

Orientation, passive transport, and sediment erosion features of the sea scallop *Placopecten magellanicus* in the benthic boundary layer

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Passive transport and orientation of sea scallops (*Placopecten magellanicus*; 27–120 mm shell height) were studied in a laboratory flume to assess flow-mediated control of movement and position on the seabed. Additional experiments were conducted to characterize patterns of sediment transport around the scallop shell in relation to recesses occupied by scallops. The critical shear velocity of scallop transport was not correlated with shell height or other size measures, and most scallops were transported with the ventral shell margin facing downstream. Frontal exposure of scallops to the flow as indicated by fineness (shell height/shell depth) was greater in larger scallops, but when pallial gape was included in fineness (shell height/shell depth + gape), frontal exposure was not correlated with scallop size. This suggests that variation in the drag component of transport was responsible for the lack of correlation between shell morphometry and critical shear velocity. Sediment transport created a horseshoe-shaped trough around the shell and several smaller erosion–deposition features downstream. The dimensions of sediment transport features were dependent on shell allometry, and it is likely that sediment transport contributes to the formation of scallop recesses typically observed in scallop beds. These results indicate that passive transport of sea scallops has a behavioural component related to gape that is independent of shell size. In contrast, scallop orientation and recessing may be explained by physical processes rather than simply by behaviour. Studies of bivalve hydrodynamics require consideration of living animals in addition to shell specimens and must include conditions of benthic boundary layer flow and sediment transport.

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Le transport passif et l'orientation ont fait l'objet d'une étude chez des Pétoncles géants (*Placopecten magellanicus*; hauteur de la coquille, 27–120 mm) placés dans un canal expérimental, en laboratoire, dans le but d'évaluer l'influence du courant sur les déplacements de ces animaux et sur leur position au fond de la mer. Des expériences additionnelles ont permis de suivre le transport des sédiments autour de la coquille et d'évaluer leur influence sur les cavités occupées par les pétoncles. La vitesse critique d'arrachement n'est pas reliée à la hauteur de la coquille ou à d'autres mesures de la taille et, lorsqu'ils sont emportés, la plupart des pétoncles ont la bordure ventrale de la coquille orientée vers l'aval. L'exposition frontale des pétoncles au courant, évaluée d'après leur finesse (hauteur de la coquille/épaisseur de la coquille), est plus importante chez les gros individus, mais lorsque la mesure de la finesse tient compte de l'ouverture palléale (hauteur de la coquille/(épaisseur de la coquille + ouverture)), il n'y a pas de corrélation entre l'exposition frontale et la taille du pétoncle. Cela semble indiquer que la variation dans la composante traînée du transport est responsable de l'absence de corrélation entre la morphométrie de la coquille et la vitesse critique d'arrachement. Le transport des sédiments crée un sillon en fer à cheval autour de la coquille et plusieurs autres effets d'érosion–dépôts en aval. Les mesures des caractéristiques du transport des sédiments sont reliées à l'allométrie de la coquille et il est probable que le transport des sédiments contribue à la formation des cavités généralement observées autour des pétoncles enfouis dans le substrat. Ces résultats indiquent que le transport passif des Pétoncles géants comporte une composante comportementale reliée à l'ouverture palléale, une caractéristique indépendante de la taille de la coquille. En revanche, l'orientation du pétoncle et son enfouissement peuvent s'expliquer par des processus physiques et il ne s'agit pas d'une simple question de comportement. L'étude de l'hydrodynamique des bivalves suppose l'observation d'animaux vivants, en plus de l'examen des coquilles, et elle doit en outre tenir compte des conditions du courant et du transport des sédiments dans la zone de contact avec le benthos.

