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Lipid composition of the giant lion's-paw scallop (Nodipecten subnodosus) in relation to gametogenesis I. Fatty acids

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Abstract: Seasonal variations in fatty acid composition in several tissues of a 1-year-old population of giant lion's-paw scallop Nodipecten subnodosus were analyzed during gonad development. Samples were taken bimonthly from December 1999 to June 2000, a period in which gonad development was occurring. Fatty acid accumulation in neutral and polar lipids of the female gonad was concomitant to the gonad development and presented a maximum in June. Among essential fatty acids, a specific accumulation was observed only for 20:5n − 3 in the female gonad, as suggested by an increase in its proportion in the neutral and the polar fractions. However, no specific accumulation was observed for 22:6n − 3, as its proportion remained relatively constant in both fractions. We suggest that a specific increase of 22:6n − 3 is not necessary during gametogenesis because its proportion was high enough for reproductive purposes (20–30%). Although some data suggest a partial mobilization of polyunsaturated fatty acids from the muscle and digestive gland to the female gonad during gonad development, the main supply came directly from the diet. The maximum increase in total and specific fatty acids in the digestive gland occurred in April and was maintained in June. These changes reflect either a higher lipid availability of the food, or the beginning of storage process in the digestive gland. However, in the female gonad, the maximum increase was observed in June, whereas gonad development and spawning were observed from April. It is suggested that different patterns of lipid accumulation in the first (April) and second (June) maturation processes could be related to the reproductive cycle of this species, which exhibits an initial facultative maturation during spring and the main reproductive activity during summer.

Keywords: Arachidonic acid; DHA; EPA; HUFA; Pectinidae; Reproduction

1. Introduction

Accumulation of lipids in female gonads during gametogenesis is well documented for several species of pectinids (Thompson, 1977; Pazos et al., 1996; Ruiz-Verdugo et al., 2001; Racotta et al., 2003). There are two postulated mechanisms by which pectinids accumulate lipids in the female gonads during maturation: (1) Transfer of lipids from the digestive gland to the gonads (Vasallo, 1973; Barber and Blake, 1981; Epp et al., 1988; Pazos et al., 1997), and (2) Lipogenesis from carbohydrates stored in the muscle, which results in a decrease of muscle carbohydrates during gametogenesis (Beninger and Lucas, 1984; Barber and Blake 1985; Mathieu and Lubet, 1993; Pazos et al., 1997; Martínez and Mettifogo, 1998; Ruiz-Verdugo et al., 2001). Synthesis *de novo* of saturated fatty acids, either directly in the gonads or in other tissues, was proposed previously by Soudant et al. (1996a). However, mollusks have a limited capacity for elongation and desaturation of long-chain polyunsaturated fatty acids (PUFA) (Waldock and Holland, 1984; Chu and Greaves, 1991, Ackman and Kean-Howie, 1995). Thus, PUFA for gonad development are probably obtained directly from diet or indirectly after previous accumulation in the digestive gland or other tissues. The role of diet in comparison to previously stored components has been addressed for general biochemical composition (Barber and Blake, 1981; Beninger and Stephan, 1985; Claere-Boudt and Himmelman, 1996; Roman et al., 1996; Pazos et al., 1997; Luna-González et al., 2000; Racotta et al., 2003), but there are few studies that analyze tissue-specific fatty acid variations in relation to gametogenesis in pectinids (Napolitano and Ackman, 1992; 1993; Caers et al., 2003).

The lion-paw scallop (*Nodipecten subnodosus*) represents an important fishery resource along the Baja California Pacific Coast in Mexico. The species is distributed from Peru to northern Mexico (Félix-Pico et al., 1999); has high commercial value for human consumption; and promising attempts have been made to implement cultivation (García-Dominguez et al., 1992; Morales-Hernández and Cáceres-Martínez,1996; Félix-Pico et al.,

1999; Barrios-Ruiz et al., 2003; Racotta et al., 2003). Although reproductive processes have been studied in wild (Reinecke-Reyes, 1996, Arellano-Martínez et al., 2004) and cultivated (Racotta et al., 2003) populations, a better understanding of specific patterns of lipid accumulation in female gonads and possible transfer from other tissues is necessary. Such an approach will be valuable to close the life cycle for this species. In a previous study, we observed that *Nodipecten subnodosus* can yield adductor muscle of 55 g after culture for 18 months concomitantly with gonad development without transfer of reserves from other tissues (Racotta et al., 2003). The present study analyzes scallops from the same growout cycle for the fatty acid levels in various tissues during gametogenesis in a one-year-old population of the lion-paw scallop.

