Marine Biology (2003) 142: 123–131
DOI 10.1007/s00227-002-0922-6

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# Ontogenetic changes in gill morphology and potential significance for food acquisition in the scallop *Placopecten magellanicus*

Received: 3 February 2002 / Accepted: 11 July 2002 / Published online: 13 September 2002


**Abstract** Sources of mortality in both wild and cultured populations of marine bivalves during postlarval stages remain largely unknown, but may be partly associated with the inability to meet energetic demands during intense morphogenesis. The development of the gills in postsettlement scallops (*Placopecten magellanicus*) from 0.35 to 14 mm in shell height (SH) was investigated using scanning electron microscopy to determine the degree of size-specific differentiation of the gills and evaluate potential ontogenetic constraints in food acquisition. Key transitional stages in morphogenesis, likely to exert pronounced effects on feeding function, were identified and correlated with scallop size. The gill was initially homorhabdic, with unreflected inner demibranchs forming a basket-like structure maintained by ciliary junctions. Gill reflection, immediately followed by accelerated proliferation of gill filaments and formation of outer demibranchs, occurred at ~1 mm SH. Outer demibranchs were fully formed at ~2 mm SH. Suspension-feeding is probably rather inefficient prior to attaining 1–2 mm sizes. The onset of the heterorhabdic, adult form of the gill, which allows bidirectional particle transport and the potential for selection and for volume regulation of ingested material on the gill, occurred fairly late in development, at ~3.3–5.0 mm SH. Full development of gill plication was delayed until scallops attained ~7 mm. Gill differentiation in this species is thus relatively protracted and punctuated by critical transitional stages, which may be important in determining feeding and growth capacity of postlarval wild and cultured populations.

Communicated by R.J. Thompson, St. John's

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## Introduction

The change from a planktonic to a benthic stage is a critical period in the life history of bivalves. Postsettlement stages often experience high mortalities during and following metamorphosis under culture conditions, yet limited information is available on postlarval morphogenesis, especially for scallops (Pectinidae). Previous structural studies have focused primarily on larval bivalves (e.g. Elston 1980; Waller 1981; see review by Cragg and Crisp 1991 for larval scallops) and adults. Descriptions of pallial organ morphogenesis in postlarval bivalves are rare, and, for pectinids, they have thus far been limited to two species: the Japanese scallop *Patinopecten* (= *Mizuhopecten*) *yessoensis* (Kingzett 1993) and the European scallop *Pecten maximus* (Beninger et al. 1994). In these studies scanning electron microscopy (SEM) and histological observations were conducted for scallops only up to 2 mm in shell height (SH) and 4 mm in shell length (SL), respectively. However, pallial organs of scallops at these sizes had not yet achieved the adult form, indicating that metamorphosis and full development of feeding structures is relatively protracted in these temperate scallop species. This contrasts with oysters (*Crassostrea* and *Ostrea* species), which generally complete metamorphosis within 48 h and undergo relatively rapid gill development compared to non-cemented bivalves (e.g. Chaparro et al. 2001). Although the structure and function of adult gills of *Placopecten magellanicus* (Morse 1982; Beninger et al. 1988, 1992; Le Pennec et al. 1988; Beninger and Le Pennec 1991) and the peribuccal organs of this species (Beninger et al. 1990a,b) have been the subject of extensive studies, no descriptions are available of morphogenesis during early ontogeny in this commercially important species. In addition, *P. magellanicus* (a member of the *Palliolum* supragenus) is a more primi-

tive pectinid than *Pecten*, and evolved later than the *Chlamys* group, which includes *P. yessoensis* (Waller 1991). These phylogenetic differences may be reflected in gill development.

The giant scallop, *Placopecten magellanicus* (Gmelin, 1791) is a major fishery species in Atlantic North America, and also shows potential for aquaculture (Dadswell and Parsons 1991), despite its relatively slow development (planktotrophic larval development lasts ~35 days at 15°C, Culliney 1974) and growth, as it has a high market value and is well adapted to cold waters. However, the processes controlling benthic recruitment and survival in wild populations are poorly known, and aquaculture of sea scallops is still heavily dependent on collection of wild postlarvae (spat) and their subsequent growout in the field. Hatchery production of sea scallop seed has met with varying, unpredictable success due to high, unexplained mortalities and arrested or slow growth during postlarval development. Poor growth and survival of postsettlement scallops (e.g. Ó Foighil et al. 1990) may reflect a poor understanding of stage-specific nutritional requirements and environmental tolerances.

Adult scallops possess two complex, heterorhabdic (two types of filaments, ordinary and principal), filibranch, plicate gills, each consisting of two demibranchs. In contrast, the gill of newly metamorphosed scallops studied to date (*Patinopecten yessoensis* and *Pecten maximus*) is homorhabdic, non-plicate and consists of a single (inner), unreflected demibranch. Gill ontogeny in this group thus appears to recapitulate the evolution of this organ. Such major morphological changes during postlarval development are likely to exert profound effects on the scallops' feeding capacity and growth potential, yet it is not clear whether they correlate with scallop age or size.

The main objectives of the present study were: (1) to document the anatomical differentiation of the gills in relation to size/age in *P. magellanicus* over a wide developmental range, from settlement (at ~0.3 mm) to ~14 mm SH, and (2) thereby to identify critical transitional stages in the ontogeny of this primary feeding organ, which may be associated with changing nutritional requirements or higher mortality risk. This study of normal development also serves as a basis for assessment of gill abnormalities that may occur in response to suboptimal environmental conditions and disease. Morphogenesis of associated pallial organs involved in food processing (labial palps, lips, mantle and foot) during early ontogeny of *P. magellanicus* will be described in a subsequent paper. These anatomical studies will provide the basis for further work designed to elucidate the functional significance of developmental changes to energetics and feeding physiology.

