of the water sampler. When the water sampler was full of air a rubber bung with a long tube inserted through it, was placed in the aperture at the base of the water sampler. The free end of the long tube was held at the appropriate sampling height, the upper tap was opened and water was drawn into the water sampler as the air escaped out of the tap. When all of the air had been replaced by water the upper tap was shut and the lower aperture closed with a bung. Great care was taken to ensure that all the air had been replaced in the sampler, otherwise the air expansion that occurred during the ascent to the surface could cause the lower bung to be forced out.

When the animals were removed from the cages three sediment samples were taken from within each cage. Buckets with a diameter of 12 cm were pushed into the sediment. A piece of perspex was slid carefully under the rim of the bucket, and the bucket turned upright. A lid was then slid under the perspex sheet and secured to the bucket.

On return to the laboratory the animals were immediately frozen at -20^{o}C to arrest digestion. The following analyses were performed on the water and sediment samples.

Water analysis

Chlorophyll and phaeopigment concentrations

One teaspoon of magnesium carbonate was added to approximately 200 mls of distilled water, and filtered through a 45 mm Whatman GF/C filter paper. This increases the retention ability of the filter paper from 1.2 μm to approximately 0.4 μm (Takahashi *et al.*, 1985). A minimum of 1 l of seawater was then filtered, under suction, through the filter paper. Excess water was removed from the filter paper, as dilution of the 90% acetone affects the spectrophotometric readings, by drawing air through the filter paper for one minute. The filter papers were then placed in bags and frozen at -20°C.

Chlorophylls *a, b, c* and phaeopigment concentrations ($\mu g\ l^{-1} \equiv mg\ m^{-3}$) were measured using the Lorenzen method. Ten millilitres (20 mls if concentrations of pigments were thought to be high) of 90% acetone was added to tubes containing the filter papers. The papers were macerated using a glass rod, and the tubes covered to prevent the acetone from evaporating. The tubes were then placed in the dark at 4°C for 24 hours. The tubes were centrifuged for 10 minutes at 3,500 r.p.m. Ten mls of acetone was very carefully removed so that filter fibres were not resuspended (which affects the spectrophotometer readings) and placed in 4 cm glass cuvettes. The extinctions of the samples were read on a Philips PU8620 Series UV/Visible light spectrophotometer at wavelengths of 750, 664, 647, 630 and 665 nm. The samples were then acidified to breakdown the chlorophyll pigments to their breakdown products, mainly phaeopigment. This was achieved by adding 2 drops of 10% HCl and leaving the samples for 3-5 minutes. The extinctions at 750 and 665 nm were then re-read. Pigment concentrations were then calculated using the

trichromatic equations of Jeffrey & Humphrey (1975). Phaeopigments were determined using the equations given by Lorenzen (1967).

Total Particulate Matter, Particulate Inorganic Matter and Particulate Organic Matter

In order to remove any organic matter present in the filters, 45 mm Whatman GF/C filter papers were pre-ashed at 450°C for a minimum of four hours in a furnace. The temperature of the furnace was never raised above 500°C as this can alter the filtering characteristics of the paper (Parsons *et al.*, 1984). The filter papers were cooled in a desiccator for 30 minutes and weighed using a Sartorius Analytic balance to the nearest 0.1 mg. A minimum of 1l of seawater was filtered through the filter paper under suction. The filter papers were then rinsed with three 5 ml aliquots of ammonium formate isotonic with seawater to remove salts (3% w/v ammonium formate is isotonic with 33‰ seawater (Widdows *et al.*, 1984)).

The filter papers were dried at 103°C for 12-24 hours, cooled in a desiccator and weighed. The filter papers were then ashed at 450°C for 12 hours, cooled in a desiccator and weighed. Total Particulate Matter (T.P.M.), Particulate Inorganic Matter (P.I.M.) and Particulate Organic Matter (P.O.M.) were calculated according to the following equations:

T.P.M. = Dry weight - filter paper weight

P.O.M. = Dry weight - ashed filter paper weight

P.I.M. = Ashed filter weight - filter paper weight

Particle concentrations

The numbers and volumes of particles in the seawater were recorded using a Coulter Counter Multisizer. Particles from 1.4-35 μm were counted using a tube with a 70 μm aperture. Particle counting continued until at least 80,000 particles had been counted or until 200 seconds of sampling time had elapsed.

Phytoplankton

250 mls of each seawater sample was placed in 250 ml cylinders and 1-2 mls of Lugol's iodine added. The samples were then covered and left to sediment in the dark for at least one week (see Hasle, 1978). The water was then carefully siphoned off until approximately 5 mls remained. The concentrated samples were then stored in tubes in the dark, to prevent oxidation of the Lugol's iodine.

Sediment analysis

The buckets of sediment contained some excess water, and so were left undisturbed for 6 hours so that the sediment could settle back down (Eaton & Moss, 1966). As much water as possible was then siphoned off, until the fine surface material began to be disturbed. Any sediment that was not used in the following analyses was dried for 12 hours at 103°C and weighed.

Chlorophyll and phaeopigment concentrations

Small sub-samples of sediment were placed in tubes and frozen at -20°C until analysis. Twenty to forty mls of 90% acetone was added to the tubes and the contents macerated with a strong glass rod. The procedure

followed was then the same as for the water samples. After analysis the sediment samples were dried for 12 hours at 103°C and weighed.

Particulate Organic Matter

Only P.O.M. could be measured for the sediment, as the sediment itself is largely inorganic and would therefore give meaningless T.P.M. and P.I.M. results. Sub-samples of sediment were placed in pre-weighed crucibles and dried for 12 hours at 103°C, after which they were cooled and weighed to the nearest hundredth of a gram. The samples were then ashed for 24 hours at 450°C, cooled and weighed.

Microphytobenthos

Sediment was placed in high sided petri dishes to a depth of one to two centimetres, with enough water to create a thin layer at the surface. Two double-layer lens tissue squares (2 x 2cm pieces of Whatman 105 lens cleaning tissue) were placed on the surface to act as traps. The dishes were placed in a tall box on a windowsill that received only natural light. The tissue traps were removed from the surface between 0900 and 1100 hours the following morning (Eaton & Moss, 1966), and placed in vials containing 3 mls of Lugol's iodine in 40% glycerol.

Diatom analysis

Each months samples were treated in one batch. The volume of each water sample was measured to the nearest 0.1 mm and the sample poured into a centrifuge tube. The sample vial and measuring cylinder were rinsed with approximately 5 mls of distilled water, which was then added to the centrifuge tube.

The liquid from each sediment sample was poured into a centrifuge tube. In order to free diatoms that may be trapped in the tissue fibres, the tissues were ripped 12 times using two pairs of tweezers, and then placed in the centrifuge tube. The sample vial was rinsed with two 3 ml aliquots of distilled water, which was added to the centrifuge tube.

The *P. maximus* and *A. opercularis* were defrosted, and the gut contents removed using glass Pasteur pipettes inserted through the mouth. A small volume (0.5-1 ml) of distilled water was then injected into the gut using the pipette. As much of the water as possible was then removed and added to the centrifuge tube. This served to remove as much of the gut contents as possible.

Many different methods of cleaning the diatoms were tested, for example, various concentrations of sulphuric, nitric and chromic acids, sulphuric acid and potassium permanganate, and hydrogen peroxide (see Round *et al.*, 1990). These methods, though proven to be effective and commonly used, would almost certainly destroy weakly silicated planktonic species. Also, although these methods worked well with planktonic and sediment samples, some methods reacted with the gut content samples to form very viscous liquids, which then proved very difficult to treat further. It was thought that the problem was that the gut content samples contained a lot of lipids from the digestive gland surrounding the stomach, which was usually punctured. Fairy liquid is known to effectively remove flocculent material from diatom samples without damaging the silicon frustules, as it has a neutral pH (Hendey, pers. comm.). Since a detergent would be very effective at removing fatty substances and the method would be extremely gentle, Fairy Excel liquid was eventually chosen to clean the

frustules. In trials using this method weakly silicated planktonic species remained identifiable.

One drop of Fairy Excel detergent was added to each tube. Each tube was filled with distilled water, mixed thoroughly and left for 45-60 minutes. The samples were then centrifuged at 2,000 r.p.m. for 10 minutes and the supernatant removed. The tubes were filled with distilled water and left for a minimum of 5 hours, which is considered sufficient time for the diatoms to sediment down to the bottom of the tube (Eaton & Moss, 1966; Hendey, 1974a; Hendey, pers. comm.). The samples were rinsed five times using this decantation method, which is thought to be more satisfactory than centrifuging as there is more time for the cleaning agent to diffuse out of the minute pores of the diatom frustule (Hendey, pers. comm.). Much less physical damage would also occur to the frustules.

After the fifth rinse the samples were decanted to approximately 1 ml, the sediment and gut content samples were carefully sieved through a large mesh tea strainer to remove large pieces of tissue or animal material. The pipette and sieve were thoroughly rinsed with distilled water, which was added to the sample tube. The tube was filled with distilled water and again left for at least 5 hours before the water was decanted. One drop of concentrated ammonia was added to each sample so the diatoms would spread more evenly over the coverslip (Hendey, 1974a; Hendey, pers. comm.). Coverslips (Borosilicate, 22 x 22 mm, Thickness No. 0) were pre-washed in a solution of 1% HCl in 70% ethanol before the samples were dried onto them. Samples should not be dried directly onto the slide as it may prove impossible to focus on diatom specimens when using immersion lenses (Round *et al.*, 1990).

Two slides were made of each gut content and water sample, but only one slide was made of each sediment sample, but more samples were analysed. This strategy was followed in an to attempt to reduce the sample variance (Eaton & Moss, 1966), as the chlorophyll levels in the sediment were often found to be very variable between samples.

The coverslips were dried at 50°C for at least 3 hours, after which 5 drops of Naphrax were dropped on to the coverslip. The coverslips were then returned to the oven for at least 3 hours to drive off the Naphrax solvent (toluene). Slides (1.0-1.2 mm thick) were heated to approximately 250°C (Hasle & Fryxell, 1970) on a hot plate and the coverslips placed on them. When the Naphrax had melted (it usually boiled, producing bubbles) the slide was moved to a cooler part of the hotplate. The coverslip was then gently pressed downwards using a pair of tweezers and a mounted needle, to force the bubbles out from under the coverslip. The slides were then labelled, each month being allocated a random numerical code so that the slides would be analysed 'blind'.

Diatom counting strategy

One hundred diatoms were identified to genus from each slide. This was decided from pilot studies plotting the number of genera found against the number of diatoms identified. Random fields of view were analysed from randomly chosen transects. If the diatom numbers present were very low a maximum of 70 fields of view were analysed. Certain families proved to be difficult to identify readily and confidently: members of the family Fragilariaceae and Naviculaceae were often too small and too easily obscured to be easily analysed. In an attempt to be consistent between samples these were allocated to larger taxonomic groups (Boalch, pers.

comm.). The first 20 diatoms encountered were also measured (length and width) using a calibrated eyepiece graticule.

The books and papers most commonly used for identification purposes were: Smith (1853), Van Heurck (1896), Hendey (1964), Cleve-Euler (1968), Cardinal *et al.* (1984), Poulin *et al.* (1984a, 1984b, 1984c, 1987), Berard-Therriault *et al.* (1986), Cardinal *et al.* (1986) and Berard-Therriault & Giroq (1987). The nomenclature used followed that of Hendey (1974b) and Hartley (1986).

Statistical analysis

The diversities of the diatom assemblages were measured using Shannon's diversity index (equation 1), and Hill's N1 (equation 2) and N2 (equation 3). Evenness was measured using Pielou's J' (equation 4). All equations are taken from Ludwig & Reynolds (1988).

$$H' = -\sum_{i=1}^{S}\left[\left(ni/n\right)\ln\left(ni/n\right)\right] \qquad 1$$

where ni is the number of individuals belonging to the ith of S species in the sample and n is the total number of individuals in the sample

$$N1 = e^{H'} \qquad 2$$

$$N2 = 1/\lambda \qquad 3$$

where $\lambda = \sum_{i=1}^{S} p_i^2$ (Simpson's index)

$p_i = n_i/N$, where ni is the number of individuals of the ith species and N is the known total number of individuals for all S species in the population.

$$J' = H'/\ln(S) \qquad 4$$

The similarities of the diatom assemblages were examined using both Sørensen's similarity index based on presence/absence data (equation 5) and Czekanowski's abundance weighted similarity index (also called percent similarity, PS, equation 6). The rare species were removed from the species matrix used for the calculation of these indices. A species was evaluated as being rare if the total abundance, summed for all the samples, was less than 5% of the total, and if it occurred in fewer than five of the samples. A rare species usually fulfilled both criteria. Clusters were determined using the complete linkage (furthest neighbour) method.

$$qs = 2a/2a + b + c \qquad 5$$

where a is the number of shared taxa between the two sampling units (SUs), b is the number of taxa found only in SU 1, and c is the number of taxa found only in SU 2.

$$PS_{jk} = \left(2W/A + B\right) \qquad 6$$

where $W = \sum_{i=1}^{S}\left[\min\left(X_{ij}, X_{ik}\right)\right]$ $\quad A = \sum_{i=1}^{S} X_{ij}$ $\quad B = \sum_{i=1}^{S} X_{ik}$

X_{ij} represents the abundance of the ith species in the jth SU, X_{ik} is the abundance of the ith species in the kth SU.

Various combinations of the samples were used in the cluster analysis. Firstly, the water and sediment samples were analysed together to assess any seasonal trends that may have occurred. The gut content samples were then added to the matrix to analyse any broadscale patterns which may be present. Finally, the samples from each month were analysed together, to check whether the gut content samples clustered more closely to one particular dietary source. Various statistical packages were employed to interpret the data. A package programmed by T.R. Williams (University of Liverpool) was used to produce similarity matrices, which were then clustered using Systat.

RESULTS

Water analyses

The chlorophyll concentrations plotted are those determined using the Lorenzen (1967) technique; values corrected for the presence of phaeopigment. These values are generally different from those obtained using the trichromatic equations developed by Jeffrey & Humphrey (1975), since the absorbance readings are sensitive to the presence of accessory chlorophyll pigments and phaeopigments (Patterson & Parsons, 1963; Lorenzen, 1967).

The total chlorophyll levels did not differ greatly between the two heights sampled (Fig. 3.1a), but there were considerable seasonal differences. Chlorophyll concentrations peaked in July in 1991 and, in March 1992 towards the end of the study. From October to February concentrations remained between approximately 4 and 10 $\mu g\ l^{-1}$. Phaeopigment concentrations were usually above 5 $\mu g\ l^{-1}$, although occasionally negative values were recorded. Phaeopigment concentrations peaked in July and August at heights of 1 m and 2 cm above the seabed respectively (Fig. 3.1b). The ratio of chlorophyll to phaeopigment remained generally stable, except for a large peak in February 1992 (Fig. 3.1c).

T.P.M., P.I.M., and P.O.M. in the water samples also did not differ much between sampling heights except in May 1991 and May 1992 (Figs 3.2a-c). It should be noted that the standard errors were large on these occasions. P.I.M. was greater at a height of 1 m than at 2 cm in June 1991, with the reverse occurring in May 1992. T.P.M. remained greater than 2 $mg\ l^{-1}$ throughout the sampling period, reaching a maximum of almost 20 $mg\ l^{-1}$ in May 1991. After May 1991 the T.P.M. gradually declined to lower levels,

remaining relatively stable between August 1991 and February 1992, after which concentrations increased (Fig. 3.2a). P.I.M. peaked at both sampling heights in June and November 1991, and in May 1992 at the 2 cm sampling height (Fig. 3.2b), but remained below 2 mg l^{-1} during the rest of the sampling period. P.O.M. concentrations fluctuated considerably from April to July 1991, but showed a general decline and then remained low from August until January 1992, after which concentrations increased (Fig. 2.c). The ratio of P.I.M. to P.O.M. was always less than 3, and usually less than 1, but displayed maxima in June and November 1991 at both sampling heights (Fig. 3.2d).

The volume of particles in the water (Fig. 3.3a) was always greater than 0.25 mm^3 l^{-1}, and usually more than 0.5. The highest values occurred in the July 1 m sample (3.07 mm^3 l^{-1}) followed closely by the May 1992 2 cm sample (2.74 mm^3 l^{-1}). A peak also occurred in the water sampled from both heights in March 1992. The number of particles greater than 2.4 μm in the water varied between 4 and 49 particles μl^{-1}, but was usually between 7 and 15 particles μl^{-1}(Fig. 3.3b). Small particles (< 5 μm) were dominant in the water samples taken at both sampling heights. Particles less than 10 μm (and often those less than 5 μm) account for 50% of the total volume of particles.

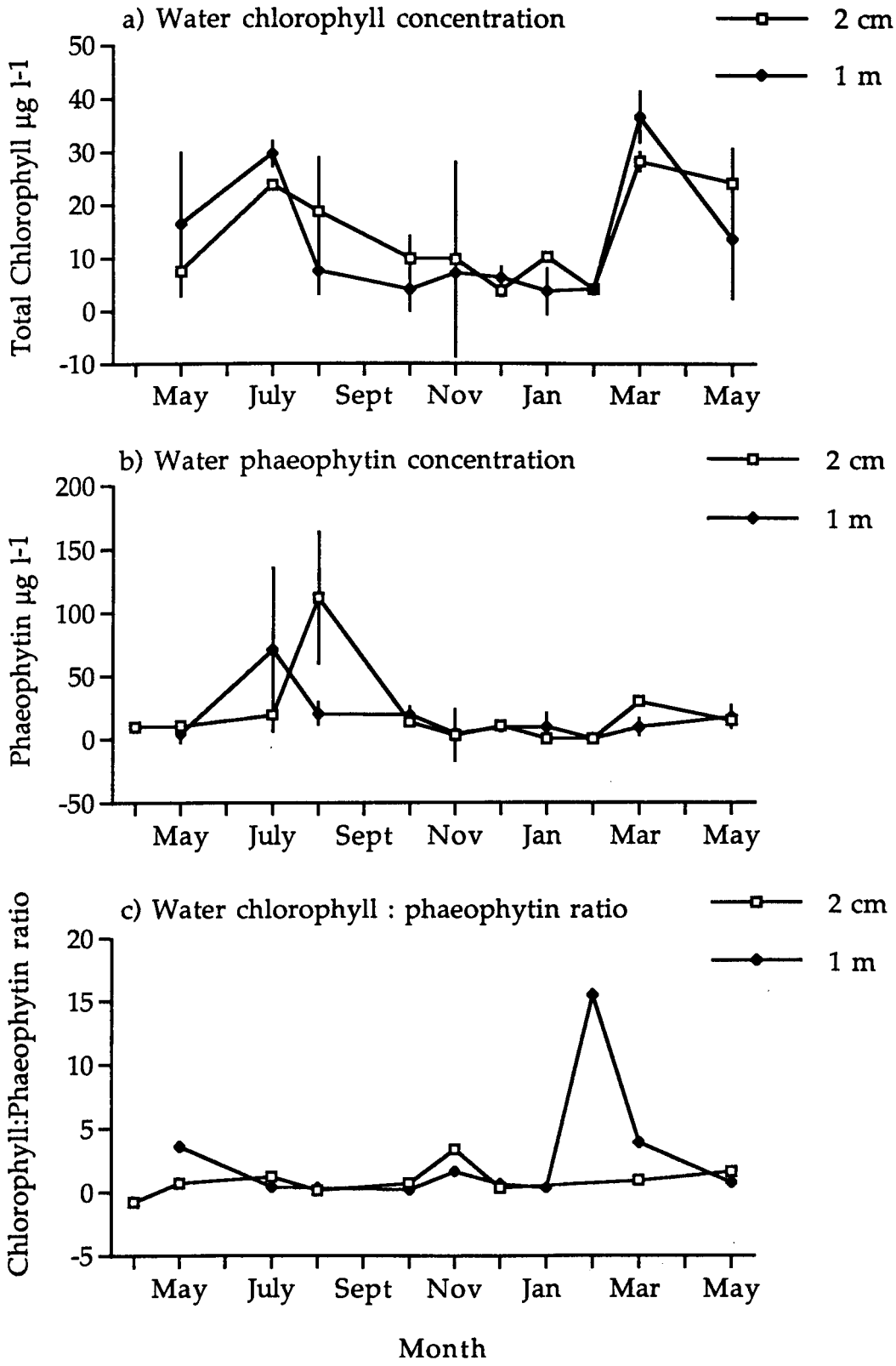


Fig. 3.1a-c) Total chlorophyll and phaeophytin concentrations and the chlorophyll : phaeophytin ratio in the water samples taken from April 1991 to May 1992. Water samples were taken at heights of 2 cm and 1 m from the seabed. Points represent means of 2 determination (± standard errors where large enough, for chlorophyll and phaeophytin graphs).

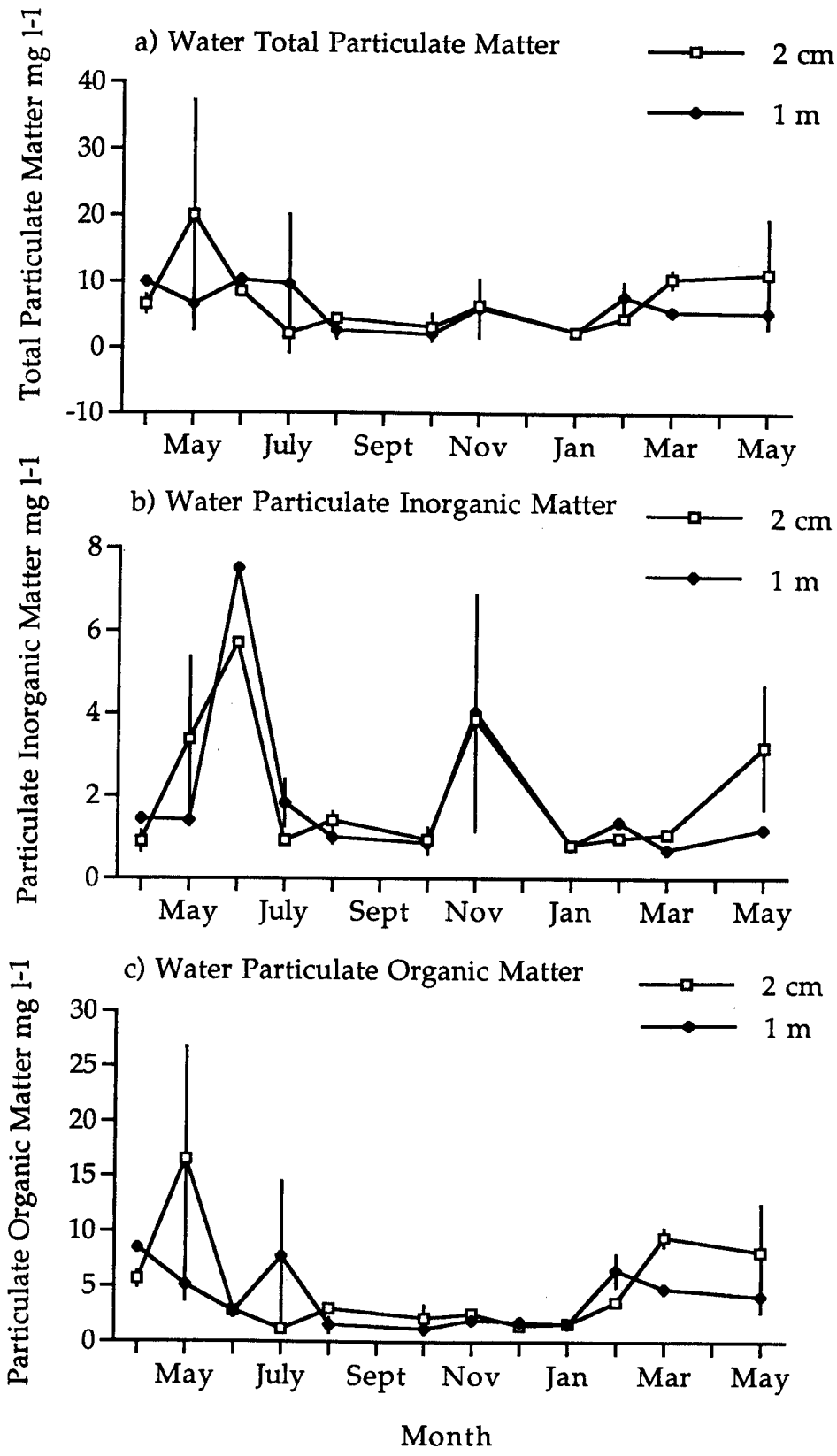


Fig. 3.2a-d) Total particulate matter, particulate organic matter, particulate inorganic matter, and the P.I.M.:P.O.M. ratio in the water samples taken from April 1991 to May 1992. Water samples were taken at heights of 2 cm and 1 m from the seabed. Points represent means of 2 determination (± standard errors where large enough, for graphs a-c).

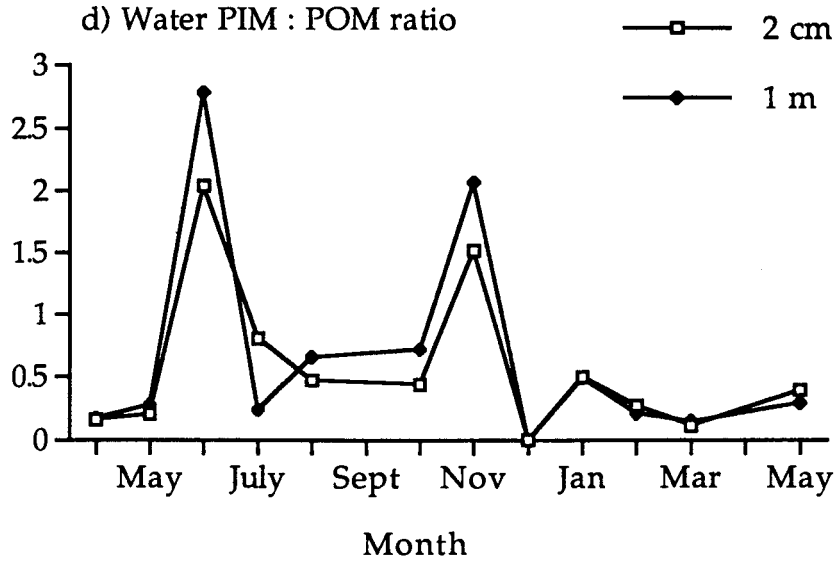


Fig. 3.2a-d) continued Total particulate matter, particulate organic matter, particulate inorganic matter, and the P.I.M.:P.O.M. ratio in the water samples taken from April 1991 to May 1992. Water samples were taken at heights of 2 cm and 1 m from the seabed. Points represent means of 2 determination (± standard errors where large enough, for graphs a-c).

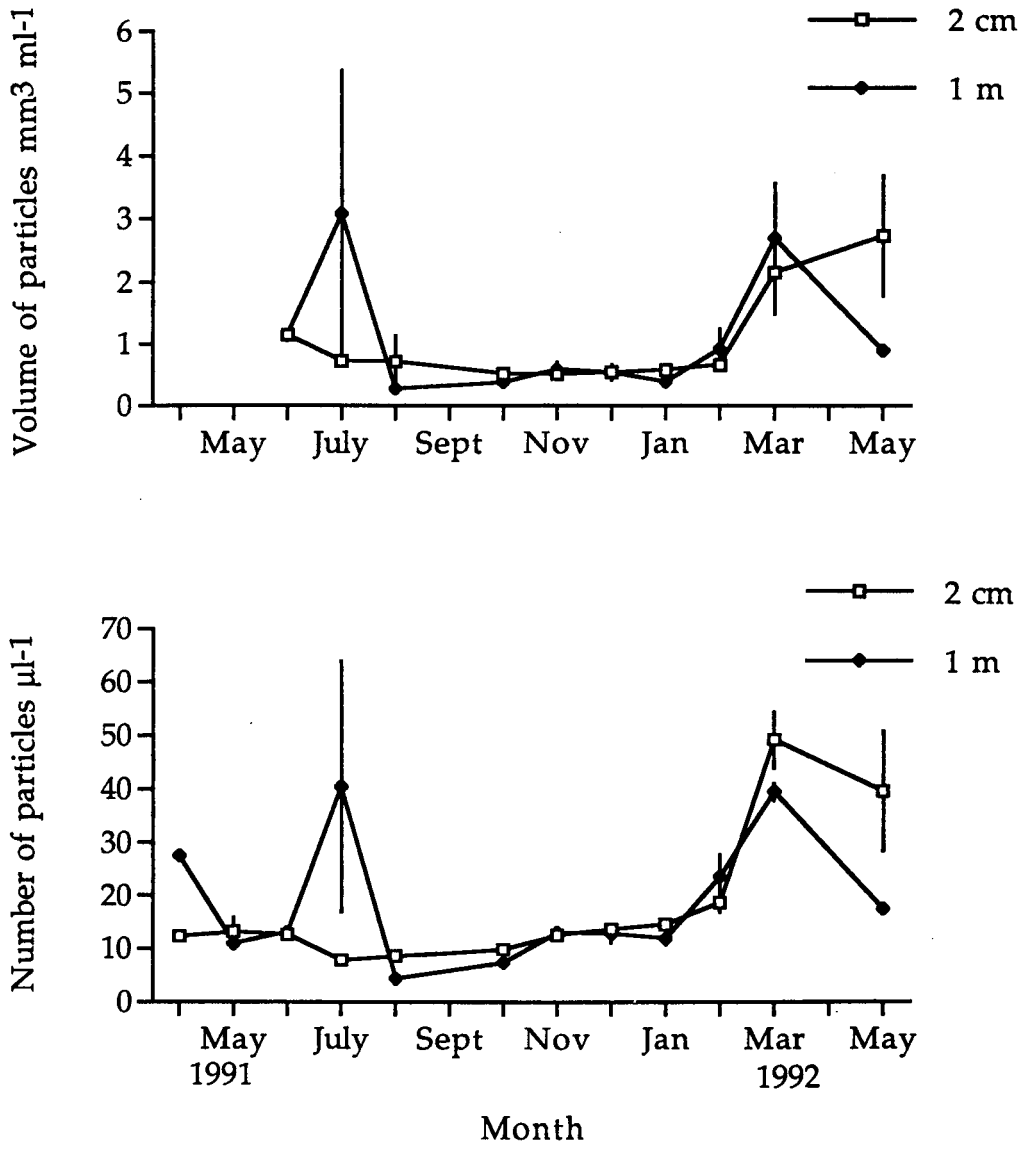


Fig. 3.3 The mean (± standard errors where large enough to be plotted) number and volume of particles in water sampled at 2 cm and 1 m above the seabed from April 1991 to May 1992.

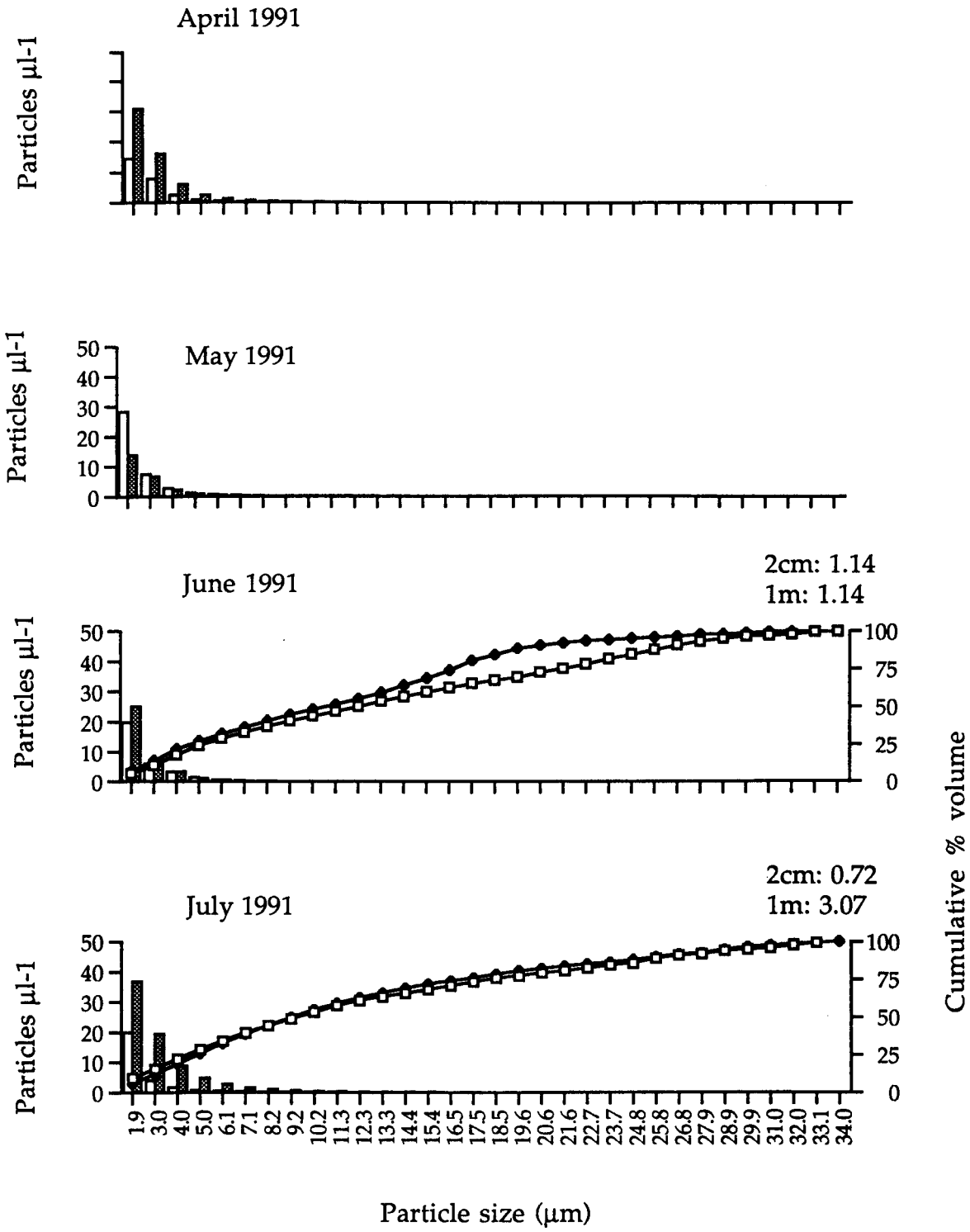


Fig. 3.4 Size frequency histograms of the particles in water sampled at 2 cm and 1 m above the seabed during the months indicated. Note that the size frequency data are plotted on two scales. The cumulative percentage volume of particles is also shown, as well as the total volume of particles (in µm-3 ml-1) in the sample (shown above the cumulative % volume axis).