2. Materials and methods

Growout and sampling of scallops used in this study were previously described in Racotta et al. (2003). Briefly, mature wild scallops were collected from Guerrero Negro, B.C.S. and induced to spawn (October 1998) at CIBNOR in La Paz, Mexico. At spat stage, the scallops were transported to the growout area in Rancho Bueno (Bahía Magdalena Lagoon complex, B.C.S.), and grown in Nestier trays at a density of 110 scallops per tray. For lipid analyses, five scallops were collected bimonthly from December 1999 until June 2000 (12 and 18 months old, respectively) and transferred to the laboratory at CIBNOR. Upon arrival, samples of mantle, digestive gland, adductor muscle, and female gonads were stored at –80^{o}C. Dissection of male gonads sufficient for lipid analyses was done only in June 2000.

Lipids were analyzed at the Université de Bretagne Occidental, France. Lipids were extracted with 2:1 chloroform: methanol according to Bligh and Dyer (1959), and extracts were stored in chloroform in a Teflon-lined screw-cap glass vial at –

20°C under a nitrogen atmosphere until further analysis. Neutral and polar lipid fractions were separated in a silica-gel microcolumn and collected in vials containing 23:0 as internal standard, with 1% butylated hydroxytoluene (BHT) as the antioxidant (Marty et al., 1992). Fatty acids were transesterified with boron-trifluoride methanol (BF_3 14% methanol, Supelco), and purified using a high-precision liquid chromatogram (HPLC, Merck) as described by Marty et al. (1992). Purified fatty acid methyl esters were analyzed in a Chrompak 9001 gas chromatograph (GC) equipped with DB-WAX capillary column (25 m × 0.32 mm, 0.2-µm film thickness) flame ionization detector with hydrogen as the carrier gas and a temperature gradient from 150 to 250°C at 3°C min^{-1}. Fatty acids were identified by comparing their retention times with those of standards run in the polar DBWAX column and in a non-polar CP8 capillary column (50 m × 0.25 mm, 0.2-µm film thickness) with the concentration of each fatty acid corrected by correlation with the response of the corresponding standard. The concentration of each fatty acid was corrected in relation to its molecular weight, and fatty acids are reported in µmol/g wet weight.

Only fatty acids, consisting on average of more than 1% of total fatty acids, were reported and considered for statistical analysis. The concentration of 20:1n-x represents the sum of three fatty acids: 20:1n-11, 20:1n-9, and 20:1n-7. The polyunsaturation index (PUI) was calculated, as described by Napolitano and Ackman (1993), but molar concentrations were used instead of percentage of total fatty acids.

All data are reported as mean ± standard error. One-way ANOVA, followed by Tukey tests for mean comparison (Statistica version 5.0) were used to assess significant differences between sampling months. Fatty acids from the neutral and polar fractions of each tissue were analyzed separately.

3. Results

There were two general accumulation patterns in female gonad tissue of fatty acid concentration in the neutral fraction (Table 1): significantly higher fatty acid concentrations in June (18:0, 18:1n-7, 18:2n-6, 18:4n-3, 22:6n-3, DMA, NMID, MUFA, and PUFA), or progressive increases that were traced from February (16:0, 16:1n-7, 18:1n-9, 18:3n-3, 20:1n-x, and SAT) or April (18:3n-3, 22:4(n-9)13t and total fatty acids). Only the concentration of 20:4n-6 showed an irregular pattern, with higher values in February and June. In the polar lipid fraction of gonads, a steep increase in fatty acids concentrations, similar to that observed in the neutral lipid fraction, was observed in June for 16:0, 18:0, 18:1n-9, 18:2n-6, 18:3n-3, 18:4n-3, 20:5n-3, 22:4(n-9)13t, 22:6n-3, SAT, PUFA, and total fatty acids. The 14:0, 18:1n-7, 20:1n-x, 22:4(n-9)13t, and MUFA concentrations increased in February, decreased in April, and finally increased in June.

