Demonstration of Nutrient Pathway From the Digestive System to Oocytes in the Gonad Intestinal Loop of the Scallop *Pecten maximus* L.

PETER G. BENINGER1*, GAEL LE PENNEC2, AND MARCEL LE PENNEC2

1 Laboratoire de Biologie Marine, Faculté des Sciences, Université de Nantes, 44322 Nantes Cédex, France; and 2 Institut Universitaire Européen de la Mer, Université de Bretagne Occidentale, Site Technopôle Brest-Iroise, 29280 Plouzané, France

Abstract. The mechanism of nutrient transfer from the digestive system to the gonad acini and developing oocytes was investigated in the gonad-intestinal loop system of the queen scallop *Pecten maximus* L. Ferritin was injected directly into the purged intestine of specimens from the wild. Subsequently, a histochemical reaction and transmission electron microscopy were used to localize ferritin in various cell types. Ferritin was rapidly absorbed by the intestinal epithelium, and then appeared in hemocytes in the surrounding connective tissue. In the hemocytes, ferritin was stored in variously sized inclusions, as well as in the general cytoplasm. In all sections examined for the 12 experimental individuals, hemocytes were always found in association with connective tissue fibers extending from the base of the intestinal epithelium to gonad acini. After 30-min incubation, ferritin appeared inside the acini of all individuals. Ferritin-bearing cells were rarely found in association with male acini or gametes, nor with mature female gametes, but often with developing female gametes. Not all individuals showed the same temporal dynamics of ferritin transport, suggesting that nutrient transfer to oocytes is either not a continuous process, or that among individuals, transfer is not synchronized on short time scales. This is the first demonstration of a pathway of nutrient transfer from the intestine, and more generally the digestive system, to developing oocytes in the Bivalvia.

Introduction

In the Bivalvia, the digestive and reproductive systems are closely situated and often intertwined, either within the visceral mass (the majority of bivalves), or more distinctly separated from the visceral mass, as in the Pectinidae (Galtsoff, 1964; Morales-Alamo and Mann, 1989; Beninger and Le Pennec, 1991; Morse and Zardus, 1997). The ultrastructural characteristics of gametogenesis have only recently begun to be elucidated in this class (Pipe, 1987a, b; Dorange and Le Pennec, 1989; Eckelbarger and Davis, 1996a, b). However, gametogenesis must rely on the transfer of nutrients, which are acquired almost exclusively by other tissues or organs and transferred to the gonad.

Transfer of nutrients from storage or digestive sites to the gonad has been inferred or demonstrated in a number of bivalve species (Goddard and Martin, 1966; Vassallo, 1973; Ansell, 1974; Comely, 1974; Gabbott, 1975, 1983; Adachi, 1979; Zaba, 1981; Lubet et al., 1987; Le Pennec et al., 1991a, b). Although successful gamete production relies on such transfers, very little is known about the underlying pathways and mechanisms. The elaboration of oocyte reserves has been the subject of considerable research in many invertebrates, but is largely lacking in bivalves (see Eckelbarger and Davis, 1996a, for review). Regardless of whether bivalve gametes ultimately elaborate vitelline reserves using autosynthetic (Suzuki et al., 1992) or heterosynthetic pathways (as suggested by Eckelbarger and Davis, 1996a), or both, it is clear that nutrients must be made available, largely from the diet, for the synthesis of the gametes and their reserves.

A summary of known or inferred pathways that transfer nutrients to the gonad acini and gametes has been outlined.
Materials and Methods

Twelve specimens of *Pecten maximus* (size range 9–10 cm shell length, antero-posterior axis) were collected from the Bay of Brest (Finistère, France). The valves of each scallop were kept open with a wedge in the posterior dorsal region, and the proximal part of the descending intestinal loop was located by directing a cold light source at the male portion of the translucent gonad (see Fig. 1). Into this portion of the intestine in each scallop, 1 ml of a 4 mg ml$^{-1}$ solution of cadmium-free ferritin (Sigma horse spleen Type...
Figure 2. Transmission electron micrographs of uncontrasted oocytes and hemocytes in posterior (female) region of gonad, from individuals which had not been injected with ferritin. 2.1, 2.2 Details of early-developing oocytes at two magnifications (20,000 and 40,000 x, respectively). 2.3 Detail of rounded hemocyte, showing non-ferritin-containing inclusions (I). 2.4 Detail of pseudopod-bearing hemocyte. Note absence of ferritin clusters in all micrographs. N, nucleus.

