RESEARCH ARTICLE

Swimming away or clamming up: the use of phasic and tonic adductor muscles during escape responses varies with shell morphology in scallops

Isabelle Tremblay[1,2,*], Helga E. Guderley[1,2] and John H. Himmelman[1]

[1]Département de Biologie, Université Laval, Québec city, Québec, Canada and [2]Réseau Aquaculture Québec, Institut des Sciences de la Mer de Rimouski, Université du Québec à Rimouski, Rimouski, Québec, Canada

*Author for correspondance (Isabelle.Tremblay.26@ulaval.ca)

SUMMARY

The simple locomotor system of scallops facilitates the study of muscle use during locomotion. We compared five species of scallops with different shell morphologies to see whether shell morphology and muscle use change in parallel or whether muscle use can compensate for morphological constraints. Force recordings during escape responses revealed that the use of tonic and phasic contractions varied markedly among species. The active species, *Amusium balloti*, *Placopecten magellanicus* and *Pecten fumatus*, made more phasic contractions than the more sedentary species, *Mimachlamys asperrima* and *Crassadoma gigantea*. Tonic contractions varied considerably among these species, with the two more sedentary species often starting their response to the predator with a tonic contraction and the more active species using shorter tonic contractions between series of phasic contractions. *Placopecten magellanicus* made extensive use of short tonic contractions. *Pecten fumatus* mounted an intense series of phasic contractions at the start of its response, perhaps to overcome the constraints of its unfavourable shell morphology. Valve closure by the more sedentary species suggests that their shell morphology protects them against predation, whereas swimming by the more active species relies upon intense phasic contractions together with favourable shell characteristics.

Key words: locomotion, muscle contraction, force recording, interspecific comparisons, bivalve.

INTRODUCTION

Animals use diverse styles of locomotion that rely upon a range of morphological, physiological and biochemical attributes. In vertebrates, bone structure and cardiovascular capacity as well as muscle size, fibre types, energetic reserves and metabolic capacity reflect the species' style of locomotion. For example, high-performance swimming fish, such as tuna and lamnid sharks, have a hydrodynamic body shape as well as many physiological characteristics (centrally positioned red muscle, regional endothermy and enhanced tissue oxygen delivery) that increase swimming efficiency (Bernal et al., 2001). The large leg muscles and short wings of deep-diving cormorants compromise flying but favour diving (Watanabe et al., 2011). Sustained flight by pigeons requires highly aerobic flight muscles (Pennycuick, 1968; Davis and Guderley, 1987), whereas burst flight by pheasants relies upon powerful anaerobic muscles that fatigue rapidly (Kiessling, 1977; Davis and Guderley, 1987; Marden, 1994; Askew and Marsh, 2002). Although it is clear that muscle morphology, metabolic capacity and fibre-type composition differ with locomotory style, the complex musculoskeletal structures of vertebrates make it difficult to study the use of muscle during movement and to identify how body morphology influences muscle use. The study of simpler locomotor systems could indicate whether body morphology and muscle use change in parallel or whether muscle use can compensate for morphological constraints.

Scallop swimming primarily involves one muscle, one ligament and the hinged shells. This mode of swimming is shared by scallops exhibiting a wide range of shell morphologies and lifestyles, ranging from the highly hydrodynamic *Amusium balloti* to the cemented rock scallop, *Crassadoma gigantea*. In response to disturbance, particularly contact with their predators, scallops swim using water jets produced by successive contractions during which rapid adductions (closure) alternate with abductions (opening) of the valves (Drew, 1906; Dakin, 1909; Bruddenbrock, 1911). The phasic adductor muscle is responsible for rapid valve closure (Lowy, 1954; Millman, 1967), whereas the uncalcified hinge ligament with its rubber-like properties (Alexander, 1966; Marsh et al., 1976) acts like a spring to open the valves when the adductor relaxes. The phasic adductor is composed of cross-striated fibres whereas the smaller tonic adductor is composed of smooth fibres, which contract slowly, allowing prolonged valve closure or low-energy maintenance of a constant valve opening during filter feeding (Lowy, 1954; Chantler, 2006).

Shell and muscle morphology, as well as metabolic capacity and use of the adductor muscle, should determine the swimming ability of scallop species. A swimming scallop has to produce thrust to overcome drag, and lift to overcome gravity. Thrust is produced by expulsion of water following contraction of the phasic adductor muscle, drag and lift are influenced by shell shape, swimming angle and swimming speed, whilst gravitational effects are primarily influenced by shell mass and organismal buoyancy. For a given scallop species, size and swimming angle as well as current speed and direction help determine lift production and swimming capacity (Gruffydd, 1976; Thorburn and Gruffydd, 1979; Millward and White, 1992). Scallops with good swimming abilities generally have a high aspect ratio, an upper valve that is slightly more convex than

the lower valve, and light valves with smooth surfaces (Gould, 1971; Seomodihardjo, 1974). Swimming ability varies positively with the ratio of phasic to tonic adductor muscle surface area (Gould, 1971; Seomodihardjo, 1974) and with the obliqueness of the phasic adductor, in a plane perpendicular to the hinge (Thayer, 1972). Shell size and the energetic status of the adductor muscle also influence swimming ability, as the ability of individual scallops to swim and recover from exhausting exercise changes with size, acclimation temperature and reproductive stage (Manuel and Dadswell, 1991; Manuel and Dadswell, 1993; Brokordt et al., 2000a; Brokordt et al., 2000b; Bailey and Johnston, 2005; Guderley et al., 2009; Labrecque and Guderley, 2011). Whereas interspecific comparisons of shell morphology and muscle characteristics can predict relative swimming abilities, little is known about how the phasic and tonic adductor muscles are used during activity and of the influence of shell morphology. We reasoned that, as the intensity of phasic contractions should influence the development of thrust and lift, the pattern of utilisation of the phasic and tonic adductor muscles should vary with swimming ability and shell morphology.

Phasic muscle contractions are better understood than tonic contractions, primarily because phasic contractions are visible and more readily quantified. As the phasic adductor relies upon phosphagens for fuel and has limited endurance, it is analogous to fast glycolytic fibres in vertebrates (Grieshaber, 1978; de Zwaan et al., 1980; Livingstone et al., 1981). In contrast to the case in vertebrate fast muscle, glycogen breakdown provides limited metabolic support for scallop swimming, but is used during anaerobic and aerobic recovery (Livingstone et al., 1981). Tonic contractions have no direct analogue in vertebrate skeletal muscle. In the context of swimming escape responses, tonic contractions are used in a variety of situations. Prolonged tonic contractions occur once the phasic adductor muscle is fatigued, when most scallop species close their valves. Short tonic contractions separate series of phasic contractions during escape responses in both *Placopecten magellanicus* (Fleury et al., 2005) and *Argopecten purpuratus* (Pérez et al., 2009). Prolonged tonic contractions allow partial metabolic recovery of the phasic adductor (Pérez et al., 2008), potentially facilitating subsequent phasic contractions.

The objective of this study was to quantify the pattern of utilisation of phasic and tonic contractions by different species of scallops during escape responses to evaluate whether these patterns vary with morphology and lifestyle. Using a force gauge, we recorded phasic and tonic forces generated by different scallop species during responses stimulated by contact with predators. For each scallop species, we used the predator that elicited the strongest escape response, as identified from the literature and personal observations. Scallop performance was measured at habitat temperature (12.5–18.5°C). We used the number of phasic and tonic contractions, the duration of tonic contractions and the frequency of phasic contractions to characterise the use of the adductor muscle during simulated escape responses. We predicted that active scallops should make more phasic contractions, have a higher rate of phasic contractions and sustain these phasic contractions for longer periods compared with less active scallops. Less active scallops should rely more on tonic contractions when faced with predators.