In the neutral fraction of the digestive gland, the concentrations of 16:0, 18:0, 18:2n-6, 18:3n-3, 18:4n-3, 22:6n-3, TMTD, SAT, MUFA, PUFA, and total fatty acids were higher in April and June than in December and February (Table 2). The concentrations of 14:0, 16:1n-7, 18:1n-7, and 20:5n-3 increased progressively from December to June, while 18:1n-9 and 20:4n-6 were highest in April. In the polar lipid fraction of the digestive gland, concentrations and proportions of 18:4n-3 and 20:5n-3 increased progressively during gametogenesis. Concentrations of DMA were higher in April and June, but TMTD was higher in February. No significant differences were observed for the concentration of other fatty acids.

In the neutral lipid fraction of the muscle, concentrations of 18:0, 18:1n-7, 20:5n-3, DMA, and total fatty acids were higher in April and June compared to December and February (Table 3). The lowest concentrations of 16:0, 18:1-9, 18:3n-3, 20:1n-x, 20:4n-6, 22:6n-3, MUFA, PUFA, and SAT were observed in February. Some of these fatty acids

reached by April similar levels than in December (16:0, 20:1, 18:1n-9, 18:3n-3), while others (20:4n-6, 22:6n-3, SAT, MUFA and PUFA) were significantly higher in April and/or June compared to December. In the polar lipid fraction of muscle tissue, the concentration of 18:4n-3 increased progressively during gametogenesis. The other fatty acids did not present significant variation except for 20:4n-6 and NMID, which had their lowest values in June.

Concentrations of the neutral fraction from the mantle of 18:0, 18:1-7, 20:4n-6, 20:5n-3, 22:4(n-9)13t, 22:6n-3, DMA, NMID, SAT, PUFA, and total fatty acids increased in April and June, compared to December and February (Table 4). In the polar lipid fraction from the mantle, concentrations of 14:0, 16:0, 18:0, 16:1n-7, 18:1n-7, 18:4n-3, 20:5n-3, SAT, MUFA, and total fatty acids increased progressively as gametogenesis progressed.

Figure 1 depicts variation of PUI, calculated from the total concentration of fatty acids in the neutral and polar fractions, in relation to gametogenesis. PUI increased significantly during April and June in the digestive gland and in June in female gonads. In muscle, there was an increase in April, but no significant differences were found in the mantle.

4. Discussion

The scallops used in this study were sampled for fatty acid analyses starting in December of 1999, when they were one year old and at the end of their first maturation. A summary of data indicating the gonad development during the four months were adapted from Racotta et al. (2003) to discuss fatty acid accumulation in relation to gametogenesis (Table 5). Oocyte diameter in December (first sampling) was 13 μm, and some scallops had partially spawned. After reproductive quiescence in January 2000 (oocyte diameter = 8 μm), an increase in gametogenesis activity was observed in February (second sampling), and oocyte diameter increased to 12 μm. A peak in sexual maturity was observed in April (third sampling), when oocyte diameter reached 48 μm, and some scallops had already

spawned. Thus, results for April include data for completely mature (67%) and partially spawned (27%) scallops. When the last samples were taken for fatty acid analyses in June, scallops that had spawned in April were maturing again (100% mature scallops with oocyte diameter of 36 μm), and we did not find spawned scallops. These results coincide with those for a closely related species, the tropical scallop *Nodipecten nodosus*, in which spawning occurred between late May and late July (Lodeiros et al., 1998).

Gametogenesis and oocyte growth during this study involved either a steep increase in the concentration of most fatty acids in both lipid fraction (especially in neutral lipids) of the gonad in June, or a progressive increase during the sampling period. A progressive increase in triacylglycerol concentration was also observed for the same scallops during this sampling period (Racotta et al., 2003). The concentrations of SAT in the neutral fraction of gonad tissue increased from 2.5 to 12.6 μmol/g, and of MUFA from 0.4 to 5.3 μmol/g. The concentrations of SAT and MUFA are particularly important in this fraction (acylglycerides) because most organisms readily catabolize SAT and MUFA to generate energy (Sargent et al., 1999). The concentration of SAT in the polar fraction of gonad tissue also increased (2.1 to 6.2 μmol/g), but not to the same degree as the neutral fraction. However, the concentration of MUFA in the polar fraction was lower in December and in April. The decrease of MUFA in April could be a result of a partial spawning observed in some scallops, a process that requires energy. However, if this was the case, we would expect a steeper decline in the SAT and MUFA of the neutral fractions, as has been described for post-spawned *Placopecten magellanicus* scallops (Napolitano and Ackman, 1992).

