A qualitative and quantitative study of the reproductive cycle of the giant scallop, *Placopecten magellanicus*, in the Bay of Fundy (New Brunswick, Canada)

PETER G. BENINGER
Département de biologie, Université de Moncton, Moncton (Nouveau-Brunswick), Canada E1A 3E9
and
Huntsman Marine Laboratory, Brandy Cove, St. Andrews, N.B., Canada E0G 2X0
Received May 7, 1986

BENINGER, P. G. 1987. A qualitative and quantitative study of the reproductive cycle of the giant scallop, *Placopecten magellanicus*, in the Bay of Fundy (New Brunswick, Canada). Can. J. Zool. **65**: 495–498.

The reproductive activity of a nearshore giant scallop (*Placopecten magellanicus*) population in the Bay of Fundy was studied over a 17-month period using qualitative histological staging, quantitative stereology, and gonosomatic index techniques. The major spawning period extended from August to late September in both years, and no winter resting period was observed. Larval metamorphosis and settlement from this major spawning could be expected from early September to early October. Histological examination revealed that 33% of the males sampled were in advanced stages of maturity in December and January. Although direct histological observation and stereology provide the most information, the gonosomatic index coupled with macroscopic gonad examination allows a rapid and accurate assessment of reproductive activity.

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Le cycle reproducteur d'une population côtière du pétoncle géant (*Placopecten magellanicus*) a été étudié pendant une période de 17 mois dans la Baie de Fundy, en utilisant les techniques de l'histologie qualitative, la stéréologie et l'indice gonosomatique. La période de ponte principale a eu lieu du mois d'août jusqu'à la fin de septembre les 2 années; aucune période de repos hivernal n'a été observée. La métamorphose larvaire et l'établissement des individus issus de cette ponte ont été prévus pour la période allant du début de septembre au début d'octobre. L'examen histologique a révélé que 33% des mâles échantillonnés étaient dans un état de maturité avancé en décembre et janvier. Bien que l'examen histologique et la stéréologie soient les techniques qui fournissent le plus d'information, l'indice gonosomatique et l'examen macroscopique de la gonade permettent une évaluation rapide et correcte de l'activité reproductrice.

Introduction

The giant scallop, *Placopecten magellanicus* (Gmelin), is an important commercial bivalve species on the east coast of Canada and the northeastern United States. In addition to the regional fishery, there is a growing interest in the aquaculture of this species both in St-Pierre and Miquelon and in Canada (Dupouy 1983; G. Newkirk, Department of Biology, Dalhousie University, Halifax, personal communication). Detailed knowledge of the reproductive cycle constitutes a fundamental aspect of fishery or aquaculture management. However, despite the extended natural range of *P. magellanicus* from Labrador to Cape Hatteras, little is known about its reproductive cycles. Three such studies have been performed in Newfoundland (Naidu 1970; Thompson 1977; most recently, MacDonald and Thompson 1986) and one in Maine (Robinson et al. 1981). Furthermore, the techniques used in these studies have varied: histological staging and macroscopic examination only were employed by Naidu (1970), a gravimetric gonad index and gonad DNA determinations were used by Thompson (1977), while both histological staging and index methods were used by Robinson et al. (1981). Histological staging is a subjective, semiquantitative technique which is currently being replaced by quantitative stereological methods in the evaluation of bivalve reproductive activity (Bayne et al. 1978; Lowe et al. 1982; Newell and Bayne 1980; Newell et al. 1982; Sundet and Lee 1984; Kennedy and Van Huekelem 1985; Pipe 1985; MacDonald and Thompson 1986). Recently, the validity of gravimetric gonad indices has been questioned in fish studies (DeVlaming et al. 1982; Cayré and Laloe 1986).