## Materials and methods

Terminology used in previous studies has sometimes been confusing, as the terms postlarvae, spat and juvenile have often been used interchangeably. In this study, the term "postlarvae" designates scallops from settlement (marked by the disappearance of the larval velum, appearance of the dissoconch shell and adoption of a benthic, crawling habit) up to achievement of the adult form of the gill. The term "juvenile" is here applied to scallops measuring >5–7 mm SH, from attainment of the heterorhabdic, plicate form of the gill (see "Results") to the time when they reach reproductive maturity, as evidenced by spawning.

Observations of sea scallops (*Placopecten magellanicus*) were derived from three cohorts obtained from two commercial hatcheries in Atlantic Canada. The first cohort was sampled during the summer of 1997. Samples were narcotized and fixed on site at a commercial hatchery in Mahone Bay (Nova Scotia, Canada). The first sample was taken on 3 June 1997, at a mean SH (=maximum dimension along the dorso-ventral axis excluding the umbo) of 178 μm. The second cohort was air-shipped from a hatchery in Quebec (Canada) on 16 July 1999, at a mean SH of 389 μm. Scallop postlarvae were reared in 1000-l recirculating tanks equipped with downwellers (on a Nitex screen, square mesh size=153 μm) maintained in a temperature-controlled room at IMB's (Institute for Marine Biosciences) Aquaculture Research Station (ARS). Spat (50–100 depending on size) were sampled at regular intervals to allow observations at approximate mean cohort SH increments of ~100 μm in early stages, and ~1000 μm in later stages (≥6 mm). The third cohort consisted of hatchery-reared juveniles obtained from a field growout site in Quebec, which were air-shipped on 5 July 2000 at an initial mean SH of ~5 mm. These were maintained in recirculating upwellers (on a 1 mm square mesh).

Scallops at ARS were kept at a constant temperature of 14°C, in 1-μm-cartridge-filtered seawater (salinity=30 ppt). In 1999, scallop postlarvae were offered a mixed algal diet consisting of *Pavlova lutheri* and *Chaetoceros gracilis* (50:50 ratio by volume, 40 cells $\mu l^{-1}$ total cell density). The juveniles sampled in 2000 were fed a mixed algal diet of *P. lutheri*, *C. gracilis* and *Tetraselmis striata* (40:40:20 ratio by volume).

### Preparation of specimens for SEM

Postlarvae were kept refrigerated at 4°C for 1–2 h prior to narcotization. Spat sampled in 1997 and early 1999 were narcotized using gradual exposure to ascending concentrations of magnesium chloride up to 7.5%. However, the valves of postlarvae remained closed, and the animals remained relatively contracted, rendering dissection difficult. Gaping valves and relaxation were finally achieved on later 1999 samples using gradual additions of a 1 mg $ml^{-1}$ stock solution of tricaine methanesulfonate (MS-222), a popular fish narcotizing agent, prepared in 0.22-μm-filtered seawater.

Sea scallops were fixed in slightly hyperosmotic 1G4F for a minimum of 48 h at 4°C to ensure tissue penetration. Animals were dehydrated in an ascending ethanol series after removal of the fixative with 0.2 M $PO_4$ buffer (pH 7.2) and dried in a critical-point dryer. They were then glued to aluminum stubs using double-sided conductive carbon tape, which facilitated measuring and dissection of spat. Dissection most often involved removal of the flatter, lower or right valve. The exact position and shell height of each specimen on the stub was recorded. The stubs were sputter-coated with gold, and observations were made with a JEOL 5200 SEM at the University of Moncton (New Brunswick) or with a Hitachi model S-3000 N SEM at IMB. Approximately 10–20 postlarvae of a given size class were typically observed at each sampling date.

## Results

Major changes in the gill anatomy of *Placopecten magellanicus* were observed over the course of development, which suggest varying efficacy in particle retention, transport and selection. Five key stages in gill

morphogenesis were identified: (1) formation of the ''gill basket'', composed of two opposing inner demibranchs, and elongation and slow multiplication of ordinary filaments (homorhabdic, unreflected gill); (2) reflection of inner demibranchs to form ascending and descending lamellae; followed by (3) formation of the outer demibranchs and accelerated multiplication of ordinary filaments; (4) differentiation of the principal filaments and thus development of the heterorhabdic condition; and (5) gill plication (heterorhabdic, plicate gill characteristic of adult scallops).

The morphological developmental stage of scallops was correlated with shell size rather than age. Gill reflection started between 950 μm and 1.1 mm SH in both 1997 and 1999 cohorts. However, the age of the postlarvae (in days from settlement) in this size range was between 38 and 42 days for the 1997 cohort and between 26 and 111 days for the 1999 cohort. The wide range of ages in the 1999 cohort was due to a period of arrested growth, which occurred between August and November. Another example of size-related morphogenesis was the development of the interconnecting vessels of the dorsal expansions in juveniles (see below). They appeared at approximately 5.0–5.2 mm SH, even in animals with a 4-month age difference.

Postlarvae measuring up to ~950 μm possessed homorhabdic, unreflected, non-plicate gills, each composed of a single (inner) demibranch (Fig. 1). The two opposing demibranchs formed a basket-like structure (Fig. 1A, B, F) termed ''gill basket'' (Beninger et al. 1994), which is maintained by a number of interfilamentar ciliary junctions. These include ciliary junctions between adjacent ordinary filaments from the same demibranch (length of cilia ~15 μm; Fig. 1D, E) and a ciliary junction between the first free filaments from opposing demibranchs (Fig. 1F). The first, anteriormost filament, fused to the mantle along its entire length, is connected to the first free filament by a ciliary junction (Fig. 1B). At 350 μm SH, the gill comprised one anterior mantle-fused filament, five ordinary filaments and a few (~2) gill buds or primordia at the posterior end (Fig. 1A).

