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POSSIBLE PREDICTION OF SCALLOP SWIMMING STYLES FROM SHELL AND ADDUCTOR MUSCLE MORPHOLOGY

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ABSTRACT Modifications in shell structure, mantle, and adductor muscle are considered derived adaptations that allowed scallops to swim. This suggests that morphological properties of the adductor muscle and shell should relate to swimming performance in scallops. Various morphological characteristics of the shell (mass, aspect ratio, and volume between the valves) and the adductor muscle (size, position, and attachment to the shell) were measured in six scallop species (*Amusium balloti*, *Placopecten magellanicus*, *Equichlamys bifrons*, *Pecten fumatus*, *Mimachlamys asperima*, and *Crassadoma gigantea*) with distinct swimming strategies, as documented by measurements of muscle use during induced escape responses. Morphological characteristics of the shell and adductor muscle differed markedly between the species, but did not always follow their swimming strategies. Principal components analysis revealed that shell width, shell and muscle masses, and associated morphological attributes were closely linked with swimming endurance. The intensity of the escape response was best predicted by the aspect ratio and the obliqueness of the adductor muscle.

KEY WORDS: scallop, swimming strategies, shell morphology, adductor muscle

INTRODUCTION

Diverse morphological, physiological, and biochemical attributes underlie the wide range of locomotor styles developed by animals. Even within the generally sedentary bivalves, one finds a range of locomotor strategies accompanied by specific morphological attributes. Some bivalves, such as the softshell clam *Mya arenaria* (Linnaeus, 1758), use a hydraulic mechanism to burrow into the substrate (Trueman 1954, Checa & Cadée 1997). The elongated and tubular shape of the shell, with siphonal and pedal gapes, facilitates penetration into the substrate, whereas ejection of water through the pedal gape liquefies the surrounding substrate (Stanley 1975, Checa & Cadée 1997). Other bivalves, such as the cockle *Cardium tuberculatum* (Linnaeus, 1758), developed a large, powerful foot. In response to contact with a predator, the cockle pushes itself away with its foot, resulting in jumps of 15–20 cm (Gäde 1980). Only a few bivalves, almost exclusively monomyarian (i.e., only one adductor muscle), have acquired the ability to swim. Modifications in the structure of the shell, mantle, and adductor muscle are derived adaptations that allowed swimming in monomyarians (Yonge 1936). Swimming capacity is found only in a few species confined to the Pectinidae, Amussiidae, and Limidae. The file shell *Lima hians* (Gmelin, 1791) swims with its ventral edge leading using propulsive forces generated by coordinated rowing movements of the pallial tentacles and by water jets formed by rapid adductions of the valves (Gilmour 1967). Scallops swim via water jets produced by rapid contractions of the phasic adductor muscle and move with their ventral edge leading, seeming “to take a series of bites out of the water” (Dakin 1909 as cited by Yonge 1936).

The scallop locomotor system is mainly composed of two valves, an adductor muscle and a ligament. In response to a disturbance, such as contact with a predator, scallops can swim away by expelling jets of water through lateral openings.

Swimming is produced by rapid cycles of valve closures and openings (Drew 1906, Dakin 1909, Buddenbrock 1911). Contractions of the phasic adductor muscle rapidly close the valves (Lowy 1954; Millman 1967), whereas the hinge ligament (Alexander 1966, Marsh et al. 1976) acts as a spring to open the valves when the adductor muscle relaxes. The size and direction of the water jets are controlled by the muscular mantle during valve closure. The phasic adductor muscle is composed of cross-striated fibers, whereas the smaller tonic adductor muscle is composed of slow-contracting smooth fibers that allow prolonged valve closure (Lowy 1954, Chantler 2016). This mode of swimming is shared by scallops exhibiting a wide range of shell morphologies and life styles ranging from the highly active *Amusium balloti* (Bernardi, 1861) to the byssally attached *Mimachlamys asperima* (Lamarck, 1819).

Logically, the swimming capacity of bivalves should be reflected in their morphological characteristics, including adductor muscle size and position and shell characteristics. Several studies have compared these properties in swimming and nonswimming monomyarian bivalves, inferring swimming capacities from the literature, and have generated numerous predictions as to characteristics that should enhance swimming performance. Swimming monomyarians are thought to have smaller bodies, relative to the shell volume, than their nonswimming counterparts, presumably to increase the volume of water ejected during valve closure (Thayer 1972). The obliqueness (see illustration Fig. 1) of the phasic adductor muscle in a plane perpendicular to the hinge is greater in swimming monomyarians, presumably to increase the angular velocity of valve closure (Thayer 1972) and generate more powerful water jets (Yonge 1936, Thayer 1972, Soemodihardjo 1974). The ratio of phasic to tonic adductor muscle areas (Yonge 1936, Gould 1971, Soemodihardjo 1974) is greater in scallops thought to swim more, reflecting the central role of phasic contractions. A greater phasic moment (cross-sectional area of the phasic muscle times its distance from the hinge) would enhance force production when the scallop claps its valves (Gould 1971). Scallops with good swimming capacities generally have light

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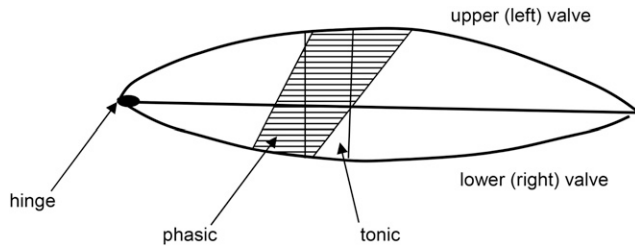


Figure 1. Side view of a schematic representation of a scallop. Valves are treated as transparent and insertions of both parts of the adductor muscle are shown. Phasic muscle, stripes; tonic muscle, white.

smooth shells, an upper valve that is slightly more convex than the lower one and a high aspect ratio (calculated either as valve length/valve height or valve length²/valve area) (Gould 1971, Soemodihardjo 1974). A greater aspect ratio increases the lift/drag ratio when movement is perpendicular to the anterior–posterior axis (Stanley 1970). Finally, the cemented scallop sinks rapidly (Gould 1971), but more active scallops have an approximately circular shape that slows sinking (Cheng & DeMont 1996). Although these interspecific differences in shell and muscle morphology have been interpreted in light of swimming capacities, these studies did not measure swimming capacities, but inferred them from literature anecdotes. Despite the oversimplifications in the previous studies, two conclusions are clear from the existing literature: (1) nonswimming bivalves and scallops differ considerably in their muscle and shell morphologies and (2) the smoothness and lightness of the shells of *Amusium* sp. favor its capacity for active and long-distance swimming (e.g., Gould 1971, Morton 1980). The literature does not, however, reveal whether differences in shell and muscle morphology are quantitatively linked with the wide range of scallop swimming strategies.

The objective of this study was to determine whether morphological characteristics of the shell and adductor muscle in a range of scallop species reflect their swimming strategies and muscle use. Six scallop species (*Amusium balloti*, *Placopecten magellanicus*, *Equichlamys bifrons*, *Pecten fumatus*, *Mimachlamys asperima*, and *Crassadoma gigantea*) with different shell shapes (Fig. 2) and distinct swimming strategies, as documented by our measurements of muscle use during induced escape responses (Tremblay et al. 2012; summarized in Table 1), were compared. The scallops *A. balloti* and *P. magellanicus* (Gmelin, 1791) are active swimmers and perform phasic contractions throughout the escape response (duration 355 sec; Tremblay et al. 2012), with *A. balloti* making phasic contractions at a quicker pace than *P. magellanicus*. The scallop *P. fumatus* (Reeve, 1852) performs intense bursts of phasic contractions at the beginning of its escape response, but fatigues quickly and then makes prolonged tonic contractions. The scallop *M. asperima* performs short series of phasic contractions at the beginning of the response with a slower phasic contraction rate than the foregoing species. Finally, the purple-hinge rock scallop *C. gigantea* (J. E. Gray, 1825) is free living in early life (<30-mm shell height) and then cements its lower, right valve to rocky surfaces (Yonge 1951, Parsons et al. 2016). Adult *C. gigantea* generally respond to predators by closing their valves, and only rarely make phasic contractions. Muscle use during an escape response was not recorded in

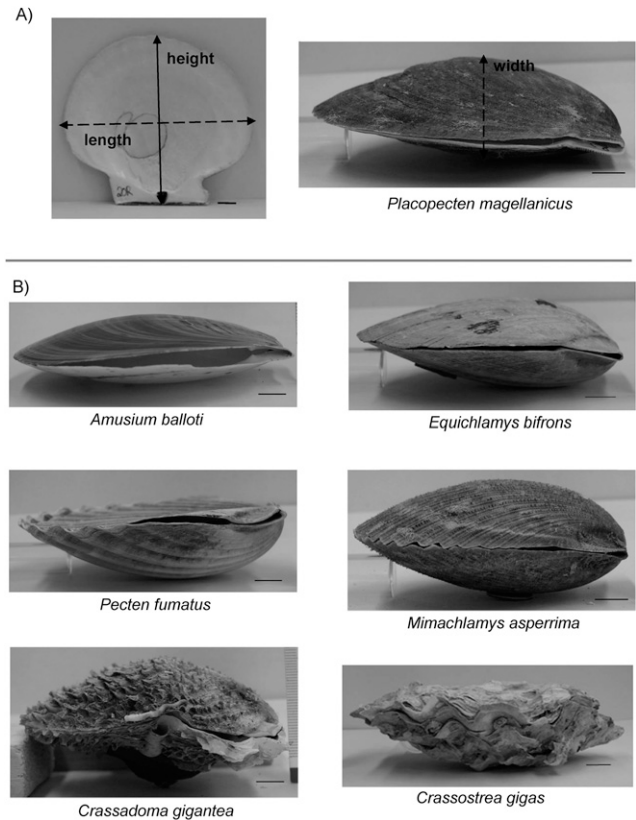


Figure 2. Shell dimensions and side view of experimental species. (A) Shell dimensions. Full line corresponds to shell height and dash line is shell length on the left image and width on the right image. (B) Side view of experimental species. Scale is 1 cm. (Photographs by Isabelle Tremblay.)

adult *E. bifrons* (Lamarck, 1819), only visual assessment of the swimming behavior was done (see Tremblay et al. 2015 for details). Olsen (1955) suggests that *E. bifrons* is less active than *M. asperima* and *P. fumatus*, although shell characteristics predict that the swimming behavior of *E. bifrons* would be similar to that of *P. magellanicus* (Minchin 2003). The oyster *Crassostrea gigas* (Thunberg, 1793) serve as a nonswimming outlier as it possesses one striated adductor muscle similar to the one in scallops.