1. 10-12 nm diameter molecules) was slowly injected. Complete distribution of ferritin throughout the length of the intestinal lumen was monitored visually by the appearance of the colored solution in the ascending branch. The scallops were divided into four groups of three individuals each, corresponding to 10, 30, 120, and 300 min of exposure to the ferritin solution. Exposure was carried out in 15°C filtered seawater, which was aerated with a pump and airstone. Following the designated period of exposure, the scallops were immediately dissected. Transverse slices of the gonad (about 1-2 mm thick) were removed at three levels along the antero-posterior axis of the gonad as shown in Figure 1, and immediately processed for histology and electron microscopy. To control for the eventual presence of clusters of endogenic ferritin molecules or other electron-dense particles, a control group of three individuals was injected with 0.8 μm filtered seawater, and processed for histology as detailed below.

Histology

Slices of gonad were fixed for histology in aqueous Bouin’s solution (24 h), dehydrated in an ascending ethanol-xylene series, and embedded in paraffin. Transverse sections corresponding to each exposure time and gonad level were cut at 5 μm, and each exposure series for a given level were positioned on a single microscope slide. The slides were then immersed in 35% ammonium sulfite for 2 h and rinsed with Milli-Q-filtered ultrapure water (all glassware at this stage was also prerinsed with ultrapure water). Sections were stained using the Turnbull blue protocol,
Figure 3. Dynamics of ferritin distribution in the *Pecten maximus* gonad for the three individuals at each exposure time. A, anterior region of gonad; M, median region of gonad; PO, posterior region of gonad; C, male portion of gonad; F, female portion of gonad; AB, tissues of ascending branch of intestine-gonad complex; DB, tissues of descending branch of intestine-gonad complex; 1, uptake into intestinal epithelium; 2, appearance in hemocytes within connective tissue surrounding intestine; 3, appearance in hemocytes at the outer faces of the acini; 4, appearance in hemocytes within the acini; 5, appearance in hemocytes/follicle cells appressed to oocytes. Thin line represents one individual; medium line represents two individuals; thick line represents three individuals.

Transmission electron microscopy

For transmission electron microscopy (TEM), the gonad slices were fixed for 10 h in cold (4°C) 2.5% glutaraldehyde −0.1 M sodium cacodylate buffer at pH 7.3 and 1100 mOsm. They were then cut into pieces of about 1 mm³, rinsed twice with the sodium cacodylate buffer solution, and post-fixed in cold 1% osmium tetroxide in buffer for 1 h. The tissue pieces were then rinsed with 70% ethanol, dehydrated in an ascending ethanol-xylene series, and embedded in Epon 812 resin. Transverse sections (400–600 nm) were cut with a Reichert ultracut-S ultramicrotome and examined without further contrast using a JEOL 100CX transmission electron microscope. The lack of further contrasting allowed ferritin granules to be identified without ambiguity in the resulting micrographs. However, lack of contrast and the very small size of the free ferritin molecules and masses render observation via the fluorescent TEM screen somewhat challenging.

Results

As will be shown below, it is important to distinguish between oocytes in different states. Oocytes may be in development (previtellogenic and vitellogenic oocytes), or
Figure 5. *Pecten maximus*. Uncontrasted transmission electron micrographs of cells in the intestine-gonad complex following ferritin injection in the intestinal lumen. 5.1 Detail of cytoplasm of absorptive cell from intestinal epithelium, in median (male + female) level of gonad showing ferritin clusters (F) in inclusions (FCI). 5.2 Enlargement of indicated region in Fig. 4.1. Note presence of ferritin both within the inclusions and distributed freely in the cytoplasm (>). 5.3 Detail of a large, rounded hemocyte in the connective tissue surrounding the acini in median (male + female) level of gonad. Note presence of ferritin (F) in variously sized inclusions. 5.4 Enlargement of region indicated in Fig. 4.3., showing ferritin (F) in inclusions. 5.5, 5.6 Portion
they may be mature (detached from the acinal wall). Following spawning, some oocytes of both types may remain in the acinus; these are termed residual oocytes. We will thus adopt this terminology in the present paper.

