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WHEN BEHAVIOR AND MECHANICS MEET: SCALLOP SWIMMING CAPACITIES AND THEIR HINGE LIGAMENT

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ABSTRACT Scallops swim using jet propulsion produced by expulsion of water from between the valves by rapid contraction of the adductor muscle. The valves are subsequently opened by a ligament that acts like a spring mechanism. Compared with burrowing or sessile bivalves, scallops have ligaments with greater resilience. To determine whether the ligament resilience, ligament opening force, and force deployed by the phasic and tonic adductor muscles varied with escape response strategies and shell morphology, these properties were compared in scallops (*Amusium balloti*, *Placopecten magellanicus*, *Equichlamys bifrons*, *Pecten fumatus*, *Mimachlamys asperrima*, and *Crassadoma gigantea*) with differing life habits and morphologies. The ligament opening force varied among species and was always equal to or exceeded by phasic and tonic closing forces. The species producing the greatest frequency of phasic contractions (*P. fumatus*) had the greatest ligament resilience.

KEY WORDS: resilience, hysteresis loop, muscle force, Bivalvia, scallop, swimming

INTRODUCTION

Bivalve molluscs live in a wide range of habitats and show a variety of life styles characterized by different strategies to escape predation and specific morphological attributes. For example, the softshell clam *Mya arenaria* (Linnaeus 1758) uses its pedal foot and valve adductions to burrow in the substrate (Checa & Cadée 1997). In response to contact with a predator, the cockle *Cardium tuberculatum* (Linnaeus 1758) escapes via a series of jumps produced by contractions of the foot (Gäde 1980). Other bivalves, such as the file shell *Lima hians* (Gmelin 1791), can swim via coordinated rowing movements of the pallial tentacles or via water jets formed by rapid adductions of the valves (Gilmour 1967). In addition, scallops use jet propulsion to swim with the ventral edge leading, seeming "to take a series of bites out of the water" (Dakin 1909, p. 5).

During scallop swimming, rapid closures alternate with valve openings to produce bursts of claps (Drew 1906, Dakin 1909, Bruddenbrock 1911). These rapid closures are produced by the striated phasic adductor muscle (Lowy 1953, Millman 1967) whereas the smooth tonic adductor muscle contracts slowly, maintaining constant valve positions (Lowy 1953, Chantler 2006). During adductor muscle contraction, the valves close and energy is stored in the ligament. Extensive modeling by Cheng et al. (1996) shows that most of the mechanical energy produced by phasic muscle contraction is used to produce the jet that moves the scallop. When the muscle relaxes, the energy stored in the ligament is released, opening the valves. The ligament acts as a spring, applying a force that pushes the valves apart. This force must counteract the mass of the valves as well as the added mass of the water displaced by the moving shell. Flow-induced forces also help to reopen the valves, but their role is small compared with that of the ligament (Vogel 1985, Cheng & DeMont 1996).

The scallop ligament is situated toward the dorsal margin of the valves. The outer and inner regions of the ligament have different structures and functions. The outer laminated part connects the valves at the dorsal margin and acts as a hinge (Fig. 1) (Trueman 1953b). The inner part of the ligament is a dark-brown pyramid with a base that bulges ventrally—particularly when the valves are closed (Fig. 1) (Trueman 1953b). Although in bivalves such as mussels or oysters the inner ligament is calcified throughout, in scallops it has a large, noncalcified center and two lateral calcified regions attaching the ligament to the valves (Trueman 1953a, Trueman 1953b, Alexander 1966, DeMont 1990). The calcified parts of the ligament contain aragonite (Kahler et al. 1976), whereas the center of the inner ligament is composed of abductin, a protein with properties similar to those of elastin and resilin (Alexander 1966, Kelly & Rice 1967).

The mechanical properties of scallop ligaments differ from those of sedentary bivalves (Trueman 1953a, Kahler et al. 1976). The ligaments of *Pecten maximus* (Linnaeus 1758) and *Aequipecten opercularis* (Linnaeus 1758) are more resilient than those of sedentary bivalves (Kahler et al. 1976), with the resilience corresponding to the ability of the ligament to return to its original state after being compressed. Scallop ligaments also have a lower opening moment (applied moment value, measured in grams per millimeter, when the valves are just starting to open during the unloading cycle) per gram of shell than those of nonswimming bivalves such as *Cyprina islandica* (Linnaeus 1767), *Mytilus edulis* (Linnaeus 1758), *Mya arenaria*, and *Crassostrea virginica* (Gmelin 1791) (Trueman 1953a, Kahler et al. 1976). Last, the area enclosed by the hysteresis loop from stress–strain curves of intact ligaments is markedly smaller in *P. maximus* and *A. opercularis* than in the nonswimming bivalves. This indicates that scallop ligaments are more efficient during closing and opening cycles (Trueman 1953a).

Scallops exhibit a wide range of lifestyles, ranging from the highly active *Amusium* species to the more sedentary and byssally attached *Chlamys* species (Minchin 2003, Alejandrino et al. 2011), and they differ in their use of phasic and tonic muscles during escape responses (Tremblay et al. 2012). It was reasoned that ligament properties—in particular, resilience—could reflect the escape response strategies of scallops. Specifically, this study proposed that the ligaments of scallop species that show a vigorous escape response, as reflected by high rates of phasic contractions, should have greater resilience than those