Despite a significant commercial fishery, no detailed study of the reproductive cycle of *P. magellanicus* has been performed in the Bay of Fundy. Knowledge has been limited to estimations of spawning times inferred from macroscopic appearance of the gonad (Dickie 1955). The purpose of the present study is to elucidate the reproductive cycle of a nearshore population of *P. magellanicus* in the Bay of Fundy using three techniques: histological staging, stereology, and a gravimetric gonad index. In addition to providing basic knowledge of the reproductive cycle of this species, the results of the three techniques can be compared and recommendations made for methodology in future work.

Materials and methods

The population was situated in Chamcook Bay near St. Andrews (New Brunswick) in the Bay of Fundy (45°07′ N, 67°04′ W). Fifteen individuals from 6 to 41 cm shell width (dorso-ventral axis) were randomly sampled at 4-week intervals by divers from May to November 1983 and from May to September 1984; a scallop drag was used in the intervening winter months. The shells were cleaned and the animals were placed in an open-circuit aquarium overnight. For each individual, the soft parts were divided into somatic and gonadal tissue. The crystalline style was removed from the gonad and included with the somatic tissue; contents of the gonad intestinal loop were squeezed out and discarded. The tissue components were then blotted with absorbent paper and the fresh weights determined using a Mettler P 1200 digital balance. The gonosomatic index (GSI) was defined as fresh gonad weight/fresh body weight (Giese and Pearse 1979; Robinson et al. 1981; DeVlaming et al. 1982).

Two tissue sections were removed from the mid-dorsal region of each previously weighed gonad and fixed in aqueous Bouin's solution

for a minimum of 48 h. The sections were rinsed under running tap water for 24 h and subsequently embedded in Paraplast (mp 56°C, Fisher Scientific) following a dehydration sequence of ethanol–Hemo-De (Fisher Scientific). Hemo-De was found to be an excellent, low-toxicity substitute for aromatic solvents at all stages of tissue preparation and staining.

The paraffin-embedded sections were cut at 7.5 μm and stained using the following modified Masson trichrome protocol: Hansen's trioxyhematein for nuclear material (Gabe 1968); running water rinse; aqueous acetic erythrosine for acidophilic cytoplasmic structures (Martoja and Martoja 1967); acetic acidified water (Humason 1979); phosphomolybdic Orange G to reinforce the cytoplasmic stain (Martoja and Martoja 1967); acetic acidified water; fast green for collagen and glycoproteins (Humason 1979); acetic acidified water. All staining and rinse times were standardized to 5 min. This protocol gave excellent tissue color contrast, enabling easy identification of tissue types for stereologic analysis.

The ongoing gametogenic activity was assessed using both qualitative staging and quantitative stereology. The qualitative staging and gametogenic value technique used by Robinson et al. (1981) was employed in the present study. The stereological technique consisted of examination of gonad sections using a Wild M20 projection microscope equipped with a 7 × 7 point matrix (Briarty 1975). The volume fractions of interfollicular tissue (IFT), developing gametes (DG), mature gametes (MG), and empty follicles (EF) were determined (Kennedy and Van Huekelem 1985). Three counts were made for each tissue type and for each tissue section; three tissue sections were examined for each individual. The arcsine-transformed mean volume fractions and standard deviations for each tissue type were calculated for each animal (Sokal and Rohlf 1981) and sample means were then calculated for males and females for each monthly sampling.

Preliminary observations of serial sections of the entire gonad confirmed the structural homogeneity of this organ, as reported by MacDonald and Thompson (1986).

Results and discussion

Reproductive cycle

This population showed a relatively consistent reproductive cycle in both 1983 and 1984 (Fig 1). The major spawning period extended from August to late September in both years; this is consistent with the spawning periods for southeastern Newfoundland (Thompson 1977; MacDonald and Thompson 1986) and the inferred spawning period for the Bay of Fundy in general (Dickie 1955), and also with the histological observations of *P. magellanicus* populations in Boothbay, Maine (Robinson et al. 1981). It would thus appear that an August–September spawning is characteristic of these populations, whereas the more northerly west-coast Newfoundland population studied by Naidu (1970) presented a spawning period from September to late October.