No ferritin was detected using either the Turnbull method or TEM observation (Fig. 2) in any of the control individuals; we may thus conclude that the ferritin observed in our histological and electron microscopical sections was injected.

The histological observations of the entire set of individuals and gonad levels revealed that the distribution of ferritin in the sampled tissues could be divided into 5 sequential steps: (1) uptake into intestinal epithelium, (2) appearance in hemocytes among the connective tissue surrounding the intestine, (3) appearance in hemocytes at the exterior faces of acini, (4) appearance in hemocytes within the acini, and (5) appearance in hemocytes/follicle cells appressed to oocytes. It is not possible to ascertain whether these cells were hemocytes or follicle cells in the histological sections (only TEM profiles can distinguish these cell types). The TEM profiles of these cells described below do not correspond to follicle cells, which are rich in rough endoplasmic reticulum (Dorange and Le Pennec, 1989), absent in the two pectinid hemocyte types (Beninger and Le Pennec, 1991) and in the cells observed appressed to the oocytes; however, as the TEM sections were uncontrasted, it is not possible to distinguish these cells with certainty. Although ferritin-containing hemocytes were very rarely observed associated with male spermatogonia, they were never observed appressed to developing male gametes. The distribution of ferritin among the sections is summarized in Figure 3, which presents each step in the sequence, for each gonad level, and each intestinal branch (ascending and descending), for each exposure time.

Light microscopy of the histological sections showed that ferritin was distributed in cells of the intestinal epithelium at all three antero-posterior levels of the gonad-intestinal complex, from the apex to the basal region of the columnar intestinal cells (Fig. 4). Ferritin appeared very rapidly in the intestinal cells, and was observed in all preparations, even after 10 min of exposure. TEM micrographs revealed that ferritin appeared predominantly in variously sized inclusions of the intestinal cells, although isolated granules could also be found in the cytoplasm (Fig. 5.1, 5.2). Large, round, ferritin-containing hemocytes were also detected beneath the intestinal basal lamina within the surrounding connective tissue after only a 10-min exposure (Fig. 4.2). Ferritin appeared in these hemocytes in variously sized inclusions, as well as being generally distributed within the cytoplasm (Fig. 5.3–5.6). In all sections examined for the 12 experimental individuals, ferritin-containing hemocytes were always observed in close association with connective tissue fibers extending from the basal lamina of the intestinal epithelium and the acini (Fig. 4.2, 4.3).

Further transport of ferritin to the gonad acini and oocytes appeared to be somewhat independent of exposure time (Fig. 3). Specimens in which further ferritin transport was observed showed ferritin-containing hemocytes/follicle cells both at the outside faces of gonad acini (including those which were remote from the intestine) and inside the gonad acini (Fig. 4.3–4.8). These hemocytes/follicle cells were typically found appressed to developing oocytes (Fig. 4.3–4.8). Although no positive Turnbull blue reaction was observed in female gametes, transmission electron micrographs revealed dispersed ferritin clusters within the cytoplasm of oocytes to which ferritin-containing hemocytes/follicle cells were appressed (Fig. 5.7, 5.8).

The localization and distribution of ferritin within the various cell types involved in the transfer sequence presented notable differences, which also explains the absence of a visibly positive Turnbull reaction in some cell types. Both the intestinal cells and the transport hemocytes possessed variously sized inclusions with considerable concentrations of ferritin, and these cells presented visibly positive Turnbull reactions.