The species chosen for this study correspond to the 'ecomorphs' established by Minchin (Minchin, 2003) according to swimming abilities and lifestyles, ranging from the most to the least active as follows: *Amusium balloti* (Bernardi 1861), *Placopecten magellanicus* Gmelin 1791, *Pecten fumatus* Reeve 1852, *Mimachlamys asperrima* (Lamarck 1819) and *Crassadoma gigantea* (J. E. Gray 1825). The morphological characteristics of *A. balloti*

suggest that it is the most accomplished swimmer (Yonge, 1936; Stanley, 1970; Gould, 1971; Thayer, 1972). Its shell is very light, symmetrical and slightly biconvex, with internalised ribs, small auricles and very smooth outer valve surfaces (Fig. 1). In its natural habitat, *A. balloti* is free living and found exposed or partly recessed on the seabed. As the maximum single-swim distance of *A. balloti* is greater than that recorded for any other scallop, Joll (Joll, 1989) suggested that *A. balloti* is a more active swimmer than *P. magellanicus* and *Amusium pleuronectes*. *P. magellanicus* is an active swimmer (Caddy, 1968; Dadswell and Weihs, 1990) and lives mainly exposed on the seabed. Its upper valve is more convex than the lower valve, providing a good hydrodynamic shape (Fig. 1) (Stanley, 1970; Thorburn and Gruffydd, 1979). As *P. magellanicus* grows, its valves become heavier and its swimming performance declines (Manuel and Dadswell, 1991). Like other members of the genus *Pecten*, the upper valve of *P. fumatus* is flat and the lower one convex (Fig. 1), a combination that is disadvantageous for swimming (Stanley, 1970; Gruffydd, 1976). Usually *Pecten* spp. lie recessed in the substrate in small depressions with their upper valves covered and roughly level with the seabed. *P. fumatus*, like other *Pecten*, is considered to have a moderate swimming ability, although it is capable of intense swimming when disturbed (Olsen, 1955; Baird and Gibson, 1956; Thomas and Gruffydd, 1971). Like many scallops of the subfamily *Chlamydinae*, *M. asperrima* is frequently byssally attached, but is capable of detaching and swimming when touched by its predator (Olsen, 1955; Vahl and Clausen, 1981; Brand, 2006). The valves of *M. asperrima* are biconvex, covered by external ribs and have asymmetical auricles (Fig. 1). The similar shell shape and aspect ratio of *Chlamys islandica* and *M. asperrima* suggests that these scallops have a limited swimming ability (Gruffydd, 1976). Finally, the purple-hinge rock scallop, *C. gigantea*, is free-living in early life (<20–30 mm shell height) and then cements its lower, right valve, to rocky surfaces (Yonge, 1951; Lauzier and Bourne, 2006). Once cemented, *C. gigantea* shells become heavily calcified and irregularly shaped, with shell height generally exceeding length (Fig. 1). *Crassadoma gigantea* is normally cryptic and its shell is covered by other organisms.

MATERIALS AND METHODS
Scallop sampling and experimental conditions
Amusium balloti
Mature *A. balloti* (89.5–113.4 mm shell height) were collected in August 2007 near Gladstone (Queensland, Australia) and were kept in holding tanks with running seawater (18.5°C, salinity ~35 p.p.t.) at the Bribie Island Aquaculture Centre (Woorim, Bribie Island, Queensland, Australia). Scallops were left undisturbed for 1 week before the escape response experiments.

Placopecten magellanicus
Mature *P. magellanicus* (85–95.9 mm shell height) were obtained from Cultimer (Cap-Aux-Meules, Îles-de-la-Madeleine, Québec, Canada) in September 2008. Approximately 1 week before the experiments, the scallops were transferred to holding tanks with seawater pumped in from the neighbouring lagoon (salinity ~30 p.p.t.) in the Ministère des Pêcheries et de l'Alimentation du Québec laboratory and were left undisturbed in the tanks. This period allowed them to recover from the transfer and to adjust to the laboratory conditions. Initially, the temperature was 17.5°C, but after a week, it dropped to 14°C and remained constant. We left the scallops another 3 days to habituate to this temperature prior to the escape response experiments.
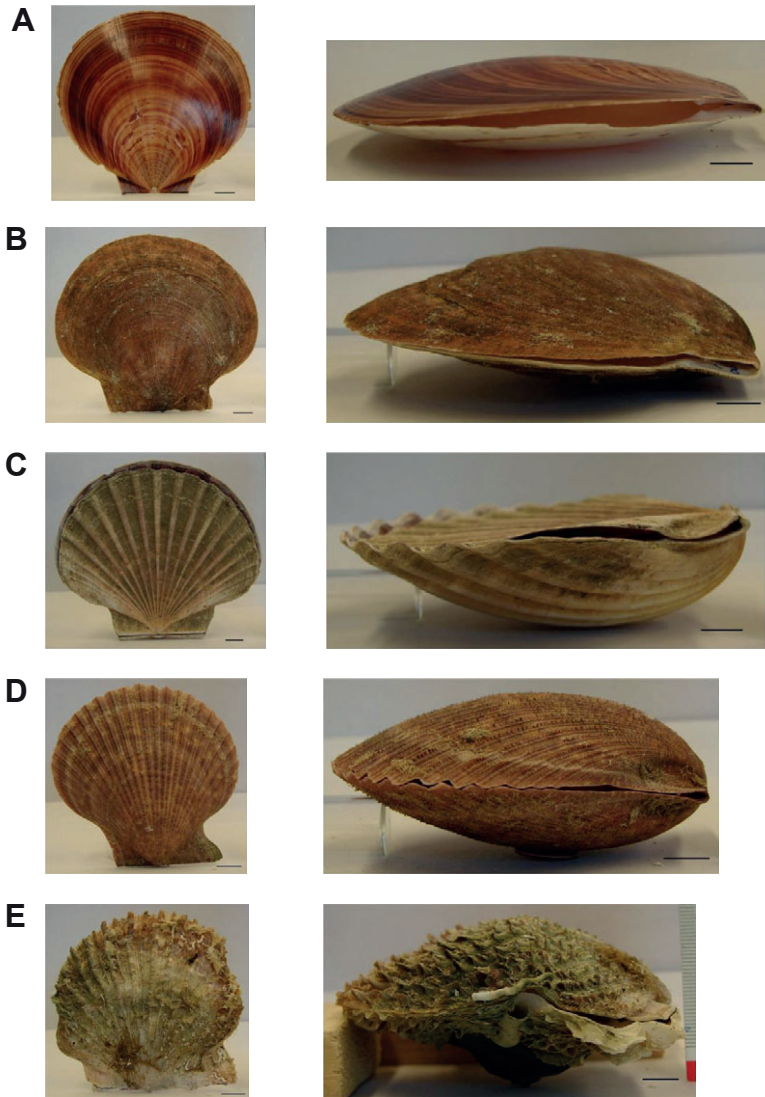
Fig. 1. Upper valve and side view of experimental scallops. (A) *Amusium balloti*, (B) *Placopecten magellanicus*, (C) *Pecten fumatus*, (D) *Mimachlamys asperrima* and (E) *Crassadoma gigantea*. Scale bars, 1 cm.

Pecten fumatus

Mature (85.7–103.7 mm shell height) *P. fumatus* were collected by SCUBA near Satellite Island (43°32′491″S and 147°23′297″E, Channel d'Entrecastreux, Tasmania, Australia) in September 2007. Scallops were transferred to the Tasmanian Aquaculture and Fisheries Institute (Taroona, Tasmania, Australia) where they were kept in tanks with running seawater (12.5°C, 34 p.p.t.). Scallops were left undisturbed in the tank for 1 week prior to the escape response tests.

Mimachlamys asperrima

Mature *M. asperrima* (70.5–95.2 mm shell height) were collected at the same time and locality as *P. fumatus* and were transferred to the Tasmanian Aquaculture and Fisheries Institute laboratory where they were kept in tanks with running seawater (12.5°C, 34 p.p.t.). Scallops were left undisturbed for 1 week prior to the escape response experiments.

Crassadoma gigantea

Mature *C. gigantea* were collected in May 2010 from oyster-rearing systems that had been in the water for the past 4–5 years near Espinosa Inlet (Vancouver Island, British Columbia, Canada). After collection, scallops (73.3–130.1 mm shell height) were transferred to the Centre for Shellfish Research (Vancouver Island University, Nanaimo, British Columbia, Canada) where they remained in tanks with running seawater (12.5°C, ~28 p.p.t.) for 1 week prior to the escape response experiments.

