MUSCULAR MECHANICS AND THE ONTOGENY OF SWIMMING IN SCALLOPS

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ABSTRACT. Swimming ability declines, and may disappear, during the ontogeny of scallops that swim well as juveniles. The mechanics of swimming at increased sizes provides two reasons for decline during isometric growth: (1) Scallops are much denser than water; the gravitational force scales as the cube of the length (L^3) while all lifting forces that could balance it scale at smaller powers of L. (2) The maximum velocity that a scallop can generate is independent of its size; yet larger scallops must move faster than small ones in order to swim at all (minimum take-off velocity scales as $L^{0 \cdot 5}$).

Actual scallops undergo allometric changes in ontogeny that partly offset this loss in swimming ability. I measured these changes in shell shape, muscle size, and muscle position in the growth of three Recent and one Miocene pectinid species. (1) The relative width of three free-living species increased; this improves the shell's aspect ratio and augments the lift–drag ratio. Cemented *Hinnites* becomes relatively longer, an unsurprising exception to the general trend. (2) The area of the quick muscle insertion increases relative to the area of the right valve. (3) The quick muscle insertion moves from a dorsal to a more central position; in concert, these last two trends produce a relative increase in the closing moment that the adductor can exert in clapping the valves. (4) The quick muscle insertion moves from a posterior to a more central position; this lengthens the muscle by bringing it to a more convex portion of the shell, thus increasing its mass and power reserve.

THE fundamental feature of bivalve design, enclosure of a soft-bodied, headless animal between two valves of density 2·7 g/cm^3, would seem to preclude the idea of a swimming clam; yet this adaptation has evolved several times (Stanley, in press). It is not only our intrinsic fascination for peculiarity that motivates the study of unusual adaptations in designs evolved for other purposes; for these adaptations are experiments that test the limits of form just as manufacturers expose their products to extreme conditions before marketing them for ordinary ones. One swimmer, one rock-borer, or one cementer can instruct us more in the properties of bivalve design than many new shallow burrowers. And it is therefore no accident that some of our best works on the functional morphology of fossil invertebrates deal with uncoiling snails (Abel 1929), coralliform brachiopods (Rudwick 1961), or recumbent crinoids (Moore 1962).

I argued previously that modern systematics and its species concept have provided palaeontology with a science of diversity; yet, for lack of a corresponding central idea, we have no science of form (Gould 1970). I believe that this idea could be stated as a criterion for judging the relative efficiency of structures by the mechanical analysis of organic design as Rudwick proposes in his notion of the paradigm (1961, 1964, 1968). And just as our time-honoured method of studying the present elucidated the concept that built a science of diversity, so also do we need a palaeontology of the present to develop our functional morphology into a science of form. This study of scallop swimming is presented here not because one fossil species is included in the data, but because it is a palaeontological problem, based on the mechanics of hard parts and organs recorded therein, that requires a knowledge of behaviour and physiology for a solution that can be applied to the past.

Although some solenids, solemyids, and cardiids swim occasionally (Stanley, in press), this peculiar bivalve adaptation is best developed within the Pectinacea. I

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consider here only scallops that swim with the commissure plane at 0° to approximately 45° to horizontal; Limidae swim with the commissure plane vertical. Basically, a scallop swims with the thrust provided by water jets. These are produced by rapid, repeated cycles of ligamental extension and adductor contraction. This produces the characteristic 'clapping' of the valves. (The movement of fluids by adductor contraction also powers the 'hydraulic machine' of burrowing bivalves [Trueman 1966, p. 525] and the cleansing reactions that Yonge [1936] regards as precursors to swimming.) In addition, the scallop must avoid sinking by achieving hydraulic lift, by directing its motion partially upward to compensate for sinking between claps or by directing a separate water jet downwards as Buddenbrock (1911) believed and Stanley (in press) denies.

In this work I am concerned almost entirely with the most neglected and most pervasive aspect of mechanical problems—the effect of size or scale (reviews in Bonner 1952 and 1968, Cock 1966, Gould 1966, and Thompson 1942). The performance of virtually any machine will alter if it maintains its shape as size increases. The most familiar reason for this involves the different scaling of areas (L^2) and volumes (L^3). But other effects may be more important. Kinetic energy, for some problems, scales as L^5; some amusing consequences are developed by Went (1968). From a mechanical point of view, an outstanding feature of organisms is that they must deal with such different balances of forces at various stages of their life-cycle. Thus, when compared with a man-made device, an organism not only must often use inferior materials (hence no wheeled organisms or really heavy fliers), but must also adapt to the varying requirements of very different sizes.

The literature is full of unassembled, undigested, and unassimilated data on the influence of size upon form and habits. In the absence of a theory to collate these observations, they stand as scattered bits of pure, and therefore unenlightening, information. One set of similar bits, in fact, inspired this project. Over and over again, it has been recorded that the large scallops of any swimming species swim rarely, poorly, or not at all (Yonge 1936 in general; Bayliss *et al.* 1930 for *Pecten maximus*; Verrill 1897 and Waller 1969 for *Argopecten irradians*; Verrill 1897 and Caddy 1968 for *Placopecten magellanicus*; Fairbridge 1953 for *Notovola meridionalis*; Olsen 1955 for *Equichlamys*); no-one has ever asked why.

For such a change in habits, there are two possible types of explanation:

1. Large scallops do not swim because they need not. Large, heavy valves might provide the protection from predators that active escape furnished for small scallops.
2. Large scallops do not swim because they cannot. (In either case, of course, the new and more sluggish habit of large scallops entails no loss of adaptation. In fact, large scallops use the same quick adductor contractions that had previously powered their swimming to 'recess' into self-formed depressions for protection; Baird 1958, p. 68; Waller 1969, pp. 16–17.)

Whatever our *a priori* preference, we should, as a method of procedure, begin with (2) as a working hypothesis and seek a reason why large scallops might be unable to swim. Continuing failure would lead us to suspect (1), though not prove the point, while an initial assumption of (1) closes the matter prematurely, for the demonstration of no need says nothing of the original impetus for such adaptations as recessing and shell thickening. Since scallops are still with us, they have obviously accommodated themselves to any problems imposed by size.

The problems of increased size are met by allometric growth (Gould 1966), i.e. by changes in shape that allow an organism to avoid the unfavourable aspects of geometric similarity in scaling. The empirical part of this study, therefore, is an attempt to define allometric patterns in important structures that can be detected in fossils, i.e. basic shell shape and muscular size and position. It is extraordinary how little work has been done on the basic description of allometry in scallops, not to mention its adaptive significance. Of the adductor musculature, Waller (1969, p. 22) writes: 'Positional and dimensional changes of the adductor during growth have been poorly described. . . . The meaning of these changes in terms of function is unknown.' Merrill (1961) records the movement of adductors in *Placopecten magellanicus* from a posterior dorsal to a more central position. Waller (1969) found a similar shift in most members of the *Argopecten gibbus* stock and also noted a tendency for the muscles to increase in relative size. No one has given explicit consideration to the ontogeny of differences in relative size and movement between quick and slow portions of the adductor musculature. The only information here is Waller's set of drawings for *Argopecten comparilis* from the Miocene of Florida (1969, p. 22). Ontogenetic allometry of musculature has been reported by Sandberg (1964) and Benson (1967) for ostracods and by Spjeldnaes (1957) for brachiopods, again without much consideration for adaptive significances.

It is perhaps even more surprising that so little functional analysis has been offered for the obvious and easily quantified changes of basic shell form with growth. Thus, increase in relative shell width has been noted a number of times, but only recently did Stanley (in press) relate this to an improvement in aspect ratio. Aspect ratio is *the* basic parameter of shape in aerodynamics (see p. 87); all major texts in engineering give it prominent consideration in discussions on the motion of lifting bodies.

The argument of this paper will therefore proceed as follows:

1. To show that there are physical reasons why large scallops would have greater difficulty in swimming than small ones;
2. To demonstrate that the major allometries of shell and muscle can all be interpreted as providing some aid in meeting these difficulties.

We often think that the adaptive significance of size-required allometry (Gould 1966, p. 588) lies in *maintaining* such properties as the surface to volume ratio. Often, however, when size places ever more stringent requirements upon given functions (increased wing loading for flight in birds, for example), large animals will possess designs of greater efficiency than those needed in smaller models. Rashevsky writes (1960, p. 273): 'For larger animals, like birds, the profile of the wing must be made more perfect an aerodynamic profile than it needs to be for insects.' And Bainbridge (1958) has noted, in fishes, the same improvements in muscles and body shape that characterize the growth of scallops.

MATERIALS AND METHODS

From collections of the Departments of Invertebrate Palaeontology and Molluscs at the Museum of Comparative Zoology, Harvard University, I selected five samples of four species that cover the range of pectinid swimming ability:

1. *Placopecten magellanicus*, Recent from Penobscot Bay, Maine. M.C.Z. No. 71965 (Molluscs); 30 right valves ranging from 0·3 to 131·4 g in weight. *P. magellanicus* is the common sea scallop of the western Atlantic and is considered to be an excellent swimmer (Stanley, in press, Caddy 1968).

2. *P. magellanicus*, Recent from 10 miles SE. of Block Island, Rhode Island. M.C.Z. No. 225815 (Molluscs); 19 right valves ranging from 0·4 to 123·8 g in weight.

3. *Amusium balloti*, Recent from Queensland. M.C.Z. Nos. 213682 and 213828 (Molluscs); 13 right valves ranging from 2·4 to 22·5 g in weight. I know of no actual observations, but every major feature of its design (pp. 79–81) marks *Amusium* as the most accomplished bivalve swimmer.

4. *Hinnites multirugosus*, Recent from San Diego Bay, California. M.C.Z. Nos. 70320, 87050 and 115251 (Molluscs); 8 right valves ranging from 0·4 to 176·5 g in weight. Young are byssally attached, swimming if dislodged; permanent attachment by cementation at dorso-ventral diameter of 2·2–4·2 cm (Yonge 1951).

5. *Chlamys* (*Lyropecten*) *jeffersonius*, Miocene, Yorktown Formation, Virginia. M.C.Z. No. 17498 (Invertebrate Palaeontology); 19 right valves ranging from 0·1 to 466·6 g in weight. I have no information for this common fossil, but species of *Chlamys* are either byssally attached throughout life or free living during part, or all, of growth.

The adductor musculature of pectinids (and most clams) consists of two portions performing two functions. The more central, striate quick muscle (text-fig. 1) contracts rapidly but cannot hold the valves together for long; it produces the rapid, cleansing contractions of many clams and the 'clapping' of valves for swimming in pectinids. The posterior, smooth, slow muscle is not involved in swimming; it contracts slowly but holds the valves tightly shut for long periods with little expenditure of energy. The more common designation, 'catch muscle', refers to a theory of its action that is still under debate—to von Uexkull's notion of a 'molecular ratchet' (Hoyle 1964, p. 333) that, once set, allows the muscle to remain in a state of tension without consuming energy. I prefer to speak of 'slow muscle', a descriptive term of undisputed application. Hill (1950, p. 227), moreover, has shown that the smooth adductor must be slow in order to maintain a state of contraction for long periods, for speed of shortening and economy in maintaining force are opposing properties of muscle. In this observation we are also provided with an explanation for the large size of quick *v.* slow muscle in swimming clams; to provide power for continual, rapid clapping of the valves, the uneconomical quick muscle must be large. The impressions of these muscles are distinct on right valves, but fused on left valves; since the study of swimming requires their distinction, only right valves were used. The following measurements were made (text-fig. 1):

1. Basic shell dimensions:

(*a*) Weight in grams.