For each species, the adductor muscle proportions, size, position, and obliqueness, as well as mass, were measured. The sinking rate and shell width, height, and length, as well as the aspect ratio and volume between the valves, were measured. Principal component analysis (PCA) of these morphological characteristics was used to examine links among the morphological characteristics and how they differentiated our experimental scallop species. Next, a PCA on our data for patterns of muscle use during induced escape responses (Tremblay et al. 2012) was carried out to evaluate links among the principal components (PC) describing morphology and those describing behavior in our experimental scallop species. The underlying premise was that the morphological characteristics of the experimental scallops' shell and adductor muscle should reflect their swimming strategies. Scallops that are active swimmers and mainly rely on phasic contractions during an escape response should have light shells, a high aspect ratio, and sink slowly, and these species should have a higher proportion of phasic muscle (relative to tonic muscle) than scallops using prolonged

TABLE 1.
Behavioral parameters during induced escape responses in experimental scallops.

Behavioral parameters	<i>Amusium balloti</i>	<i>Placopecten magellanicus</i>	<i>Pecten fumatus</i>	<i>Mimachlamys asperima</i>	<i>Crassadoma gigantea</i>
Total number of phasic	40.9 ± 1.37	27.5 ± 1.65	32.7 ± 2.86	18.0 ± 1.61	1.8 ± 0.84
Minimum interval between two phasics, sec	0.38 ± 0.036	1.12 ± 1.44	0.32 ± 0.042	0.64 ± 0.123	–
Number of phasic contractions during the first series	9.4 ± 1.3	5.9 ± 1.0	22.4 ± 3.4	3.0 ± 0.4	0.4 ± 0.01
Phasic contraction rate during first series, nb/sec	0.92 ± 0.07	0.72 ± 0.07	2.39 ± 0.15	1.25 ± 0.14	–
Time to fatigue, sec	229 ± 12.5	217 ± 15.3	76 ± 14.3	111 ± 13.8	45 ± 21.1
Total number of tonic	12.5 ± 0.76	20.9 ± 1.67	8.0 ± 1.12	9.9 ± 0.88	2.3 ± 0.86
Mean duration of tonic, sec	20.9 ± 1.71	16.2 ± 2.17	46.4 ± 10.95	33.2 ± 2.94	276.0 ± 31.4
% time in tonic contraction	67 ± 3.5	82 ± 3.2	65 ± 6.1	83 ± 1.6	93 ± 5.2

Data are means ± SE. Sample size: *A. balloti* 30, *P. magellanicus* 15, *P. fumatus* 15, *M. asperima* 16, and *C. gigantea* 19. The minimal interval between two phasics is for consecutive phasic contractions. Number of phasics during the first series: a series of phasic contractions is defined as consecutive phasic contractions separated by less than 3 sec. Time to fatigue: a scallop was considered fatigued when it made no phasic contractions during 1 min of stimulation with its predator.

tonic contractions. Moreover, the phasic muscle in scallops performing mostly phasic contractions should have both a greater moment and obliqueness, in a plane perpendicular to the hinge, than that in species using prolonged tonic contractions.

MATERIALS AND METHODS

Experimental Scallops

The individuals of *Amusium balloti*, *Placopecten magellanicus*, *Pecten fumatus*, *Mimachlamys asperima*, and *Crassadoma gigantea* characterized were those used in a complementary behavioral study (Tremblay et al. 2012). The scallop *Equichlamys bifrons* was collected with and kept in the same conditions as *P. fumatus* and *M. asperima* (Table 2). Oysters, *Crassostrea gigas*, were collected at low tide on the beach and were immediately transferred to the Center for Shellfish Research (Nanaimo, British Columbia, Canada). Capture and holding conditions are summarized in Table 2. All species were kept in temperature-controlled flow-through tanks for at least 2 wk prior to measurements. All scallops were adult with mature gonads and had similar condition indices (Tremblay et al. 2012). The shell and morphological characteristics of the experimental species are summarized in Table 3.

Sinking Test

The time taken by living scallops to sink in a 35-cm water column was measured. Scallops were disturbed slightly to make them shut their valves and then held in the tank, containing seawater, with the upper valve level with the water surface. Using a stopwatch, the time from when the scallop was released to when it touched the bottom was measured. Three trials were made with each individual and the average sinking time was calculated. Because experimental *Pecten fumatus* and *Crassadoma gigantea* had a screw attached to their lower valve, another sample of scallops was used for this test. In both species, the individuals were a similar size as those used for measurements of swimming behavior. As the shells of oysters were encrusted with shells, barnacles, and rocks that could not be removed without damaging the oyster, sinking time was not measured.

Given the slight size differences between the samples of the experimental species, the sinking time was adjusted to a shell height of 90 mm (a size present in our samples for each species). First, the regressions between shell height and sinking time were determined. These regressions were used to calculate T_1 , T_2 , and T_3 where T_1 was the sinking time expected for a 90-mm shell height scallop, T_2 the sinking time expected for a scallop with the size of the experimental scallop, and T_3 the measured

TABLE 2.
Capture method and holding conditions of the experimental scallops.

Species	Capture method	Capture location	Year	Temperature (°C)	Salinity (psu)
<i>Amusium balloti</i>	Trawling	Northern Hervey Bay, Australia	2007	18.5	35
<i>Placopecten magellanicus</i>	Aquaculture pearl nets	Cap-Aux-Meules, Îles-de-la-Madeleine, Canada	2008	14	30
<i>Equichlamys bifrons</i>	Scuba	Satellite Island, Canal d'Entrecasteux, Australia	2007	12.5	34
<i>Pecten fumatus</i>	Scuba	Satellite Island, Canal d'Entrecasteux, Australia	2007	12.5	34
<i>Mimachlamys asperima</i>	Scuba	Satellite Island, Canal d'Entrecasteux, Australia	2007	12.5	34
<i>Crassadoma gigantea</i>	Scuba	Espinosa Inlet, Vancouver Island, Canada	2010	12.5	28
<i>Crassostrea gigas</i>	Hand	Deception Bay, Vancouver Island, Canada	2010	12.5	28

TABLE 3.
Shell and morphological characteristics of experimental scallops.