[Traduit par la rédaction]

Introduction

Swimming in scallops has been extensively studied owing to the commercial importance of pectinids as well as the specialized bioenergetics and hydrodynamics involved in this activity (Hartnoll 1967; Gould 1971; Thorburn and Gruffydd 1979; Thompson et al. 1980). Several scallop species are believed to undertake large-scale (km) migrations, on the basis of their swimming abilities (see Joll 1989). Owing to the high-energy nature of many scallop habitats (continental shelves), passive transport of individuals interacting with swimming may pro-

vide an alternative explanation for the active migration of scallops (Gruffydd 1976; Thouzeau et al. 1991). Previous studies have examined the influence of sediment transport on the redistribution of infaunal bivalves (Emerson and Grant 1991), but there is no corresponding information for epifaunal bivalves, which are more exposed to flow at the sediment surface. Although the postmortem transport of shells has been studied in relation to sediment transport (Al-Dabbas and McManus 1987) and paleoecological significance (Allen 1984; Powell et al. 1989), there are few empirical data on the factors that control the erosion and transport of living molluscs.

Shell morphology will influence the passive transport of

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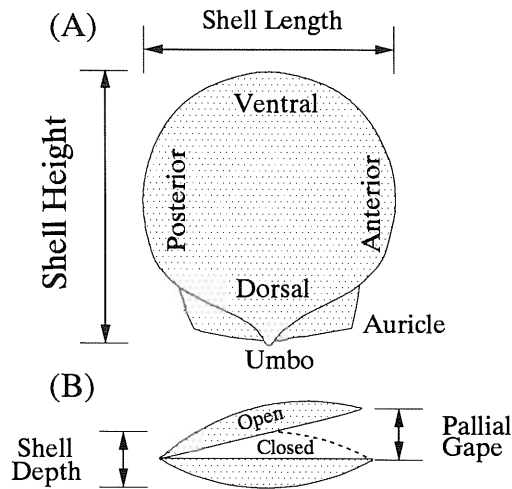


FIG. 1. Shell dimensions and orientation of living sea scallops (*Placopecten magellanicus*) as referred to in the text. (A) Plan view. (B) Anterior view showing shell in open and closed position. In a resting scallop in the open position, mantle tissue would occupy most of the perimeter of the valves. Shell depth measurements were taken from the closed shell as indicated.

molluscs and other shelled benthic invertebrates owing to its influence on the drag and lift forces experienced by the animal at the seabed. Shell hydrodynamics have thus been examined in various studies, e.g., flow patterns around brachiopod shells (LaBarbera 1981) or yield strength of byssally or pedally attached molluscs (Denny 1988, 1989). Although similar analyses have been applied to drag and lift of scallop shells, these studies consider animals swimming in the water column rather than resting on the bottom (e.g., Thorburn and Gruffydd 1979). In the benthic boundary layer, scallops are exposed to a velocity gradient that may affect their transport and orientation differently than when they are swimming off the bottom.

On soft sediments, changes in the ambient flow owing to the shell may also affect the surrounding bed, causing distinct erosion and deposition features (Allen 1982). Sediment recesses inhabited by pectinids have usually been attributed to the activities of the animal (Brand 1990) without consideration of flow regimes around the scallop; scour may provide an alternative explanation for the occurrence of scallops in sediment depressions.

In the present study, we have examined the passive transport and orientation of the sea scallop *Placopecten magellanicus* (Gmelin), a widespread and commercially important species in the western North Atlantic. A laboratory flume was used to impose unidirectional boundary layer flow on individuals of various sizes on soft sediment and on a Plexiglas flume bed. We hypothesized that more work would be required to transport larger (older) individuals passively along the bottom than smaller individuals, relative to their size. The objectives of the study were to (i) determine a threshold shear stress for live scallops in relation to shell size, weight, allometry, and orientation and (ii) characterize sediment transport features caused by flow around the shell. We have attempted to assess the role of passive physical processes in the movement, orientation, and habitat of *P. magellanicus*, as well as changes in the importance of these processes with scallop size and behaviour.

Materials and methods

Scallops were collected by SCUBA divers from Passamaquoddy Bay, New Brunswick, in June 1988 and transported to the laboratory, where they were kept in flowing seawater (6–9°C, 31‰). A diet of natural food particles in the sand-filtered seawater was supplemented by addition of cultured phytoplankton. Flume experiments were conducted using a 3-m flow-through flume channel described in Muschenheim et al. (1986). Water depth in the flume ranged from 4 to 9 cm.

