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Maike Schmidt [a]; Eva E. R. Philipp [a]; Doris Abele [a]

[a] Department of Biosciences, Shelf Sea Ecology, Alfred-Wegener-Institute for Polar and Marine Research, Bremerhaven, Germany

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ORIGINAL ARTICLE

Size and age-dependent changes of escape response to predator attack in the Queen scallop *Aequipecten opercularis*

MAIKE SCHMIDT, EVA E. R. PHILIPP⋆ & DORIS ABELE⋆

Alfred-Wegener-Institute for Polar and Marine Research, Department of Biosciences, Shelf Sea Ecology, Bremerhaven, Germany

Abstract
Physiological fitness and exercise capacity decrease with age in humans and rodents, a finding for which, among other causes, the decline of cellular and especially mitochondrial functions with age is held responsible. We investigated changes of escape response to predator attacks in swimming scallops (*Aequipecten opercularis*) with size using the natural predator *Asterias rubens*. *Aequipecten opercularis* swim mainly to avoid predators and a decrease in swimming abilities would increase risk of capture and lower survival. The queen scallop *A. opercularis* is a very active, epibenthic species with a short lifespan of 8–10 years and a shell height up to 90 mm in the investigated fishing ground around the Isle of Man. No difference in clap rate was found between smaller and bigger *A. opercularis* individuals, but differences were found in swimming mode (jumping and swimming) and valve opening and closure behaviour between the two size groups in response to predator attack. Smaller individuals showed less jumping movements and closed valves more often and remained closed for longer time than bigger animals. The difference in swimming behaviour is discussed in respect to size and age-dependent changes in morphology and cellular physiology as well as interactions of different main predators (sea stars, crabs) with the different size classes.

Key words: *Predators, scallops, size, swimming*

Introduction

As animals grow in size and age they transform morphologically and biochemically, often involving changes of behaviour and physiological responsiveness to environmental stressors (Castagna & Chanley 1973; Paul 1980; Tatar et al. 1997). These may either be abiotic stressors like temperature or salinity extremes in marine environments, but may also consist of organisms' interactions through predation, competition or parasitism. *Aequipecten opercularis* (Linnaeus, 1758), also called queen scallop or queens, belongs to the pectinid family which, together with the cephalopods, represent the only molluscs which developed jet propulsion swimming. The scallop has a wide geographical distribution on the European continental shelf from Northern Norway to Gibraltar and within the Mediterranean (Waller 1991). Maximum lifespan of *A. opercularis* around the Isle of Man is about 8–10 years with a maximum shell height of about 90 mm. Young *A. opercularis* are often attached by byssus while older individuals lie freely on the sediment (Ansell et al. 1991). The species has a high commercial value and is fished, for example in the north Irish Sea around the Isle of Man. *Aequipecten opercularis* are active swimmers and sensitive to disturbance. Danger is sensed over astonishing distances so that a swimming escape reflex is initiated up to 1.5 m away from approaching divers or fishing gear (Chapman 1981). Around the Isle of Man *A. opercularis* damaged by fishing gear, but also undamaged *A. opercularis*, are preyed upon by starfish *Asterias rubens*, crustaceans *Pagurus* spp., *Cancer pagurus* and the demersal fish *Callionymus lyra* (Veale et al. 2000).

Two pioneers in describing the swimming ability of scallops were Buddenbrock (1911) and Yonge (1936). Both interpreted this movement as a modification of the mantle cavity cleansing mechanism. The cooperative action of shell, adductor muscle

and mantle enables the scallops to locomote by swimming (Moore & Trueman 1971). A typical swim series is divided into three phases: in the first phase the scallop lifts from the ground and rises at an angle of 30–50° into the water column, the second phase consists of horizontal swimming in the water column and is characterized by high frequent clapping of the valves, the animal moving with the ventral edge foremost. The third phase is the passive sinking to the sea floor (Brand 1991). In situ studies of Chapman and co-workers (1979) on the queen scallop yielded swimming velocities between 29 and 40 cm per second and a distance of 1.5 m covered within one swim series. In many scallop species an escape response to various forms of stress has been documented (Paul 1980; Wong & Barbeau 2003). The response seems to be versatile, and a single species can show graded response reactions upon attack of different sea stars, meaning that the animals react stronger to predatory than non-predatory sea stars (Thomas & Gruffydd 1971).