(*b*) Area of the right valve. The valve outlines were traced and measured with a compensating polar planimeter. Variation in valve convexity presents difficulties that will be considered later.

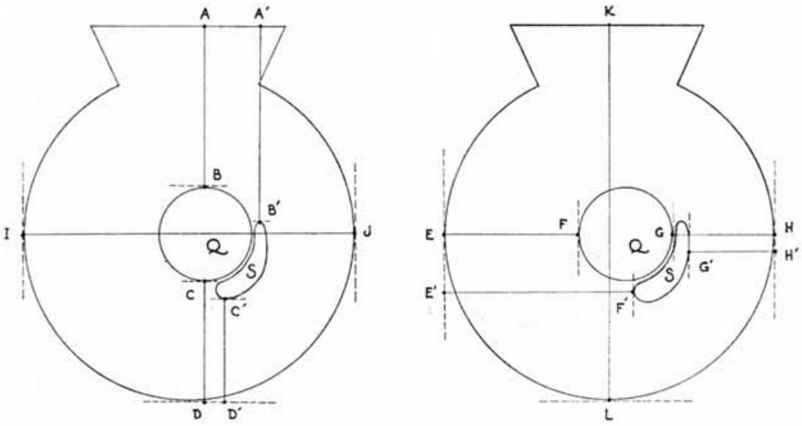
(*c*) Antero-posterior width of shell (IJ of text-fig. 1).

(*d*) Dorso-ventral length of shell (KL of text-fig. 1).

2. Size of muscles:

(*e*) Area of slow muscle insertion projected to plane of commissure.

(*f*) Area of quick muscle insertion projected to plane of commissure. The scar peripheries were outlined in black and traced on to thin paper held tautly in the plane of commissure. Valve outlines were traced on the same sheet to produce drawings like text-fig. 1. Marceau (1936) made similar measures by drawing on glass placed upon the plane of commissure.



TEXT-FIG. 1. Measures used in this study (see text for explanation).

3. Position of the muscles:

(*g* and *h*) Position of quick and slow muscles in dorso-ventral axis. The shortest distances between the hinge line and the muscle measured parallel to KL (AB and A′B′) and between the most ventral extension of the muscles and the tangent to point L (CD and C′D′) were measured. The ratios AB/CD and A′B′/C′D′ define muscle positions with respect to the dorso-ventral axis.

(*i* and *j*) Position of quick and slow muscles in antero-posterior axis. By analogy with the method used in (*g*) and (*h*), the ratios EF/GH and E′F′/G′H′ define the positions of quick and slow muscle, respectively, in the antero-posterior axis.

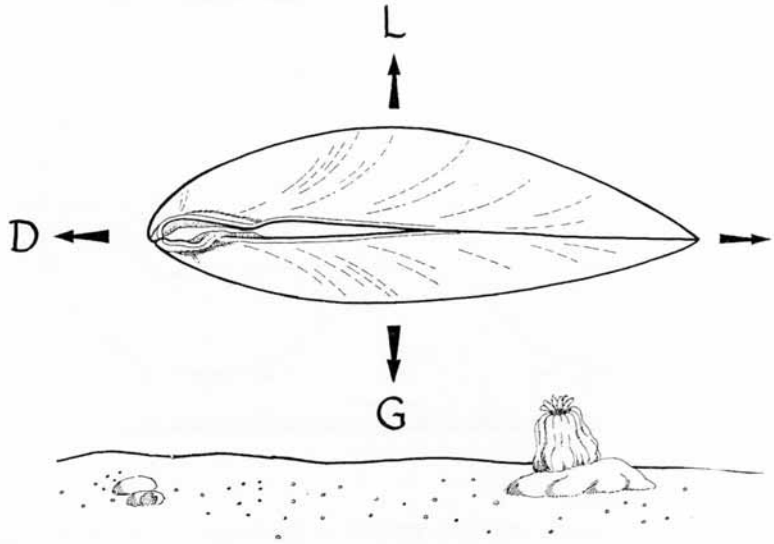
SIZE AND SWIMMING IN SCALLOPS: A THEORETICAL ANALYSIS

In this section, I present two reasons why large scallops should have more difficulty in swimming than small ones of the same shape. In presupposing geometric similarity (constant shape at all sizes) in this discussion, I purposely misrepresent actual scallops in order to detect the problems they alleviate by allometric growth.

Forces on a swimming scallop

A swimming scallop is subject to four major forces, two that impede its motion and two that aid it (text-fig. 2).

1. A drag force resists its horizontal motion. Drag is a compound force of three major components: frictional drag arising from surface stresses, form drag from normal pressures (these designated, collectively, as profile drag) and induced drag generated when lifting vortices lose connection with the shell at its lateral tips where their energy degrades as heat (Weis-Fogh 1961; Goldstein 1965).



TEXT-FIG. 2. The forces acting on a swimming scallop. Lift (*L*) counteracts gravity (*G*), while thrust (*T*) overcomes drag (*D*). *Placopecten magellanicus*; note the more convex upper valve, enabling the shell to function as a lifting hydrofoil.

2. A thrust force to overcome drag and propel the shell is generated by the expulsion of water jets at the anterior and posterior auricles.

3. The gravitational force, if not counteracted, limits forward motion by causing the scallop to sink to the bottom. Other pelagic molluscs avoid this problem with a fascinating array of buoyancy mechanisms: gelatinous, low density tissues of pteropods and heteropods; floating (on mucus-coated air bubbles in *Ianthina*, on mucous floats in *Peringia ulva*); low-density coelomic fluid in cranchid squids; and gas filled buoyancy chambers in many cephalopods (Denton 1964). But all scallops are much denser than the medium in which they swim (specific gravity of the shell is near 2·7, while the tissues are near sea water in density). For this analysis, it is imperative that we recognize the proper analogy: the swimming of scallops is comparable to flight, not to the normal

swimming of neutrally buoyant pelagic animals. 'How the fish or dolphin swims, and how the bird flies, are up to a certain point analogous problems. . . . But the bird is much heavier than the air, and the fish has much the same density as the water, so that the problem of keeping afloat or aloft is negligible in the one, and all-important in the other' (D'Arcy Thompson 1942, p. 43). Hence, 'swimming and flying have much in common, by flying involves an additional complication in that *lift* to overcome the *gravitational pull* must be produced as well as *thrust* to overcome the *drag* of the body moving through the fluid' (Weis-Fogh and Jensen 1956, p. 418, italics in original). The rapid sinking of non-clapping scallops has often been recorded (Gutsell 1931, Moore and Marshall 1967, p. 77).

4. A lift force must be generated to balance the gravitational force and prevent sinking. Some scallops are designed as lifting aerofoils; their upper (left) valve exceeds the right in convexity and lift is achieved in the usual way, in accordance with Bernoulli's Theorem. But most scallops are either equiconvex or have more convex lower (right) valves. This is apparently related to the common tendency for unattached scallops to recess in the substrate into self-excavated depressions. Greater right-valve convexity permits deeper recession and provides greater protection; I assume, with Waller (1969, p. 17), that it is disadvantageous for the plane of commissure to be far below the surface of the substrate. Verrill (1897) and Baird (1958) noted that this right convexity should impart a negative lift. If this seems to be a poor design for swimming, we are probably faced with a problem of conflicting demands upon form that result in compromises optimal for neither function. In fact, in a second solution to the problem of lift, such scallops swim with their planes of commissure inclined as much as 45° from the horizontal (Jackson 1890, p. 339; Gutsell 1931, p. 597; Stanley, in press). Although they fall between claps, the upward force provided by expelling water downwards as well as backwards is sufficient to prevent sinking. Some pteropods maintain themselves in the nekton with a similar propulsive rise and passive fall mechanism (Morton 1954; Kornicker 1959). Jeffries and Minton (1965) assumed a similar mode of locomotion in their model experiments on swimming in the Jurassic bivalve *Bositra buchi*. They concluded that *Bositra* could have maintained its swimming only if it were provided with a long fringe of tentacles as in modern limids. This conclusion points to a shortcoming of the present work. In discussing the structures that generate the swimming jets, I have considered only the shell and musculature and have ignored the pallial curtain (inner mantle lobe) which is not recorded in fossils. This curtain, or velum, is certainly important. It forms a 'valve' (engineer's, not conchologist's) to prevent ventral expulsion of water when the valves close and may even create a water jet without adductor contraction by its withdrawal from beyond the ventral margin towards the hinge (Waller, personal communication). Stanley (in press) reports that many right-convex scallops are not long-distance swimmers but move primarily to escape from predators and unfavourable micro-environments. Some scallops may possess a third lifting mechanism if Buddenbrock (1911) is correct in claiming that, in addition to the posterior jets, water is expelled downwards at the anterior margin; the observation has not been repeated, and Stanley (in press) doubts that it is of much importance.

To achieve equilibrium in swimming, therefore, a scallop must provide thrust to balance drag and lift to overcome gravity.

The scaling of forces on a swimming scallop

How do these forces change as a scallop grows? I should begin with a disclaimer. The dimensional approach, although easy to apply in its simplest form, is rarely adequate for all complexities (see criticism of Weis-Fogh and Jensen 1956, p. 436, for insect flight). A scallop is not an experimental sphere, cylinder, or even an aerofoil (though *P. magellanicus* is close to one). It performs such odd tasks as swimming right into the turbulent eddies of its own clapping. We know neither the regimes of flow over its complex surface nor the potential effect of pressure differentials produced by its anterior ingestion of water. We have no information on its behaviour in relation to the primary way that aerofoils increase lift, that is by increasing the angle of attack (Weis-Fogh and Jensen 1956, p. 417; Jacobs 1963, p. 348; Thom and Swart 1940). Stanley (in press) has claimed that *P. magellanicus* swims with its plane of commissure horizontal (i.e. with an angle of attack = 0°); but the minutest changes in this property can increase lift enormously. Jacobs (1963, p. 348) reports a three-fold rise in lift coefficient for an increase of 0–2° in the angle of attack of his experimental aerofoil.