Scallop transport experiments

The threshold shear velocity for passive scallop entrainment on the Plexiglas flume bed was used to examine scallop transport in relation to size without the confounding effects of sediment transport. Individual scallops (27–120 mm shell height) were placed in the center of the flume working section in slow flow ($\sim 5 \text{ cm} \cdot \text{s}^{-1}$), until they exhibited a constant pallial gape with tentacles extended. Each scallop was positioned in three orientations in random order: (i) ventral shell margin facing upstream or (ii) downstream, and (iii) anterior or posterior margin facing upstream (Fig. 1). The latter orientation was random with respect to side chosen, but the influence of anterior and posterior positioning on transport direction was subsequently examined from these results. Gape was estimated to the nearest millimetre with a scale on the flume wall. For each trial, flow was increased until the scallop was transported downstream, and orientation during transport was recorded. After the three trials, shell height, shell length, and shell depth, whole wet weight, and volume displacement were measured (Fig. 1).

After the scallop was removed, flow velocity profiles were measured using a thermistor anemometer at a minimum of 1-mm vertical intervals (usually 10–11 points over 40 mm) logged on a micro-computer (Muschenheim et al. 1986). Thermistors were calibrated in pipe flow. Velocity profiles were used to calculate a critical shear velocity, u^* , for scallop transport as follows:

$$[1] \quad u_c = u^* / \kappa \ln(z/z_0)$$

where \bar{u}_z is the free-stream velocity at height z above the bed, κ is von Karman's constant (0.4), and z_0 is the roughness length. Values of u^* were rejected for linear regressions of \bar{u}_z versus $\ln z$ with $r < 0.9$. Details of these calculations may be found in Muschenheim et al. (1986).

Sediment transport features

Sediment erosion features were observed around 12 live scallops ranging in shell height from 50 to 106 mm. A basin insert in the test section of the flume (18 × 18 × 7 cm deep; see Muschenheim et al. 1986) was filled with washed and ashed medium-fine sand (median diameter $\sim 250 \mu\text{m}$), with a shallow layer of sand spread upstream. Scallops were placed on the flume bed in the center of the basin insert, with the ventral margin facing upstream. After a normal pallial gape and extension of tentacles were observed, flow was slowly increased until the critical threshold of the sediment was just exceeded. Trials were standardized with respect to erosion features rather than flow velocity, by allowing erosion to proceed until the progressing horseshoe feature (see below) reached the dorsal shell margin (maximum 24 min). After the flow was reduced, the scallop was carefully removed and the flume slowly drained. A ruler was then used to measure transport features on the bed.

Results

Scallop transport experiments

Free stream velocity ($z \geq 30 \text{ mm}$) at transport for scallops of all sizes ranged from 11 to 37 $\text{cm} \cdot \text{s}^{-1}$, with a mean value ranging from 20.6 to 21.7 (CV = 33–35%) for the three orientations. The u^* causing scallop transport (upstream of the shell) ranged from 0.15 to 1.92 $\text{cm} \cdot \text{s}^{-1}$, with a mean ranging from 0.57 to 0.73 (CV = 45–74%) for the three orienta-