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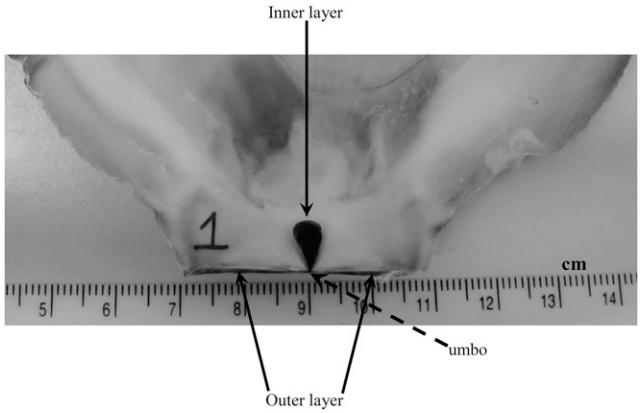

Figure 1. Interior of the dorsal region of the left valve of *Amusium balloti* showing the ligament cut in longitudinal section. Scale is in centimeters (photograph courtesy of Isabelle Tremblay).

of species with a weaker escape response. Because the ligament must counteract the mass of the valves, as well as the added mass of the water displaced by the moving shell, it was reasoned that the force deployed by the ligament when opening the valves should vary with shell mass. Logically, the force deployed by the phasic and tonic adductor muscles to close the valves must exceed that deployed by the ligament that opens them. Because a greater phasic force produces stronger water jets, it was predicted that scallops performing a vigorous escape response should have a greater divergence between the phasic force and the ligament opening force than more sedentary species. It was also reasoned that the tonic force would remain similar to the ligament opening force, regardless of the escape response strategy.

To examine these predictions, ligament resilience, ligament opening force, and the force deployed by the phasic and tonic adductor muscles during escape responses in scallop species with distinct escape responses and shell morphologies were determined (Fig. 2). The ligament opening force was assessed by measuring the mechanical force required to close the valves. The scallops *Amusium balloti* (Bernardi 1861) and *Placopecten magellanicus* (Gmelin 1791) perform phasic contractions throughout the escape response. Phasic contractions occur at a faster pace in *A. balloti* than in *P. magellanicus*, as shown by the short interval between phasic contractions and the high phasic contraction rate (Fig. 2). Intense bursts of phasic contractions occur at the start of escape responses by *Pecten fumatus* (Reeve 1852), whereas *Mimachlamys asperrima* (Lamark 1819) makes a short series of phasic contractions at the beginning of the response, with a slower overall rate of phasic contraction (Fig. 2). Adult *Crassadoma gigantea* (J.E. Gray 1825) are cemented to the substrate and make phasic contractions only rarely in response to predators (Fig. 2) (Tremblay et al. 2012). Last, *Equichlamys bifrons* (Lamark 1819) is supposedly more sedentary than *M. asperrima* and *P. fumatus* (Olsen 1955). Its escape response was assessed visually.

MATERIALS AND METHODS

Experimental Scallops: Shell and Behavioral Characteristics

The experimental scallops used in this study (*Amusium balloti*, *Placopecten magellanicus*, *Pecten fumatus*, *Mimachlamys asperrima*, and *Crassadoma gigantea*) were the same individuals used for the behavioral tests in Tremblay et al. (2012). An additional species, *Equichlamys bifrons*, was collected with and kept in the same conditions as *P. fumatus* and *M. asperrima* (Table 1). Holding conditions are given in detail in Tremblay et al. (2012) and are summarized in Table 1. Scallops were kept in temperature-controlled flow-through tanks for at least 2 wk before measurements were taken. All scallops were adults with mature gonads. Shell heights of experimental individuals were similar. Anatomic characteristics and behavioral parameters of the experimental scallops are summarized in Table 2 and Figure 2, respectively.

Muscle Force Measurements, Data Recordings, and Analysis

Force production of scallops during an escape response was characterized using the technique described by Fleury et al. (2005), as modified by Guderley et al. (2008). Technically, the scallops were not able to escape because their lower valve was fixed to the bottom of a tank; only the upper valve was free to move (Fig. 3). A lever, attached to a force gauge (recording frequency, 0.1 Hz; AFG-50 N, Quantrol Advanced Force Gauge, Dillon, Fairmont, MN), was placed under the ventral edge of the upper valve. The force gauge was mounted on a test stand, allowing adjustments of the lever to separate the valves by a distance corresponding to that observed in scallops at rest and ventilating normally. Only downward movements of the upper valve were recorded by the force gauge. The escape response was elicited by repeatedly touching the mantle of the scallop with its predator for the duration of the test (355 sec; see Tremblay et al. [2012] for details about the predators).

The force gauge was connected to a personal computer in which the recordings were stored using Dataplot-X software (Dillon, Fairmont, MN). Recordings from the force gauge were transferred to an Excel spreadsheet for analysis of the phasic and tonic muscle contractions during the escape response test. On the force recordings, phasic contractions were apparent as sharp peaks; sustained force production indicated tonic contractions (Fig. 4). The escape response of each scallop was characterized in terms of number, rate, and duration of phasic and tonic contractions (see Tremblay et al. [2012] for more details). Because ligament efficiency is important during closing and opening cycles, the variables related to the intensity of the escape response were examined—namely, minimal interval between two consecutive phasic contractions, number of phasics during the first series, phasic contraction rate during the first 30 sec of the escape response test, and overall phasic contraction rate. A series of phasic contractions was defined as consecutive phasic contractions separated by less than 3 sec. The overall phasic contraction rate was calculated relative to the test duration of 355 sec for all species except *Equichlamys bifrons*. For *E. bifrons*, the escape response was characterized via visual observations. Therefore, the overall phasic contraction rate was calculated relative to the time to fatigue (which corresponds to when the scallop made no phasic contractions during 1 min of stimulation with its predator).