1. Drag. The drag on a body is given by the equation

$$D = 1/2\, \rho\, v^2\, AC_d \tag{1}$$

where D is the drag, ρ the density of the medium, v the velocity, A a characteristic area and C_d the drag coefficient. The density of sea water is approximately constant. I shall argue on p. 72 that large scallops swim at the same speed as small ones. The area A might be measured as total surface area or frontal area (projected area in the direction of flow); in any event, it scales as L^2 in our hypothetical series of scallops that increase in size without altering their shape. The drag coefficient, C_d, depends on the shape of the body and on Reynolds number (Alexander 1968, p. 215). Our shape is invariant, but Reynolds number, the dimensionless quantity that represents the ratio of inertial to viscous forces and specifies the flow regime past objects, is given by

$$R_e = vl/\gamma \tag{2}$$

where R_e is Reynolds number, v is velocity, l is length of the body in the direction of flow, and γ is the kinematic viscosity of the medium (see Alexander 1968, pp. 209–78 on the interpretation and importance of Reynolds number). Since this discussion is based on scallops designed as lifting aerofoils, we shall use the Western Atlantic sea scallop *Placopecten magellanicus* as a model. Caddy (1968) reported that *P. magellanicus* swims at speeds 'in excess of 67 cm/sec'; individuals greater than 10 cm in length rarely swim at all. Setting maximum velocity as 75 cm/s (constant throughout the size range—see p. 72), entering the kinematic viscosity of water as 0·01 and taking the size range of swimming as 1 cm (freedom from juvenile byssal attachment) to 10 cm (adults cease to swim), the range of Reynolds number for this species is, from (2), 7500 to 75 000; or, being somewhat more generous, approximately 10^3 to 10^5. Now, a great number of experiments on bodies of various shapes (Alexander 1968, fig. 90, p. 216; Zeigler and Gill 1959, fig. on p. 5a; Goldstein 1965; Jacobs 1963) show that this is just the range of R_e in which the drag coefficient tends to be invariant: 'The drag coefficient is nearly constant for a body of given shape, moving in a given direction, at Reynolds numbers between about 10^3 and 10^5 (Alexander 1968, p. 217). Hence, in our range of R_e and shell size, A is the only right-hand term of (1) that will change in a regular manner with increase in size. The drag force should therefore scale as L^2.

2. Thrust. To balance drag and keep larger scallops swimming at equilibrium, thrust will have to scale as L^2 as well. But, let us ask a different question, for the problem is more one of endurance. How many times can a scallop clap before fatiguing; for how long can it supply a thrust force scaling as the square of length? In other words, what is the effect of size upon power output? Power is work (force × distance or cross-sectional area of muscle × length through which it contracts) per unit time. As an initial expectation we might assume that power should increase as the mass of musculature, i.e. as L^3. But power can increase only so fast as oxygen is supplied to the muscles and the heat generated by their action is dissipated; since both these processes are mediated by surfaces, power should scale as L^2 (Smith 1968, pp. 8–11, Hill 1950, pp. 218–19, Thompson 1942, p. 32). The argument, despite impressive support and supporters, is not without its weaknesses. Thompson (1942) points out that, for short spurts before too much heat accumulates or an oxygen debt is incurred, power should scale as L^3. (We must then ask whether the swimming periods of some scallops are short and in this range, or short because muscles fatigue rapidly when clapping several times per second.) Due to some unusual metabolic properties insect wing muscle may never encounter a problem with oxygen supply. 'Oxidative recovery processes have been speeded up to such rates that, on the average, they are completed within the duration of a single contraction cycle. . . . All major enzyme systems must operate at least ten to thirty times faster than in human muscle' (Weis-Fogh 1961, p. 291). There is no evidence for similar mechanisms in birds or bats, not to mention scallops (Weis-Fogh 1961, p. 292). Some fishes can increase the slope of their log oxygen consumption *v.* log weight curve in response to changing salinity and swimming speed (Farmer and Beamish 1969), but the slope does not reach 1 (scaling as L^3). The only evidence I have found for oxygen consumption *v.* size in scallops (Montuori 1913) is presented as Table 1. Since oxygen consumption ratios are similar to weight$^{2/3}$ ratios and smaller than straight weight ratios, scaling as L^2 is implied. (The data, ironically, are from an author who attempted to disprove such scaling by counting the scallop data as exceptional.) In any event, the data are for resting metabolism and need have little to do with swimming.

TABLE 1. Oxygen consumption of resting metabolism in *Pecten jacobeus* and *P. varius* at two sizes (from Montuori, 1913)

Species	*Weight (in g)*	*Absolute oxygen consumption in 2 h (in cm³)*	*Ratio of consumptions for two weights*	*Ratio of weights*	*Ratio of weights 2/3*
P. jacobeus	62·0	1·026	4·48	7·75	3·92
	8·00	0·229			
P. varius	5·0	0·183	1·29	2·50	1·84
	2·0	0·142			

In summary, dimensional considerations lead to the conclusion that muscular power should scale as L^2. Scaling at higher exponents of L may occur for short bursts or when special adaptations are present. It is unlikely that power could scale at exponents of L as high as 3; I shall assume in future discussion that power scales as L^2.

3. Gravity. The gravitational force scales as weight, or L^3.

4. Lift. The formula for lift is like that for drag

$$Li = 1/2\ \rho\ v^2\ AC_l \tag{3}$$

where ρ and v (density of the medium and velocity) remain constant with size increase, the area A scales as L^2 and C_l (the lift coefficient) again depends on shape and Reynolds number but not in the same way as it does for drag. Here we encounter a difficulty not met in considering drag, for there is very little information on variation of C_l with R_e in a scallop's range, though there is no want of knowledge for aeroplanes. This lack of data has been decried by Weis-Fogh (1956*a*, p. 547) and Vogel (1967, p. 431). Goldstein (1965, pp. 444–5) reports on an aerofoil at R_e ranging from 5×10^4 to 3×10^5. C_l rises with increase in R_e; the rise may be abrupt but it is always very small (maximum increase from 1·2 to 1·6 compared with very rapid increases of C_l for tiny changes in the attack angle, p. 68). For various aerofoil shapes and turbulence in the medium, Millikan (1934) found virtually no relation between C_l and R_e at R_e slightly above the scallop range. Thom and Swart (1940) studied the behaviour of an aerofoil at very low R_e. C_l is very high at $R_e = 1$, but it declines rapidly, by $R_e = 10$ it has stabilized and remains almost constant well into the scallop range, to the limits of their data at $R_e = 10^4$. These patchy observations have led Jacobs (1963, p. 330) and Von Kármán and Burgers (1963, p. 4) to state that aerofoil size may usually be neglected in calculating C_l. 'In most cases, C_l and C_d can be treated as approximately independent of the velocity and (for geometrically similar airfoils) of the dimensions of the airfoil, though actually they depend on the Reynolds number connected with the flow around it' (Von Kármán and Burgers 1963, p. 4). Hence, for geometrically similar aerofoils at a constant orientation, lift will scale as L^2.

Swimming and size: the first argument

There lies, in the previous section, an obvious problem for large scallops—the gravitational force that impedes their motion increases faster than any force that could balance gravity. There are some potential solutions to this dilemma.

Most animals that swim or fly through a medium less dense than themselves manage to generate enough lift to balance their increasing weight. How is this done? We just argued that lift scales as L^2, weight as L^3. The ratio of lifting surface/body weight must decline with growth; this is the classic problem of increased 'wing-loading' in birds (Meunier 1959*a*, *b*; Holst and Kuchemann 1942; Gray 1968). The answer is that lift scales as L^2 only under the restrictive conditions of constant shape and orientation; animals possess an impressive repertory of devices for increasing lift at greater rates. Sharks lack a swim bladder and many are denser than sea water (Bone and Roberts 1969); they have two lifting devices, one on each side of their centre of gravity: the heterocercal tail (Grove and Newell 1936; Affleck 1950) and pectoral fins shaped as aerofoils (Harris 1936; Alexander 1965). To obtain more lift they can increase the amplitude of tail-beat and raise the angle of attack of their pectoral fins. Insects regulate lift by changing the angle of wing attack (Nachtigall 1967), and by appropriate and complex wing twisting at various points of the stroke (Weis-Fogh 1956*b*, Bennett 1970).

In noting that desert locusts maintain a constant lift even when the incidence angle of their body is forcibly changed from 0 to 15°, Weis-Fogh (1956*b*, p. 574) proposed 'a lift-sensitive receptor system which controls the motor impulses'. Birds use such subtle mechanisms as a slotted wing (Brown 1963; Alexander 1968, p. 239) to increase the angle of attack at which stalling occurs; even so, large birds cannot hover as hummingbirds do, while gliding and thermal soaring on warm updrafts become very important to large albatrosses and buzzards (Alexander 1968, pp. 240–50; Pennycuick 1960). Which of these devices are available to scallops? Scallops have no flexibility and cannot bend their lifting surface. Their medium does not provide sufficient turbulence for gliding or riding on upwelling currents. I even doubt that they can use, to any great extent, the most common device for increasing lift: raising the angle of attack. For whereas sharks can incline their pectorals, birds and insects their wings, and still move forward horizontally, a scallop's lifting surface is his entire outer covering. If this is inclined, the whole body must move in that direction and sacrifice part of its horizontal component (as do, indeed, the poorer swimmers among scallops that are not designed as aerofoils).

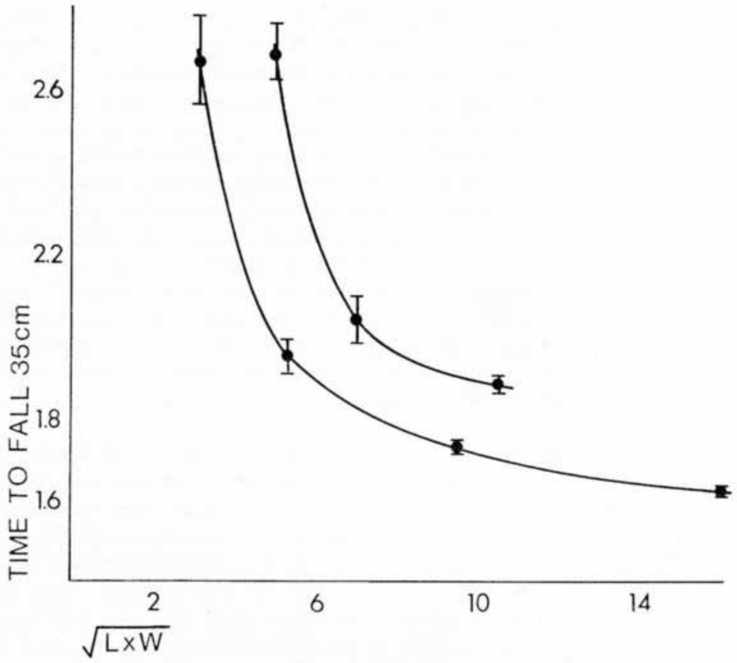
Another way to increase lift is to increase velocity (equation 3). Moreover, increased velocity would also benefit non-lifting scallops that swim upward and sink between claps; for even though larger animals would sink more quickly than smaller ones, they might cover an equal horizontal distance in this shorter time by moving faster.

I could find no data on sinking speed in scallops and therefore performed the following rough experiment. Double valves of *Placopecten magellanicus* and *Amusium ballotti* were selected to represent the available size range; each pair was held together by modelling clay equal to $\frac{1}{25}$ the weight of the valves. These were dropped, ten times each, in swimming position, through 35 cm of sea water. (Caddy 1968, reports that the largest, swimming *P. magellanicus* reach a height of 40 cm from the bottom.) The density of soft tissues probably does not differ much from that of the sea water that occupied the body space in this experiment; the shell, on the other hand, has a specific gravity near 2·7. Tamura (1929) reports an average tissue weight/total weight ratio of $\frac{1}{84}$ in *Patinopecten yessoensis*. I plotted the mean time for a 35-cm fall against the square root of length times height (text-fig. 3). I thought that the falling time might scale as L^{-1} since the ratio of drag forces that resist sinking to gravitational forces that encourage it is L^2/L^3.