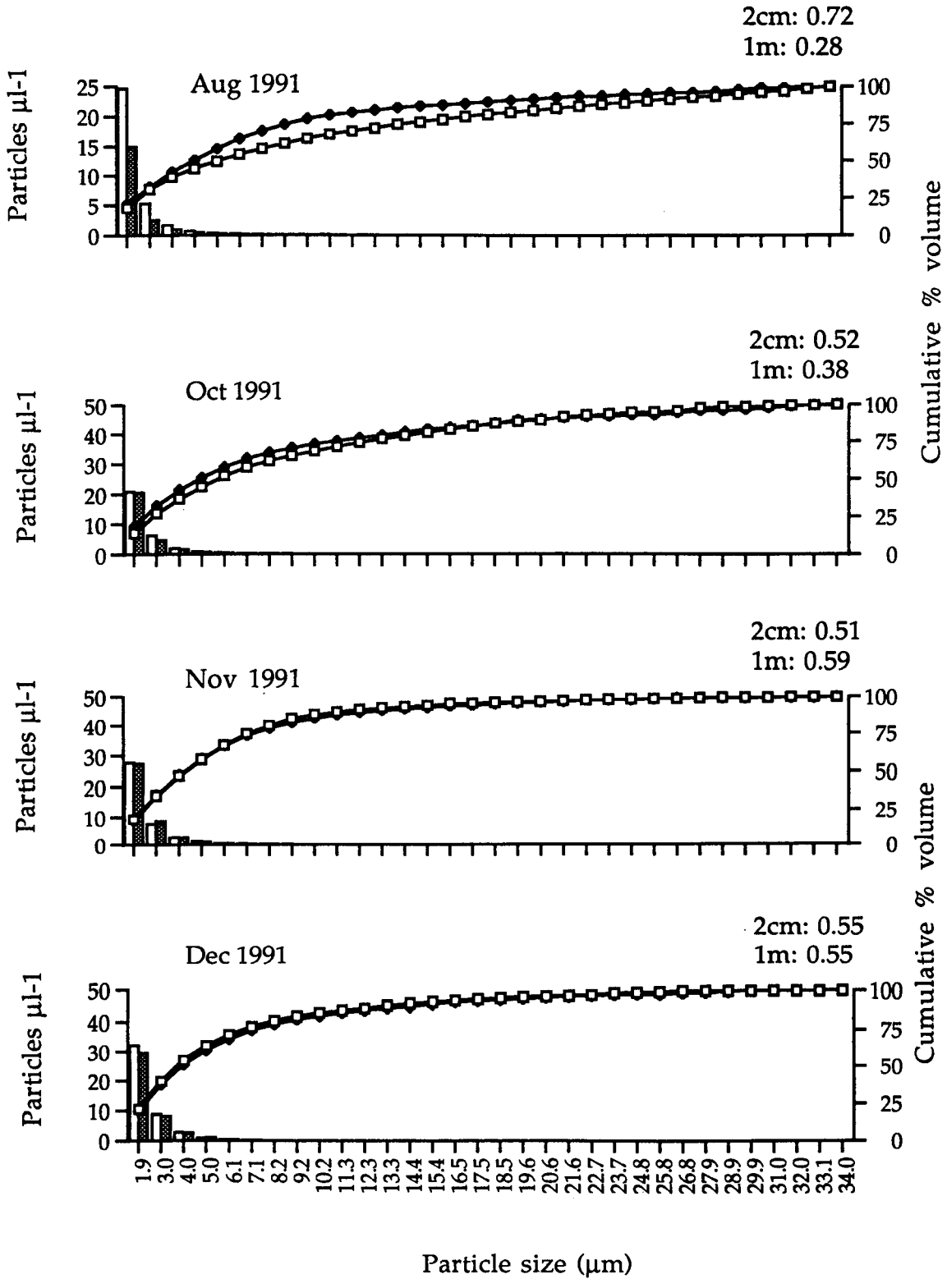


Fig. 3.4 continued. Size frequency histograms of the particles in water sampled at 2 cm and 1 m above the seabed during the months indicated. Note that the size frequency data are plotted on two scales. The cumulative percentage volume of particles is also shown, as well as the total volume of particles (in µm-3 ml-1) in the sample (shown above the cumulative % volume axis).

□ 2 cm ▩ 1 m —□— 2 cm —◆— 1 m

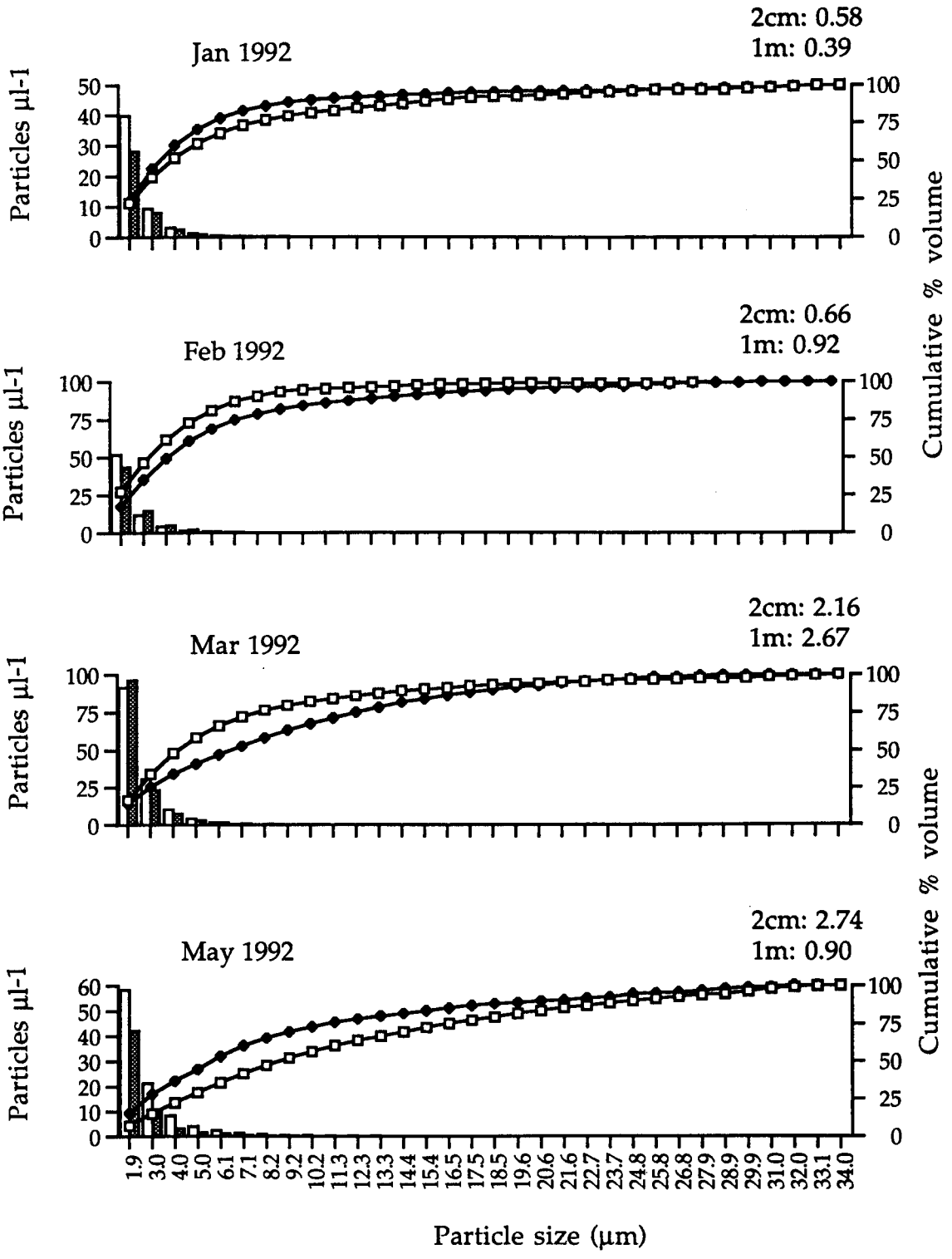


Fig. 3.4 continued. Size frequency histograms of the particles in water sampled at 2 cm and 1 m above the seabed during the months indicated. Note that the size frequency data are plotted on two scales. The cumulative percentage volume of particles is also shown, as well as the total volume of particles (in µm-3 ml-1) in the sample (shown above the cumulative % volume axis).

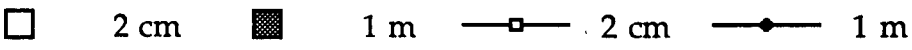


Table 3.1 The approximate particle size (μm) below which accounts for 50% and 75% of the total volume of particles in the water samples taken from 2 cm (W0) and 1 m (W1) above the seabed.

	50 % threshold		75 % threshold	
MONTH	W0	W1	W0	W1
June 1991	11	11	22	17
July 1991	9	9	20	17
Aug 1991	5	5	14	9
Oct 1991	6	5	12	10
Nov 1991	5	5	7	7
Dec 1991	4	4	7	8
Jan 1992	4	4	8	6
Feb 1992	3	4	6	7
Mar 1992	4	7	7	12
May 1992	8	5	15	9

Particles less than 20 μm, and often those less than 10-15 μm, account for 75% of the total volume of particles (Fig. 3.4 and Table 3.1). Little difference in cumulative percent volume occurred between the two sampling heights. Where differences did occur there was no consistent pattern; the particle size spectra were not consistently different between heights.

Sediment analyses

The sediment chlorophyll reached maximum levels in August 1991 (Fig. 3.5a), later than the water samples, but phaeopigment levels peaked in July (Fig. 3.5b). The ratios of chlorophyll to phaeopigment of the sediment samples were also more variable than in the water samples, but showed a general, though erratic, rise (Fig. 3.5c).

The P.O.M. in the sediment gradually increased from April 1991 to maximum levels in July 1991, after which the P.O.M. declined until March

1992 when concentrations began to rise again (Fig. 3.6). There were also smaller increases during November and December 1991.

Diatom assemblages

Due to the sampling differences between the water, sediment and gut content samples, Figure 3.7 can only be considered as semi-quantitative at best. Comparisons within certain sample types can be made however.

The number of diatoms in the water sampled at 2 cm above the seabed decreased from May to July, and from July to December 1991, and increased again in March 1992. The number of diatoms in the water from 1 m above the seabed followed the same pattern as that from 2 cm, except in July, when the number of diatoms remained high. Except for the samples taken in July the number of diatoms at the two sampling heights were very similar. Within the sediment samples, the number of diatoms increased from May to July, then declined to very low numbers in December, before increasing again in March 1992. The numbers of diatoms in the gut contents of *P. maximus* were highest and at similar levels in May, July and December 1991, but dropped in March 1992. In the gut contents of *A. opercularis* the numbers of diatoms were again usually high for most of the year, but dropped considerably in December.

The size frequency distributions (Fig. 3.8) of the centric and cocconeid diatoms from the gut contents of *P. maximus* and *A. opercularis* were significantly different in July and December 1991 and in March 1992, but not in May 1991 (Table 3.2). The majority of the centric and cocconeid diatoms measured were less than 35 μm in diameter, except in July, when the majority were less than 25 μm.

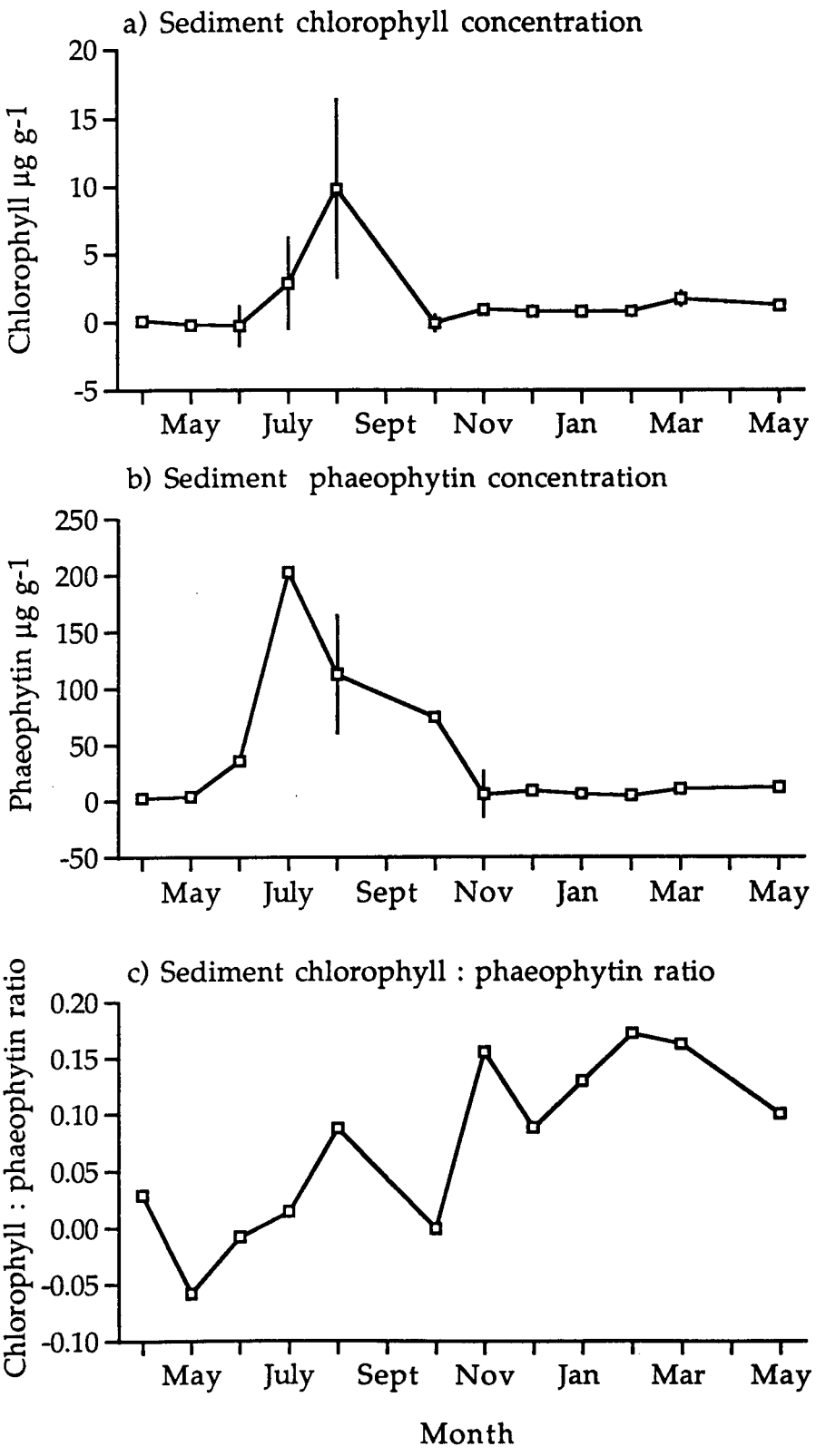


Fig. 3.5a-c) Total chlorophyll and phaeophytin concentrations and the chlorophyll : phaeophytin ratio in the sediment samples taken from April 1991 to May 1992. Points represent means of 3 to 6 determinations (except October 1991, where n=9). Standard errors are plotted, where large enough, for the chlorophyll and phaeophytin graphs.

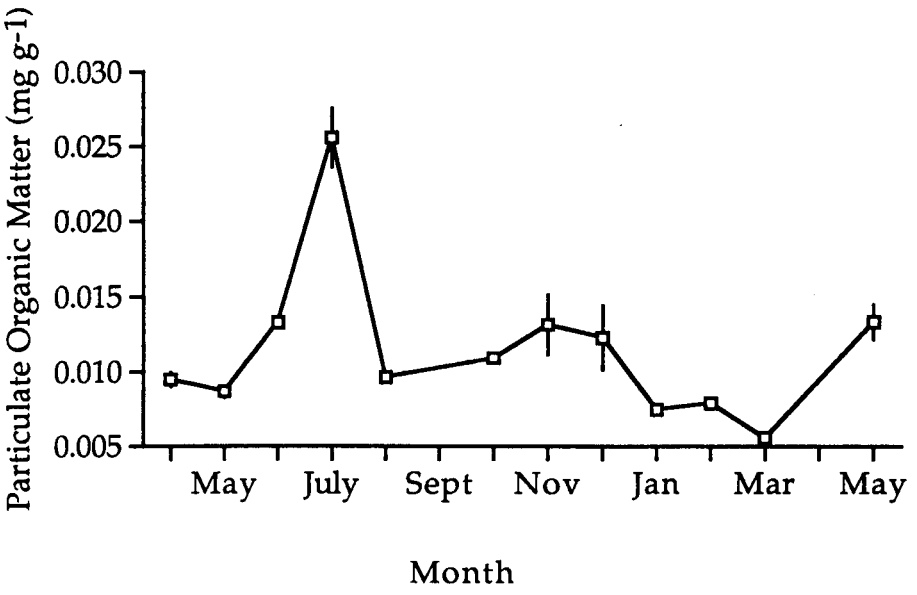


Fig. 3.6 Particulate organic matter in the sediment samples taken from April 1991 to May 1992. Points represent means of 3 to 6 determinations (except October 1991, where n=9). Standard errors are plotted where large enough.

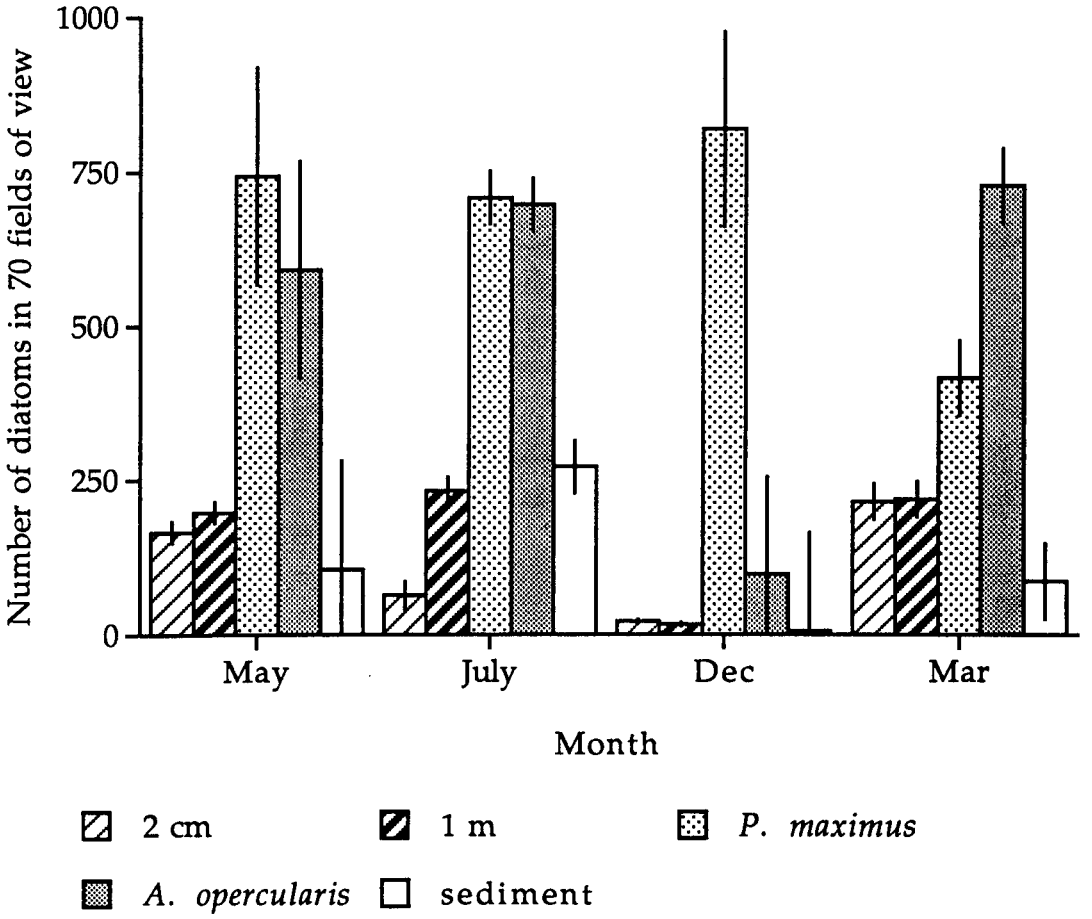


Fig. 3.7 The number of diatoms counted in water samples collected from heights of 2 cm and 1 m above the seabed, *P. maximus* and *A. opercularis* gut contents, and sediment samples collected from cages on the seabed. Counts are totals standardized to 70 fields of view at a magnification of x500, each bar represents the mean number (± standard error) found during the months of May 1991, July 1991, December 1991 and March 1992. n = 4 for water samples and n = 8 for gut content and sediment samples.

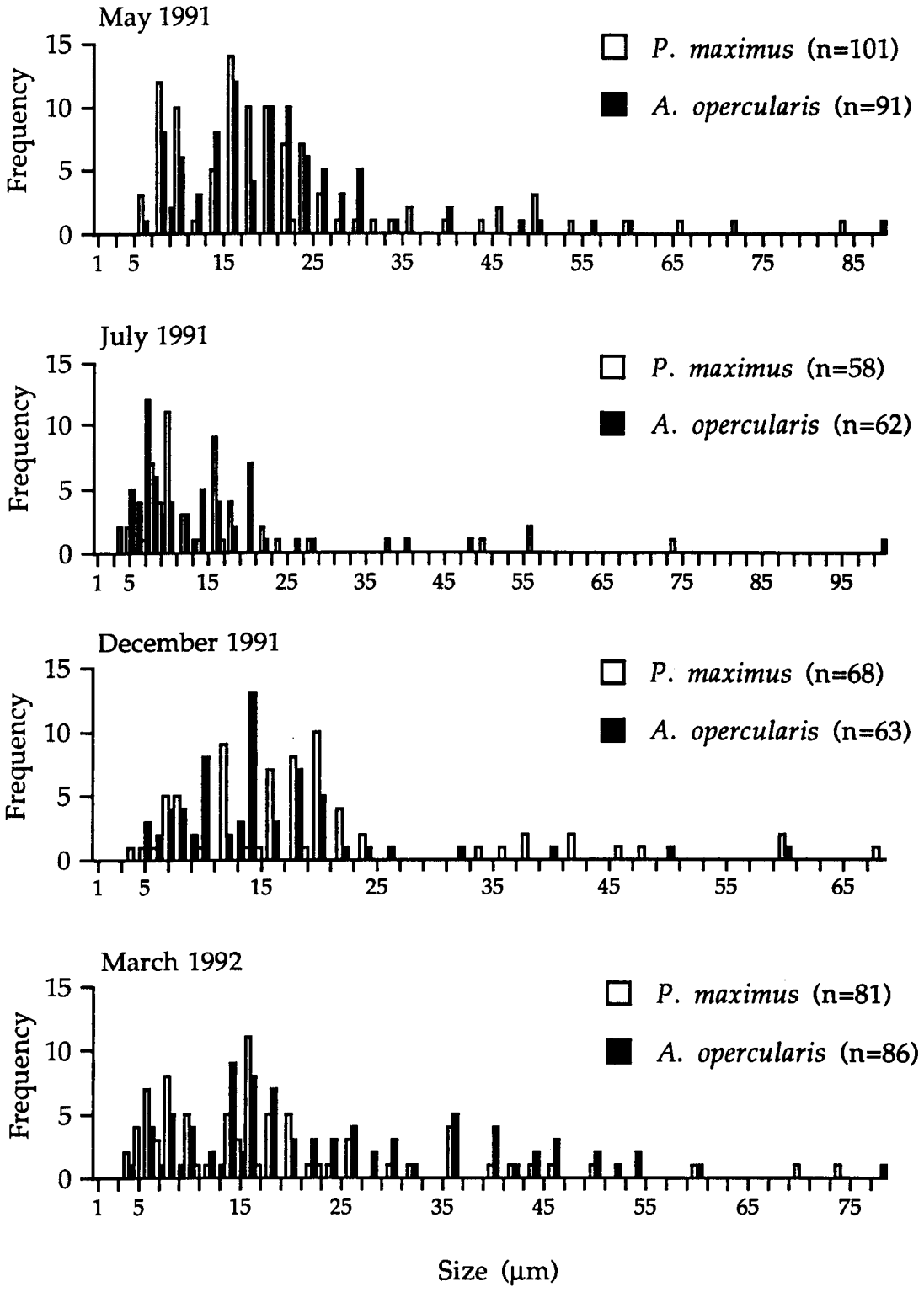


Fig. 3.8 Size frequency histograms of the centric and cocconeid diatoms measured in the gut contents of *P. maximus* and *A. opercularis* collected from cages on the seabed during the months of May 1991, July 1991, December 1991 and March 1992. Size frequency distributions of the diatoms in the gut contents of *P. maximus* and *A. opercularis* were significantly different during the months of May 1991, July 1991, December 1991 and March 1992 (Kolmogorov-Smirnov two sample tests).

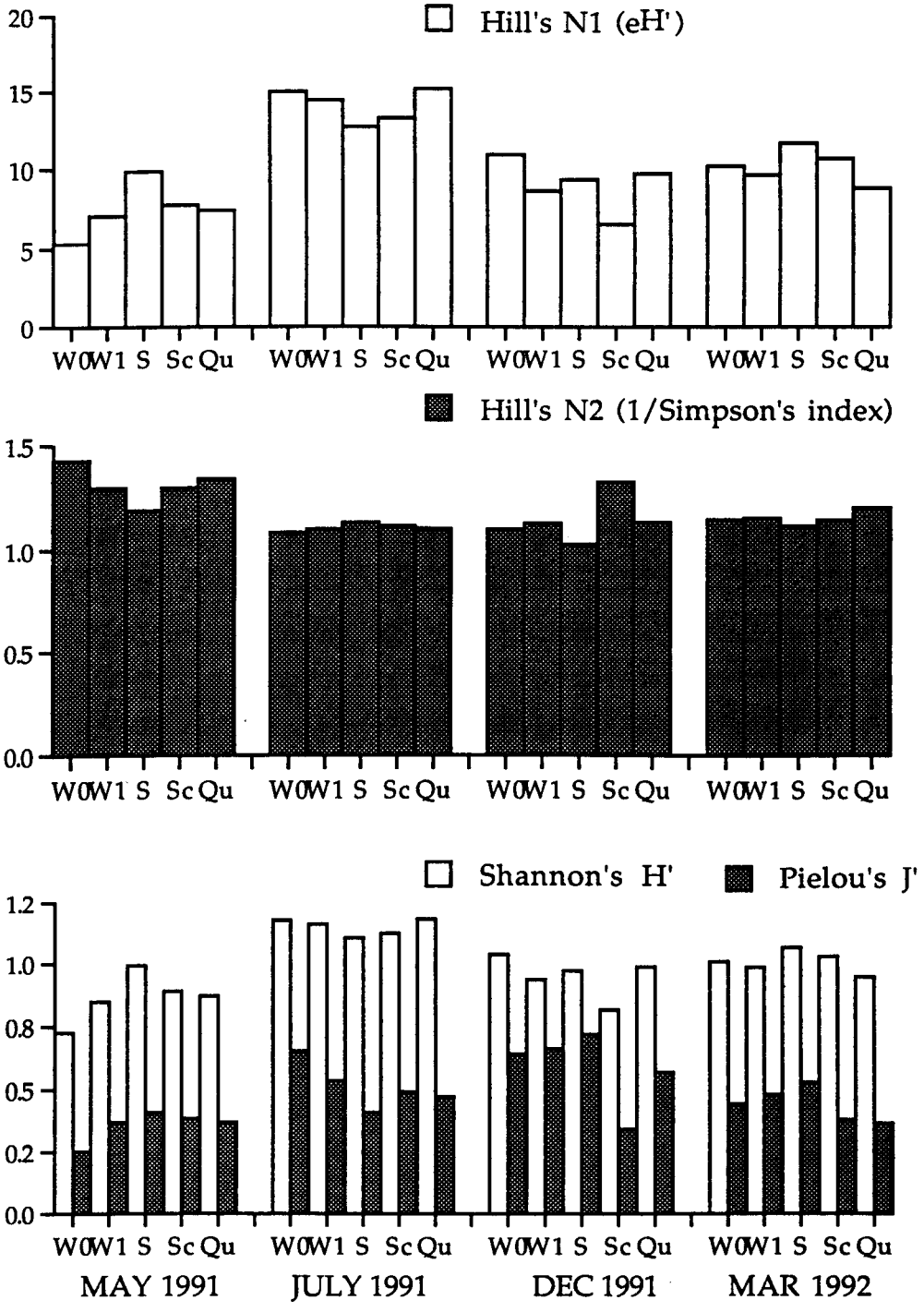


Fig. 3.9 Diversity (Shannon's H' and Hill's N1 and N2) and evenness (Pielou's J') indices of the diatom assemblages found in water sampled at heights of 2 cm (W0) and 1 m (W1) above the seabed, *P. maximus* (Sc) and *A. opercularis* (Qu) gut contents, and sediment (S) sampled from the seabed. n=4 for water samples and n=8 for sediment and gut content analyses.

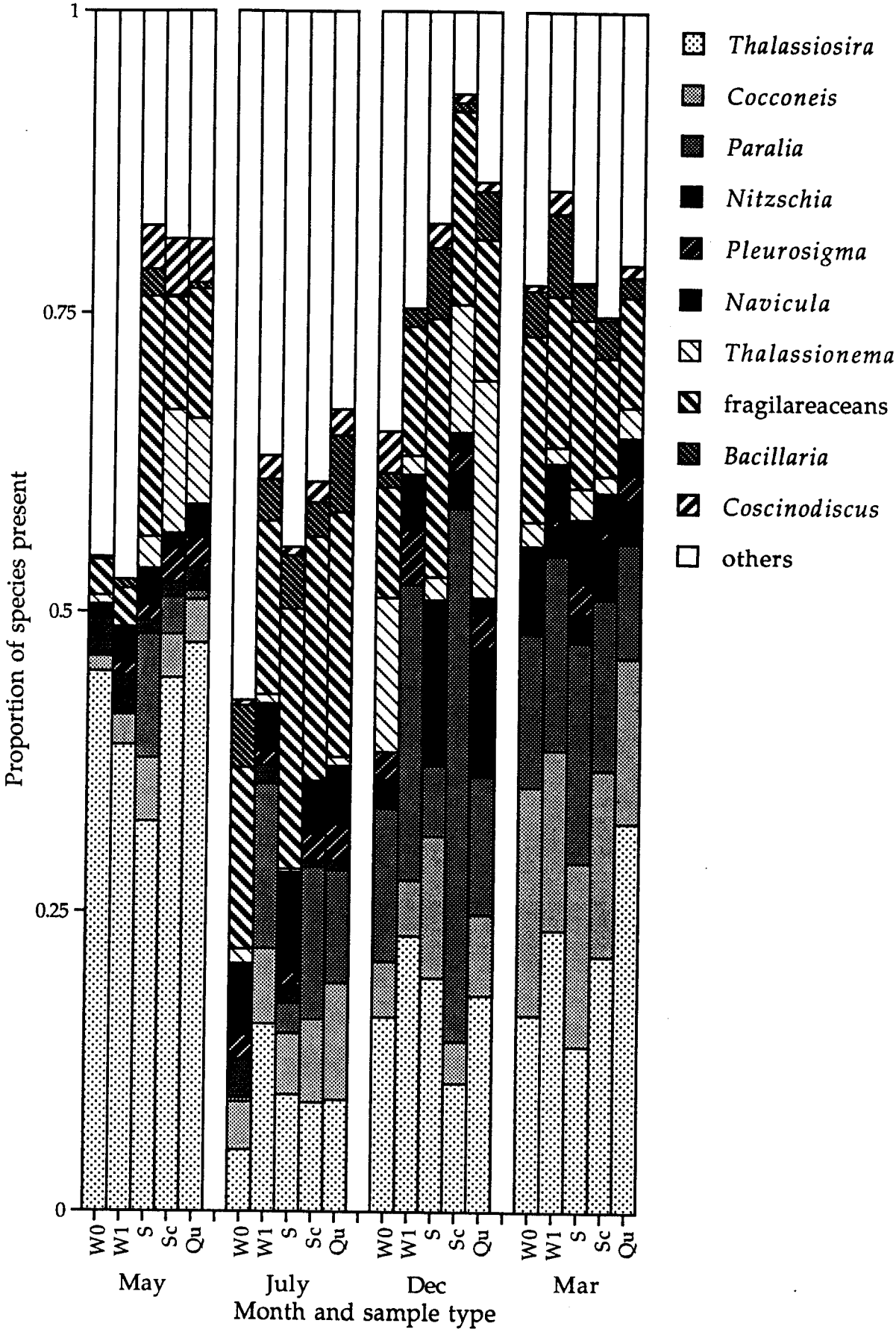


Fig. 3.10 The proportions of the ten most overall abundant diatom species in the water sampled at heights of 2 cm (W0) and 1 m above the seabed, *P. maximus* (Sc) and *A. opercularis* (Qc) gut contents, and sediment (S) sampled from the seabed.

Table 3.2 Kolmogorov-Smirnov tests to compare the size distributions of the centric and cocconeid diatoms measured in the gut contents of *P. maximus* and *A. opercularis* sampled during May, July and December 1991, and March 1992. n1 and n2 represent the sample sizes from the gut contents of *P. maximus* and *A. opercularis* respectively.

Month	n1	n2	K	P
May 1991	101	91	0.951	NS
July 1991	58	62	2.044	< 0.002
Dec 1991	68	63	3.343	< 0.002
Mar 1992	81	86	2.557	< 0.002

The species diversity indices (Shannon's H' and Hill's N1), gave very similar patterns of results (Fig. 3.9). Species diversity was highest during July, with the water and *A. opercularis* gut content samples being the most diverse. In May the species diversity was generally lower than in the other months analysed. Within the May samples the species diversity was highest in the sediment samples, and lowest in the water sampled from 2 cm above the seabed. In December the species diversities of the sediment, water from 1 m above the seabed, and the *A. opercularis* gut contents were very similar, whilst that of the water from 2 cm above the seabed was slightly higher. The species diversity of the *P. maximus* gut contents in December was lower than on any other sampling occasion. In March 1992 the species diversity was greater than that in December, and was slightly higher in the sediment and in *P. maximus* gut content samples. The species diversity index Hill's N2 was highest in May 1991, but was generally constant between July and December 1991, and March 1992, except for a peak in the diversity of the diatom assemblage in the gut contents of *P. maximus* in December 1991.

The proportions of the ten overall most abundant diatom species in the samples analysed are shown in Fig. 3.10. The proportions of these species

in the gut content samples were usually very similar to the proportions available in the water and sediment. In some months some diatom species were represented in the gut contents of both scallops and queens out of proportion to their availability. In May 1991, for example, the gut contents contained a larger proportion of *Thalassionema* than was available in the environment, the same occurred in December with regard to the *Thalassionema* and *Nitzschia* present in the *A. opercularis* gut content samples and *Paralia* in the gut contents of *P. maximus* . The proportions of species in the various samples in March 1992 were remarkably similar to each other.

The dendrograms formed in the cluster analysis were interpreted by inspection (Ludwig & Reynolds, 1988). Clusters were deemed to occur where there was a large change in distance between one linkage point and the next. The dendrogram formed from analysing the water and sediment samples showed, using both similarity coefficients, that two obvious clusters were present (Fig. 3.11). The samples taken during December formed one clearly separate cluster. The samples within the second cluster should be regarded as being fairly homogenous, although several sub-groups were apparent within it. The March 1992 samples tended to group closely together, and usually near the December samples. Using the Sørensen index, the water sample from 1m (W1) was determined to be rather distinct from the others, and clustered the water sample from immediately above the seabed (W0) from May with W0 from July. The Czekanowski index grouped both May water samples together, distinct from the other samples, with the July W0 sample linking the next closest to them.