PUFA contents of gonads increased from 4 to 30 μmol/g in the neutral fraction and from 7 to 20 μmol/g in the polar fraction. Fatty acid composition in gonads of pectinids has often been characterized as having a high degree of unsaturation (Besnard et al., 1989;

Napolitano and Ackman, 1993; Soudant et al., 1996a; Heras et al., 1997). Soudant et al. (1996a) found that PUFA content of the neutral lipid fraction in gonads of *Pecten maximus* scallops was approximately 45%, and the PUFA content of the neutral lipid fraction in gonads of *Placopecten magellanicus* was 44% during the summer (Napolitano and Ackman, 1992). PUFA content in the lion-paw scallop was also high, approximately 60% in the neutral fraction and 70% in the polar fraction. PUFA can be used as an energy source, as precursors of prostaglandins, and as structural components of phospholipids (Ackman and Kean-Howie, 1995). An accumulation of 20:5n-3 is suggested by an increase in its proportion in both the neutral (from 13% in December to 21% in June) and polar fractions (from 14% in December to 20% in June). In the polar fraction, this could be a result of its role in membrane function, mediated by some phospholipids (Soudant et al., 1996b). While mollusks can use 20:5n-3 as an energy source during embryogenesis, the maximum content of 20:5n-3 is probably regulated because it can compete with eicosanoid production from 20:4n-6 (Sargent et al., 1999). However, no accumulation of 22:6n-3 was observed in the gonads during gametogenesis. The concentration of 22:6n-3 tends to remain constant during larval development (Whyte et al., 1990; Whyte and Boutillier, 1991; Soudant et al., 1998), although its synthesis is limited in mollusks (Waldock and Holland, 1984; Chu and Greaves, 1991; Ackman and Kean-Howie, 1995; Soudant et al., 1996a). The 22:6n-3 is conserved and incorporated into cellular membranes where it modulates several membrane functions (Di Constanzo et al., 1983; Rabinovich and Ripatti, 1991; Farkas et al., 2000; Wu et al., 2001; Turner and Hulbert, 2003), rather than used as an energy source because it is a poor substrate for energy-generating fatty acid oxidation than more saturated fatty acids (Ackman and Kean-Howie, 1995; Sargent et al., 1999).

The variation of 20:4n-6 is interesting because its levels were higher in February and June in the neutral fraction of female gonads. Although the role of 20:4n-6 as an energy-yielding fatty acid is probably negligible because of the low concentration in most tissues,

it has an important role in prostaglandin production and as a component of phosphatidylinositol (Foegh and Ramwell, 1983; Oliw et al., 1983; Stanley-Samuelson, 1987; Burgoyne and Morgan, 1990; Deridovich and Reunova, 1993; Soudant et al., 1998). The decreased concentration of 20:4n-6 in the neutral fraction in December and April could be associated with spawning (Table 5) and its role in prostaglandin production, which stimulates muscle contraction and egg release (Martinez et al., 1996, 2000).

One of our objectives was to determine the storage site of long-chained PUFA during maturation. PUI of the digestive gland was significantly higher in April and June, whereas in female gonad it was higher only in June (Fig. 1). In muscle, PUI was higher in April, and no differences in PUI were found in the mantle. Thus, mantle provides little or no PUFA to gonads during maturation, and the levels of PUFA in muscle, particularly those from the neutral fraction, are negligible compared to those in digestive gland, in accordance to these being lean tissues, as pointed out by Napolitano and Ackman (1992). However, some specific fatty acids could be transferred from muscle to gonad during periods of less food availability. A negative correlation was found between muscle and gonad for 20:5n-3, but only in April ($r = –0.65$; $P < 0.05$), probably indicating a transport of this fatty acid from muscle to gonad. In addition, a decrease in the proportion of 22:6n-3 in the polar fraction of muscle (from 32% in December to 26% in June) could indicate a selective mobilization of this fatty acid to gonads.