Parameters related to phasic and tonic force were estimated from the force–time curves (Fig. 4). Before a phasic contraction, the adductor muscle relaxes and the valves open widely, filling the mantle cavity with water. At this point, the upper valve of the scallop is well above the force gauge lever. Then, a rapid

Figure 2. Behavioral variables and side view of experimental scallops. Data are mean ± SE. Scale bar is 1 cm. Different letters indicate significant differences (Kruskal–Wallis followed by multiple comparisons; $P < 0.05$). *Overall rate was calculated relative to the time to fatigue for *Equichlamys bifrons* and relative to test duration of 355 sec for other species (see Tremblay et al. [2012] for details). The minimal interval between two phasics is for two consecutive phasic contractions. For the number of phasics during the first series, a series of phasic contractions is defined as consecutive phasic contractions separated by less than 3 sec. The contraction rate during 30 sec refers to the first 30 sec of the escape response test (photographs courtesy of Isabelle Tremblay).

phasic contraction leads the edge of the upper valve to hit the lever during its downward movement. The force recorded corresponds to the impact of the upper valve on the lever and reflects the force deployed by the phasic muscle, as well as inertial forces and water resistance. Shell velocity is needed to evaluate inertial forces. Because this variable was not available, the exact force deployed by the phasic adductor muscle could not be estimated. Nonetheless, it was reasoned that the impact

TABLE 1.

Origin and holding conditions of the experimental scallops.

Species	Capture method	Capture location	Temperature (°C)	Salinity
Amusium balloti	Trawling	Northern Hervey Bay, Australia	18.5	35
Placopecten magellanicus	Aquaculture pearl nets	Cap-Aux-Meules, Îles-de-la-Madeleine, Canada	14	30
Equichlamys bifrons	Scuba	Satellite Island, Canal d'Entrecastreux, Australia	12.5	34
Pecten fumatus	Scuba	Satellite Island, Canal d'Entrecastreux, Australia	12.5	34
Mimachlamys asperrima	Scuba	Satellite Island, Canal d'Entrecastreux, Australia	12.5	34
Crassadoma gigantea	Scuba	Espinosa Inlet, Vancouver Island, Canada	12.5	28

TABLE 2.

Experimental scallops anatomic characteristics.

	Amusium balloti	*Placopecten magellanicus*	*Equichlamys bifrons*	*Pecten fumatus*	*Mimachlamys asperrima*	*Crassadoma gigantea*
Shell						
Height (mm)	96.3 ± 1.1^{a}	$90.4 \pm 0.9^{b,c}$	96.2 ± 2.5^{a}	$94.4 \pm 1.7^{a,c}$	84.2 ± 2.0^{b}	$97.0 \pm 4.5^{a,c}$
Mass (g)	34.6 ± 1.6^{a}	49.4 ± 1.7^{b}	61.6 ± 3.6^{c}	$53.9 \pm 2.5^{b,c}$	27.3 ± 2.0^{d}	162.2 ± 15.5^{e}
n	27	15	20	15	16	19
Soft tissue dry mass (g)						
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}
Tonic muscle	0.05 ± 0.004^{a}	0.25 ± 0.01^{b}	0.51 ± 0.01^{c}	0.23 ± 0.01^{b}	0.17 ± 0.01^{c}	0.29 ± 0.02^{d}
n	18	15	20	15	16	19
Condition index (g/mL)*	0.48 ± 0.01^{a}	0.51 ± 0.01^{a}	0.71 ± 0.06^{b}	0.42 ± 0.02^{c}	0.41 ± 0.01^{c}	0.61 ± 0.02^{b}
n	18	15	20	15	16	19

* The condition index is the total animal wet mass divided by the volume inside the shell. In a given row, different letters indicate significant differences (Kruskal–Wallis followed by multiple comparisons, $P < 0.05$). Data are mean ± SE. Soft tissue dry mass was adjusted for a 90 mm shell height.

of the upper shell on the lever of the force gauge represents the force deployed by the moving valve, which ultimately produces jet propulsion. Therefore, in this study, this measure is the best estimate of force produced by the phasic muscle for swimming and is designated as the phasic closing force.

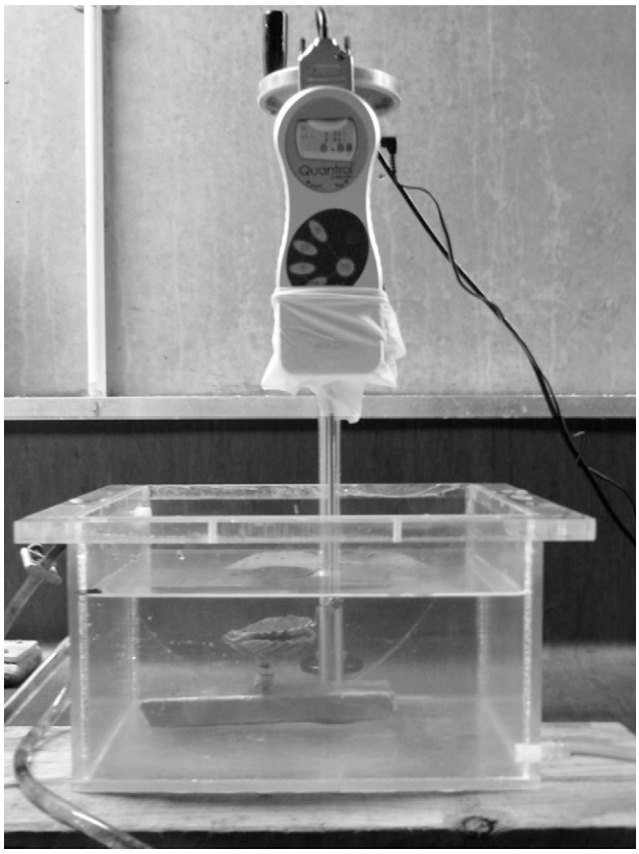

Figure 3. Force gauge, mounted on the test stand, used for recording force measurements. The lower valve of the scallop (*Pecten fumatus*) is fixed at the bottom of the tank and the lever, attached to the force gauge, is placed under the ventral edge of the upper valve (photograph courtesy of Isabelle Tremblay).