Predator–prey experiments with diverse animal phyla indicate that a decline in physiological fitness leads to lower survival probability in prey organisms with active escape response, so that it seems advantageous for such species to stabilize physiological fitness over lifetime. This is in line with theoretical studies by Abrams (1993) and Williams & Day (2003), who presented a general rationale saying that increased probability of extrinsic mortality (e.g. higher predation pressure) early in life improves selection for slower senescence deterioration. In other words: subcritical stress at a young age may improve late survival. A recent study by Reznick et al. (2004) on guppies indeed indicates such a relation to exist between predation pressure and senescence.

These concepts would assume conservation of swimming capacities with increasing size and age in *A. opercularis*. However, degenerative processes were also observable and significant in the queen scallop, albeit less obvious than in mud clams, with increasing size (Philipp et al. 2005a,b, 2006). Mitochondrial respiration and key metabolic enzyme activities [citrate synthase (CS) and cytochrome oxidase (COX)] in mantle tissue of *A. opercularis* declined with increasing size and age (Philipp et al. 2006). The question arises whether these changes are already sufficient to lead to impaired physiological function in bigger, older animals compared to smaller, younger animals. In general it is observed in scallops that large individuals swim less readily and often (Jenkins et al. 2003; for review see Brand 1991). Thus, although swimming behaviour of scallops has been thoroughly investigated (Grieshaber 1978; Thompson et al. 1980; Chih & Ellington 1983;

Bailey et al. 2003) the important question as to whether or not swimming activity and physiological fitness change with size and age have not been resolved. In the present study we tested the changes of swimming activity and escape response to sea star attack in smaller and bigger *A. opercularis* to investigate if there is a general loss in physiological fitness with size and age in queen scallops.

Material and methods

Sampling and maintenance

Irish Sea queen scallops, *Aequipecten opercularis*, were dredged 12 miles south of Port St. Mary, Isle of Man in July 2005 at about 50 m water depth. Animals were transported to the Port Erin Marine Laboratory and kept in natural seawater flow-through aquaria at $\sim 14°C$ and 34 PSU for 2 weeks. Animals were transported in thermoboxes with wet cotton wool and supplemented with oxygen and cold packs to the Alfred-Wegener-Institute of Polar and Marine Research, Germany. *Aequipecten opercularis* individuals were kept in flow-through aquaria at $\sim 10°C$ (mean in-situ temperature) and 34 PSU for 2 weeks prior to experimentation and fed live plankton twice a week (DT's Live Marine Phytoplankton®).

Individuals grouped in two size classes: small animals from 39 to 58 mm and thus below marketable size (Jenkins et al. 2003) and bigger animals from 63 to 77mm shell height. Age was determined from shell size, using the von Bertalanffy growth function (VBGF) of Philipp et al. (2006) based on animals of the same sampling location. Mean age of the small animals was 2 years (SD 0.5), and 4 years (SD 0.5) for the large animals.

Swimming experiments

Experimental setup. Twenty-four hours before the experiment, a Teflon nut was glued to the lower shell of each individual using plastic glue (Artisil Adeseal, Innotec Dtld.G.Pannenbecker KG) as described in Jenkins et al. (2003). A Teflon screw was fixed in the experimental setup aquarium in a constant temperature (cT) room at a 10°C. Salinity was 34 PSU. The aquarium sides were covered with black plastic foil to avoid irritation of the experimental animals by people moving in the cT room. A small gap was kept free for the video camera (DCR-VX2000E, Sony) to record shell adductions (claps) during the experiment. The video camera was connected to a Computer (Toughbook RC-29, Panasonic), to control the camera and store the movies. For swimming experiments, individuals were screwed to the experimental set-up. This

technique was used to standardize the experimental conditions, e.g. to avoid swimming being hampered by swimming against the aquaria walls.

Swimming was triggered with the sea star *Asterias rubens*, a natural predator of Isle of Man scallops. The sea star was held in the aquarium so that one arm touched the mantle tissue of the experimental animal. Shading of the scallop with the sea star or the scientist was avoided. When swimming had been triggered, visible in clapping movements of the scallop, the sea star was immediately withdrawn. During every 1 min swimming interval, *A. opercularis* were touched 10 times with the sea star, even when the shell remained closed. After each experiment the water in the experimental aquaria was exchanged, to avoid irritation of the experimental individual by traces of the sea star or the previous scallop in the water.