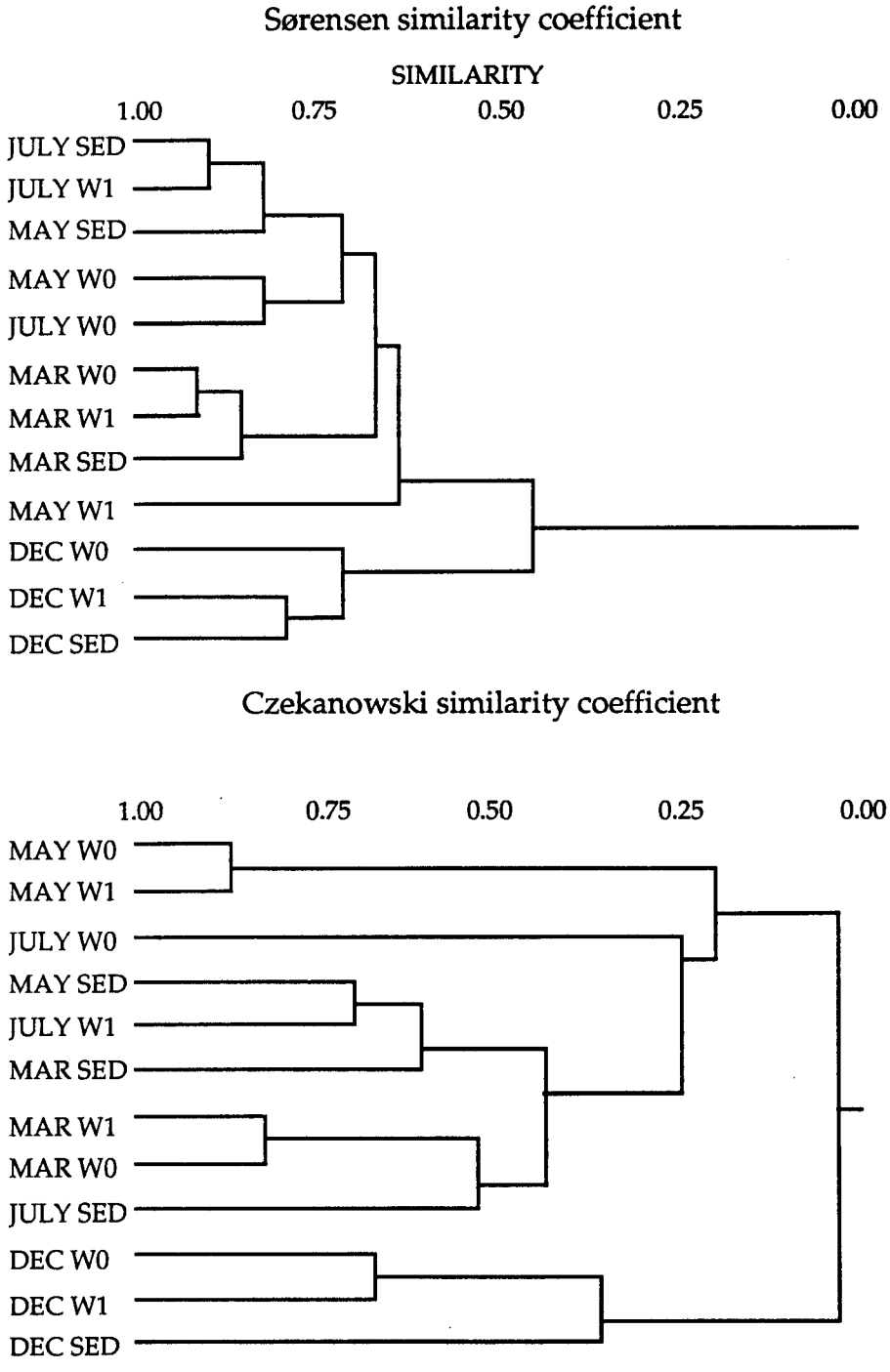


Fig. 3.11 Hierarchical cluster analysis of the diatom assemblages in water samples taken from 2 cm (W0) and 1 m (W1) above the seabed, and sediment samples (SED). The samples from all of the months were analysed together using the complete linkage (furthest neighbour) method of clustering on both Sørensen and Czekanowski similarity coefficients.

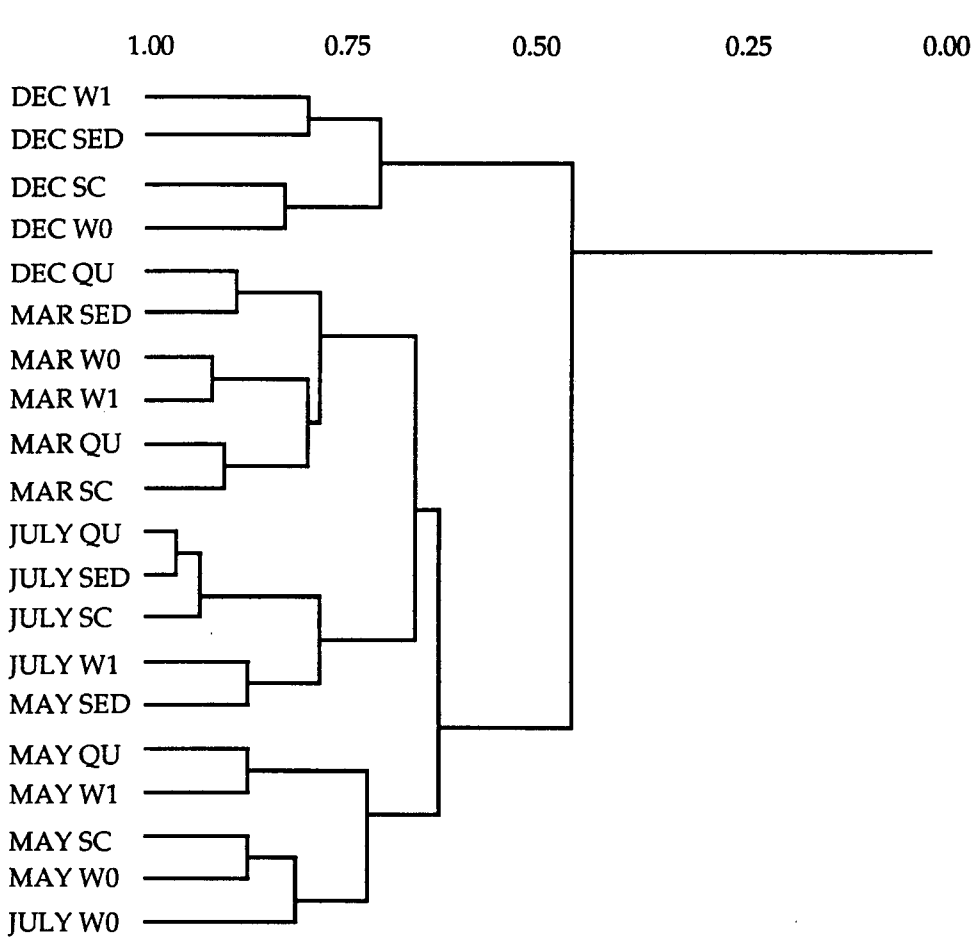


Fig. 3.12a Hierarchical cluster analysis of the diatom assemblages in water samples taken from 2 cm (W0) and 1 m (W1) above the seabed, sediment samples (SED) and the gut contents of *P. maximus* (SC) and *A. opercularis* (QU). The samples from all of the months were considered together, using the complete linkage (furthest neighbour) method of clustering on Sørensen similarity coefficients.

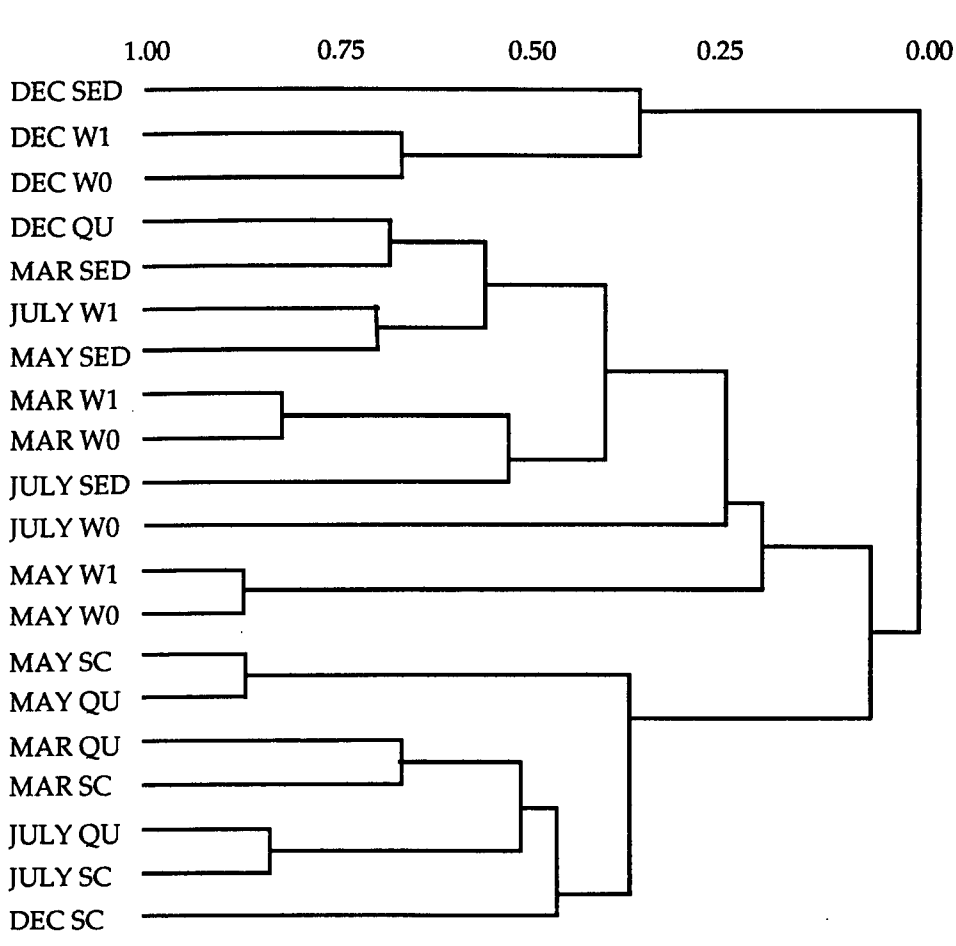


Fig. 3.12b Hierarchical cluster analysis of the diatom assemblages in water samples taken from 2 cm (W0) and 1 m (W1) above the seabed, sediment samples (SED) and the gut contents of *P. maximus* (SC) and *A. opercularis* (QU). The samples from all of the months were considered together, using the complete linkage (furthest neighbour) method of clustering on Czekanowski similarity coefficients.

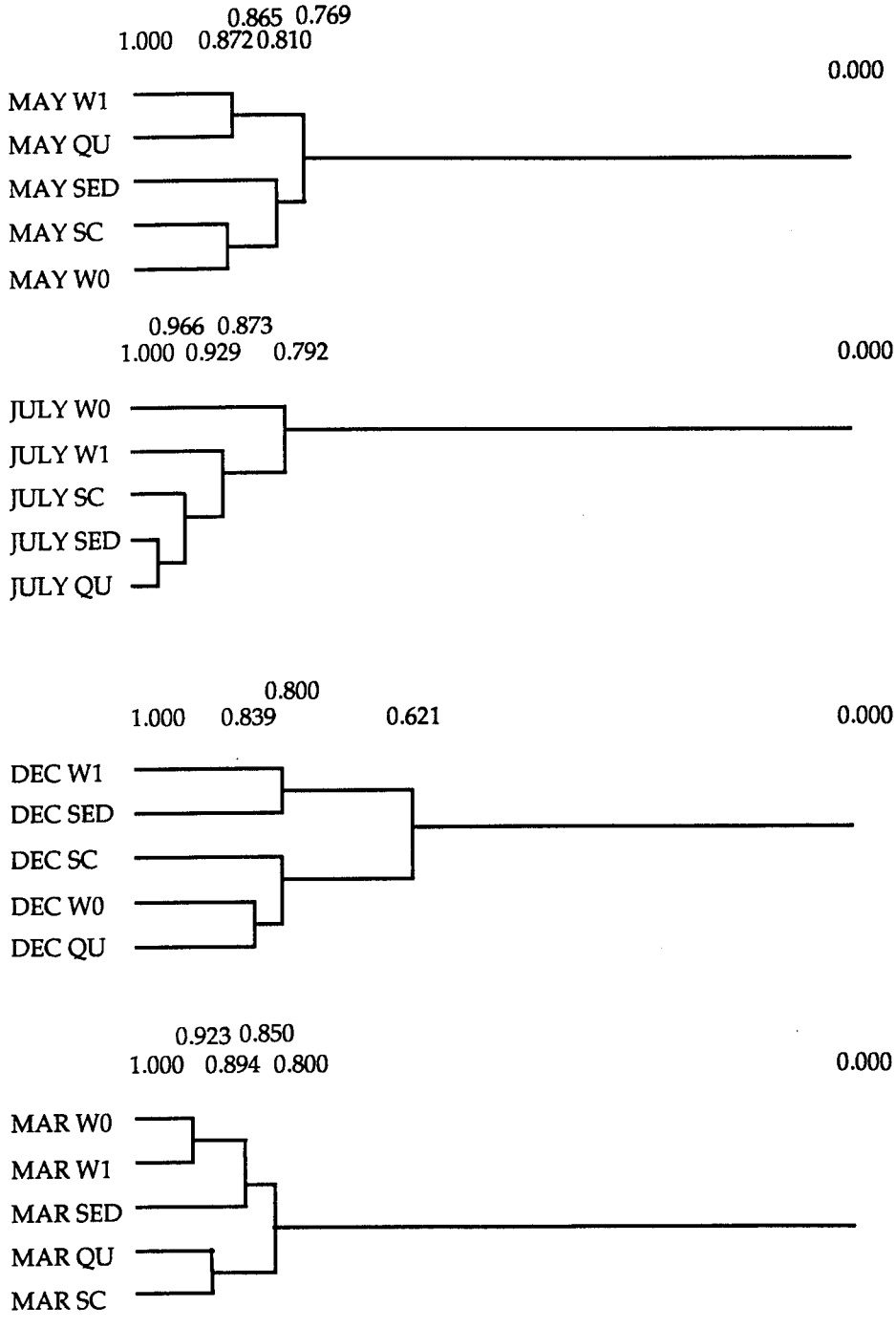


Fig. 3.13a Hierarchical cluster analysis of the diatom assemblages in water samples taken from 2 cm (W0) and 1 m (W1) above the seabed, sediment samples (SED) and the gut contents of *P. maximus* (SC) and *A. opercularis* (QU). Each month was considered individually using the complete linkage (furthest neighbour) method of clustering on Sørensen similarity coefficients.

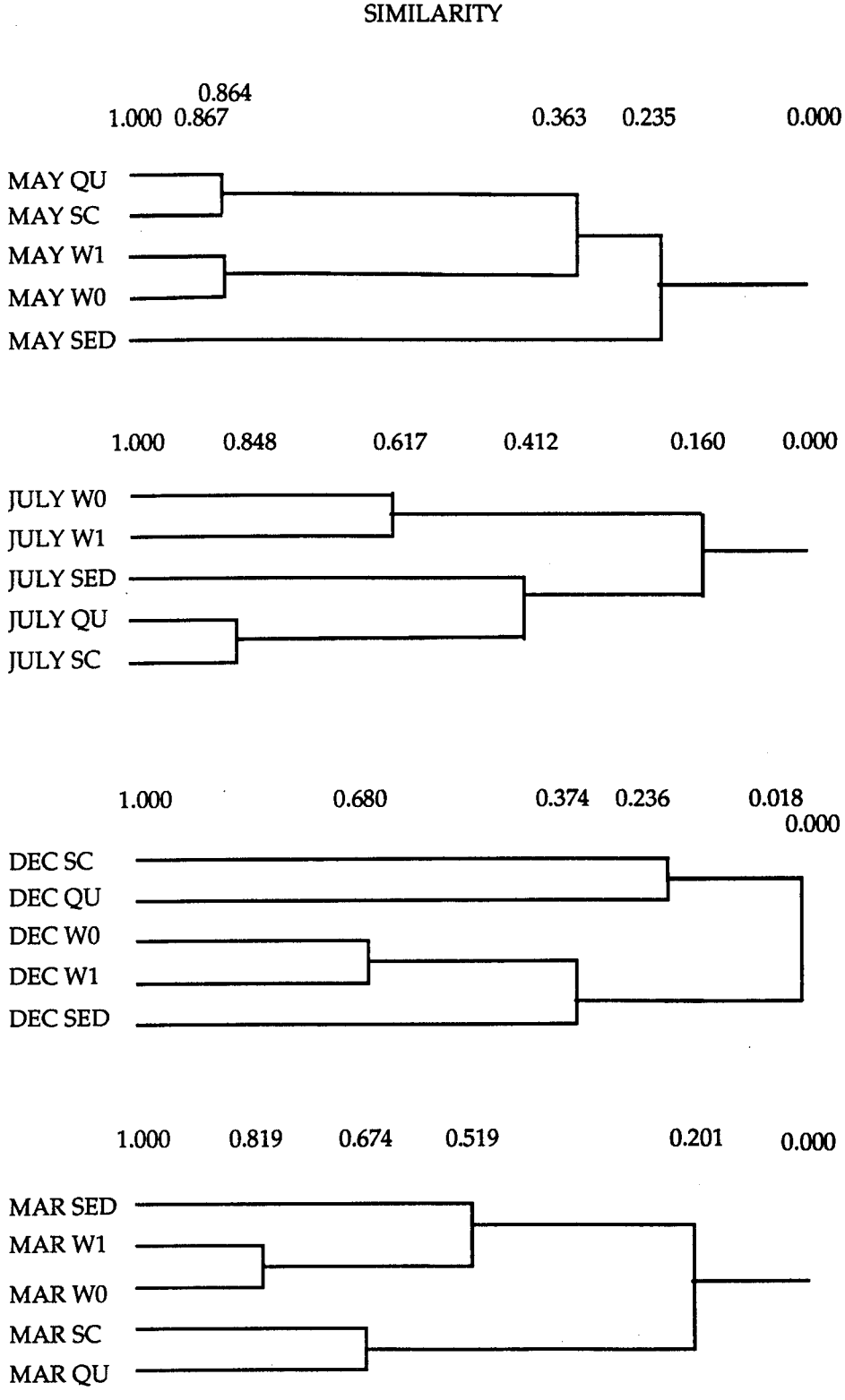


Fig. 3.13b Hierarchical cluster analysis of the diatom assemblages in water samples taken from 2 cm (W0) and 1 m (W1) above the seabed, sediment samples (SED) and the gut contents of *P. maximus* (SC) and *A. opercularis* (QU). Each month was considered individually using the complete linkage (furthest neighbour) method of clustering on Czekanowski similarity coefficients.

The dendrograms formed using all the samples again showed that two clusters occurred (Fig. 3.12). Using the Sørensen index, each month's samples generally clustered together - although there were several samples that were more similar to samples from other months, for example, the *A. opercularis* gut content assemblages in December, the July W0 and the May sediment samples. These samples still tended to cluster near the other samples taken within the same month.

Three clusters were formed from the Czekanowski similarity matrix. The gut content samples clustered together, except for the December *A. opercularis* sample, and the sediment and water samples taken in December formed a second cluster. Within the remaining cluster, the May W0 and W1 samples clustered together, as did the March W0 and W1 samples: the other samples were mixed together.

The interpretation of the dendrograms created for each month (Fig. 3.13) must be regarded as being very tentative, as the linkages are usually so close together that they could be regarded as being homogenous. When the Sørensen index was used, in July and December the gut content samples of *A. opercularis* clustered more closely than the *P. maximus* sample to one of the dietary sources. In May 1991 the *A. opercularis* gut content assemblage clustered most closely to that of the W1 sample, whilst *P. maximus* clustered most closely to the W0 sample. The sediment sample was more similar to the W0 and *P. maximus* group than the *A. opercularis* group. In March 1992 the gut content samples clustered most closely to each other, with the sediment sample being the next closest neighbour. The Czekanowski index gave more consistent results: the gut content samples always clustered most closely to each other, and in July, December and March the next most similar sample was the sediment

sample. In May the water samples were more similar to the gut content samples.

DISCUSSION

Methodological constraints

One of the problems encountered in this experiment was comparing diatom samples that originated from different sources. This was because they were necessarily sampled differently, and the gut content samples could not be easily quantified. One hundred diatoms were counted from each slide to alleviate this problem. The diatoms in the gut contents would also have undergone some digestion, which would bias the samples against the more weakly silicated planktonic species. Weakly silicated planktonic species such as *Chaetoceros* were observed in large numbers in the gut content samples, therefore this was probably not a serious problem.

The two similarity coefficients used employ different descriptors of the species in the sample (sampling unit or SU): the Sørensen index is based on a presence/absence matrix of species, whereas the Czekanowski index uses the actual abundance values. The Sørensen method therefore effectively regards all the species as being equally abundant; it is weighted towards rare species. The Czekanowski index on the other hand, is weighted towards the more common species. Elimination of the rare species within a data set is often employed: the occurrence of a rare species is often a matter of chance (Gauch, 1982) and would therefore be strongly influenced by sampling differences between samples. Most of the techniques used are only influenced slightly by rare species, as they represent such a small percentage of the overall information (Gauch, 1982). This last factor would not apply to presence/absence indices such as Sørensen's index. The elimination of the rare species from the data would reduce the bias of the Sørensen index, but increase it when using the

Czekanowski index. The two similarity indices are acknowledged to be different, but were chosen to counteract the biases within each of them.

Euclidean distance is a very commonly used coefficient of dissimilarity. It was not used in this study as it has been shown to occasionally produce spurious results (Wolda, 1981; Ludwig & Reynolds, 1988). It also weights common species very heavily, as it uses the square of the difference in abundance between species. The Czekanowski index (Percent Similarity or PS) has been shown to produce ecologically more interpretable results than many other measures, including Euclidean distance (Beals, 1984). Percent Dissimilarity (1 - PS) weights species abundance linearly, it is an intermediate measure between Euclidean distance and the coefficient of dissimilarity (1 - Sørensen's index, also called the coefficient of community, or CC) (Gauch, 1982).

Sørensen's index and the Jaccard coefficient are regarded as being the most satisfactory of the presence/absence indices in common usage (Clifford & Stephenson, 1975).

A commonly used method for clustering data is hierarchical cluster analysis (CA). Two different methods of hierarchical CA can be used: monothetic and polythetic. Monothetic methods sub-divide a group of SUs using first one characteristic, then another, in sequence. Polythetic methods assess the overall similarity of the SUs by considering several attributes simultaneously (Clifford & Stephenson, 1975). This is usually the preferred approach. In agglomerative polythetic methods clusters are formed by grouping individual SUs into clusters, until they form a single large cluster. Divisive polythetic classification starts with all the SUs in a

single cluster, and splits the cluster until each SU is the only member of a cluster.

The different agglomerative polythetic techniques use basically the same algorithm, but differ in how they determine the distance between SUs and clusters. Since the merging of SUs or clusters depends on the distance between them, different methods of measuring that distance can result in the formation of different clusters. Several different methods of CA should be tried and the results compared (Gauch, 1982; Ludwig & Reynolds, 1988). Single linkage CA is most often used in taxonomy, but it produces straggly clusters and quickly agglomerates very dissimilar samples. It is not usually appropriate for community ecology. The median, centroid and Ward's minimum variance techniques should be used with squared Euclidean distances (Norusis, 1990). The single linkage (nearest neighbour), complete linkage (furthest neighbour) and average linkage methods were tested in this study: the complete linkage method was used as it gave the most readily interpretable results. This method produces tight clusters of similar samples (Sokal & Sneath, 1963; Sneath & Sokal, 1973; Gauch, 1982). In complete linkage CA the distance between a sample and a cluster is defined as being equal to the distance to the furthest (least similar) sample in that cluster. When clusters merge, the distance between the clusters is the greatest distance found between a pair of samples, one coming from each cluster.

Temporal patterns in the benthic boundary layer

In temperate waters with marked seasonal changes in the pelagic system, a corresponding seasonality can be expected to occur in the benthos (Graf *et al.*, 1982; Graf, 1989). The patterns of seasonal changes in the water were

very similar at both sampling heights, showing peaks in July 1991 and March 1992. The only available surface chlorophyll *a* measurements are those taken routinely at the 'Cypris' station at 54° 05.5′ N, 4° 50′ W. Peak chlorophyll *a* concentrations were recorded in May 1991 and in July 1992.

The peak that occurs in my data in the March 1992 water samples is likely to have been caused by resuspension due to poor weather conditions. In the days immediately before the samples were collected there were north-westerly winds. Wind from this direction would probably cause the greatest resuspension of bottom sediments as the wind would have the greatest fetch, and the site would not be sheltered by nearby headlands. Although the winds were only force 3-5 (gentle-fresh breeze) the strongest gusts were force 7-8 (near gale and gale). It was also noted during the dive that the visibility at the seabed was less than 1 m. It is also possible that an increase in phytoplankton numbers occurred: Graziano (1988) found a small pre-bloom peak in diatom numbers in March 1987 at the Cypris site.

A small peak in the chlorophyll to phaeopigment ratio, the P.I.M. to P.O.M. ratio and the P.I.M. was also recorded in November 1991. The wind on the day of sampling and the two previous days swung from SE to SW to NW, at a force of 4-6 (moderate to strong breeze) with gale force gusts recorded on every day. It is therefore possible that there was resuspension of benthic sediment above the normal 'seasonal' levels. There was also a peak in the sediment chlorophyll to phaeopigment ratio and P.O.M. present. The sediment P.O.M. and phaeopigment concentration peaked in July due to the influx of sedimenting phytoplankton. The chlorophyll, however, peaked in August. This possibly reflects increased primary production by the microphytobenthos,

which may be caused by the increased nutrient availability due to the breakdown of phytoplankton species.

In August, October, November and January the chlorophyll levels (and during some months the T.P.M. and P.O.M.) were slightly higher at the 2 cm height than at the 1 m sampling height. Due to the high standard errors recorded (which probably reflect the patchy nature of plankton, Venrick, 1978) the differences between the two sampling heights would almost certainly not prove to be significant. The pattern was repeated on several occasions, however, and therefore may be of note. The resuspension of benthic diatoms has been demonstrated in field and laboratory studies (Grant *et al.*, 1986a; Grant & Bathmann, 1987; Shaffer & Sullivan, 1988; Wainright, 1990). Parmenter *et al.* (1983) also found, at depths of 62 m, resuspended diatoms in traps 3 m above the seabed after storms. Delgado *et al.* (1991) found that as much as 41% of the microphytobenthos was resuspended in field experiments. The presence of diatoms can also stabilize the sediment (Grant *et al.*, 1986a; Madsen *et al.*, 1993) by the production of mucus films, but most biological activity decreases the stability by bioturbation (Rhoads, 1973; Grant, 1983; Probert, 1984).

The value of the food in the benthic boundary layer

Although much of the resuspended sediment is refractory in nature (Grant & Hargrave, 1987) its food value is enhanced by the attached bacterial flora (Widdows *et al.*, 1979; Schleyer, 1981; Grant *et al.*, 1990; Wainright, 1990). The influx into the lower water column of resuspended sediment and its associated algal and bacterial microflora may be of great importance to benthic filter feeders during periods of the year when

production in the water column is low. Resuspended material would probably be more concentrated immediately adjacent to the sediment, which may explain the slightly higher chlorophyll concentrations at the 2 cm sampling height. Davis & Marshall (1961) found that the number of live resuspended benthic algae in the water column increased with increasing proximity to the sediment. Particles with a low specific gravity tend to have a higher organic content and are more labile than particles of a higher specific gravity (Taghon & Greene, 1992). On a unit volume basis low specific gravity particles will have a lower settling rate (Taghon & Greene, 1992), therefore the residence time of more labile particles will be longer than that of more refractory particles, with the net effect of increasing food quality.

Oviatt & Nixon (1975) found that resuspended sediment deposited in traps was significantly higher in total organic matter, organic carbon and nitrogen than the near-surface sediments on the bottom. Resuspended material also stimulated the production of heterotrophic bacteria and Protozoa, both free forms and, to a lesser extent, those attached to the sediment that remained in suspension (Wainright, 1987). The resuspended diatoms may also remain in the plankton for some time, where they have been found to contribute significantly to plankton productivity (Shaffer & Sullivan, 1988).

Field evidence of the effect of resuspension of sediments on growth of bivalves is contradictory. Undoubtedly there is a fine line between the enhancement and retardation of growth by resuspended sediment. Grant *et al.* (1990) demonstrated that the growth of *Ostrea edulis* was enhanced by moderate levels of resuspension of sediment, and Rhoads *et al.* (1984) predicted that the particulate organic nitrogen in the B.T.Z. would support

the growth of commercially important mollusc species. Frechette & Grant (1991) did not find that wind-driven resuspension enhanced the growth of *Mytilus edulis*. The amount of pseudofaeces produced will presumably influence whether resuspended sediment is beneficial, due to the energetic losses incurred.

The ratio of chlorophyll to phaeopigment is used as an indicator of food quality: the higher the ratio the better the quality of the food. The chlorophyll to phaeopigment ratio of the sediment increased in the autumn/winter, peaking in February after which it declined. This suggests that the quality of the sediment, as a potential food source, is higher during the autumn and winter than in the summer. During the summer the influx of phytoplankton to the sediment is great (Graf *et al.*, 1982; Davies & Payne, 1984). Much of the material will be decomposing resulting in high phaeopigment levels and low chlorophyll to phaeopigment ratios, but this food source is still likely to be nutritious.

Vahl (1980b) predicted that absorption of organic matter by *Chlamys islandica* would decline to zero when P.I.M. comprised 80% or more of the seston. Wallace & Reinsnes (1985) likewise predicted adverse effects on the growth of *C. islandica* if the P.I.M. : P.O.M. ratio exceeded 3.5 (if P.I.M. accounted for 78% of the seston). The P.I.M. : P.O.M. ratio did not exceed 3 on any sampling occasion, suggesting that the overall quality of food was good.

The influx of sedimenting phytoplankton to the benthos during the bloom period is considerable. Davies & Payne (1984) calculated that in the northern North Sea, during the period before the spring bloom, 50 mg C m^{-2} d^{-1} (20% of primary production) was sedimenting down to the seabed.

During the bloom this rose to 185 mg C m^{-2} d^{-1}, dropping to 115 (35% and 25% of primary production respectively) in early summer. Graf *et al.* (1982) calculated that the total input from the spring phytoplankton bloom (25th March to 19th April) was 11.5 g C m^{-2}. Using heat production budgets they found that the influx of phytoplankton material was 'burned' within 21 days. Graf *et al.* (1984) concluded that the transport of particles through the water column alone would not be sufficient to sustain the benthos, and that near-bottom transport of organic material must occur.

The effect of the sedimenting bloom on the benthos has also been studied. (Graf *et al.*, 1984; Christensen & Kanneworff, 1985) found it to be the trigger for enhanced benthic activity. Christensen & Kanneworff (1985) demonstrated a time lag between the occurrence of peak phaeopigment levels in the sediment and the gut contents of four benthic species. Peak concentrations were found first in *A. opercularis*, then in a second suspension feeder, then in the sediment, and finally in the gut contents of two infaunal deposit feeders. The phaeopigment peaks found in the gut contents of the suspension feeders were much narrower than those of the deposit feeders. This led the authors to suggest that suspension feeders have less time to utilize the sedimenting bloom.

This time lag in the utilization of the sedimenting bloom between the epifaunal and infaunal macrobenthos may be important with respect to behavioural differences between *P. maximus* and *A. opercularis*; *P. maximus* recesses and *A. opercularis* does not. Christensen & Kanneworff (1986) found that the uppermost part of the sediment is changed during the bloom to a 'fluid medium' with variable, but high, concentrations of phytoplankton material. Presumably this would have a greater impact on a recessed animal than one on the sediment surface.

The composition of the benthic boundary layer diatom communities

The diatom species found in the water and sediment consisted of two components: firstly a 'baseline' population of species (mainly *Thalassiosira, Paralia sulcata, Bacillaria paxillifer, Pleurosigma, Cocconeis, Actinoptychus senarius, Coscinodiscus, Thalassionema, Navicula* and *Nitzschia*). Within these genera the species present did sometimes vary. Throughout most of the year the *Thalassiosira* species present were *T. tenera* and *T. anguste-lineata,* with occasional *T. eccentrica.* However, in May 1991 *T. nordenskioldii, T. gravida, T. tenera, T. anguste-lineata* and *T. eccentrica* were found. This agrees with previous work performed in Port Erin Bay (Johnstone *et al.,* 1925) and at the Cypris site (Marasigan, 1986; Graziano, 1988).

The second group of species found were the more transient members of the phytoplankton bloom and summer species. This included species such as *Rhizosolenia, Chaetoceros, Guinardia flaccida, Licmophora, Grammatophora oceanica* var *subtilissima, G. marina, G. serpentina* and *Ditylum brightwellii.* The *Rhizosolenia* species found in July were thought to be *R. setigera.* This was found at the Cypris site from November 1982 to early March 1983 (Marasigan, 1986) and in Port Erin Bay in large numbers from March to May and again from September to October (based on mean data compiled during 1907-1920 by Johnstone *et al.,* 1925). Graziano (1988) also recorded its presence, but does not indicate in which month it was found. The *Chaetoceros* species found changed from being a mixture of *C. radicans* and *C. socialis* with some *C. cinctus* in May, to being dominated by *C. cinctus* in July. *C. cinctus* was not recorded by any of the previous authors, so the species may have been misidentified, as one form of *C. radicans* is very similar. (*C. cinctus* is

referred to as *C. cinctum* in Hendey, 1964, but as *C. cinctus* in Lebour, 1930, Hendey, 1974b and Hartley, 1986).

Graziano (1988) also recognized two distinct diatom assemblages; an autumn-winter group and a late-spring-summer group. His autumn-winter assemblage was comprised mainly of large benthic species such as *Paralia sulcata, Bacillaria paxillifer, Coscinodiscus* spp., *Actinoptychus,* and *Biddulphia* (mainly *B. sinensis* and *B. mobiliensis*). He did not find *Paralia* or *Bacillaria* throughout the year and does not include further details of his other autumn-winter assemblage species; presumably they did not occur in any great numbers during the rest of the year. Marasigan (1986) did find *Paralia* and *Bacillaria,* as well as *Thalassionema,* throughout the year. Graziano (1988) found *Thalassiosira* species throughout the year, but Marasigan (1986) only found them during the period August to October. No *Cocconeis* species were found by either author.

Although the results of Marasigan and Graziano differ in some respects, the broad pattern agrees with this study: the year-round presence of a 'core' group of species. Significant numbers of these omnipresent species were found throughout the sampling period, the presence of *Cocconeis* and *Pleurosigma* reinforcing the suggestion that most of the species are resuspended from the sediment. The species which form Graziano's autumn-winter group are therefore actually present throughout the year near the seabed. In the autumn and winter the seas are presumably rough enough to thoroughly mix the water column, bringing the benthic species to the surface. The turbulent transfer processes instigated by the movement of the water body over the seabed, combined with tidal mixing and wind-driven resuspension, must be sufficient to resuspend diatoms

into the lowest one metre of the water column throughout the whole year, but ordinarily not throughout the whole water column.

Hill's N1 and N2 indices represent the number of abundant and the number of very abundant species in the sample respectively (Ludwig & Reynolds, 1988). The various diversity indices indicate that overall no species were particularly dominant. Dominance by a small group of species was least apparent in May and July. At other times of the year the diatom assemblage was dominated by a few abundant species.