Initial growth of the ascending filaments of the inner demibranch (known as ''reflection'') began at scallop sizes ranging between 0.95 and 1.1 mm SH and marked the formation of a V-shaped gill and separation between the suprabranchial and infrabranchial chambers (Fig. 2A). In addition to the ciliary junctions between the distal tips of the filaments described above (also see Fig. 4E), ciliary junctions were also observed between filaments at the ventral bend of the reflected gill (Fig. 2C, D). At this stage the gill is similar to the homorhabdic filibranch gill type (e.g. as observed in adult mussels), although its function likely differs, as sea scallops lack a distinct ventral food groove (see Fig. 3F). Prior to reflection, the most prominent features in gill development were elongation and slow proliferation of the filaments, which are added at the posterior end of the gill, as indicated by the presence of gill buds (Fig. 2A). The mantle-fused, anteriormost filament

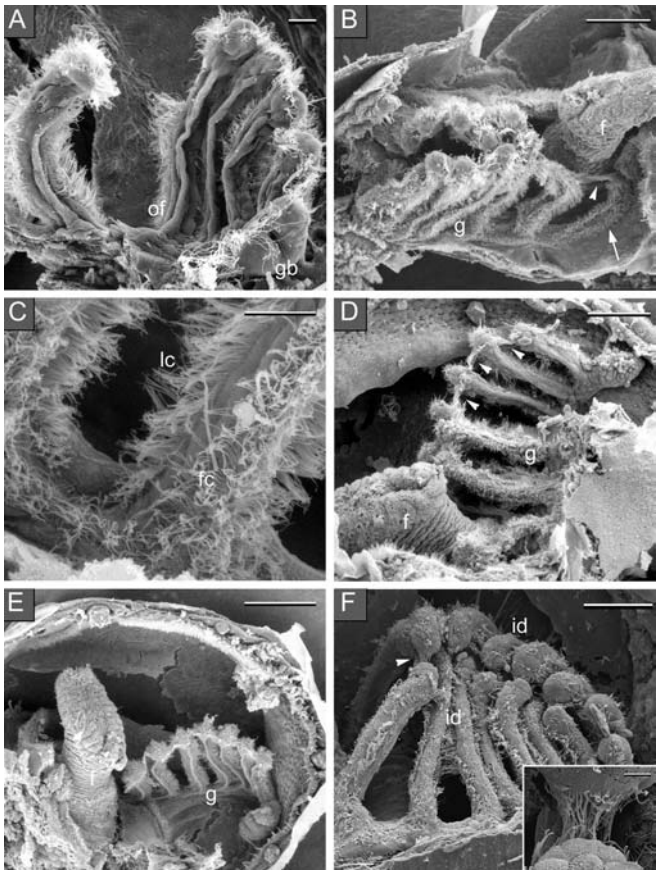


**Fig. 1A–F** *Placopecten magellanicus*. SEM micrographs showing gill development of postlarvae prior to reflection (350–867 μm). **A** Abfrontal view of the ordinary gill filaments (*of*) and gill bud (*gb*) at 350 μm shell height, foot removed. The two opposing demibranchs form a basket-like structure referred to as the gill basket. *Scale bar*: 10 μm. **B** Gill (*g*) of a 500 μm scallop, showing a ciliary junction (*arrowhead*), the fusion of the anteriormost filament to the mantle (*arrow*) and the spatial relationship between the foot (f) and the two inner demibranchs forming the gill basket. *Scale bar*: 50 μm. **C** Close-up of frontal surface of ordinary filaments showing the frontal cilia (*fc*) and lateral cilia (*lc*). Note absence of the laterofrontal cilia. Mean shell height (SH) of the sampled cohort was 440.9 μm. *Scale bar*: 10 μm. **D** Abfrontal surface of the inner demibranch showing the interfilamentar ciliary junctions (*arrowheads*). Note absence of cilia on the abfrontal surface. *Shell height*: 684 μm, *scale bar*: 50 μm. **E** Gill prior to reflection in a 835 μm scallop. *Scale bar*: 100 μm. **F** View of the gill basket and the ciliary junction (*arrowhead* and *inset*) between the first free filaments of opposing inner demibranchs (*id*). *Shell height*: 867 μm, *scale bar*: 50 μm (*inset*: 5 μm)

persisted in larger postlarvae (was still visible in 1 mm scallops). The free filaments numbered over nine per demibranch (~14 including the gill buds) at the time of reflection (Fig. 2A).

At these stages the abfrontal gill surface was completely devoid of cilia (Figs. 1A, D, E and 2A, and confirmed at higher magnifications). The frontal surface of the filaments (Figs. 1C and 4F) and the thickened distal extremities of the filaments or capitula (Fig. 4E) were densely covered with simple cilia in all spat observed. Abundant lateral cilia were also present

