

Scallops visually respond to the size and speed of virtual particles

Daniel I. Speiser* and Sönke Johnsen

Biology Department, Duke University, Durham, NC 27708, USA

*Author for correspondence (e-mail: dis4@duke.edu)

Accepted 16 April 2008

SUMMARY

The unique eyes of scallops are abundant along the right and left valve mantle margins. These eyes form images by reflection off a concave spherical mirror, and give scallops an angular resolution of around 2° , far better than the $13\text{--}40^\circ$ angular resolution provided by the eyes of other bivalves. It has been argued that bivalve mantle eyes primarily act as predator detectors, but behavioral studies have suggested that vision may serve additional purposes in scallops. By placing specimens of the bay scallop *Argopecten irradians* (Lamarck 1819) in a tank with $5\text{--}10\text{ cm s}^{-1}$ flow, showing them simulated images of moving particles, and recording their behavior, we tested whether visual cues may influence feeding behavior in these animals. We found that scallops opened their anterior mantle gapes significantly more often when they were shown $1.5\times 1.5\text{ mm}$ virtual particles (with angular sizes of 3.4°) than when they were shown $0.6\times 0.6\text{ mm}$ particles (1.4° ; $P<0.001$) or no particles at all ($P<0.05$). We also found that scallops opened their anterior mantle gapes significantly more often when they were shown virtual particles moving at 2.5 cm s^{-1} ($P<0.01$) or 5 cm s^{-1} ($P<0.05$) than when they were shown particles moving at 10 cm s^{-1} . Because scallops must open their anterior mantle gapes to feed, our findings suggest that these animals may visually detect the size and speed of moving particles and use this information to help identify favorable feeding conditions.

INTRODUCTION

The bay scallop *Argopecten irradians* (Lamarck 1819) has up to one hundred bright blue eyes at the tips of short tentacles on the middle mantle fold. These eyes line the edges of the right and left valves from the anterior to the posterior ends of the hinge. These mantle eyes contain a lens, two distinct retinas and a concave spherical mirror, morphologically similar to that of previously described scallop eyes (Dakin, 1928; Barber et al., 1966; Morton, 2000). Light reflected off the mirror is thought to form a focused image on the distal retina (Land, 1965), which appears to be well-suited for the detection of movement (Land, 1966).

Because scallops close their valves in the presence of large moving objects, it has been argued that their eyes primarily act as predator detectors (Nilsson, 1994; Morton, 2000). Although predator detection is almost certainly one task of the mantle eyes, evidence suggests that other scallop behaviors are also visually influenced. For example, scallops have been observed extending their tentacles in response to visual stimuli (von Buddenbrock and Moller-Racke, 1953; Wilkens, 2006) and visually navigating toward a preferred habitat (von Buddenbrock and Moller-Racke, 1953; Hamilton and Koch, 1996).

Measurements of optical resolution also imply that predator detection may be only one of several functions performed by scallop eyes. Behavioral (von Buddenbrock and Moller-Racke, 1953), morphological (Land, 1965) and physiological (Land, 1966) studies all conclude that scallop eyes have an angular resolution of around 2° . In comparison, the predator-detecting eyes of other bivalves have angular resolutions ranging from 13° to 40° (Nilsson, 1994; Land, 2003). Although coarse, an angular resolution within this range would still probably allow scallops to spot major predators, such as crabs, gastropods, rays and starfish (Brand, 2006; Myers et al., 2007), at ecologically relevant distances. Therefore, while predator detection may explain some aspects of scallop vision, it does not account for these bivalves' diverse visual behaviors or why they see so relatively well.

We have tested the hypothesis that scallops visually detect the presence and speed of moving particles when assessing feeding conditions. Scallops actively feed on suspended organic particles and can open their valves to see without opening their mantle gape. Thus, the visual detection of particle presence and speed may let these animals monitor feeding conditions without exposing the vulnerable structures of their mantle cavity. We placed specimens of *A. irradians* in a flow tank, showed them simulated particles of different sizes moving at a range of different speeds, and recorded and analyzed their responses. We worked with *A. irradians* because it lives in bright, shallow water and has been used in previous studies of scallop vision (e.g. Hamilton and Koch, 1996).