Experimental design. The swimming experiment (Figure 1) consisted of a 30 min acclimation phase to experimental conditions (unstressed animals, group 0), run 1 = 1 min predator stress (group 1) and 15 min recovery (group 2), run 2 = again 1 min predator stress (group 3) and 15 min recovery (group 4). Individuals of each group were removed from the aquarium directly after the respective event, quickly dissected and the adductor muscle snap frozen in liquid nitrogen.

Morphological measurements. For each *Aequipecten opercularis* individual, shell weight (SW), height (SH), length (SL) and thickness (ST) (Figure 2) were recorded, and weight of gonad, adductor muscle and residual soft body determined.

Fineness, which mathematically describes the drag resistance of a given form in a medium, was calculated after Dadswell & Weihs (1990) as:

$$F = SH/ST.$$

Gonadosomatic index (GSI) and condition indices of each experimental animal were calculated as follows.

The GSI was determined after Jenkins et al. (2003) on the basis of wet mass:

$$(\text{gonad weight [g]}/\text{adductor muscle weight [g]}) \times 100$$

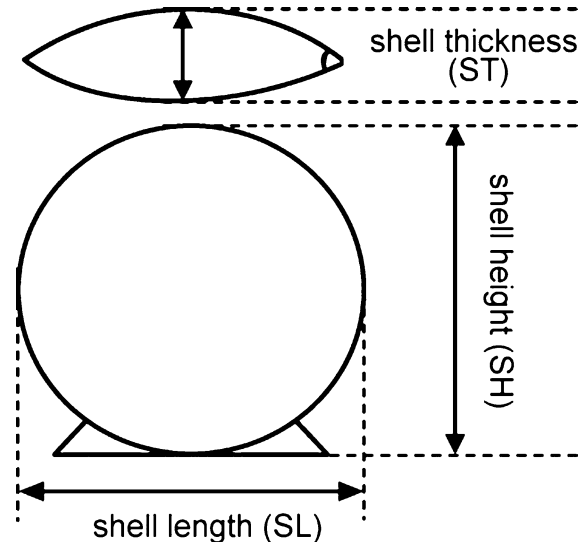Condition index (CI) was calculated as:

Figure 2. Morphological measurements of scallop shells (modified after Dadswell & Weihs 1990).

$$CI\ (\%) = (\text{wet soft body wet weight [g]}\ /$$
$$\text{shell dry weight [g]}) \times 100.$$

Muscle index (MI) was calculated as:

$$MI\ (\%) = (\text{wet adductor muscle [g]}/\text{wet soft body}$$
$$\text{weight [g]}) \times 100.$$

Escape responses

Analysing the escape videos, three different responses of *Aequipecten opercularis* touched by a sea star were distinguished following Thomas & Gruffydd (1971) with slight modifications: (A) swimming, (B) jumping, and (C) shell closure. Swimming (A) was defined as a series of more than three shell claps, whereas all escape responses of three claps and less were defined as jumping behaviour (B). The mathematical argument that a series of three or fewer claps describes jumping and a series of more than three claps describes swimming is based on the information gained from the videos and the behavioural studies following the descriptions of Thomas & Gruffydd (1971) and Brand (1991).

30 min acclimation = group 0	1. Run		2. Run	
	Sea star attacks 1 min = group 1	15 min recovery = group 2	Sea star attacks 1 min = group 3	15 min recovery = group 4

Figure 1. Systematization of experimental groups.

Statistics

Statistical analysis was undertaken using GraphPad Prism 4. Student's *t*-test was used for identification of significant differences between two groups after testing for normality and difference in variance. Analysis of Variance (ANOVA) was used to identify differences between slopes.

For identification of differences in clap response of small and large individuals, clap number per attack were transformed (log (clap + 1)) to achieve normality, and a full interaction model of ANCOVA using JMP 5.1 software was applied.

Results

Morphology

Small and large *Aequipecten opercularis* individuals showed no significant differences in condition index or gonadosomatic index (Table I).

Animal weight increased exponentially with shell height (Figure 3) which resulted from the increase in shell weight (SW) and soft body wet weight (SBWW) to equal proportion, as no significant difference in the rate constant (k) of the slopes of increase of both parameters with shell size was found (see legend for Figure 3).