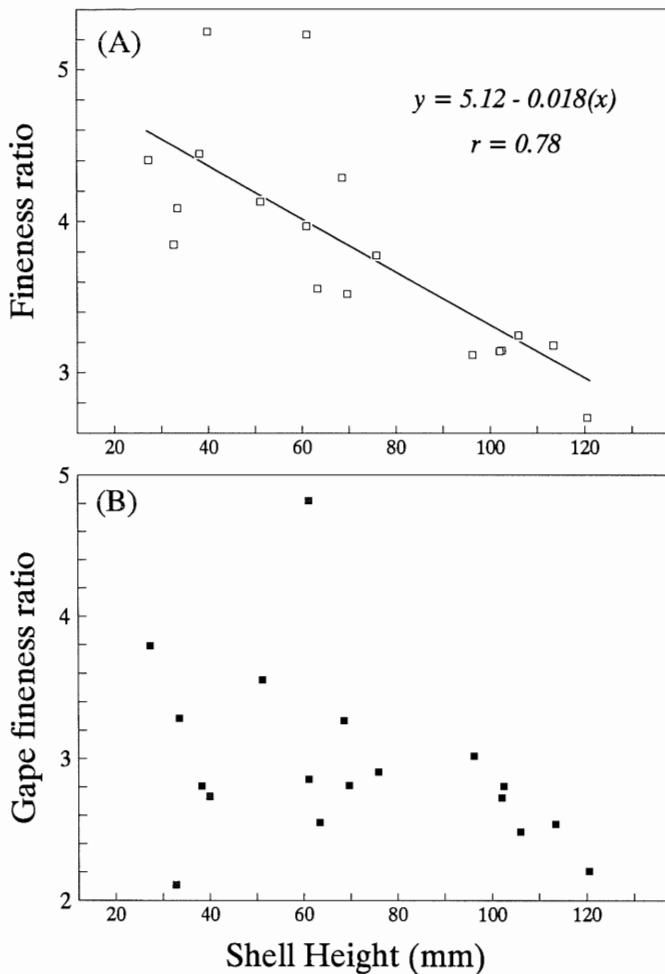


FIG. 2. Fineness ratio as a function of shell size of living scallops utilized in flume experiments. (A) Fineness is calculated as shell height/shell depth. The significance of the regression equation given for the line is $p < 0.01$. (B) Gape fineness is calculated as shell height/(gape + shell depth) for scallops facing ventrally into the flow. A linear regression between gape fineness and shell height was not significant ($p > 0.05$; see text).

tions. Free-stream velocity and u^* showed no relationship with shell height or initial orientation. Other independent variables such as scallop area, scallop volume, scallop weight, and various shape indices were not correlated with free-stream velocity or u^* ($p > 0.05$).

The pallial gape of scallops resting in the flume prior to transport ranged from 1 to 11 mm. Gape appeared to be a response to some unknown behavioural stimulus but was not correlated with water velocity or scallop size ($p > 0.05$). The initial orientation of animals to the flow had no influence on gape. Because the fineness ratio of shell shape (shell height/shell depth) decreases significantly with shell height ($p < 0.01$, Fig. 2A), older scallops have a thicker profile with greater frontal exposure and thus increased drag (Gould 1971; Dadswell and Weihs 1990). However, when gape was used to calculate an alternative fineness ratio (shell height/(shell depth + gape)), there was no relationship with shell height ($r = 0.35$, $p > 0.05$, Fig. 2B). The trend in Fig. 2A is disrupted by variance in gape, which contributes to the increased spread in fineness in Fig. 2B. Moreover, the generally smaller fine-

ness values calculated with gape (Fig. 2B) suggest that the profile of a living animal produced more drag than indicated solely by shell dimensions (Fig. 2A). The density of whole live scallops ($1.60 \pm 0.52 \text{ g} \cdot \text{cm}^{-3}$, mean \pm SD) was not related to shell height ($p > 0.05$), suggesting that this factor need not be considered as an allometric variable.

During transport, scallops rotated on the lower valve and slid downstream on the flume bed, often with a subsequent spinning motion ($\leq \pm 180^\circ$). Regardless of their initial orientation to the flow, 70–84% of scallops were transported with the ventral shell margin facing $\pm 45^\circ$ downstream (Fig. 3). The remaining scallops were transported with the anterior–posterior axis normal to the flow. Scallops with the posterior margin facing into the flow tended to remain in their initial position during transport more than individuals with the anterior margin facing upstream (Figs. 3C, 3D), but in both cases transport orientation was primarily ventrally $\pm 45^\circ$ downstream. Scallop transport never occurred with the umbo facing downstream. Many scallops reduced the gape or closed the shell upon initiation of movement, but no swimming off the bottom was ever observed. Several of the small scallops attached the foot onto the flume bottom. Transport of one individual (39.9 mm shell height) began ($u = 16 \text{ cm} \cdot \text{s}^{-1}$), but the animal did not wash away owing to anchoring by the foot.