Relative importance of planktonic and benthic food

The importance of benthic diatoms in the diets of *P. maximus* and *A. opercularis* supports previous work performed on various pectinid species. The diatom species found in the gut contents of *A. opercularis* by Hunt (1925) were very similar to those found in this study. He also found the dinoflagellate *Dinophysis* in the gut contents in July, as found in this study (60 *Dinophysis* were recorded in 11 fields of view in one animal in my study). Aravindakshan (1955) reported the presence of diatoms in the gut contents of *A. opercularis,* but did not mention which species were found or their origin. Davis & Marshall (1961) found that benthic diatoms were more abundant than planktonic species in the gut contents of *Argopecten irradians.* This was also found to be the norm in the gut contents of *Placopecten magellanicus,* from depths of both 20m and 180m (Shumway *et al.,* 1987). Vernet (1977) examined the gut contents of the Patagonian scallop, *Chlamys tehuelcha,* in relation to the diatom assemblages in the plankton above the seabed and bottom sediment samples. She again found that benthic species were the dominant component of the gut contents. Interestingly, during the phytoplankton

bloom periods, consisting largely of *Thalassiosira* and *Chaetoceros*, the bloom species were found only very rarely in the gut contents (Vernet, 1977). This was not the case in my study, which is probably because it was carried out in strongly tidally mixed waters. For example, in July 11% of the diatoms in the gut contents of *A. opercularis* were *Chaetoceros*. Graf *et al.* (1984) found that bloom species took four days to sediment a depth of 19m (to the bottom sediment trap suspended in 21m of water). It is possible that in Vernet's study the bloom diatom species were not readily available to the scallops. Mikulich & Tsikhon-Lukanina (1981) found a wide range of animal and plant material in the gut contents of *Patinopecten yessoensis*, they also recorded the presence of large quantities of *Chaetoceros* and other planktonic species such as *Dytilum brightwellii*. Blevgrad (1915) gave no specific details of the gut contents of *Pecten septemradiatus*, *Pecten varius* and *A. opercularis*, but concluded that they were detritus feeders. Detritus and diatoms were also recorded in the gut contents of *Placopecten magellanicus* by Stevenson (1932, 1936, cited in Shumway *et al.*, 1987).

Work on the gut contents of other bivalve species includes that on the burrowing species *Macoma balthica* (Hummel, 1985) and the cockle *Anadara antiquata* (Kasigwa & Mahika, 1991), both of which found a greater occurrence of species from the phytoplankton. Newell *et al.* (1989) found that over two-thirds of the species in the gut contents of *Mytilus edulis* were benthic in origin. Field (1911, cited in Newell *et al.*, 1989) also found a large proportion of the diatoms in the gut contents were benthic in origin. Paulmier (1972) found that benthic species of diatoms dominated the gut contents of the oyster *Ostrea edulis* from March to December, except in July when phytoplanktonic species accounted for over 68% of the diatoms found. Petersen (1908) and Petersen & Jensen (1911)

likewise concluded that the oyster was a detritus eater. It is interesting that Blevgrad (1915) found small infaunal bivalves such as *Abra alba* and *Nucula nitida* had very different gut contents than larger infaunal and epifaunal bivalves such as *Mytilus edulis*. He attributed the difference in diet to be due to the small infaunal species feeding at a lower level than the other species. This makes an important point about the source of the diet in different bivalve species: being an infaunal species does not necessarily mean that the diet will consist of a greater proportion of benthic diatom species. Presumably it will depend upon the height that the siphons extend above the seabed. The polychaete *Spio setosa* has been shown to receive a lower organic quality diet when its sand tube is shortened to seabed level (Muschenheim, 1987b), and that its optimum tube height is 4-5 cm above the seabed (Muschenheim, 1987a). Since *P. maximus* and *A. opercularis* do not have siphons, it could be possible that the two species encounter different assemblages of particles, due to the small, but possibly significant, difference in feeding height (Grizzle *et al.*, 1992). *P. maximus* would presumably receive a greater proportion of mineral particles and particles of higher specific gravity, which are usually of low quality (Taghon & Greene, 1992). Under high flow conditions pectinids reduce feeding (Wildish *et al.*, 1992; Wildish & Saulnier, 1992) whereas infaunal species can continue within their burrows (Levinton, 1991).

The cluster analysis (Figures 3.11 and 3.12) also suggested the presence of two groups of diatom assemblages. December formed the most distinct cluster, probably due to a combination of the relatively small number of species found, and the low abundance of diatoms. The May samples were also distinct, more so when using the Czekanowski index, which could be

due to the large number of *Thalassiosira* found during that month, more than on any other occasion.

When analysing all of the samples using the Czekanowski index, which is not biased towards rare species, all of the gut content samples clustered together (except the December *A. opercularis* sample). This suggests that both species feed on a similar group of species throughout the year - that is, the 'baseline' species *Cocconeis, Thalassiosira, Pleurosigma, Bacillaria* etc. The gut content samples of P. *maximus* and *A. opercularis* within each month always clustered more closely to each other than to any other month, indicating a high degree of similarity between the common items in the diets of the two species. This is also suggested by the results of the individual month clusters when using the Czekanowski index. The gut content samples in the individual month dendrograms usually cluster more closely to the sediment samples, except in May when they were more similar to the water samples. Since the sediment is probably the major source of the diatoms in the water samples this is not unexpected. In May the sediment chlorophyll concentration is lower than at any other time of the year. There would therefore be fewer diatoms to resuspend than usual, and the diet would be influenced more by sedimenting phytoplankton species.

When using the Sørensen index the individual month analyses gave more variable results. The *A. opercularis* gut content samples clustered more closely to a single dietary source than the gut content samples of P. *maximus* did, except in March when the gut content samples clustered most closely to each other, and then to the sediment (as occurred when using the Czekanowski index). It could be expected that, since *P. maximus* are recessed, their gut content samples would cluster more closely to the

sediment samples than the gut content samples of *A. opercularis* would. This does not occur, however. During July, for example, when the chlorophyll concentration in the sediment was high, the gut content sample of *A. opercularis* clusters more closely to the sediment.

P. maximus may be exhibiting a greater degree of selectivity than *A. opercularis*. If so, it is probably against the rare species, since when the common items in the diets of *P. maximus* and *A. opercularis* are compared the diatom assemblages are very similar. Alternatively, *P. maximus* may be encountering diatom assemblages which were not adequately sampled in this experiment. Whether *P. maximus* can actually sort and utilize resuspended seston to a greater degree than *A. opercularis* will be addressed in Chapter 4.

The diets of *P. maximus* and *A. opercularis* both contain the same core of diatom species, which are present throughout the year. *P. maximus* does not feed on exactly the same dietary items as *A. opercularis*. This may be due to either behavioural differences between them; *P. maximus* recessing into the sediment and receiving a different diet, or that *P. maximus* is exhibiting more selection. If *P. maximus* is selecting to a greater extent than *A. opercularis* it may be because *P. maximus* receives a lower quality diet, due to being recessed.

CONCLUSIONS

The diatom species present in the benthic boundary layer fall into two categories. Firstly, there are the species which are resuspended from the benthos and which are present throughout the year. Secondly, there is a group of more transient species which sediment from the upper water

column or are resuspended from the benthos during times of increased productivity. This will obviously be a very important flux of energy into the water column.

The species resuspended from the sediment are resuspended to a height of at least one metre: microalgae were found to be available in suspension in the water throughout the year. Whether this algae can be utilized when it is present with resuspended refractory sediment particles will be discussed in Chapter 4.

The diatom assemblages in the gut contents of P. *maximus* appear to be less closely associated with a single dietary source than those of *A. opercularis*. This may imply that *P. maximus* is exhibiting greater selection that *A. opercularis* during feeding, which would produce a diatom assemblage in the gut contents unlike that of any dietary source.

CHAPTER 4. THE EFFECT OF RESUSPENDED SEDIMENT ON THE FEEDING PHYSIOLOGY OF *PECTEN MAXIMUS* AND *AEQUIPECTEN OPERCULARIS*

INTRODUCTION

Recent studies designed to elucidate the behavioural feeding responses of bivalves to changing diets have moved away from using pure algal diets such as those used by Davids (1964), Bayne & Thompson (1970), Bayne (1973a) and Palmer & Williams (1980). It has been recognised that the response to particle concentration is very complex: it depends upon both dietary quality and quantity (Widdows *et al.*, 1979; Griffiths, 1980b; Berry & Schleyer, 1983; Bricelj, 1984; Bayne *et al.*, 1987, 1989; Cranford & Grant, 1990; Iglesias *et al.*, 1992; Navarro *et al.*, 1992).

Resuspension of bottom sediment occurs due to the movement of water over the seabed (Nowell & Jumars, 1984; Frechette *et al.*, 1989), and is a common feature of shallow water habitats (Grant *et al.*, 1990). The benthic boundary layer thus contains variable amounts of resuspended sediment, depending on tidal and weather conditions, which will be a mixture of benthic microalgae, macroalgal fragments, mineral particles and detrital organic matter (Zeitzschel, 1970). Reports on the effect of silt or sediment in the diet on the feeding and growth of bivalves are apparently contradictory: some authors report beneficial effects (Winter, 1975; Kiørboe *et al.*, 1981; Møhlenberg & Kiørboe, 1981; Rhoads *et al.*, 1984; Bayne *et al.*, 1987), whilst others the opposite (Bricelj & Malouf, 1984; Bricelj *et al.*, 1984; Robinson *et al.*, 1984). The reasons suggested for the enhanced feeding or growth rates include the absorption of sedimentary organics (Kiørboe *et al.*, 1981; Bricelj & Malouf, 1984), dilution of the organic matter by

inorganic material, which is beneficial due to its influence on the absorption efficiency (Widdows *et al.*, 1979; Bricelj and Malouf, 1984), increased grinding of the food (Bricelj and Malouf, 1984), or increased clearance rates and absorption efficiencies (Navarro *et al.*, 1992). Adverse reactions to sediment in the diet could be due to the decline in diet quality as the organic matter becomes diluted, or the bivalve gill becomes clogged (Grant *et al.*, 1990).

Bivalves may respond to increased particle loads in the diet by reducing clearance rates and/or increasing pseudofaecal production, or by exhibiting discontinuous feeding. Short term feeding experiments have illustrated that complex interactions controlling the ingestion rate, gut capacity and the digestive processes are involved, the physiological mechanisms of which are unclear (Iglesias *et al.*, 1992). In reality the relative importance of altering clearance rates or pseudofaecal production depends on the composition of the food (Iglesias *et al.*, 1992).

Some species have been shown to acclimate to long-term exposure to sediment in the diet, for example, *Mytilus edulis* (Bayne *et al.*, 1987), *Cerastoderma edule* (Navarro *et al.*, 1992), and *Spisula solidissima* (Robinson *et al.*, 1984). Other species apparently do not acclimate, such as *Mercenaria mercenaria* (Bricelj *et al.*, 1984), *Placopecten magellanicus* (Cranford & Grant, 1990), and *Mya arenaria* (Grant & Thorpe, 1991). Acclimation to diets containing resuspended sediment or macroalgal debris can involve changes in various physiological traits, such as oxygen consumption, ammonia excretion and absorption efficiency (Bayne *et al.*, 1987; Grant & Thorpe, 1991; Navarro *et al.*, 1992).

Most of the work designed to elucidate feeding responses of bivalves to natural seston or sediment in the diet have involved mytilids. Less work has been performed on the feeding and digestion of pectinids. With regard to European species, Vahl (1980b) has studied the absorption efficiency of *Chlamys islandica*, and Richardson *et al.* (1984) examined the effect of iron particles on the growth of *Aequipecten opercularis*. More work has been carried out on North American and Canadian species: Pierson (1983) assessed the absorption efficiency of *Argopecten irradians concentricus* when fed different pure algal diets; Cranford & Grant (1990) and Grant & Cranford (1989) studied the feeding and energy balance of *Placopecten magellanicus* when fed a variety of diets.

There are ecological differences between *P. maximus* and *A. opercularis* which may result in them receiving different quantities and qualities of food. *P. maximus* recesses into a shallow pit, whereas *A. opercularis* sits upon the sediment. This difference in feeding height may result in *P. maximus* receiving a lower quality diet since refractory particles tend to have a heavier specific gravity (Taghon & Greene, 1992), and would concentrate lower in the water column (Muschenheim, 1987a, 1987b; Muschenheim & Newell, 1992). It is possible, therefore, that the feeding responses of the two species to changing dietary quality and quantity may be different. Both species will certainly receive resuspended sediment in their diets, thus it is of significance to study the potential contribution of sediment to the energy balance of *P. maximus* and *A. opercularis*.

My study used both long and short-term durations of exposure to sediment in the diet, to assess short-term behavioural responses, and whether long-term acclimation occurs. My study aimed to determine the effect of suspended bottom sediment on the feeding rate and selectivity of

Pecten maximus and *Aequipecten opercularis*, whether any differences between the two species were evident, and whether the sediment can be utilized. In the long-term exposure experiment the scope for growth and oxygen to nitrogen ratios were also calculated, to determine if *P. maximus* and *A. opercularis* could maintain a positive net energy balance over a longer time scale, when sediment was present in the diet.

MATERIALS AND METHODS

Two year old *Pecten maximus* and *Aequipecten opercularis* of approximately 57-74 and 51-67 mm shell height respectively, were collected from a longline system situated in Bay Fine, Isle of Man. The animals were maintained in a constant temperature (C.T.) room at 10 ± 0.5°C for one week before use. The experiment used the same experimental system as that described in Chapter 2, except that an extra block of feeding chambers was added. Each block consisted of eight feeding chambers, two of which were randomly designated as control feeding chambers. Two control chambers were used to increase the accuracy of the control evaluation. The sediment was collected from a sub-tidal site beyond the Breakwater at Port Erin, Isle of Man. In the laboratory it was vigorously stirred, and allowed to settle for one minute. The supernatant was then siphoned off and stored in a dimly lit C.T. room, while being constantly aerated. Sufficient sediment was collected to supply both experiments, to ensure an homogenous supply throughout.

Short term feeding responses to resuspended sediment

The algae *Rhinomonas reticulata, Isochrysis galbana* and *Monoisochrysis lutherii* were used in an approximately 1:1:1 ratio by number in the experiment. A three by three factorial design of diets was used. Diet concentrations are described in Table 4.1. Algae and sediment concentrations were chosen to try to provide chlorophyll and total particulate matter (T.P.M.) values within the range of those found in the water immediately above the seabed. This was determined from samples taken during the experiment detailed in Chapter 3. The algal concentrations (zero, low and high - A0, AL and AH) chosen were 0, and approximately 3.5 and 20 cells μl^{-1} respectively. The sediment levels (zero,

low and high - S0, SL and SH) chosen were 0, and approximately 7 and 80 particles μl^{-1}. Deviations from these theoretical levels did occur due to the difficulty in maintaining high concentrations of resuspended sediment, since it tended to settle out in the diet supply tank.

Table 4.1 The mean number, volume, and standard deviations (SD) of particles greater than 2.4 μm per ml of experimental diet.

DIET	DIET CODE	N	MEAN No. ml^{-1}	SD	N	MEAN vol. mm^3 l^{-1}	SD
Zero algae, low sediment	A0SL	12	7130	1154	16	0.336	0.056
Zero algae, high sediment	A0SH	12	105939	8586	16	5.169	0.803
Low algae, zero sediment	ALS0	12	3606	270	16	0.550	0.078
Low algae, low sediment	ALSL	12	15579	2376	15	1.899	0.663
Low algae, high sediment	ALSH	6	84618	18111	8	5.225	0.777
High algae, zero sediment	AHS0	12	21132	5812	16	3.343	0.874
High algae, low sediment	AHSL	12	20216	2142	16	3.501	0.117
High algae, high sediment	AHSH	9	126683	14739	11	9.099	0.319

Diet analysis

Samples of each diet were analysed to determine the total particulate matter (T.P.M.), particulate organic matter (P.O.M.) and particulate inorganic matter (P.I.M.) present. This was achieved using the methods described in Chapter 3. . Total chlorophyll and phaeopigment concentrations were determined using the method developed by Lorenzen (1967), described in Chapter 3. The total number and volume of particles greater than 2.4 μm were recorded using a Coulter Counter Multisizer, as described in Chapter 2.

Clearance rates and particle selection

Four repeat measurements of clearance rate and particle size selection efficiency (Jacob's electivity index, D) were made for each diet, as described in Chapter 2.

Biodeposit production

Biodeposits (which refers to a mixture of both the faeces and pseudofaeces) produced during the first hour of the experiment were discarded. After one hour the faeces ejected should consist of material originating from the experimental diet, since in radioactive labelling experiments using *Mercenaria mercenaria* radioactive faeces were produced after one hour of feeding (Bricelj, 1984).

Absorption efficiency

Half of the biodeposits were placed in centrifuge tubes and rinsed with two 2 ml aliquots of ammonium formate isotonic with sea water (3 % w/v). Rinsing was achieved by centrifuging the biodeposits for 10 minutes at 3500 r.p.m. and discarding the supernatant. The biodeposits were rinsed from the centrifuge tube into small foil dishes using two 2 ml aliquots of ammonium formate. The biodeposits were dried in an oven for 12 hours at 103°C, cooled in a desiccator and weighed to the nearest tenth of a milligram. The biodeposits were then ashed in a muffle furnace (450°C for 3 hours), cooled in a desiccator and weighed to the nearest tenth of a milligram. The absorption efficiency (AE) was then determined according to the method described by Conover (1966):

$$AE = \frac{F - E}{(1 - E)F} \qquad 1$$

where F and E are the ash-free dry weight to total weight ratios of the food and biodeposits respectively; that is, the proportion of organic material present. Biodeposits were used to determine the absorption efficiency so that the energetic losses due to metabolic faecal loss (Hawkins & Bayne, 1984, 1985; Bayne *et al.*, 1987; Hawkins *et al.*, 1990), and mucus in the pseudofaeces, would be taken into account in subsequent calculations. The absorption efficiency equation was only intended for use in feeding studies where no selection occurred (Conover, 1966; Kiørboe & Møhlenberg, 1981; Bricelj & Malouf, 1984) - using biodeposits circumvents this problem.

Chlorophyll selection efficiency and digestion efficiency

A sample of faeces was separated from the remaining biodeposits, and the faeces and biodeposits placed in pre-weighed fluorometer tubes for pigment analysis. The faeces and pseudofaeces were freeze-dried in darkness, and weighed to the nearest tenth of a milligram. The total chlorophyll and phaeophytin levels were determined using a Turner 10-005R fluorometer fitted with Kodak Wratten emission filters c/s 29 nearest the photomultiplier, with a 16 c/s over it to reduce its inherent fluorescence and the consequent scatter that occurs. These emission filters measure the total chlorophyll and phaeophytin, if only chlorophyll *a* is required the filter Corning CS.2-64 should be used.

The method developed by Yentsch & Menzel (1963) and described in Strickland & Parsons (1965) and Parsons *et al.* (1984) was followed. 4.2 mls of 90% acetone was added to the samples, which were then macerated with a glass rod. The samples were left for 24 hours to complete the extraction of the chlorophyll. The fluorescence of the samples was then recorded and three drops of 10% hydrochloric acid added to reduce the chlorophyll

pigments to their breakdown products, phaeopigments. After 3-5 minutes the sample fluorescence was re-measured.

The pigment concentrations were then calculated using the equations:

$$\text{Chlorophyll } mg / m^3 = F_D x 1.83(R_B - R_A) x \frac{v}{V} \qquad 2$$

$$\text{Phaeopigment } mg / m^3 = F_D x 1.83(2.2R_A - R_B) x \frac{v}{V} \qquad 3$$

where R_B and R_A are the fluorescence readings before and after acidification, v and V are the volumes of acetone and water sample filtered respectively (in this case the weight of biodeposits or faeces was used in place of V). F_D is a calibration factor calculated by determining the chlorophyll concentration of pure chlorophyll using a spectrophotometer, and relating that to the fluorescence reading:

$$F_D = \frac{C_a}{R} \qquad 4$$

Where Ca is the chlorophyll *a* concentration determined spectrophotometrically, and R is the fluorescence reading. Some fluorometers need this calibration factor to be calculated for each sensitivity setting, but this is not necessary for the Turner 10-005R model (Parsons *et al.*, 1984).

The chlorophyll concentration in the pseudofaeces was calculated as the difference between the chlorophyll in the biodeposits and in the faeces (Bricelj & Malouf, 1984; Robinson *et al.*, 1984). Further calculations were then made using the pseudofaeces and faeces chlorophyll concentrations:

Consumed chl = (chl in diet)-(chl in pseudofaeces) 5

Digested chl = (consumed chl)-(chl in faeces) 6

There was also considerable pigment loss during the digestion of the food; that is, breakdown of chlorophyll and/or phaeopigments to non-fluorescent end-products. Pigment concentrations can be converted to chlorophyll equivalents to assess this loss (Landry *et al.*, 1984; Downs & Lorenzen, 1985; Conover *et al.*, 1986). If the major breakdown product is phaeophorbide, then phaeopigment concentrations should be divided by 0.66 (the ratio of the molecular weights of chlorophyll and phaeophorbide: 590.65/893.48). If the major breakdown product is phaeophytin the ratio becomes 869.16/893.48, or 0.97, which would produce a much less significant error (Shuman & Lorenzen, 1975; Conover *et al.*, 1986).

The major breakdown product during the digestion of chlorophyll *a* by zooplankton is usually phaeophorbide (Shuman & Lorenzen, 1975; Conover *et al.*, 1986), and in *Mytilus edulis* 61-80% of the end-products have been found to be phaeophorbide-like pigments (Hawkins *et al.*, 1986). Robinson *et al.* (1989) also found that the major phaeopigment present in the digestive glands of *Placopecten magellanicus* was phaeophorbide. Gelder & Robinson (1980) concluded that the pigments they detected in *Mytilus edulis* were probably phaeophorbides, and Bricelj (1984) found that phaeophorbide accounted for 92-99% by weight of the phaeopigments in the faeces of *Mercenaria mercenaria*. Therefore the phaeopigment concentrations were multiplied by 0.66 to estimate the chlorophyll equivalents.

Various indices of selection and digestion efficiency were calculated:

$$\text{Selection efficiency (SE1)} = \frac{\text{Chl}\mu\text{g / g D}}{\text{Chl}\mu\text{g / g P}} \qquad 7$$

$$\text{Digestion efficiency (DE)} = 1 - \frac{\text{Chl}\mu\text{g / g F}}{\text{Chl}\mu\text{g / g Consumed}} \qquad 8$$

$$\text{Proportion of pigment destroyed (PD)} = 1 - \frac{\text{Chl}\mu\text{g / g equivalents B}}{\text{Chl}\mu\text{g / g equivalents D}} \qquad 9$$

$$\text{Acid ratio index} = (R_B/R_A)\ B - (R_B/R_A)\ F \qquad 10$$

The codes used in the equations represent: P pseudofaeces, D diet and B biodeposits. R_B and R_A are the fluorescence readings before and after acidification of the samples, respectively.

Physiological responses to a long-term diet of resuspended sediment

The experimental system used was the same as that described for the short-term feeding response experiment, except that the feeding chambers were replaced by tanks containing five individuals. Within each block of the experimental system four tanks contained *P. maximus* and four tanks contained *A. opercularis*. One tank of each species was supplied with each diet. The lengths, heights and blotted wet weights of the animals were recorded at the beginning and end of the experiment. At the end of the experiment the dry weights were also measured after the animals had been dried at 103°C for 48 hours.

The algae *Rhinomonas reticulata* and the sediment used in the first experiment, were used in four different combinations to produce diets with chlorophyll and T.P.M. concentrations within the range of those

found in the water immediately above the seabed. Diet particle concentrations and volumes are described in Table 4.2.

Table 4.2 The mean number, volume, and standard deviations (SD) of particles greater than 2.4 μm per ml for four experimental diets (AL, SL, ALSL and ALSH).

DIET	DIET CODE	N	MEAN No. ml^{-1}	SD	N	MEAN vol. $mm^3 l^{-1}$	SD
Low algae	AL	12	8314	3127	12	1.160	0.51
Low sediment	SL	12	8384	2017	12	0.498	0.13
Low algae. low sediment	ALSL	12	8671	2362	12	0.859	0.30
Low algae, high sediment	ALSH	12	19524	6357	12	1.308	0.41

The tanks were supplied with these diets continuously for 19 days. On days 16 to 19 the oxygen consumption, ammonia excretion and clearance rates were measured and the biodeposits collected and analysed.

Diet analysis

On days 14, 18 and 19 water samples were taken from the inflow of each tank. These samples were analysed for T.P.M., P.I.M., P.O.M., chlorophyll and phaeopigment concentrations, total number and volume of particles according to the methods described in Chapters 2 and 3.

Clearance rates

Clearance rates were estimated from the depletion of particles by all of the animals in the tank; measurements were made for five animals at a time. Particle concentrations and clearance rates were measured according to the methods described in Chapter 2.

Biodeposit production

The biodeposits produced by the animals during the measurement of clearance rates were collected from each tank. The samples were treated as described in the short-term response experiment in this Chapter, except that the pigment concentrations were measured using the spectrophotometric method described in Chapter 3.

Oxygen consumption rates

The measurement of oxygen consumption is outlined in Widdows (1985b). The Strathkelvin 781 oxygen meter used was calibrated at the start of every experimental run using a zero oxygen solution (0.01M disodium tetraborate, to which crystalline sodium sulphite is added to excess) and oxygen-saturated seawater (aerated for at least 5 minutes). Oxygen concentrations for the calibration were calculated using the oxygen saturation tables of Green & Carritt (1967).

The oxygen consumption of each individual was measured in duplicate in 0.5 l Kilner jars. The Kilner jars were modified so that they had perspex, rather than glass, lids, which were drilled with 13 mm diameter holes. One animal from each tank was measured at any one time, and 3 jars acted as controls to measure any microbial activity or drift of the oxygen meters. The animals were carefully placed in the jars, this operation was performed beneath the surface of the water so that no air was introduced to the jar, and so that as little mechanical disturbance to the animal occurred as possible. Any bubbles that were present in the jars were carefully dislodged with a fine paint brush.

The jar was carefully partially sealed, and supplied with the appropriate diet through a hole in the lid. The animals were left undisturbed for one

hour to resume normal feeding. The jars remained on stands beneath the surface of the water, so that the animals experienced essentially the same conditions as previously. The water in the jars was not stirred, partly because the use of magnetic stirrers would necessitate removing the animals from their tanks, but also to avoid disturbing the animals during the incubation (Bricelj, 1987).

If any bubbles entered the chamber with the seawater after the jar had been partially sealed, but before the jars were completely sealed, bent pipe cleaners were used to move the air bubbles to the exit hole. After one hour a sample of 0.5 mls of water was removed from the chamber using a glass syringe, and the chamber sealed using rubber bungs. The oxygen concentration in the water was recorded using a 70 µl incubated oxygen chamber (Strathkelvin, MC100), the floor of which is a Strathkelvin 1302 electrode, connected in turn to a Strathkelvin 781 oxygen meter. The water samples were carefully injected into the chamber via fine polypropylene tubing, which has very low oxygen diffusion across its walls. Samples must be injected slowly and smoothly otherwise the Strathkelvin F.E.P. oxygen membrane distorts, which results in incorrect readings. A constant sample volume was used so that differences in chamber rinsing would not occur. Pilot studies using zero oxygen solutions and saturated oxygen solutions indicated that 0.5 mls of water was sufficient to flush the chamber. After allowing exactly 90 seconds for the membrane to equilibriate the oxygen concentration was recorded. Initial studies showed that there was a peak in the oxygen recording immediately after the sample was injected into the chamber but a stable level was reached after 70-90 seconds, after which it remained essentially constant for another minute or more.

After approximately one hour, the bung was carefully removed and the water very gently stirred. The oxygen concentration was recorded, and the chamber re-sealed. After a further hour another sample was taken and analysed, the animal removed from the jar and the volume of water in the jar recorded.

The oxygen readings were corrected to atmospheric pressure before being used, and the oxygen consumption rate (V_{O_2}) calculated using the equations:

$$\frac{\text{mmHg at } t_o}{760 \text{ mmHg}} \times C\left(\text{ml } O_2\ l^{-1}\right) = \text{ml } O_2\ l^{-1} \text{ at } t_0 = A \qquad 11$$

and

$$\frac{\text{mmHg at } t_1}{760 \text{ mmHg}} \times C\left(\text{ml } O_2\ l^{-1}\right) = \text{ml } O_2\ l^{-1} \text{ at } t_1 = B \qquad 12$$

then

$$V_{O2}\left(\text{ml } O_2\ h^{-1}\right) = (A - B) \times V \times \frac{60}{t_1 - t_0} \qquad 13$$

where t_o and t_1 are the times (in minutes) at the start and end of the incubation, and V is the volume of water in the jar.

Ammonia excretion rates

The measurement of ammonia excretion rate is outlined in Widdows (1985b). The ammonia excretion was measured once for each animal. Each sample was analysed in duplicate using an ALPKEM 320 autoanalyser. The animals were incubated in 300 mls of seawater, that had been filtered to 0.2 μm, for 20 minutes. Pilot experiments were carried out to determine the best combination of water volume and incubation time to ensure that ammonia concentrations did not become high enough to

inhibit ammonia excretion (above 10 μM NH^4-N l^{-1} ≡ 140 μg l^{-1}, Widdows (1985b)). Four chambers containing 300 mls of 0.2 μm filtered seawater, but no experimental animals, were used as controls.

The ammonia excretion rate was calculated as:

$$\mu g NH_4 - N \ \ h^{-1} = (\text{test} \ \ \mu M - \text{control} \ \ \mu M) x \frac{14}{1000/V} x \frac{1}{t} \qquad 14$$

where V is the volume (in mls) of water in which the animal was incubated, and t is the duration of incubation (h). The test and control concentrations are those of the animal and control samples respectively.

The O:N ratio

The rate of oxygen consumption relative to the nitrogen excreted was calculated using atomic equivalents:

$$O:N = \frac{ml \ \ O_2 x 1.428}{16} \Big/ \frac{mg \ \ NH_4 - N \ \ h^{-1}}{14} \qquad 15$$

The oxygen consumption rate is multiplied by 1.428 to convert ml O_2 h^{-1} to mg O_2 h^{-1}, and then divided by 16 to convert it to atomic equivalents. The ammonia excretion rate is converted to atomic equivalents by dividing by 14.

Scope for growth

When the oxygen consumption rates, ammonia excretion rates and clearance rates are used to calculate scope for growth and the net growth

efficiency, they must be corrected to a standard body weight using the equation:

$$\log Y_C = \log Y_o - \left(b \log X_o - b \log X_C\right) \qquad 16$$

where Yc is the corrected value for a standard body mass X_C, and Y_O and X_O are the individual's measured rate and body mass respectively, and b is the weight exponent. The physiological rates were corrected to a standard body mass of 2.43g, the average weight of the animals used. The weight exponents used were b=0.72 for clearance rates, b=0.75 for oxygen consumption, and b=0.65 for ammonia excretion. The exponents for oxygen consumption and clearance rate were calculated from work on pectinids by various authors who are listed in Bricelj & Shumway (1991). The weight exponent for ammonia excretion (b=0.65 ± 0.10 SD, n=7) was calculated as the mean of the values found by several authors working on various species of bivalve at similar temperatures to that of my experiment: Bayne *et al.* (1976), Bayne & Widdows (1978), Widdows (1978), Mann (1979), Widdows *et al.* (1981) and Worrall *et al.* (1983).

The components of the scope for growth equation $P(J\ h^{-1})=A-(R+U)$ were calculated as follows, using the conversion factors in Widdows (1985b):

Energy absorbed from the seston (A) = $C(J\ h^{-1}) \times e$ 17

where e is the absorption efficiency, and C = CR x P.O.M. x energy content of P.O.M., which was assumed to be 23.5 J mg^{-1} (Widdows *et al.*, 1979). The absorption efficiency was calculated using biodeposits, therefore the net absorption efficiency was calculated, rather than the gross absorption efficiency which is calculated if faeces are used. The use of net absorption

efficiency in the scope for growth calculation will account for the loss of energy from the animals due to mucus loss in the pseudofaeces.

Energy respired (R) = V_{O_2}(ml O_2 h^{-1})x20.33 18

Energy excreted (U) = (µg NH_4-N h^{-1})x0.0249 19

Net growth efficiency

The net growth efficiency (K_2) was calculated from the energy components used in the scope for growth equation:

$$K_2 = \frac{A - (R + U)}{A} \qquad 20$$

Statistical analysis

The normality and homoscedascicity of the data were checked using the statistical procedures outlined in Chapter 2: 'Nscores', the Fmax test and visual assessment of the fits and residuals from initial ANOVAs. In the short-term response experiment the electivity index D that was calculated could not be analysed directly (see Chapter 2), therefore the particle size class at which maximum selection occurred was analysed, as well as the summed values of D. No transformation of the summed values of D could be found that provided adequate homogeneity of variance (homoscedascicity). A higher significance threshold was therefore used (Underwood, 1981); probabilities less than 1%, rather than 5%, were accepted as being significant. The ANOVAs and ANCOVAs performed on the data from the short-term response experiment are shown in Table 4.3.

Table 4.3 The ANOVAs and ANCOVAs performed on the variables calculated in the short-term response experiment. The transformations required, if any, are indicated, as well as whether any covariates were included in the analysis.

VARIABLE	TRANSFORMATION	FACTORS	COVARIATES
Selection efficiency	$\log_{10}$	species diet	none
Digestion efficiency	arcsine	species diet	none
Absorption efficiency	arcsine	species diet	none
Pigment destroyed	arcsine	species diet	none
Weight-standardized clearance rate	Box-Cox λ =-0.1	species diet block	dry body weight control concentration
Size class where maximum D occurred	none	species diet block	dry body weight control concentration
Summed values of D	none (see text)	species diet block	dry body weight control concentration

Regression analyses were carried out on the following variables: arcsine transformed absorption efficiency, the arcsine transformed proportion of pigment destroyed, and weight-standardized clearance rate (l h-1 g-1 dry body weight), to ascertain which methods of describing diet quality and quantity were more useful in analysing feeding responses. Fifteen different ways of describing the diet were used to predict the above mentioned variables: number ml^{-1}, volume (mm^3 l^{-1}), total particulate matter, particulate organic matter, particulate inorganic matter, the arcsine proportions of P.O.M. and P.I.M., the ratio of P.I.M. to P.O.M., particulate organic matter per mm^3, chlorophyll and phaeopigment l^{-1}, chlorophyll and phaeopigment g^{-1}, the ratio of chlorophyll to phaeopigment, and chlorophyll per mm^3.

The ANOVAs and ANCOVAs performed on the data from the long-term feeding experiment are shown in Table 4.4.

Table 4.4 The ANOVAs and ANCOVAs performed on the variables calculated in the long-term response experiment. The transformations required, if any, are indicated, as well as whether any covariates were included in the analysis.