However, when SBWW is divided into residual soft body wet weight (RSBWW = SBWW – AM) and adductor muscle weight (AM), the slopes of RSBWW and AM growth with shell height were significantly different, with adductor muscle growing slower than the residual body. RSBWW and AM slopes were not, however, different from the increase in shell weight (SW).

In line with the parallel increase in shell weight and the different compartments of soft body with shell height, a linear relationship between shell weight and soft body wet weight is found (Figure 4, open dots). However, again, when the soft body is partitioned into adductor muscle and residual body mass, the slope of growth plotted against shell weight is significantly different for both body segments with slower growth in the adductor muscle (Figure 4).

This finding is supported by comparing the muscle index in both groups (Figure 5). Moreover,
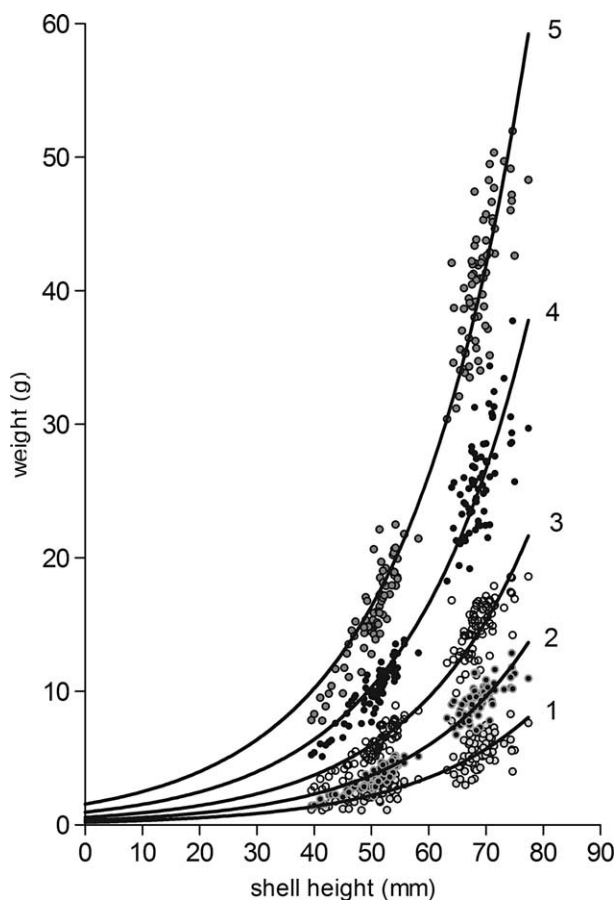

Figure 3. Relationship of (1) adductor muscle weight (AM), (2) residual soft body wet weight (RSBWW), (3) soft body wet weight (SBWW), (4) shell dry weight (SW) and (5) whole animal weight (SBWW + SW) to shell height of different sized *Aequipecten opercularis* individuals. Equation: Exponential growth with $Y = \text{Start} \times \exp (k \times X)$. Results for Start are 0.2906 (AM), 0.3173 (RSBWW), 0.5947 (SBWW), 0.9708 (SW), 1.565 (SBWW + SW) and for k are 0.04227 (AM), 0.04879 (RSBWW), 0.4635 (SBWW), 0.4728 (SW), 0.4694 (SBWW + SW). $N = 145$.

when adductor muscle weight is plotted either against the shell weight or residual soft body wet weight, inter-individual variance was significantly higher ($p < 0.001$) in bigger compared to smaller animals (Figure 4).

Fineness, as a measure of the amount of drag individuals encounter when swimming in sea water, was significantly higher in smaller (3.05 ± 0.022, $N = 73$) compared to bigger individuals (2.90 ± 0.020, $N = 72$) with $p < 0.0001$.

Table I. Size and age ranges as well as condition index and gonadosomatic index of smaller and bigger *Aequipecten opercularis* individuals. Data shown are means $\pm$ SD. Data are combined values of smaller and bigger individuals from group 0–4 as no significant difference between groups 0 to 4 were found for any parameter.