Sediment transport features

Transport of sediment around the scallop shell occurred in the shape of a horseshoe, with areas of both erosion and deposition (see examples in Allen 1982). Characteristic transport features (obstacle marks) were consistent for all scallops (Fig. 4). Erosion was first apparent at the ventral shell margin, where flow separation presumably deflected fluid onto the bed. This horseshoe-shaped trough (also known as a current crescent; Paola et al. 1986) gradually proceeded around the shell, with eroded sediment deposited in two elongate crests at each end of the trough. Four small elliptical pits were eroded behind the shell at the reattachment point, where the flow recovered from separation. The inner pair of pits were symmetrical about the streamwise center line of the shell. These were flanked on the downstream side by symmetrical crests. Further from the center line, two more pits separated by about one shell length occurred immediately behind the ends of the horseshoe trough. During transport, sediment was deposited on the scallop shell auricles and dorsal margin.

As expected, the dimensions of the transport features were related to shell morphometrics (Table 1, Fig. 4). Because shell height, length, and depth were intercorrelated, most correlations with sediment features apply to all of these variables. The downstream length of the horseshoe feature was correlated with all three shell dimensions, but the width of the central depression was correlated only with shell length. The most significant relationships occurred between length and width of the downstream pits and linear shell dimensions. Depth of neither these pits nor the central pit was correlated with shell size. The width of the central plateau (3.5–6 cm) was not correlated with any shell dimension.

Discussion

Scallop orientation

The orientation and movement of scallops observed in natural beds must be reinterpreted in terms of physical processes as well as in terms of scallop behaviour. In short-

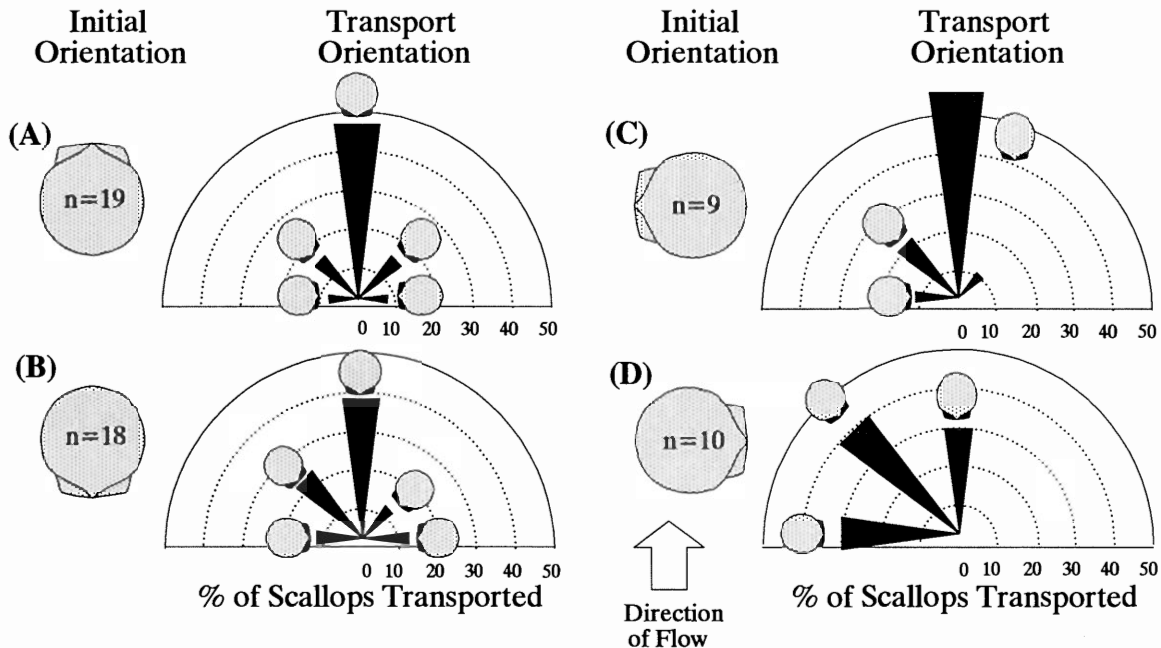


FIG. 3. Orientation of sea scallops during downstream passive transport in the flume. Auricles indicate the dorsal shell margin. Initial orientation (A–D) is the direction scallops were placed in the flume prior to transport; n is the number of trials for each orientation. Vectors indicate the direction and the percentage of trials in which scallops were transported in the orientation shown.