Experimental design and force recordings

We characterised force production of scallops during an escape response using a modified version (Guderley et al., 2008) of a previously described technique (Fleury et al., 2005). Although we refer to the recordings as escape responses, the scallops could not escape as they had their lower valve fixed, while the upper valve was free to move during stimulation by the predator. The lower valve of the scallop was attached to the bottom of a waterbath filled with seawater, whereas a lever, attached to a force gauge (AFG-50 N, Quantrol Advanced Force Gauge, Dillon, Fairmont, MN, USA), was placed under the ventral edge of the upper valve. The force gauge was mounted on a test stand that allowed us to use the lever to separate the valves by a distance corresponding to that observed in scallops at rest and ventilating normally. This distance was previously evaluated for each species. The upper valve was free to move and only downward movements were recorded by the force gauge. In *P. magellanicus*, this technique slightly reduces the total number of phasic contractions compared

with the number assessed by visual observations of the response of unattached scallops to their predator, but escape performance differences between age groups of *P. magellanicus* were independent of the measurement technique (H.E.G., unpublished observations). We chose the force gauge method as it provides considerable information concerning the use of the tonic and phasic adductor muscles. Once attached, the scallop was stimulated to contract by continuously stroking the mantle of the scallop with a predator. Each scallop was stimulated for 355 s, as preliminary tests showed that this was enough to exhaust all scallop species. We changed the water after every second scallop tested to keep the temperature constant. As each species presented specific morphological constraints, certain aspects of the experimental design differed, as detailed below.

Each *A. balloti* was identified with a permanent marker and the lower valve was attached to the bottom of the waterbath with a suction clamp. We used slipper lobsters, *Thenus orientalis* (~13 cm long), to induce escape responses, as this predator induces the strongest escape response in *A. balloti* (Himmelman et al., 2009).

Placopecten magellanicus were identified individually with a permanent marker. They were attached to the bottom of the waterbath using a suction clamp and the sea star *Asterias vulgaris* (~15 cm diameter) was used to induce escape responses.

Each *P. fumatus* had a plastic tag glued on its lower valve for subsequent identification. A nylon screw was fixed on the lower valve using Araldite glue and then the scallops were left at rest for 1 week prior to the experiments. For the escape response experiments, the scallops were attached *via* a bolt to an aluminium platform attached to lead weights in the waterbath. The escape response was stimulated by the sea star *Coscinasterias muricata*. As the sea star was too big for the experimental chamber, we removed an arm of the sea star and used it to stimulate the scallops.

Each *M. asperrima* was identified with a numbered plastic tag glued on the lower valve. We attached the scallops to the bottom of the waterbath with a suction clamp and used an arm of the sea star *C. muricata* to elicit the escape response.

We glued a screw to the lower valve of each *C. gigantea* using Araldite glue and etched a number in the glue to identify the individuals. For the escape response experiments, we attached the scallops to an aluminium frame that was attached to the bottom of the waterbath. We used the sea star *Pycnopodia helianthoides* (~20 cm diameter) to elicit the escape response.

Data recordings and analysis

Recordings from the force gauge (Fig. 2) were stored on a personal computer using Dataplot-X software (Dillon) and were then transferred to an Excel spread sheet for analysis of phasic and tonic muscle performance during the tests. As one person stimulated the scallop with the predator and controlled the computer, manipulations had to be done in a specific sequence. First, the scallop was fixed on the experimental setup and then the computer recording was started. Stimulation of the scallop with the predator started at the fifth second of the recording. Thus, we analysed the force recordings from the 5th to the 360th second, giving 355 s of force recording for analysis.

Phasic contractions are apparent as sharp peaks in the force recordings whereas sustained force production indicates tonic contractions (Fig. 2). We counted the total number of phasic contractions made by the scallop during the test. As the initial intensity of the response is important for survival upon encounters with a predator, we noted the number of phasic contractions during the first series, the minimal interval between two consecutive phasic

contractions and the contraction rate during the first 30 s (i.e. 5–35 s) of the test. We defined a series of phasic contractions as consecutive phasic contractions separated by <3 s. As the capacity to maintain swimming activity may be important when escaping a predator, we quantified the number of phasic contractions before fatigue, the number before the first tonic contraction, the percentage time spent in phasic contractions and the time to fatigue. We considered a scallop was fatigued when it made no phasic contractions during 1 min of stimulation with its predator.

Tonic contractions lead to sustained valve closure. For scallops that cannot close their valves tightly, valve closure does not offer protection against predators. Given the low energetic cost of tonic contractions, valve closure offers metabolic respite to the adductor muscle (Pérez et al., 2008). On the force recordings, tonic contractions were defined as sustained force production lasting more than 0.5 s (Fig. 2). We characterised tonic contractions by evaluating their total number, the number that lasted ≥5 s, the percentage of time spent in tonic contractions, the mean duration of contraction, the time until the initiation of the first tonic contraction and total number of phasic contractions relative to the total number of tonic contractions.

Anatomical and morphological measurements

We measured the height, length and width of the shells of each individual using a digital calliper (±0.01 cm). Shell height corresponded to the maximum distance between the dorsal (hinge) and ventral margins, whereas shell length was the maximum distance between the anterior and posterior margins and was perpendicular to shell height (Fig. 3). Shell width was measured at the point of maximum convexity with the two valves placed in their natural closed position (Fig. 3). Wet tissue mass was obtained after removing all the tissues from the shell and placing them on absorbent paper to remove excess water. We weighed the phasic and tonic adductor muscles, gonad and remaining soft tissues separately using a digital balance (0.01 g). Tissues were subsequently dried for 48 h at 60°C to assess dry mass and percentage water content. We assessed the total damp-dried shell mass of each individual. As the lower shell of *P. fumatus* and *C. gigantea* had a screw attached to it with Araldite glue, we used another sample of shells to establish the damp-dried shell mass and the relationship between shell dimensions and damp-dried shell mass.

The condition index was expressed as the wet mass of all soft tissues (g)/volume between the two valves (ml). The volume between the two valves was estimated by weighing the upper and lower valves filled with sand (500 µm sifted sand) level with the shell margin. As we knew the mass of a given volume of sand, we could estimate the volume in each valve to estimate the total volume.

Shell and soft tissue dry masses were adjusted to a shell height of 90 mm using the following formula:

$$\text{Corrected mass} = (A_1 \,/\, A_2) \times A_3 \,, \tag{1}$$

where A_1 was the mass expected for a 90 mm shell height scallop in the allometric series, A_2 the mass expected for a scallop the size of the experimental scallop in the allometric series and A_3 the measured mass for the experimental scallop. We adjusted mass to that of a standard scallop measuring 90 mm shell height as this size was present in the samples of all species studied.