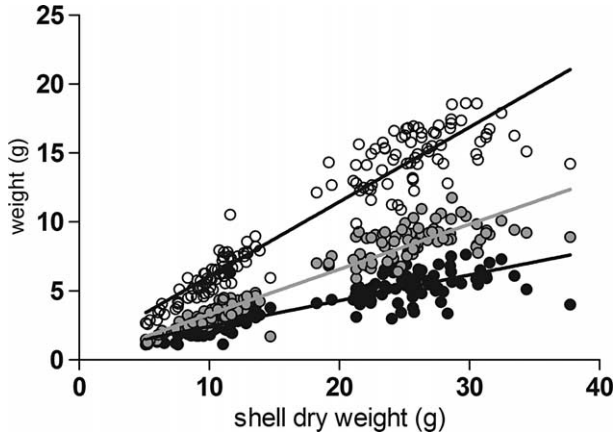|	Small	Big	N	p
Size range (mm)	50.23 ± 4.03	68.95 ± 2.86	72 (small), 73 (big)	< 0.5
Age range (years)	2.0 ± 0.5	4.0 ± 0.5	72 (small), 73 (big)	< 0.05
Condition index (%)	57.75 ± 6.80	57.93 ± 7.44	72	> 0.05
Gonadosomatic index (%)	13.55 ± 6.41	15.22 ± 6.13	71 (small), 72 (big)	> 0.05

Figure 4. Relationship of adductor muscle (AM, black dots), residual soft body (RSBWW = SBWW – AM; grey dots) and whole soft body wet weight (SBWW open dots) to shell dry weight (SW) in different sized *Aequipecten opercularis*. Slopes are significantly different from each other ($n = 145$, $p < 0.0001$).

Behaviour

Touching the mantle edge of *Aequipecten opercularis* with a sea star resulted in a swimming response of all animals in the first run. The number of claps decreased significantly with each attack ($p < 0.0001$, Figure 6). In the second run, initial clap number was significantly lower compared to the first run and, again, decreased with each subsequent attack (Figure 6). While in the first run, 100% of smaller and bigger individuals (small $n = 52$, large $n = 54$) showed swimming or jumping reactions to sea star attack, in the second run 91.2% of the bigger ($n = 34$) and only 44% of smaller animals ($n = 32$) reacted (data not shown). Number of claps following an attack was not significantly different between the two size classes in the first run. In the second run, the smaller individuals showed lower clap numbers
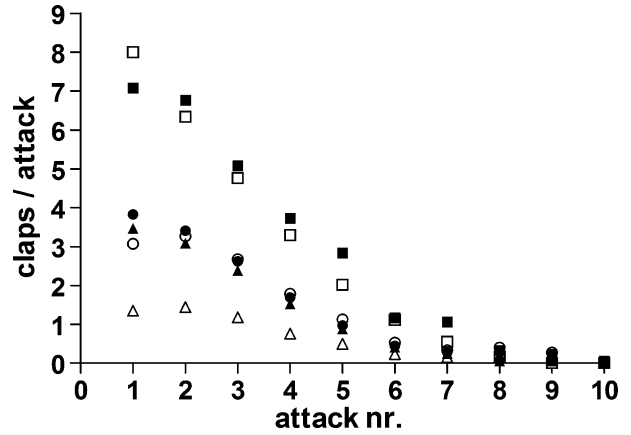
Figure 6. Clap number of smaller ([S], open symbols) and bigger ([B], closed symbols) individuals per attack nr. 1–10 in the first run (squares, $n = 52$ [S]; 53 [B]) and second run (triangles, $n = 34$ [S]; 32 [B]). Dots show data of the second run ($n = 15$ [S]; 29 [B]) when all animals which did not respond to a sea star attack were excluded. For better overview, only means without standard deviation are shown.

per attack compared to bigger individuals (Figure 6, triangles). This resulted from the high number of individuals which performed zero claps per attack in the second round. When all animals, which did not react were excluded from the analysis of the second run data set (small $n = 19$, large $n = 3$), again no difference in clap number per attack was found between the two size groups (open and closed dots, see legend of Figure 6).

Maximum clap number in a series, which did not always take place in the first sea star attack, and mean clap number during predator attacks in run 1 and run 2 did also not differ between *A. opercularis* individuals of the two size groups (Table II).

Additionally to clap number, shell opening and closing behaviour of the *A. opercularis* individuals in response to predator attack were recorded. For better comparison of the runs, only data of animals which underwent run 1 and 2 (i.e. group 4) were used for calculation. In both runs, smaller animals closed their shell more often (Figure 7A: first run = 47% and seond run 41%) compared to bigger individuals (Figure 7B: first run = 3% and second run = 13%).