	<i>Amusium balloti</i>	<i>Placopecten magellanicus</i>	<i>Equichlamys bifrons</i>	<i>Pecten fumatus</i>	<i>Mimachlamys asperima</i>	<i>Crassadoma gigantea</i>	<i>Crassostrea gigas</i>
Shell							
Height, mm	96.3 ± 1.1 ^a	90.4 ± 0.9 ^{b,c}	96.2 ± 2.5 ^a	94.4 ± 1.7 ^{a,b}	84.2 ± 2.0 ^c	97.0 ± 4.5 ^{a,b}	105.9 ± 3.3 ^d
Length, mm	95.5 ± 1.4 ^a	99.6 ± 1.0 ^b	100.8 ± 2.9 ^{b,c}	107.0 ± 1.6 ^c	82.4 ± 2.1 ^d	92.9 ± 3.5 ^a	70.2 ± 2.2 ^d
Width, mm	19.8 ± 0.4 ^a	27.7 ± 0.4 ^b	29.6 ± 0.6 ^{b,d}	22.6 ± 0.4 ^c	31.3 ± 1.1 ^{b,d}	34.5 ± 2.0 ^d	36.6 ± 1.6 ^d
<i>N</i>	27–30	15	20	15	16	16–19	18
Dry mass at 90 mm, g							
Soft tissue	2.00 ± 0.08 ^a	6.71 ± 0.26 ^b	7.16 ± 0.14 ^c	4.96 ± 0.30 ^{d,e}	5.45 ± 0.17 ^e	8.87 ± 0.55 ^c	4.61 ± 0.23 ^d
Phasic muscle	0.86 ± 0.05 ^a	3.08 ± 0.13 ^b	3.08 ± 0.10 ^b	2.05 ± 0.16 ^c	1.92 ± 0.09 ^c	3.60 ± 0.24 ^b	0.31 ± 0.02 ^d
Tonic muscle	0.05 ± 0.004 ^a	0.25 ± 0.01 ^{b,d}	0.51 ± 0.01 ^c	0.23 ± 0.01 ^d	0.17 ± 0.01 ^e	0.29 ± 0.02 ^b	0.19 ± 0.01 ^e
Shell	26.5 ± 0.4 ^a	48.8 ± 1.1 ^b	54.9 ± 0.8 ^c	45.9 ± 1.4 ^b	32.7 ± 0.7 ^d	136.4 ± 9.9 ^e	94.8 ± 4.5 ^f
<i>N</i>	18–27	15	19–20	9–15	16	18–19	18
Ratio*							
Adductor muscle/total animal	0.37 ± 0.01 ^{a,c}	0.39 ± 0.01 ^b	0.38 ± 0.01 ^{b,c}	0.36 ± 0.01 ^a	0.30 ± 0.01 ^d	0.36 ± 0.01 ^a	0.09 ± 0.005 ^e
Soft tissue/shell volume, g/ml	0.48 ± 0.01 ^a	0.52 ± 0.01 ^b	0.63 ± 0.01 ^c	0.42 ± 0.02 ^d	0.41 ± 0.01 ^d	0.61 ± 0.02 ^c	0.41 ± 0.01 ^d
<i>N</i>	18	13–15	18–20	15	16	19	18
Aspect ratio							
Shell length ² /valve area	1.29 ± 0.01 ^a	1.21 ± 0.01 ^b	1.26 ± 0.02 ^{a,b}	1.52 ± 0.02 ^c	1.10 ± 0.01 ^d	1.24 ± 0.05 ^b	1.00 ± 0.05 ^d
<i>N</i>	27	15	20	15	16	19	18
Muscle area/valve area							
Phasic							
Left valve	0.10 ± 0.002 ^{a,d} †	0.08 ± 0.001 ^b †	0.10 ± 0.004 ^{a,c}	0.11 ± 0.01 ^c †	0.09 ± 0.003 ^d	0.10 ± 0.01 ^c	0.03 ± 0.002 ^e †
Right valve	0.08 ± 0.002 ^a †	0.06 ± 0.002 ^b †	0.10 ± 0.002 ^c	0.07 ± 0.002 ^b †	0.09 ± 0.01 ^a	0.09 ± 0.005 ^c	0.02 ± 0.002 ^d †
Tonic							
Left valve	0.009 ± 0.001 ^a †	0.012 ± 0.001 ^a †	0.019 ± 0.001 ^b †	0.018 ± 0.001 ^b †	0.018 ± 0.002 ^b	0.021 ± 0.006 ^b	0.019 ± 0.002 ^b
Right valve	0.006 ± 0.0002 ^a †	0.015 ± 0.001 ^{b,d} †	0.028 ± 0.001 ^c	0.014 ± 0.001 ^d †	0.020 ± 0.002 ^e	0.023 ± 0.005 ^{b,e}	0.017 ± 0.002 ^{b,e}
<i>N</i>	30	15	9–10	15	13–14	15–17	13–14
Moment phasic muscle							
Left valve	31.5 ± 2.0 ^a †	30.8 ± 1.0 ^{a,b} †	38.0 ± 4.2 ^b †	35.3 ± 2.5 ^b †	22.4 ± 2.3 ^c	40.4 ± 6.2 ^{a,b} †	6.5 ± 0.6 ^d
Right valve	22.5 ± 1.5 ^{a,d} †	17.1 ± 0.9 ^b †	28.8 ± 2.2 ^{c,d} †	17.6 ± 1.2 ^{a,b} †	19.9 ± 2.6 ^{a,b,d}	34.4 ± 5.5 ^{c,d} †	6.5 ± 0.8 ^e
<i>N</i>	30	15	10–20	15	14	17	13–15

Data are means ± SE. In a given row, different letters indicate significant differences (Kruskal–Wallis and multiple comparisons, $P < 0.05$). Volume: refers to the volume between the two empty valves. Aspect ratio: was calculated for the left valve. Soft tissue dry mass was adjusted for 90-mm shell height. Soft tissue refers to all soft tissues including the adductor muscle.

* Masses are the wet mass. Adductor muscle includes the phasic and tonic muscles. Moment phasic muscle: phasic muscle area × distance between phasic muscle center and hinge (cm³).

† Indicates a difference between the left and right valves in a given species (paired *t*-test, $P < 0.05$).

sinking time for the experimental scallop. Finally, the adjusted sinking time, at 90-mm shell height, was calculated using the following formula:

$$\text{Adjusted sinking time} = (T_1/T_2) \times T_3$$

Morphological Measurements

Shell height, length and width of each individual were measured using a digital caliper (± 0.01 cm). The shell height corresponded to the maximum distance between the dorsal (hinge) and ventral margins, whereas length was the maximum distance between the anterior and posterior margins and was perpendicular to shell height (Fig. 2A). Shell width was measured at the point of maximum convexity with the two valves placed in their natural closed position (Fig. 2A).

Because of the variable chord of scallop shells, it was decided to measure the aspect ratio as the square of the shell length divided by valve area as done by Dadswell and Weihs (1990). Digital photos were taken of the valves with an adjacent ruler as a reference (Fig. 3A). Valve area was determined from photographs of the shell using image analysis software (ImageJ, ver. 1.42, National Institutes of Health).

Following the behavioral tests, all tissues were removed from the valves. Wet tissue mass was obtained after carefully removing soft tissues from the shell and placing them on absorbent paper to remove excess water. The phasic and tonic adductor muscles and remaining soft tissues were weighed

separately (± 0.01 g). All soft tissues were dried for 48 h at 60°C to assess dry mass and percentage water content. Once the soft tissues had been removed, shells were wiped dry and weighed. As the lower shell of *Pecten fumatus* and *Crassadoma gigantea* had a screw attached to it, other individuals were used to establish the relationship between shell dimensions and shell mass and then the shell mass for our individual scallops was calculated (see Table A1).

The volume between the valves was estimated by weighing the upper and lower valves filled with sifted sand (500 μm) leveled with the shell margin. Using the weight of a given volume of sand, the volume in each valve was estimated. The sum gave the total volume.

The shell and soft tissue dry masses were adjusted to a shell height of 90 mm using the formula described for sinking time.

Measurement of Attachment Position of Adductor Muscles

Following tissue removal, the shells were wiped dry before retracing the phasic and tonic muscle impressions with a permanent marker inside both valves (Fig. 3A). Digital photos of both valves with an adjacent ruler as a reference were taken (Fig. 3A). Photographs of the shells with retraced muscle impressions were used to determine the area of the valves and adductor muscles using image analysis software (ImageJ). Muscle position on both valves was defined in terms of ratios as in Gould (1971) and Soemodihardjo (1974) (Fig. 3B). The dorso-ventral position of the phasic muscle corresponded to the ratio of line EF to line GH. Line EF was the shortest distance between the phasic muscle and the ventral most edge of the valve, whereas line GH was the shortest distance between the phasic muscle and the hinge (Fig. 3B). Similarly, the ratio IJ/KL represented the dorsoventral position of the tonic muscle. The antero-posterior position of the phasic and tonic muscles was defined by the ratios OP/MN and ST/QR, respectively (Fig. 3B). The obliqueness of the adductor muscle, relative to the valve, was defined as the ratio between the dorsoventral position of the muscle on the left valve over that on the right one. Accordingly, the obliqueness of the phasic adductor muscle was $EF \times G'H'/E'F' \times GH$, whereas that of the tonic muscle was $IJ \times K'L'/I'J' \times KL$ (Fig. 3B). The more the ratio departs from one, the greater the obliqueness.

The moment of the phasic muscle was estimated as the product of the area of the muscle impression on the valve and the distance between its center and the hinge (Gould 1971).

As some of the species in this study have valves with a strong curvature, it had to be demonstrated that measurements of muscle area and position on photographs of the valves were not biased. The muscle impression was retraced on a clear plastic paper that closely fitted shell curvature. Muscle area was then measured from photographs of the flattened plastic paper using image analysis software (ImageJ). For muscle position, the measurements were made directly on the shell using a thin plastic ruler that could closely fit the shell. No significant differences were observed between measurements based on photographs of the valves and measurements that took shell curvature into account.

Statistical Analysis

Normality was tested using a Shapiro-Wilks test and the homogeneity of variances was analyzed visually by plotting

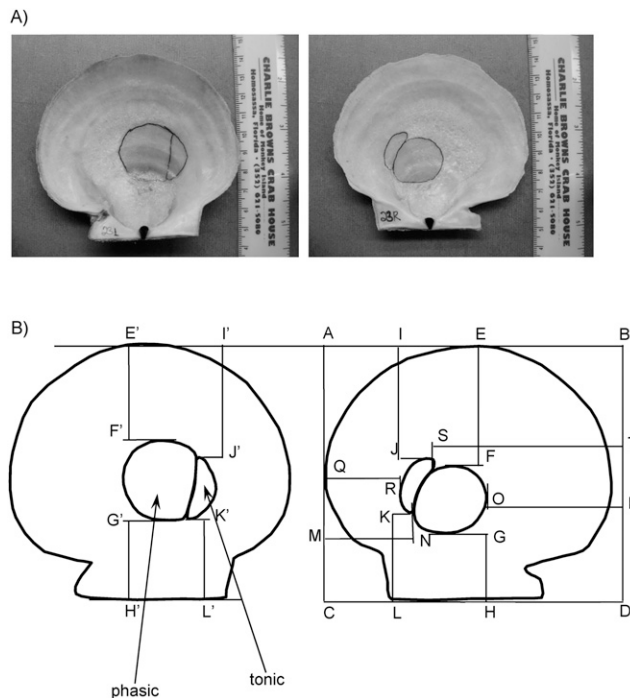


Figure 3. Retraced impressions of adductor muscle on the scallop valves and diagram used for muscle positioning measurements. (A) Phasic and tonic muscle impressions retraced on the inside of the scallop valves. (Photographs by Isabelle Tremblay.) (B) Diagram representing the various measurements taken to determine the position of the phasic and tonic adductor muscle. Valve on the left represents the left or upper valve, whereas the one on the right represents the right or lower valve. (B: Inspired of Soemodihardjo 1974)

residuals relative to predicted values. Because of the non normality of residuals and non homogeneity of variances, non parametric tests were used. Comparisons between the different scallop species and the oyster were made using Kruskal–Wallis tests. The non-parametric Wilcoxon signed-rank test was used when data were expressed in terms of ratios to assess if these ratios differed from one. Intra-specific differences in muscle area and position on the left and right valves were assessed using paired *t*-tests. Spearman's correlations were used to assess whether shell mass and aspect ratio were correlated with sinking time.