The resistance to sinking provided by the plate-like valves is really quite impressive when you realize that it takes only 2 seconds for a quartz sphere ($\rho = 2{\cdot}65$) only 1·13 mm in diameter to fall 35 cm in fresh water (Zeigler and Gill 1959).

In fact, the falling time decreases very rapidly at first and slowly thereafter because the drag on small, unstable scallops is sufficiently strong to cause them to rock back and forth while sinking, whereas large shells drop straight down. This is reflected in the larger standard deviations (actual standard deviations, not standardized coefficients of variation) for small scallops (vertical lines of text-fig. 3).

Attractive as it seems as a mechanism for generating lift, increased velocity is not often attained by larger animals. Most authors agree that the maximum velocity of geometrically similar animals is largely independent of their size (Hill 1950, on cetaceans, Smith 1968, Thompson 1942). Some of the standard reasons are applicable to scallops and new ones can be developed to relate scallop swimming to this common argument.



TEXT-FIG. 3. Time to fall 35 cm in sea water *v.* size in *Amusium ballotti* (upper curve) and *Placopecten magellanicus* (lower curve). Passive drop experiment on double valves. Each point is the mean time (10 trials) required for a single specimen. The vertical line through each point is the standard deviation of these 10 trials.

1. The scallop as a hydraulic pump. Let us assume that the forward velocity of a scallop is in constant proportion to the backward velocity of expelled water and demonstrate that this backward velocity is independent of size. The mass of water expelled should equal $\rho\Delta V$ where ρ is density and ΔV the change in scallop volume during a closing stroke. Then

$$\rho\Delta V = \rho vTA \tag{4}$$

where v is the velocity of the existing water, T the stroke time and A the cross-sectional area of the gap through which water is expelled. Now T is proportional to the contraction time of the quick muscle. Since the contraction time of muscle is directly proportional to its length, T should scale as L. The slower speed of larger pumps and levers is recorded in the reduced pulse rate of large mammals (Smith 1968, Gould 1966), tail beat frequency of large fishes (Gray 1968) and wing-beat frequency of large insects (Chapman 1969, Reed *et al.* 1942, Weis-Fogh and Jensen 1956) and birds (Hill 1950, Rashevsky 1960). Therefore

$$v = \frac{\rho\Delta V}{\rho TA} \propto \frac{L^3}{L^1L^2} = \mathbf{1} \tag{5}$$

and velocity is independent of size.

2. Scallop power (argument adapted from Smith 1968). The power exerted by a scallop is equal to (force × velocity). The force must balance the drag force which, from (1), and remembering that C_d is constant for R_e in a scallop's range, scales as L^2v^2; the power required is therefore $L^2v^2 \times v$ or L^2v^3. Since the power available is L^2 (p. 69)

$$L^2 \propto L^2v^3 \tag{6}$$

and

$$v^3 \propto \frac{L^2}{L^2} = 1. \tag{7}$$

Velocity, again, is independent of size.

I conclude, therefore, that scallops probably cannot generate enough lift to balance increasing weight as they grow.

Swimming and size: the second argument

A second, and stronger, argument depends on our conclusion that maximum velocity is independent of size. D'Arcy Thompson (1942, p. 46) enunciated a 'principle of necessary speed' and explained it as follows (p. 41) (and here we must remember that the appropriate analogy for scallop swimming is flight, not the swimming of teleosts): 'In running, walking, or swimming, we consider the speed which an animal can attain. . . . But in flight there is a certain necessary speed—a speed (relative to air) which the bird must attain in order to maintain himself aloft, and which must increase as its size increases.' The idea that minimum take-off velocity must scale as some positive power of L is an old one. Thompson (1942, p. 48) reminds us that it formed the basis for one of Borelli's propositions in *De motu animalium* (1685): *Est impossibile ut homines propriis viribus artificiose volare possint. Propriis viribus* (by their own strength) is the key. Large birds can glide (as did the pioneers of human aviation before adding motored power), scallops cannot.

Gray (1968) presents a dimensional argument that is incorrect as a generalization, but valid within a scallop's range. Since the lift force must balance weight in order to keep an object aloft, from (3)

$$1/2\,\rho\, v^2AC_l = mg \tag{8}$$

and

$$v_m = \sqrt{\left(\frac{2}{C_l\rho}\,\frac{mg}{A}\right)}, \tag{9}$$

where v_m is the minimal velocity needed for take-off. Gray then errs in assuming that $2/C_l$ is constant. Since C_l depends on Reynolds number, it is not independent of size; however, at Reynolds number in a scallop's range, C_l is approximately constant (p. 70). Therefore

$$v_m = k\sqrt{\frac{mg}{A}} \propto \sqrt{\frac{L^3}{L^2}} \propto L^{0.5} \tag{10}$$

and a scallop four times the length of another must swim twice as fast to get off the bottom. Since the maximum velocity of a scallop is independent of size (p. 72), if small scallops swim at anywhere near their maximum speed, large scallops will not be able to swim at all. In fact, large *Placopecten magellanicus* do execute quick contractions, but do not take off (Caddy 1968, p. 2131).

Theoretical arguments aside, Thompson's principle of necessary speed is validated by the swimming and flight behaviour of many animals that are heavier than their enclosing medium. Large birds have difficulty rising from the ground and 'must fly quickly or not at all' (Thompson 1942, pp. 45–6); insects and hummingbirds can hover in almost stationary flight. The three largest elasmobranchs swim very slowly, in apparent contradiction to our principle; yet two of these have oily livers that provide neutral buoyancy, while the third, *Mobula* the ray, has an enormous lifting surface (Bone and Roberts 1969). Small bats and birds can take off directly from their perch; 'condors and the larger fruit bats take to the heights so that they may plunge fully into open air' (Breder 1930, p. 115). Adult flying fish (Cypselurinae) 'taxi' before a flight, accelerating on the speedboat principle by driving the caudal fin through water while the body encounters less drag in moving through the rarer medium of air. Yet young flying fish do not taxi before their flights (Hubbs 1933, p. 603). Hubbs attributed this difference in behaviour to recapitulation in the evolution of flight (primitive flying fish, he believed, merely leap out of water with no preliminary manœuvre). It seems quite clear, however, that behavioural differences in the flight of young and old cypselurids are size-required adaptations for commensurate efficiency in motion, not the signposts of an antiquated rule of phylogeny. Young horseshoe crabs 'swim briskly up and down, skimming about on their backs' (Packard 1871, p. 500). Yet Clarke and Ruedemann (1912, p. 73) describe the almost comic performance of a large limulid which, in trying to take off, climbed a rock, fell into the water and landed on its tail spine.

There are, in summary, two major reasons why scallops that do not change their shape during growth will experience continually greater difficulties in swimming as they increase in size. (I note that size increase causes a scallop to cease swimming not once, but twice during its ontogeny. We have just documented the loss at large sizes. But the prodissoconch swims by the beating of velar cilia (Gutsell 1931) and the insufficiency of ciliary locomotion at large sizes is a classic example of surface/volume problems (Gould 1966, p. 638), the cilia number increases as the external surface; the weight they must support as volume).

1. The gravitational force scales as L^3. All forces that could balance it, in principle, scale at smaller powers of L.

2. Maximum velocity is independent of size; yet larger scallops must move faster than small ones in order to swim at all.

ALLOMETRY AND SWIMMING IN SCALLOPS: AN EMPIRICAL ANALYSIS

If swimming becomes continually more difficult as scallops increase in size, we can expect that growth will be accompanied by allometric changes, selected to alleviate these difficulties. (Since large scallops do not swim, solutions are not complete; but any favourable allometry will slow down the rate at which swimming ability is lost and prolong the range of swimming to larger sizes. Scallops may retain the ability to swim until they are large enough for defence against predators that could only be evaded by flight at smaller sizes. The more massive valves and greater absolute muscle force of large scallops will afford protection [see Hancock 1965, on the relation of muscle size to starfish predation in *Mytilus*]).

On pp. 63–5 I discussed the species that were studied and defined the measures that were made. Table 2 presents some summary statistics calculated from these data. The

TABLE 2. Summary of statistics for allometry of shell and musculature in five samples of scallops (for regressions: first line is y-intercept, second is slope, and third is correlation coefficient; columns 9–12 at right valve area = 60 mm², columns 13–14 at length = 8·9 cm)

Species	N	1. *Quick muscle area* v. *valve area*	2. *Slow muscle area* v. *quick muscle area*	3. *Log quick muscle area* v. *log weight*	4. *Valve width* v. *length*	5. *Dorso-ventral position of quick muscle* v. *length*	6. *Dorso-ventral position of slow muscle* v. *length*	7. *Antero-posterior position of quick muscle* v. *width*
Placopecten magellanicus (Penobscot Bay)	30	− 0·067 0·054 0·967	0·038 0·204 0·947	− 0·662 0·649 0·979	− 0·398 1·148 0·994	0·415 0·040 0·747	0·694 0·013 0·272	1·650 − 0·062 − 0·647
Placopecten magellanicus (Block Island)	19	− 0·224 0·068 0·987	0·145 0·182 0·984	− 0·657 0·655 0·961	− 0·246 1·058 0·995	0·498 0·017 0·693	0·907 − 0·051 − 0·676	1·453 − 0·008 − 0·095
Amusium ballotti	13	− 1·317 0·109 0·893	0·043 0·090 0·891	− 0·452 0·820 0·926	− 0·254 1·097 0·996	0·421 0·055 0·675	0·659 0·063 0·398	1·335 − 0·041 − 0·473
Hinnites multirugosus	8	− 0·957 0·102 0·979	0·296 0·232 0·946	− 0·941 0·615 0·958	0·521 0·749 0·931	0·440 0·145 0·843	0·626 0·106 0·520	1·832 0·157 − 0·633
Chlamys jeffersonius	19	− 0·637 0·076 0·946	− 0·010 0·415 0·960	− 0·039 0·461 0·968	− 0·178 1·118 0·994	0·681 0·018 0·324	1·141 − 0·021 − 0·257	1·901 − 0·115 − 0·839

Species	8. *Antero-posterior position of slow muscle* v. *width*	9. *Quick muscle area*	10. *Slow muscle area*	11. *Slow muscle/quick muscle*	12. *Weight*	13. *Width*	14. *Width/length*
Placopecten magellanicus (Penobscot Bay)	2·192 − 0·015 − 0·130	3·17	0·678	0·213	16·41	9·20	1·03
Placopecten magellanicus (Block Island)	2·013 0·059 0·607	3·83	0·842	0·220	21·18	8·79	0·99
Amusium ballotti	1·659 0·043 0·328	5·22	0·512	0·098	13·02	9·09	1·02
Hinnites multirugosus	2·700 − 0·071 − 0·170	5·16	1·493	0·289	66·57	7·97	0·90
Chlamys jeffersonius	2·202 − 0·003 − 0·027	3·92	1·617	0·410	21·07	9·50	1·07

first eight columns include regression parameters (least squares y on x), three lines for each column (y-intercept, slope, and correlation coefficient in that order). For this linear model,

$$y = ax+b \tag{11}$$

allometry is measured by the y-intercept; y increases faster than x if the y-intercept is negative, vice versa if positive. The ratio of increments y/x per unit x is constant during growth, but since these increments are being added to an initial shape of different proportions, total shape changes during growth (Gould 1968, p. 84; Waller 1969, pp. 23–5). The single exception is column 3, where quick muscle area is plotted against shell weight. Here the increments cannot be constant, since y scales near L^2 and x near L^3. Here we use a power function

$$\log y = a\,(\log x)+\log b \tag{12}$$

and we *are* interested in the slope. Allometry is measured by change in the ratio of increments, and we look for variation from the ideal slope of 2/3 to detect departure from geometric similarity.