VARIABLE	TRANSFORMATION	FACTORS	COVARIATES
Digestion efficiency	arcsine	species diet	none
Absorption efficiency	arcsine	species diet	none
Weight specific VO_2	none	species diet block	dry body weight
Weight specific NH_4-N	square root	species diet block	dry body weight
Oxygen to Nitrogen ratio	$\log_{10}$	species diet block	dry body weight
Scope for growth	none	species diet block	none
Net growth efficiency, K_2	none	species diet block	none

If a factor proved to be significant in the ANOVA or ANCOVA, Bonferroni Least Significant Differences (L.S.Ds) were calculated to ascertain between which levels of the factor significant differences occurred. If diet proved to be significant in the short-term response experiment, there were more pairwise combinations (28) than could be tested using the available statistical tables. A complete pairwise examination is also not necessarily useful, as some comparisons will not yield relevant information. Therefore, before the results were examined, ten comparisons were chosen, five to examine the effect of increasing sediment, and five to examine the effect of increasing algae in the diet. The combinations chosen were:-

1. No algae, low sediment (A0SL) vs. No algae, high sediment (A0SH)
2. Low algae, low sediment (ALSL) vs. Low algae, high sediment (ALSH)
3. High algae, low sediment (AHSL) vs. High algae, high sediment (AHSH)
4. Low algae, no sediment (ALS0) vs. Low algae, low sediment (ALSL)
5. High algae, no sediment (AHS0) vs. High algae, low sediment (AHSL)
6. Low algae, No sediment (ALS0) vs. High algae, no sediment (AHS0)
7. No algae, low sediment (A0SL) vs. Low algae, low sediment (ALSL)

8. No algae, high sediment (A0SH) vs. Low algae, high sediment (ALSH)
9. Low algae, low sediment (ALSL) vs. High algae, low sediment (AHSL)
10. Low algae, high sediment (ALSH) vs. High algae, high sediment (AHSH)

RESULTS

Short term response experiments

Particle size selection efficiency

The particle size class that was selected to the greatest extent was not affected by any factor in the ANCOVA except animal dry weight ($F_{0.05}$, 1, 311 = 4.51 P= 0.035, Table 4.5).

Table 4.5 Analysis of covariance of the size class at which maximum particle selection occurred, using control particle concentration and animal dry body weight as covariates. * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
Control concentration	1	1.829	2.384	2.384	0.75	0.388	
Dry body weight	1	7.515	14.383	14.383	4.51	0.035	*
Diet	7	26.615	25.917	3.702	1.16	0.325	
Block	1	6.180	6.211	6.211	1.95	0.164	
Species	1	2.102	3.092	3.092	0.97	0.326	
Diet & block	7	28.182	27.705	3.958	1.24	0.280	
Diet & species	7	7.196	7.229	1.033	0.32	0.943	
Block & species	1	10.119	11.337	11.337	3.55	0.060	
Diet & block & species	7	24.182	24.182	3.455	1.08	0.374	
Error	311	992.081	992.081	3.190			
Total	344	1106					

The summed values of D (Table 4.6) were significantly affected by the covariate control concentration ($F_{0.05}$, 1, 205 = 6.02 P = 0.015), diet ($F_{0.05}$, 7, 205 = 11.05 P = <0.001) and block ($F_{0.05}$, 1, 205 = 7.76 P = 0.006). Bonferroni L.S.Ds showed that significant increases in the extent of selection occurred when sediment concentrations were increased at constant algal concentrations, except between the high algae, no sediment (AHS0) diet and the high algae, low sediment (AHSL) diet. At constant sediment concentrations increasing the algal concentration did not affect the degree

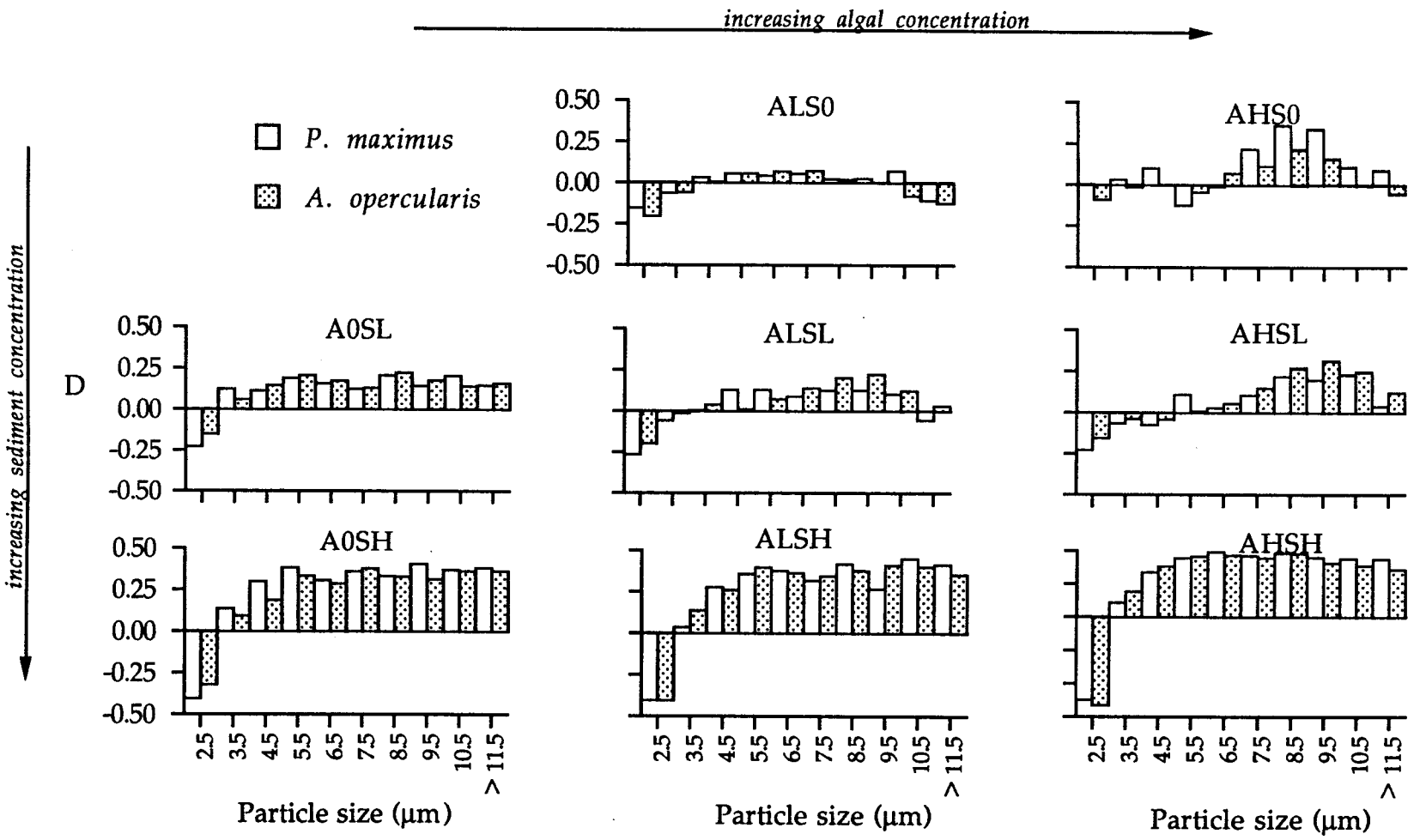


Fig. 4.1 The particle selection (Jacobs' electivity index, D) of *P. maximus* and *A. opercularis* when fed different combinations of sediment and algae. Each bar represents the mean of 1-4 determinations on each of six individuals.

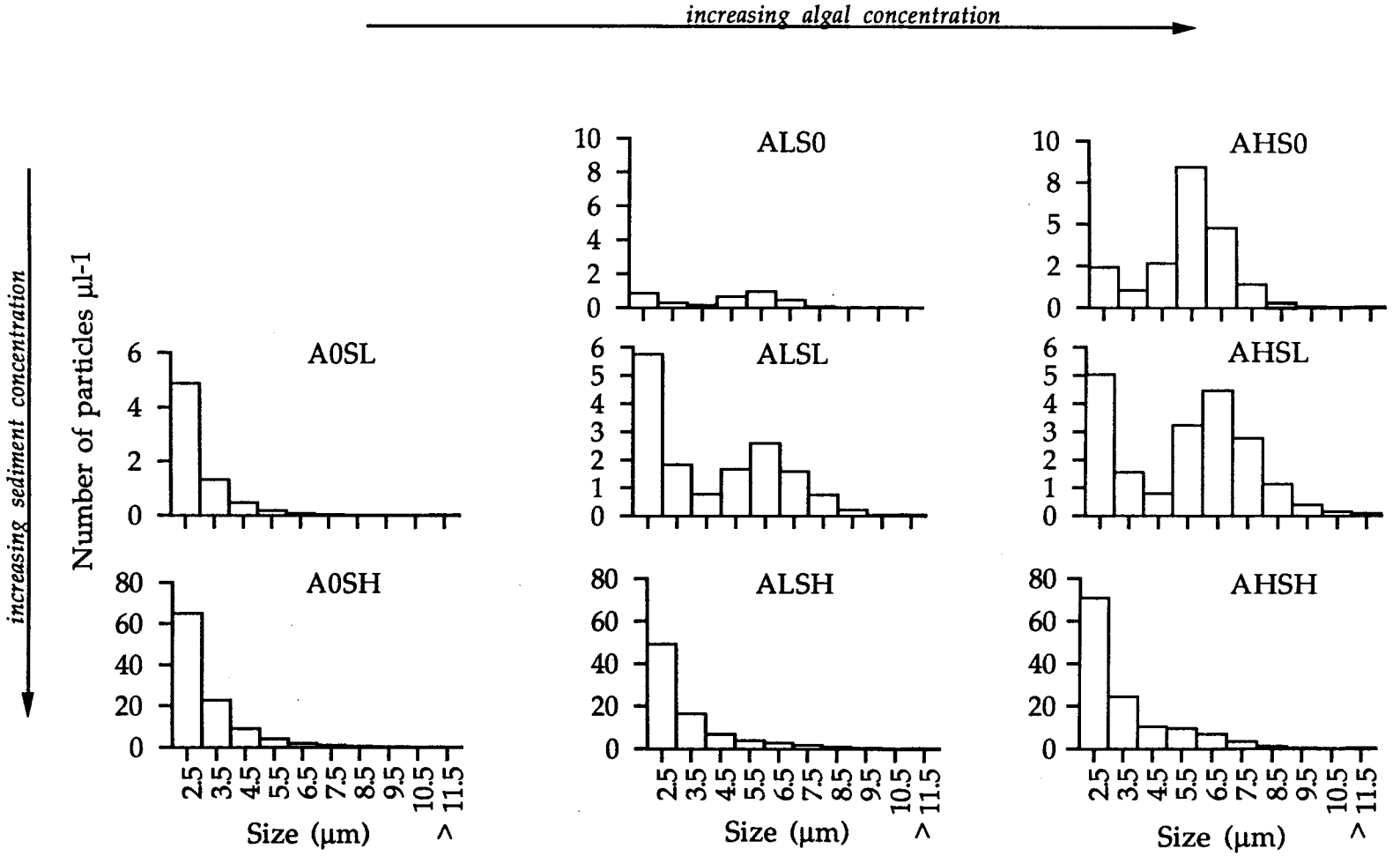


Fig. 4.2 The particle size spectra of the diets used in the short term response experiment. Each bar represents the mean of 5-8 determinations. Note that the ordinate axes are drawn to different scales.

of selection, except between the no algae, low sediment (A0SL) diet and the low algae, low sediment (ALSL) diet, when the extent of selection decreased. This pattern can be seen in Fig. 4.1, and compared to the diet particle size spectra in Fig. 4.2, where the peaks of particle selection reflect the most available particle size class.

Table 4.6 Analysis of covariance of the summed values of D, using control particle concentration and animal dry body weight as covariates. Selected comparisons were made between levels of significant factors by calculating Bonferroni L.S.Ds (using an EER of 0.05). Due to problems finding an appropriate transformation for the data, results were deemed to be significant at below a 1% threshold, rather than 5%. * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
Control concentration	1	242.424	3.404	3.404	6.02	0.015	*
Dry body weight	1	0.445	0.265	0.265	0.47	0.494	
Diet	7	46.955	43.690	6.241	11.05	<0.001	**
Block	1	3.334	4.382	4.382	7.76	0.006	**
Species	1	0.936	0.409	0.409	0.72	0.396	
Diet & block	7	4.472	3.854	0.551	0.97	0.451	
Diet & species	7	4.840	5.064	0.723	1.28	0.262	
Block & species	1	0.069	0.000	0.000	0.00	0.999	
Diet & block & species	7	4.996	4.996	0.714	1.26	0.270	
Error	205	115.834	115.834	0.565			
Total	238	424.305					

Bonferroni L.S.Ds. S and NS represent significant and non-significant differences respectively, between the indicated diets.

Comparison	N1	N2	MS Error	F Crit	LSD	Significance
A0SL vs. A0SH	35	32	0.565	8.06	0.522	S
ALSL vs. ALSH	41	19	0.565	8.06	0.592	NS
AHSL vs. AHSH	24	27	0.565	8.06	0.599	S
ALS0 vs. ALSL	36	41	0.565	8.06	0.487	S
AHS0 vs. AHSL	25	24	0.565	8.06	0.610	NS
ALS0 vs. AHS0	36	25	0.565	8.06	0.556	NS
A0SL vs. ALSL	35	41	0.565	8.06	0.491	NS
A0SH vs. ALSH	32	19	0.565	8.06	0.618	NS
ALSL vs. AHSL	41	24	0.565	8.06	0.548	NS
ALSH vs. AHSH	19	27	0.565	8.06	0.639	NS

Clearance rates

The clearance rates of both species showed a similar response to increasing concentrations of algae and silt (Fig. 4.3). This is confirmed by the ANCOVA performed on the weight-standardized clearance rates (Table 4.7) which showed that there is no significant difference between the two species ($F_{0.05}$, 1, 287 = 3.77 P = 0.053), although the results are close to being significant, with *A. opercularis* having a higher overall clearance rate than *P. maximus*.

Table 4.7 Analysis of covariance of the Box-Cox transformed (λ optimized at -0.1) weight-standardized clearance rates, using control particle concentration and animal dry body weight as covariates. Selected comparisons were made between levels of significant factors by calculating Bonferroni L.S.Ds (using an EER of 0.05). * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
Dry body weight	1	1.961	0.802	0.802	3.19	0.075	
Control concentration	1	30.240	1.724	1.724	6.86	0.009	**
Diet	7	44.739	43.738	6.248	24.87	<0.001	**
Block	1	0.015	0.096	0.096	0.38	0.536	
Species	1	1.074	0.948	0.948	3.77	0.053	
Diet & block	7	2.756	2.795	0.399	1.59	0.138	
Diet & species	7	2.737	2.663	0.381	1.51	0.162	
Block & species	1	0.797	0.612	0.612	2.44	0.120	
Diet & block & species	7	1.225	1.225	0.175	0.7	0.675	
Error	287	72.110	72.110	0.251			
Total	320	157.654					

Bonferroni L.S.Ds. S and NS represent significant and non-significant differences respectively, between the indicated diets.

Comparison	N1	N2	MS Error	F Crit	LSD	Significance
A0SL vs. A0SH	45	36	0.251	7.88	0.315	S
ALSL vs. ALSH	48	21	0.251	7.88	0.368	S
AHSL vs. AHSH	44	36	0.251	7.88	0.316	S
ALS0 vs. ALSL	47	48	0.251	7.88	0.289	S
AHS0 vs. AHSL	44	44	0.251	7.88	0.300	S
ALS0 vs. AHS0	47	44	0.251	7.88	0.295	S
A0SL vs. ALSL	45	48	0.251	7.88	0.292	S
A0SH vs. ALSH	36	21	0.251	7.88	0.386	S
ALSL vs. AHSL	48	44	0.251	7.88	0.294	S
ALSH vs. AHSH	21	36	0.251	7.88	0.386	S

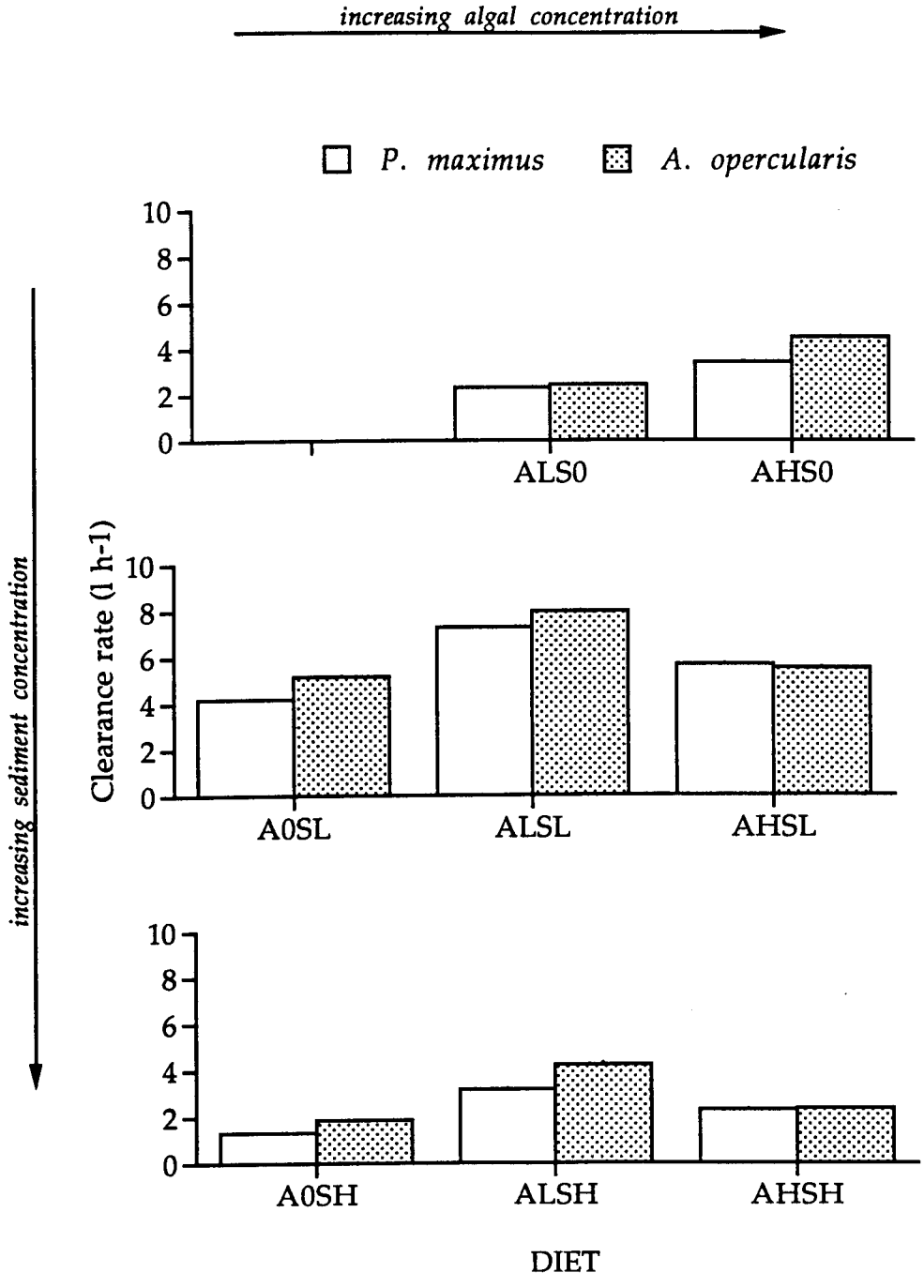


Fig. 4.3 Clearance rates (l h-1) of *P. maximus* and *A. opercularis* when fed different combinations of sediment and algae. Each bar represents the mean (± standard errors where large enough to be plotted) of 1-4 determinations on each of six individuals.

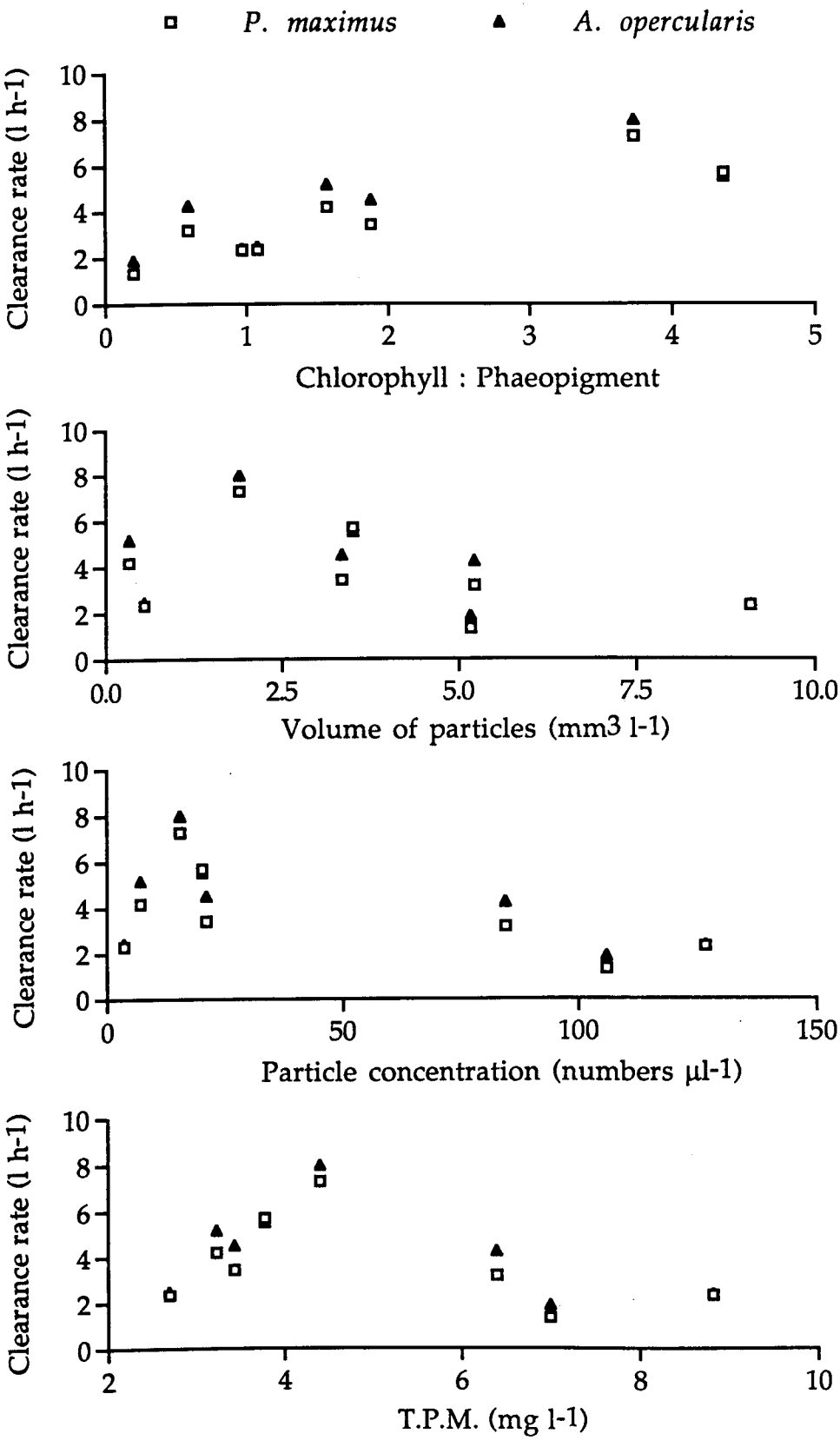


Fig. 4.4 The clearance rates of *P. maximus* and *A. opercularis* expressed in terms of diet particle number, particle volume, total particulate matter (T.P.M.) and the chlorophyll to phaeopigment ratio. Points represent the mean values (± standard errors where large enough to be plotted) of 1-4 determinations on each of 6 individuals.

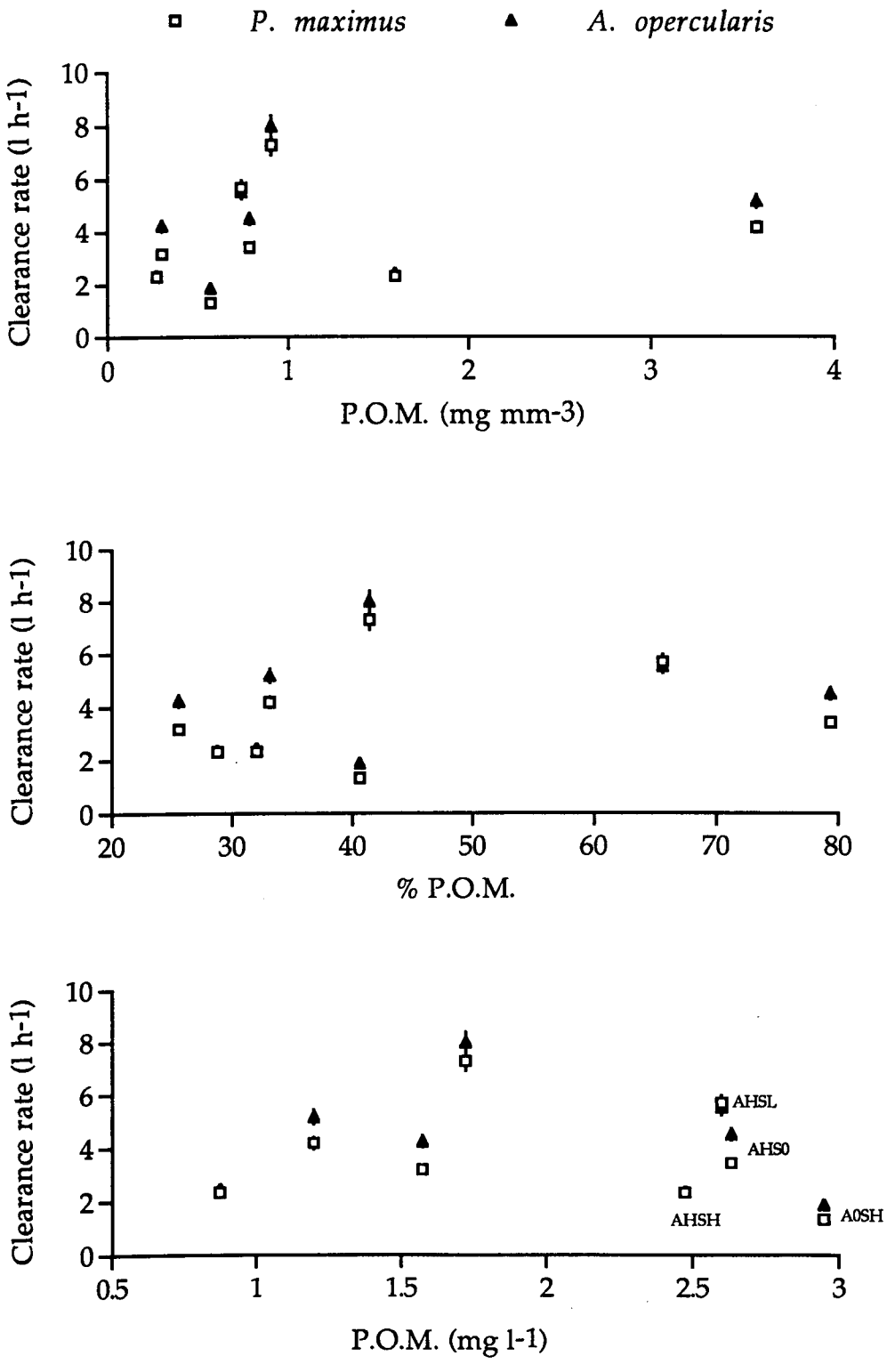


Fig. 4.4 continued. The clearance rates of *P. maximus* and *A. opercularis* expressed in terms of diet particulate organic matter (P.O.M.) mm-3, % P.O.M., and P.O.M. mg l-1. Points represent the mean values (± standard errors where large enough to be plotted) of 1-4 determinations on each of 6 individuals.

At every algal and sediment concentration the addition of low concentrations of the other dietary substance to the diet increases the clearance rate, and a further increase in the concentration of the second substance decreases the clearance rate (Fig. 4.3). At the highest algal concentration the addition of the highest sediment concentration decreases the clearance rates to below the high algae, no sediment (AHS0) diet level. When no sediment is present, increasing algae increases the clearance rates, but with no algae present, increasing sediment decreases the clearance rate. The lowest clearance rates were recorded when the animals were fed the no algae, high sediment (A0SH) diet.

The only factors in the ANCOVA of weight-standardized clearance rates which proved significant were the covariate control concentration and diet ($F_{0.05}$, 7, 287 = 24.87 $P < 0.001$). Bonferroni L.S.D. tests showed that there was a significant difference between every combination of diets examined (Table 4.7).

The clearance rates were related to both the quality of the diet, measured using the ratio of chlorophyll to phaeopigment, and physical parameters of the diet such as particle number, volume, and T.P.M. (Fig. 4.4). The clearance rates peaked at 16 particles μl^{-1}, 1.9 mm^3 l^{-1} and 4.4 mg l^{-1}, for particle number, volume, and T.P.M. respectively.

The amount of material cleared from suspension, when expressed as mm^3 removed per hour, increased with increasing concentration of sediment or algae (Fig. 4.5). When expressed as the amount of P.O.M. removed per hour, the amounts cleared at the high sediment concentration increased only slightly, especially with regard to *P. maximus*.

Biodeposit production

The amount of biodeposits produced increased substantially when the animals were fed diets containing high sediment concentrations (Fig. 4.5). This was due almost entirely to the large amount of pseudofaeces produced.

Absorption efficiency

The effect of increasing one component of the diet whilst keeping the other constant did not produce a clear-cut pattern of response that proved statistically significant (Fig. 4.6). Generally, however, at the constant algal concentrations of no algae (A0) and low algae (AL), increased sediment in the diet produced an increase in the absorption efficiency, although the differences were not always significant (Table 4.8). The reverse occurred at the high algal concentration. When the sediment concentration was kept at constant low levels (no sediment (S0) and low sediment (SL)), increased algae in the diet tended to increase the absorption efficiency. Again, the reverse occurred at high sediment concentrations.

ANOVA (Table 4.8) showed that diet ($F_{0.05}$, 7, 76 = 56.86 P = <0.001) and the diet and species interaction terms ($F_{0.05}$, 7, 76 = 4.53 P = <0.001) were significant. Within the diet and species interaction term, the absorption efficiencies of *P. maximus* and *A. opercularis* only proved to be significantly different when fed the low algae, no sediment (ALS0) and the no algae, low sediment (A0SL) diets.

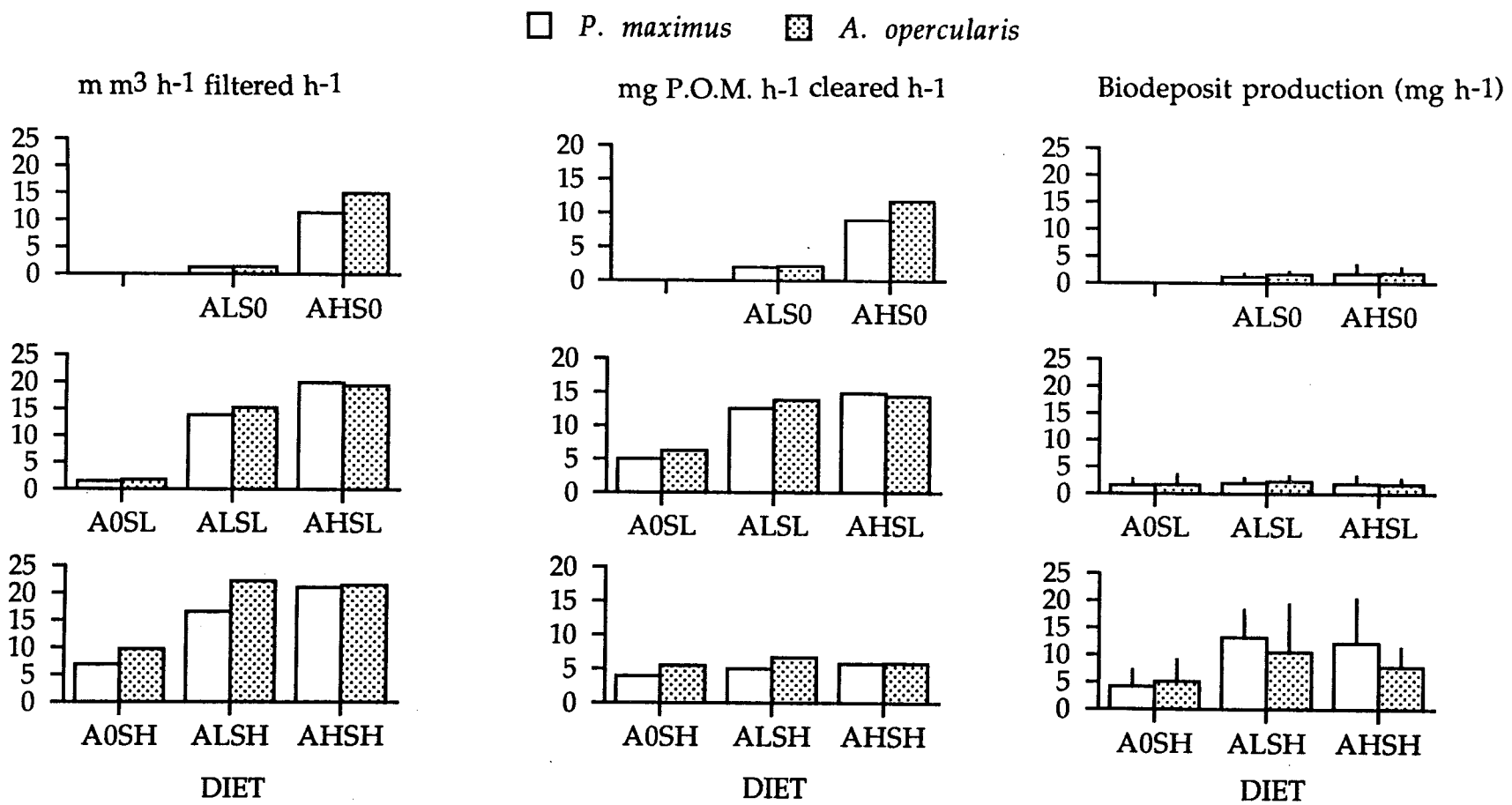


Fig. 4.5 The amount of material cleared from suspension, expressed in terms of mm3 and mg P.O.M. cleared per hour (bars represent the mean values of 1-4 determinations on each of 6 individuals), and the approximate rate of biodeposit production (bars represent the mean, ± standard errors where large enough to be plotted, of one determination on 5-6 animals), of *P. maximus* and *A. opercularis*, when fed diets of different combinations of algae and sediment.