Upon histological examination, 3 of the 12 experimental scallops were observed to be mature and ready to spawn, while the remaining 9 had already spawned and had begun producing a new cohort of female gametes. Although ferritin appeared in the intestinal epithelium and surrounding connective tissue of the mature scallops, ferritin-containing hemocytes were virtually never observed, either in the acini, or appressed to the oocytes of these individuals. Moreover, despite the presence of mature residual oocytes in the acini of the individuals which had spawned previously, ferritin-containing hemocytes/follicle cells were never observed appressed to them. Ferritin-containing hemocytes/follicle cells were, however, observed appressed to late-developing residual oocytes in these individuals (Fig. 4.8).

**Discussion**

The uptake of ferritin in the intestinal epithelium of *Pecten maximus*, observed in the present study, demon-
strates that proteinaceous substrates are absorbed by the scallop intestinal epithelium, at least some of which subsequently appear in hemocytes at the cell bases. The rapidity and ubiquity of this uptake, observed in the present study, as well as the cytological and enzymatic equipment of the intestinal epithelium (Le Pennec et al., 1991b), suggest that the scallop intestine is well-adapted for both a digestive and a transfer function. This result is consistent with the view of the intestine as a digestive organ in bivalves (Zacks, 1955; Reid, 1966; Payne et al., 1972; Mathers, 1973; Teo and Sabapathy, 1990). The development of the gonad around the intestine optimizes the potential for the transfer of nutrients to developing gametes.

The results of the present study allow us to identify the various cell categories and pathways that mediate the entero-gonadal transfer system in bivalves: intestine epithelial cells; large hemocytes which concentrate ferritin in cytoplasmic inclusions, in addition to that present freely in the cytoplasm; and connective fibers which are often associated with the hemocytes. Previous studies have shown that hemocytes may move across the intestinal epithelium: those containing material of little or no nutritional value move toward the lumen, while those containing nutritionally valuable material move from the lumen to the tissues surrounding the intestinal epithelium (see Cheng, 1996, for review of bivalve hemocyte types and functions). The present study shows that the scallop intestinal cells may, themselves, move nutrients from the lumen to the basal lamina; hemocytes subsequently act as transport vectors to the surrounding gonad tissue. This line of investigation does not seem to have been pursued previously, despite long-held anatomical knowledge of the scallop intestine-gonad relationship.

The pathway of intestine-oocyte transfer seems to conform largely to that postulated by Le Pennec et al., based on detailed histological observations (1991a). These authors proposed that nutrients assimilated by the intestinal epithelium are transferred to hemocytes at the base of the basal lamina, as observed in the present study. They further proposed that the efficiency of this transport relied upon connective tissue fibers linking the basal lamina to the acini, such that incorporated nutrients could be directed specifically to acini. In the present study, ferritin-containing hemocytes were always observed in association with connective tissue fibers between the base of the intestinal epithelium and the bases of the acini.

The asymmetry in ferritin distribution between the male and female parts of the simultaneous hermaphroditic gonad is consistent with the difference in the composition and consequent energetic demand of male and female gametes. While ferritin-containing hemocytes/follicle cells were readily observed appressed to developing oocytes, which elaborate substantial vitelline reserves, they were rarely observed within male gonad acini, which produce small spermatozoa with few energy reserves (see Beninger and Le Pennec, 1991, for the sizes of spermatozoa and oocytes inpectinids, and Beninger and Le Pennec, 1997, for the sizes of spermatozoa and oocytes in bivalves generally); and ferritin-containing hemocytes were never observed appressed to developing male gametes. This asymmetry suggests that the entero-gonadal pathway is specific to female gametes. Another such possible distinction is described below.