For each individual, the force of all phasic contractions was averaged to assess its mean phasic closing force. For each species, mean phasic closing force (Table 3) was estimated by averaging values for all individuals. Because phasic contractions decrease in force during escape response tests, the mean phasic closing force corresponded to 55%–78% of the maximal phasic closing force.

The sustained contraction of tonic muscle facilitates the determination of its force production. Mean tonic force was estimated by dividing the area under the force–time curve by recording duration. This was feasible because phasic contractions represent a minimal proportion of the recordings. When the valves are prevented from moving, the force measured at the edge of the shell is less than that measured near the muscle (Pérez et al. 2009). Indeed, when the force measured was 7.55 N at the shell edge, it was 13.95 N near the muscle for a scallop with its muscle situated 4.5 cm from the edge (Pérez et al. 2009). Because the force measurements in the current study were made at the shell edge, mean tonic force was corrected for the distance between the shell edge and the tonic muscle for each individual based on the relationship in Pérez et al. (2009).

Experimental Setup and Measurement of Ligament Resilience

Following the behavioral tests, all tissues were removed from the valves without touching the ligament; ligament resilience was measured immediately to reduce air exposure and to prevent drying. The method used to measure ligament resilience was inspired by Trueman (1953a). Emptied valves were placed on a base with an adjacent ruler as a reference (Fig. 5). The force gauge, equipped with a disc-shaped tip, was used to apply a force at the center of the phasic adductor muscle attachment area on the upper valve. The force gauge was attached to a manual stand, which allowed fine control of force application while closing the valves and while releasing the force during valve opening. The valves were closed and opened in steps to photograph the separation of the valves and to record the force. Photographs were taken regularly during the closing and opening cycle, with approximately 30 photographs per individual. The time between consecutive photographs did not exceed 5 sec, and the entire test lasted less than 5 min. In *Placopecten*

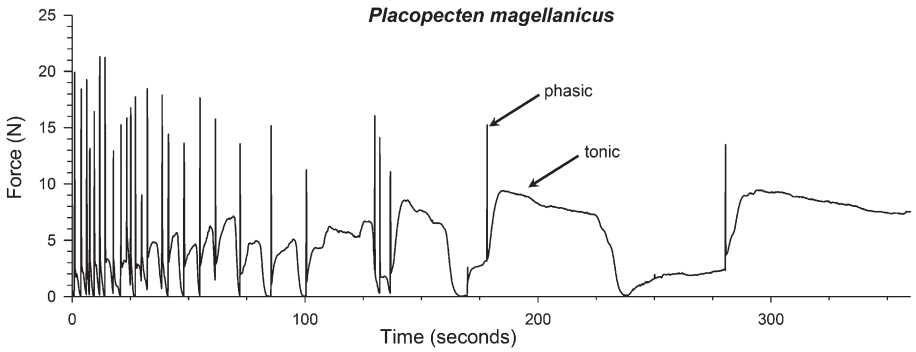

Figure 4. Force production of the phasic and tonic muscle during an escape response in *Placopecten magellanicus*.

magellanicus, ligament resilience measured in two consecutive closing/opening cycles did not differ. Therefore, only one closing and opening cycle was measured for each individual in all species.

Each photograph (Fig. 5) was analyzed using ImageJ (v. 1.42, National Institutes of Health) to determine the force applied and the separation between the valves during closing and opening. From these photographs, data points from the loading (valve closing) and unloading (valve opening) phases were graphed and joined by straight lines (SigmaPlot 11.0), giving a hysteresis loop for each individual (Fig. 6). Using image analysis, the areas under the loading and unloading curves were measured and then used to calculate ligament resilience (area under unloading curve divided by area under loading curve). The force required to close the valves mechanically was assessed as the force applied when the valves are completely closed (distance 0 cm on the hysteresis loop; Fig. 6), and this measure was used as a proxy for the ligament opening force. The force required to close the valves of each individual mechanically was averaged to assess the mean ligament opening force for each species (Table 3).

Statistical Analysis

Normality was tested using the Shapiro–Wilk test, and homogeneity of variance was analyzed visually by plotting residuals relative to predicted values. Because of the non-normality of residuals and nonhomogeneity of variances, non-parametric statistics were used.

Interspecific comparisons of ligament resilience were made using the Kruskal–Wallis test and multiple comparisons. Spearman's correlations were used to assess whether the mean ligament opening force correlated with shell mass, and to assess whether ligament resilience correlated with phasic contractile activity during escape responses in the different species. Spearman's correlations were also used to assess whether the mean phasic force correlated with shell mass and phasic muscle mass, and to assess whether the mean tonic force correlated with shell mass. These correlations were examined inter- and intraspecifically. Because the behavior of *Equichlamys bifrons* was assessed visually, the phasic contraction rate could be estimated relative to time to fatigue only. Therefore, data for *E. bifrons* were not included in the interspecific correlations. All analyses were done using SAS 9.2 (SAS Institute). Significance was accepted at $P < 0.05$.

RESULTS

Shell Characteristics

Shell heights of the experimental scallop species overlapped, although *Mimachlamys asperrima* (84.2 ± 2.0 mm) was slightly smaller than the other species (Table 2). The scallop *Crassadoma gigantea* had the heaviest shell (162.2 ± 15.5 g), and *Amusium balloti* and *M. asperrima* the lightest (34.6 g and 27.3 g, respectively; Table 2). The biggest phasic muscle was associated with *C. gigantea*; *A. balloti* had the smallest (Table 2). The smallest tonic muscle belonged to *A. balloti*; *Pecten fumatus* had the biggest (Table 2).