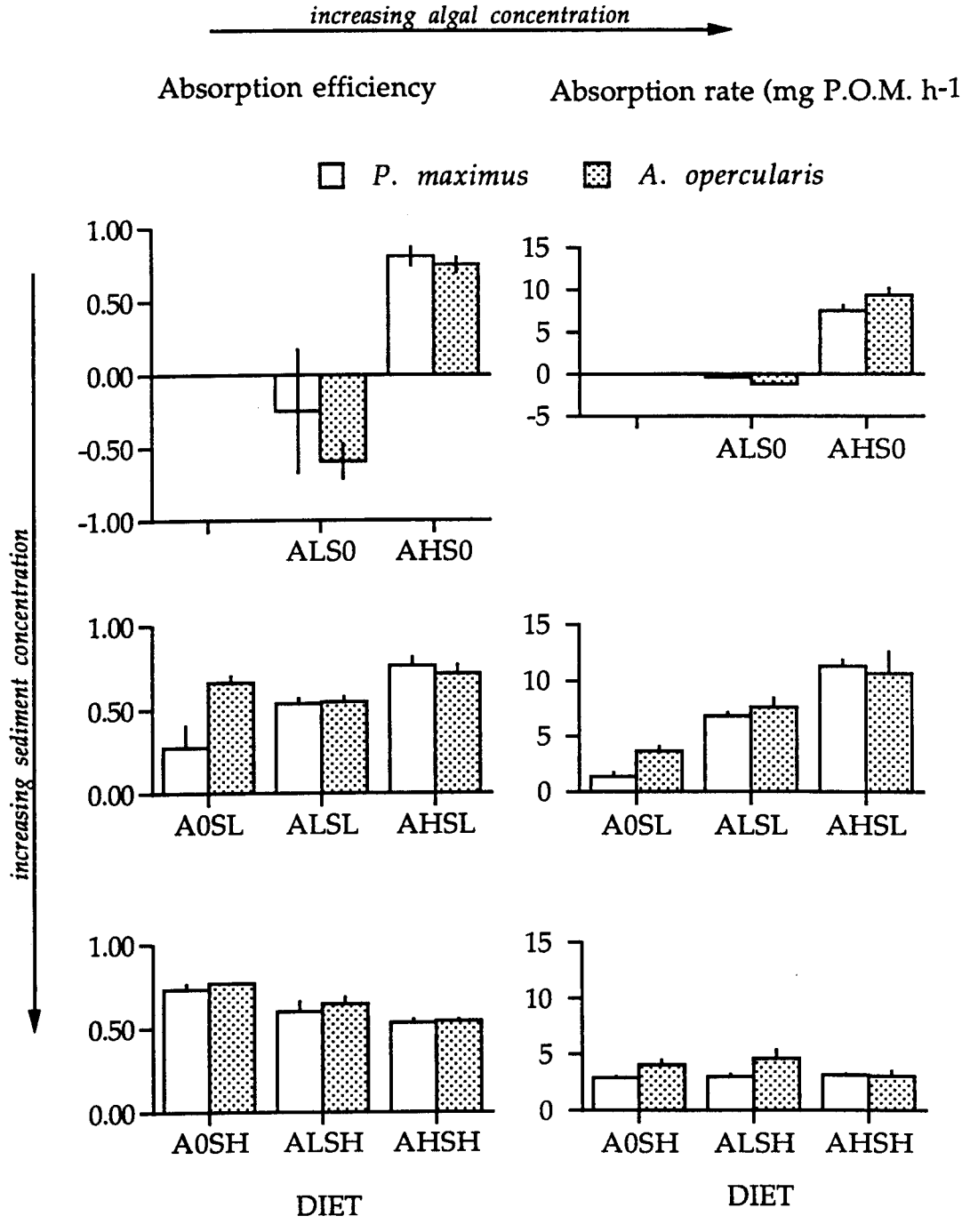


Fig. 4.6 The absorption efficiency and the amount of particulate organic matter (P.O.M.) absorbed by *P. maximus* and *A. opercularis* when fed different combinations of sediment and algae. Bars represent mean values of single measurements from 5-6 animals, ± standard errors where large enough to be plotted.

Table 4.8 Analysis of variance of the arcsine transformed absorption efficiency. Selected comparisons were made between levels of significant factors by calculating Bonferroni L.S.Ds (using an EER of 0.05). * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
Diet	7	15.233	13.827	1.975	56.86	<0.001	**
Species	1	0.002	0.000	0.000	0.01	0.922	
Diet & species	7	1.103	1.103	0.158	4.53	<0.001	**
Error	76	2.641	2.641	0.035			
Total	91	18.977					

Bonferroni L.S.Ds. S and NS represent significant and non-significant differences respectively, between the indicated diets. P represents *P. maximus* and A *A. opercularis*.

Comparison	N1	N2	MS Error	F Crit	LSD	Significance
A0SL vs. A0SH	12	12	0.035	8.37	0.220	S
ALSL vs. ALSH	12	12	0.035	8.37	0.220	NS
AHSL vs. AHSH	12	11	0.035	8.37	0.225	S
ALS0 vs. ALSL	10	12	0.035	8.37	0.231	S
AHS0 vs. AHSL	11	12	0.035	8.37	0.225	NS
ALS0 vs. AHS0	10	11	0.035	8.37	0.235	S
A0SL vs. ALSL	12	12	0.035	8.37	0.220	NS
A0SH vs. ALSH	12	12	0.035	8.37	0.220	NS
ALSL vs. AHSL	12	12	0.035	8.37	0.220	S
ALSH vs. AHSH	12	11	0.035	8.37	0.225	NS
		Diet & Species				
A0SL P vs. A	6	6	0.035	7.92	0.303	S
A0SH P vs. A	6	6	0.035	7.92	0.303	NS
ALS0 P vs. A	4	6	0.035	7.92	0.338	S
ALSL P vs. A	6	6	0.035	7.92	0.303	NS
ALSH P vs. A	6	6	0.035	7.92	0.303	NS
AHS0 P vs. A	6	5	0.035	7.92	0.317	NS
AHSL P vs. A	6	6	0.035	7.92	0.303	NS
AHSH P vs. A	6	5	0.035	7.92	0.317	NS

The actual amount of P.O.M. absorbed (Fig. 4.6) increased with increasing concentrations of algae or sediment only at zero or low levels of sediment. At high sediment concentrations the amount of material absorbed was held very constant, especially by *P. maximus*. When the P.O.M. absorbed is expressed relative to the amount of material cleared from suspension (Fig. 4.7), a positive linear relationship was observed. No change in the

absorption efficiency was apparent with regard to the amount of material cleared from suspension (Fig. 4.7).

Pigment destroyed

Diet significantly affected the destruction of fluorescent pigments ($F_{0.05}$, 7, 74 = 28,21 P = <0.001, Table 4.9 and Fig. 4.8). When no algae was present, increasing the sediment concentration increased the proportion of pigment that was destroyed during digestion. At low levels of algae, adding sediment to the diet resulted in an increase in pigment destruction (although it was not significant), increasing the sediment concentration further decreased the proportion of pigment destroyed. At high levels of algae adding sediment to the diet increased the pigment destroyed. Increasing the concentration of sediment further did not significantly alter the destruction of pigment, but the species appeared to react differently: the pigment destruction by *P. maximus* decreased, while that of *A. opercularis* increased.

When the sediment concentration was held constant, peak destruction at sediment concentrations of no sediment (S0) and low sediment (SL) occurred at low concentrations of algae (AL), conversely at high sediment levels (SH) the lowest levels of pigment destruction occurred at the low algae concentration (AL).

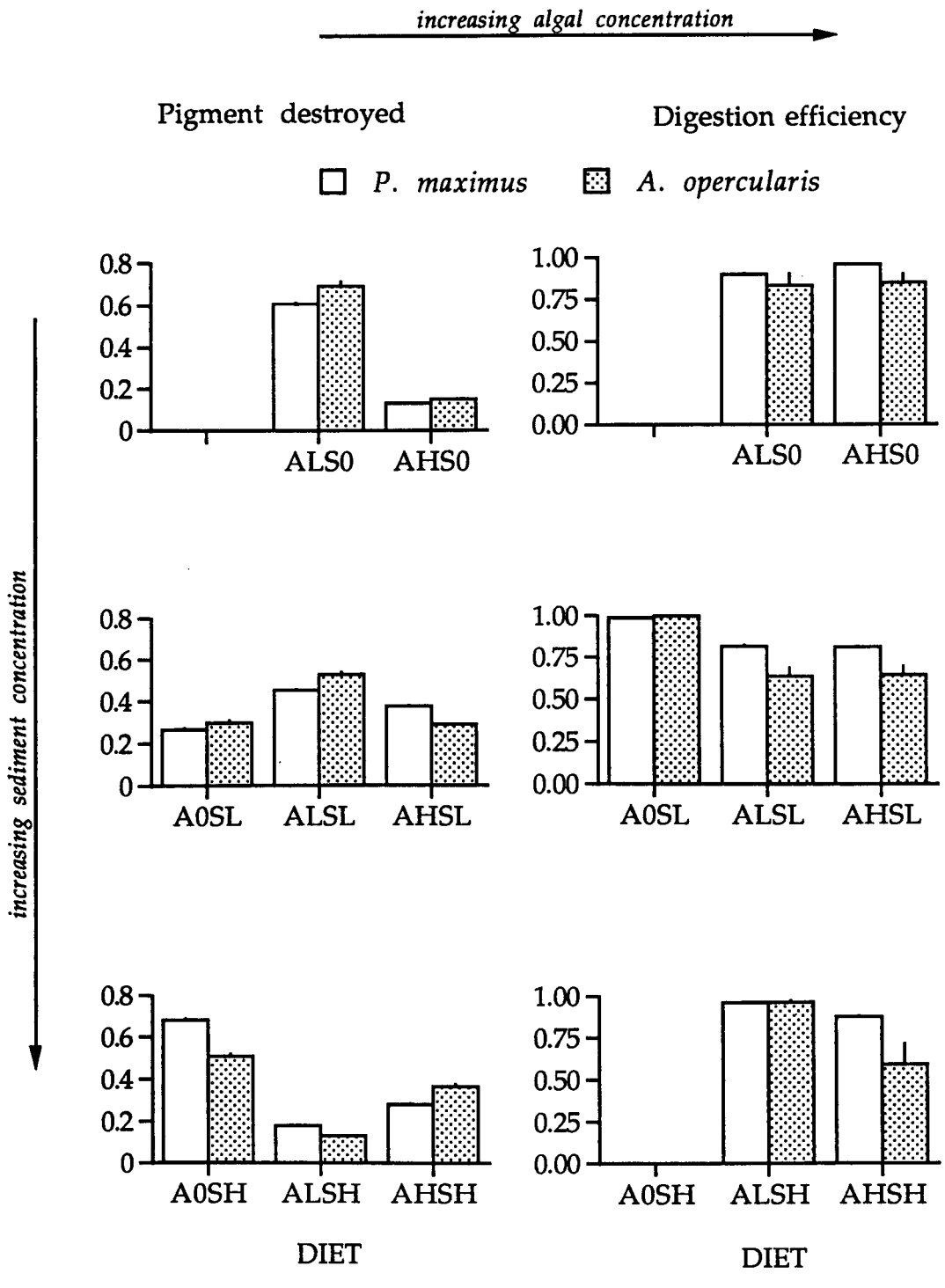


Fig. 4.8 The proportion of pigments destroyed (when expressed as chlorophyll equivalents) and the digestion efficiency index (DE) of *P. maximus* and *A. opercularis* when fed different combinations of sediment and algae. The bars represent the mean values of single measurements from 1-6 animals, ± standard errors where large enough to be plotted.

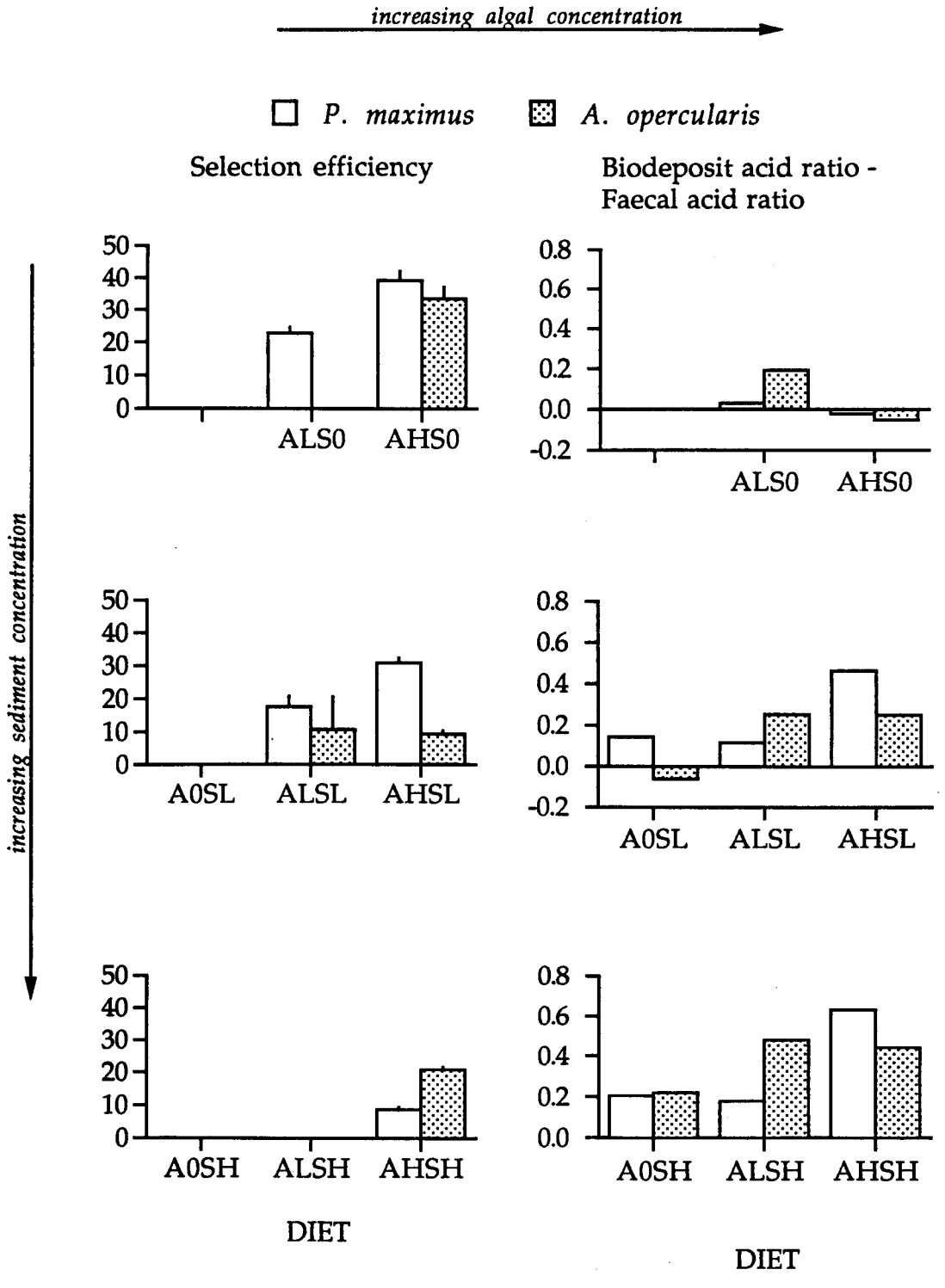


Fig. 4.9 The selection efficiency (measured using the chlorophyll per gram of the pseudofaeces compared to that of the diet) and the acid ratio index of *P. maximus* and *A. opercularis* when fed different combinations of sediment and algae. Bars represent the mean of single measurements from 1-6 individuals, ± standard errors where large enough to be plotted.

Table 4.9 Analysis of variance of the arcsine transformed proportion of pigment destroyed during digestion. Selected comparisons were made between levels of significant factors by calculating Bonferroni L.S.Ds (using an EER of 0.05). * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
Diet	7	4.959	4.917	0.702	28.210	<0.001	**
Species	1	0.001	0.000	0.000	0.000	0.950	
Diet & species	7	0.253	0.253	0.036	1.450	0.198	
Error	74	1.843	1.843	0.025			
Total	89	7.055					

Bonferroni L.S.Ds. S and NS represent significant and non-significant differences respectively, between the indicated diets.

Comparison	N1	N2	MS Error	F Crit	LSD	Significance
A0SL vs. A0SH	10	12	0.025	8.37	0.195	S
ALSL vs. ALSH	12	11	0.025	8.37	0.191	S
AHSL vs. AHSH	12	11	0.025	8.37	0.191	NS
ALS0 vs. ALSL	11	12	0.025	8.37	0.191	NS
AHS0 vs. AHSL	11	12	0.025	8.37	0.191	S
ALS0 vs. AHS0	11	11	0.025	8.37	0.195	S
A0SL vs. ALSL	10	12	0.025	8.37	0.195	S
A0SH vs. ALSH	12	11	0.025	8.37	0.191	S
ALSL vs. AHSL	12	12	0.025	8.37	0.186	S
ALSH vs. AHSH	11	11	0.025	8.37	0.195	S

Digestion efficiency

The digestion efficiency of *P. maximus* was greater than that of *A. opercularis* ($F_{0.05}$, 1, 49 = 22.74 P = < 0.001). Diet also significantly affected the digestion efficiency ($F_{0.05}$, 6, 49 = 4.77 P = 0.001). Increasing the algal concentration had no effect when there was no sediment in the diet, but at both the low and high sediment levels (SL and SH), increasing the algal concentration decreased the digestion efficiency (Fig. 4.8). At low algal concentrations adding sediment to the diet decreased the digestion efficiency, a further increase in sediment increased it. At high algal concentrations the addition of sediment to the diet resulted in a decrease in digestion efficiency, a further increase in sediment did not significantly

affect the digestion efficiency, but the two species did seem to react differently: the digestion efficiency of *P. maximus* increased slightly, whereas that of *A. opercularis* declined further.

Table 4.10 Analysis of variance of the arcsine transformed digestion efficiency. Selected comparisons were made between levels of significant factors by calculating Bonferroni L.S.Ds (using an EER of 0.05). * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
Diet	6	1.632	1.361	0.227	4.77	0.001	**
Species	1	1.080	1.080	1.080	22.74	<0.001	**
Error	49	2.328	2.328	0.048			
Total	56	5.040					

Bonferroni L.S.Ds. S and NS represent significant and non-significant differences respectively, between the indicated diets.

Comparison	N1	N2	MS Error	F Crit	LSD	Significance
A0SL vs. A0SH	1		0.048	8.13	no data	
ALSL vs. ALSH	11	4	0.048	8.13	0.363	S
AHSL vs. AHSH	11	11	0.048	8.13	0.265	NS
ALS0 vs. ALSL	8	11	0.048	8.13	0.289	NS
AHS0 vs. AHSL	11	11	0.048	8.13	0.265	S
ALS0 vs. AHS0	8	11	0.048	8.13	0.289	NS
A0SL vs. ALSL	1	11	0.048	8.13	0.649	NS
A0SH vs. ALSH		4	0.048	8.13	no data	
ALSL vs. AHSL	11	11	0.048	8.13	0.265	NS
ALSH vs. AHSH	4	11	0.048	8.13	0.363	S

Digestion efficiency was inversely related to diet quality, when expressed as the ratio of chlorophyll to phaeopigment present. *A. opercularis* also showed a positive relationship with the percentage of P.O.M. in the diet (Fig. 4.8).

Selection efficiency

These data must be interpreted very cautiously, since much of the available estimates for chlorophyll and phaeopigment in the pseudofaeces

Table 4.11 Results of regression analyses using different descriptors of the diets as predictors of the clearance, the absorption efficiency and the proportion of pigment destroyed. The upper table gives the analysis of variance probability results, the lower table the adjusted r2 value for the regression analysis. Figures which are underlined indicate significance at the 0.05 probability level.

	DIET DESCRIPTOR								
INDEX	Number/ml	Vol mm3/l	TPM mg/l	POM mg/mm3	PIM mg/l	POM mg/l	arc PIM/TPM	arc POM/TPM	PIM:POM
Arcsine proportion of pigment destroyed	0.762	0.075	0.824	0.670	0.896	0.332	0.054	<u>0.013</u>	0.824
Clearance rate	<u><0.001</u>	<u><0.001</u>	<u><0.001</u>	0.188	<u><0.001</u>	0.202	<u>0.015</u>	<u>0.024</u>	<u>0.006</u>
Arcsine absorption efficiency	<u>0.005</u>	<u><0.001</u>	<u>0.005</u>	<u>0.006</u>	0.548	<u><0.001</u>	<u><0.001</u>	<u><0.001</u>	<u>0.001</u>

	Chl/l	Ph/l	Chl/g	Ph/g	Chl : Ph	Chl µg/mm3
Arcsine proportion of pigment destroyed	<u><0.001</u>	<u><0.001</u>	<u><0.001</u>	<u><0.001</u>	0.875	0.252
Clearance rate	<u><0.001</u>	<u>0.004</u>	<u><0.001</u>	<u>0.037</u>	<u><0.001</u>	<u>0.003</u>
Arcsine absorption efficiency	<u><0.001</u>	<u>0.001</u>	<u>0.003</u>	0.059	0.107	0.069

	DIET DESCRIPTOR								
INDEX	Number/ml	Vol mm3/l	TPM	POM mg/mm3	PIM mg/l	POM mg/l	arc PIM/TPM	arc POM/TPM	PIM:POM
Arcsine proportion of pigment destroyed	0.0	2.5	0.0	0.0	0.0	0.0	3.1	<u>5.8</u>	0.0
Clearance rate	<u>24.7</u>	<u>12.2</u>	<u>13.1</u>	0.8	<u>12.8</u>	0.7	<u>5.3</u>	<u>4.4</u>	<u>7.3</u>
Arcsine absorption efficiency	<u>7.4</u>	<u>12.9</u>	<u>7.6</u>	<u>7.2</u>	0.0	<u>45.2</u>	<u>16.0</u>	<u>16.6</u>	<u>11.3</u>

	Chl/l	Ph/l	Chl/g	Ph/g	Chl : Ph	Chl µg/mm3
Arcsine proportion of pigment destroyed	<u>23.7</u>	<u>40.9</u>	<u>16.7</u>	<u>34.9</u>	0.0	0.4
Clearance rate	<u>15.6</u>	<u>7.5</u>	<u>13.6</u>	<u>0.0</u>	<u>55.8</u>	<u>8.0</u>
Arcsine absorption efficiency	<u>15.1</u>	<u>10.9</u>	<u>8.7</u>	2.8	1.8	2.5

had to be discarded (see discussion). However, a general pattern emerged from the data: *P. maximus* exhibited greater selection efficiency than *A. opercularis*, except when fed the diet consisting of a high concentration of both algae and sediment (Fig. 4.9). The efficiency with which particles were sorted increased with increasing algal concentration when no sediment was present. At low sediment concentrations, increasing the algal concentration increased the selection efficiency of *P. maximus*, but decreased the selection efficiency of *A. opercularis*. When the algal concentration remained constant increasing the sediment resulted in decreased selection efficiency. This is confirmed if the acid ratio index is examined.

Methods of describing diet quantity and quality

Table 4.11 shows the results of regression analyses performed to relate clearance rate, absorption efficiency, and the proportion of pigment destroyed during digestion to different descriptors of the diet. The clearance rate and absorption efficiency tended to correlate significantly with many different descriptions of the diet, though interestingly the clearance rate did not correlate with the amount of P.O.M. per mm^3. The proportion of pigment destroyed correlated with the pigment concentrations and the arcsine proportion of P.I.M.

Physiological responses to a long-term diet of resuspended sediment

Clearance rates

The clearance rates were low per individual in both species (Fig. 4.10). The clearance rates of *A. opercularis* were marginally higher on the diets which included sediment, and tended to be slightly greater than *P.*

maximus. *P. maximus* showed a similar trend, but with slightly depressed clearance rates when fed the low algae, high sediment (ALSH) diet.

Oxygen consumption

P. maximus showed depressed rates of oxygen consumption when fed diets consisting of only resuspended sediment or high levels of resuspended sediment (the low algae, high sediment (ALSH) diet). *A. opercularis* exhibited more constant results (but the associated errors were greater), with slightly depressed rates of oxygen consumption when fed the diets the low algae, low sediment (ALSL) diet and the low algae, high sediment (ALSH) diet (Fig. 4.10). The ANCOVA did not detect any significant influences (Table 4.12).

Table 4.12 Analysis of variance of the weight-specific oxygen consumption rates of *P. maximus* and *A. opercularis*. * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Dry body weight	1	0.005	0.008	0.008	1.21	0.275
Diet	3	0.009	0.009	0.003	0.49	0.689
Species	1	0.010	0.010	0.010	1.54	0.218
Block	1	0.015	0.015	0.015	2.36	0.129
Diet & species	3	0.011	0.011	0.004	0.58	0.633
Error	70	0.438	0.438	0.006		
Total	79	0.488				

Ammonia excretion

The ammonia excretion of *P. maximus* was significantly higher than that of *A. opercularis* ($F_{0.05}$, 1, 65 = 37.18 P = <0.001), and exhibited elevated ammonia excretion rates when fed diets containing resuspended sediment (Fig. 4.10). The excretion rates of *A. opercularis* declined when fed diets

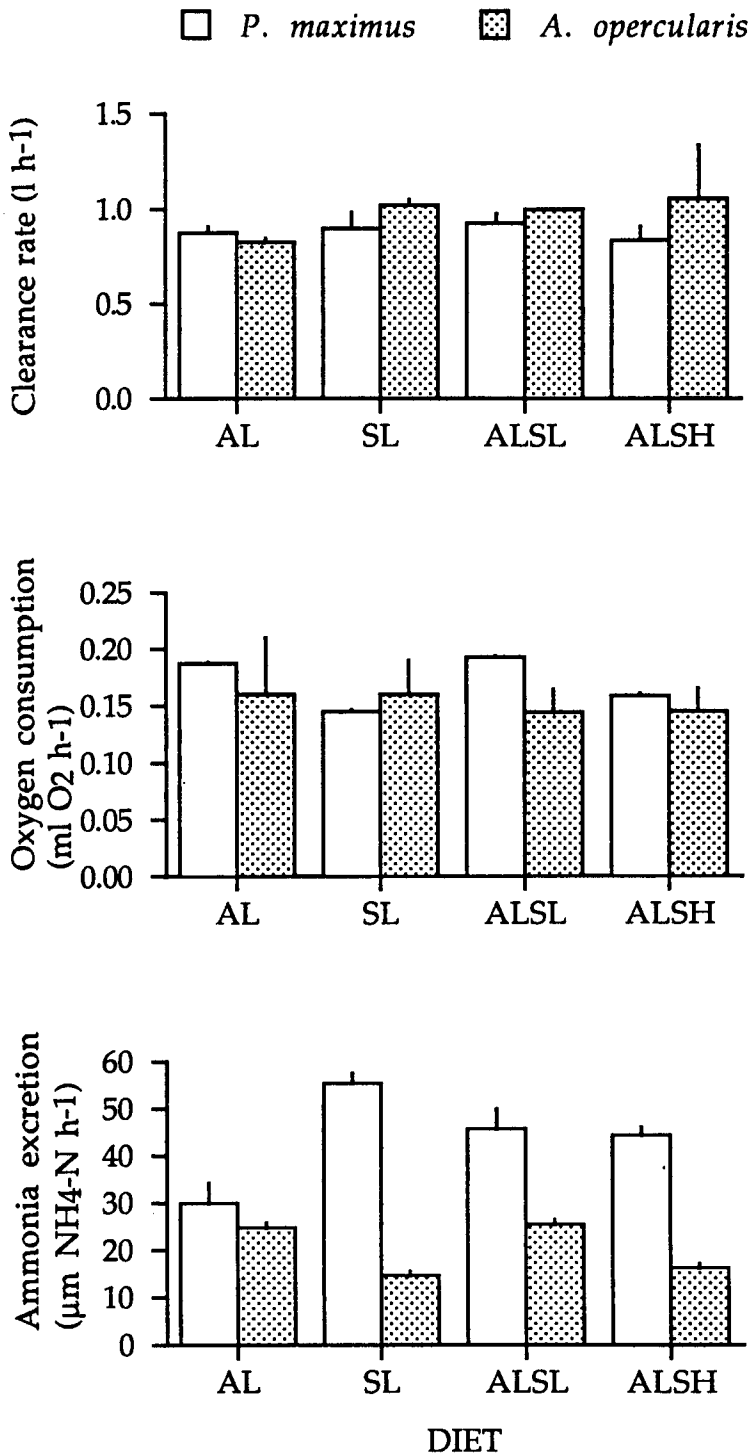


Fig. 4.10 The weight-specific clearance rates, weight-specific ammonia excretion rates and weight-specific oxygen consumption rates of *P. maximus* and *A. opercularis* when fed different combinations of algae and resuspended sediment for 19 days. The bars are mean values (± standard errors, where large enough to be plotted) of two measurements per tank for the clearance rates, and the mean of two-three measurements on each of ten animals for the oxygen consumption and ammonia excretion evaluations.

consisting of only sediment (SL) or high levels of sediment (the low algae, high sediment (ALSH) diet).

Table 4.13 Analysis of variance of the square root transformed ammonia excretion rates. Selected comparisons were made between levels of significant factors by calculating Bonferroni L.S.Ds (using an EER of 0.05). * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
Dry body weight	1	5.731	7.291	7.291	3.18	0.079	
Diet	3	2.841	2.117	0.706	0.31	0.820	
Species	1	87.462	85.282	85.282	37.18	<0.001	**
Block	1	2.654	2.550	2.550	1.11	0.296	
Diet & species	3	18.974	20.055	6.685	2.91	0.041	*
Diet & block	3	17.721	17.211	5.737	2.50	0.067	
Species & block	1	6.539	6.539	6.539	2.85	0.096	
Error	65	149.104	149.104	2.294			
Total	78	291.025					

Bonferroni L.S.Ds. S and NS represent significant and non-significant differences respectively, between the indicated species at each diet. P represents *P. maximus* and A *A. opercularis.*

Comparison	N1	N2	MS Error	F Crit	LSD	Significance
AL P vs. A	10	10	2.294	6.60	1.740	NS
SL P vs. A	10	9	2.294	6.60	1.788	S
ALSL P vs. A	10	10	2.294	6.60	1.740	NS
ALSH P vs. A	10	10	2.294	6.60	1.740	S

Absorption rate

The amount of T.P.M. or P.O.M. cleared from suspension was largely a reflection of what was available, since the clearance rates did not vary much. The subsequent P.O.M. absorption rate showed that the amount of P.O.M. absorbed from the low sediment (SL) and the low algae, high sediment (ALSH) diets were considerably greater than from the other diets (Fig. 4.11).

Absorption efficiency

The absorption efficiencies of *P. maximus* and *A. opercularis* were not significantly different (Table 4.14), but were significant affected by diet ($F_{0.05}$, 3, 8 = 17.57 P = 0.001). The absorption efficiencies were greater when the diets contained sediment (Fig. 4.12), the highest values being recorded for the diets containing only sediment (SL) and high concentrations of sediment (the low algae, high sediment (ALSH) diet).

Table 4.14 Analysis of variance of the arcsine absorption efficiencies. Selected comparisons were made between levels of significant factors by calculating Bonferroni L.S.Ds (using an EER of 0.05). * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
Diet	3	1.110	1.110	0.370	17.57	0.001	**
Species	1	0.018	0.018	0.018	0.86	0.382	
Diet & species	3	0.005	0.005	0.002	0.08	0.968	
Error	8	0.169	0.169	0.021			
Total	15	1.302					

Bonferroni L.S.Ds. S and NS represent significant and non-significant differences respectively, between the indicated diets.

Comparison	N1	N2	MS Error	F Crit	LSD	Significance
AL vs. SL	4	4	0.021	12.10	0.357	S
AL vs. ALSL	4	4	0.021	12.10	0.357	NS
AL vs. ALSH	4	4	0.021	12.10	0.357	S
SL vs. ALSL	4	4	0.021	12.10	0.357	S
SL vs. ALSH	4	4	0.021	12.10	0.357	NS
ALSL vs. ALSH	4	4	0.021	12.10	0.357	NS

Digestion efficiency

The digestion efficiency did not differ between species ($F_{0.05}$, 1, 7 = 0.34 P = 0.576). Diet did significantly affect the digestion efficiency, but no significant differences between diets were apparent from the Bonferroni L.S.Ds (Table 4.15), though the low algae (AL) diet versus the low sediment

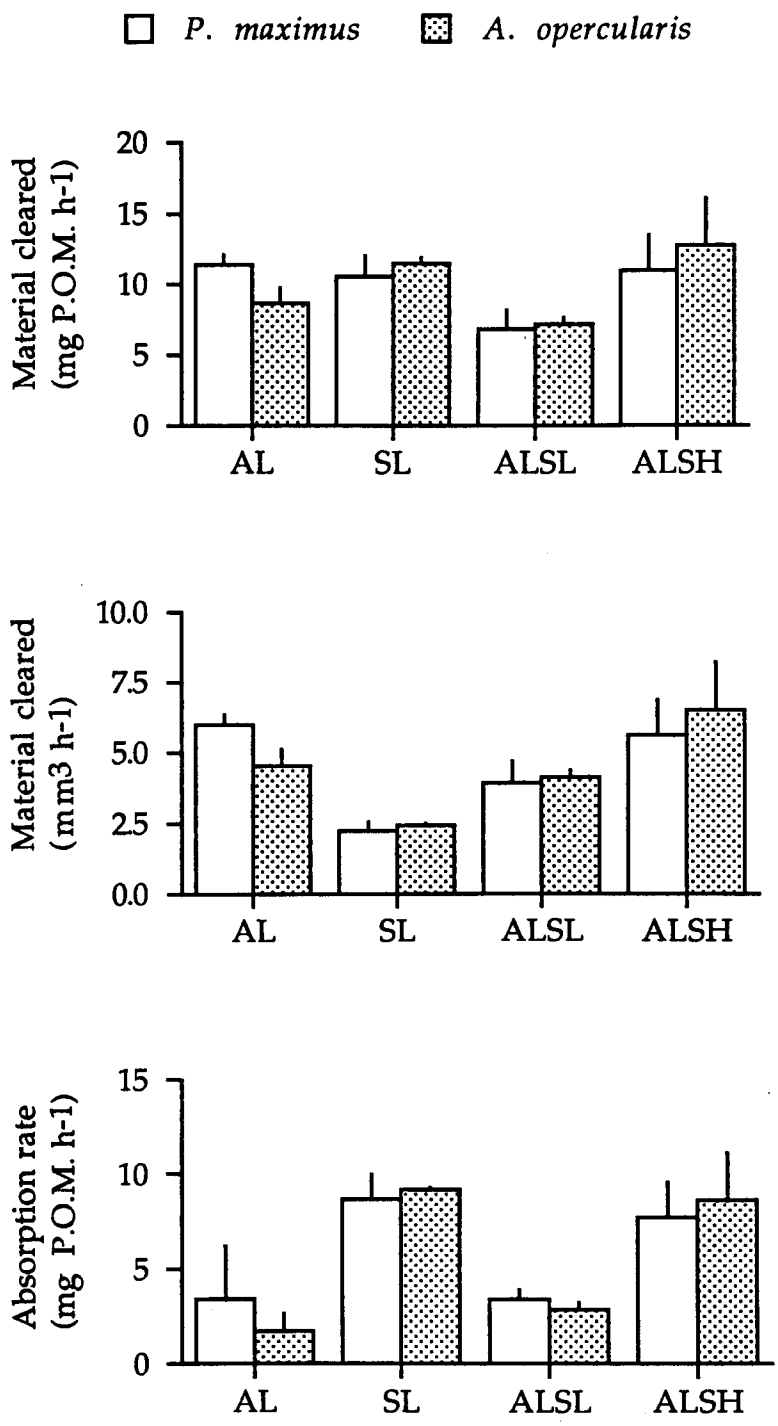


Fig. 4.11 The absorption rate and amount of material cleared fom suspension per hour by *P. maximus* and *A. opercularis* expressed as mg particulate matter (P.O.M.) and mm3 of material. Bars represent mean values (± standard errors) for two tanks.