MATERIALS AND METHODS

Specimen collection and care

Specimens of *A. irradians* were obtained from Middle Marsh, NC, USA (6 km east of Beaufort, NC, approximately 34.72°N , 76.59°W) on 25 May and 12 July 2006 and on 10, 17 and 31 May 2007. Animals were collected from eelgrass (*Zostera* sp.) beds at low tide (water depth of 30–60 cm). Animals collected in 2006 were immediately transported to Duke University (Durham, NC, USA), where they were kept in 40 l aquaria under natural light with bi-weekly water changes. Salinity was kept at 28–30‰ (Instant Ocean sea salt, Aquarium Systems, Inc., Mentor, OH, USA). Animals collected in 2007 were immediately transported to the Duke University Marine Laboratory (Beaufort, NC, USA), where they were kept in sea tables with continually flowing filtered sea water. At both sites, animals remained in apparent good health for over a month. Experiments were conducted on animals 1–3 weeks after they were collected.

Experimental apparatus

The experimental set-up included a computer monitor, laptop computer, small flow tank, video camera, and recorder (Fig. 1). The

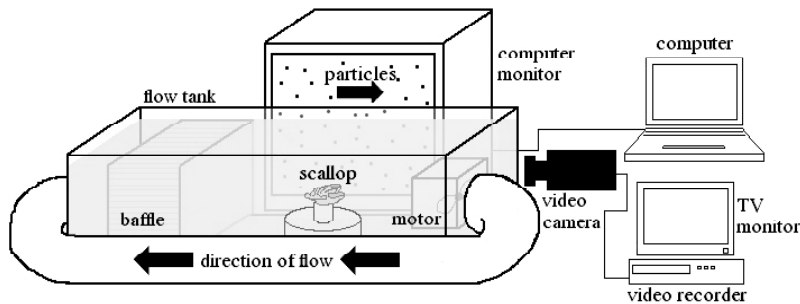


Fig. 1. The experimental arena used in this study. Flow direction matched virtual particle direction and scallops were mounted right valve down, so that their anterior faced away from oncoming flow.

flow-tank was a Plexiglas box (64 cm \times 14 cm \times 18 cm, L \times W \times H) attached at each end to a curved length of 6 cm diameter PVC pipe. A 1200 l h⁻¹-rated submersible pump (Penguin 1140, Marineland Aquarium Products, Moorpark, CA, USA) and a 13 cm-long baffle made of plastic drinking straws created a laminar flow of 5–10 cm s⁻¹ within the tank, well within the normal range of flow rates encountered by scallops in nature (MacDonald et al., 2006). Flow was used because scallops, in preliminary trials, rarely opened their valves in still water.

The flow-tank was placed in front of a 46 cm monitor attached to a laptop computer that ran the particle simulation program. The behavior of *A. irradians* was recorded with a video camera attached to a time-lapse VHS video recorder. Video camera output was displayed on a second monitor so that proper aperture and focus could be maintained from trial to trial. In both 2006 and 2007, trials were conducted in light-tight rooms. The only illumination in these rooms was provided by the two monitors.

Experimental procedure

The flow tank was rinsed and filled to a depth of 14 cm with newly mixed artificial sea water on each day that trials were run. Trials were conducted during daylight hours and with one animal at a time. To prevent scallops from swimming during trials, while allowing a full range of valve motion, specimens of *A. irradians* were glued, right valve down, to a short length of PVC pipe that was then attached to a mount at the bottom of the flow-tank. Specimens were mounted so that the anterior (inhalant) opening faced the video camera and was downstream with regards to flow. The flow-tank was positioned so that the computer monitor was, at most, 2.5 cm from the nearest point on a test animal.