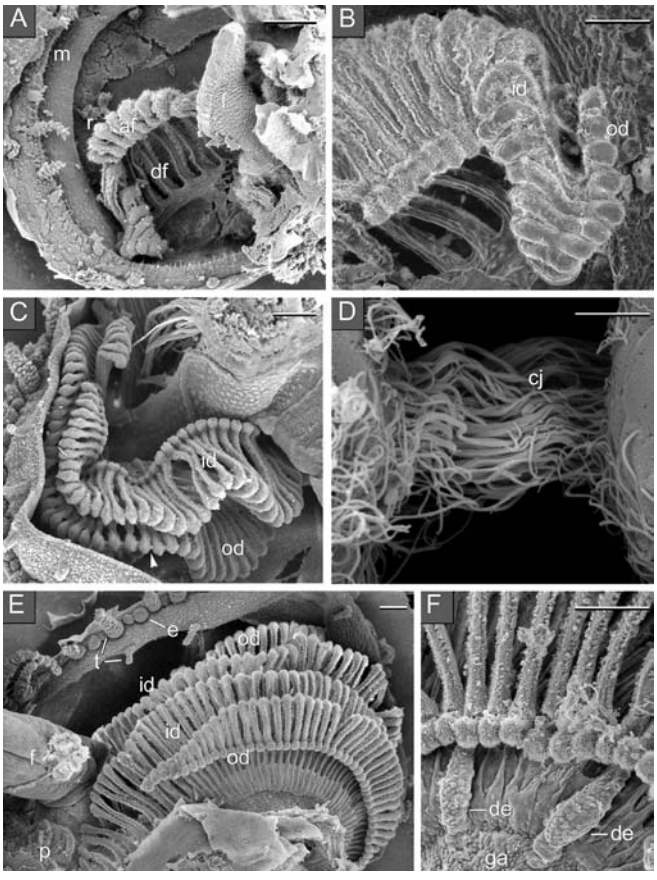


**Fig. 2A–F** *Placopecten magellanicus*. Gill development of sea scallop postlarvae between 1.1 and 5.5 mm SH. **A** Reflection (*r*) of the inner demibranch; ascending filaments (af) and descending filaments (*df*) (*m* mantle) (*f* foot). *Shell height*: 1140 μm, *scale bar*: 100 μm. **B** Initial development of the outer demibranch (*od*) (*id* inner demibranch).*Shell height*: 1320 μm, *scale bar*: 50 μm. **C** Completion of the outer demibranch. *Arrowhead* marks ciliary junctions between filaments at the ventral bend. *Shell height*: 1784 μm, *scale bar*: 125 μm. **D** Close-up of interfilamentar junctional cilia (*cj*) at the ventral gill margin shown in B. *Scale bar*: 10 μm. **E** Paired gills, each composed of an outer and inner demibranch, of a 3000 μm SH scallop. Note first appearance of rudimentary dorsal expansions at the base of the gills (*e* eyes; *t* tentacles) (*p* labial palp). *Scale bar*: 100 μm. **F** Rudimentary precursor of the dorsal expansions (*de*) (*ga* gill axis). *Shell height*: 3560 μm, *scale bar*: 100 μm

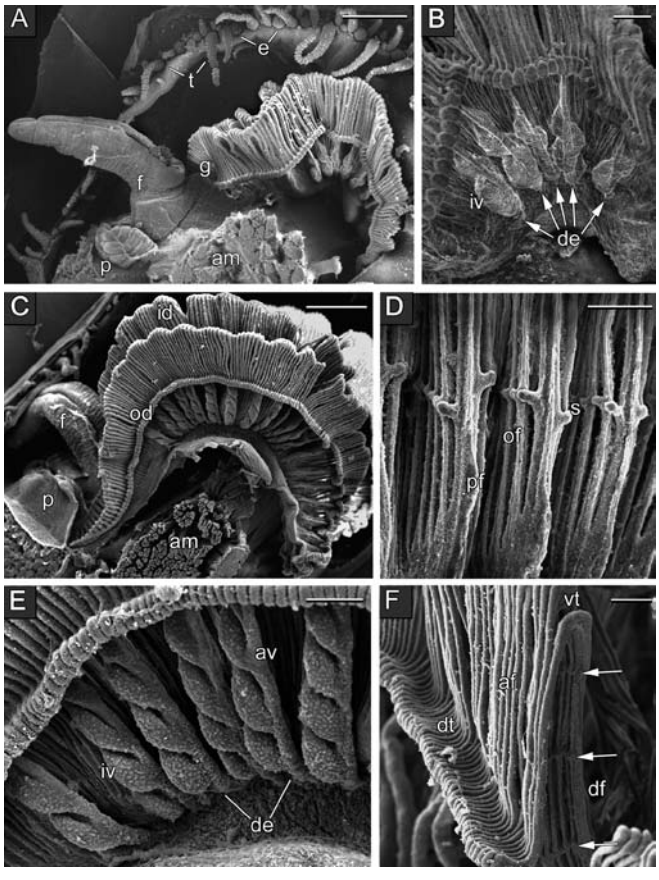


**Fig. 3A–F** *Placopecten magellanicus*. Gill morphology in sea scallops from 6 to 14 mm SH. **A** Onset of plication and further development of dorsal expansions on the abfrontal gill (*g*) surface (right gill removed) (*e* eyes; *t* tentacles on the mantle edge; *f* foot; *p* labial palp; *am* posterior adductor muscle). *Shell height*: 5520 μm, *scale bar*: 500 μm. **B** Close-up of the dorsal expansions (*de*) seen in A, showing development of interconnecting vessels (*iv*). *Scale bar*: 100 μm. **C** Whole view of a 7 mm SH scallop gill, showing well-developed dorsal expansions on the centralmost filaments and well-developed plicae. Note the spatial relationship between the palp (*p*) and the ventral margin of the gill (*id* inner demibranch; *od* outer demibranch). *Scale bar*: 50 μm. **D** Ciliated spurs (*s*) forming a row in an 8 mm scallop, connecting the principal filament (*pf*) and the ordinary filaments (*of*). *Scale bar*: 100 μm. **E** Close-up of C, showing interconnecting vessels of the dorsal expansions and the afferent vessel (*av*). *Scale bar*: 100 μm. **F** Gill of a 14 mm (SH) juvenile, showing several rows of spurs (*arrows*), the ventral tract (*vt*) and a well-developed dorsal tract (*dt*) (*af* ascending ordinary filaments). *Scale bar*: 100 μm

(Figs. 1C and 4F); however, latero-frontal cilia were absent in this and later stages (at least up to 7.5 mm SH; see inset Fig. 4F). Interfilamentar ciliary junctions were first observed in spat measuring 450 μm SH. This does not exclude their presence at smaller sizes in which apposition of filaments may obstruct the view of these junctions. Wide interfilamentar spaces (up to 21–29 μm in width) were characteristic of unreflected gills (Fig. 1D, E), whereas adjacent filaments were more closely apposed in larger specimens (Fig. 2E). Particle capture prior to reflection may therefore be less efficient than in later stages.