The large number of morphological parameters measured increases the risk of erroneous identification of significant relationships between morphological and behavioral characteristics in our experimental scallops. Therefore, a PCA was performed to create new combined variates (PC, i.e., random variables; Legendre & Legendre 1998) of the morphological characteristics in our experimental scallops. A second PCA was performed with the behavioral data measured on our experimental scallops (Tremblay et al. 2012). As only visual evaluations of behavior for *Equichlamys bifrons* were available, the PCA for morphology and behavior used data for *Amusium balloti*, *Placopecten magellanicus*, *Pecten fumatus*, *Mimachlamys asperrima*, and *Crassadoma gigantea*. After running the PCA, an orthogonal rotation was applied to have uncorrelated PC that would be easier to interpret. Only the PC that explained more than 10% of the overall variance were interpreted. Each variable was linked with the PC on which it had the greatest loading. Each PC was named and interpreted according to the variables assigned to it.

Principal component analysis omits observations that have missing values for any variable. Because of the presence of scattered missing values in the morphological data set, Monte Carlo multiple imputations (20 imputations) were performed to replace the missing values. The morphological PCA was performed using the 20 data sets that resulted from the multiple imputations. As fewer values were missing in the behavioral data set, such imputations were not needed.

To examine interspecific differences for the PC for the morphological and behavioral data of our experimental scallops, a score was calculated for each individual for each PC. Then, an analysis of variance (ANOVA) was performed to see if these scores differed between the scallop species.

The links between morphological and behavioral characteristics in the experimental scallops were examined by performing regressions of the individual scores calculated for each morphological PC against the individual scores calculated for each behavioral PC.

All analyses were done using SAS 9.2 (SAS Institute). Significance was accepted at $P < 0.05$.

RESULTS

In the tables and figures, the species are placed in approximate order of their swimming capacity, starting with *Amusium balloti* and ending with *Crassadoma gigantea* and the oyster *Crassostrea gigas*. Swimming capacity of all species except *Equichlamys bifrons* and *C. gigas* was based on Tremblay et al. (2012). Initially, interspecific differences in the morphological parameters were evaluated. Then PCA were used to examine how these parameters were related and how the resulting PC differentiated the experimental scallop species. Next, the behavior during induced escape responses (Tremblay et al. 2012) was examined to see whether it was related to morphology, first using PCA to create behavioral PC. After examining how the behavioral PC differed between the experimental species, regressions were used to evaluate how the PC for morphology were linked to those for escape response behavior in the scallop species.

Shell Characteristics

The individuals studied had similar shell heights, although the sample of *Mimachlamys asperrima* was slightly smaller and that of the oyster *Crassostrea gigas* was slightly bigger than those of the other species (Table 3). After adjusting shell and tissue masses to a common shell height (90 mm), *Crassadoma gigantea* had the heaviest shell followed by *Pecten fumatus* and *Placopecten magellanicus* (Table 3). The shells of *M. asperrima* and *Amusium balloti* were considerably lighter than those of the other species (Table 3). The expectation that scallops that are active swimmers have lighter shells than less active and non-swimming species was only partially borne out.

The aspect ratio was highest in *Pecten fumatus*, whereas it was lowest in *Mimachlamys asperrima* and *Crassostrea gigas* (Table 3). The scallop *Amusium balloti*, *Placopecten magellanicus*, *Equichlamys bifrons*, and *Crassadoma gigantea* had intermediate aspect ratios (Table 3). This pattern only partly conformed to the prediction that a high aspect ratio characterizes good swimmers.

Sinking Test

Absolute and adjusted (90-mm shell height) sinking times are shown in Table 4 and both values follow the same trends. The scallop *Amusium balloti* took the most time to sink (Table

TABLE 4.
Sinking time in experimental species.

	<i>Amusium balloti</i>	<i>Placopecten magellanicus</i>	<i>Equichlamys bifrons</i>	<i>Pecten fumatus</i>	<i>Mimachlamys asperrima</i>	<i>Crassadoma gigantea</i>	<i>Crassostrea gigas</i>
Time (sec)	2.58 ± 0.04 ^a	2.29 ± 0.03 ^b	2.14 ± 0.06 ^c	2.06 ± 0.03 ^c	2.42 ± 0.04 ^b	1.27 ± 0.04 ^d	–
Time (sec) for 90 mm*	2.68 ± 0.03 ^a	2.30 ± 0.03 ^b	2.07 ± 0.05 ^c	2.08 ± 0.03 ^c	2.36 ± 0.04 ^b	1.29 ± 0.04 ^d	–
N	22	15	20	15	16	19	–

Mean ± SE. Kruskal–Wallis and multiple comparisons, $P < 0.05$.

* Sinking time adjusted for 90-mm shell height. See material and methods section for details about the adjustment.

4). The scallops *Mimachlamys asperima* and *Placopecten magellanicus* took slightly but significantly less time, whereas *Equichlamys bifrons* and *Pecten fumatus* sank more quickly (Table 4). The scallop *Crassadoma gigantea* plummeted to the bottom in only 1.29 ± 0.04 sec (Table 4). Sinking time (adjusted to 90 mm) was correlated with shell mass (correlation coefficient = -0.943 , $P = 0.005$), but not with the aspect ratio (correlation coefficient = -0.086 , $P = 0.872$). The expectation that sinking time reflects swimming capacity was partly supported.

Soft Tissue and Adductor Muscle Characteristics

The ratio of the soft tissue wet mass to shell volume was highest in *Equichlamys bifrons* and *Crassadoma gigantea* followed by *Placopecten magellanicus* with a slightly but significantly lower ratio (Table 3). The lowest ratios were found in *Amusium balloti*, *Pecten fumatus*, *Mimachlamys asperima*, and *Crassostrea gigas* with less than half of the shell volume filled with soft tissues (Table 3). The highly active *Amusium*, the byssally attached *M. asperima*, and the oyster shared a reduced body volume relative to the interior shell volume, contradicting the prediction that this characteristic favors active swimming.

The phasic adductor muscle (corrected to 90-mm shell height) was heaviest in *Crassadoma gigantea*, *Placopecten Magellanicus*, and *Equichlamys bifrons* (Table 3). The scallop *Pecten fumatus* and *Mimachlamys asperima* had intermediate phasic muscle masses, whereas *Amusium balloti* had the smallest phasic muscle among the scallops (Table 3). The oyster had a much smaller phasic muscle than all scallops (Table 3). The heaviest tonic muscle was found in *E. bifrons*, whereas *A. balloti* had by far the smallest and the other species were intermediate (Table 3). The ratio of adductor muscle to soft tissue wet mass was lowest in the oyster, whereas scallops all had considerably higher ratios (Table 3). Muscle mass was not simply related to swimming capacity.

The portion of the valves covered by the phasic muscle scar differed among species (Table 3). Interspecific differences were greater for the ratio on the right valve. Here, *Equichlamys bifrons*, *Mimachlamys asperima*, and *Crassadoma gigantea* had the highest value, followed by *Amusium balloti* and then *Placopecten magellanicus* and *Pecten fumatus*. Phasic muscle size, as assessed by the muscle scar, was not a predictor of swimming capacity.

The proportion of the valves covered by tonic muscle differed among scallops (Table 3). On the left valve, four scallops (*Equichlamys bifrons*, *Pecten fumatus*, *Mimachlamys asperima*, and *Crassadoma gigantea*) shared high values with the oyster, whereas *Amusium balloti* and *Placopecten magellanicus* had considerably lower values. The proportion of the right valve covered by tonic muscle also differed among species, with *A. balloti* having the lowest value, *E. bifrons* the highest value, and the other species having intermediate values. Generally, tonic muscle area was lower in most active swimmers.

The moment exerted by the phasic adductor muscle varied among species (Table 3). When calculated for the left valve, *Amusium balloti*, *Placopecten magellanicus*, *Equichlamys bifrons*, *Pecten fumatus*, and *Crassadoma gigantea* had the highest moments, whereas *Mimachlamys asperima* had an intermediate moment and the oyster had the lowest. When the phasic moment was calculated for the right valve, interspecific differences among scallops changed. The scallop *E. bifrons* and

C. gigantea had the highest moments, whereas *A. balloti*, *P. magellanicus*, *P. fumatus*, and *M. asperima* had intermediate values. The oyster had the lowest moment. Again, simple predictions based on swimming capacities do not explain these patterns.