In our experiment, we observed the behavior of scallops shown moving, simulated particles of different sizes and speeds. The particle simulation program was written in JavaScript (Ecma International, Geneva, Switzerland) and run as an HTML file. In our first set of trials, particles in the no particle treatment were grey (grey value=80 out of 255) and invisible against the grey background (grey value=80 out of 255) and particles in the 0.6 \times 0.6 mm (1.4 $^\circ$ angular size) and 1.5 \times 1.5 mm (3.4 $^\circ$ angular size) particle treatments were black (grey value=0 out of 255). All particles in our first set of trials moved at 2.5 cm s⁻¹. In our second set of trials, black virtual particles were 1.5 \times 1.5 mm in size and moved at 2.5, 5, or 10 cm s⁻¹ against the grey background. In all treatments, particles appeared at random positions on the left edge of the screen at a rate of ten per second and moved left to right, the same direction as the flow in the tank. Flow speed was not altered between trials. Monitor refresh rate was 50 Hz and irradiances at the scallop (integrated from 400 to 700 nm) were nearly identical between trials, with readings of 1.20 \times 10¹⁴ photons cm⁻² s⁻¹ and 1.21 \times 10¹⁴ photons cm⁻² s⁻¹ for the no particle and particle treatments, respectively. Furthermore,

no observed scallop behaviors differed significantly when the monitor background was changed from white (grey value=255; $N=23$) to grey (grey value=80; $N=23$) to black (grey value=0; $N=24$) in an independent set of trials. The irradiance values at the scallop for the white, grey and black backgrounds were 6.61 \times 10¹⁴, 1.20 \times 10¹⁴ and 5.11 \times 10¹¹ photons cm⁻² s⁻¹, respectively. No virtual particles were displayed in these treatments. The results from this set of trials suggest that the slight differences in irradiance values between the virtual particle treatments did not influence scallop behavior.

Trials for the no particle and 1.5 \times 1.5 mm, 2.5 cm s⁻¹ virtual particle treatments were conducted in 2006 and trials for the 0.6 \times 0.6 mm, 2.5 cm s⁻¹ and the 1.5 \times 1.5 mm, 5 and 10 cm s⁻¹ treatments were conducted in 2007. Different animals were used for each trial within a given treatment. Because some animals were used in both the 0.6 \times 0.6 mm, 2.5 cm s⁻¹ and the 1.5 \times 1.5 mm, 5 cm s⁻¹ treatments, these two conditions were not compared in our analysis. Trials for the black, grey and white background conditions were conducted in 2006 and 2007, different animals were used for each trial within a treatment, and no animals were used in more than one treatment.

Data collection and analysis

The particle simulation program was initiated and behavioral recording begun immediately after scallops were placed in the flow tank. All trials lasted 10 min, measured from the onset of recording. For our recordings of each trial, scallop mantle gapes were scored as open or closed and tentacles were scored as extended or not extended at 24 s intervals. Mantle gapes were scored as open if there was a gap in the anterior mantle folds and the gills were exposed (Fig. 2A). Mantle gapes were scored as closed if no gap was visible between the anterior mantle folds and the gills were not exposed (Fig. 2B). We also counted the number of times that each scallop clapped its valves during a trial. Scallops can see as long as their valves are open, but it is unlikely that they are able to see when their valves are closed. Therefore, we only analyzed trial data recorded after a scallop first opened its valves. This resulted in a variable number of observations per trial. However, the total number of observations varied little between treatments (Table 1).

We calculated the proportion of observations in each trial in which a scallop's mantle gape was open or its tentacles were extended (Table 1). These proportions were arcsine square-root transformed for analysis and comparisons between treatments were made using one-way ANOVAs and Bonferroni pairwise multiple comparison *t*-tests. The numbers of valve claps per trial were not consistent with a normal distribution, so Kruskal–Wallis one way ANOVAs on rank order were used to compare valve claps between treatments.