term SCUBA observations (~ 1 h), Caddy (1968) found that in populations of *Placopecten magellanicus* in the Gulf of St. Lawrence, individuals were oriented with their ventral margins facing into or oblique to unidirectional flow. Hartnoll (1967) showed that *Pecten maximus* faced ventrally into a unidirectional tidal flow. In reversing tidal currents, *Pecten maximus* was found to be aligned dorsoventrally $\pm 180^\circ$ with respect to the ebb–flood axis (Mathers 1976). These studies have assumed that orientation depends on behaviour rather than on physical conditions. Laboratory flume observations with *Chlamys islandica*, however, indicated passive control of orientation with the ventral margin facing downstream (Gruffydd 1976). Eckman et al. (1989) found similar results with *Argopecten irradians concentricus*, byssally attached to eelgrass blades.

Our flume experiments similarly demonstrated that *P. magellanicus* was most unstable when the ventral margin faced the flow and that immediately prior to transport, the scallop was rotated to a more stable orientation, usually with the hinge oriented upstream. Because currents likely cause a nonrandom orientation, the observed correspondence between position and flow in scallop populations may be due to physical processes as well as directed movement. This conclusion is consistent with Olsen's (1955) data showing that *Notovola meridionalis* (*Pecten fumatus*) was oriented ventrally toward the flow in strong tides; weaker flow produced no pattern in orientation. In reversing flows, passive orientation should reflect both flow directions as found by Mathers (1976) for *Pecten maximus*. Studies of scallop orientation in the field must include stages of tidal flow that exceed the transport threshold for scallops. The resolution of the passive and active components of orientation in the field requires high-frequency monitoring (h^{-1}) of current velocity and direction, and scallop position and orientation.

In subcritical flows, recent laboratory work suggests that scallops orient with the anterior margin (inhalant opening) fac-

ing the flow (Wildish et al. 1987; Eckman et al. 1989). Positioning of the posterior side (exhalant opening) into the flow may be suboptimal owing to the negative pressure gradient opposing the excurrent water (Wildish et al. 1987; Wildish and Saulnier 1992) and result in lower rates of shell growth (Eckman et al. 1989). MacDonald and Bajdik (1992) suggested that the orientation of *Placopecten magellanicus* populations in Newfoundland indicated avoidance of posterior positioning toward the flow. In field experiments, *Placopecten magellanicus* fixed with umbo facing the flow showed greater shell growth than those facing ventrally into the current, but orientation did not affect soft tissue growth (Fr chet te 1989). Regardless of how active and passive processes influence shell orientation, it is apparent from the above studies that scallops in the field spend considerable time facing ventrally into the flow, a position which is hydrodynamically unstable (Fig. 3) and potentially unfavourable for growth (Fr chet te 1989). Another position unfavourable for growth, posterior upstream (Wildish et al. 1987), is hydrodynamically stable, since our experiments (Fig. 3D) showed that scallops were often transported in that orientation. These conflicting results suggest that the fluid dynamic requirements of suspension feeding, positioning on the seabed, and swimming would not necessarily lead to a single set of behavioural and (or) morphological adaptations (Gould 1971). Various strategies to meet these ecological requirements are apparent within the Pectinidae in which there are diverse behaviours and abilities with respect to swimming, recessing, and byssal attachment.