The fact that ferritin-containing hemocytes/follicle cells were always found in association with developing oocytes, and never in association with mature oocytes, suggests that the ferritin-containing cells might be able to distinguish between these two states, and can supply nutrients to the oocytes most in need, i.e., developing oocytes. It should be noted that the follicle cells detach from the mature oocytes of Pecten maximus (Dorange and Le Pennec, 1989). Although both residual mature and residual developing oocytes were observed in individuals that had recently spawned, ferritin-containing cells were only observed appressed to the residual developing oocytes, and never to the residual mature oocytes. This finding suggests that the spawning status (i.e., prespawning or postspawning) does not influence nutrient transport; rather, the oocyte developmental stage appears to be the determining feature of such transport, even when these gametes are destined for atresia and metabolic recycling (Pipe, 1987b; Dorange and Le Pennec, 1989; Le Pennec et al., 1991a). The data of Figure 3 show that ferritin transfer to developing oocytes does not occur at a uniform rate for all individuals; indeed, after 300 min, some individuals had no ferritin-containing cells appressed to developing oocytes. While this could be due to the stress induced by the experimental procedure, it could also indicate that nutrient transfer from the intestine is not a continuous physiological activity, or that among individuals, transfer is not synchronous on such short time scales. We are unaware of any studies that present the dynamics of oogenesis on such short time scales, but this is an interesting physiological question.

While the particular scallop gonad-intestine anatomical relationship is not common in bivalves, the digestive system and gonad are generally closely associated and intertwined, with loose connective tissue containing abundant fibers between these epithelia (Galtsoff, 1964; Morales-Alarcon and Mann, 1989; Morse and Zardus, 1997). These similarities to the pectinid system suggest that transfer from digestive epithelia to developing oocytes via a pathway similar to that described above may be a general feature of bivalve physiology.

Acknowledgments

The authors wish to thank Dr. Ita Widowati, Diponegoro University, Semarang, Indonesia, for having carried out
previous unpublished experiments on this subject, which guided the methodology of the present work. We are indebted to the staff of The Biological Bulletin for their very rigorous editorial work on this paper, which allowed us to substantially improve earlier versions of the manuscript. As a study of no direct economic or medical impact on humans, it is not possible to acknowledge funding from any of the French funding agencies.

Literature Cited

Adachi, K. 1979. Seasonal changes of the protein level in the adductor muscle of the clam, Tapes philippinarum (Adams and Reeves) with reference to the reproductive season. Comp. Biochem. Physiol. 64A: 85–89.

Ansell, A. D. 1974. Seasonal changes in the biochemical composition of the bivalve Chlamys septemradiata from the Clyde Sea area. Mar. Biol. 25: 85–99.

Beninger, P. G., and M. Le Pennec. 1991. Functional anatomy of scallops. Pp. 133–223 in Scallop: Biology, Ecology and Aquaculture, S. E. Shumway, ed. Elsevier Science Publishers B. V., Amsterdam.

Beninger, P. G., and M. Le Pennec. 1997. Reproductive characteristics of a primitive bivalve from a deep-sea reducing environment: giant gametes and their significance in acharas aline (Cryptodonta: Solemyidae). Mar. Ecol. Prog. Ser. 157: 195–206.

Block, J., A. A. Mulder-Stapel, L. A. Ginsel, and W. T. Daems. 1981. Endocytosis in absorptive cells of cultured human small-intestinal tissue: horse-radish peroxidase, lactoperoxidase and ferritin as markers. Cell Tissue Res. 216: 1–13.

Bockman, D. E., and W. B. Winborn. 1966. Light and electron microscopy of intestinal ferritin absorption. Observations in sensitized and non-sensitized hamsters (Mesocricetus auratus). Anat. Rec. 155: 603–622.

Bonaventura, C., and J. Bonaventura. 1983. Respiratory pigments: structure and function. Pp. 1–50 in The Mollusca, Vol. 2: Environmental Biochemistry and Physiology, P. W. Hochachka, ed. Academic Press, New York.

Booth, C. E., and C. P. Mangum. 1978. Oxygen uptake and transport in the lamellibranch mollusc Modulus demissus. Physiol. Zool. 51: 17–32.

Bottke, W., and I. Sinha. 1979. Ferritin as an exogenous yolk protein in snails. Wilhelm Roux's Arch. 186: 71–75.

Bottke, W., I. Sinha, and I. Kiel. 1982. Coated vesicle-mediated transport and deposition of vitellogenic ferritin in the rapid growth phase of snail oocytes. J. Cell Sci. 53: 173–191.