Between 1 and 2 mm SH, following reflection of the inner demibranch and thus breakdown of the "gill basket" structure, the outer demibranch underwent rapid development. Gill buds of the outer demibranch were sometimes seen with the onset of reflection of the inner demibranch (Fig. 2A). Short filaments were visible by 1.3 mm SH (Fig. 2B). Subsequently, there was a rapid increase in the number of filaments of the outer demibranch and their reflection occurred almost immediately. This development differed from that of the inner demibranch (in scallops $< 1.2$ mm SH), in which reflection was preceded by a period of filament elongation and multiplication. The outer demibranch was fully developed in scallops ranging from 1.78 to 1.95 mm SH (Fig. 2C). The formation of the outer demibranch

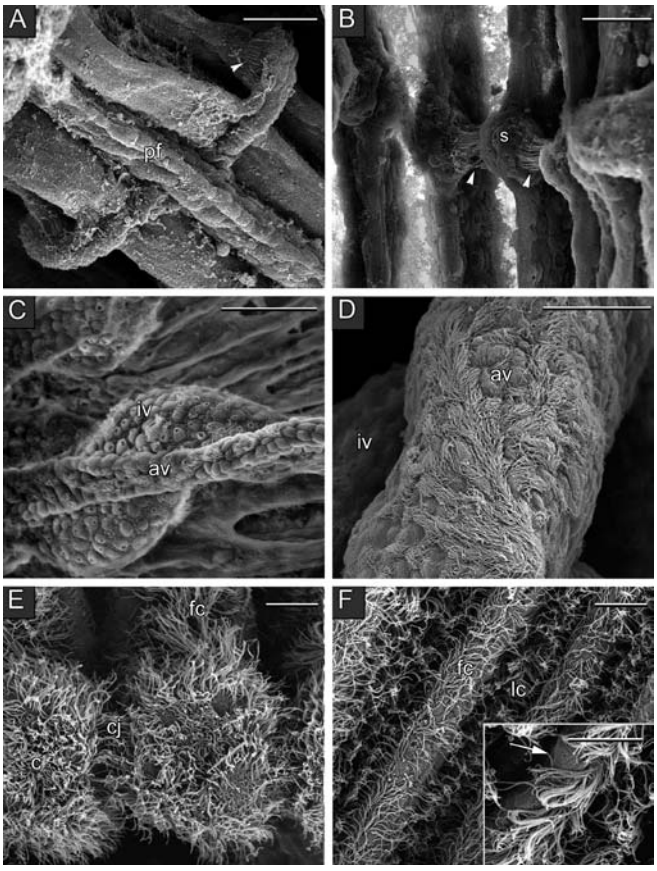


**Fig. 4A–F** *Placopecten magellanicus*. Details of gill ciliation during scallop ontogeny: ciliary junctions between filaments (*upper panels*), abfrontal surface ciliation of principal filaments (*middle panels*) and frontal surface ciliation of ordinary filaments (*lower panels*). **A** Close-up of ciliated spur connecting the principal filament (*pf*) with adjacent ordinary filaments, in distended position. Note ciliation on one side of the spur only (*arrowhead*). *Shell height*: 6 mm; *scale bar*: 50 μm. **B** Ciliated spurs (*s*) showing the ciliary junctions (*arrowheads*) between ordinary filaments in a 7.5 mm scallop. These spurs are ciliated on both sides. *Scale bar*: 20 μm. **C** Afferent vessel (*av*) and interconnecting vessels (*iv*) on the abfrontal gill surface, showing sparse ciliation and abundant mucocytes in a 5.5 mm juvenile. *Scale bar*: 50 μm. **D** Surface of the afferent vessel of a dorsal expansion (abfrontal gill surface), showing patchy but abundant ciliation. *Shell height*: 15 mm, *scale bar*: 25 μm. **E** Close-up of the tips of the ascending filaments or capitula (*c*) of a reflected inner demibranch, showing dense ciliation and a ciliary junction (*cj*) (*fc* frontal cilia). *Shell height*: 1.56 mm, *scale bar*: 10 μm. **F** Detail of the ciliation of the frontal surface of ordinary filaments in a 7.5 mm SH scallop (*fc* frontal cilia; *lc* lateral cilia). *Scale bar*: 10 μm. *Inset* shows absence of the latero-frontal cilia. *Scale bar*: 10 μm

undoubtedly provides a sharp increase in the effective gill surface area for particle capture.

Above 2 mm SH, a rapid increase in the genesis of filaments in both demibranchs was observed, resulting in a further increase in gill surface area. The principal filaments typically began differentiating at ~3.3 mm SH (although they were first observed in a 2.7 mm specimen), as marked by the presence of rudimentary dorsal expansions [shown in a 3.0 mm (Fig. 2E) and 3.6 mm specimen (close-up in Fig. 2F)]. In adult *P. magellanicus* (Beninger et al. 1988), dorsal expansions are associated only with principal filaments, not ordinary filaments, and they consist of an abfrontal afferent vessel, an efferent vessel contained within the wall of the principal filament and a number of interconnecting vessels (Beninger and Le Pennec 1991). During ontogeny the dorsal expansions formed on the centralmost filaments first and showed the most advanced stage of development in this region (Fig. 3A, C). They developed incipient interconnecting vessels (Fig. 3B) in specimens of approximately 5 mm. The onset of plication (shown for a 5.5 mm specimen in Fig. 3A) occurred at approximately 4.7 mm. Full development of plication was observed at 7 mm SH (Fig. 3C). Close association of the anterior, tapered end of the gill and the base of the labial palp (as shown in Fig. 3C, and characteristic of adults) indicates that the gill can deliver particles to the palps and has become fully functional in suspension-feeding.