Proportions of Tonic and Phasic Adductor Muscle

The impression of the phasic and tonic adductor muscles on the valves varied among the species (Fig. 4). When the percentage of tonic adductor muscle in the overall adductor muscle was calculated from the impression on the right valve, *Amusium balloti* was shown to have very little tonic muscle compared with the other species (Fig. 5). The scallop *Placopecten magellanicus*, *Pecten fumatus*, *Mimachlamys asperima*, and *Crassadoma gigantea* had intermediate proportions of tonic muscle, whereas the oyster had the highest proportion of tonic muscle (Fig. 5). The proportion of phasic and tonic adductor muscles was also calculated from the masses of each part of the muscle and interspecific differences in phasic and tonic muscle proportions were similar to those observed from muscle impressions on the shell (data not shown). Although muscle proportions separated *Amusium balloti* from the other scallops, these proportions did not follow differences in swimming strategy among the other scallop species.

Muscle Obliqueness: Adductor Muscle Impression on Left versus Right Valves

Having a larger area of muscle attachment on one valve than the other is one means by which muscle obliqueness can be

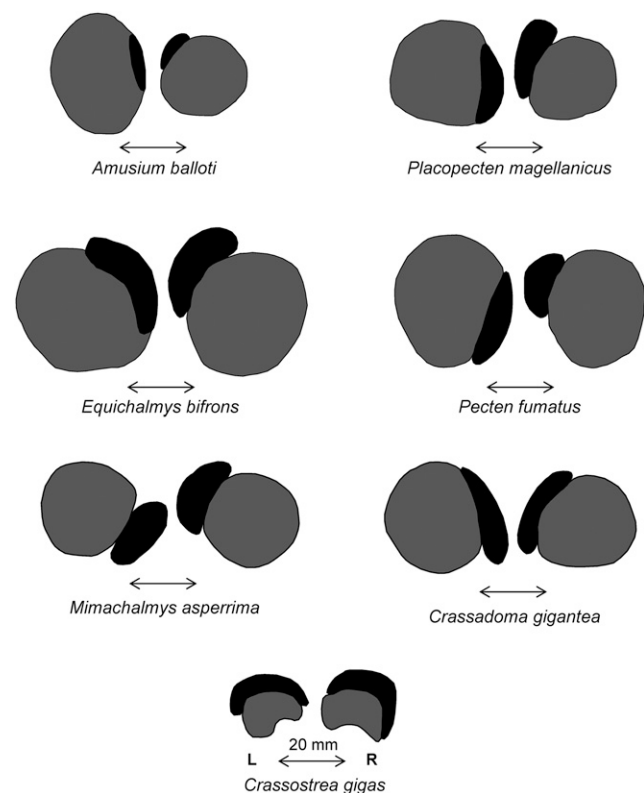


Figure 4. Typical phasic (gray) and tonic (black) adductor muscle impressions on left (L) and right (R) valves in experimental species. Arrowed line corresponds to scale: 20 mm for all species.

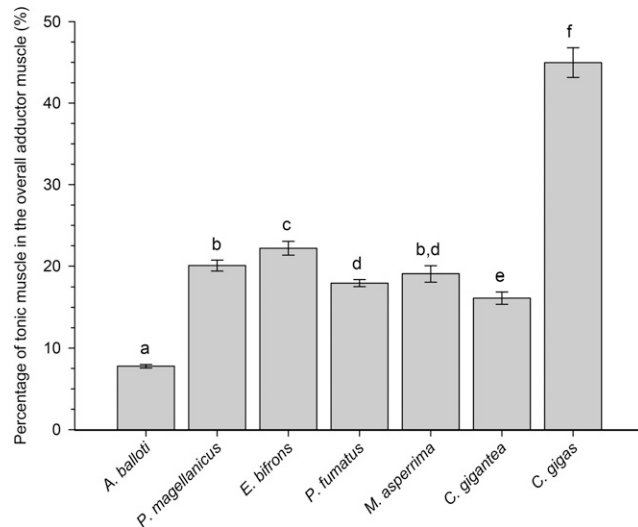


Figure 5. Percentage of tonic muscle in the overall adductor muscle calculated from the impression on the right valve. Mean $\pm$ SE. Kruskal–Wallis and multiple comparisons ($P < 0.05$). Sample size: *Amusium balloti*, $N = 30$; *Placopecten magellanicus*, $N = 15$; *Equichlamys bifrons*, $N = 20$; *Pecten fumatus*, $N = 15$; *Mimachlamys asperima*, $N = 14$; *Crassadoma gigantea*, $N = 15$; and *Crassostrea gigas*, $N = 13$.

increased. In agreement with a role of muscle obliqueness in increasing the angular velocity of valve closure, the size of the adductor muscle attachment on the two valves differed more in actively swimming scallops than in less active and sedentary species (Fig. 6). The area of the phasic adductor muscle was larger on the left than right valve in *Amusium balloti*, *Placopecten magellanicus*, *Equichlamys bifrons*, and *Pecten fumatus*, whereas no significant differences were observed in *Mimachlamys asperima*, *Crassadoma gigantea*, and *Crassostrea gigas*. The ratio was approximately 1.50 in *P. magellanicus* and *P. fumatus*, significantly higher than in *A. balloti* and *E. bifrons*. This mechanism of increasing phasic muscle obliqueness followed overall swimming strategy.

The impressions of the tonic adductor muscle did not differ between the two valves in any species except *Equichlamys bifrons* in which the area of the tonic muscle was larger on the right than the left valve (Fig. 6).

Muscle Obliqueness: Muscle Position on Right and Left Valves

The relative positions of the adductor muscle attachment on the right and left valves also influence obliqueness. All the species, including the oyster, exhibited this type of obliqueness for the phasic adductor (Fig. 7). The insertion on the right valve was always closer to the hinge than on the left valve. Phasic muscle obliqueness was much more pronounced in *Pecten fumatus* than in the other species. In most species, the tonic muscle was oblique in the opposite direction than the phasic muscle, with the insertion on the left valve being closer to the hinge. In *P. fumatus* and the oyster, tonic and phasic adductor muscles showed obliqueness in the same direction.

Obliqueness of the muscles in *Pecten fumatus* was slightly overestimated due to the curvature of the lower valve. When this was taken into account, obliqueness of the phasic muscle remained much higher than in other scallops, whereas obliqueness of the tonic muscle was similar to that of the other scallops.

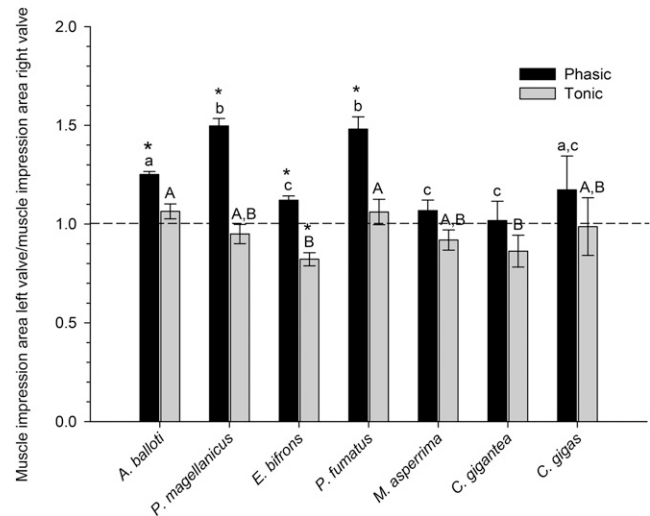


Figure 6. Ratio of the area of the muscle impression on left valve relative to area of the muscle impression on right valve. Mean $\pm$ SE. Different letters indicate significant differences (Kruskal–Wallis and multiple comparisons, $P < 0.05$). Lowercase letters refers to phasic muscle, whereas capital letters refer to tonic muscle. The dashed line indicates when the areas on the left and right valves are the same size. Ratios significantly different than unity are identified by a star (Wilcoxon signed-rank test, $P < 0.05$). Sample size *Amusium balloti*, $N = 30$; *Placopecten magellanicus*, $N = 15$; *Equichlamys bifrons*, $N = 19$; *Pecten fumatus*, $N = 15$; *Mimachlamys asperima*, $N = 14$; *Crassadoma gigantea*, $N = 16$; and *Crassostrea gigas*, $N = 12$.

Principal Component Analysis of Scallop Morphology and Behavior

Principal component analysis included only the scallop species for which swimming behavior during induced escape responses was available (Tremblay et al. 2012). The first three PC of the PCA for morphology accounted for 30%, 19%, and 12% of the variance, respectively (Fig. 8). The first PC was influenced by sinking time, shell and tissue mass, and various tissue proportions and was named “mass and proportions.” Sinking time and proportion of phasic muscle had negative loadings, whereas shell and muscle masses had positive loadings on this PC. The shared positive loadings of tonic muscle area and shell and muscle masses reflected the fact that poor swimmers have heavy shells and larger tonic muscles. The second PC was mainly influenced by the phasic muscle moment, relative size of the phasic muscle on the left valve, and valve dimensions and was named “phasic moment and size.” The last component, named “obliqueness and aspect ratio,” was influenced by parameters related to the obliqueness of the adductor muscle and the aspect ratio. The scores of the morphological PC differentiated the scallop species (Fig. 9). For the first PC (mass and proportions), *Crassadoma gigantea* had the highest score and *Amusium balloti* the lowest. The scallop *Placopecten magellanicus*, *Pecten fumatus*, and *Mimachlamys asperima* had intermediate scores. For the second PC (phasic moment and size), *M. asperima* had the lowest score, whereas the other species were similar and slightly higher, partly as the *M. asperima* sampled were slightly smaller than the other species. For the third PC (obliqueness and aspect ratio), *P. fumatus* had the highest score, whereas *M. asperima* and *C. gigantea* had the lowest. The scallop *A. balloti* and *P. magellanicus* had intermediate scores, with *P. magellanicus* being slightly higher than *A. balloti*.