Statistical analysis

Normality was tested using a Shapiro–Wilks test and the homogeneity of variance was analysed visually by plotting residuals relative to predicted values. Because of the non-normality
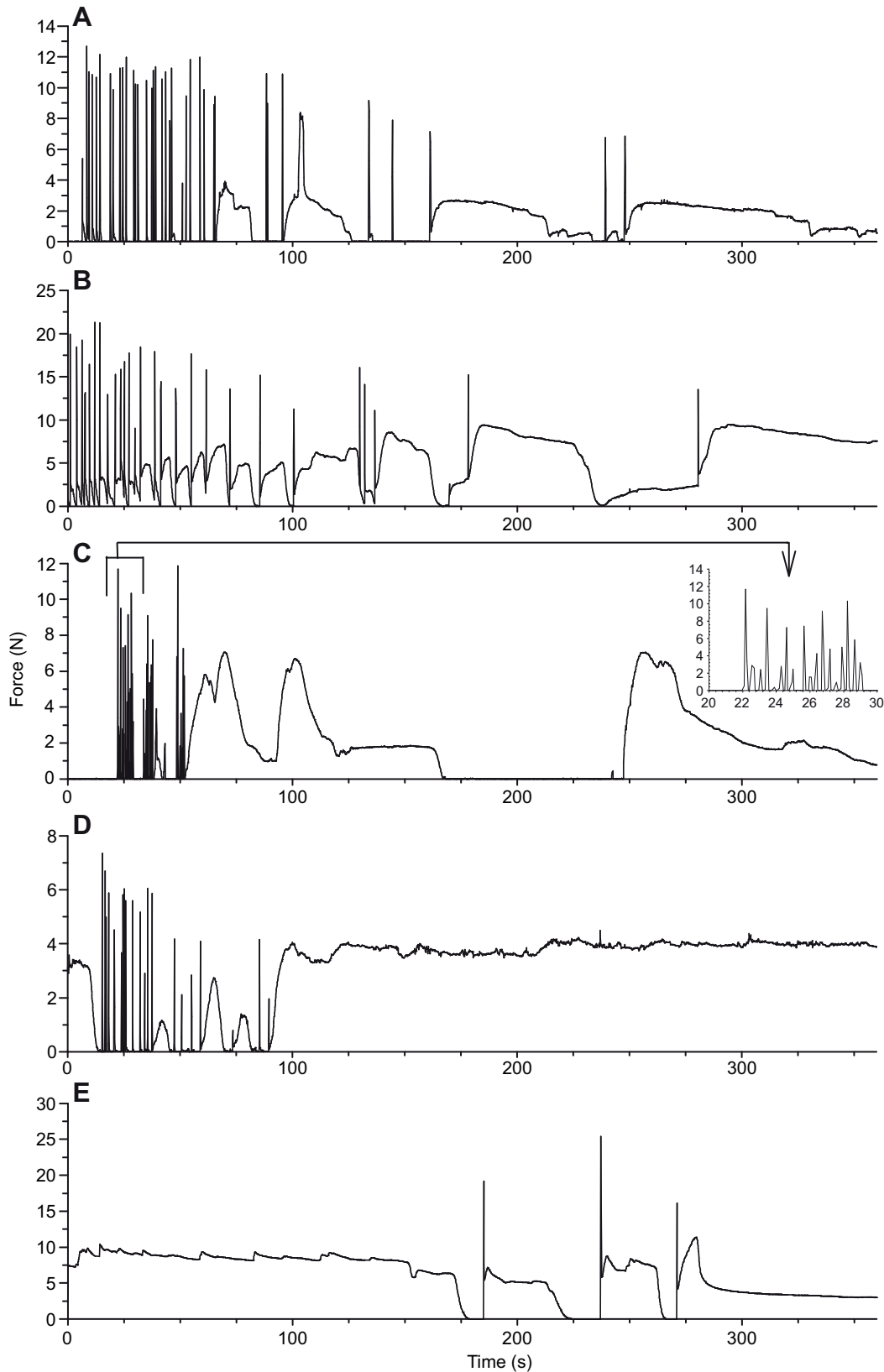
Fig. 2. Typical force recording during an escape response for each experimental scallop species: (A) *A. balloti*, (B) *P. magellanicus*, (C) *P. fumatus*, (D) *M. asperrima* and (E) *C. gigantea*. Sharp peaks correspond to phasic contractions whereas sustained force production indicates tonic contractions.

of residuals and non-homogeneity of variance, we used non-parametric tests. Comparisons between the different scallop species were made using Kruskal–Wallis tests. All analyses were done using SAS 9.2 (SAS Institute). Significance was accepted at $P<0.05$.

RESULTS

Shell and anatomical characteristics

The shell height of the different experimental scallop species overlapped, although the *M. asperrima* studied had a mean shell height of 84.2 mm and were slightly smaller than the other species
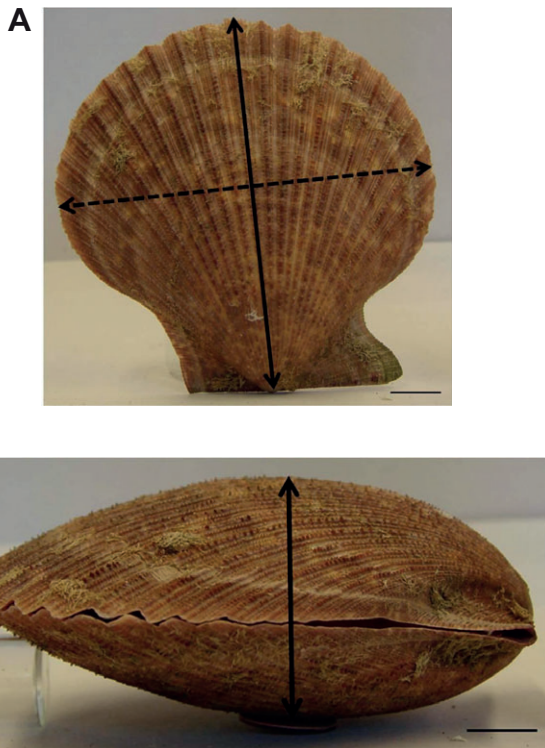
Fig. 3. Shell dimensions. (A) Solid line corresponds to shell height and dashed line is shell length. (B) Solid line corresponds to shell width.

gigantea (Table 1). Interspecific differences in the soft tissue dry mass were marked: *C. gigantea* usually had the largest mass and *A. balloti* had the lowest (Table 1). Tissue water content varied slightly between species with *A. balloti* having the highest (85.5%) and *C. gigantea* the lowest (79.2%) values (Table 1). *Crassadoma gigantea* had the highest condition index (0.61 g ml⁻¹) and *M. asperrima* the lowest (0.41 g ml⁻¹) (Table 1). All the species, except *A. balloti*, had mature gonads and a relatively high gonadosomatic index (Table 1).

Escape response recordings

For *A. balloti*, phasic contractions were spread throughout the tests, although most were made during the first 120 s (Fig. 2A). The first tonic contraction appeared quite late in the test. Tonic contractions were of relatively short duration, becoming longer as the test progressed. *Placopecten magellanicus* also spread its phasic contractions throughout the test, but alternated them with short tonic contractions (Fig. 2B). *Placopecten magellanicus* made many very short tonic contractions that became longer as the test progressed. *Pecten fumatus* made an intense burst of phasic contractions at the beginning of the test followed by relatively long tonic contractions (Fig. 2C). *Mimachlamys asperrima* started its response with a short tonic contraction, followed by a few series of phasic contractions interspersed with tonic contractions, ending with a prolonged tonic contraction that lasted until the end of the test (Fig. 2D). *Mimachlamys asperrima* made its phasic contractions at a slower rate than *A. balloti* and *P. fumatus*. *Crassadoma gigantea* usually made a prolonged tonic contraction that lasted throughout the test, but sometimes made a few phasic contractions (Fig. 2E).

Interspecific comparisons: phasic contractions

The scallop species considered to be active swimmers used their phasic muscle more than the less active scallops. *Amusium balloti* made the highest number of phasic contractions (41.0, Fig. 4A) and spent the greatest proportion of time in phasic contractions (2.8%, Table 2). *Pecten fumatus* and *P. magellanicus* were next in line, making respectively one-fifth and one-third fewer phasic

(Table 1). To compare the anatomical characteristics of the species, we adjusted shell and tissue masses to a common shell height of 90 mm. After this adjustment, *C. gigantea* had the heaviest shell (136.4 g) followed by *P. fumatus* and *P. magellanicus*, which had similar shell masses, equivalent to one-third the mass of *C. gigantea* (Table 1). The shells of *M. asperrima* and *A. balloti* were the lightest, being respectively 4 and 5 times less heavy than the shells of *C.*

Table 1. Shell and anatomical characteristics of experimental scallops

	Amusium balloti	Placopecten magellanicus	Pecten fumatus	Mimachlamys asperrima	Crassadoma gigantea
Shell					
Height (mm)	96.3±1.1[a]	90.4±0.9[b,c]	94.4±1.7[a,c]	84.2±2.0[b]	97.0±4.5[a,c]
Length (mm)	95.5±1.4	99.6±1.0	107.0±1.6	82.4±2.1	92.9±3.5
Width (mm)	19.8±0.4	27.7±0.4	22.6±0.4	31.3±1.1	34.5±2.0
Aspect ratio	1.01±0.004[a]	0.91±0.06[b]	0.88±0.0.01[b]	1.02±0.005[a]	1.04±0.03[a]
Mass at 90 mm height (g)	26.5±0.4[a]	48.8±1.1[b]	45.9±1.4[b]	32.7±0.7[c]	136.4±9.9[d]
N	27	15	15	16	19
Soft tissue dry mass (g)					
Total animal	2.00±0.08[a]	6.71±0.26[b]	4.96±0.30[c]	5.45±0.17[c]	8.87±0.55[d]
Phasic muscle	0.86±0.05[a]	3.08±0.13[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]	0.23±0.01[b]	0.17±0.01[c]	0.29±0.02[d]
N	18	15	15	16	19
Tissue indicators					
Water content in total animal (%)	85.5±0.2[a]	80.2±0.3[b]	84.1±0.4[c]	84.6±0.3[c]	79.2±0.3[d]
Water content in gonad (%)	87.3±0.7[a]	86.2±1.0[a]	82.8±0.8[b]	81.9±0.5[b]	80.3±0.4[d]
Condition index (g ml⁻¹)	0.48±0.01[a]	0.51±0.01[b]	0.42±0.02[c]	0.41±0.01[c]	0.61±0.02[d]
Gonadosomatic index (%)	5.4±0.3[a]	10.5±0.7[b,c]	11.5±0.7[c]	17.8±0.9[d]	9.9±0.6[b]
N	18	15	15	16	20

Data are means ± s.e.m.