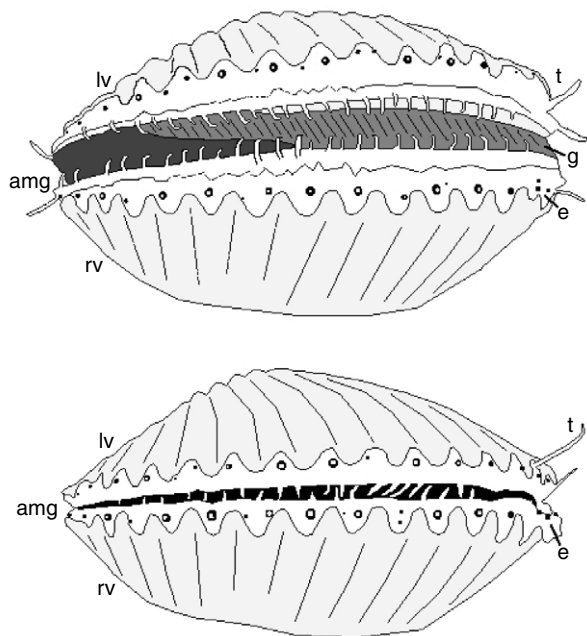


Fig. 2. Drawings of *A. irradians* with (A) open anterior mantle gape (amg) and (B) closed amg. Abbreviations: e, eye; g, gill; lv, left valve; rv, right valve; t, tentacle.

RESULTS

Effect of size of virtual particles moving at 2.5 cm s⁻¹

Scallop anterior mantle gapes were open in 52±13% (mean ± 2 s.e.m.) of the observations per trial for the 1.5×1.5 mm particle treatment ($N=25$), but in only 23±10% and 29±10% of the observations per trial for the treatments with 0.6×0.6 mm particles ($N=24$) and no particles ($N=24$), respectively (Fig. 3). One-way ANOVA revealed that scallop behavior was influenced by virtual particle size ($F_{2,70}=7.270$; $P<0.001$). Bonferroni t -tests indicated that scallop anterior mantle gapes were open significantly more often in the larger particle treatment than in either the smaller particle ($t=3.660$; $P=0.001$) or no particle ($t=2.726$; $P=0.024$) treatments.

Effect of speed of 1.5×1.5 mm virtual particles

Scallop anterior mantle gapes were open in 52±13% and 49±11% of the observations per trial for the 2.5 and 5 cm s⁻¹ particle treatments ($N=25$ for both), but in only 26±10% of the observations per trial for the 10 cm s⁻¹ particle treatment ($N=24$; Fig. 4). As previously noted, scallop anterior mantle gapes were open in 29±10% of the observations per trial from the no particle treatment. We found that scallop behavior was influenced by virtual particle speed ($F_{3,94}=5.397$, $P=0.002$; one-way ANOVA), and that scallop

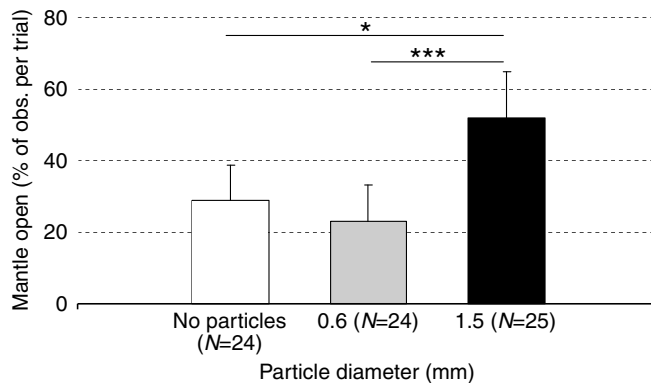


Fig. 3. The percentage of observations per trial in which scallop anterior mantle gapes were open. Particle diameter varied between trials, but particle speed was held constant at 2.5 cm s⁻¹. Background radiance in each trial was identical. Error bars represent + 2 s.e.m. $N=24$, 24 and 25 for the no particle, 0.6 mm particle, and 1.5 mm particle treatments, respectively. * $P=0.05$; *** $P=0.001$.

anterior mantle gapes were open significantly less often in the 10 cm s⁻¹ particle treatment than in either the 2.5 ($t=3.305$, $P=0.008$; Bonferroni t -test) or 5 cm s⁻¹ ($t=2.860$; $P=0.031$; Bonferroni t -test) treatments.