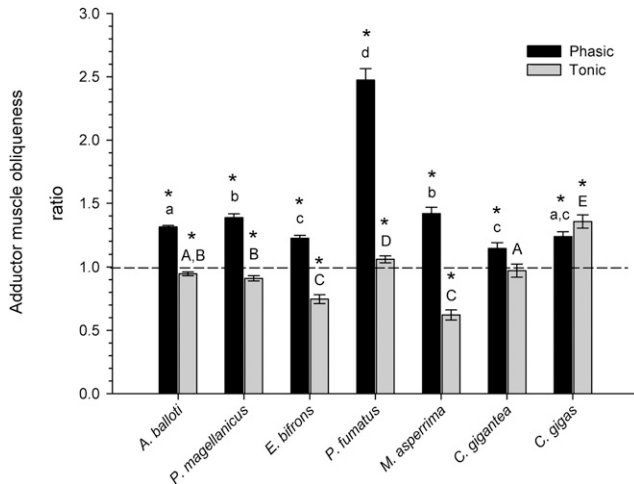


Figure 7. Adductor muscle obliqueness. Obliqueness is the ratio of the dorsoventral position of the adductor muscle on the left valve to that on the right valve. Mean $\pm$ SE. Different letters indicate significant differences (Kruskal–Wallis and multiple comparisons, $P < 0.05$). Lowercase letters refers to phasic muscle, whereas capital letters refer to tonic muscle. If the value is above the dashed line, the insertion on the right valve is closer to the hinge. Ratios significantly different than unity are identified by a star (Wilcoxon signed-rank test, $P < 0.05$). Sample size *Amusium balloti*, $N = 30$; *Placopecten magellanicus*, $N = 15$; *Equichlamys bifrons*, $N = 9$; *Pecten fumatus*, $N = 15$; *Mimachlamys asperima*, $N = 14$; *Crassadoma gigantea*, $N = 14$; and *Crassostrea gigas*, $N = 11$.

The PCA on behavioral parameters, measured during escape response tests on these scallops (see Tremblay et al. 2012 for details), identified two PC that together explained 70% of the observed variability (Fig. 10). The first PC explained 47% of the variability. It included parameters related to endurance during an escape response (total number of phasics, time to fatigue, number of phasics before fatigue, mean duration of tonic contractions, number of tonic contractions > 5 sec). As when tonic contractions are prolonged, they are fewer in number, a high number of tonic contractions was negatively related to the time spent in tonic contractions. For this PC, *Amusium*

balloti and *Placopecten magellanicus* had the highest scores, *Pecten fumatus* and *Mimachlamys asperima* had intermediate scores and *Crassadoma gigantea* the lowest score (Fig. 11). The second PC explained 23% of the variability and it included parameters related to the intensity of the escape response (number of phasics in the first series, number of phasic contractions before the first tonic, number of phasics over number of tonics, time at first tonic) (Fig. 10). Here, *P. fumatus* had the highest score, *A. balloti* had an intermediate score, whereas *P. magellanicus*, *M. asperima*, and *C. gigantea* had the lowest scores (Fig. 11).

Finally, links between morphological and behavioral parameters were examined by calculating regressions between the three morphological PC and the two behavioral PC (Table 5) in the experimental scallop species. The PC “endurance” during an induced escape response was highly related to the PC “proportions and mass.” The PC “intensity” of escape responses was strongly related to the obliqueness of the adductor muscle and the aspect ratio, as well as the proportions and mass of tissues in the scallop. Morphological parameters linked to force and size (PC2) were not significantly linked with either of the PC for behavior.

DISCUSSION

Morphological characteristics of the shell and adductor muscle differed markedly among the experimental scallops as well as with the oyster, but when examined individually, the morphological differences among scallop species did not always follow their swimming strategies. The PCA revealed links among morphological parameters that nicely differentiated the experimental scallop species and revealed the morphological parameters that were linked with specific escape response behaviors. The relationship between scallop behavior and morphology is not simple, as it is the result of compromises imposed by habitats, lifestyle, and predators. To understand how the combinations of morphological parameters relate to the swimming behavior of each experimental species, it is important to interpret these results in the overall context of the habitats in which these scallops live.

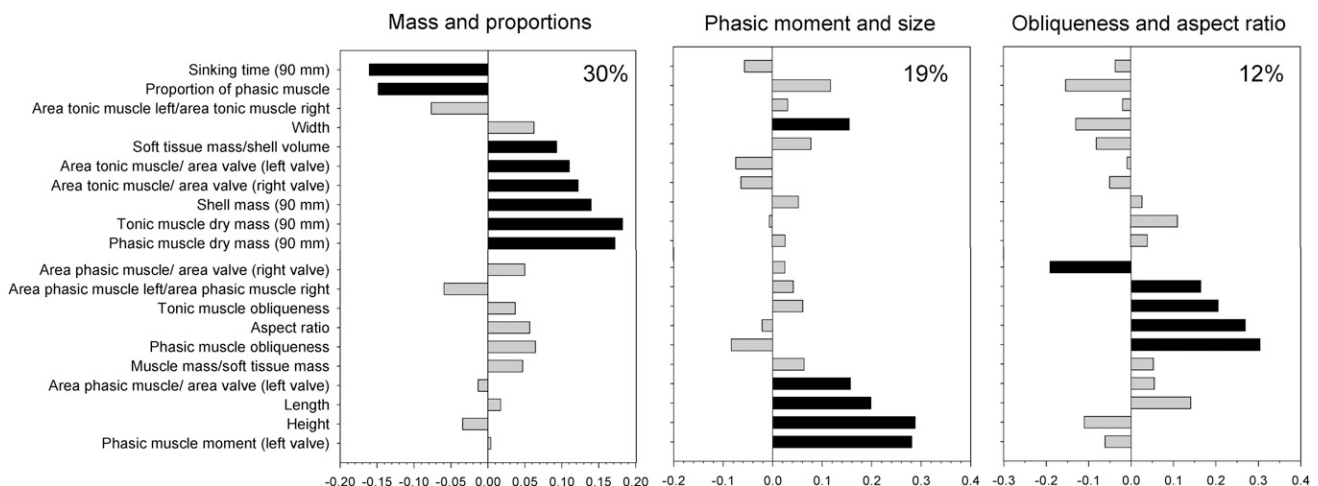


Figure 8. The normalized scores for the morphological variables associated with the first three PC. Black bars identify variables assigned to each component. The percentages indicate the proportion of variance explained by the principal component.

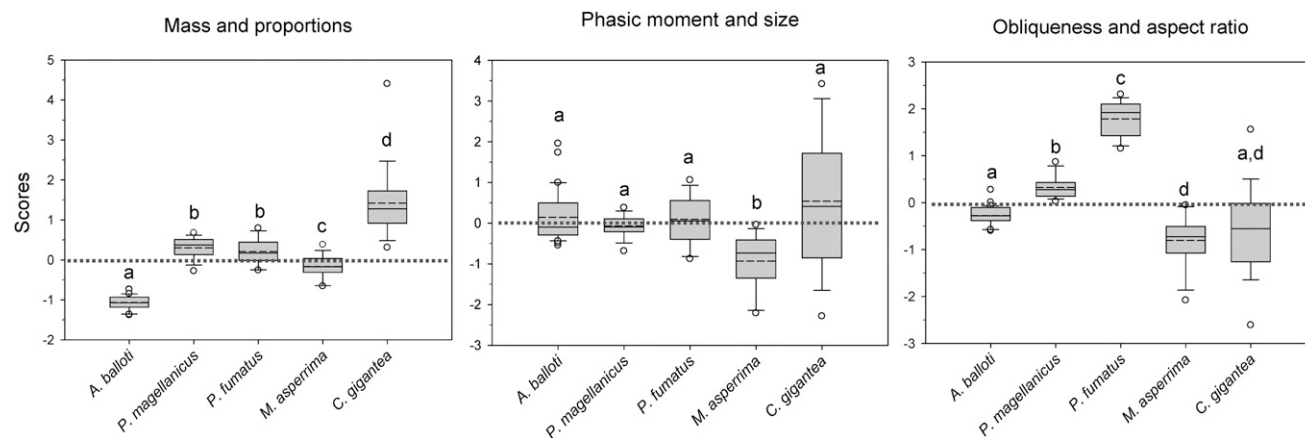


Figure 9. Scores for each scallop species for each principal component from the PCA. The boundary of the box closest to zero indicates the 25th percentile and the boundary of the box farthest from zero indicates the 75th percentile. The full line within the box marks the median, whereas the dashed line marks the mean. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles. Open circles are outlying data. ANOVA and multiple comparisons, $P < 0.05$. Sample size: *Amusium balloti*, $N = 30$; *Placopecten magellanicus*, $N = 15$; *Pecten fumatus*, $N = 15$; *Mimachlamys asperima*, $N = 16$; and *Crassadoma gigantea*, $N = 19$.