For the digestive gland, no correlations were found between female gonads for 22:6n-3, but partial mobilization of this fatty acid from digestive gland is suggested by the decrease in its proportion from December to February in the neutral (from 22% to 18%) and in the polar fractions (from 31 to 27%). However, this was observed only at the beginning of gametogenesis and no further decrease was observed during the months of more advanced gonad development. This indicates that the main supply of 22:6n-3 in gonad during maturation probably came directly from diet, without previous accumulation in the

digestive gland. The sampling site, Bahía Magdalena, is particularly rich in phytoplankton (Nienhius and Guerrero-Caballero, 1985; Gárate-Lizárraga and Siqueiros-Beltrones, 1998) and the concentration of nutrients, chlorophyll a, and particulate matter at the site during the same sampling period is reported in a parallel work (Cervantes-Duarte et al., 2004).

There was a negative correlation for 20:4n-6 between gonads and digestive gland in April ($r = –0.77$; $P < 0.05$), when the levels of this fatty acid in the neutral fraction of digestive gland were highest, and in June ($r = –0.61$; $P < 0.05$), but no other negative correlations were found. Positive correlations were found between 20:4n-6 in gonads and 20:4n-6 in muscle and mantle during December, February, and April, and with digestive gland in December, indicating a parallel accumulation during algae blooms.

The content of trimethyltridecanoic acid (TMTD) in the digestive gland was 8% in the polar fraction and 2% in the neutral fraction. TMTD is a metabolic product of degradation of phytol, a fatty alcohol side chain of chlorophylls (Napolitano and Ackman, 1993), and is found mostly in the triacylglycerols of the digestive gland of scallops (Napolitano and Ackman, 1993; Heras et al., 1997). The reason we found TMTD in the polar fraction could be the timing of the digestion process. The majority of chlorophylls are associated with photosynthetic pigments and photo systems in the thylakoid membranes of algae (Ramus, 1981). If samples of scallops were taken during initial digestion of algae, it is possible that TMTD still would be attached to thylakoid membranes and be separated into the polar fraction. We did not eliminate digestive gland contents prior to extraction, so it is probable that its fatty acid composition reflected that of algae on which the scallop specimens were feeding. Sampling of scallops during more advanced digestion could result in separation of TMTD into the neutral fraction.

Like other pectinids, *N. subnodosus* had low total levels of non-methylene-interrupted fatty acids (NMID) (Ackman and Hooper, 1973; Dembitsky et al., 1992; Napolitano et al., 1992; Marty et al., 1999; Freites et al., 2002). NMID concentrations were less than 1% in

the neutral fractions, although higher than expected concentrations of NMID of 20 and 22 carbons were found in the polar fraction of all tissues (1-3% of the total). In addition to NMID, we also found 22:4(n-9)13t, which was reported recently in certain pectinids by Marty et al. (1999). As with NMID, the highest concentrations of 22:4(n-9)13t were found in mantle tissue and the lowest in muscle tissue. When comparing the levels of 22:4(n-9)13t during gametogenesis, we found an increase of the compound in the gonads and the neutral fraction of mantle tissue.

5. Conclusion

Little transfer of essential PUFA from other tissues (muscle and digestive gland) to gonads occurs during gametogenesis in *N. subnodosus* at the culture site at Bahía Magdalena. These results are in accord with the high food availability at this site, sufficient to sustain the energy and essential fatty needs for gonad development.