As described in the Material and methods section, two different types of swimming reaction to sea star attack were distinguished and defined as jumping (≤ 3 claps) and swimming (> 3 claps). In both runs, larger individuals showed a higher percentage of jumping reactions compared to smaller animals and in both groups the percentage of jumping increased from the first to the second round of attacks (Figure 8).
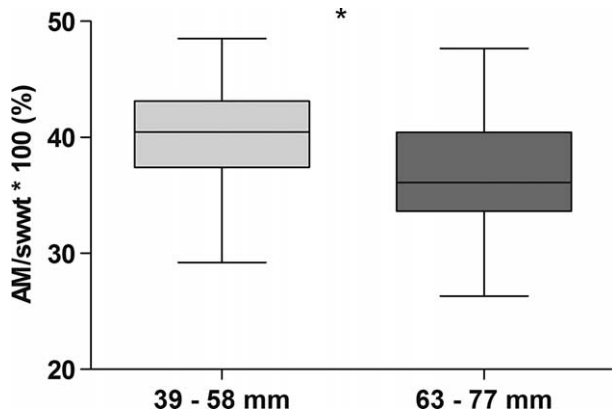

Figure 5. Muscle index: percentage of adductor muscle (g) of whole body wet weight (g) in smaller (light box, 39–58 mm, 2.0 (0.5) years) and bigger (dark box, 63–77 mm, 4.0 (0.5) years) scallops. Groups are significantly different with $p < 0.0001$, $n = 71$–72.

Table II. Maximal number of claps in a series and sum of claps during the attack of smaller and bigger *Aequipecten opercularis* individuals. Mean (SD, *n*). Individuals which did not react in the second round were excluded from this analysis (19 of smaller and 3 of bigger individuals).

	Smaller ind., first run	Smaller ind., second run	Bigger ind., first run	Bigger ind., second run
Maximal number of claps in a series	9.32 (3.68, 53)	4.47 (1.85, 15)	9.15 (3.82, 52)	4.86 (2.66, 29)
Sum of claps	26.3 (9.75, 53)	12.5 (8.42, 15)	28.3 (7.94, 52)	13.4 (6.1, 29)

Discussion

The change in morphology and behaviour response to predator attacks was studied in smaller and bigger sized *Aequipecten opercularis* from the Irish Sea, Isle of Man. The gonadosomatic index did not differ between the two size groups, thus differences in adductor muscle mass found between individuals cannot be related to differences in gonad development. In many scallops the adductor muscle glycogen is used as energy source to build up gonads and thus reproduction significantly influences adductor muscle mass (for a review see Barber & Blake 1991). The condition index used in the present study compares the shell mass and corresponding soft tissue. A low condition index indicates that an individual has allocated less energy to maintenance of body mass, which may relate to under-nutrition, but also to energy investments into stress defence. The condition index did not differ between smaller and bigger individuals of the present study, indicating similar investments of energy into maintenance in small and big animals. Using the size-age curve of Philipp et al. (2006) of *A. opercularis* from the same sampling station as the animals of the present study, we calculated age from size for the investigated *A. opercularis* individuals. Although age determination from size is not as precise as counting year rings of individual shells, the size–age curve of Philipp et al. (2006) shows that in *A. opercularis* of the investigated population, age and size is tightly correlated so that we can assume that the two size classes given in the present paper represent also different age classes.

Shell and soft body weight and thus whole animal weight of *A. opercularis* increased exponentially with shell height. Compared to residual soft body mass, adductor muscle weight increased more slowly with shell size. Thus in bigger *A. opercularis* a relatively small adductor muscle has to contract large and heavy shells which is bound to affect swimming capacity. Dadswell & Weihs (1990) investigated the hydrodynamic capacities of *Placopecten magellanicus*, a scallop which belongs to the same active swimming ecomorph as *A. opercularis* (Minchin 2003), and, for that matter, found hydrodynamic efficiency to first increase and then decrease with size in *Placopecten magellanicus* and to be highest in medium-sized individuals. In the present study the smaller animal group (39–58 mm) represents the medium-sized *A. opercularis* as maximum height (H_∞) in the Isle of Man populations is 75–95 mm (Allison 1993). Thus the smaller group in our study may be the hydrodynamically most efficient group. Calculations of the fineness of the shells of the investigated individuals after Dadswell & Weihs (1990) corroborates this assumption, as indeed it indicates less drag is experienced by smaller compared to bigger animals. Thus, bigger and much heavier individuals with a proportionally smaller adductor muscle additionally suffer from less favourable hydrodynamic quality, i.e. higher water resistance during swimming, than smaller animals. These factors together are bound to compromise swimming response in the large size group.