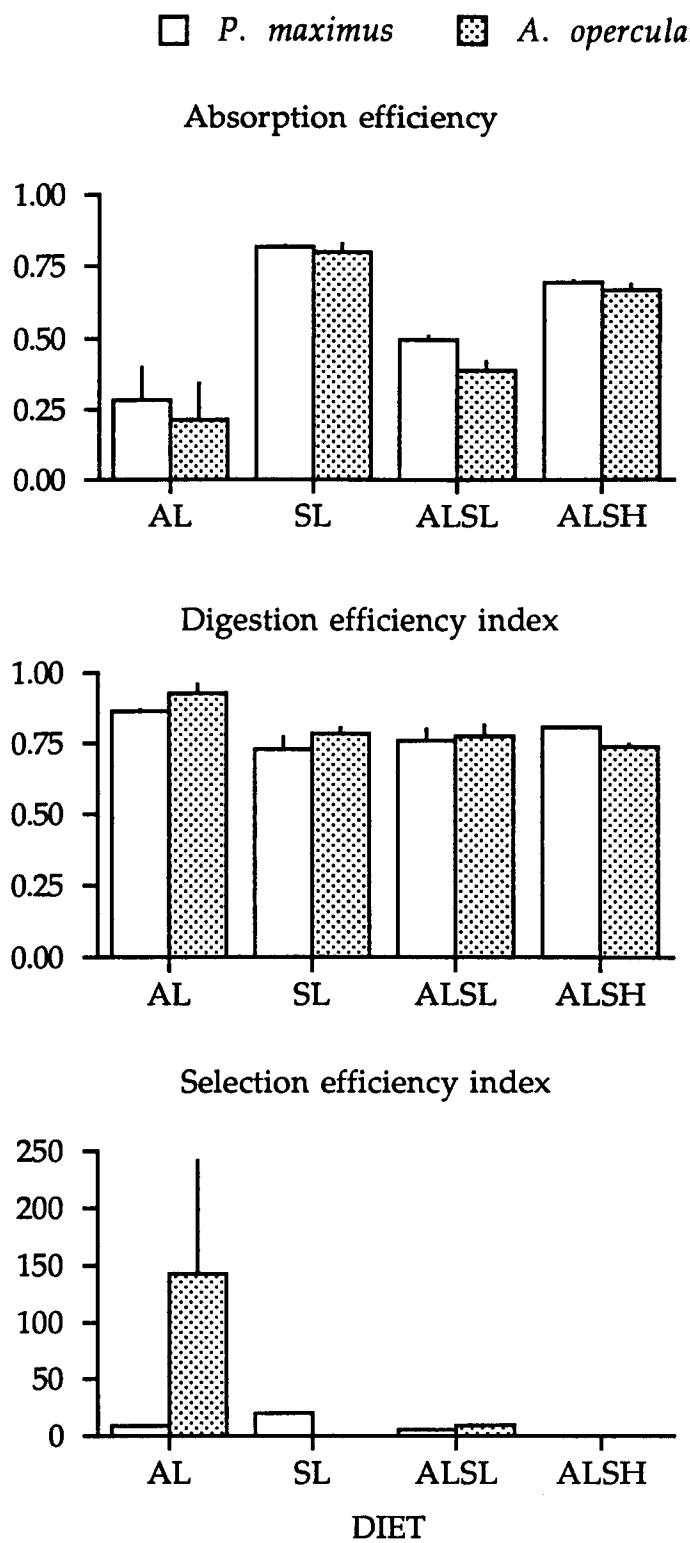


Fig. 4.12 The mean absorption efficiency, digestion efficiency and chlorophyll selection efficiency (± standard errors, where large enough to be plotted) of *P. maximus* and *A. opercularis* when fed different combinations of algae and sediment for 19 days.

(SL) diet, and the low algae (AL) vs. the low algae, high sediment (ALSH) diet were close to being significantly different. The digestion efficiency of the animals when fed the pure algal diet was slightly greater than when fed the other diets (Fig. 4.12).

Table 4.15 Analysis of variance of the arcsine absorption efficiencies. Selected comparisons were made between levels of significant factors by calculating Bonferroni L.S.Ds (using an EER of 0.05). * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
Diet	3	0.180	0.172	0.057	4.75	0.041	*
Species	1	0.008	0.004	0.004	0.34	0.576	
Diet & species	3	0.029	0.029	0.010	0.81	0.529	
Error	7	0.085	0.085	0.012			
Total	14	0.302					

Bonferroni L.S.Ds. S and NS represent significant and non-significant differences respectively, between the indicated diets.

Comparison	N1	N2	MS Error	F Crit	LSD	Significance
AL vs. SL	4	4	0.012	13.22	0.283	NS
AL vs. ALSL	4	4	0.012	13.22	0.283	NS
AL vs. ALSH	4	4	0.012	13.22	0.283	NS
SL vs. ALSL	4	4	0.012	13.22	0.283	NS
SL vs. ALSH	4	4	0.012	13.22	0.283	NS
ALSL vs. ALSH	4	4	0.012	13.22	0.283	NS

Chlorophyll selection efficiency

No clear pattern emerged from the available data (Fig. 4.12). The percentage of chlorophyll rejected as pseudofaeces suggested that *P. maximus* was rejecting more chlorophyll; and hence selecting less efficiently.

The oxygen to nitrogen ratio

The oxygen to nitrogen ratio was significantly different between species ($F_{0.05}$, 1, 65 = 5.20 P = 0.026 Table 4.16), with *P. maximus* having lower O : N ratios. The species and diet interaction term was also significant. Bonferroni L.S.Ds showed that there was a significant difference between species when fed the low sediment diet (SL), there was also almost a significant difference between the species when fed the low algae, high sediment (ALSH) diet.

Table 4.16 Analysis of variance of the log_{10} transformed oxygen to nitrogen ratios. Selected comparisons were made between levels of significant factors by calculating Bonferroni L.S.Ds (using an EER of 0.05). * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
Dry body weight	1	0.400	0.337	0.337	2.06	0.156	
Diet	3	0.035	0.027	0.009	0.06	0.983	
Species	1	0.893	0.852	0.852	5.20	0.026	*
Block	1	0.012	0.012	0.012	0.07	0.787	
Diet & species	3	1.453	1.474	0.491	3.00	0.037	*
Diet & block	3	0.195	0.188	0.063	0.38	0.766	
Species & block	1	0.182	0.182	0.182	1.11	0.295	
Error	65	10.642	10.642	0.164			
Total	78	13.813					

Bonferroni L.S.Ds. S and NS represent significant and non-significant differences respectively, between the indicated species at each diet. P represents *P. maximus* and A *A. opercularis*.

Comparison	N1	N2	MS Error	F Crit	LSD	Significance
AL P vs. A	10	10	0.164	6.60	0.465	NS
SL P vs. A	10	9	0.164	6.60	0.478	S
ALSL P vs. A	10	10	0.164	6.60	0.465	NS
ALSH P vs. A	10	10	0.164	6.60	0.465	NS

The O:N ratio of *P. maximus* was low when fed the low sediment diet (SL) and the low algae, high sediment (ALSH) diet, but slightly higher when

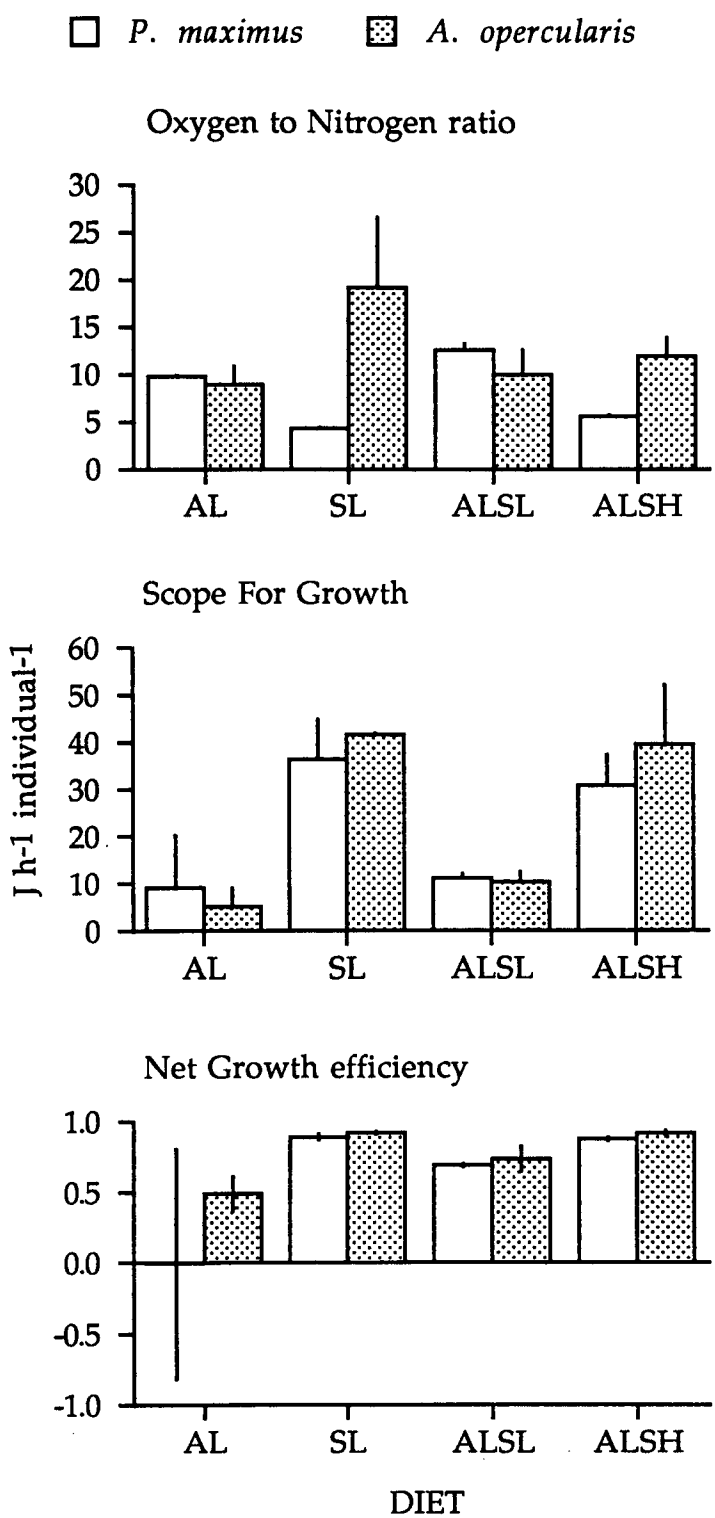


Fig. 4.13 The physiological indices scope for growth, oxygen to nitrogen ratio, and the net growth efficiency (K2) of *P. maximus* and *A. opercularis* when fed different combinations of algae and resuspended sediment. Each bar represents the mean value of two tanks, ± standard errors, where large enough to be plotted.

fed the low algae (AL) diet, and higher again when fed the low algae, low sediment (ALSL) diet. The O:N ratios of *A. opercularis* were more regular, except when fed the low sediment (SL) diet, when the ratio was considerably higher (Fig. 4.13).

Scope for growth

The scope for growth did not differ significantly between species, but diet did play a significant rôle ($F_{0.05}$, 3, 3 = 25.04 P = 0.013). The scope for growth of the animals fed the low sediment (SL) diet was significantly higher than when fed pure algae (AL) (Table 4.17), and the low algae (AL) and low sediment (SL) diets were very close to being significantly different from the low algae, high sediment (ALSH) diet and the low algae, low sediment (ALSL) diet respectively. However, it can be seen that the scope for growth was highest when the animals were fed low levels of resuspended sediment and low levels of algae with high levels of sediment (Fig. 4.13).

Table 4.17 Analysis of variance of the scope for growth of *P. maximus* and *A. opercularis*. Selected comparisons were made between levels of significant factors by calculating Bonferroni L.S.Ds (using an EER of 0.05). * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
Diet	3	3247.41	3247.41	1082.47	25.04	0.013	*
Species	1	20.44	20.44	20.44	0.47	0.541	
Block	1	374.56	374.56	374.56	8.67	0.060	
Diet & species	3	101.50	101.50	33.83	0.78	0.577	
Diet & block	3	273.60	273.60	91.20	2.11	0.278	
Species & block	1	30.85	30.85	30.85	0.71	0.460	
Error	3	129.68	129.68	43.23			
Total	15	4178.03					

Bonferroni L.S.Ds. S and NS represent significant and non-significant differences respectively, between species at the indicated diets.

Compare	N1	N2	MS Error	F Crit	LSD	Significance
AL vs. SL	4	4	43.23	38.83	28.971	S
AL vs. ALSL	4	4	43.23	38.83	28.971	NS
AL vs. ALSH	4	4	43.23	38.83	28.971	NS-just
SL vs. ALSL	4	4	43.23	38.83	28.971	NS-just
SL vs. ALSH	4	4	43.23	38.83	28.971	NS
ALSL vs. ALSH	4	4	43.23	38.83	28.971	NS

Net growth efficiency

The net growth efficiency did not differ significantly with diet or species (Table 4.18), however, it was slightly lower when the animals were fed the diets AL and the low algae, low sediment (ALSL) diet (Fig. 4.13).

Table 4.18 Analysis of variance of the net growth efficiencies of *P. maximus* and *A. opercularis*. Selected comparisons were made between levels of significant factors by calculating Bonferroni L.S.Ds (using an EER of 0.05). * and ** signify significance at the 0.05 and 0.01 probability levels respectively.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Diet	3	1.151	1.151	0.384	2.34	0.160
Species	1	0.094	0.094	0.094	0.57	0.474
Diet & species	3	0.155	0.155	0.052	0.31	0.815
Block	1	0.201	0.201	0.201	1.22	0.305
Error	7	1.149	1.149	0.164		
Total	15	2.749				

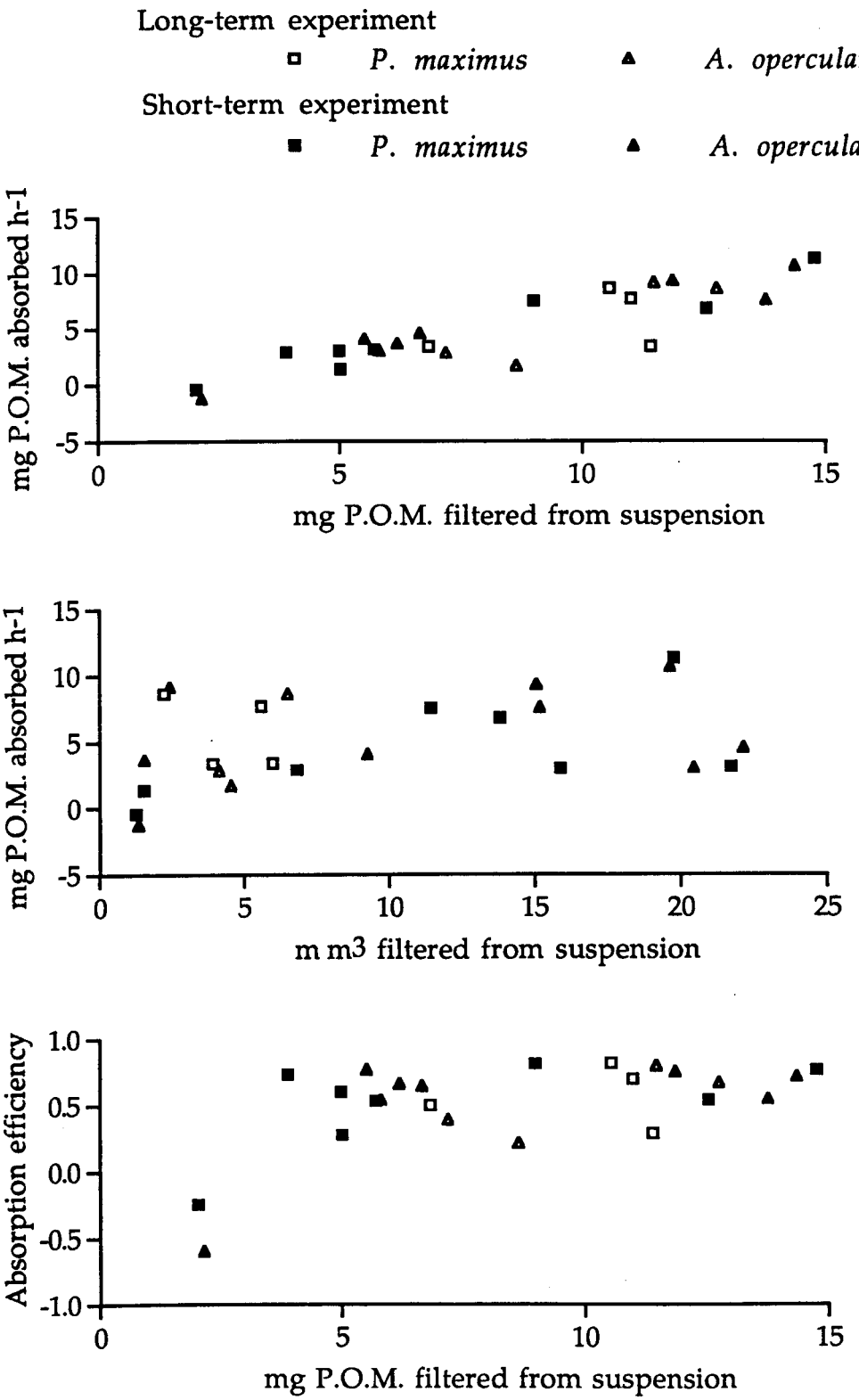


Fig. 4.14 A comparison of the amount of particulate organic matter absorbed and the absorption efficiency in the long-term and short-term experiments, when related to the P.O.M. or the volume of material filtered from suspension.

Comparison of the long-term and short-term experiments

Since the diet quantities and qualities varied between the long-term and short-term experiments, the experiments were compared by examining the amount of P.O.M. absorbed and the absorption efficiency, in relation to the amount of P.O.M. or the volume of material filtered from suspension (Fig. 4.14). There were no appreciable differences in absorption efficiencies or absorption rate between experiments when a similar amount of material was filtered from suspension.

DISCUSSION

Methodological problems

The major difficulty in my experiments concerned the analysis of chlorophyll and phaeopigment concentrations in the biodeposits and faeces. The pigment concentrations were often not high enough to be detected by the methods employed: the sensitivities of the spectrophotometric and fluorescent methods are related to the quantity of water filtered or amount of material analysed (Lorenzen, 1967; Parsons *et al.*, 1984). The quantities used in my experiments were obviously inadequate.

The presence of accessory pigments (chlorophylls *b* and *c* and degradation products) can introduce significant errors to the estimation of chlorophyll *a* and phaeopigment concentrations in both spectrophotometric and fluorometric methods. Acidification of the sample degrades the chlorophyll to phaeophytin by removing a magnesium ion from the phytol chain. More acidic conditions degrade the phaeophytin further, removing the phytol chain by breaking an ester bond, to phaeophorbide (Patterson & Parsons, 1963; Holm-Hansen *et al.*, 1965). The breakdown to the degradation products results in a reduction in the absorbency of the sample, whichever chlorophyll pigments were originally present (Lorenzen, 1967). However, the fluorescence of the sample will decrease if only chlorophylls *a* and *c* are present, but the fluorescence of chlorophyll *b* degradation products actually increases relative to that of chlorophyll *b* (Lorenzen, 1967). This can cause problems in fluorometry when samples contain significant quantities of chlorophyll *b*. The accessory pigments alter the acid ratio (the ratio of the fluorescence or absorbance readings before and after acidification). The acid ratio is used to estimate the

amount of material that has been degraded by acidification to phaeopigments, and hence the amount of chlorophyll present.

In fluorometry, high ratios of chlorophyll *c* to chlorophyll *a* result in an overestimation of chlorophyll *a* concentrations, and an underestimation of phaeopigment concentrations. The opposite occurs if significant quantities of chlorophyll *b* are present (Holm-Hansen *et al.*, 1965; Lorenzen, 1967; Trees *et al.*, 1985). The alteration of the acid ratio from 2.2 (as used in the fluorometric equations) can result in negative phaeopigment values (Holm-Hansen *et al.*, 1965), phaeopigment concentrations being the most sensitive to changes in the acid ratio (Trees *et al.*, 1985). Various combinations of pigments can result in apparent negative values of both chlorophyll and phaeophytin (Trees *et al.*, 1985). Pure chlorophyll *c* extracts from two algal species had acid ratios of 5-6, which illustrates how significant the presence of accessory pigments can be (Holm-Hansen *et al.*, 1965). Accessory pigments may also reabsorb fluoresced light, which will result in an underestimate of the chlorophyll *a* concentration (Holm-Hansen *et al.*, 1965).

In summary, the variability of the fluorometric technique depends upon the presence or absence of chlorophylls *b* and *c*, and phaeophorbide *a*. Phaeophorbide has been found in large quantities in marine sediments (Patterson & Parsons, 1963), and has been found to be the dominant pigment in the digestive glands of *Placopecten magellanicus* (Robinson *et al.*, 1989) and *Mytilus edulis* (Gelder & Robinson, 1980; Hawkins *et al.*, 1986), and the stomachs of oysters (Patterson & Parsons, 1963).

As previously mentioned, the spectrophotometric trichromatic technique (Strickland & Parsons, 1965; Parsons *et al.*, 1984) is also sensitive to the

presence of accessory pigments (Patterson & Parsons, 1963; Lorenzen, 1967). The error associated with the determination of chlorophyll increases with increasing phaeopigment concentrations (Lorenzen, 1967).

The faeces and biodeposits collected during the long-term exposure experiment were analysed using the spectrophotometric technique of Lorenzen (1967). It was evident that this technique was unsatisfactory, since negative values occurred. This was probably due to a combination of the small amount of fluorescing pigment present (in particular the faecal material, where readings taken at 665 nm, after correction for the blank, should ideally be greater than 0.2 (Lorenzen, 1967)), and to the complex mixtures of pigments present. The faeces and biodeposits from the short-term response experiment were therefore analysed fluorometrically. The use of this technique did not solve the problem of apparent negative concentrations, even though the method is more sensitive to low chlorophyll concentrations (Holm-Hansen *et al.*, 1965; Lorenzen, 1965). The lower limit of detection of chlorophyll is about 0.01 μg, approximately 5% of that required for spectrophotometric methods.

Altering the combinations of filters used in the fluorometer may reduce the errors involved, the use of the 2-64 emission filter should reduce the sensitivity of the method to changes in the acid ratio (Holm-Hansen *et al.*, 1965). Alternatively, the acid ratio in the equation could be reduced (to less than 2) to minimize interference from accessory pigments, but other errors are then introduced (Trees *et al.*, 1985). Ideally high-performance liquid chromatography should be employed (Trees *et al.*, 1985; Hawkins *et al.*, 1986).

In the short-term response experiment, the errors associated with the fluorometric method were compounded by the apparent destruction of pigments to non-fluorescing end-products during digestion. The overall result was either negative values of chlorophyll or phaeophytin, or the determination of pseudofaecal chlorophyll (biodeposit - faecal chlorophyll) resulted in negative values. Thus the pigment budget did not balance. All negative results were discarded, which resulted in low sample sizes.

The apparent destruction of fluorescent pigments to non-fluorescent end-products is in itself interesting, especially as it did not occur in the long-term response experiment. This apparent destruction may be due to the fact that different methods were used in the short-term response experiment to measure the chlorophyll in the diets and in the biodeposits. However, the fluorometer is calibrated using the spectrophotometer. In addition, the amount of pigment lost may perhaps be expected to be similar between samples, which was not the case (although the differences between the methods that produce apparent pigment destruction, may be related to concentration). Pigment destruction has also been reported in grazing experiments performed on copepods (Conover *et al.*, 1986; Kiørboe & Tiselius, 1987; Lopez *et al.*, 1988; Head, 1992a). The extent of pigment destruction has been shown to be very variable, both within and between species (Lopez *et al.*, 1988). The variation has been attributed to several different sources: the food concentration (Lopez *et al.*, 1988), the feeding history over the preceding days (Kiørboe & Tiselius, 1987; Lopez *et al.*, 1988; Head, 1992a), and the ingestion rate (Conover *et al.*, 1986; Wang & Conover, 1986).

In my experiment, the proportion of pigment destroyed was positively related to the pigment concentration in the diet, and less strongly to the

proportion of P.O.M. in the diet. The correlation to the pigment concentrations is probably due to the fact that pigment destruction is calculated from pigment concentrations. The proportion of organic material in the diet will affect the gut passage time and the absorption efficiencies (Bayne *et al.*, 1987), and hence probably the digestion efficiencies. The reliability of this pigment destruction data is such that further speculation is unwarranted.

One further problem encountered during the short-term response experiment was that the low algal concentration diet produced results unlike those expected for a pure algal diet - which is a reasonably good quality diet. Upon examination of the diet chlorophyll and phaeopigment data, an almost one to one ratio of pigments was observed. This value was unexpectedly low, and may reflect either a large input of detrital material via the natural seawater system of the laboratory, or that one of the algal species had begun to deteriorate. The first theory is more likely to be correct, since the particle size spectra revealed a large proportion of very small (that is probably non-algal) particles in the diet.

The patterns of response that *P. maximus* and *A. opercularis* showed to increasing sediment or algae concentrations in the short-term response experiment were very similar, so the changes will be discussed collectively. There were some differences, and these will be mentioned in the appropriate section.

Short-term changes in the clearance rates

Generally both species responded to increasing particle numbers, volume or T.P.M. by increasing clearance rates up to a threshold value, after which

clearance rates declined. This is a commonly described pattern of response for bivalves (see reviews by Winter, 1978; Bayne & Newell, 1983; Griffiths & Griffiths, 1987; Bricelj & Shumway, 1991), which illustrates the volumetric constraint on feeding imposed by the gut capacity (Winter, 1975; Bayne *et al.*, 1987, 1989; Willows, 1992).

It must be remembered that the response to a particular diet is also controlled by the dietary quality: the observed clearance rate will be dictated by the interaction between quality and quantity. The expression of diet quality is an important aspect of the interpretation of feeding responses (Bayne *et al.*, 1987, 1988; Willows, 1992). In my experiment, with regard to clearance rates, the best descriptor of diet quality was found to be the ratio of chlorophyll to phaeopigment. This index accounted for 72 and 62% of the variability in clearance rates of *P. maximus* and *A. opercularis* respectively. Contrary to the results of other studies (Bayne *et al.*, 1987, 1989; Iglesias *et al.*, 1992; Navarro *et al.*, 1992), the descriptor P.O.M. mg per mm^3 was not as useful when describing the diet with respect to predicting clearance rates.

To illustrate the usefulness of the chlorophyll to phaeopigment ratio as a predictor in my experiment, the low algae, no sediment (ALS0) and the high algae, high sediment (AHSH) diets will be considered. These diets consisted of very different numbers, volumes and weights of particles: 3.5 and 127 particles μl^{-1}, 0.55 and 9.10 $mm^3\ l^{-1}$, 2.7 and 8.8 mg l^{-1} for the low algae, no sediment (ALS0) diet and the high algae, high sediment (AHSH) diet, respectively. However, the chlorophyll to phaeopigment ratios were very similar (1.08 and 0.97), and likewise the clearance rates recorded were very similar: 2.30 and 2.45 l h^{-1} for *P. maximus* and *A. opercularis* fed the low algae, no sediment (ALS0) diet , and 2.39 and 2.25 l h-1 for those fed

the high algae, high sediment (AHSH) diet. The disadvantage of this predictor is that it does not take into consideration any physically limiting aspects of the diet.

Short-term responses to changing dietary quality

Responses to changing dietary quality and quantity can differ over different time-scales of exposure (Bayne *et al.*, 1987; Bayne, 1992; Navarro & Iglesias, 1992). In the short-term, changes may include the alteration of clearance rates and the level of pseudofaecal production. Over a longer period of exposure, changes in the digestive investment may occur (enzyme production rate and the suite of enzymes present) and very long exposure times (many weeks) may ultimately result in changes to the morphology of the digestive tubules, gills and labial palps (see Bayne, 1992 for references).

In my experiment the feeding behaviour response to changing quality and quantity of diet was complicated, which is to be expected since it depends on both quality and quantity. Work with *Cerastoderma edule* has shown that the response triggered by increased particle concentrations depends upon the dietary quality (Iglesias *et al.*, 1992). This seems to be the case in my experiment: diets that do not contain high sediment loads trigger different responses in the feeding. If the diets that do not contain high sediment concentrations are considered, then within a particular level of algae or sediment in the diet, clearance rates reflect the changing concentration of P.O.M. mg mm^{-3}; clearance rates increase with decreasing quality. Within the high sediment group of diets, the clearance rates also increase with decreasing quality, but clearance rates are much lower.

Since energetically it is important to optimize the food absorbed from the diet (Willows, 1992), it is important to note that at the no (S0) or low (SL) sediment concentrations the absorption rate is enhanced by increasing sediment concentrations, and that no regulation of the P.O.M. absorbed occurs, except at high sediment concentrations. At high sediment concentrations the absorption efficiencies also no longer increase with increasing amounts of material removed from suspension - the pattern reverses. Thus at high sediment concentrations, clearance rates, in conjunction with pseudofaecal production, are adjusted to control the clearance of P.O.M.. Slight changes in gut passage time and/or digestive enzyme investment then maintain the P.O.M. absorbed at a very constant level, especially in *P. maximus*. *P. maximus* also generally exhibited greater selection efficiency than *A. opercularis*, except at the high sediment concentration, when the reverse occurred. This index was calculated using the chlorophyll data, and therefore should be interpreted with caution.

My experiment does not elucidate whether the absorption efficiency or the gut passage time (or both) alter, since the absorption efficiency measured here is the so-called apparent absorption efficiency (Navarro *et al.*, 1992). The apparent absorption efficiency was measured since it takes into account the energetic losses that may occur due to metabolic faecal loss (Hawkins & Bayne, 1984, 1985; Bayne *et al.*, 1987; Hawkins *et al.*, 1990), and the use of mucus in pseudofaecal packaging. When actual absorption efficiencies are used to calculate absorption rate the actual net gain is measured. Since the digestion efficiencies also decreased with increasing amounts of material cleared from suspension, it is reasonable to suggest that gut passage times were decreasing with increasing food quality; the amount of P.O.M. being processed per unit time was maintained at a

constant rate. Further circumstantial evidence that gut passage times were changing, is that this pattern of changing digestion efficiencies occurred over the whole range of diets. The enzymatic investment may also change, but this is less likely since changes in digestive investment are not theoretically very cost-efficient (Willows, 1992). However, increased enzyme production has been shown to occur in the digestive glands of *Cerastoderma edule*, in response to enhanced diet quality (Ibarrola, unpublished results, cited in Navarro & Iglesias (1992)).

Since it is acknowledged that both quantity and quality influence the feeding response to the addition of sediment to the diet, it is not surprising that so many apparently conflicting results occur in the literature (see Bayne & Newell, 1983 for a table of results). Some work has reported that absorption efficiency increases with increasing quality (for example, Vahl, 1980b; Navarro & Winter, 1982; Berry & Schleyer, 1983; Bricelj & Malouf, 1984; Hawkins *et al.*, 1986, 1990; Bayne *et al.*, 1987; Cranford & Grant, 1990; Navarro *et al.*, 1991, 1992). Other work has reported the opposite, or that absorption efficiency is inversely related to concentration or ration (Foster-Smith, 1975a; Griffiths, 1980a; Møhlenberg & Kiørboe, 1981; Bricelj & Malouf, 1984; Hawkins & Bayne, 1984). It should be noted, though, that these results were mainly obtained using pure algal monocultures. Experiments that use pure algal diets usually give different results from those which employ more natural assemblages of particles (Bayne *et al.*, 1984). The way in which diet quality is expressed is also important in determining the relationship between diet quality and absorption efficiency (Navarro, pers. comm., 1992).

In my experiment absorption efficiency increased with increasing quality (P.O.M. mm^{-3}) only when the diets contained high sediment

concentrations. It must be remembered that the above studies were usually performed on faeces, rather than biodeposits. When only the diets that did not contain high sediment concentrations are considered, absorption efficiency increased with increasing ration, and with diet quality when it was expressed as the ratio of chlorophyll to phaeopigment. Other work with pectinids has shown that the absorption efficiency of *Placopecten magellanicus* increases with the percentage of organic matter in the diet (Cranford & Grant, 1990), which also broadly occurred in my experiment. Pierson (1983), using radioactively labelled algae, found that *Argopecten irradians concentricus* assimilated different species of algae with efficiencies ranging between 17.4 and 99.0%.

It should also be noted here that post-ingestion selection may also occur (Shumway *et al.*, 1985), and that possible sorting devices have been reported at the entrances to the digestive diverticula (Morton, 1983). There are also unpublished reports that gut passage times have been observed to differ for different quality particles (silt, diatoms and naked flagellates) within a diet (Hawkins & Bayne, unpublished data, cited in Bayne, 1992). This adds further evidence to the suggestion that selection between particles within the gut may occur.

There are further ways in which the digestive component of the feeding response can alter. For example, the gut volume can change (Bayne *et al.*, 1984; Hawkins & Bayne, 1984; Hawkins *et al.*, 1990). An increase in gut volume will allow greater absorption of organic matter; for a constant ingestion rate gut passage times will be increased.

Another consideration in the analysis of short-term feeding responses is that the previous feeding history will probably affect the response (Landry

et al., 1984; Lopez *et al.*, 1988; Bayne, 1992). Also, the observed response of the animal may in fact not optimize the feeding strategy in the short-term, but may be operating in some 'time-averaged' optimal way (Hawkins *et al.*, 1983, 1985; Hawkins & Bayne, 1985).

Taghon (1981) predicted that the energetically optimal response to increasing dietary quality would be to increase the rate of feeding, even if that necessitated a reduction in gut passage time and absorption efficiency. This occurred in my experiment when the diets did not contain high concentrations of sediment. When the diets contained high sediment concentrations, the pattern was repeated, but from a much lower baseline value. Within a dietary level the ingestion rate was also negatively related to absorption efficiency, as was proposed by Bayne *et al.* (1984). Willows (1992) suggested that, at high food concentrations, gut passage times will be short and absorption efficiencies will not respond to the qualitative composition of the food. Filtration rates will increase with increasing concentration to utilize the more abundant high quality particles, if the low quality particles are selectively removed. Otherwise, filtration rates will decline. The relationship in my experiment between P.O.M. absorbed and the volume of diet removed from suspension suggests that the feeding response is one involving the alteration of gut passage times. This would explain the absorption efficiency results, when combined with the large amounts of mucus in the pseudofaeces reducing the apparent absorption efficiency at high sediment concentrations. Thus the absorption efficiency in my study is related to ration, which was also found by Foster-Smith (1975a) and Bricelj & Malouf (1984). This suggests that *P. maximus* and *A. opercularis* increase filtration rates with increasing food availability, except at high concentrations, when clearance

rates are reduced but the P.O.M. cleared is maintained through increasing the production of pseudofaeces.