Soft tissue dry mass was adjusted for 90 mm shell height.

Aspect ratio is the ratio of height/length. Total animal refers to all soft tissues including the adductor muscle. Condition index is the total animal wet mass/shell volume. Gonadosomatic index is calculated as (gonad tissue wet mass/total animal wet mass)×100.

In a given row, different letters indicate significant differences (Kruskall–Wallis and multiple comparisons, *P*<0.05).
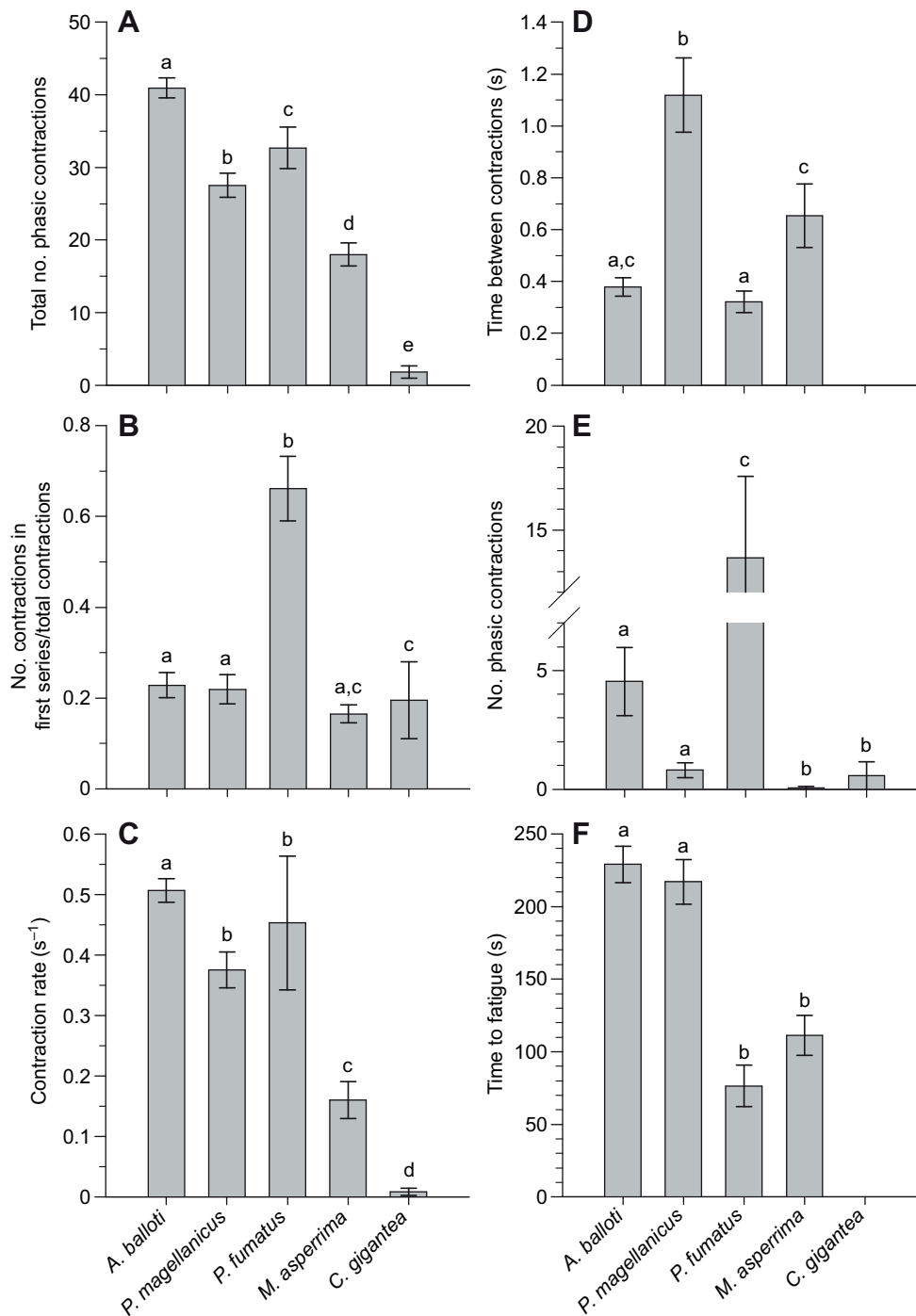
Fig. 4. Escape response parameters related to phasic contractions. (A) Total number of phasic contractions. (B) Total number of phasic contractions during the first series relative to the total number of phasic contractions. (C) Contraction rate during the first 30 s. (D) Minimum interval between two phasic contractions. (E) Number of phasic contractions before the first tonic contraction. (F) Time to fatigue. Data are means ± s.e.m. Different letters indicate significant differences (Kruskall–Wallis and multiple comparisons, $P<0.05$). Sample size: *A. balloti* N=30, *P. magellanicus* N=15, *P. fumatus* N=15, *M. asperrima* N=16, *C. gigantea* N=19.

contractions than *A. balloti* (Fig. 4A) and spending half to a third less time in phasic contractions than *A. balloti* (Table 2). *Mimachlamys asperrima* only made half the number of phasic contractions compared with *A. balloti* and spent the same proportion of time in phasic contractions as *P. magellanicus* (Table 2). Finally, *C. gigantea* primarily kept its valves closed and spent the lowest proportion of time in phasic contraction (Table 2).

The distribution of phasic contractions during the escape response varied among the scallop species. *Amusium balloti* and *P. magellanicus* spread phasic contractions throughout the tests, whereas *P. fumatus* and *M. asperrima* tended to concentrate theirs (Fig. 2), generally at the beginning of the test. The timing of phasic contractions by *C. gigantea* was unpredictable (Fig. 2E). Most of

the scallop species made ~20% of their phasic contractions during the first series (phasic contractions not separated by more than 3 s), but *P. fumatus* made 66% of its phasic contractions during the first series (Fig. 4B). The phasic contraction rate during the first 30 s was highest for *A. balloti* (0.51 phasic contractions s^{-1}, Fig. 4C), slightly less for *P. fumatus*, and still less for *P. magellanicus* (Fig. 4C). The rate for *M. asperrima* was approximately one-third that of *A. balloti* and *C. gigantea* had the lowest rate (Fig. 4C) compared with that of *A. balloti*. *Amusium balloti* and *P. fumatus* could make phasic contractions in quick succession as shown by the short minimal interval between two successive phasic contractions (0.38 and 0.32 s, respectively, Fig. 4D). In contrast, repetition of phasic contractions by *P. magellanicus* and *M. asperrima* was much slower and *P.*

Table 2. Behavioural parameters related to phasic contractions during escape responses by the different scallop species

	Amusium balloti	Placopecten magellanicus	Pecten fumatus	Mimachlamys asperrima	Crassadoma gigantea
Number of phasic contractions before fatigue	39.1±1.5[a]	26.7±1.7[b]	32.0±2.8[c]	13.3±1.4[d]	1.4±0.7[e]
Percentage of time spent in phasic contractions	2.8±0.1[a]	1.0±0.1[b]	1.3±0.1[c]	0.9±0.1[b]	0.2±0.1[d]

Phasic parameter data are means ± s.e.m. Sample size: *A. balloti* N=30, *P. magellanicus* N=15, *P. fumatus* N=15, *M. asperrima* N=16, *C. gigantea* N=19.
In a given row, different letters indicate significant differences (Kruskall–Wallis and multiple comparisons, $P<0.05$).

magellanicus had the longest gap between phasic contractions of the species studied, except *C. gigantea* (Fig. 4D). Given the sporadic nature of phasic contractions by *C. gigantea*, we did not calculate its minimal interval between contractions.