A second adult characteristic of the ordinary filaments on the abfrontal gill surface, i.e. the presence of ciliated spurs or cilifers (Fig. 3D), was first noted in 6 mm scallops. The spurs of adjacent ordinary filaments were connected by interdigitating cilia (Fig. 4B), forming multiple rows (Fig. 3D, F). In addition, the number of rows of spurs along the length of the principal filament, between the gill axis and the ventral margin of the gill, increases as the gill enlarges and requires additional structural support. The ciliated spur connecting the principal filament to the adjacent ordinary filaments appeared distended in some specimens (Fig. 4A). In most cases, however, the spurs were not elongated. This may reflect varying degrees of expansion or contraction of the gill. The ultrastructure of the junctional cilia between adjacent cilifers has been described in detail for adult *P. magellanicus* (Morse 1982) and *Argopecten irradians* (Reed-Miller and Greenberg 1982).

The frontal surface of the ordinary filaments was abundantly ciliated throughout development (Figs. 1C and 4E, F). The abfrontal surface remained unciliated prior to differentiation of the principal filaments (Fig. 1A, D). Sparse and patchy ciliation of the afferent vessel and interconnecting vessels was observed (Fig. 4C) until scallops attained ~8 mm SH. However, in larger (14 mm) juveniles, the afferent vessels of the dorsal expansions were abundantly ciliated (simple cilia are shown in Fig. 4D), as also described for adults (Dufour and Beninger 2001).

Figure 5 shows the ontogenetic relationship between the number of filaments of the inner demibranch and scallop shell height (350 μm to 7.5 mm). Only intact gills were used for these determinations, and the number of filaments excluded the first filament fused to the mantle, but included those of the gill bud region, as shown in the inset. A single power curve did not adequately fit the data in that it consistently underestimated the number of filaments in larger scallops. The best fit was provided by two linear regressions, with a predicted inflection point at ~1 mm, which coincides with the size at which gill reflection was observed to occur. The inflection point

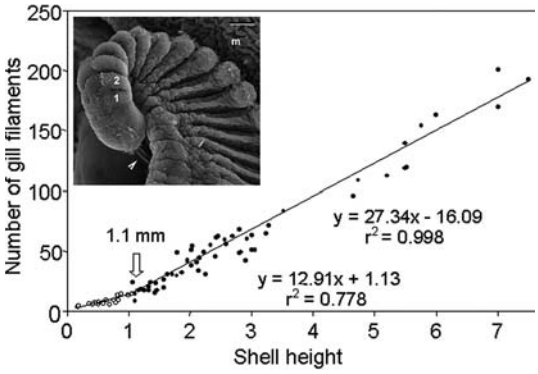


**Fig. 5** *Placopecten magellanicus*. Linear relationships between the number of filaments of the inner demibranch, *y*, and scallop shell height in millimeters, *x* ($r^2$ coefficient of determination of the linear regression equation). *Arrow* marks the inflection point at 1.1 mm (see "Results"). *Inset* illustrates the method used to count individual filaments starting at the gill bud region (*m* mantle). *Scale bar*: 25 μm

was determined by iterative regression analysis rather than visual inspection, as follows: linear regression equations were recalculated after sequential addition of individual data points (and subtraction from the second regression line) to determine those fitted equations yielding the highest coefficients of determination for the two lines ($r^2$ in Fig. 5) as well as a systematic increase in $r^2$ (for example, inclusion of filament data for scallops ranging from 167 to 780 μm yielded an $r^2$ of 0.48, which increased to 0.64 when the range was 167–879 μm, and finally to 0.78 when the range was extended to 1.04 mm). An alternate, but not dissimilar, approach based on moving regression analysis was used by Forbes and Lopez (1989) to identify departures from single-power curve scaling and potential critical developmental periods or breakpoints. Thus, the rate of proliferation of gill filaments (as determined by the slope of the regression equations) increased from ca. 12.9 filaments $mm^{-1}$ SH prior to reflection, to ~27.3 filaments $mm^{-1}$ following reflection.

## Discussion

The pronounced changes in gill morphogenesis of sea scallops (*Placopecten magellanicus*) documented in the present study suggest that the feeding mechanisms and efficiency of particle retention and transport are likely to vary considerably during postlarval development. During early stages, especially prior to reflection, the gill may not be very effective in suspension feeding, and alternate, supplementary methods of food acquisition may be important, such as the uptake of dissolved organic matter (DOM) by pallial organs or palp-pedal feeding on benthic microfilms. This could result in suboptimal growth rates using traditional culture methods that rely only on suspended microalgae. Thus, the presence of epiflora on an artificial settlement substrate greatly enhanced growth of early (< 1 week old) *Patinopecten yessoensis* postlarvae (O Foighil et al. 1990). Uptake of DOM (labeled amino acids) was demonstrated in *P. magellanicus* veligers (Marshall and Lee 1991), and, in newly settled *Pecten maximus*, autoradiography confirmed that DOM uptake was largely localized in the gill filaments and mantle (Manahan and Crisp 1982). Pedal feeding involves deposit feeding on benthic films by the ciliated distal portion of the foot or propodium and subsequent transfer of particles trapped in mucus secreted by pedal mucocytes to the labial palps for ingestion. This feeding mode has been documented in postlarval *P. yessoensis* and *Tridacna* (Reid et al. 1992; Kingzett 1993) and in geoducks, *Panope abrupta*, using video cinematography (King 1986). Pedal cilia can also contribute to the generation of the anterior, inhalent current in postlarval bivalves (Caddy 1969), including scallops. It has been suggested that palp-pedal feeding may indeed be a ubiquitous and primitive mechanism of food capture in all postlarval bivalves (reviewed by King 1986).