Histological observations showed that all animals retained the follicular structure of the gonad throughout the winter, as previously reported by MacDonald and Thompson (1985) and in contrast to the observations of Naidu (1970). Indeed, new gametes began developing immediately after spawning in most follicles, with no postspawning resting period such as that reported in a population from Maine (Robinson et al. 1981). However, the latter conclusion was based on subjective staging and gametogenic values only, which do not reveal the quantitative variations of tissue types. Moreover, the "gonad mass index" used by Robinson et al. (1981) did not reach a minimum until the month of January.

The volume fraction of interfollicular connective tissue increased immediately following spawning in both 1983 and 1984, and remained elevated during winter and early spring, decreasing steadily from November to August (Fig. 1). Such an inverse relationship between developing gametes and interfollicular connective tissue has previously been observed using qualitative histological evaluations in *Placopecten magellanicus* (Naidu 1970) and in several other bivalve species (see review by Mackie 1984). Such a relationship has also been observed in a recent independent study of *P. magellanicus* using quantitative stereology (MacDonald and Thompson 1986). These results support previous findings that in pectinid bivalves the gametogenic cells receive their nourishment directly from the interfollicular connective tissue (Coe 1943).

Predicted larval appearance and settlement

At 15°C, straight-hinge larvae have been obtained 4 days after spawning in the laboratory, while maximum settlement occurred 28 days after spawning (Culliney 1974). The mean surface temperature of Passamaquoddy Bay is 13°C in September (Trites and Garrett 1983) and with the usual *caveat* of extrapolation from laboratory to field, most larval settlement could be expected from early September to early October, with a maximum in late September for both 1983 and 1984, based on the postmaturity decreases in the mature gamete fraction.

Winter maturity

Macroscopic evidence indicating an advanced stage of maturity was obtained for three of the nine (33%) males sampled in each of the months of December and January. The macroscopic appearance of the gonad corresponded to that described by Posgay and Norman (1958) and Naidu (1970) for spawning males; the remaining six males in both December and January all showed gonads typical of very early developmental stages (small, translucent; alimentary canal visible). Subsequent histological examination confirmed that all of the macroscopically mature males were indeed in the late stages of gametogenesis (late developing, mature, partially spawned), whereas the macroscopically immature males were all in early developmental stages, as were all of the males examined in November and in March. Although only one male in December appeared partially spent, the other mature males all presented mature spermatozoa in their evacuating ducts. Although it may be argued that the stress of sampling could have induced spawning, no evidence of this was observed in the aquaria. Moreover, mechanical induction of spawning is only possible with mature animals. Comparison between summer and winter mature gonad sections revealed no histological difference. Although no females were observed to be mature in winter ($n = 6$ for December, $n = 6$ for January), these preliminary observations suggest that some males may remain mature into midwinter. A more extensive study should be performed, preferably in conjunction with larval samplings, to evaluate the precise extent and nature of scallop winter maturity in the Bay of Fundy.

Comparison of stereological, staging, and GSI data

In most bivalves quantitative separation of gonadal and somatic tissue is not possible, and hence rapid methods of assessing ongoing gametogenic activity usually involve the use of whole-body condition indices (Lucas and Beninger 1985). However, the near-total anatomical separation of pectinid gonad from somatic tissue allows the use of simple, rapid gravimetric gonad maturity indices. Two such indices have previously been used to study the reproductive cycle of *Placopecten magellanicus*: the "gonad weight index" (dry gonad weight/dry body weight; Thompson 1977), and the "gonad mass index" (wet gonad weight/wet body weight; Robinson et al. 1981). The latter index is widely used and