We have still another concern when ratios, rather than raw measures, are plotted against a linear dimension. Here (as in columns 5–8) our test for allometry is any significant correlation coefficient or slope $\neq 0$. (Ratios are dimensionless parameters of shape and must remain constant during growth if geometric similarity is to be maintained. Any significant correlation of a ratio with a linear measure indicates allometry.)

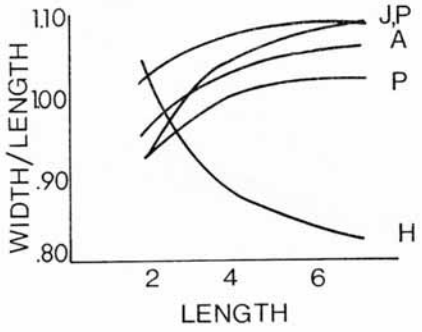
Allometric trends and interspecific variation

I shall first describe the allometric changes and then present interpretations for each as improvements in swimming design that partly offset the detrimental effects of increasing size. With the initial descriptions, I shall also discuss interspecific differences and their relation to varying modes of life. (Interspecific differences are shown in Table 2 in columns 9–14; entries are predicted values for given variables at common size-standards for large scallops still well within the swimming range of *Placopecten magellanicus*—columns 9–12 at right valve area = 60 cm^2; columns 13–14 at length = 8·9 cm.)

1. Basic dimensions. We see, from y-intercept values of column 4, that width/length ratios increase in all species except the cemented *Hinnites multirugosus*. Increasing relative width, I shall argue on p. 87, provides advantages in swimming. It has been noted before in free-living scallops. It was the most consistent of Waller's 'size-correlated morphological trends' (1969, p. 24); relative width increased during the ontogeny of all 56 samples of various species of the *Argopecten gibbus* stock. Yonge (1951, p. 409) recognized the correlation of this trend with mode of life when he stated, of the family Pectinidae, that 'only in those that lose all attachment . . . is the anteroposterior diameter the greater'. *Hinnites multirugosus* begins its post-larval life conventionally as a byssally attached juvenile. It is, at this stage, capable of swimming movements when dislodged. But at a dorso-ventral diameter of 2·2–4·2 cm it cements permanently to the substrate (Yonge 1951). Thereafter it undergoes progressive elongation rather than widening, an unsurprising exception for a scallop in this oyster-like role. *Pedum spondyloideum*,

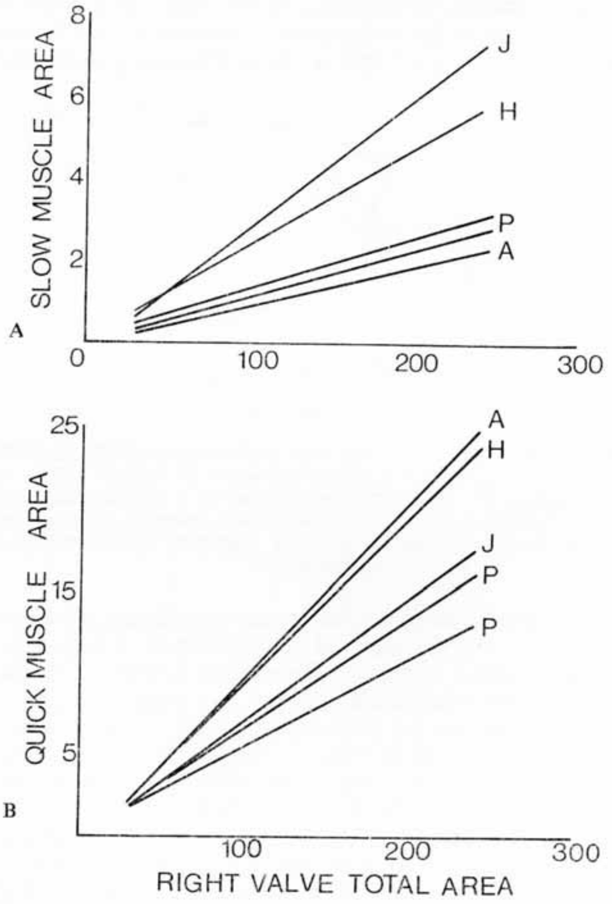
another sedentary pectinid, also becomes more elongated as it grows (Yonge 1967*b*). Text-fig. 4 plots the width/length ratio against size in all five samples.

2. Size of the quick muscle. In column 1 (Table 2), we see that the area of quick muscle insertion increases faster than the area of the entire valve during ontogeny in all samples. The relationship, as shown in text-fig. 5, seems to convey the odd impression that non-swimming *Hinnites* has a larger quick muscle at any standardized stage of growth than the accomplished swimmer *Placopecten magellanicus*. However, this results only from the use of area as a size standard. If we plot quick muscle area against shell weight (text-fig. 6 and Table 2, column 3), this anomaly is resolved. *Amusium*, our best swimmer, bears the greatest quick muscle area per unit weight at any weight. But now the two *Placopecten* samples are not only closer together, but also lie near *Amusium*'s line, while non-swimming *Hinnites* and fossil *Chlamys jeffersonius* are further removed to a region of high weight per unit muscle area. Since *Hinnites* cements by the right valve, its quick muscle, in executing cleansing contractions, need only move the lighter left valve. A massive right valve therefore imposes no mechanical penalties and offers undoubted aid for stability and protection. *Hinnites* lies close to *Amusium* in text-fig. 5*b* because it has the most convex right valve among our species; this produces a misleading high value for quick muscle area in relation to valve area projected to the plane of commissure.



TEXT-FIG. 4. Width/length ratio of the right valve plotted against length (in inches). Based on predicted values from the width *v.* length regressions of Table 2. Letters as follows: J = *Chlamys jeffersonius*; P = *Placopecten magellanicus*; A = *Amusium ballotti*; H = *Hinnites multirugosus*. Relative width increases during the ontogeny of all species but the cemented *Hinnites*. Increased relative width aids swimming by augmenting the shell's aspect ratio.

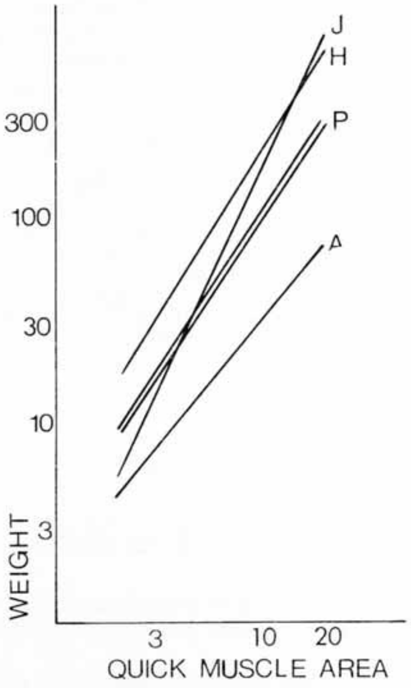
The line for *Chlamys jeffersonius* in text-fig. 6 is peculiar in one respect. It passes from an area occupied by good swimmers early in its ontogeny, finally to cross the *Hinnites* line at large sizes. Although this unusual scallop lacks close living relatives and has not yielded palaeoecological data to reveal its mode of life, I feel confident that the ontogeny of its swimming behaviour can be deciphered from this mechanical analysis. Young *C. jeffersonius* are vèry light, yet the shell thickens during ontogeny at a rate approached, to my knowledge, by no living scallop. Despite its coarse ribbing I suspect that the young could swim, not only because their valves were so light, but especially because the width/length ratio increases with growth (pp. 76 and 87). Yet the remarkable shell thickening that places this species second only to the abalone as a favoured object for shell ash-trays surely precludes swimming at large sizes; *C. jeffersonius* could generate neither the velocity to raise its adult shell nor the lift to keep it aloft. The adults must have rested free on the bottom, stable by the sheer weight of their valves and protected both by this weight and by the strength of their massive slow muscle (see next paragraph).



TEXT-FIG. 5. Muscle areas *v.* total area of the right valve; based on calculated slopes and intercept of Table 2 (in cm^2). A: slow muscle area. B: quick muscle area. Letters as in text-fig. 4.

3. Size of the slow muscle. Text-fig. 5 clearly distinguishes the good swimmers from *Hinnites* and *C. jeffersonius* by the small size of their slow muscle. Since *Placopecten* and *Amusium* respond to predators by flight (photographs in Rees 1957), they need not maintain the slow muscle strength that sedentary scallops require. (Kim 1969, found that starfish could open *Patinopecten yessoensis* more quickly than they opened a variety of cemented and slow-moving forms. He claims that *Patinopecten* is, nonetheless, comparatively difficult prey because valve movements tend to drive the starfish off. This is surely not the major reason. The scallop was firmly attached to a wood plate in this experiment; Kim's kymograph merely recorded the quick muscle contractions of the scallop's escape reaction.)

The slow muscle of *C. jeffersonius* is particularly massive (text-fig. 7), even on the small specimens that were, if my previous contention is correct, capable of swimming. This poses no problem, for there are two ways for an adult to produce a structure that need be relatively large only late in ontogeny. The structure will either grow with marked positive allometry (which may impose a heavy metabolic load and markedly increase variation at large sizes), or it can be relatively large to begin with and grow at normal rates. German writers on allometry refer to this second mode as *Vorbereitungswachstum* (or preparatory growth) and cite such obvious examples as the fully developed wings of nestling birds (Kramer 1959). In such cases, the functional significance of features at small sizes can only be determined by studying the mechanics and behaviour of adults.

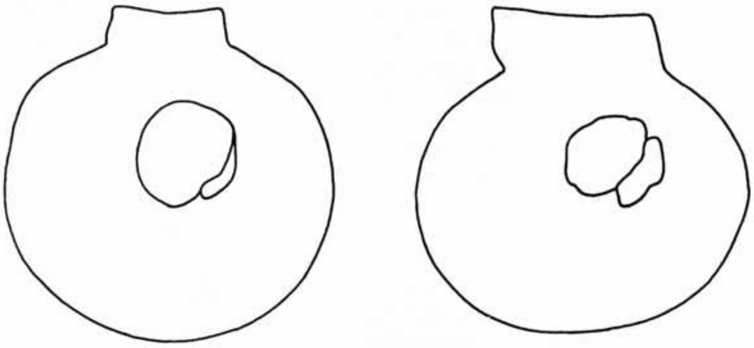


TEXT-FIG. 6. Weight (in g) *v.* quick muscle area (cm^2) on logarithmic coordinates. Letters as in text-fig. 4.