Tentacle extension and valve claps

Scallops had extended tentacles in 53±14% to 69±12% of the observations per trial for the different particle treatments (Table 1). Particles of different size ($F_{2,70}=1.031$, $P=0.362$; one way ANOVA) or speed ($F_{3,94}=1.091$, $P=0.357$; one way ANOVA) did not have an influence on scallop tentacle extension. Scallops also clapped their valves between 1.4±0.7 and 1.9±0.8 times per trial (Table 1). Kruskal–Wallis ANOVAs revealed that the number of valve claps per trial did not vary significantly between treatments when particle size ($H_2=3.330$; $P=0.189$) or particle speed ($H_3=2.032$; $P=0.566$) varied.

DISCUSSION

A. irradians opened their anterior mantle gapes significantly more often when they were shown larger, slower virtual particles than when they were shown smaller or faster particles. Scallops open their mantle gape to collect food particles on their gills (MacDonald et al., 2006), and other bivalves, such as mussels, have been found to increase their mantle gape in response to the presence of feeding cues (Riisgård et al., 2003). It is likely, therefore, that the scallops in our study responded to the size and speed of virtual particles with a feeding-related behavior. Scallops must also regularly open their mantle gape to respire (MacDonald et al., 2006), which may account for why open

Table 1. Individual trials yielded a variable number of observations, but treatments had a similar number of total observations

	Particle treatments				
	No particles	0.6 mm 2.5 cm s ⁻¹	1.5 mm 2.5 cm s ⁻¹	1.5 mm 5 cm s ⁻¹	1.5 mm 10 cm s ⁻¹
Number of trials (M)	24	24	25	25	24
Total observations	533	556	555	584	542
Open mantle observations	156	125	287	284	144
Percentage of open mantle observations per trial	29±10	23±10	52±13	49±11	26±10
Extended tentacle observations	342	300	376	365	292
Percentage of extended tentacle observations per trial	63±14	54±14	69±12	64±14	53±14
Valve claps per trial	1.8±1.4	1.4±1.4	1.8±1.2	1.5±1.4	1.9±1.6

When appropriate, data are given as means ± 2 s.e.m. (to give a 95% confidence interval).

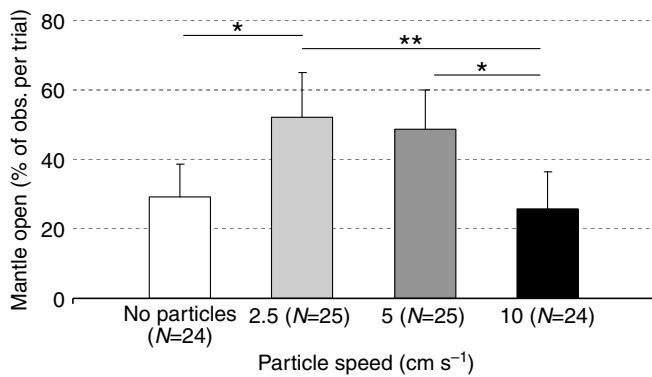


Fig. 4. The percentage of observations per trial in which scallop anterior mantle gapes were open. Particle speed varied between trials, but particle size was held constant at 1.5×1.5 mm. Background radiance in each trial was identical. Error bars represent $+2$ s.e.m. $N=24$, 25, 25, and 24 for the no particle, 2.5 cm s⁻¹, 5 cm s⁻¹ and 10 cm s⁻¹ treatments, respectively. * $P=0.05$; ** $P=0.01$.

mantle gapes were observed during trials in which no particles, or any other feeding cues, were present. Respiratory conditions were identical between trials, so it is unlikely that respiration accounted for the differences observed between treatments.