Facing ventrally into the flow may confer certain trophic advantages to the scallop that offset any hydrodynamic detriment of this position. For example, near-bottom particle loads and nutrition could be enhanced by resuspension of sediment organic matter around the shell (Grant and Cranford 1991; see below). In addition, the downstream position of the inhalant opening may be located in a stagnation region that facilitates water intake in an otherwise rapid flow. Our sediment trans-

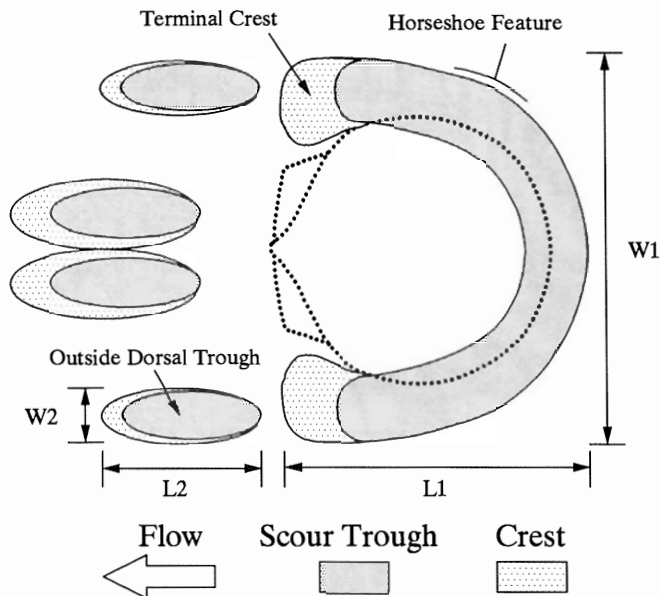


FIG. 4. Erosion and deposition features formed by sediment transport around sea scallops in flume experiments. Features are drawn to scale relative to scallops of shell height from 50 to 106 mm. The actual dimensions of specified erosion features may be assessed from the regression equations given in Table 1. The position of the scallop is indicated by the broken line. The length (L) and width (W) features designated are related to the scallop shell dimensions given in Table 1.

port experiments (Fig. 4) and previous measurements of skin friction around obstacles (Eckman and Nowell 1984; Paola et al. 1986) have shown the presence of variable stress regions at different locations around roughness elements. The relationship between scallop orientation and feeding or growth requires further study of flow fields and their interaction with particle fluxes around the shell.

Scallop transport

The decreased fineness ratio of the shell with increasing shell height (Fig. 2A) suggests increased exposure normal to the flow in larger scallops. Dadswell and Weihs (1990) measured a wider size range of scallops from Passamaquoddy Bay and suggested that fineness is a nonlinear function of shell height in *Placopecten magellanicus* (shells only), with smaller values on either side of a peak at ~ 40 mm shell height. Our data do not cover a wide-enough size range to define a similar trend (Fig. 2A), but an indication of the variance in fineness of smaller scallops is also present in our data. By incorporating gape measured under flow conditions into a fineness ratio (Fig. 2B) we suggest that there is increased drag on living scallops because gape increases the cross-sectional area and frontal exposure of scallops normal to the flow. Moreover, owing to variation among individuals in the gape of the pallial curtain, the consistent relationship between fineness and shell height is disrupted. One cannot generalize that for scallops resting on the seabed, smaller individuals create less drag than larger individuals. We conclude that both shell allometry and behavioural variation in gape are important to the passive transport of living *Placopecten magellanicus*, as is true of the forces acting on swimming scallops (Gould 1971; Vogel 1985).

Although we have emphasized drag, lift forces are potentially important in enhancing the passive transport of scallops

TABLE 1. Regression statistics relating scallop shell width to the size of sediment erosion features, on the basis of laboratory flume experiments

	a	b	n	r	p
Width of horseshoe trough ($W1$)	1.33	36.63	12	0.60	0.04
Length of horseshoe trough ($L1$)	0.89	-6.76	6	0.93	0.007
Erosion of outside dorsal trough ($W2$)	0.35	1.86	8	0.92	0.001
Length of outside dorsal trough ($L2$)	0.81	-3.34	11	0.80	0.003
Height of terminal crest on horseshoe trough	0.06	2.72	9	0.68	0.04