Interspecific comparisons: tonic contractions

Our escape response recordings revealed considerable interspecific variation in the use of tonic contractions. *Placopecten magellanicus* made the highest number of tonic contractions with a mean of 20.9 (Fig. 5A). *Amusium balloti* made approximately half as many and *P. fumatus* and *M. asperrima* made about one-third as many (Fig. 5A). *Placopecten magellanicus* and *A. balloti* made the shortest tonic contractions (mean of 16.2 and 20.9s, respectively, Fig. 5B). The tonic contractions of *M. asperrima* and *P. fumatus* were 2–3 times longer than those of *P. magellanicus* but those of *C. gigantea* were by far the longest (276.3s, Fig. 5B). For *C. gigantea*, all tonic contractions lasted longer than 5s, whereas for the other species, half of the tonic contractions lasted 5s or less (Fig. 5F). The pronounced differences in the number (and duration) of tonic contractions led to considerable variability in the ratio of phasic to tonic contractions; from 5.3 for *P. fumatus* and 4.0 for *A. balloti* to 1.6 for *M. asperrima* and 1.4 for *P. magellanicus* (Fig. 5C).

Generally, the more active species spent less time in tonic contractions and began them later than the less active species. *Pecten fumatus* spent the least time in tonic contraction (65%) and *A. balloti* spent slightly but not significantly longer (Fig. 5E). The time spent in tonic contractions was similar for *P. magellanicus* and *M. asperrima* (about 82%). This was surprising given that *M. asperrima* is a less active swimmer (Fig. 5E). *Crassadoma gigantea* spent almost all the test in tonic contraction (93%, Fig. 5E). The less active scallops, *M. asperrima* and *C. gigantea*, started using tonic contractions when first touched by their predator (Fig. 5D). *Placopecten magellanicus* made their first tonic contraction within seconds of the beginning of the test (Fig. 5D). Both *A. balloti* and *P. fumatus* made numerous phasic contractions before their first tonic contraction (Fig. 2A,C). *Amusium balloti* took eight times longer than *P. magellanicus* to make its first tonic contraction and *P. fumatus* took 30 times longer (Fig. 5D).

DISCUSSION

Although all scallops use jet propulsion to swim at some point in their lives, the species we compared varied considerably in their use of the adductor muscle during escape responses. Both the timing and frequency of phasic contractions varied markedly. The use of tonic contractions varied greatly among the species. Some species made many short tonic contractions throughout the escape response, others only used tonic contractions after a major phasic effort, and still others started the tests with tonic contractions. Effectively, each species adopted a specific combination of phasic and tonic contractions that presumably facilitates escape from predators within the constraints of their morphology, habitat and lifestyle. Our analysis suggests that differential use of the adductor muscle can

facilitate swimming despite quite marked differences in shell morphology, including some morphologies that appear hydrodynamically unfavourable. Alternatively, when scallop species can avoid predation by closing their valves, they can use the more energetically efficient tonic contractions, avoiding the costs of phasic contractions.

Eco-morphological classification *versus* phasic and tonic contractions

In general, the eco-morphological classification (Minchin, 2003) of our scallop species predicted the patterns of use of phasic contractions during escape response tests. The most hydrodynamic species, *A. balloti*, relied the most on phasic contractions. We tested *A. balloti* in August, during the Australian winter and after spawning. Even during this period of relatively low natural responsiveness (Himmelman et al., 2009), *A. balloti* showed more phasic activity than the other species. *Placopecten magellanicus* and *P. fumatus* were next in sequence for high phasic activity. Presumably because of its hydrodynamically unfavourable shell morphology (Stanley, 1970), *P. fumatus* makes a particularly intense series of phasic contractions at the start of its response to get up off the seabed. By contrast, the timing of the bursts of phasic contractions by *M. asperrima* was much less predictable than for *P. fumatus*. Finally, *C. gigantea* only occasionally made phasic contractions in response to stimulation by their predator, this not being their primary response.

Only some of the interspecific variation in the use of tonic contractions could be predicted from the use of phasic contractions or from the eco-morphological classification. Species making many phasic contractions (*A. balloti*, *P. magellanicus* and *P. fumatus*) made more and shorter tonic contractions than species making few phasic contractions. The more sedentary species, *M. asperrima* and *C. gigantea*, often initiated the response to the predator with tonic rather than phasic contractions. The time spent in tonic contractions did not follow any obvious correlation with the eco-morphological classification. For example, *P. magellanicus* is considered a good swimmer but its frequent use of short tonic contractions, appearing early in the escape response test, led it to spend a similar proportion of time in tonic contractions to *M. asperrima*. The numerous brief tonic contractions by *P. magellanicus* were unexpected and their role remains to be elucidated.

Initiation of prolonged tonic contractions: metabolic fatigue or energy saving?

The initiation of prolonged tonic contractions presumably reflects fatigue of the phasic adductor muscle in active scallops, whereas it may be the preferred response to predators in more sedentary scallops. Fatigue is presumably caused by an inability of the phasic adductor to contract as a result of its metabolic status. *Amusium balloti* and *P. magellanicus* made phasic contractions throughout the escape response, and fatigued much later in the tests than the three other species (Fig. 4F). By contrast, despite being quite active,
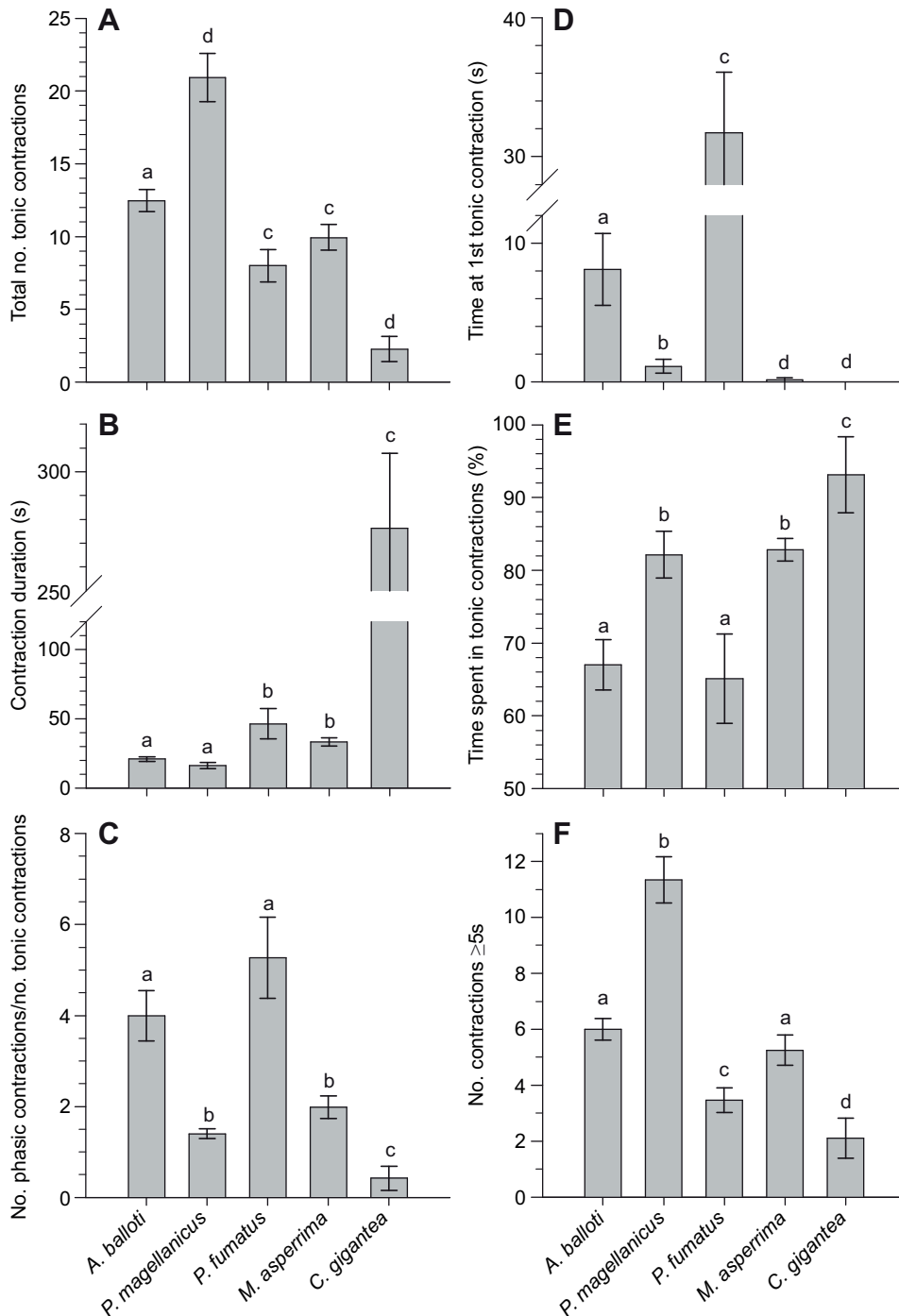
Fig. 5. Escape response parameters related to tonic contractions. (A) Total number of tonic contractions. (B) Mean duration of tonic contractions. (C) Total number of phasic contractions relative to the total number of tonic contractions. (D) Time at the first tonic contraction. (E) Percentage of time spent in tonic contractions. (F) Number of tonic contractions of a duration of 5 s or more. Data are means ± s.e.m. Different letters indicate significant differences (Kruskall–Wallis and multiple comparisons, $P<0.05$). Sample size: *A. balloti* N=30, *P. magellanicus* N=15, *P. fumatus* N=15, *M. asperrima* N=16, *C. gigantea* N=19.