Scallop behaviors other than mantle gape position, including tentacle extension and valve clapping, varied little between treatments (Table 1). Scallops extended their tentacles within the first 2 min of most trials, indicating that this behavior may be a general response to new environmental conditions. Valve clapping, however, did not display a temporal pattern and may have represented behavior related to respiration, swimming attempts or pseudo-feces expulsion. These findings support our hypothesis that *A. irradians* responded to different virtual particle sizes and speeds with specific behaviors consistent with increased or decreased levels of feeding activity.

The response of *A. irradians* to virtual particle size was consistent with the estimated 2° inter-receptor angle of its eyes (Speiser and Johnsen, in press). An angular resolution of 2° would probably have let *A. irradians* see the 1.5×1.5 mm particles, which had angular sizes of 3.4° . However, it is less likely that scallops were able to detect the 0.6×0.6 mm particles, which had angular sizes of 1.4° . This strongly implies that the differences in scallop behavior we observed between treatments were due to the detection of the virtual particles by visual means.

Scallops may respond to the presence of virtual particles with feeding-related behavior because they visually monitor feeding conditions. Scallops feed on suspended organic particles ranging from 5 to 950 μ m in diameter (Mikulich and Tsikhon-Lukanina, 1981; Shumway et al., 1987). Objects in the upper half of this range would be visible to scallops at a distance of a few millimeters, provided that scallop eyes are capable of focusing at such short distances. Alternately, scallops may detect larger, inorganic particles and use this information as a proxy for the presence of smaller, organic particles.

Coastal scallops, such as *A. irradians*, encounter highly variable feeding conditions (Fegley et al., 1992). For example, re-suspensions of bottom sediment by tide or wind (Grant et al., 1997) and changes in phytoplankton abundance (Fr chet te and Bourget, 1987) may cause food particle concentrations to fluctuate. Previous studies have clearly established that scallops track these fluctuations using tactile and chemosensory cues (MacDonald et al., 2006). However, we

hypothesize that the visual detection of suspended particles may be a safe and efficient method for scallops to initially assess new feeding conditions. For example, although scallops may be able to continually test for the presence of food particles by opening their mantle gapes and sampling water with their gills, this action may increase their vulnerability to mantle cavity parasites such as pinnotherid crabs (Kruczynski, 1972) and odostomid gastropods (Leibovitz et al., 1984). Because scallops can see even when their mantle gape is closed, visually monitoring for food particles may allow them to avoid these risks. Furthermore, the detection of food particles on the gills may, like feeding in most bivalves (Widdows and Hawkins, 1989), incur a metabolic cost in scallops. This cost may be avoided if scallops are able to visually detect food particles.

A. irradians responded not only to differences in particle size, but to differences in particle speed as well. We found that *A. irradians* had open anterior mantle gapes significantly more often when they were shown virtual particles moving at 2.5 or 5 cm s⁻¹ than when they were shown particles moving at 10 cm s⁻¹. Laboratory experiments suggest that scallop feeding may be inhibited by flow rates over 10 – 15 cm s⁻¹ (Kirby-Smith, 1972; Wildish and Saulnier, 1993). Therefore, our findings suggest that *A. irradians* exhibited higher rates of feeding-related behavior when they were shown simulations that indicated favorable feeding conditions. This implies that scallops may visually monitor aspects of their environment related to feeding efficiency, such as particle speed, not just food availability.

Scallops process visual information in the lateral lobes of their visceroparietal ganglion (VPG), an organ that innervates the adductor muscle and probably controls mantle gape position (Wilkens, 2006). Processing may be simplified if visual input is filtered at the level of the scallop eye. For example, scallops may optimally respond to a range of environmental conditions if they simply close their mantle gape when they are unable to visually detect suspended particles. Electroretinograms (ERGs) indicate that scallop eyes have an integration time of around 200 ms [for *Amusium japonicum* (Kanmizutaru, 2005)]. Moving at a speed of 10 cm s⁻¹ and at a distance of 2.5 cm, the 1.5×1.5 mm particles in our study probably traveled the entire distance across *A. irradians* retinas in less than a single visual cycle. It is unlikely, therefore, that the scallops in our study were able to detect the virtual 10 cm s⁻¹ particles that they were shown. As previously mentioned, flow rates over 10 – 15 cm s⁻¹ may inhibit scallop feeding (Kirby-Smith, 1972; Wildish and Saulnier, 1993), so an inability to distinguish between rapidly moving and non-existent particles may help scallops link a single behavioral output, mantle gape position, to a wide range of visual conditions. This sort of visual system, which filters information at the level of the eye, may be a common feature in animals that lack the neural complexity to process large amounts of visual input (Wehner, 1987; Nilsson et al., 2005).