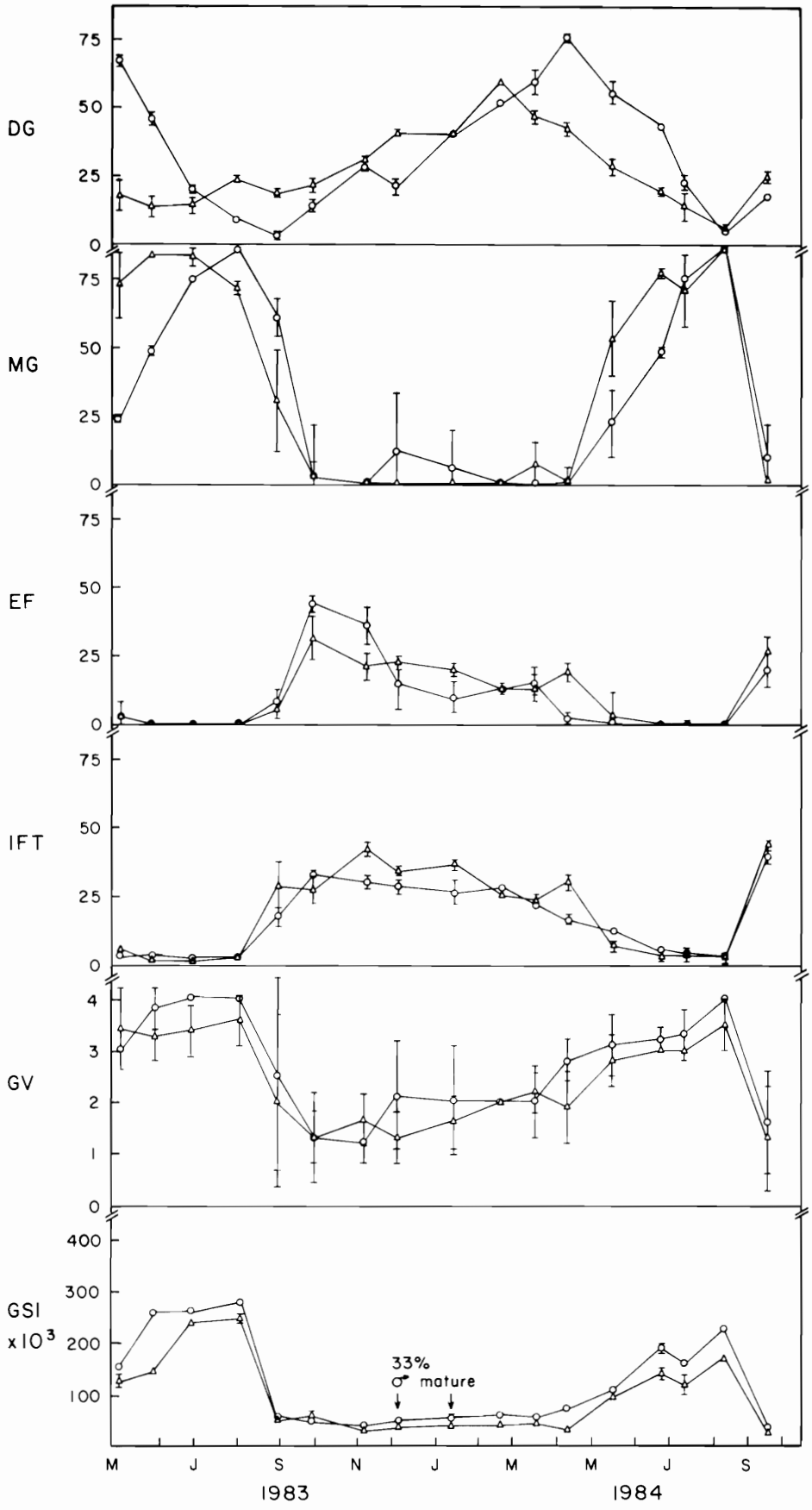

FIG. 1. Mean ± SD gonosomatic index (GSI: wet gonad weight/wet body weight), gametogenic value (GV: subjective staging), and gamete volume fraction (% gonad volume) values of male (○) and female (△) *P. magellanicus* from Chamcook Bay (Bay of Fundy), May 1983 – September 1984. Abbreviations for gamete volume fractions: IFT, interfollicular tissue; EF, empty follicular space; MG, mature gametes; DG, developing gametes. Note: Gametogenic values were assigned as in Robinson et al. (1981).

referred to as the "gonosomatic index" (GSI) in fish studies, so in the interests of universality this term is used in the present work.