Hysteresis Loops and Muscle Force Production

The ligament opening force showed considerable interspecific variation (Table 3 and Fig. 6), but did not correlate significantly with shell mass (correlation coefficient = 0.77,

TABLE 3.

Force measured in experimental scallops.

	Amusium balloti	*Placopecten magellanicus*	*Equichlamys bifrons*	*Pecten fumatus*	*Mimachlamys asperrima*	*Crassadoma gigantea*
Ligament opening force (N)	4.2 ± 0.1^{a}	3.5 ± 0.3^{b}	$4.6 \pm 0.3^{a,c}$	5.3 ± 0.3^{c}	2.8 ± 0.2^{d}	$5.1 \pm 0.7^{a,c}$
Phasic closing force (N)	10.10 ± 0.25^{a}	15.31 ± 0.96^{b}	—*	8.16 ± 0.90^{c}	7.57 ± 0.55^{c}	$14.21 \pm 3.42^{a,b}$
Tonic closing force (N)	4.73 ± 0.30^{a}	8.94 ± 0.94^{b}	—*	8.17 ± 1.33^{b}	7.54 ± 0.82^{b}	9.97 ± 1.39^{b}
n	30	15	18	15	15–16	7–16

* Because *E. bifrons* behavior was assessed visually, phasic and tonic closing forces could not be determined. Data are mean ± SE. In a given row, different letters indicate significant differences (Kruskall–Wallis followed by multiple comparisons; $P < 0.05$).

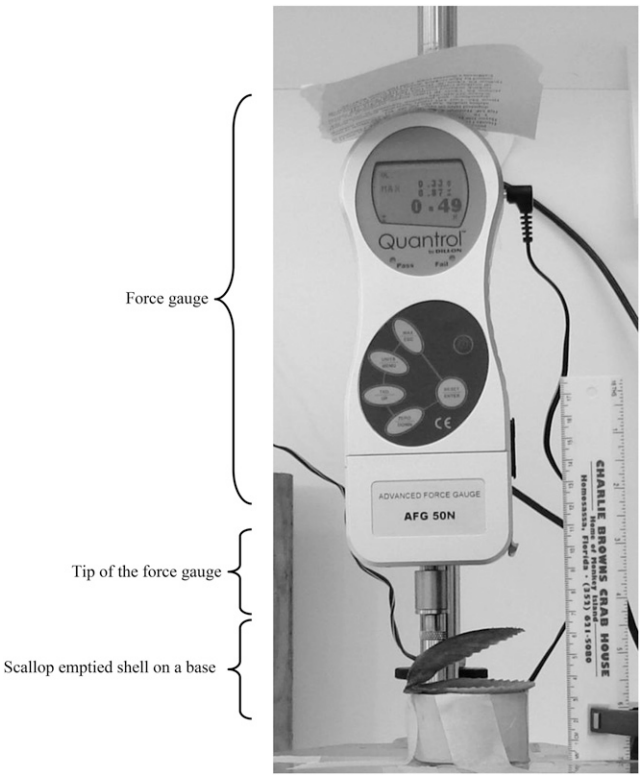

Figure 5. Experimental setup for examining ligament resilience. The emptied shell is placed on a fixed base, alongside an adjacent ruler, under the force gauge used to apply the force on the upper shell of the scallop (photograph courtesy of Isabelle Tremblay).

$P = 0.07$, $n = 6$). The scallops *Mimachlamys asperrima* and *Placopecten magellanicus* had the lowest mean values of the ligament opening force, with 2.8 N and 3.5 N; *Amusium balloti* and *Equichlamys bifrons* had intermediate levels at 4.2 N and 4.6 N; and *Crassadoma gigantea* and *Pecten fumatus* had the highest at 5.1 N and 5.3 N, respectively (Table 3). For all species, mean phasic closing force exceeded the ligament opening force markedly (range, 1.5–4.4 times; Table 3). The mean phasic closing force was greater in species that rely on phasic contractions throughout their escape responses (*A. balloti* and *P. magellanicus*), as well as in *C. gigantea* (Table 3). The mean phasic closing force did not correlate with shell or phasic muscle mass (correlation coefficient = 0.50 and 0.60, $P = 0.39$ and 0.28, respectively; $n = 5$). The mean tonic closing force also exceeded the ligament opening force, but to a lesser degree than the mean phasic force (Table 3). The mean tonic closing force did not correlate with shell mass (correlation coefficient = 0.80, $P = 0.10$, $n = 5$) and was markedly less in *A. balloti* than in the other species (Table 3).

Ligament resilience was greatest in *Pecten fumatus* at 0.91 ± 0.01 followed by *Amusium balloti* with a slightly lower resilience (Fig. 7). The scallops *Placopecten magellanicus* and *Crassadoma gigantea* had similar measures of ligament resilience, but they were less than those of *A. balloti* (Fig. 7). The scallops *Equichlamys bifrons* and *Mimachlamys asperrima* had the lowest ligament resilience at 0.70–0.76 (Fig. 7). When comparing mean values per species, ligament resilience did not correlate with parameters describing rates of phasic contraction during escape responses (Table 4). However, when the pattern produced by data points for all individuals was examined, individuals showing greater rates of phasic contraction (as shown by the number of phasic contractions during the first series and the phasic contraction rate during the first 30 sec of the escape response) showed greater ligament resilience (Fig. 8). The wide cloud in *P. fumatus* data points reflects the behavioral diversity among individuals. Although *P. fumatus* typically start the tests with a burst of phasic contractions, this burst is sometimes separated into a few series of phasic contractions or, in some cases, the burst of phasic contractions starts later (after 30 sec). Last, *P. magellanicus* showed a significant correlation between ligament resilience and phasic contraction rate during the first 30 sec of the escape response (correlation coefficient = 0.65, $P = 0.009$, $n = 15$).