Ciliation of the gill filaments (presence of well-developed lateral and frontal simple cilia) was present even in the smallest specimens observed (175 μm pediveligers) and was therefore not an acquired feature during early development. This contrasts with findings for *Ostrea chilensis*, in which ciliation of the gill filaments does not become apparent until ~475 μm SH (Chaparro et al. 2001). The ciliation pattern of the ordinary filaments in early stages of sea scallops is thus similar to that of the adult, except for the absence of reduced latero-frontal cilia, a characteristic of adult Pectinidae. This finding in *P. magellanicus* postlarvae agrees with Kingzett's (1993) observations of *P. yessoensis*, in which these cilia were absent at least up to 2 mm SH. In adult scallops poor development of the latero-frontal cirri has been suggested as an explanation for the poor retention efficiency of small (< 6–7 μm) particles of the pectinid group (reviewed by Bricelj and Shumway 1991). Kingzett found that, in contrast to adults, scallop postlarvae (*P. yessoensis*, 600 μm SH) were able to clear *Chateoceros calcitrans* (2.5–4.8 μm size range) effectively relative to larger (but ≤ 10 μm) algae offered in unialgal suspensions. At ≤ 1000 μm SH they also ingested 2, 6.5 and 9 μm fluorescent beads at similar rates (Kingzett 1993). The upper size limit for ingestion at 600 μm SH was ca. 20–25 μm, the approximate width of the interfilamentar space determined for early *P. magellanicus* postlarvae in the present study. Future determinations of particle retention efficiency in mixed suspensions by scallop postlarvae that lack latero-frontal cilia may help to elucidate conflicting information on the role played by these cilia in particle retention. It is difficult, however, to make direct comparisons of gill ciliary function between adult scallops (heterorhabdic) and postlarvae (homorhabdic), as these two stages also have vastly different gill morphologies.

The complete absence of ciliation on the abfrontal surface of ordinary filaments in these early stages differs

from adult bivalves of all gill types studied, which show varying degrees of ciliation on this surface, with greatest reduction marked by the presence of short, simple cilia in advanced homorhabdic filibranchs, such as *Abra zebra*, and the more evolved eulamellibranchs (Dufour and Beninger 2001). Therefore, in early *P. magellanicus* postlarvae (homorhabdic condition), the abfrontal surface cannot play a role in cleansing of the gill, the main function ascribed to this surface in primitive deposit-feeding protobranchs, or in generating water currents and thus aiding in water flow through the gills, as suggested for adult *Mytilus edulis* (Jones et al. 1990). Dufour and Beninger (2001) suggested that in adult suspension-feeding bivalves the abfrontal gill surface, which retains a variable density of cilia and mucocytes depending on gill type and species, constitutes a vestigial mucociliary particle transport surface retained from the ancestral protobranchs. However, in the present study there was no evidence of vestigial ciliation of the abfrontal gill surface during early ontogeny. The presence or absence of abfrontal mucocytes in these stages remains to be determined.

Reflection of the inner demibranch at ~1 mm SH led to breakdown of the gill basket, and coincided with an inflection point in the allometric relationship between filament number and scallop size and a doubling of the rate of multiplication of gill filaments, suggesting that this size may represent a critical transition during development. Yonge (1947) concluded that the bivalve gill cannot function effectively in suspension-feeding until reflection occurs, allowing formation of ventral particle tracts. However, Stasek (1962) concluded, based on observations of two non-pectinid bivalves, that the inner demibranch could function as a food-collecting organ in young stages even in the absence of distinct marginal food tracts and before development of the outer demibranch. Ciliary currents along the free margins of the gill could actively transport food particles to the mouth despite the absence of anatomically distinct food tracts. This discrepancy may simply reflect differences in the effectiveness of suspension feeding during early ontogeny. Kingzett (1993) measured size-specific clearance rates in *P. yessoensis*, and found that scallops $\leq 400$ μm SH were characterized by a constant and very low clearance rate and experienced a sudden increase in this parameter at 600 μm SH and again at sizes exceeding 1 mm SH. In this context it is noteworthy that inner demibranch reflection occurred in this species at approximately the same size (~1.0 mm) as in *P. magellanicus*, although in the Japanese scallop it started at sizes $>600$ μm SH and filaments were fully reflected at 1.2–1.5 mm. It is noteworthy that the size range 600–1000 μm also coincided with high mortalities or reduced growth of *P. yessoensis* postlarvae in culture (Ó Foighil et al. 1990).