Amusium's very small slow muscle (text-fig. 7) may provide an example of material compensation in Rensch's sense (1960, pp. 179–91), and offers further testimony to this animal's presumed abilities as a swimmer. No one, it seems, has reported on the actual behaviour of *Amusium*; yet the anatomical and structural evidence is strong, despite the fact that *Amusium* is not an aerofoil because its lower valve is the more convex.

(i) The remarkably small convexity of the valves, reduced, as Yonge (1936, p. 78) states, to a minimum raises the fineness ratio chord (= width)/maximum thickness to its highest value among scallops. In hydrodynamics the fineness ratio is second in importance only to the aspect ratio (p. 87) as a measure of efficiency in aerofoils; the drag coefficient rises markedly as relative thickness of an aerofoil increases.

(ii) The extreme lightness of the valves reduces the gravitational force, thereby reducing the speed of sinking (text-fig. 3) and specifying a minimum velocity for take-off smaller than that of any other scallop at any comparable size. Most scallops increase the relative thickness of their valves as they grow, *Amusium* does not. It is, in fact, the only one of our four species in which the log quick area *v.* log weight regression maintains a slope greater than the predicted 2/3 for isometry ($k = 0{\cdot}820$). *Amusium* possesses an extraordinary adaptation for sufficient strength in the presence of such lightness; it has *internal* ribs that allow the outer surface to remain smooth. The emphasis on lightness extends to shell micro-architecture: 'Where these [internal] ribs are covered by the crossed-lamellar inner layer, there is a reciprocal thickness variation, so that the relief of the central part of the shell is greatly reduced' (Taylor, Kennedy, and Hall 1969, p. 94).



TEXT-FIG. 7. Valve outlines, quick and slow muscle scar traces of actual specimens. Left: *Amusium ballotti*. Right: *Chlamys jeffersonius*. Specimens in correct relative proportions to each other. Actual width of *A. ballotti* = 10 cm.

(iii) I have already alluded to the uncommon smoothness of the valves. This surely reduces turbulence, as does the absence of a byssal notch and very small size of the auricles. There is another intrinsic reason why *Amusium* needs to be smooth. The higher the fineness ratio of an object, the greater the percentage contribution of skin-friction drag to its total drag (Goldstein 1965, p. 425). By being smooth *Amusium* minimizes the most important component of its drag.

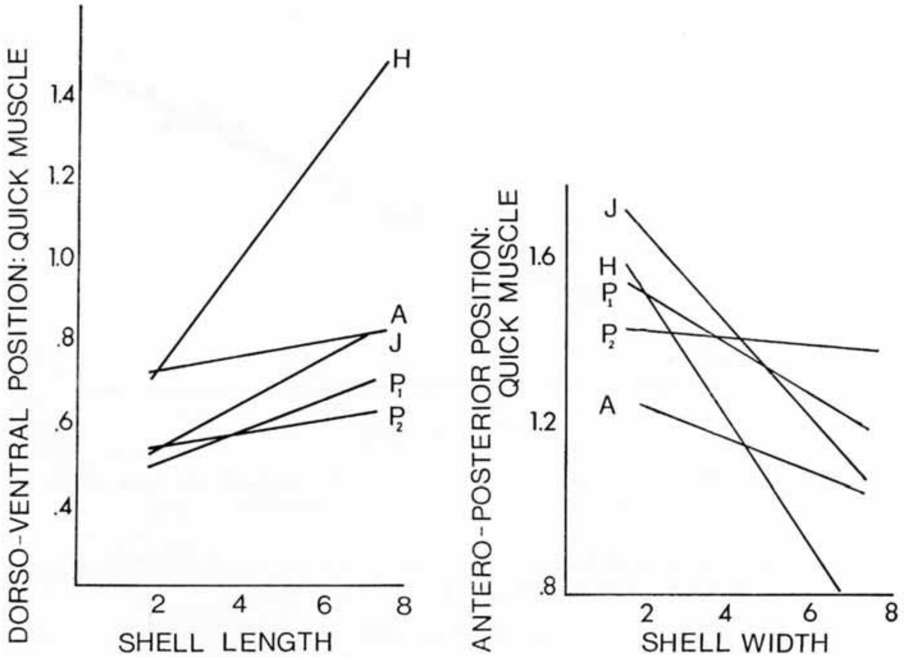
(iv) Considerations of flow provide other evidences of good swimming design. The point of maximum convexity is more anterior than in most other scallops. The gradual posterior taper from this point helps prevent separation of the flow. In addition, the postero-lateral edges of the upper (left) valve are turned upwards. With an axis of maximal convexity running down the centre of the valve, this upbowing at the edges produces two lateral channels that should direct the flow and prevent separation.

(v) The large quick muscle and small slow muscle have already been discussed.

(vi) Waller (1969, p. 21) mentions that while the slow muscle is inserted normal to the valves,. the quick muscle is quite oblique. This lengthens the quick muscle and increases its capacity for performing work (cross-sectional area × length).

(vii) Yonge (1967*b*, p. 315) reports the 'circumstantial evidence' of Pelseneer who showed that the right posterior pedal retractor is large in byssally attached scallops and small in unattached forms. It is absent in *Amusium*.

4. Movement of the quick muscle; movement in the dorso-ventral axis. Text-figure 8 *a* and column 5 of Table 2 show that the quick muscle moves to a progressively more ventral position during the ontogeny of all samples. (I shall resolve, on p. 89, the apparent anomaly that this motion is greatest in cemented *Hinnites*.) This motion has been noted before, by Waller (1969) and, particularly, by Merrill (1961, pp. 12–13) who claims that, in *Placopecten magellanicus*, the adductor moves to a more ventral position until the shell reaches a length of about 50 mm. Thereafter, the position of the adductor is said to be stable. Thus, for Merrill, there are two distinct phases in ontogeny, one of motion and one of stability. I should like to point out that this appearance is illusory and that both supposed phases are the consequences of a single process.

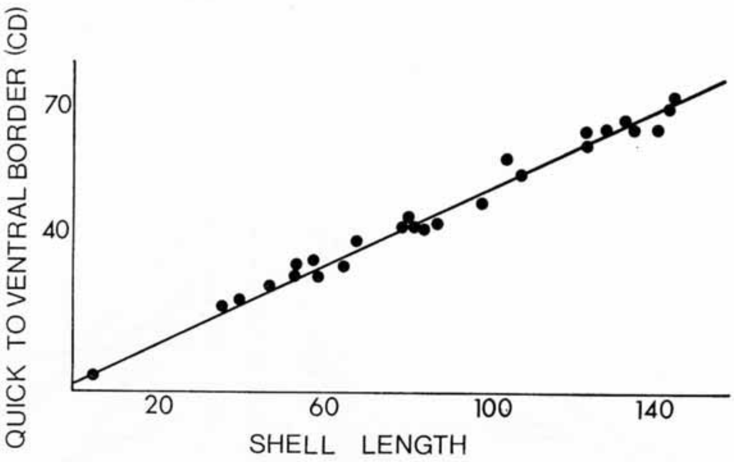


TEXT-FIG. 8 (*a*)

TEXT-FIG. 8 (*b*)

TEXT-FIG. 8. (*a*) Dorso-ventral position of the quick muscle (AB/CD of text-fig. 1) *v*. shell length (in). Relative motion is dorsal to central in all species. (*b*) Antero-posterior position of the quick muscle (EF/GH of text-fig. 1) *v*. shell width (in). Relative motion is posterior to central in all species.

During allometric growth on the linear model (equation 11), the rate of change in y/x must decrease as size increases. This occurs because such allometry consists of adding increments of unvarying y/x to an initial shape of different proportions. As the initial shape becomes a progressively smaller part of the whole, y/x of the whole approaches the constant incremental y/x and the rate of change in shape diminishes. Now, text-fig. 9 shows that the linear model applies in a quite precise and unvarying fashion throughout growth. The regression line of text-fig. 9 was computed simply by connecting points for my largest scallop and that for the 5-mm shell figured by Merrill 1961, p. 14 (and far smaller than any I could measure). My measured points are well distributed with small variance about this line for CD *v.* shell length (text-fig. 1)



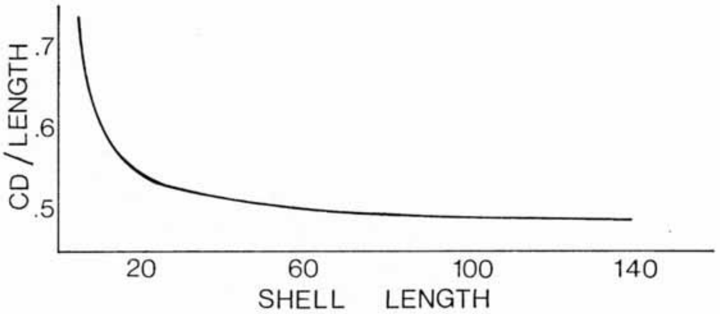
TEXT-FIG. 9. Distance from ventral border of quick muscle to ventral border of the shell *v.* shell length in *Placopecten magellanicus* from Penobscot Bay (in mm).

$$y = 0{\cdot}478x + 1{\cdot}28 \tag{13}$$

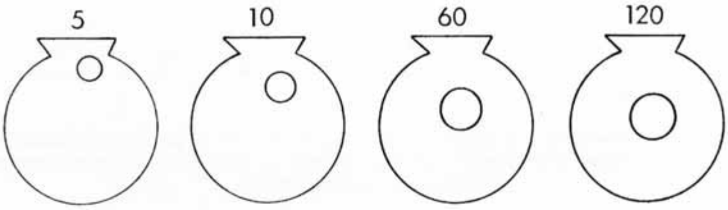
and the positive y intercept indicates that the muscle approaches the ventral border as growth proceeds. The diminishing rate of change in y/x that this equation yields is plotted directly as text-fig. 10. Text-fig. 11 then shows, for theoretical scallops conforming to this equation, how the appearance of stability at large sizes arises (the rate of change between 60 and 120 mm is quite slow). Finally, the plot for our ratio measure of dorso-ventral position (AB/CD of text-fig. 1) *v.* size (text-fig. 12) shows that, while the rate of movement does indeed diminish beyond Merrill's 50 mm, its direction never changes. Of 8 scallops that equal or exceed 0·6 for this measure, 5 are larger than 125 mm in length; (there are only 6 shells in the > 125 mm category). Given the wide variation in this measure, the qualitative impression of two growth phases is almost unavoidable.

Movement in the antero-posterior axis: column 7 of Table 2 and text-fig. 8*b* show that, in all samples, the quick muscle moves from a posterior to a more central position during growth. I have separated the dorso-ventral from this antero-posterior component because I believe that the adaptive significances of the two are different (pp. 87–91). Of course, they represent a single vector in growth—a single motion from a dorso-posterior to more ventral and central position.