Links between Morphology and Behavior

The PCA for morphological characteristics differentiated the scallop species by groups of parameters. The first PC, “proportions and mass,” separated the most active swimmer (*Amusium balloti*) and the non swimming scallops (*Crassadoma gigantea*) from the other species. The scallop *A. balloti* had the shortest sinking time, lowest width, and lightest shell and muscle masses, whereas *C. gigantea* had the fastest sinking time, greatest width, and heaviest shell and muscle masses. Major attributes of muscle morphology influencing this PC were the relative valve area occupied by tonic muscle and the proportion of phasic muscle. The adductor muscle contains virtually no tonic muscle in *A. balloti* but contains substantially more in heavy, sedentary species, particularly *C. gigantea*. The second PC, “phasic moment and size,” distinguished *Mimachlamys asperima*, the byssally attached species, from the others. Although the third PC, “obliqueness and aspect ratio,” only explained 12% of the variability, it separated the scallops into three groups: the swimmers, *A. balloti* and *Placopecten magellanicus*, the byssally attached *M. asperima* and the cemented *C. gigantea*, and finally *Pecten fumatus* alone with a much higher score than all the others. The scallop *P. fumatus* had the highest values for the aspect ratio and obliqueness of the phasic and tonic muscles, whereas *A. balloti* and *P. magellanicus* had relatively high aspect ratios and values of muscle obliqueness.

The PCA for behavioral parameters yielded two PC that explained much of the variability in the data. The first behavioral PC (endurance) nicely positioned the scallop species in order of their swimming endurance: *Amusium balloti*, *Placopecten magellanicus* followed by *Pecten fumatus*, *Mimachlamys asperima*, and finally *Crassadoma gigantea*; a similar rank order as for the first PC of morphology (mass and proportions). The swimming endurance in the scallops was best predicted by the slimness (width) and lightness of the shell and muscles and the ensuing changes in muscle morphology. The second behavioral PC (intensity) primarily highlighted *P. fumatus*. The swimming intensity of the scallops was best predicted by the obliqueness of the adductor muscle and aspect ratio, as well as the tissue mass and proportions. Neither behavioral PC was

correlated with the second morphological PC, “phasic moment and size,” presumably as none of the behavioral data were expressed in terms of muscle force.

Obliqueness of the adductor muscle can be achieved by having the insertion of the muscle closer to the hinge on one valve than the other or by having the muscle impression larger on one valve than the other. Adductor muscle obliqueness has been observed for many years (Thayer 1972), but this study is the first to demonstrate its role and adaptive significance. Yonge (1936) suggested that the oblique arrangement increases the length of the muscle allowing the valves to open wider to take in more water and generate a more powerful water jet. Gould (1971) argued that increased length of the phasic muscle, due to its oblique arrangement, increases its capacity for work (cross-sectional area $\times$ length). Thayer (1972) demonstrated via calculations that the obliqueness of the phasic adductor muscle, in a plane perpendicular to the hinge, increases the angular velocity of valve closure. Finally, Soemodihardjo (1974) proposed that the increased diameter of the phasic muscle on the left valve relative to the right one, allows a pinnate arrangement of the muscle fibers that ultimately produces greater force. This present analysis showed that the obliqueness of the phasic muscle is linked to the intensity of induced escape response in the experimental scallop species. As high velocities of valve closure and powerful water jets are both important determinants of the intensity (initial bursts of phasic contractions) of the escape response, the conclusions of this study support the earlier proposals. An increase of valve closure velocity requires that the ligament allow rapid opening of the valves. Indeed, the resilience of the ligament tended to be higher in scallops with more intense escape responses (Tremblay et al. 2015).

Shell Characteristics

The experimental scallop species were chosen based on visible differences in shell shape and texture, as well as on differences in swimming strategies (Tremblay et al. 2012). Shell structure reflects a compromise between conflicting requirements. Light and smooth shells facilitate swimming by decreasing drag and gravity, but are more easily broken by

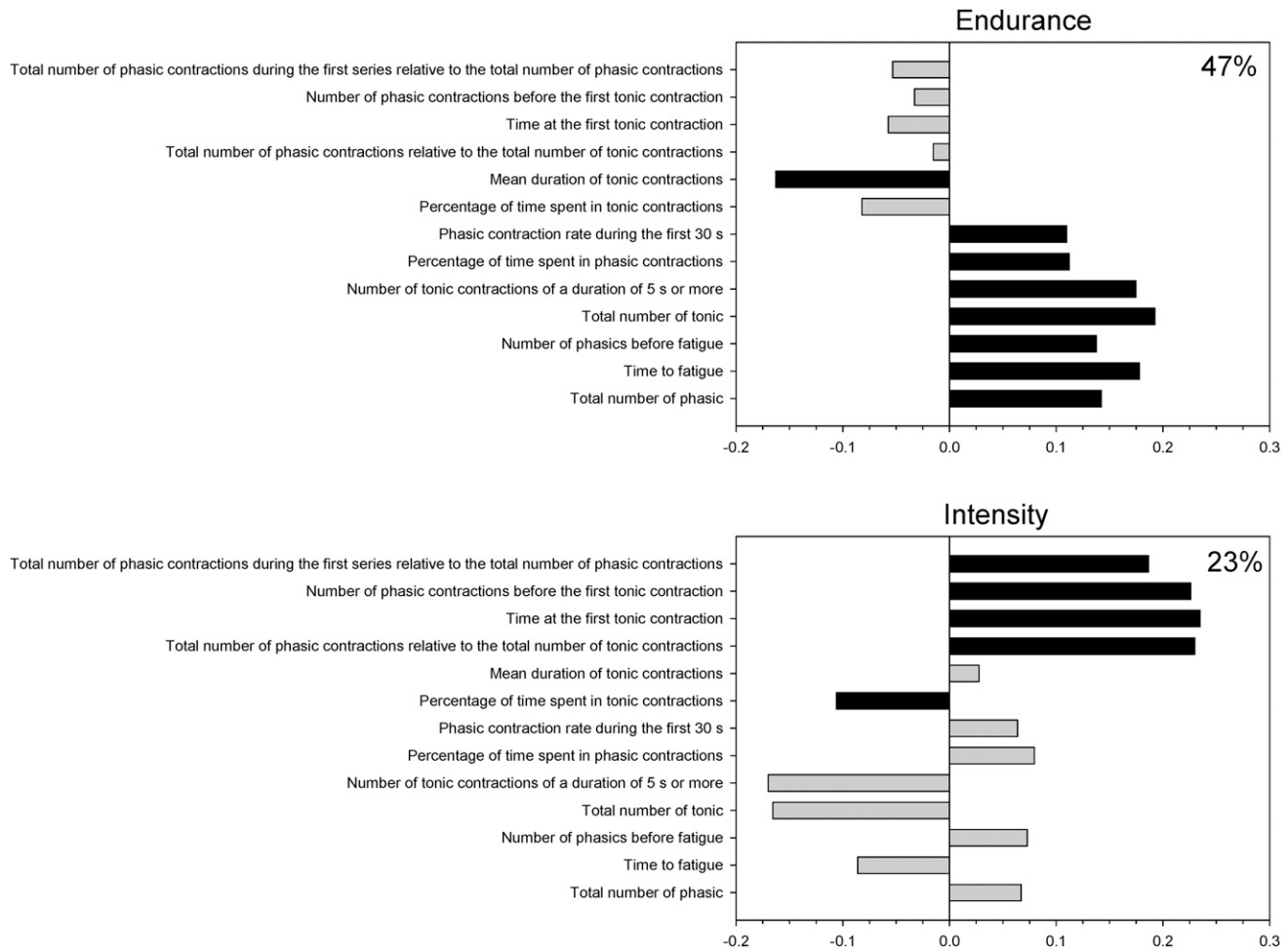


Figure 10. Normalized scores of the behavioral variables associated with the first two PC. Black bars identify variables assigned to each component. The percentages indicate the proportion of variance explained by the principal component.

predators than the thick heavy shells that restrict movement. At one end of the range of species, the non swimming scallop *Crassadoma gigantea* has a thick, tightly sealed, heavy shell cemented to the substrate that gives efficient protection against predators when closed. On the other extreme, *Amusium balloti* and *Mimachlamys asperima* have very light shells that facilitate swimming, but can easily be crushed or opened by predators. In response to its crustacean predator, *A. balloti*'s strategy is to swim away, whereas in seeming contradiction to the fragility of its shell, *M. asperima* tends to keep its valves closed for prolonged periods. The shell of *M. asperima* is frequently covered by sponges known to inhibit predation by sea stars (Pitcher & Butler 1987). Furthermore, the valves of *M. asperima* fit closely together, hindering access by predators. Therefore, *M. asperima* seems to have sufficient protection against predation without having a heavy shell or an extensive escape response.