The position in which scallops were mounted in the flow tank may have influenced our results. Evidence suggests that high flow rates strongly inhibit scallop growth when posterior (exhalant) openings face oncoming flow, as they did in our study, and that juvenile *A. irradians* actively turn their anterior (inhalant) opening to face oncoming flow when flow speeds exceed 9 cm s⁻¹ (Eckman et al., 1989). This suggests that we may not have observed a decrease in feeding-related behavior at virtual flow speeds of 10 cm s⁻¹ if *A. irradians* had been positioned in the flow tank in their preferred anterior-to-flow orientation. However, given that scallops are probably unable to detect objects moving faster than 10 cm s⁻¹ (Kanmizutaru, 2005), it is doubtful that the observed visual response of *A. irradians* to virtual particle speed was influenced by flow

direction. Future experiments will explore whether scallops use vision to help assess flow direction, as well as other environmental conditions relevant to feeding, such as turbidity levels, and whether these responses may be interpreted through a 'matched filters' model of information processing.

We would like to thank Alison Sweeney, Sam Boyarsky, Mark Hooper, Bill Kirby-Smith, Richard Forward and Steve Vogel for their help on this project. S.J. was supported in part by a grant from the National Science Foundation (IOB-0444674).

REFERENCES

- Barber, V. C., Evans, E. M. and Land, M. F.** (1966). The fine structure of the eye of the mollusc *Pecten maximus*. *Cell Tissue Res.* **76**, 295-312.
- Brand, A. R.** (2006). Scallop ecology: distributions and behaviour. In *Scallops: Biology, Ecology, and Aquaculture* (ed. S. E. Shumway and G. J. Parsons), pp. 651-744. New York: Elsevier.
- Dakin, W. J.** (1928). The eyes of *Pecten*, *Spondylus*, *Amusium* and allied lamellibranchs with a short discussion on their evolution. *Proc. R. Soc. Lond. B Biol. Sci.* **103**, 355-365.
- Eckman, J. E., Peterson, C. H. and Cahalan, J. A.** (1989). Effects of flow speed, turbulence, and orientation on growth of juvenile bay scallops *Argopecten irradians concentricus* (Say). *J. Exp. Mar. Biol. Ecol.* **132**, 123-140.
- Fegley, S. R., MacDonald, B. A. and Jacobsen, T. R.** (1992). Short-term variation in the quantity and quality of seston available to benthic suspension feeders. *Estuar. Coast. Shelf Sci.* **34**, 393-412.
- Fréchette, M. and Bourget, E.** (1987). Significance of small-scale spatio-temporal heterogeneity in phytoplankton abundance for energy flow in *Mytilus edulis*. *Mar. Biol.* **94**, 231-240.
- Grant, J., Cranford, P. J. and Emerson, C. W.** (1997). Sediment resuspension rates, organic matter quality, and its utilization by sea scallops (*Placopecten magellanicus*) on Georges Bank. *J. Mar. Res.* **55**, 965-994.
- Hamilton, P. V. and Koch, K. M.** (1996). Orientation toward natural and artificial grassbeds by swimming Bay scallops, *Argopecten irradians* (Lamarck, 1819). *J. Exp. Mar. Biol. Ecol.* **199**, 79-88.
- Kanmizutaru, T.** (2005). Light perception capability of the pallial eyes in the Japanese moon scallop *Amusium japonicum* as determined by electroretinogram. *Nippon Suisan Gakkai Shi* **71**, 928-934.
- Kirby-Smith, W. W.** (1972). Growth of the bay scallop: the influence of experimental water currents. *J. Exp. Mar. Biol. Ecol.* **8**, 7-18.