Although widely used, the validity of gonad maturity indices such as the GSI has recently been questioned (DeVlaming et al. 1982; Cayré and Laloe 1986). In the present work, the GSI clearly reflected the information given by the histological staging technique, with one important difference. The histological examination of the gonads confirmed winter maturity in 33% of the males, whereas the GSI data did not indicate such a phenomenon. Indeed, the mean GSI of the winter mature animals was 71.7 and 116.7 for December and January, respectively, while the mean GSI for summer mature animals ranged from 171 to 307.

The mean gametogenic values of the postspawning months reveal some gametogenic activity in the males, whereas the stereologic means indicate the presence of both developing and mature gametes immediately following spawning. The stereologic technique thus gives a more precise evaluation of ongoing reproductive activity, and may in fact belie the existence of some supposed postspawning "resting" periods observed using only mean gametogenic values (Robinson et al. 1981).

There thus appears to be no substitute for direct histological observation, preferably using stereology, where a complete and unequivocal evaluation of reproductive activity is necessary. A convenient index of reproductive effort may be associated with such an evaluation, to yield a composite index, for example, total gamete volume fraction × gonad weight, as has recently been suggested (B.A. MacDonald, Biology Department, University of New Brunswick, personal communication). However, a combination of GSI data and macroscopic maturity assessment according to the descriptions of Posgay and Norman (1958) and Naidu (1970) should allow the routine evaluation of most important reproductive events in *Placopecten magellanicus*.

Acknowledgements

The author thanks Prof. A. Lucas and Dr. J. C. Martinez for their help in developing the histological protocol, as well as Mad. S. Argouarch, E. Lachance, and S. Dionne for their excellent technical assistance. Draft versions of this manuscript were reviewed by Drs. A. Boghen, V. Kennedy, B. MacDonald, and R. Thompson; their comments and suggestions are greatly appreciated. The secretarial work of Mad. L. Briard is gratefully acknowledged. This study was funded by the Conseil de recherche de l'Université de Moncton grant Nos. 10-531-54-105 and 10-531-54-13 and by Summer Canada and Challenge 85 contract Nos. 7027YE7, 5510BE0, and 4023EE2.

BAYNE, B. L., D. L. HOLLAND, M. N. MOORE, D. M. LOWE, and J. WIDDOWS. 1978. Further studies on the effects of stress in the adult on the eggs of *Mytilus edulis*. J. Mar. Biol. Assoc. U.K. **58**: 825–841.

BRIARTY, L. G. 1975. Stereology: methods for quantitative light and electron microscopy. Sci. Prog. **62**: 1–32.

CAYRÉ, P., and F. LALOE. 1986. Review of the gonad index (GI) and an introduction to the concept of its "critical value": application to the skipjack tuna *Katsuwonus pelamis* in the Atlantic Ocean. Mar. Biol. (Berlin), **90**: 345–351.

COE, W. R. 1943. Development of the primary gonads and differentiation of sexuality in *Teredo navalis* and other pelecypod molluscs. Biol. Bull. (Woods Hole, Mass.), **84**: 178–186.

CULLINEY, J. L. 1974. Larval development of the giant scallop *Placopecten magellanicus* (Gmelin). Biol. Bull. (Woods Hole, Mass.), **147**: 321–332.

DEVLAMING, V., G. GROSSMAN, and F. CHAPMAN. 1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. A, **73A**: 31–39.

DICKIE, L. M. 1955. Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy. J. Fish. Res. Board Can. **12**: 797–857.

DUPOUY, H. 1983. La pectiniculture à Saint-Pierre et Miquelon. Sci. Pêche, **337**: 17–29.

GABE, M. 1968. Techniques histologiques. Masson et Cie, Paris.

GIESE, A. D., and J. S. PEARSE. 1979. Introduction: general principles. *In* Reproduction of marine invertebrates. *Edited by* A. C. Giese and J. S. Pearse. Academic Press, New York. pp. 1–49.