Although the shell of *Pecten fumatus* is not hydrodynamic, its plano-convex shape facilitates recessing into the substrate and provides certain advantages for swimming. Plano-convex scallops produce significant lift when the commissural plane is in line with current flow (Gruffydd 1976, Millward & White 1992). The high aspect ratio of *P. fumatus* shell means a high lift/

drag ratio, helping it to rise in the water column and swim (Stanley 1970). The plano-convex shell is particularly important for recessing and camouflaging the scallop in soft substrate habitats. The compromises embodied in the shell shape of *P. fumatus* extend to its behavior, muscle morphology, and metabolic capacities. Effectively, the intensive burst of phasic contractions by *P. fumatus* at the start of its escape response (Tremblay et al. 2012), the obliqueness of its phasic muscle, and its muscle metabolic capacities (Tremblay & Guderley 2014) can be seen as means of compensating for a shell shape that is unfavorable for swimming but useful for camouflage and feeding.

Muscle and Body Morphology

In response to the presence of its predator, a scallop will either swim away or close its valves for prolonged periods. Swimming has been suggested to benefit from a reduction of body mass relative to shell volume, a bigger phasic adductor muscle, or an oblique arrangement of the phasic adductor muscle (Thayer 1972). The volume of water expelled per unit of time (t) and the force of the water jets could be increased by these mechanisms. Taken individually, muscle size and proportions did not differentiate swimming strategies in this study.

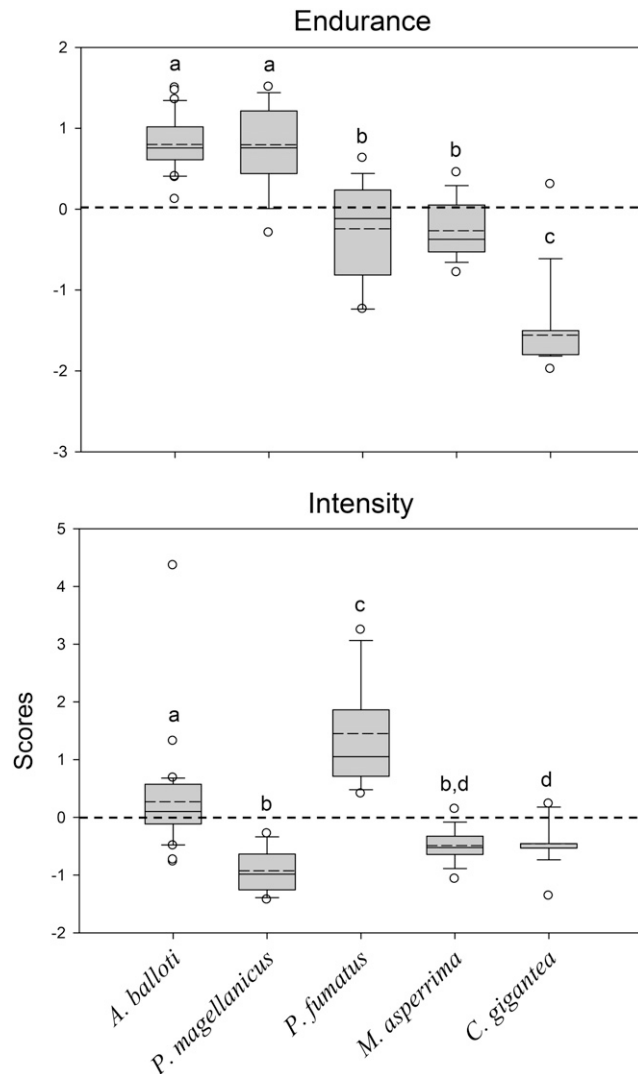


Figure 11. Scores for the two behavioral PC from the PCA of our behavioral data (Tremblay et al. 2012). The boundary of the box closest to zero indicates the 25th percentile and the boundary of the box farthest from zero indicates the 75th percentile. The full line within the box marks the median, whereas the dashed line marks the mean. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles. Open circles are outlying data. ANOVA and multiple comparisons, $P < 0.05$. Sample size: *Amusium balloti*, $N = 30$; *Placopecten magellanicus*, $N = 15$; *Pecten fumatus*, $N = 15$; *Mimachlamys asperima*, $N = 16$; and *Crassadoma gigantea*, $N = 18$.

These characteristics, however, were linked on the first PC of the morphological PCA (mass and proportions) and in turn were strongly correlated with the PC for endurance during an escape response. Heavy shells require large muscles, increase the soft tissue volume, and reduce sinking times and the proportion of phasic muscle in the overall adductor muscle. Thus, in combination, muscle size and proportions were strongly linked with the endurance and intensity during an escape response in the experimental scallops.

When a scallop claps its valves, the phasic muscle moment rotates the valves toward each other around the hinge and counteracts the opening moment of the ligament (Trueman 1953). This phasic muscle moment can be assessed as the cross-sectional

TABLE 5.

Links between the morphological and behavioral PC.

	Endurance		Intensity	
	<i>t</i> value	Pr > <i>t</i>	<i>t</i> value	Pr > <i>t</i>
Mass and proportions	-7.28	<0.0001	-2.51	0.012
Phasic moment and size	-1.93	0.054	1.07	0.286
Obliqueness and aspect ratio	0.41	0.685	5.23	<0.0001

Regression of the individual scores calculated for each morphological PC against the individual scores calculated for each behavioral PC ($P < 0.05$).

area of the phasic muscle times its distance from the hinge (Gould 1971). The moment exerted by the phasic muscle was a major determinant of the second morphological PC (phasic moment and size). As none of the escape response behaviors we had quantified in Tremblay et al. (2012) compared the force exerted by the scallop species, the second morphological PC was not linked with escape response behaviors. Finally, the moment exerted by the phasic muscle was much higher in our scallops than in the oyster as expected from the swimming condition of scallops.

The behavioral PCA did not yield a PC highlighting tonic contractions, rather the performance of the tonic and phasic contractions was closely intertwined in both PC. The frequent use of short tonic contractions in some actively swimming species (Tremblay et al. 2012) was apparent in the association of numbers of phasic and tonic contractions in the PC “endurance” of the behavioral data. Prolonged valve closure by tonic contractions provides time for phasic muscle recuperation (Pérez et al. 2008) as well as protecting against predation in sedentary species. Scallop species that use mainly prolonged tonic contractions did not have a bigger proportion of tonic muscle than scallops performing mainly phasic contractions. On the other hand, the scallop *Amusium balloti* had a much smaller tonic muscle and developed less tonic force than the other species (Tremblay et al. 2012). In the presence of predators, *A. balloti* cannot use tonic contractions as the large lateral openings of its shell give little protection against predators. With the use of phasic contractions as the main swimming strategy in *Amusium* species, it seems that the tonic muscle has become virtually vestigial.

This study allowed the identification of parameters of swimming behavior that are linked with specific aspects of muscle and shell morphology in several scallop species. Throughout evolution, scallops underwent various modifications in morphology and behavior, with an ancestral byssally attached form giving rise to the various modern scallop species (Alejandrino et al. 2011). Although most of the life habits observed in scallops (gliding, free living, recession, byssally attached) can be either ancestral or transitory, the cemented form did not give rise to any other life-forms that scallops can assume (Alejandrino et al. 2011). This bias in life habit transitions may indicate constraints due to the complexity in the physiological and morphological changes necessary for the transition from one life habit to another (Alejandrino et al. 2011). Although this study examined how interspecific differences in shell and adductor muscle morphology are linked to swimming strategies, the underlying question is that of evolutionary plasticity in these attributes. Data from this study show that scallops can compensate for unfavorable shell morphology

by changes in their behavior (Tremblay et al. 2012), and that their muscle metabolic capacities follow these changes (Tremblay & Guderley 2014). Although the behavior and the metabolism of an organism are plastic on relatively short time scales, morphological plasticity is manifested at a longer time scale. Morphological components, such as soft tissue mass and muscle arrangement within the shell, would change more rapidly than shell morphology; but even shell morphology shows plasticity. Indeed, shell strength is influenced by the presence of predators with wild scallops having stronger shells than cultured ones (Lafrance et al. 2003, Grefsrud & Strand 2006). The time scale required for changing shell shape (plano-convex to biconvex) or surface texture would be greater than the lifespan of individuals. Therefore, we view such aspects of shell morphology as constraints to which the morphology of soft tissues, behavior, and muscle metabolic capacities of scallops must adapt.

Throughout their lifespan, scallops go through important changes in structure and activity. Indeed, shell morphology, soft tissue and muscle arrangement, muscle metabolic capacities, and swimming behavior change as scallops grow (Gould 1971, Dadswell & Weihs 1990, Manuel & Dadswell 1993, Schmidt et al. 2008, Labrecque & Guderley 2011). Those modifications mostly take place during juvenile stages and tend to stabilize when scallops reach maturity and put more energy into reproduction than into growth. Thus, the relationships between shell and adductor muscle morphology and swimming strategy may change during ontogeny.

Overall, the differing swimming strategies of the experimental scallop species are associated with specific morphological

attributes without which these behavioral strategies would not work. Scallops have exploited different mechanisms to deal with the constraints of shell morphology, ranging from modifications of muscle size, position, and proportions, to adjustments of muscle metabolic capacities and use during escape responses. The mechanisms that best enhance survival against predation reside on multiple levels.

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APPENDIX

TABLE A1.

Regression between shell height and shell mass of the scallops used to estimate the shell mass of the scallops of the behavioral study.

Species	Regression equation	R ²
<i>Pecten fumatus</i>	$y = 1.5187 \times -89.217$	0.8659
<i>Crassadoma gigantea</i>	$y = 3.4072 \times -168.27$	0.6518