Interestingly, in our experiments, swimming activity was not diminished in bigger animals. Smaller and bigger animals performed similar clap numbers on predator attack. However, the response mode to the predator attack was indeed different with respect to shell opening and permanent closure, as well as with respect to swimming or jumping. Smaller individuals closed their shells more often in the first and second run compared to bigger animals. Nearly 50% of the smaller individuals closed shells tightly
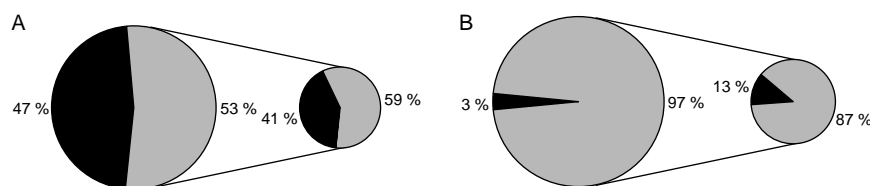

Figure 7. *Aequipecten opercularis* group 4: percentage of individuals keeping their shells open (grey part) during attack and closing their shell during sea star attack and keeping their shells closed until dissection (black part). In the first run (big circles) all animals are shown; in the second run (small circles) the individuals which closed their shell during the first run were excluded and residual animals are shown. A: smaller animals, *n* = 32 (39.5–58.2 mm shell height); B: bigger animals, *n* = 34 (64.4–77.4 mm shell height).
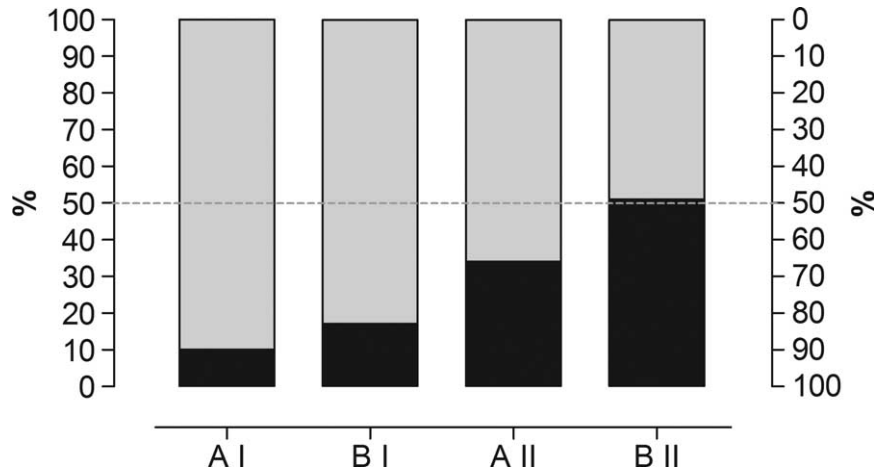
Figure 8. Percentage of jumping (lower black part) and swimming (upper grey part) of all swimming movements for smaller (A, $n = 34$) and bigger (B, $n = 32$) individuals in the first (I) and second (II) predator presence. Only those animals which underwent both runs were counted.

during repeated predator attack and kept the shell closed thereafter for the rest of the experiment, whereas only 3–13% of the bigger individuals behaved this way.

What explains the different behaviour of the smaller and bigger *A. opercularis* individuals? Is it driven by the change in morphology and physiological capacities or a response to a change in predator–prey relationships with increasing size? Eventually it seems a combination of all three parameters.