*P. magellanicus* are typically transferred from the hatchery to field nurseries by commercial growers at relatively smaller sizes (ca. 1–2 mm SH) than other bivalves, such as quahogs, *Mercenaria mercenaria*, and oysters, *Crassostrea virginica*, for which culture methods are more established. However, the present study demonstrates that the gills of *P. magellanicus* are relatively undifferentiated at these sizes, and long after benthic recruitment of natural populations. Completion of the outer demibranch (observed at ca. 1.8–1.9 mm SH) may also signal a critical developmental stage, as it leads to an increase in the total surface area for feeding and may result in an increase in clearance rate. Development of the outer demibranch (at 15°C) occurred at similar sizes in *P. yessoensis*, in which the primordia of the outer demibranch were first observed at 1.0–1.2 mm SH, and the outer demibranch was equal in size to the inner demibranch at ~2 mm SH (Kingzett 1993). The appearance of the outer demibranch has been proposed as a morphological indicator of the end of the byssal plantigrade stage and the beginning of the juvenile plantigrade stage (King 1986). It is of interest to note that *P. magellanicus* spat $>3$ mm had higher survival rates than smaller spat when deployed for field growout (Dabinett et al. 1997). Thus, once hatchery rearing conditions, including diets, are optimized for this species, it may be advantageous to delay transfer of these vulnerable stages to suspended culture in the field until the gills are more completely differentiated and the animals better able to cope with a more variable and potentially suboptimal food supply.

The heterorhabdic condition develops relatively late in *Placopecten* spp., starting at ~3.3 mm SH when incipient dorsal expansions were first observed. Their functional role as respiratory surfaces has been questioned by Morse (1982), who suggested that they may serve as a hemolymph reservoir when the gill is contracted. The significance of the increased ciliation on the abfrontal surface of the afferent vessel of the principal filaments observed during ontogeny in the present study remains unclear, although it may be associated with increased water flow at this surface. In adult *P. magellanicus* the density of abfrontal cilia is much greater and more uniform on the principal than on the ordinary filaments, and ciliation of the dorsal expansions is found mainly on the afferent vessel and is much sparser on the interconnecting vessels (Dufour and Beninger 2001). Abfrontal mucocytes were suggested to play a role in lubricating and thus protecting the adult gill during contraction associated with valve clapping and swimming.

Most of the significant changes in gill morphology occurring above ~3.3 mm SH were detectable at the abfrontal surface of the gill and involved the gradual differentiation and increasing complexity of the principal filaments. The heterorhabdic condition allows the possibility of bidirectional flow and thus control of particle selection and ingested volume at the gill. Video endoscopy of adult *P. magellanicus* showed that when the gill is overloaded, algae were transported dorsally to the dorsal food tract on principal filaments, whereas they were moved ventrally towards the ventral tract on ordinary filaments (Beninger et al. 1992). Since pectinids

do not have a well-developed ventral particle groove, particles transported along the ventral tract are more likely to be rejected as pseudofeces. Adult *P. magellanicus* are known to be capable of ingestion selectivity based on particle quality (MacDonald and Ward 1994), but the site of selection (presumably the labial palps and/or gills) and mechanisms involved remain uncertain. Beninger et al. (1990a) found no evidence of sensory receptors on the labial palps and, thus, argued that they were more likely to play a role in the regulation of volume entering the mouth than in qualitative selection.

Full plication of the gill at ~7 mm SH allows the concertina response (contraction of the principal filaments which modifies the orientation of the ciliated spurs), a mechanism used by adults for cleansing the gill and thus regulating volume (Beninger et al. 1992).

Remarkable similarities were found between the timing of major events in gill development at comparable rearing temperatures between the more primitive pectinid, *P. magellanicus* (present study, 14°C), and *P. maximus* (13–14°C) (Beninger et al. 1994). For example, gill reflection in the latter species began at 900–1000 μm SL, and dorsal expansions were first observed at 4 mm SL (compared to 3.6 mm SH in sea scallops). [Note that the mean ratio of SH/SL in *P. magellanicus* postlarvae ranges from 0.825 at 300 μm SH to 0.995 at 1000 μm SH (authors' unpublished data) indicating that size thresholds given in SH and SL are comparable]. Observations on these two relatively long-lived species, phylogenetically separated for 65 million years (Waller 1991), suggest a considerable degree of conservatism in the ontogeny of the heterorhabdic, filibranch gill. However, investigation of the timing (size) of key developmental events needs to be extended to other pectinid species. Additionally, the effect of temperature on gill ontogeny has not been studied for any bivalve species, and temperature-dependent variations in ontogenetic chronology could potentially have a significant influence on recruitment of wild scallop populations. Future studies should address this question.

In conclusion, postmetamorphic development in *P. magellanicus*, a cold-adapted species (and presumably also in *P. maximus* given the parallels mentioned above) is relatively protracted compared to that of other bivalves, as acquisition of the adult gill structure (heterorhabdic, plicate gill) does not occur until scallops exceed ca. 7–8 mm SH. Additional work on mucocyte distribution and mucus characterization of pallial organs and on feeding physiology, behavior and energetics during early ontogeny are required to gain further insights into the functional morphology of the organs described. However, the results of the present study identify critical transitions that will help to narrow the focus of future studies and suggest that gill morphology may be a determining factor in postmetamorphic growth and survival of pectinids, both in the wild and in culture. Our findings also set the stage for development of stage-specific diets and rearing conditions that may allow land-based aquaculture of sea scallops to larger and less vulnerable sizes prior to their transfer to the field.

**Acknowledgements** We especially thank D. O'Neil and the IMB microscopy staff for initial development of the protocols for SEM work and general guidance in microscopy, C. Barré (trainee at IMB) for SEM assistance and confirmatory observations, and S. McKenna (IMB) for husbandry of scallop postlarvae. We thank the Département de Biologie, Université de Moncton, for use of their scanning electron microscope and laboratory facilities, and Pec-Nord Inc., Quebec, and Lunenberg Shellfish Inc., Nova Scotia, for supplying scallops for this study. We also thank C. Bird (IMB) for reviewing the manuscript. This research was funded by NSERC through a Strategic Grant and National Centers of Excellence (NCE) AquaNet grant to Dr. V.M. Bricelj in collaboration with Memorial University of Newfoundland. This publication is NRCC contribution no. 42361.

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