HUMASON, G. L. 1979. Animal tissue techniques. 4th ed. W. H. Freeman and Co., San Francisco.

KENNEDY, V. S., and L. E. VAN HUEKELEM. 1985. Gametogenesis and larval production in a population of the introduced Asiatic clam, *Corbicula* sp. (Bivalvia: Corbiculidae) in Maryland. Biol. Bull. (Woods Hole, Mass.), **168**: 50–60.

LOWE, D. M., D. L. MOORE, and B. L. BAYNE. 1982. Aspects of gametogenesis in the marine mussel *Mytilus edulis* L. J. Mar. Biol. Assoc. U.K. **62**: 133–145.

LUCAS, A., and P. G. BENINGER. 1985. The use of physiological condition indices in marine bivalve aquaculture. Aquaculture, **44**: 187–200.

MACDONALD, B. A., and R. J. THOMPSON. 1985. Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. II. Reproductive output and total production. Mar. Ecol. Prog. Ser. **25**: 295–303.

——— 1986. Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. III. Physiological ecology, the gametogenic cycle and scope for growth. Mar. Biol. (Berlin), **93**: 37–48.

MACKIE, G. L. 1984. Bivalves. *In* The Mollusca. Vol. 7. Reproduction. *Edited by* K. M. Wilbur. Academic Press, New York. pp. 351–418.

MARTOJA, R., and M. MARTOJA. 1967. Initiation aux techniques de l'histologie animale. Masson et Cie, Paris.

NAIDU, K. S. 1970. Reproduction and breeding cycle of the giant scallop *Placopecten magellanicus* (Gmelin) in Port au Port Bay, Newfoundland. Can. J. Zool. **48**: 1003–1012.

NEWELL, R. I. E., and B. L. BAYNE. 1980. Seasonal changes in the physiology, reproductive condition, and carbohydrate content of the cockle *Cardium* (= *Cerastoderma*) *edule* (Bivalvia: Cardiidae). Mar. Biol. (Berlin), **56**: 11–19.

NEWELL, R. I. E., T. J. HILBISH, R. K. KOEHN, and C. J. NEWELL. 1982. Temporal variation in the reproductive cycle of *Mytilus edulis* L. (Bivalvia, Mytilidae) from localities on the east coast of the United States. Biol. Bull. (Woods Hole, Mass.), **162**: 299–310.

PIPE, R. K. 1985. Seasonal cycles in and effects of starvation on egg development in *Mytilus edulis*. Mar. Ecol. Prog. Ser. **24**: 121–128.

POSGAY, J. A., and K. D. NORMAN. 1958. An observation on the spawning of the sea scallop, *Placopecten magellanicus* (Gmelin), on Georges Bank. Limnol. Oceanogr. **3**: 142.

ROBINSON, W. E., W. E. WEHLING, M. P. MORSE, and G. C. MCLEOD. 1981. Seasonal changes in soft-body component indices and energy reserves in the Atlantic deep-sea scallop, *Placopecten magellanicus*. Fish. Bull. **79**: 449–458.

SOKAL, R. R., and F. J. ROHLF. 1981. Biometry. W. H. Freeman and Co., San Francisco. pp. 427–428.

SUNDET, J. H., and J. B. LEE. 1984. Seasonal variation in gamete development in the Iceland scallop, *Chlamys islandica*. J. Mar. Biol. Assoc. U.K. **64**: 411–416.

THOMPSON, R. J. 1977. Blood chemistry, biochemical composition, and the annual reproductive cycle in the giant scallop, *Placopecten magellanicus*, from southeast Newfoundland. J. Fish. Res. Board Can. **34**: 2104–2116.

TRITES, R. W., and C. J. R. GARRETT. 1983. Physical oceanography of the Quoddy region. *In* Marine and coastal systems of the Quoddy region, New Brunswick. *Edited by* M. L. H. Thomas. Can. Spec. Publ. Fish Aquat. Sci. **64**: 9–34.