Boucher-Rodoni, R., and E. Boucard-Camou. 1987. Fine structure and absorption of ferritin in the digestive organ of Loitge vulgaris and L. forbesi (Cephalopoda, Teuthoidea). J. Morphol. 193: 173–184.

Cheng, T. C. 1996. Hemocytos: forms and functions. Pp. 299–333 in The Eastern Oyster Crassostrea virginica, V. S. Kennedy, R. I. E. Newell, and A. F. Eble, eds. Maryland Sea Grant College, College Park, MD.

Comely, C. A. 1974. Seasonal variations in the flesh weights and biochemical content of the scallop Pecten maximus L. in the Clyde Sea area. J. Cons. Cons. Int. Explor. Mer 35: 281–295.

Dorange, G., and M. Le Pennec. 1989. Ultrastructural study of oogenesis and oocytic degeneration in Pecten maximus from the Bay of St. Brieuc. Mar. Biol. 103: 339–348.

Eckelbarger, K. J., and C. V. Davis. 1996a. Ultrastructure of the gonad and gametogenesis in the eastern oyster, Crassostrea virginica. I. Ovary and oogenesis. Mar. Biol. 127: 79–87.

Eckelbarger, K. J., and C. V. Davis. 1996b. Ultrastructure of the gonad and gametogenesis in the eastern oyster, Crassostrea virginica. II. Testis and spermatogenesis. Mar. Biol. 127: 89–96.

Gabbott, P. A. 1975. Storage cycles in marine bivalve molluscs: a hypothesis concerning the relationship between glycogen metabolism and gametogenesis. Pp. 191–211 in Proceedings of the 9th European Marine Biological Symposium, H. Barnes, ed. Aberdeen University Press, Aberdeen, Scotland.

Gabbott, P. A. 1983. Development and seasonal metabolic activities in marine molluscs. Pp. 165–217 in The Mollusca, Vol. 2, P. W. Hochachka, ed. Academic Press, London.

Gabe, M. 1968. Techniques Histologiques. Masson & Cie, Paris.

Galtsoff, P. S. 1964. The American oyster Crassostrea virginica Gmelin. Fish. Bull. 64: 1–480.

Goddard, C. K., and A. W. Martin. 1966. Carbohydrate metabolism. Pp. 275–308 in Physiology of Molluscs, Vol. 2, K. M. Wilbur and C. M. Yonge, eds. Academic Press, New York.

Heneine, I. F., G. Gazzinelli, and W. L. Tafuri. 1969. Iron metabolism in the snail Biomphalaria glabrata: uptake, storage and transfer. Comp. Biochem. Physiol. 28: 391–399.

Ito, T., H. Kitamura, Y. Inayama, A. Nazawa, and M. Kanisawa. 1992. Uptake and intracellular transport of cathionic ferritin in the brachioserial and alveolar epithelia of the rat. Cell Tissue Res. 268: 335–340.

Kiernan, J. A. 1990. Histological and Histochemical Methods: Theory and Practice. P. 226. Academic Press, New York.

Le Pennec, M. P. G., Beninger, G., Dorange, and Y. M. Paulet. 1991a. Trophic sources and pathways to the developing gametes of Pecten maximus (Bivalvia Pectinidae). J. Mar. Biol. Assoc. UK 71: 451–463.

Le Pennec, M. G., Dorange, P. G., Beninger, A. Donval, and I. Wido-wati. 1991b. Les relations trophiques anse intestinale-gonade chez Pecten maximus (Mollusque, Bivalve). Haliotis 21: 57–69.

Lubet, P., J. Y. Besnard, R. Faveris, and I. Robbins. 1987. Physiologie de la reproduction de la coquille Saint Jacques (Pecten maximus). Oceans 13: 265–290.

Matthers, N. F. 1973. A comparative histochemical survey of enzymes associated with the processes of digestion in Ostrea edulis and Crassostrea angulata (Mollusca: Bivalvia). J. Zool. Lond. 169: 169–179.