DISCUSSION

The extensive morphological variation among scallops is reflected in a wide range of escape response strategies (Tremblay et al. 2012) and metabolic attributes (Tremblay & Guderley 2014). The current study demonstrated that the properties of the hinge ligament also differ among scallop species with distinct escape response behaviors. Ligament hysteresis loops differed in terms of ligament opening force and in terms of resilience. The mean phasic closing force was greatest in species that rely on phasic contractions throughout the escape response and in the cemented scallop *Crassadoma gigantea*. The mean phasic force exceeded ligament opening force to a greater extent than the mean tonic closing force. The ligament opening force did not correlate with phasic or tonic closing forces (correlation coefficient = 0.10 and 0.30, respectively; $P = 0.87$ and $P = 0.62$, respectively; $n = 5$). Because the ligament opening force was measured in the air, and the phasic and tonic forces were measured in the water, their respective contributions during scallop swimming are difficult to quantify. Clearly, complex forces are involved in cycles of valve closing and opening in swimming scallops (Cheng & DeMont 1996), and the measurements acquired in the current study were not from free-swimming scallops. That said, the current study did demonstrate considerable variation in ligament resilience and opening force among scallop species.

Ligament resilience varied with escape response strategies. As hypothesized, more active scallops tended to have a more resilient ligament, with species that reached the greatest frequency of phasic contraction having the greatest resilience. Among the experimental species, *Pecten fumatus* showed the most intense response at the beginning of the test by executing a burst of phasic contractions. This is reflected by the short interval between two consecutive phasic contractions, the high number of phasic contractions performed during the first series, and the high phasic contraction rate during the first 30 sec of the escape response test (Fig. 2). That *Pecten fumatus* had the ligament with the greatest resilience supports the principal hypothesis of the current study. On the other hand, ligament resilience in *Crassadoma gigantea* was similar to that in *Placopecten magellanicus* and greater than that in *Mimachlamys asperrima*. As adults, the latter species performs phasic contractions at much greater rates than *C. gigantea*. The scallop *C. gigantea* is free living during its early life (shell height, <20–30 mm) before cementing its lower valve to rocky surfaces (Yonge 1951, Lauzier & Bourne 2006). Although new material is