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3. Mickaël Dutertre, Peter G. Beninger, Laurent Barillé, Mathias Papin, Philippe Rosa, Anne-Laure Barillé, Joël Haure. 2009. Temperature and seston quantity and quality effects on field reproduction of farmed oysters, Crassostrea gigas , in Bourgneuf Bay, France. *Aquatic Living Resources* **22**, 319-329. [CrossRef]
4. Dale C. Z. Arendse, Sissel Andersen, Norman J. Blake, Grant C. Pitcher. 2008. The Reproductive Cycle of the Scallop Pecten sulcicostatus from the Southern Benguela Upwelling System. *Journal of Shellfish Research* **27**, 281-287. [CrossRef]
5. Antonio Remacha-Triviño, Doranne Borsay-Horowitz, Christopher Dungan, Ximo Gual-Arnau, Javier Gómez-Leon, Luisa Villamil, Marta Gómez-Chiarri. 2008. Numerical Quantification of Perkinsus marinus in the American Oyster Crassostrea virginica (Gmelin, 1791) (Mollusca: Bivalvia) by Modern Stereology. *Journal of Parasitology* **94**, 125-136. [CrossRef]
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10. Marcela Cantillanez, Miguel Avendaño, Gérard Thouzeau, Marcel Le Pennec. 2005. Reproductive cycle of Argopecten purpuratus (Bivalvia: Pectinidae) in La Rinconada marine reserve (Antofagasta, Chile): Response to environmental effects of El Niño and La Niña. *Aquaculture* **246**, 181-195. [CrossRef]
11. Rozenn Cannuel, Peter G. Beninger. 2005. Is oyster broodstock feeding always necessary? A study using oocyte quality predictors and validators in Crassostrea gigas. *Aquatic Living Resources* **18**, 35-43. [CrossRef]
12. James R. Williams, Russell C. Babcock. 2004. Comparison of multiple techniques to evaluate reproductive variability in a marine bivalve: application to the scallop Pecten novaezelandiae. *Marine and Freshwater Research* **55**, 457. [CrossRef]
13. Marcel Le Pennec, Peter G Beninger. 2000. Reproductive characteristics and strategies of reducing-system bivalves. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **126**, 1-16. [CrossRef]
14. M Avendaño, M Pennec. 1997. Intraspecific variation in gametogenesis in two populations of the Chilean molluscan bivalve, Argopecten purpuratus (Lamarck). *Aquaculture Research* **28**, 175-182. [CrossRef]
15. Marcel Le Pennec, Peter G. Beninger. 1997. Ultrastructural characteristics of spermatogenesis in three species of deep-sea hydrothermal vent mytilids. *Canadian Journal of Zoology* **75**:2, 308-316. [Abstract] [PDF] [PDF Plus]
16. Richard McGarvey, Fredric M. Serchuk, Ian A. McLaren. 1993. Spatial and Parent-Age Analysis of Stock–Recruitment in the Georges Bank Sea Scallop (Placopecten magellanicus) Population. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:3, 564-574. [Abstract] [PDF] [PDF Plus]
17. P.J. Cranford, D.C. Gordon. 1991. Chronic sublethal impact of mineral oil-based drilling mud cuttings on adult sea scallops. *Marine Pollution Bulletin* **22**, 339-344. [CrossRef]
18. Marcel Le Pennec, Peter Gerard Beninger, Germaine Dorange, Yves Marie Paulet. 1991. Trophic Sources and Pathways to the Developing Gametes of Pecten Maximus (Bivalvia: Pectinidae). *Journal of the Marine Biological Association of the United Kingdom* **71**, 451. [CrossRef]
19. D.J. Wildish, D.D. Kristmanson, R.L. Hoar, A.M. DeCoste, S.D. McCormick, A.W. White. 1987. Giant scallop feeding and growth responses to flow. *Journal of Experimental Marine Biology and Ecology* **113**, 207-220. [CrossRef]