In a previous study we showed that citrate synthase (CS), cytochrome c oxidase and also whole protein content decreased with increased size in mantle tissue of *A. opercularis* (Philipp et al. 2006), indicating lower aerobic capacities in bigger individuals. Investigating parameters of aerobic and anaerobic energy metabolism, as well as the tissue redox ratio in small and large animals in the different groups of the same swimming experiment, we found the adductor muscle of bigger individuals to have lower mitochondrial volume densities, less specific CS activity, lower ATP and generally lower adenylate concentrations compared to muscle tissue of smaller individuals. Moreover the content of the energetic reserve glycogen was lower in bigger animal adductor muscle (Philipp et al. 2008). The differences in shell closing/opening behaviour might thus reflect lower anaerobic capacities in bigger individuals and indicate that they rely more on aerobic energy generation after exhaustion and therefore keep their shells open to the air-saturated sea water. Further the higher jumping rate with shorter clap sequence of bigger compared to smaller *A. opercularis* might point towards a less energetic capacity of bigger individuals and hence the need to

minimize energy used for escape responses. Thus the behaviour described in the present paper can, at least in part, be explained by changes in energy capacities with size and age.

Still, predator–prey relationships have to be considered as yet another reason for different swimming behaviour. Predator–prey relationships have been shown to change with size, as different predators prefer different prey sizes, and thus likely stimulate different escape response in differently-sized individuals (Barbeau & Schreibling 1994). According to Barbeau & Scheibling (1994; c.f. Bailey et al. 2003), closing of the shell does not necessarily prevent predation, as, for example, crabs can crush the shells of scallops. So from the ecological point of view the closing of the shell does not make sense at any age or size. However, it depends on the predator and the prey. In the environment of *A. opercularis* of the present study, the sea stars *Asterias rubens* and *Astropecten irregularis* are the most abundant scavengers (Veale et al. 2000), and Barbeau & Scheibling (1994) showed for *P. magellanicus* that smaller scallops are preferred by the sea stars, whereas crabs prefer middle and large-sized scallops. Veale et al. (2000) showed that around the Isle of Man *A. rubens* scavenges on damaged but also undamaged live *A. opercularis*. Deduced from the results for *P. magellanicus*, with sea stars as the main predators, shell closing might indeed help smaller individuals to survive attacks when energy reserves are too low for a swimming response. For older individuals, crabs seem to be the most dangerous predators, in which case shell closure does not prevent being eaten.

Thus, on the one hand, the behaviour may change with size to optimize survival in a specific and size-

dependent predator–prey setting; on the other hand, bigger individuals may not be able to close their shells for longer times probably due to energetic deficiencies (Philipp et al. 2006, 2008).

The general lifestyle of a prey animal may lead to different physiological and behavioural adjustments in predator–prey response. Minchin (2003) described different ecotypes of scallops (ecotype A–E) exhibiting different lifestyles, e.g. byssaly attached or free-living inside or above the sediment. These lifestyles will certainly involve behavioural and physiological adjustments with respect to the response to predation and change of physiology with size and age. Other size-dependent physiological studies of scallop swimming on predator attack contrast the results of our study. Tremblay et al. (2006) compared two studies that investigated smaller (Tremblay et al. 2006) and bigger (Brokordt et al. 2000) *Chlamys islandica* from the same region, and found that bigger *C. islandica* keep their valves closed for longer times compared to smaller individuals. Also in *P. magellanicus* it was observed that bigger individuals closed their valves more often than smaller ones when exhausted (c.f. Lafrance et al. 2003). Thus, the change of behaviour with growth in different species may be different and moreover relate to lifestyle and life expectancy: in species which are long-lived and grow to large maximum sizes, older and larger animals seem to be less active swimmers and need to modify their response to the different predators (example: *Pecten maximus*). In species which are generally small, light and short-lived, behavioural changes with size may be less pronounced, as in the present case.

In summary, bigger *A. opercularis* have smaller adductor muscles relative to shell weight than smaller individuals. Still, they maintain the same clap rate as smaller animals when attacked by a sea star predator. This supports our idea that in queen scallops physiological adjustments are made for optimal functioning throughout lifetime, to avoid predation or to be able to change location when abiotic living conditions become unfavourable. However, behaviour changes with bigger animals showing more jumping than swimming in response to predator attack compared to smaller individuals, and, moreover, only occasionally close their valves fully after the attack only to quickly open them again. This difference in behaviour of small and larger *A. opercularis* may be rooted in a combination of a change in morphology and physiology (aerobic and anaerobic energy generation capacity) over size and age, but also it may be a response to a change in predator attracted by the different sized scallops (sea stars, crabs).

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Editorial responsibility: Alan C. Taylor