P. fumatus fatigued quickly, presumably as a consequence of the intense deployment of phasic contractions in its initial response to the predator. Much like the burst flight of pheasants, the burst of phasic contractions by *P. fumatus* is needed to propel this awkwardly shaped scallop through the water, but requires an unsustainable power output. Scallops use phosphoarginine as the major source of ATP for phasic contractions (Livingstone et al., 1981; Bailey et al., 2003). *Pecten fumatus* probably used much of its phosphoarginine in its initial burst of phasic contractions, explaining the rapid fatigue. For the active scallops, *A. balloti*, *P. magellanicus* and *P. fumatus*, it is likely that the initiation of relatively long tonic contractions reflects depletion of phosphoarginine and a decrease in the free energy of ATP hydrolysis in the phasic adductor (Bailey et al., 2003;

Pérez et al., 2008). The less active species, *M. asperrima* and *C. gigantea*, made few phasic contractions and often made prolonged tonic contractions during the initial responses to the predator. Such early use of tonic contractions is unlikely to be due to metabolic fatigue of the phasic adductor. This reliance on tonic contractions probably reflects an alternative defence against predation whereby prolonged closure of a robust, tightly closing shell provides adequate protection. Our observations of the gaps between the closed valves of our scallops allowed us to see differences between experimental species (Fig. 1). We can rank the species from the most to least tightly closed shells as follows: *C. gigantea*, *M. asperrima*, *P. fumatus*, *P. magellanicus* and *A. balloti*. If valve closure is an effective defence against predation, the use of energetically efficient tonic contractions

would decrease the need for phosphoarginine-powered phasic contractions. This suggests that interspecific differences in the total number of phasic contractions may be paralleled by differences in the phosphoarginine content of the phasic adductor. In turn, interspecific differences in time to 'fatigue' would reflect the phosphoarginine content, the intensity of phosphoarginine use during phasic contractions and the efficacy of valve closure as a defence against predation.

Interspecific differences in the use of tonic contractions raise the question as to their role and importance. The best known roles of tonic contractions are in prolonged valve closure and maintenance of specific valve opening during routine ventilation. In both, the lower energetic cost of tonic contractions is beneficial. Force recordings revealed that *P. magellanicus* alternate between phasic and tonic contractions during escape responses (Fleury et al., 2005) leading to the suggestion that tonic contractions facilitate metabolic recovery of the phasic adductor muscle. In *P. magellanicus*, long tonic contractions (1 min) do allow partial metabolic recovery of the phasic adductor muscle as the adenylate energy charge returns to control levels (Pérez et al., 2008). However, replenishment of phosphoarginine takes longer (Grieshaber, 1978; Livingstone et al., 1981; Chih and Ellington, 1983; Bailey et al., 2003; Pérez et al., 2008). Comparison of force recordings of electrically stimulated *versus* sea star-stimulated *P. magellanicus* [fig. 4 in Pérez et al. (Pérez et al., 2008)] shows that short (<5 s) tonic contractions are absent in electrically stimulated scallops, although prolonged tonic contractions begin at a similar time in scallops stimulated electrically and by sea stars. We believe that improvement of the energetic status of the phasic adductor is unlikely to occur during short duration tonic contractions. Given the lack of a plausible metabolic role for short tonic contractions, interspecific differences in the use and duration of tonic contractions may reflect functional attributes of the tonic adductor muscle. Scallop tonic adductor muscles use the catch mechanism typical of molluscan smooth muscle, which allows maintenance of tension at a relatively low cost of ATP (Lowy and Millman, 1963). Tonic muscle contains a high quantity of paramyosin at the core of the myosin-containing thick filaments (Chantler, 1983). In addition to its structural role, paramyosin may play an indirect role in the maintenance of catch (Chantler, 2006). Most of our knowledge of molluscan catch muscle physiology comes from studies of the anterior byssus retractor muscle of *Mytilus edulis*. It is unknown whether these characteristics apply to scallops and if they vary between species. Interestingly, Bayliss and colleagues observed that *in vitro* 'contracture' (tonic contraction) of the tonic adductor muscle diminished in an hour in *P. maximus*, while that of *P. magellanicus* fell to low values much more quickly (Bayliss et al., 1930). Possibly, interspecific differences among scallops in the catch mechanism and in tension development during tonic contractions underlie the differences in the use of tonic contractions during escape responses.

Habitat temperature and escape response patterns

In designing this study, we characterised each species at habitat temperatures at sampling and timed our sampling to have similar measurement temperatures for these species. Thus *C. gigantea*, *M. asperrima* and *P. fumatus* were measured at 12.5°C, *P. magellanicus* at 14°C and *A. balloti* at 18.5°C. Many aspects intervene to establish the impact of temperature upon performance. Each species has its thermal optimum for performance and individual thermal history can modify the position of this optimum (Guderley et al., 2009). Intraspecific thermal sensitivities provide a guide to the potential impact of the differences in measurement temperature in

our study. In *P. magellanicus*, total number, overall rate and minimum interval between phasic contractions differed little between 12 and 18°C but clapping rate in the first series increased (Guderley et al., 2009). This suggests that although *A. balloti* was measured at the highest temperature, its performance was not markedly enhanced by this thermal difference. Furthermore, as 18.5°C is a cool temperature for *A. balloti*, we may be underestimating its performance. Thus, we conclude that the interspecific performance differences we observed are not a reflection of the differences in measurement temperature.

Potential influence of ontogenetic changes on escape responses

Our study of interspecific differences in the use of the phasic and tonic adductor muscles during scallop escape responses aimed to interpret these patterns in the context of morphology and lifestyle (habitat and activity levels). Nonetheless, morphology and lifestyle change during ontogeny and these changes may affect escape response performance. Although we compared scallops within a similar size range to reduce the influence of size, as the species we studied reach different maximal sizes (*A. balloti* 110 mm, *P. magellanicus* 150 mm and sometimes up to 200 mm, *P. fumatus* 145 mm, *M. asperrima* 110 mm and *C. gigantea* 250 mm) [Lauzier and Bourne (Lauzier and Bourne, 2006) and references therein] (see also Edgar, 2001; Dredge, 2006; Naidu and Robert, 2006), we must consider the potential influence of ontogenetic state in interpreting interspecific differences in adductor muscle use.