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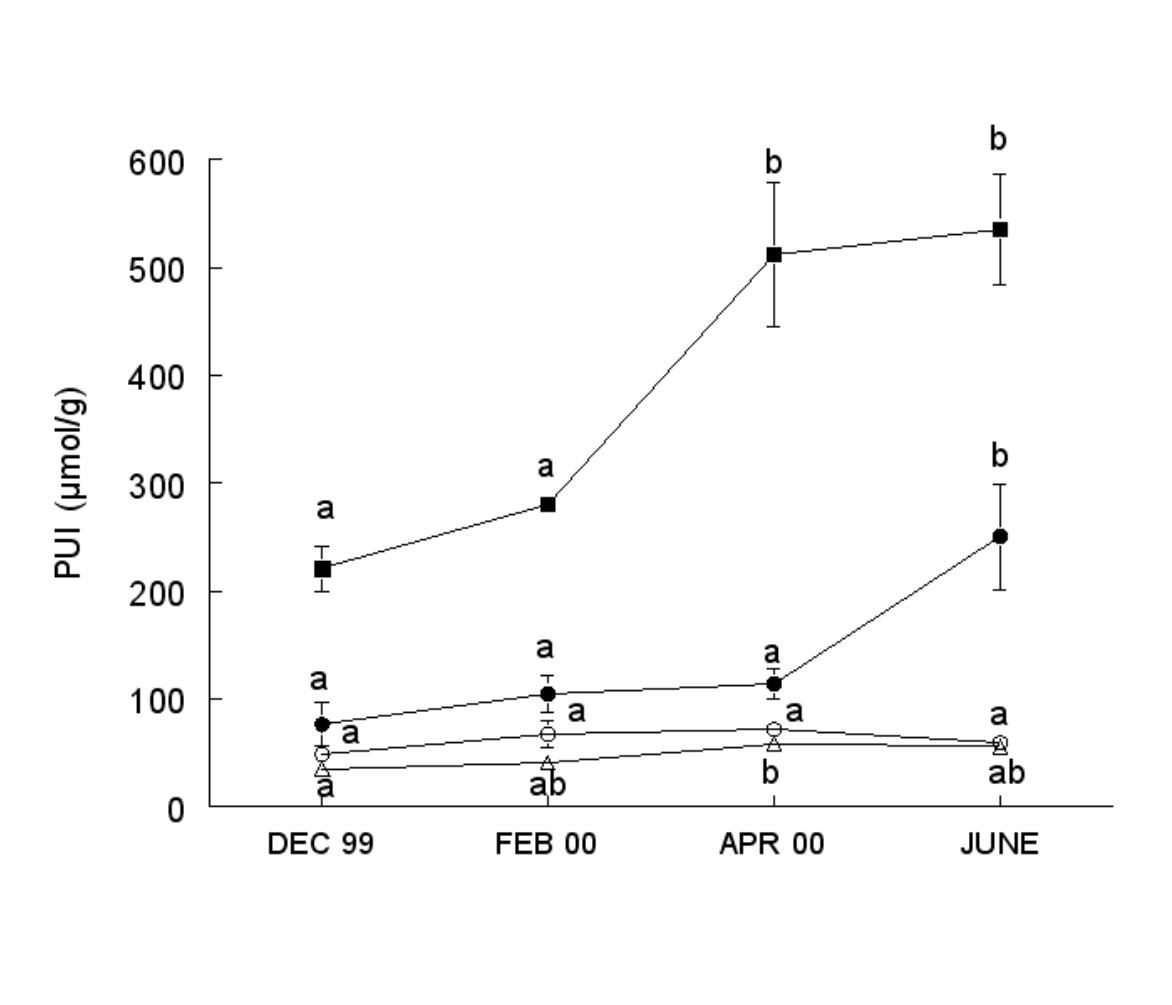

1

2 Fig.1. Variation in PUI (µmol/g, w/w) in relation to gametogenesis of *Nodipecten*
3 *subnodosus*, where female gonad = black circles; digestive gland = black squares; muscle
4 = white triangles; mantle = white circles. Unifactorial ANOVA followed by Tukey post-
5 hoc analyses were applied to assess differences among means within the same tissue. n = 5
6 scallops for each sampling. Means sharing the same superscript were not significantly
7 different ($P < 0.05$).

8

Table 1. Gonad fatty acid concentrations (µmol/g, w/w) in neutral and polar fractions of *Nodipecten subnodosus* scallops sampled from December 1999 to June 2000. Unifactorial ANOVA followed by Tukey post-hoc analyses were applied to assess differences among means. Means sharing different superscript in a row were significantly different ($P < 0.05$). Neutral and polar fractions were analyzed separately (n = 5).