Thus the suggestion that bivalve species which regulate ingestion primarily by reducing clearance rates will be more vulnerable to suspended sediment (Bricelj & Shumway, 1991) applies to a certain extent to *P. maximus* and *A. opercularis*. However, they do seem to be capable of employing pseudofaecal production to maintain the quality of the ingested ration. *P. maximus* in particular maintained the level of absorbed P.O.M. very well. The amount of P.O.M. removed at high sediment concentrations will not necessarily be high enough to support growth. It must be noted though that the addition of silt to the diet resulted in enhanced absorption rates of P.O.M., which would presumably enhance growth (assuming that metabolic costs of feeding are not disproportionately increased). Bricelj (1984) demonstrated that the increased absorption efficiency of *Mercenaria mercenaria* upon the addition of sediment to the diet was not due to the sediment increasing the grinding of the food, but that sedimentary organics were being utilized. Indeed, Bricelj & Malouf (1984) found that 21-22 % of the available organic material in the sediment was absorbed. A further suggestion is that the absorption efficiency of the algae in the diet is increased due to 'dilution' of the food by the inorganic material (Widdows *et al.*, 1979). This does not incorporate the idea that selective ingestion may occur, which would largely counter this effect.

To investigate whether the amount of P.O.M. absorbed in my experiments was sufficient to maintain a positive net energy balance, oxygen consumption rates have been calculated for 2.43g animals (Table 4.19) using the weight exponents and energetic conversion factors in the

methods section, and the data in Mackay & Shumway (1980, calculated from McLusky, 1973) for *A. opercularis*, and that of Roberts (1973) for *P. maximus*. Two values are given for *P. maximus* as only size range information (11-17g) was given in Roberts (1973). It can be seen that episodic feeding on all of the diets should have provided sufficient energy to support the basic metabolic energy requirements. The P.O.M. absorbed from the low algal concentration would not have been sufficient to achieve a positive net energy balance.

Table 4.19 The estimated oxygen consumption rates and energy respired per hour of *P. maximus* and *A. opercularis*, and the P.O.M. that would need to be absorbed per hour to maintain a net positive energy balance (excluding ammonia excretion).

Species	ml O_2 h^{-1}	J h^{-1}	P.O.M. required h^{-1}
P. maximus	0.74	13.62	0.58
P. maximus	0.84	15.04	0.64
A. opercularis	0.67	17.08	0.73

Long-term physiological responses to sediment

In the long-term response experiment clearance rates were low due to low water flow rates through the tanks. Thus the amount of material removed from suspension was limited by flow rate rather than alteration in clearance rate and the clearance rates remained essentially constant. The oxygen consumption and the ammonia excretion rates when the animals were fed diets including sediment showed different patterns for the two species: *A. opercularis* maintained more constant oxygen consumption rates and less elevated ammonia excretion rates. *P. maximus* showed greater signs of food limitation: reduced oxygen consumption and enhanced ammonia production (Bayne, 1973a, 1973b;

Bayne & Scullard, 1977; Grant & Thorpe, 1991; Hawkins & Bayne, 1991). The oxygen consumption of *P. maximus* was especially depressed when fed the low sediment (SL) and the low algae, high sediment (ALSH) diet, and the ammonia excretion rates of *A. opercularis* were enhanced when fed the low algae (AL) diet and the low algae, low sediment (ALSL) diet; thus, increased stress occurred in the two species induced by different diets.

Unfortunately, no baseline values of ammonia excretion rates are known for these species, but they are more likely to be closer to the lower excretion rates found, since ammonia excretion is not likely to be depressed under stress. Ammonia excretion rates in my experiment varied between 4.8-14.2 and 9.8-28.2 μg g DW^{-1} h^{-1} for *A. opercularis* and *P. maximus* respectively. These may be compared with values recorded for other bivalves, Barber & Blake (1985) found excretion rates of 92 μg g DW^{-1} h^{-1} at 21°C (the lowest temperature used) in *Argopecten irradians concentricus*. Bayne & Scullard (1977) reported excretion rates for *Mytilus edulis* of approximately 32 μg h^{-1}, at the start of an experiment run at 11°C for 17 days. Bayne (1973b) reported ammonia excretion values that varied seasonally between 1 and 15 μg g DW^{-1} h^{-1}, also for *Mytilus edulis*. The values recorded by Bayne (1973b) during December (the period in which my study was performed) were less than 4 μg g DW^{-1} h^{-1}. This suggests that either the pectinids were stressed and thus excreting more ammonia, or that they normally exhibit greater excretion rates than mytilids. A combination of these features may also have occurred.

Comparing the ammonia excretion rates of pectinids with those determined for mytilids may be misleading, since pectinids utilize protein as an energy source much more commonly than mytilids (reported in *Chlamys septemratiata* (Ansell, 1974); *P. maximus* (Comely, 1974); *A.*

opercularis (Taylor & Venn, 1979); and *Placopecten magellanicus* (Robinson *et al.*, 1981)), and so excretion rates may be higher. This also causes problems in interpreting the oxygen to nitrogen ratio (O:N ratio), since little is known with regard to normal pectinid O:N ratios. Barber & Blake (1985) found that seasonal values of the O:N ratio were generally lower than those found for mytilids, ranging from 6 to 22. Volckaert (1988, cited in Grant & Cranford, 1991) reported O:N ratios of 31.2 for juvenile *Placopecten magellanicus* fed on *Chaetoceros* and *Isochrysis*, and 12.7 for starved scallops. Experiments using thermally stressed *Placopecten magellanicus* recorded an O:N ratio of 8.9 (Grant & Cranford, 1991). The O:N ratio of mytilids usually exceeds 50 during periods of tissue growth (range 17-120 (Bayne & Newell, 1983), but much higher values do occur).

The apparently lower range of O:N ratios found in pectinids may be due to the more important contribution of protein to the overall metabolism (Epp *et al.*, 1988). An O:N ratio of approximately 9 indicates exclusive protein catabolism while a value between 12 and 19 indicates lipid catabolism and above 22 indicates carbohydrate catabolism (Mayzaud, 1972; Bayne, 1975; Barber & Blake, 1985). The utilization of ammonia in synthetic pathways, or the incomplete oxidation of the amino acids will also result in low O:N ratios (Bayne, 1975).

The fact that nothing is known regarding baseline ammonia excretion rates of *P. maximus* and *A. opercularis*, and consequently about the O:N ratio, means that interpreting my data is difficult. This is especially so when the S.F.G. and O:N results apparently contradict each other. The O:N ratios of *P. maximus* when fed the low sediment (SL) or the low algae, high sediment (ALSH) diets indicate that the animals were stressed, whereas the S.F.G. results suggest that they were not.

The adductor muscle of pectinids acts as a storage site for protein and carbohydrate, while the digestive gland stores lipids (Ansell, 1974; Comely, 1974; Taylor & Venn, 1979; Barber & Blake, 1981; Sundet & Vahl, 1981; Barber & Blake, 1985; Epp *et al.*, 1988). In *A. opercularis* and *P. maximus* peak levels of storage products in the adductor muscle occur in September-October and November respectively (Comely, 1974; Taylor & Venn, 1979). Comely (1974) and Taylor & Venn (1979) reported that the energetic demands of gametogenesis in *P. maximus* and *A. opercularis* were supported by adductor muscle protein and glycogen. Barber & Blake (1991) concluded that adductor muscle glycogen appeared to be the energy substrate most readily stored and utilized for gametogenesis, but that protein is commonly used in populations that undergo oögenesis over the winter when food levels are low (including *P. maximus* and *A. opercularis*). In contrast, mytilids rely heavily on glycogen stored in the mantle connective tissue to support gametogenesis (Bayne *et al.*, 1982).

Since pectinids utilize protein as an energetic substrate to a greater extent than mytilids (Epp *et al.*, 1988), and my experiments were carried out in December, when gametogenesis would be starting, may mean that the low O:N ratios obtained do not actually indicate that the animals were stressed. However, there must be some differences between *P. maximus* and *A. opercularis* since when fed low concentrations of sediment *A. opercularis* had both a high scope for growth and a high O:N ratio, whereas *P. maximus* had a high scope for growth but a low O:N ratio. Differences between the species may be due to the fact that there will be differences in sexual maturity: 2 year old *A. opercularis* are usually mature, but *P. maximus* are not. The scope for growth values obtained were similar, however, which perhaps would not then be expected.

The use of the O:N ratio in pectinids deserves further attention, as it is a good 'whole animal' response to stress that does not necessitate killing the animal in order to measure it (Bayne & Thompson, 1970; Bayne, 1973a, 1975; Widdows, 1978).

The scope for growth of standard (2.43g) *P. maximus* and *A. opercularis* varied between 9-36 and 5-42 J h^{-1} respectively. This is similar to the yearly range (approximately 3-33 J h^{-1}) found in 5g *Placopecten magellanicus* from a depth of 10m (MacDonald & Thompson, 1986). In my experiment the scope for growth was related to the volume of material removed from suspension; there was an inverse relationship between the amount filtered and the absorption efficiency. This determined the amount of P.O.M. absorbed which consequently determined the scope for growth. This suggests that gut passage times varied with the volume of food removed, with the longer gut passage times that occurred when less food was filtered resulting in higher absorption of material. The digestion efficiencies of the sediment diets were very similar, suggesting that some alteration of digestive investment or gut capacity may also have occurred. There also seemed to be little control of the P.O.M. removed from suspension, probably because clearance rates were very low, due to the low flow rates through the tanks.

If the calculated 'normal' oxygen consumption rates in Table 4.19 are correct (0.74-0.84 ml O_2 h^{-1} for *P. maximus* and 0.67 ml O_2 h^{-1} for *A. opercularis*), then the oxygen consumption rates determined in this study are very depressed (0.13-0.20 and 0.09-0.24 ml O_2 h^{-1}). Grant & Cranford (1991) also recorded depressed oxygen consumption rates for *Placopecten magellanicus* (using their regression equation a 2.43g animal would have

an oxygen consumption rate of 0.095 ml O_2 h^{-1} at 6°C). They attributed this to nutritive stress. Interestingly, the P.O.M. absorbed per hour in my experiment should, in theory, have provided enough energy for the animal to maintain 'normal' oxygen consumption rates; thus, the diet should not have been limiting. The diet could have been nutritionally limiting in some other way, for example, the concentrations of nitrogen or carbon that could be absorbed may have been low.

There is initial evidence that some physiological stress occurred in the short-term, as well as the long-term, experiment. At T.P.M. concentrations above 6.4 mg l^{-1} absorption rates were reduced, however, pseudofaecal production was increased, which would be energetically expensive and consequently more stressful. There does not seem to have been any acclimation to sediment in the diet. The experiments are difficult to compare, though, since different amounts of material were filtered by the animals, which would affect the consequent absorption efficiencies. It is noticeable that in both experiments *P. maximus* was more adversely affected by sediment in the diet than *A. opercularis*, but exhibited more efficient chlorophyll selection when feeding on the lower concentration diets (no algae or low algae). This is interesting in light of the ecological differences between the species. Since *P. maximus* recesses, it may be expected that it would receive a lower quality diet, which could necessitate a higher level of selection. Both species exhibited a flexible feeding response to changing dietary quality and quantity, but *P. maximus* was more adversely affected by sediment in the diet. Whether these observed differences between the two species could have any bearing on the distributional differences shown between them needs further examination. These preliminary results show that increased sediment in

the diet may be a contributory factor dictating why *P. maximus* is generally not found living in easily resuspendable sediments.

CONCLUSIONS

P. maximus and *A. opercularis* show different responses to sediment in the diet depending on the absolute amount of sediment present. At low sediment concentrations no control of the P.O.M filtered occurs; clearance rates increase with the available material. At high sediment concentrations clearance rates are reduced, but increased pseudofaecal production combined with alterations in the volume of material cleared, controls the P.O.M. removed from suspension. This results in a very tightly controlled absorption of P.O.M.. The P.O.M. absorbed from all of the diets provided, except the low algal concentration diet, should have been sufficient to maintain a positive net energy balance. The low algal concentration diet contained many small particles which suggests that high concentrations of non-algal material may have been present in the seawater system.

The scope for growth values obtained reflected the amount of P.O.M. absorbed, which was dictated mainly by the absorption efficiency. The absorption efficiency was inversely related to the volume of material filtered, which suggests that gut passage times determined the absorption efficiencies. Alterations in digestive investment and/or gut capacity may also be involved, since digestive efficiencies remained largely constant in the diets that contained sediment.

In the short-term response experiment low concentrations of sediment in the diet increased the P.O.M. absorbed compared to the algal diets, and more P.O.M. was absorbed at high, rather than low, sediment

concentrations when no algae was present. In the long-term experiment sediment in the diet also produced more favourable absorption rates than the pure algal diet. Scope for growth values obtained for the diets which included sediment were at least as good as for the pure algal diet.

This experiment has not conclusively elucidated any reason why *P. maximus* is generally not found living on easily resuspendable sediments. The O:N ratios for *P. maximus* suggest that the animals may be physiologically stressed, but no definite conclusions can be drawn due to the apparent contradictions that occur in the scope for growth and O:N ratio results. The scope for growth values were positive when both *P. maximus* and *A. opercularis* were fed diets containing sediment, but the depressed oxygen consumption rates suggest that the animals were stressed.

CHAPTER 5. GENERAL DISCUSSION

The feeding and digestion of bivalve molluscs is controlled by many different endogenous and exogenous factors (Griffiths & Griffiths, 1987; Bayne, 1992; Bayne & Hawkins, 1992; Navarro & Iglesias, 1992). The seston available will also vary seasonally and over shorter time scales, as tidal currents alter in strength and changes in the degree of resuspension of sediment occur due to wind-induced currents (Berg & Newell, 1986, 1989; Frechette & Grant, 1991). Some of the factors which were found to affect the feeding of *Pecten maximus* and *Aequipecten opercularis* in my study have been selected for further consideration in this general discussion. Firstly, methodological problems are considered since they are of fundamental importance in evaluating the results. After this the differences and similarities between *Pecten maximus* and *Aequipecten opercularis* are summarised and discussed in relation to the morphological, behavioural and ecological differences between the two species. The discussion is widened to include comparisons with other bivalves, particularly *Mytilus edulis*, on which most prior work has been carried out. Hydrographic processes, especially the conditions in the Irish Sea which affect the flux of particles to and within the benthic boundary layer, are then briefly detailed. Finally, factors which limit feeding and digestion in bivalves are appraised and suggestions made for further work.

Methodology

Several methodological problems were encountered in my study. The first involved the use of the Coulter Counter Multisizer, and concerned the fact that particles could be counted faster than they could be allocated to particle size classes. This was a problem that previous and present

colleagues who used the Multisizer were unaware of, nor is it mentioned in the operating manual. The way in which this problem was dealt with, as well as details of other known short-comings of this machine, were discussed in the General Introduction (Chapter 1). The second problem was that neither the spectrophotometric or fluorometric methods used to analyse fluorescent pigments in the biodeposits and faeces were sensitive enough to give reliable results (see Chapter 4). Most of these data were discarded, which meant that little information was available regarding the possible preferential pre-ingestion of fluorescing particles. As a compromise, the loss of chlorophyll in pseudofaeces was estimated using the acid ratios of the biodeposits and faeces. The alternative indicator of pre-ingestive selection, preferential organic matter removal, could not be used since no data were available on the organic content of the faeces - only the biodeposits. In spite of these problems my work has provided an insight into the feeding physiology of *P. maximus* and *A. opercularis*.

Comparisons between species

P. maximus exhibited greater particle size selection and higher clearance rates than *A. opercularis*, when fed an algal diet. *P. maximus* was also more efficient at pre-ingestive selection, except when the diet contained high levels of algae, when the pattern was reversed. *A. opercularis* seemed to be able to maintain more efficient selection at higher algal concentrations than *P. maximus*. The clearance rates of both species showed similar reactions to the addition of sediment in the diet, but the clearance rates and absorption rates of *P. maximus* were reduced to a greater extent when high concentrations of sediment were added to the diet. The addition of low concentrations of sediment increased the clearance rates and the subsequent absorption rates of both species. This

would suggest that low sediment concentrations have a potentially beneficial effect on the overall energy gain of the animals, due mainly to an increase in clearance rates. The response to sediment in the diet could be interpreted by examining quantitative aspects of the diet, however, quality (especially the chlorophyll to phaeopigment ratio) also played a part.

Pectinids often encounter resuspended sediment in the seston. For example, the total particulate matter in the water at my subtidal site varied seasonally between 2.0 and 19.9 mg l^{-1}. Thus the diets that I used in both the short (2.7-8.8 mg l^{-1}) and long-term (4.6-7.8 mg l^{-1}) exposure experiments spanned the lower end of the range of seston concentrations that would actually be encountered. However, even the apparently small range of sediment concentrations that I used did elicit significant feeding and physiological responses in the animals. Overall, these experiments showed that *P. maximus* is more sensitive to resuspended sediment in the diet than *A. opercularis*, and that *P. maximus* was very effective at controlling the amount of P.O.M. absorbed from diets containing between 6.4 and 8.8 mg l^{-1} of total particulate matter. In the long-term exposure experiment, the ammonia excretion results indicated that *P. maximus* was sensitive to, and stressed by, the presence of sediment in the diet, but the scope for growth results were contradictory.

This work is interesting with respect to the environment which the two species inhabit, and the morphological, behavioural and distributional differences that are evident between the two species. *P. maximus* recesses into the sediment, whereas *A. opercularis* does not. In the light of recent studies on other bivalve and polychaete species, it is possible that the difference in feeding heights between the two species affects the diet

encountered by them (Muschenheim, 1987a, 1987b; Grizzle & Lutz, 1989; Grizzle *et al.*, 1992; Muschenheim & Newell, 1992). This idea is supported by the work in my study (Chapter 3) which showed that although *P. maximus* and *A. opercularis* had a similar assemblage of common diatoms in their gut contents, *P. maximus* was not as closely linked to a single dietary source as *A. opercularis.* Either the two species encounter different diets, or *P. maximus* exhibits greater selection with regard to the diatom species that are ingested. This study has shown that *P. maximus* tends to exhibit greater selection than *A. opercularis,* but this trend can be altered by different diets.

The majority of work on the feeding of bivalves has been performed on mytilid species. In the U.K. most attention has focussed on *Mytilus edulis.* There are fundamental differences between mytilids and pectinids which warrant discussion. Mytilids are non-motile and are attached by byssal threads in dense beds, which for *Mytilus edulis* are usually intertidal and often occur in estuaries (Bayne, 1976). Pectinids are motile, occur sub-tidally, and despite reports of high densities being encountered (Mason, 1983), are usually not densely aggregated (Ansell *et al.*, 1991).

Since mytilids occur in such dense beds, food limitation and consequent population size and growth rate limitation occurs (Wildish & Peer, 1983; Wildish & Kristmanson, 1984; Frechette & Bourget, 1985a, b; Frechette & Lefaivre, 1990; Frechette *et al.*, 1992). The clearance of material from suspension in mytilids may also be physically limited by constraints imposed by neighbouring mussels (or fouling organisms) on the gape of the shell (Jørgensen *et al.*, 1988). An energetically optimal strategy in such a situation would presumably be to remove all the particles that are available. Mytilids, in contrast to pectinids, are highly efficient at filtering

small particles from the seston (Vahl, 1972a, 1972b, 1973; Møhlenberg & Riisgård, 1978; Palmer & Williams, 1980; Riisgård *et al.*, 1980; Riisgård, 1988; Cranford & Grant, 1990). Utilizing bacterioplankton from the water column is thought to be highly beneficial in supplying the nitrogen requirements of bivalves (Newell & Field, 1983; Seiderer *et al.*, 1984; Stuart & Klumpp, 1984; Seiderer & Newell, 1985). Very few free-living bacteria would be filtered by pectinids, however bacteria attached to the surface of larger particles would be utilized. Bacteria are thought by many to be an important link between benthic feeders and what may otherwise be rather refractory organic material (see Lopez *et al.*, 1989). The food available to pectinids and intertidal or estuarine populations of mytilids would also differ. The intertidal/estuarine mytilids encounter large, but predictable, fluctuations in seston due to the regular tidal influx of water which resuspends bottom sediment. The seston available to pectinids would presumably also vary as tidal currents altered sediment resuspension, but fluctuations would not be as severe. In the coastal waters around the Isle of Man, kelp fragments are common in the water immediately above the seabed. It is not known whether *P. maximus* or *A. opercularis* can ingest and utilize this material, but *Placopecten magellanicus* has been shown to absorb organic material from kelp (Cranford & Grant, 1990), as can *Aulacomya ater* (Stuart, 1982; Stuart *et al.*, 1982a). *Argopecten irradians* can also maintain slow, but steady, growth when fed a diet of the vascular plant *Spartina* (Kirby-Smith, 1976).

The study on the Irish Sea plankton by Graziano (1988) showed that primary production is almost entirely attributable to phytoplankton greater than 5 μm. My study (Chapter 3) showed that 50% of the total volume of material available seasonally was smaller than 3-11 μm, and usually below 4-6 μm. In the sediment diets of Chapter 4 the particles

were generally all smaller than 5 μm. This suggests that in the open water, coastal environment in which *P. maximus* and *A. opercularis* live, retaining particles less than approximately 5 μm may not be an energetically efficient strategy, since much of this material would probably be resuspended sediment. Also, since the flux of material in the subtidal benthic boundary layer does not exhibit such extreme variability as that in the intertidal or estuarine environment, a strategy of opportunistically removing all available particles would be less advantageous.

One very interesting difference between both *P. maximus* and *A. opercularis* and in comparison to mytilid species, is the feeding height above the seabed, and the likely differences in diet quality and quantity which result from this. Since particles of higher specific gravity have faster sedimentation rates (Taghon & Greene, 1992), and are not resuspended as high in to the water column, it may be expected that *P. maximus* would encounter the lowest quality diet (Muschenheim, 1987a, b; Muschenheim & Newell, 1992). This could potentially explain why *P. maximus* exhibits greater particle size selection and chlorophyll selection efficiency, but not why *P. maximus* shows an apparently greater sensitivity to sediment in the diet. This is in some ways surprising, since *P. maximus* recesses and would therefore presumably encounter more resuspended material, and lower quality diets. It may, on the other hand, help to explain the differences in distribution between *P. maximus* and *A. opercularis*, notably that *P. maximus* does not usually occur on fine sediment seabeds. A further consideration is that *P. maximus* may be continually buried by sedimenting soft sediment, and the recess itself alters local current patterns in a way which results in the animal being recessed further (Grant *et al.*, 1993). Sinking too low in the sediment would probably be detrimental for the animals, especially for small

individuals, thus the distribution of *P. maximus* and *A. opercularis* may be controlled by physical factors rather than, or in combination with, physiological ones.

It may reasonably be expected, though, that distributional patterns are dictated earlier in the life history due to differences in larval distribution, settlement, or early susceptibility to factors such as high sediment concentrations (turbidity). This may be especially true since Stevens (1987) found that small *Pecten novaezelandiae* (20 mm shell height) had higher mortality rates than larger animals (70 mm shell height) when exposed to suspended silt for 24 hours.

Hydrographic considerations

The area that was chosen for my field study was in a strongly tidally mixed area, within a commercially fished scallop ground. The benthic boundary layer was found to contain many suspended benthic diatoms species, and to be well mixed throughout the year. Very few differences were evident within the bottom metre of the water column. This area is typical of much of the eastern and western Irish Sea (although shallower than most of the scallop grounds), which is generally well mixed due to strong tidal currents. The exception is the stratified patch which occurs in summer further offshore to the west of the Isle of Man (Slinn, 1974). Previous studies of the phytoplankton higher in the water column have shown that resuspended benthic diatoms only occur during the autumn and winter (Marasigan, 1986; Graziano, 1988). My study showed that resuspension of benthic diatoms occurs throughout the year, providing the benthic suspension feeders with a constant supply of food. This continual resuspension of benthic material may provide a very active and efficient

link between the benthic primary producers and the benthic feeders. The benthic suspension feeders would also gain access to a large pool of detrital organic matter, which is considered to be an important source of food for the benthos (Rice & Rhoads, 1989), but which is often only available to detrital feeders. These ideas generally support the hypotheses of Brander & Dickson (1984), who suggested that the low recruitment of fish in the Irish Sea may be due to much of the primary production being channelled into benthic, rather than pelagic (providing food for fish larvae), food chains. Further support for this idea was provided by the fact that shellfish yields per unit area are relatively high, suggesting greater energy flow through the benthic food chain. The crux of this problem probably lies in the relative timing of the annual phytoplankton bloom and the fish spawning season. The relatively late phytoplankton bloom in the Irish Sea may not be beneficial for optimal larval survival and subsequent recruitment (Brander & Dickson, 1984). Pingree *et al.* (1976) showed that peaks in phytoplankton production were initiated earlier in the areas of the Irish Sea which developed stable stratification the quickest; that is, the areas with weak tidal mixing. The phytoplankton blooms in the more strongly tidally mixed waters of the Irish Sea occur later, and are more unpredictable, compared to the blooms in the more stratified waters to the west of the Isle of Man.

Commercially viable populations of pectinids, which show relatively stable annual recruitment, are often found to occur in areas of strong currents or near frontal systems (Sinclair *et al.*, 1985), for example, the western Irish Sea, the Bay St. Brieuc and the Gulf of Maine. Frontal systems are known to be biologically very productive areas, and some commercially important beds of *P. maximus* do occur near frontal systems in the Irish Sea (Murphy, 1986). The reason why areas with high ambient

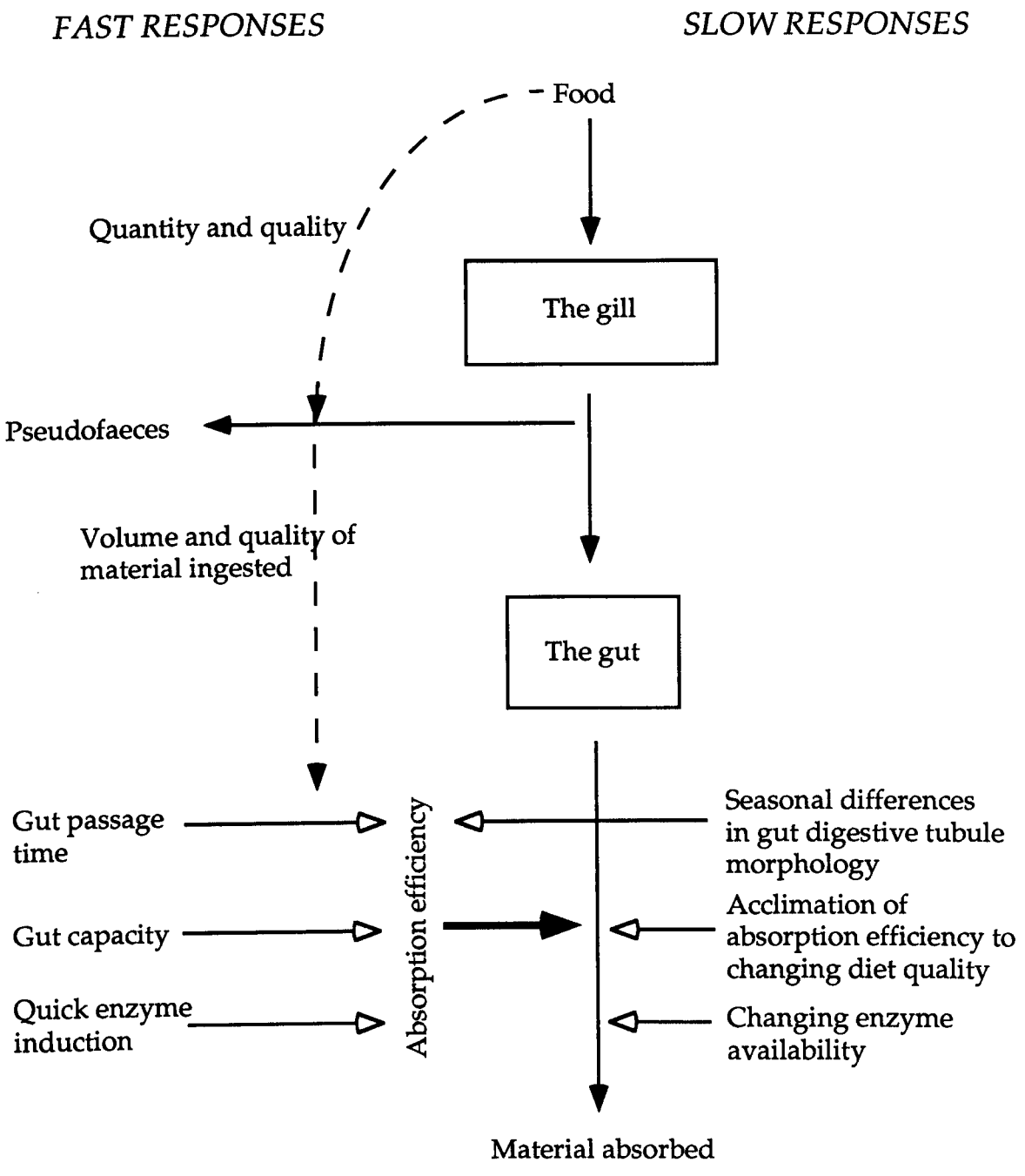


Fig. 5.1 A schematic summary of the short and long-term changes influencing feeding and digestion in bivalve molluscs

current speeds are beneficial to scallop growth and production is unclear - especially since seston uptake has been shown to be physically limited by high flows (Wildish & Saulnier, 1992; Wildish *et al.*, 1992). The influence of physical oceanographic processes on the distribution and success of commercial scallop grounds has been reviewed by Sinclair *et al.* (1985). One possibility that arises from the hypotheses of Brander & Dickson (1984) is that the production of these areas is out of phase with pelagic production cycles, and so more high quality food is available to benthic food chains. Mixing will exaggerate this effect.

The P.I.M.:P.O.M. ratio of the seston within my study area did not rise above three. Values greater than three have been suggested to be indicative of poor food quality which would be detrimental to pectinid growth (Vahl, 1980b; Wallace & Reinsnes, 1985). The adults of *P. maximus* and *A. opercularis* do not show continual growth throughout the winter (Mason, 1953; Soemodihardjo, 1974; Murphy, 1986; Allison, 1993), in the North Irish Sea, but my study suggests that food quantity may not be limiting, although food quality, or temperature may be. There may also be changes in resource allocation associated with the development of the gonads.

Rate limiting processes in feeding and digestion

Figure 5.1 summarizes some of the short and long-term factors which influence feeding and digestion. The factors mainly responsible for limiting the absorption of material filtered from suspension are the rate at which material can be processed by the gill, and the speed that the material is passed through the gut (Bayne, 1992; Navarro & Iglesias, 1992; Navarro *et al.*, 1992). Ingestion rate will be determined largely by the quantity and

quality of diet, which interact to dictate the behavioural response of the animal; that is, how clearance rates and pseudofaecal production are altered (Navarro *et al.*, 1992; de Villiers & Hodgson, 1993). This was evident in my study, where pseudofaecal production only really played an important rôle in the high sediment diets. Factors affecting the digestion rate include the quantity of material ingested, and the quality of material, which affects not only the gut passage time (Navarro *et al.*, 1992) but also the rate of enzyme production (Navarro & Iglesias, 1992). Gut capacity has been shown to increase with both quantity and quality in short-term experiments (Navarro *et al.*, 1992), and is an important mechanism which allows an increase in ingestion rate without a concomitant decline in gut passage time. One of the potentially most important features of digestion in bivalves is that particles of different quality, that are ingested at the same time, can be processed through the gut at different rates. Material that enters the gut can pass through the stomach to the intestine, or can enter the digestive gland. The material that passes straight through the stomach becomes intestinal faeces, whereas the material that undergoes further digestion in the digestive gland becomes glandular faeces (Widdows *et al.*, 1979). Thus the poorer quality particles could be expected to make up a relatively larger proportion of the intestinal, rather than the glandular, faeces. In my study (Chapter 4), the changes in absorption efficiencies were most readily explained by changes in gut passage time related to the changing volume of material ingested.

Further work

The scope for further work on the feeding and physiologies of *P. maximus* and *A. opercularis* is enormous. With regard to the physiology a seasonal study of basic physiological parameters needs to be undertaken, so that

changes due to experimental manipulation can be put in their correct context. This would also complement work on the seasonal changes in biochemical composition of *P. maximus* and *A. opercularis* that have been undertaken, highlighting time periods when the animals are under stress, or relying on different metabolic substrates. This physiological study would certainly need to cover clearance rates, oxygen consumption and ammonia excretion, but preferably also seasonal cycles in both true and apparent absorption efficiencies and gut passage time estimates. The work would need to be undertaken using naturally available seston. Using pure algal diets is of little use, even when used just as controls, except for comparison with early work which usually employed pure algal diets. However, the use of pure algal diets should not be perpetuated in physiological studies. This is not to deny that studies using algal diets have provided (and will still provide) invaluable early information regarding feeding processes, but it is now acknowledged that feeding responses may be very different when animals are fed more natural assemblages of particles (Bayne *et al.*, 1987; Griffiths & Griffiths, 1987; Navarro & Iglesias, 1992). Meaningful interpretations of any manipulative experiments can only really be made if the seasonal baseline values are known.

The flux of particles which occurs between the sediment and the benthic boundary layer, and between the upper water column and the benthos, needs to be examined. Systematic sampling needs to be undertaken over a range of sampling heights, which extend over the first few centimetres of the seabed. The effect that height above the seabed has on the quantity and quality of seston available to *P. maximus* and *A. opercularis* needs to be studied in conjunction with further physiological work on the response to long-term exposures to sediment in the diet. Additionally, studies using

radioactively labelled sediment could determine whether sedimentary organics are absorbed. This work could help to explain the observed differences in distribution between the two species, and would also be important in determining potentially useful sites for aquaculture. This would be especially important when on-growing animals in bottom culture, which is becoming an increasingly attractive aquaculture option.

CONCLUSIONS

P. maximus and *A. opercularis* exhibit variable feeding behaviour in response to diets of different quantity and quality. The presence of low levels of sediment in the diet is probably beneficial due to enhanced clearance rates and absorption of particulate organic matter. In the strongly tidally mixed region of the Irish Sea, the majority of the material encountered by *P. maximus* and *A. opercularis* is benthic in origin. The two species probably encounter slightly different diets due to differences in their behaviours - *P. maximus* recesses, and probably receives a lower quality diet. Since *A. opercularis* is often found in softer sediment areas than *P. maximus*, it is interesting to note that *P. maximus* is more sensitive to resuspended sediment in the diet. *P. maximus* is usually more efficient than *A. opercularis* at sorting the material filtered from suspension, except when high levels of algae are present. Overall, it has been shown that *P. maximus* and *A. opercularis* exhibit a more flexible feeding response to changing dietary quantity and quality than has been previously reported.

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APPENDIX 1

Chemical composition of Walne Media used for algal culture

Nutrient solution

$FeCl_3.6H_2O$	2.60g
$MnCl_2.4H_2O$	0.72g
H_3BO_3	67.20g
E.D.T.A.	90.00g
$NaH_2PO_4.2H_2O$	40.00g
$NaNO_3$	200.00g
Trace metal solution	2ml

Make up to 2l with distilled water.

Trace metal solution

$ZnCl_2$	2.1g
$CoCl_2.6H_2O$	2.0g
$(NH_4)_6MO_7O_{24}.4H_2O$	0.9g
$CuSO_4.5H_2O$	2.0g

Make up to 100ml with distilled water. Acidify with concentrated HCl to make a clear solution.

Vitamin solution

B12	10g
B1	10g
H (biotin)	200g

Make up to 200 ml with distilled water.

Add 1ml of nutrient solution (which includes the trace metal solution) and 0.2ml of vitamin solution to every litre of autoclaved seawater.