For any shell shape, basic allometric considerations predict certain aspects of swimming performance. As body mass increases in proportion to the cube of shell length (L^3) and lift requirements increase in proportion to L^2 (Gould, 1971), larger scallops need to swim more rapidly (employing more phasic contractions) to produce enough lift to compensate for their increased mass (Gould, 1971; Gruffydd, 1976). The size dependence of swimming is best known in *P. magellanicus* (Dadswell and Weihs, 1990; Manuel and Dadswell, 1991; Manuel and Dadswell, 1993). Hydrodynamic efficiency and swimming performance peak between 40 and 80 mm shell height, after which both decrease (Dadswell and Weihs, 1990). Properties of the adductor muscle in *P. magellanicus* show similar size dependence; enzymatic activities and phosphoarginine content peak at a shell height of 60 mm and decline at greater sizes (Labrecque and Guderley, 2011). Parameters related to escape response endurance, the number of phasic contractions and force production peak at 70 mm shell height and then decrease (Labrecque and Guderley, 2011). In many species, small scallops are more active than larger ones (Yonge, 1936; Olsen, 1955; Baird and Gibson, 1956; Caddy, 1968; Gruffydd, 1976; Tremblay et al., 2006; Labrecque and Guderley, 2011). The pattern of movement (swimming *versus* jumping) may also vary with size/age, with small *Aequipecten opercularis* swimming more than large individuals (Schmidt et al., 2008). Ontogenetic changes in behaviour can occur in response to the predators in an environment, as greater size can provide a refuge from predation, allowing larger scallops to reduce their response to predators (Barbeau and Scheibling, 1994; Wong and Barbeau, 2003). Ontogenetic variation in performance also reflects the increasing influence of reproductive investment as scallops become larger and favour reproductive investment over escape response capacities (Brokordt et al., 2000a; Brokordt et al., 2000b; Kraffe et al., 2008). All the species we studied were near their spawning season; only *A. balloti* had finished spawning at the time of the experiment (Table 1). Even though spawning can reduce swimming performance and recovery (Brokordt et al., 2000a; Brokordt et al., 2000b; Kraffe

et al., 2008), *A. balloti* was the most active species tested, confirming that, if anything, we underestimated its capacities relative to the other species.

Links between shell morphology, lifestyle and escape response behaviour

Interpretation of the interspecific differences in muscle use during escape responses must take shell morphology, lifestyle and potential predators into account. Of the species we studied, the shell morphology of *A. balloti* has the most attributes favouring swimming (Gould, 1971). The hydrodynamic shape and light mass of *A. balloti* allows it to climb easily in the water column and glide efficiently (Gould, 1971). Nonetheless, *A balloti* makes an intense series of phasic contractions at the beginning of its escape response. *Amusium balloti* is unusual, compared with other scallops, as it reacts very strongly to crustaceans. Of a suite of potential predators including crustaceans and a sea star, *T. orientalis* elicited the strongest escape response from *A. balloti* (Himmelman et al., 2009). *Thenus orientalis* can suddenly extend its tail to lunge forward to seize its prey at a distance of 30–50 cm (Jones, 2007). Once caught, *A. balloti* is vulnerable because the gaps between the valves provide openings through which *T. orientalis* can insert its appendages. Himmelman and colleagues suggested that the most critical step in *A. balloti*'s escape from *T. orientalis* is the time to get off the sea bottom (Himmelman et al., 2009). To escape this very active predator, *A. balloti* needs to produce significant thrust rapidly. The high rate of phasic contraction produced by *A. balloti* during the first 30 s of the escape response, as well as its highly hydrodynamic shell, should allow it to escape a predator with good swimming performance.

Placopecten magellanicus has an excellent shell shape for lift production (Stanley, 1970; Gruffydd, 1976; Thorburn and Gruffydd, 1979); however, its shell mass is relatively high compared with that of *A. balloti* (Table 1). Both juvenile and adult *P. magellanicus* responded to stimulation by crabs, but the most vigorous escape response was obtained with predatory sea stars (H.E.G., unpublished) (Wong and Barbeau, 2003). *Placopecten magellanicus*, particularly those of smaller size, are preyed upon by numerous predators (Elner and Jamieson, 1979; Naidu et al., 1986; Barbeau and Scheibling, 1994). Sea stars (*A. vulgaris*) prefer small individuals, presumably because of their greater vulnerability (Barbeau and Scheibling, 1994), and rock crabs (*Cancer irroratus*) only feed on small scallops (≤72 mm shell height) (Elner and Jamieson, 1979). Nonetheless, small juvenile scallops are less responsive to crabs than to sea stars. It is possible that, even with their good swimming capacities, juvenile *P. magellanicus* cannot escape fast moving crabs. The simultaneous decline in hydrodynamic efficiency, adductor muscle physiological capacities and swimming behaviour above a shell height of 65 mm (Labrecque and Guderley, 2011) may indicate that *P. magellanicus* no longer 'need' to swim once they have reached a certain size. This may explain the lower swimming performance of large *P. magellanicus* despite their apparently advantageous shell shape.

The flat upper valve and the convex lower valve of *P. fumatus* are not considered advantageous for lift generation or swimming (Verrill, 1897; Baird, 1958; Stanley, 1970). Like *P. magellanicus*, *P. fumatus* shells are heavy compared with those of other scallops of a similar size (Table 1). At the beginning of its escape response, *P. fumatus* carries out an intense burst of phasic contractions. This reaction indicates that *P. fumatus* uses contractile activity to overcome the constraints of its shape and mass. The intense burst of phasic contractions of *P. fumatus*, in response to its predator,

presumably allows it to attain enough speed to rise into the water column and swim away from potential predators.

For the less active *M. asperrima* and *C. gigantea*, predators may be deterred by valve closure and shell characteristics. *Mimachlamys asperrima* retains the capacity for byssal attachment throughout its life. Its shell is frequently covered by sponges, which is known to inhibit predation by sea stars (Pitcher and Butler, 1987). *Crassadoma gigantea* are free living as juveniles but cement to rocks as adults, presumably once they are sufficiently large and heavy. The shells of cemented *C. gigantea* are irregularly shaped, their outer surface is spiked and the shell is encrusted with many organisms, providing camouflage. They can also avoid predators by cementing into places that are difficult to reach. Although *C. gigantea* loses its swimming ability once cemented (Yonge, 1951; Lauzier and Bourne, 2006), phasic contractions may by retained as a means of cleansing the mantle cavity, reflecting the ancestral condition from which scallop swimming may have arisen (Yonge, 1936).

Our study is the first to examine interspecific differences in the use of phasic and tonic contractions during escape responses by scallops. Our observations revealed a variety of patterns of phasic contractions as well as marked differences in the type and deployment of tonic contractions. Short tonic contractions are widely used by more active scallop species, but their functional significance remains to be elucidated. To swim, a scallop can adjust some of its behaviour to compensate for its morphology. The use of phasic contractions to swim is energetically expensive, particularly for species with a disadvantageous shell shape. Keeping the valves shut for prolonged periods, using tonic contractions, is energetically cheap but requires tight junctions between the valves to prevent predation. Although all scallops have a simple locomotor system, our comparisons indicate that many factors intervene to determine muscle use during escape responses. Further, the position and proportions of the phasic and tonic adductor muscles, as well as the metabolic capacity of the muscles, will influence escape response performance. The properties of the hinge ligament will set an upper limit to the frequency of phasic contractions. These physiological and biomechanical properties have presumably co-evolved to facilitate escape response performance. This performance, in turn, must be adjusted to the ecological context within which each species exists. Alternatively, behavioural flexibility may allow scallops to overcome morphological constraints and to adjust to changing conditions. The marked interspecific variation in muscle use during escape responses clearly reflects such behavioural flexibility. Scallops respond to contact with a predator either by swimming away or by prolonged valve closure. Selection for these behaviours should favour different patterns of co-evolution of the underlying traits. The theory of symmorphosis postulates that the structural design of living systems is quantitatively matched to functional demands (Weibel et al., 1996). This implies a co-evolution of capacity at different levels of organisation and stipulates that no excess structure is maintained. Overall, the 'design' of oxygen and substrate use pathways in dogs and goats conforms to these principles, although pulmonary capacity exceeds that at other levels (Weibel et al., 1996). If symmorphosis also applies to scallops, the physiological and biomechanical properties favouring swimming should decrease in scallops that close their valves in response to their predator. Our analysis of the patterns of use of the adductor muscle indicates such changes of muscle use and predicts that the biochemical, biomechanical and morphological properties should show similar interspecific differences.

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