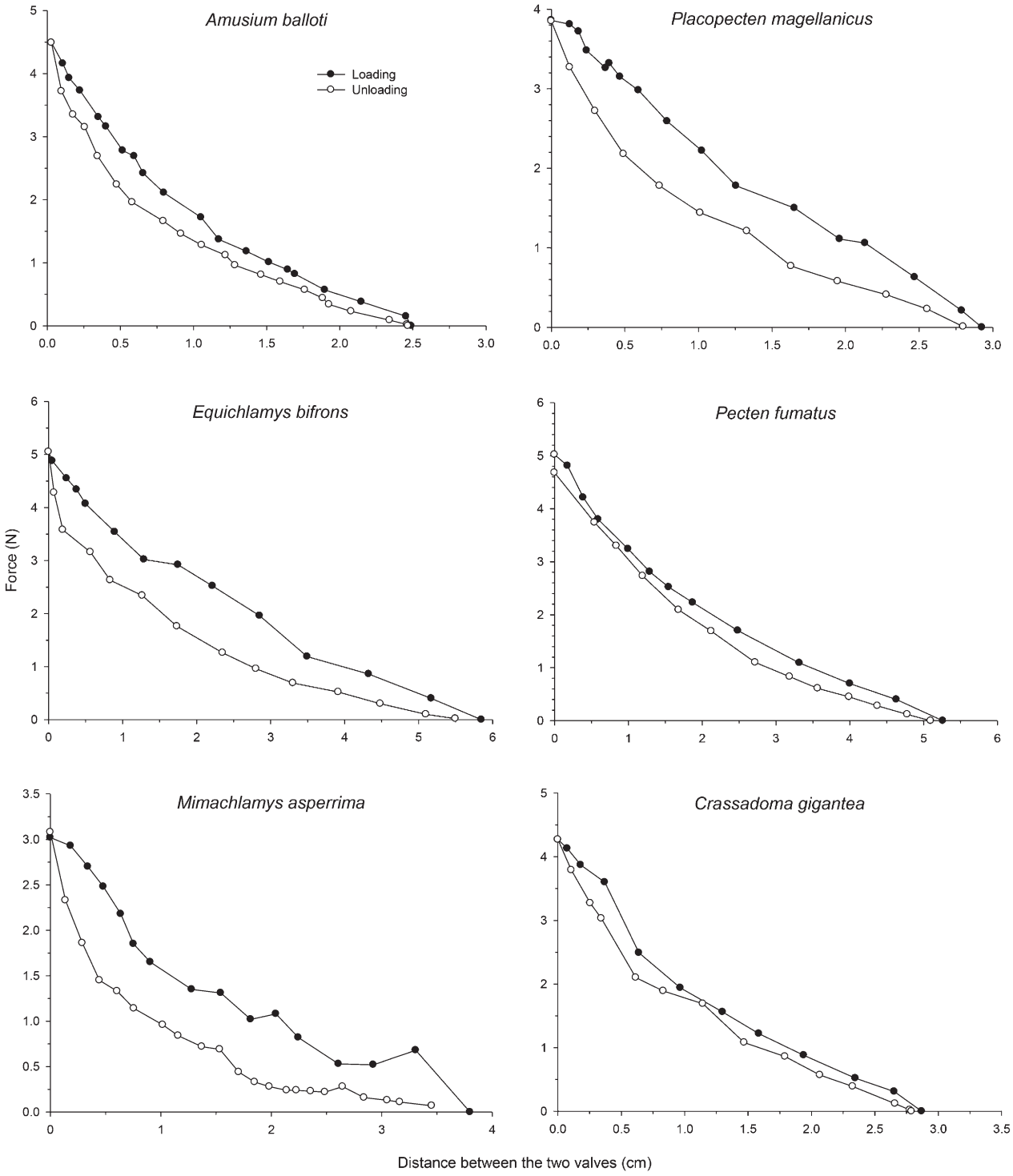

Figure 6. Example of typical hysteresis loops for each experimental species. These loops were obtained by plotting the force applied to the shell (the proxy for the ligament opening force) at the distance between the two valves. Solid circles correspond to the loading curve and open circles indicate the unloading curve.

layered on the ligament as the animal grows, older material remains. The ligament of *C. gigantea* probably retains characteristics from its juvenile period when it manifests swimming escape responses. Furthermore, it may maintain a pronounced coughing capacity for cleansing its mantle cavity. Overall, these observations show a tendency for ligament resilience to change in parallel with rates of phasic contraction during the beginning of escape responses.

The resilience of the ligament measured in the scallop species under study was similar to that observed in other studies. Alexander (1966) estimated, from graphs in Trueman (1953a), that the resilience of the ligament was 90% or more in *Pecten*

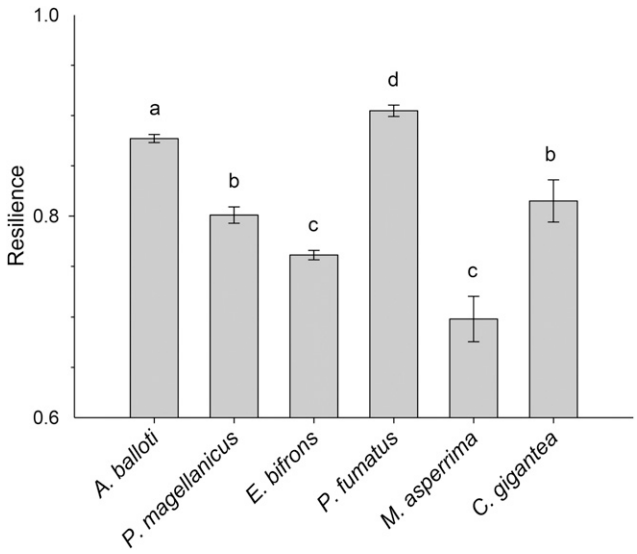

Figure 7. Ligament resilience in experimental scallop species. Data are mean ± SE. Bars with different letters are statistically different as indicated by Kruskall–Wallis and multiple comparisons tests ($P < 0.05$). Sample size is as follows: *Amusium balloti*, $n = 30$, *Placopecten magellanicus*, $n = 15$; *Equichlamys Bifrons*, $n = 20$; *Pecten fumatus*, $n = 15$, *Mimachlamys asperrima*, $n = 15$; and *Crassadoma gigantea*, $n = 16$.

maximus and *Aequipecten opercularis*. In his own experiments, Alexander (1966) measured a mean ligament resilience of 91% in *A. opercularis*. In *Placopecten magellanicus*, the resilience of the ligament was found to be 79% when measured at 10°C (Bowie et al. 1993). In these studies, ligament resilience was measured in the air (Trueman 1953a, Alexander 1966, Bowie et al. 1993). There is practically no variation in unloading and loading cycles of *A. opercularis*, *P. magellanicus*, and *Anodonta cygnea* (Linnaeus 1758) ligaments when measurements are repeated over a relatively short period of time (Trueman 1953a). Last, the resilience of the ligament in *P. magellanicus* measured at a physiological frequency of 3 Hz (Bowie et al. 1993) was similar to that measured in the current study in the same species, at a much slower frequency. Therefore, it seems that the conditions for measuring ligament resilience in the current study yield reasonable values and are particularly appropriate for the interspecific comparisons made in this study.

Ligament resilience is influenced by its arrangement in the shell and its biochemical composition (Trueman 1953b, Kahler et al. 1976) as well as by environmental temperature (Denny & Miller 2006). The scallops in the current study came from and were measured in similar thermal conditions (12–18°C); therefore, temperature is unlikely to have caused interspecific differences in ligament resilience. Although differences in ligament efficiency between nonswimming bivalves and scallops reflect in part the arrangement of the ligament in the shell (Trueman 1953b, Kahler et al. 1976), ligament anatomy is relatively constant among scallops (Trueman 1953b, Kahler et al. 1976). That said, migration of the hinge line, and thus of the ligament, to a more ventral position occurs in *Crassadoma gigantea* cementing in areas where spatial restriction could prevent the growing valves from opening (Yonge 1951). Nevertheless, the general arrangement of the *C. gigantea* ligament remains similar to that of other scallop species. Changes in ligament arrangement are unlikely to explain differences in ligament resilience among scallops. Last, differences in the biochemical composition of the ligament between nonswimming bivalves and scallops are clear (Kahler et al. 1976), but the differences among scallop species are less apparent (Denny & Miller 2006). Variation in the biochemical composition of ligaments from different scallop species may underlie the interspecific differences in resilience observed.