- Kruczynski, W. L.** (1972). The effect of the pea crab, *Pinnotheres maculatus* Say, on the growth of the bay scallop, *Argopecten irradians concentricus* Say. *Chesapeake Sci.* **13**, 218-220.
- Land, M. F.** (1965). Image formation by a concave reflector in the eye of the scallop, *Pecten maximus*. *J. Phys.* **179**, 138-153.
- Land, M. F.** (1966). Activity in the optic nerve of *Pecten maximus* in response to changes in light intensity and to pattern and movement in the optical environment. *J. Exp. Biol.* **45**, 83-99.
- Land, M. F.** (2003). The spatial resolution of the pinhole eyes of giant clams (*Tridacna maxima*). *Proc. R. Soc. Lond. B Biol. Sci.* **270**, 185-188.
- Leibovitz, L., Schott, E. F. and Karney, R. C.** (1984). Diseases of wild, captive, and cultured scallops. *J. World Maricult. Soc.* **15**, 269-283.
- MacDonald, B. A., Bricelj, V. M. and Shumway, S. E.** (2006). Physiology: energy acquisition and utilization. In *Scallops: Biology, Ecology, and Aquaculture* (ed. S. E. Shumway and G. J. Parsons), pp. 417-492. New York: Elsevier.
- Mikulich, L. V. and Tsikhon-Lukanina, E. A.** (1981). Food composition of the yesso scallop. *Oceanology* **21**, 633-635.
- Morton, B.** (2000). The function of pallial eyes within the Pectinidae, with a description of those present in *Patinopecten yessoensis*. In *The Evolutionary Biology of the Bivalvia*. Vol. 177 (ed. E. M. Harper, J. D. Taylor and J. A. Crame), pp. 247-255. London: The Geological Society.
- Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P. and Peterson, C. H.** (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**, 1846-1850.
- Nilsson, D.-E.** (1994). Eyes as optical alarm systems in fan worms and ark clams. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **346**, 195-212.
- Nilsson, D.-E., Gislén, L., Coates, M. M., Skogh, C. and Garm, A.** (2005). Advanced optics in a jellyfish eye. *Nature* **435**, 201-205.
- Riisgård, H. U., Kittner, C. and Seerup, D. F.** (2003). Regulation of opening state and filtration rate in filter-feeding bivalves (*Cardium edule*, *Mytilus edulis*, *Mya arenaria*) in response to low algal concentration. *J. Exp. Mar. Biol. Ecol.* **284**, 105-127.
- Shumway, S. E., Selvin, R. and Shick, D. F.** (1987). Food resources related to habitat in the scallop *Placopecten magellanicus* (Gmelin, 1791): a quantitative study. *J. Shellfish Res.* **6**, 89-95.
- Speiser, D. I. and Johnsen, S.** (2009). Comparative morphology of the concave mirror eyes of scallops (Pectinoidea). *Am. Malacol. Bull.* **26** (in press).
- von Buddenbrock, W. and Moller-Racke, I.** (1953). Über den Lichtsinn von Pecten. *Pubbl. Staz. Zool. Napoli* **24**, 217-245.
- Wehner, R.** (1987). 'Matched filters'-neural models of the external world. *J. Comp. Physiol.* **161**, 511-531.
- Widdows, J. and Hawkins, A. J. S.** (1989). Partitioning of rate of heat dissipation by *Mytilus edulis* into maintenance, feeding, and growth components. *Physiol. Zool.* **62**, 764-784.
- Wildish, D. J. and Saulnier, A. M.** (1982). The effect of velocity and flow direction on the growth of juvenile and adult giant scallops. *J. Exp. Mar. Biol. Ecol.* **155**, 161-168.
- Wilkens, L. A.** (2006). Neurobiology and behaviour of the scallop. In *Scallops: Biology, Ecology, and Aquaculture* (ed. S. E. Shumway and G. J. Parsons), pp. 317-356. New York: Elsevier.