	Neutral fraction				Polar fraction			
	Dec. 99	**Feb. 00**	**Apr. 00**	**Jun. 00**	**Dec. 99**	**Feb. 00**	**Apr. 00**	**Jun. 00**
14:0	0.3±0.2	1.2±0.5	0.8±0.1	1.7±0.8	0.1±0.02^{a}	0.4±0.06^{b}	0.2±0.01^{a}	0.4±0.07^{b}
16:0	1.7±1.1^{a}	2.6±1.0^{ab}	3.8±0.6^{ab}	8.8±2.7^{b}	1.0±0.1^{a}	1.9±0.2^{a}	1.5±0.1^{a}	3.2±0.4^{b}
18:0	0.4±0.2^{a}	0.5±0.1^{a}	0.7±0.1^{a}	1.7±0.4^{b}	0.8±0.1^{a}	1.2±0.1^{a}	1.1±0.1^{a}	2.4±0.3^{b}
16:1n-7	0.1±0.1^{a}	1.1±0.5^{ab}	1.0±0.2^{ab}	2.2±0.7^{b}	0.1±0.01^{a}	0.3±0.02^{ab}	0.2±0.02^{ab}	0.3±0.1^{b}
18:1n-9	0.1±0.1^{a}	0.2±0.1^{ab}	0.4±0.1^{ab}	2.0±0.3^{b}	0.1±0.01^{a}	0.2±0.02^{a}	0.1±0.02^{a}	0.3±0.1^{b}
18:1n-7	0.1±0.01^{a}	0.3±0.02^{a}	0.5±0.01^{a}	1.4±0.1^{b}	0.2±0.02^{a}	0.3±0.03^{b}	0.2±0.02^{a}	0.5±0.04^{c}
20:1n-x	0.1±0.03^{a}	0.3±0.1^{ab}	0.2±0.03^{ab}	0.5±0.1^{b}	0.3±0.04^{a}	0.5±0.06^{b}	0.2±0.01^{a}	0.4±0.06^{ab}
18:2n-6	0.1±0.02^{a}	0.2±0.1^{a}	0.3±0.1^{a}	0.9±0.3^{b}	0.1±0.01^{a}	0.1±0.01^{a}	0.1±0.01^{a}	0.2±0.02^{b}
18:3n-3	0.1±0.03^{a}	0.4±0.2^{a}	0.7±0.1^{ab}	1.4±0.5^{b}	0.1±0.01^{a}	0.2±0.03^{a}	0.1±0.02^{a}	0.3±0.05^{b}
18:4n-3	0.1±0.04^{a}	1.1±0.5^{a}	2.7±0.5^{a}	7.2±2.1^{b}	0.1±0.03^{a}	0.4±0.04^{a}	0.5±0.1^{a}	1.9±0.3^{b}
20:4n-6	0.2±0.1^{a}	0.4±0.1^{b}	0.3±0.02^{a}	0.4±0.1^{b}	0.9±0.1	1.2±0.1	0.8±0.1	0.9±0.2
20:5n-3	1.4±1.0^{a}	3.4±1.2^{a}	4.3±0.6^{a}	9.7±2.5^{b}	1.4±0.2^{a}	2.6±0.3^{a}	2.4±0.3^{a}	5.9±1.0^{b}
22:4(n-9)13t	0.1±0.02^{a}	0.1±0.02^{a}	0.2±0.02^{b}	0.3±0.05^{b}	0.4±0.05^{a}	0.5±0.05^{a}	0.4±0.02^{a}	0.7±0.1^{b}
22:6n-3	1.5±0.7^{a}	2.5±0.6^{a}	3.4±0.4^{a}	7.1±1.7^{b}	3.1±0.3^{a}	4.5±0.5^{a}	4.1±0.4^{a}	8.2±1.4^{b}
TMTD	0.03±0.01	0.2±0.1	0.1±0.02	0.1±0.04	N.D.	N.D.	N.D.	N.D.
Σ NMID	0.04±0.01^{a}	0.1±0.03^{a}	0.1±0.02^{a}	0.3±0.1^{b}	0.2±0.03^{a}	0.4±0.04^{b}	0.2±0.01^{a}	0.3±0.1^{ab}
Σ SAT	2.5±1.5^{a}	4.4±1.6^{ab}	5.7±0.9^{ab}	12.6±3.8^{b}	2.1±0.2^{a}	3.8±0.3^{a}	3.0±0.2^{a}	6.2±0.8^{b}
Σ MUFA	0.4±0.2^{a}	1.9±0.8^{a}	2.2±0.3^{a}	5.3±1.5^{b}	0.7±0.1^{a}	1.3±0.1^{b}	0.7±0.1^{a}	1.6±0.2^{b}
Σ PUFA	4.0±2.1^{a}	9.5±3.2^{a}	13.3±2.0^{a}	30.4±7.9^{b}	7.2±0.6^{a}	11.4±1.1^{a}	9.6±1.0^{a}	20.3±3.2^{b}
Total	13.5±9.9^{a}	15.9±5.7^{a}	21.4±3.2^{ab}	48.6±13.3^{b}	10.1±0.8^{a}	16.5±1.5^{a}	13.3±1.2^{a}	28.4±4.4^{b}