To close the valves, the force developed by the adductor muscle must exceed the ligament opening force. This excess was consistently greater for the phasic muscle than for the tonic muscle, although the extent of overshoot varied among species. Phasic force production not only counteracts the ligament opening force, but also it provides thrust to propel the scallops. The divergence between ligament opening force and phasic closing force was not necessarily greater in scallops that rely mainly on phasic contractions (*Amusium balloti* and *Placopecten magellanicus*; Table 3). The high mean phasic closing force in *Crassadoma gigantea* reflected its paucity of phasic contractions and may indicate a need for a strong coughing response to clean its mantle cavity (Table 3). Tonic muscle force production maintains valve closure and resists predators trying to open the valves. The low mean tonic force in *A. balloti* is commensurate with the small size of its tonic muscle (Table 2) compared with other species. Valve closure via prolonged tonic contractions in *A. balloti* is of little use against its crustacean predators, given the large gaps between the valves. For example, if *Thenus orientalis* (Leach 1815) catches *A. balloti*, it inserts its appendages into the gaps and slices away at the flesh. Therefore, *A. balloti* mainly uses phasic contractions to swim away from its predators (Tremblay et al. 2012). On the other hand, scallop

TABLE 4.

Correlations between ligament resilience and phasic contractile activity during escape responses by experimental scallop species (excluding *Equichlamys bifrons).**

	Minimal interval between two phasics	No. of phasics in the first series	Contraction rate during the first 30 sec	Contraction rate during 355 sec
Correlational coefficient	–0.80	0.70	–0.20	0.70
$P > \|r\|$	0.20	0.19	0.75	0.19
n	4	5	5	5

* The behavior of *E. bifrons* was assessed visually; therefore, the various phasic contraction rates could not be assessed in a similar way to the other species. Spearman's correlations were done using the mean value for each species, and the correlations used data from all the species with the exception of the minimal interval between two phasic contractions, which could not be estimated for *Crassadoma gigantea*.

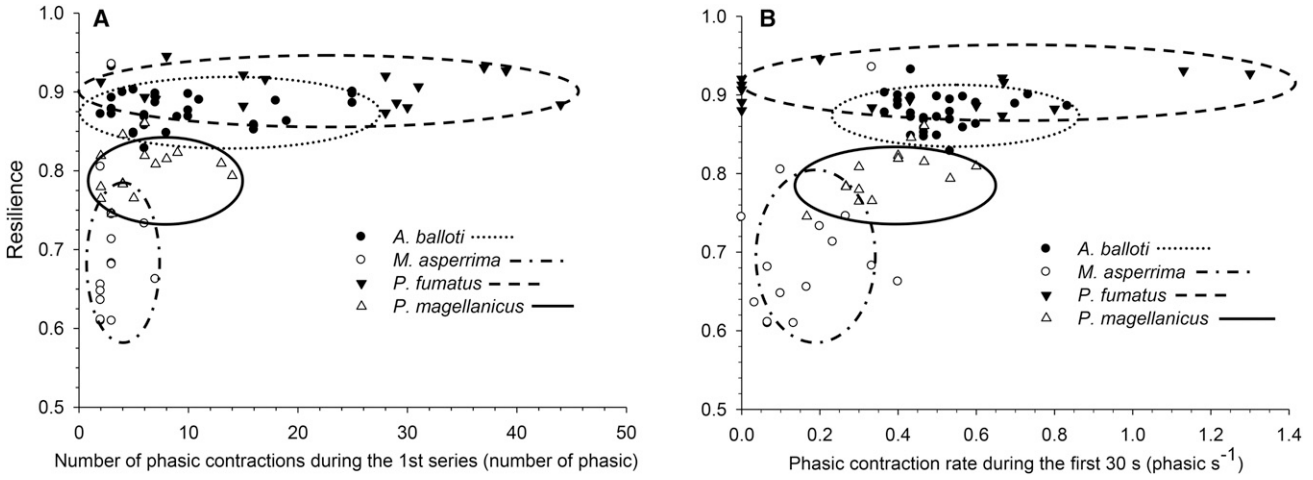

Figure 8. (A, B) Ligament resilience plotted against the number of phasic contractions during the first series ($y = 0.76 + 0.01x - 0.0002x^2$, $R^2 = 0.2650$) (A) and the phasic contraction rate during the first 30 sec of the escape response for each species ($y = 0.75 + 0.23x - 0.06x^2$, $R^2 = 0.2535$) (B). Sample size is as follows: *Amusium balloti*, $n = 30$; *Placopecten magellanicus*, $n = 15$; *Pecten fumatus*, $n = 15$; and *Mimachlamys asperrima*, $n = 16$.

species such as *Mimachlamys asperrima* and *C. gigantea,* which use prolonged tonic contractions to close their valves firmly in response to predators, had a bigger margin between tonic muscle closing force and ligament opening force (Table 3).

The hinge ligament is one component of a relatively simple, functionally elegant locomotor system. Although it was demonstrated that ligament resilience tends to reflect the frequency of phasic contractions in scallops, theory indicates that such changes in ligament resilience would have little impact on scallop swimming capacity. Indeed, Denny and Miller (2006) showed that even a drastic change in the resilience of the ligament would have only a small impact on the resonant period of the shell hinge system, and therefore on scallop locomotion. Nonetheless, the data from the current study and those of Denny and Miller (2006) show that scallops with different escape response strategies differ in ligament resilience. High ligament resilience may facilitate extensive valve gape without modifying the resonant period of the shell hinge system. The adaptive value of modifications of ligament resilience in scallops is not clear and invites consideration of other aspects of scallop movement. Although the behavior and muscle metabolic capacities of the scallop are plastic on a relatively short timescale, the plasticity of the ligament properties, as well as the shell morphology, is manifested at a longer timescale. Therefore, having a ligament with high resilience could allow a scallop to perform phasic contractions at a high rate if its muscle metabolic capacities can sustain this activity. Clearly, shell shape strongly influences swimming, and ligament properties may help muscle use in part to overcome some of the attendant morphological constraints (Tremblay et al. 2012).

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