NOTE: Regressions are in the following form: erosion feature = $a \times$ shell length + b , with all dimensions in millimetres. Experiments include scallops with shell heights ranging from 50 to 106 mm (41–111 mm shell length). Abbreviations for erosion features correspond to designations in Fig. 4.

along the bottom. Denny (1987) demonstrated significant lift forces even on a bed of attached mussels. The aspect ratio (shell length/shell height) increases in larger *Placopecten magellanicus* (Dadswell and Weihs 1987), a factor which improves the lift/drag ratio (Gould 1971; Gruffydd 1976) and would aid in the passive transport of the animals from the bottom. Moreover, increased convexity of the upper valve in larger scallops (also reflected by decreasing fineness) would enhance lift by increasing the path length of water flow over the upper valve (Stanley 1970). Both lift and drag are also influenced by the resting attitude of scallops on the bottom, a highly variable factor on a rough sand-gravel seabed.

Scallops eroded in the flume were transported along the bottom. The presence of sediment, especially gravel, would increase the scallop erosion threshold determined in our experiments and would probably decrease the transport rate owing to frictional resistance (Allen 1984). Attachment of scallops by byssus or foot, especially in juveniles, may also reduce displacement (Larsen and Lee 1978). These results suggest that transport along the bed may be important in determining local distribution and orientation. However, larger scale distribution is likely controlled by the interaction between swimming and prevailing currents (Gruffydd 1976; Brand 1990); recent evidence indicates that bank-scale dispersion of scallops with age on Georges Bank corresponds to the residual tidal circulation (Thouzeau et al. 1991).

Scallops and sediment transport

Many pectinids live in tidally energetic environments, where scallops are recessed and have sediment deposits on the dorsal shell margin and auricles (Caddy 1968; Waller 1975). Empty recesses are evident on the bottom when scallops have moved (Caddy 1968). Our flume experiments document the creation of recesses by sediment transport around scallop shells; we also observed passive sediment deposition on the dorsal shell margins. In contrast to these results, all previous descriptions of recessing behaviour in scallops have dealt primarily with active excavation (Brand 1990). *Pecten maximus* creates a recess by clapping and pumping of water jets toward the sediment surface (Baird 1958; Baird and Gibson 1956). Waller (1975) described similar behaviour in *Pecten ziczac*. Our observations with *Placopecten magellanicus* in aquaria indicated that the scallops were able to make shallow

depressions after several days, although water ejected during takeoff in swimming would also cause sediment erosion. We suggest that on sandy bottoms, recesses are formed by the interaction between passive sediment transport and active excavation of sediment by the animal.

Regions of erosion and deposition around the shell suggest that its roughness could affect resuspension and the flux of particulate material in the vicinity of the scallop. This effect will be enhanced where a large recess or scour pit traps organic matter owing to locally lowered shear stress (Nowell and Jumars 1984; Brand 1990). To examine whether scallop shells enhanced particle flux to the bed, we allowed erosion to create scallop transport features, removed the scallop, and introduced cultured diatoms (*Chaetoceros gracilis*; $\sim 8 \mu\text{m}$ diam.) to a flow of $\sim 5 \text{ cm} \cdot \text{s}^{-1}$. Using fluorescence microscopy, we could not detect the diatoms in sediment samples from various erosion–deposition locations, but we suspect that longer experiments may be required to document algal deposition, especially for small cells. Although enhanced deposition of organic matter might occur in specific locations around any roughness element on the seabed, the consequences are more significant for benthic macro- or mega-fauna that utilize these resuspended particles for food.

We conclude that passive transport by currents contributes to the orientation of *Placopecten magellanicus* with respect to flow. Similarly, passive sediment transport around the shell accounts for a component of recess formation in scallop beds. The passive transport of living scallops is a complex interaction between drag, lift, and allometry, with drag heavily influenced by pallial gape. Because scallops often occupy areas of high currents and depend on water flow for the transport of food, studies of scallop ecology and distribution must include the interaction of living scallops with the sedimentary environment.

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