Miksys, S., and A. S. M. Saleuddin. 1986. Ferritin as an exogenously derived yolk protein in Heliosoma darsi (Mollusca: Pulmonata). Can. J. Zool. 64: 2678–2682.

Morales-Alamo, R., and R. Mann. 1989. Anatomical features in histological sections of Crassostrea virginica (Gmelin, 1791), as an aid in measurements of gonad area for reproductive assessment. J. Shellfish Res. 8: 71–82.

Morse, M. P., and J. D. Zardus. 1997. Bivalvia. Pp. 7–118 in Microscopic Anatomy of Invertebrates, Vol. 6A, F. W. Harrison and A. J. Kohn, eds. Wiley-Liss, New York.

Paar, M., E. M. Liebler, and J. F. Pohlenz. 1992. Uptake of ferritin by follicle-associated epithelium in the colon of calves. Vet. Pathol. 29: 120–128.

Payne, D. W., N. A. Thorpe, and E. Donaldson. 1972. Cellulolytic activity and a study of the bacterial population in the digestive tract of Scrobicularia plana (Da Costa). Proc. Malacol. Soc. Lond. 40: 147–160.

Pipe, R. K. 1987a. Ultrastructural and cytological study on interaction between nutrient storage cells and gametogenesis in mussel Mytilus edulis. Mar. Biol. 96: 519–528.

Pipe, R. K. 1987b. Oogenesis in the marine mussel Mytilus edulis: an ultrastructural study. Mar. Biol. 95: 405–414.

Purchon, R. D. 1971. Digestion in filter feeding bivalves—a new concept. Proc. Malacol. Soc. Lond. 39: 253–262.

Read, K. R. H. 1983. Molluscan hemoglobin and myoglobin. Pp. 209–232 in Physiology of Molluscs, Vol. 2, K. M. Wilbur and C. M. Yonge, eds. Academic Press, New York.
Reid, R. G. B. 1966. Digestive tract enzymes in the bivalve Lima hians Gmelin and Mya arenaria L. Comp. Biochem. Physiol. 17: 417–433.

Suzuki, T., A. Hara, K. Yanaguchi, and K. Mori. 1992. Purification and immunolocalization of a vitellin-like protein from the Pacific oyster Crassostrea gigas. Mar. Biol. 113: 239–245.

Teo, L. H., and U. Sabapathy. 1990. Preliminary report on the digestive enzymes present in the digestive gland of Perna viridis. Mar. Biol. 106: 403–407.

Vacca, L. 1985. Laboratory Manual of Histochemistry. Raven Press. New York. 578 pp.

Vassallo, M. T. 1973. Lipid storage and transfer in the scallop Chlamys hericia Gould. Comp. Biochem. Physiol. 44A: 1169–1175.

Zaba, B. M. 1981. Glycogenolytic pathways in the mantle tissue of Mytilus edulis L. Mar. Biol. Lett. 2: 67–74.

Zacks, S. I. 1955. The cytochemistry of the amoebocytes and intestinal epithelium of Venus mercenaria (Lamellibranchiata), with remarks on a pigment resembling ceroid. Q. J. Microsc. Sci. 96: 57–71.
Beninger, Peter G, Le Pennec, Gael, and Le Pennec, Marcel. 2003. "Demonstration of Nutrient Pathway From the Digestive System to Oocytes in the Gonad Intestinal Loop of the Scallop Pecten maximus L." The Biological bulletin 205, 83–92. https://doi.org/10.2307/1543448.

View This Item Online: https://www.biodiversitylibrary.org/item/17303
DOI: https://doi.org/10.2307/1543448
Permalink: https://www.biodiversitylibrary.org/partpdf/5909

Holding Institution
MBLWHOI Library

Sponsored by
MBLWHOI Library

Copyright & Reuse
Copyright Status: In copyright. Digitized with the permission of the rights holder.
Rights Holder: University of Chicago
License: http://creativecommons.org/licenses/by-nc-sa/3.0/
Rights: https://biodiversitylibrary.org/permissions

This document was created from content at the Biodiversity Heritage Library, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.