5. Movement of the slow muscle: columns 6 and 8 of Table 2 and text-fig. 13. It would seem, at first glance, that movement of the slow muscle follows no clear pattern. Its dorso-ventral motion, for example, is dorsad in two samples, ventrad in three (with the two *Placopecten* samples showing opposite tendencies). However, when the slopes of these regressions are ranked and compared with those for quick muscle motion (Table 3) we see that, in each case, there is correspondence between the two sets. Apart from the higher slope for slow muscle than for quick muscle in dorso-ventral motion of *Amusium* and the insignificant reversal in magnitude between slow muscle slopes of *C. jeffersonius* and Penobscot Bay *P. magellanicus* for antero-posterior motion, the ranking of slow muscle slopes is the same as for quick muscle. However, for each motion, the average slow muscle slope is less than the average for quick muscles. Thus, for slow muscles, the ranking includes zero and there is reversal of direction, whereas all quick muscle slopes are in the same direction for each motion. Thus, the slow muscle tends to move less than the quick muscle, but at least part of its motion is correlated with that of the quick muscle. We have here, I suspect, a case of mechanical correlation

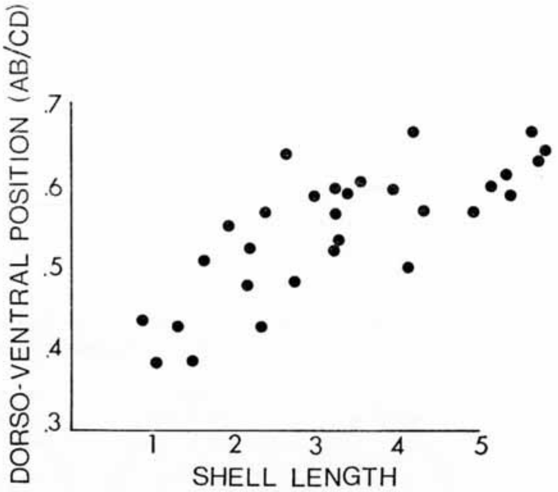


TEXT-FIG. 10. y/x of text-fig. 9 *v.* shell length (in mm). Calculated from the regression line of text-fig. 9 to show the originally rapid and subsequently slow allometric change of this ratio.



TEXT-FIG. 11. Theoretical scallops drawn to same scale. Shell length (in mm) given in figures above each drawing. The sizes and positions of the quick muscle correspond to calculations of text-fig. 9 and show that allometric changes are very rapid at small sizes and very slow later in growth.

in which slow muscle is pulled by the motion of its neighbour (the two, as diners can testify, do form a single, edible entity) or by the extension of this bordering growth field. If the goal of 'morphological integration' is to separate and explain the various, often opposing, determinants of form (Olson and Miller 1959; Gould and Garwood 1969), then we acquire useful information in identifying a component of slow muscle position that is correlated with, and perhaps controlled by, quick muscle motion.



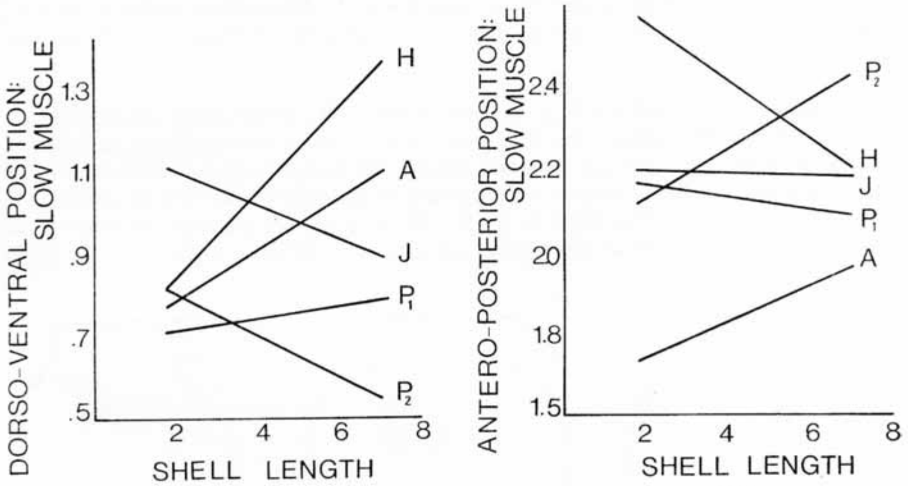
TEXT-FIG. 12. Dorso-ventral position of quick muscle (AB/CD of text-fig. 1) *v.* shell length (in inches) for *Placopecten magellanicus* from Penobscot Bay. Relative ventral movement continues throughout growth.

The net effect of these motions is that the slow muscle seems to slip around the quick muscle from a ventral-central to a more dorsal-posterior position during growth (text-fig. 14). Actually, this effect is produced primarily by ventral-central, quick muscle motion relative to a more stable slow muscle.

Hypotheses for allometric trends

I can imagine three major categories of explanation for these allometric tendencies:

1. A developmental hypothesis that does not posit specific, functional explanations for observed changes of shape; the single muscle of pectinids is, morphologically, the posterior adductor (Jackson 1890, Marceau 1936, p. 941). As Jackson (1890, p. 342) suspected and Gutsell (1931) demonstrated, larval pectinids have two adductors, situated near the dorsal hinge axis as in orthodox dimyarians. Hence, enlargement of the one muscle that remains and its motion from an original dorsal-posterior position to a more ventral and central one need represent no more than one part of an ontogenetic reorganization that converts a dimyarian clam to one in which the body is more



TEXT-FIG. 13 (*a*)

TEXT-FIG. 13 (*b*)

TEXT-FIG. 13. (*a*) Dorso-ventral position of the slow muscle (A′B′/C′D′ of text-fig. 1) *v*. shell length (in). Letters as in text-fig. 4. (*b*) Antero-posterior position of the slow muscle (E′F′/G′H′ of text-fig. 1) *v*. shell width (in). Lines in these and similar figures calculated from the regressions of Table 2.

TABLE 3. Correlation of slow and quick muscle motions (figures are slopes of regression lines)

Case 1. Dorso-ventral motion

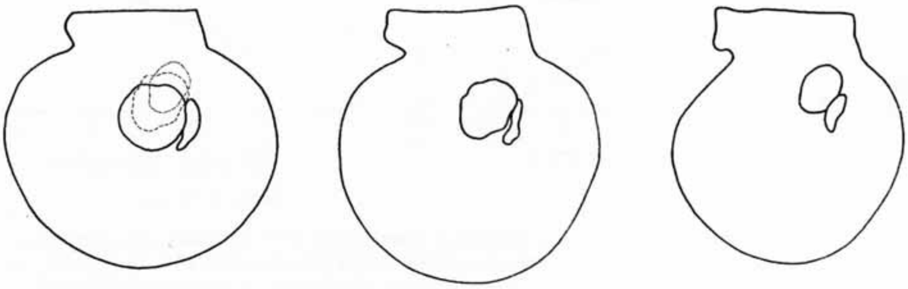
Species	*D-V motion of quick muscle* v. *shell length*	*D-V motion of slow muscle* v. *shell length*
Hinnites multirugosus	0·145	0·106
Amusium ballotti	0·055	0·063
Placopecten magellanicus (Penobscot Bay)	0·040	0·013
Chlamys jeffersonius	0·018	− 0·021
P. magellanicus (Block Is.)	0·017	− 0·051

Case 2. Antero-posterior motion

Species	*A-P motion of quick muscle* v. *shell width*	*A-P motion of slow muscle* v. *shell width*
Hinnites multirugosus	− 0·157	− 0·070
Chlamys jeffersonius	− 0·115	− 0·003
Placopecten magellanicus (Penobscot Bay)	− 0·062	− 0·015
Amusium ballotti	− 0·041	0·043
P. magellanicus (Block Is.)	− 0·008	0·059

symmetrically distributed about a more central muscle. Here there would be no need to maintain a specific, mechanical explanation for an isolated component of muscular allometry.

2. A functional hypothesis that does not explain allometric trends as adaptations to the problems of increased size. Here, we begin by admitting that the postero-dorsal placement of the larval muscle does not suit the changing functional requirements of later ontogeny. But we do not frame explanations in terms of size and its mechanical consequences, i.e. the adaptation would be advantageous at any size; the delay in its appearance simply relates to the time required for a gradual reorganization of larval proportions. A more central quick muscle, for example, would provide a better distribution of stresses on the hinge and periphery. A postero-dorsal position, near the posterior auricle, might impede the circulation of water on this side and lead to eccentricity of swimming as more water was expelled from the antero-lateral margin. For slow muscle a central position offers protection from predators that concentrate their attacks 'at the periphery of the valves where the shell is thinnest' (Waller 1969, p. 19). A very dorsal muscle leaves the whole ventral margin poorly defended as the force needed to open the valves will be some inverse function of the ratio C′D′/A′B′ (text-fig. 1).



TEXT-FIG. 14. Valve outlines and muscle scar impressions for three actual specimens of *Placopecten magellanicus* drawn to the same scale. Actual shell lengths (left to right) are 145, 71, and 25 mm. Quick muscle scars of the two smaller shells are superposed upon the largest shell to indicate the muscle's change of position. Allometry of shell shape is also well displayed by this series.

3. A functional hypothesis that relates allometric trends to size increase by explaining them as the mechanical requirements imposed by size itself. In this case, the gradual progression of a trend through ontogeny is not seen as a sign of constant improvement, but as a graded response to a mechanical problem that becomes increasingly more severe as the scallop grows.

I have no doubt that all these hypotheses contribute to the complex explanation of allometry in scallops. By discussing only the third in the following section, I am not suggesting that others do not apply, but only that each allometric trend does provide advantages for swimming that larger scallops require.

Allometric trends and size increase

Previous discussion showed that increased size will make swimming more difficult for scallops. This discussion contained one important departure from reality. It assumed an invariant shape with growth, whereas allometry is not only common in scallops, but is also the usual way in which animals overcome the mechanical problems of increased size.

1. Basic dimensions of the shell. I mentioned that lift and drag coefficients depended both on Reynolds number and on shape. For hydrodynamic considerations, the most important measure of shape is the 'aspect ratio', the quotient of the span of an aerofoil (maximum length perpendicular to direction of motion) divided by its chord (parallel to motion—Dryden, Murnaghan, and Bateman 1956, p. 75). This corresponds to the width/length ratio of scallops, a measure that increases during the ontogeny of all species, with the obvious exception of cemented *Hinnites*. As aspect ratio improves, the lift/drag ratio increases (Weis-Fogh 1961, p. 284) and flight becomes easier. 'Lifting power not only depends on area but has a linear factor besides, such that a long narrow wing is more stable and effective both for speedy and for soaring flight than a short and broad one of equal area' (Thompson 1942, p. 961). D'Arcy Thompson then (p. 964) shows an ideal bird, constructed to make the leading edges of the wings as long as possible and to produce a continuous curve with no sharp corners. The result (text-fig. 15) is a very fine picture of the ventral margin of a scallop. Stanley (in press) has related the greater relative width of free-living *v.* byssate scallops to aspect ratio.

TEXT-FIG. 15. D'Arcy Thompson's idealized bird. Note the resemblance of the leading edge of the wing to a scallop's ventral margin (its leading edge).

2 and 3. Size of the quick muscle and its dorso-ventral movement. Lest the coupling of these two trends seem peculiar, consider the mechanics of motion in scallops. At first thought we might seek an explanation for decreased swimming at increased sizes in the idea that muscular strength increases as L^2 and weight as L^3. Galileo's argument for the relatively thick legs of large terrestrial animals would then apply, by analogy, to the swimming of scallops. But muscular strength alone is not the appropriate measure; a scallop claps its valves by exerting a force to counteract the opening moment of the ligament (Trueman 1953). This force is measured not by the strength, but by the moment exerted by the quick muscle in rotating the valves towards each other about the hinge. This moment is measured by the muscular force (its cross-sectional area) times its distance from the point of rotation (linear distance from this point, approximately the centre of the muscle insertion, to the hinge). For an isometric size series, this moment will scale as L^3 and offset the increasing weight. (It is only for this reason that most clams can exhibit so little muscular allometry and still maintain their strength to move, burrow, and bore at large sizes—see Thomas, in press, on *Glycymeris*.) Both

the size of the quick muscle and its position in the dorso-ventral axis determine its moment, hence their combination in this discussion.

In an elegant series of experiments, Trueman (1953) actually measured the closing moment of the ligament in eviscerated scallops with intact ligaments. This measure, then, is not the actual moment exerted by the adductors to close the valves, but rather the minimal moment needed to close them against the opposing force exerted by the ligament. Trueman found (1953, p. 455) that this closing moment scales as L^3. Now, if allometric growth causes the muscles to increase in relative size and move to a more ventral position, then the actual moment exerted by the quick muscle will scale at a power of L greater than 3. If this improved moment allowed the valves to adduct with continually greater relative effect during growth, then large scallops might generate higher velocities than smaller ones and partly overcome both difficulties discussed on p. 74.

I measured the actual moment of each specimen as the product of quick cross-sectional area times the distance from the centre of this muscle to the hinge. I plotted these values against shell weight and obtained the following regressions:

Placopecten magellanicus, Penobscot Bay

$$y = 0{\cdot}590x^{1{\cdot}02} \tag{14}$$

where, in all formulae, y is moment and x is weight.

Placopecten magellanicus, Block Island

$$y = 0{\cdot}336x^{1{\cdot}19} \tag{15}$$

Amusium ballotti $$y = 0{\cdot}818x^{1{\cdot}17} \tag{16}$$

Hinnites multirugosus $$y = 0{\cdot}113x^{1{\cdot}22} \tag{17}$$

Chlamys jeffersonius $$y = 0{\cdot}655x^{0{\cdot}89} \tag{18}$$

Amusium continues to stand out as the best swimmer. Its rate of increase for moment is essentially the same as that for two other samples, but its y-intercept is so much greater than the others that its total moment far exceeds that of all other samples at any comparable size. (For these cases, the value $x = 1$ g [at which the y-intercept is calculated] lies within the range of measured data, and the actual value of the y-intercept may be meaningful as a measure of initial tendency. This is not usually the case; see White and Gould 1965.) *Hinnites*, on the other hand, has a slope equal to that of two swimming samples, but its y-intercept is low and its total moment smaller than that of all swimmers at sizes in our measured range. The two *Placopecten* samples behave differently: the Penobscot Bay sample does not improve its relative moment with growth, while the Block Island sample does. Shell weight at comparable valve areas is a good deal lower in the Penobscot Bay sample than in the Block Island sample (48·6 g *v.* 64·1 g at the large area of 120 cm^2). This weight differential might control the generally smaller muscle sizes (both quick and slow) in Penobscot Bay scallops (Table 2, columns 9 and 10) and their smaller rate of relative increase in moment. Perhaps scallops can exert a direct influence upon muscle sizes and positions via developmental feedback (Warburton 1955) from shell weight. *C. jeffersonius*, as expected, is the only sample that exhibits a relative decrease in moment with growth. The enormous thickening of the valves in growth causes weight to increase at a rate that cannot possibly be met by changes in the size and position of muscles. This provides yet another piece of evidence for concluding that *C. jeffersonius* lost its ability to swim when the valves thickened (p. 78).

If we isolate the two components of moment, we encounter some anomalies that need resolution. If we consider muscle size relative to weight, then relative increase appears only in our best swimmer, *Amusium* (Table 2, column 3). Relative muscle size is virtually constant for the two samples of *Placopecten* and decreases for *Hinnites* and, especially, for *C. jeffersonius*.

Since cemented *Hinnites* must move only its left valve and since the rate at which left valve weight increases is slower than that for right valves, the slope of log quick area *v.* log left valve weight might well exceed 2/3. But why should a non-swimmer show relative increase in muscle size? And does this not invalidate a claim that such relative increase therefore provides benefits to swimmers? The answer to both questions is no, because sedentary and cemented scallops also depend upon quick muscle contractions, though for functions other than swimming. Yonge (1936, p. 95) has called sediment 'the supreme danger to which all sedentary animals with ciliary feeding mechanisms are exposed'. He assumes that large quick muscles arose first as adaptations in sedentary forms for rapid and powerful cleansing contractions that would expel pseudofaeces and free the mantle cavity of sediment. In mud-dwelling *Glossus*, quick muscle is twice as large as slow muscle. But *Chama* lives in clear, intertidal or shallow water; it must stay tightly closed during exposure to air and has a larger slow than quick muscle (Yonge 1967*a*). Quick muscle is very well developed in *Placuna* (life on muddy bottoms) and *Anomia* (close application to rocks and consequent exposure to sediment, Yonge, 1936). Kauffman (1969, p. 178) attributes the large quick muscle of *Ostrea* to 'the ability of the animal to clean the mantle cavity and shell of sediment by rapid and forceful closure of the valves'. Yonge (1953, p. 460) says the same of *Hinnites*: 'The danger of sediment accumulating in the cup-shaped lower valve is countered by the great development of the striated section of the adductor.' Moreover, Caddy (1968, p. 2131) reports that large, non-swimming *P. magellanicus* use quick muscle contractions to recess into the substrate by blowing sand away from the margins of the shell. In fact, Yonge (1967*b*, p. 320) views these adaptations for quick contraction in sedentary forms as necessary precursors to the evolution of swimming: 'The capacity for swimming (i.e. movement with the free edges of the valves foremost) is due largely to prior possession of adaptations concerned with effective cleansing of the mantle cavity, notably enlargement of the quick muscle and ejection of water (with pseudofaeces) dorsally at either end of the hinge.'

It might be more appropriate, however, to consider muscle size relative to valve area since quick contractions supply thrust to overcome drag that increases as area rather than as weight (p. 68). Quick muscle area increases faster than valve area in all samples (Table 2, column 1). In *Hinnites*, this probably reflects only the increasing valve convexity, but it may record an advantage in swimming for other species.

For the second component of dorso-ventral motion, all samples show ventral displacement (Table 2, column 5, and text-fig. 8). A serious potential difficulty exists in the observation that this displacement is greatest in rate and magnitude for cemented *Hinnites*. This presents no problem for two reasons. First, we just maintained that *Hinnites* also depends upon quick contraction, but for cleansing rather than for swimming.

But secondly, and more important, this high rate is an artifact. In *Hinnites* and *Pedum*, sedentary scallops that live in crevices, Yonge (1951, 1967*b*) has demonstrated that the hinge line itself moves far ventral during ontogeny. In 1951 he viewed this motion as a response to the constraints of rock surfaces in crevices: If the hinge originally lay in the narrow part of a widening crevice, the valves of larger animals would be unable to open unless the hinge migrated to a wider area. Now (1967*b*, p. 321), since he has noted this ventral migration in cemented bivalves that do not inhabit crevices, Yonge views it as 'an inevitable consequence of cementation; only in this way can the animal increase in width dorsally during growth'. In my measures, AB (text-fig. 1) for *Hinnites* is the distance from the *original* dorsal border to the quick muscle. It is spuriously high since it includes the entire component of hinge migration as well as the actual muscle migration.

Finally, we might ask why the muscle does not move further towards the ventral border, since the moment would increase with each increment. Trueman (1967, pp. 473–4) has probably provided the answer in stating: 'If the adductor muscles were situated further from the hinge axis the mechanical advantage gained would greatly reduce the figure of muscular strength needed for adduction, but proximity to the axis ensures rapid adduction of the valves. The closer the adductor is to the hinge axis, the less the muscle will have to contract to close the shell and, provided that it shortens at a constant rate, the more rapid will adduction be.'

Another reason for this limitation in ventral motion has been provided by Thayer (in press). Thayer demonstrates that increasing obliquity of quick muscle insertion allows for more rapid adduction of the valves. Now, the quick muscle of swimming monomyarians is always inclined with its right insertion nearer the hinge than is the left insertion. Since the left insertion does not move ventrally as rapidly as the right, the total dorso-ventral obliquity decreases during growth. If ventral movement of the right insertion were greater, the advantages gained by increasing moment might be offset by the detriment of decreased dorso-ventral obliquity. As with Raup's ammonoids (1967), selection can optimize no one mechanical factor since there are conflicting demands upon form. The 'best' solution is a compromise among these factors.

Moments have occasionally been considered in studies on the functional morphology of muscles in fossil groups. Jaanusson and Neuhaus (1963) have identified several solutions evolved by brachiopods for the problem of placing diductor muscles so that their force attains its largest possible moment. Adamczak (1968, p. 25) notes that Devonian leperditiid ostracods either have a large adductor field situated dorsal to the mid-height of the valves or a smaller one situated ventral to it. I suggest that this might represent two ways of attaining a similar, required moment.

4. Antero-posterior motion of quick muscle. The movement of quick muscle from a posterior to a more central position in each sample entails no improvement in moment, since distance to the hinge does not change. This motion does, however, bring the quick muscle into an ever more convex part of the shell, thereby increasing its relative length. Although this lengthening does not raise muscular strength (= cross-sectional area), it does increase the mass of the muscle and hence its power reserve. Another proposal was advanced by Marceau (1936) who claimed that motion of the quick muscle to a more

central position brings it into closer alignment with the internal ligament, so that it may oppose the ligament's opening stress with a maximum strain.

Thus, each allometric trend proceeds in a direction that provides better design for swimming and counteracts the difficulties of increasing size. This cannot be a complete explanation. Swimming ability is lost at large sizes. Moreover, with the rate of allometry constantly decreasing as size increases, less and less compensation is provided as the problems of size become more and more severe. I am intrigued with the idea (though I doubt its truth) that, for some genetic or developmental reason, growth might be constrained as linear, thereby limiting the potential for allometric compensation. In any case, our attempts to explain adaptation suffer when we ignore the mechanical properties of form and the insights of engineering. Scallops, among other things, are swimming machines of imperfect design. This design improves as the intrinsic process of growth imposes continually greater challenges upon its operation.

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