20:1n-x = 20:1n-11, 20:1n-9, 20:1n-7; TMTD = Trimethyltridecanoic acid; NMID = Non-methylene-interrupted fatty acids; SAT = Saturated; MUFA = Monounsaturated fatty acids; PUFA = Polyunsaturated fatty acids; N.D. = Not detected.

Table 2. Digestive gland concentrations (µmol/g, w/w) and percentage (in parenthesis) in neutral and polar fractions of *Nodipecten subnodosus* scallops sampled from December 1999 to June 2000. Unifactorial ANOVA followed by Tukey post-hoc analyses were applied to assess differences among means. Means sharing different superscript in a row were significantly different ($P < 0.05$). Neutral and polar fractions were analyzed separately (n=5).

	Neutral fraction				Polar fraction			
	Dec. 99	**Feb. 00**	**Apr. 00**	**Jun. 00**	**Dec. 99**	**Feb. 00**	**Apr. 00**	**Jun. 00**
14:0	4.1±0.3^{a}	5.7±0.4^{a}	7.3±0.7^{ab}	7.8±0.7^{b}	0.4±0.1	0.9±0.2	0.8±0.2	1.1±0.4
16:0	14.0±1.1^{a}	16.2±1.0^{a}	27.1±3.5^{b}	26.2±2.7^{b}	2.4±0.4	3.7±0.7	4.1±0.8	4.8±1.5
18:0	2.0±0.2^{a}	2.1±0.2^{a}	3.5±0.6^{b}	3.5±0.4^{b}	1.4±0.2	1.9±0.13	2.0±0.2	1.8±0.3
16:1n-7	5.0±0.50^{a}	6.8±0.4^{ab}	9.2±0.8^{bc}	10.5±1.1^{c}	0.5±0.1	0.9±0.3	1.0±0.2	1.3±0.5
18:1n-9	2.3±0.1^{a}	2.4±0.2^{a}	4.4±0.6^{b}	3.4±0.4^{a}	0.4±0.1	0.4±0.1	0.5±0.1	0.6±0.2
18:1n-7	1.8±0.2^{a}	2.1±0.1^{ab}	3.3±0.5^{b}	3.3±0.4^{b}	0.3±0.1	0.5±0.1	0.6±0.1	0.7±0.2
20:1n-x	0.5±0.1	0.5±0.1	0.8±0.1	0.7±0.1	0.3±0.03	0.3±0.04	0.4±0.03	0.4±0.1
18:2n-6	1.8±0.1^{a}	1.9±0.1^{a}	4.0±0.6^{b}	3.3±0.3^{b}	0.2±0.1	0.3±0.1	0.4±0.1	0.5±0.2
18:3n-3	2.3±0.2^{a}	2.5±0.1^{a}	6.5±1.0^{b}	5.1±0.5^{b}	0.3±0.1	0.6±0.1	0.6±0.2	0.8±0.2
18:4n-3	4.8±0.5^{a}	5.1±1.3^{a}	15.0±2.2^{b}	16.6±1.2^{b}	0.6±0.2^{a}	1.3±0.2^{a}	1.7±0.4^{ab}	3.1±0.7^{b}
20:4n-6	0.7±0.1^{a}	1.1±0.1^{b}	1.6±0.2^{c}	1.2±0.2^{b}	1.2±0.02	1.1±0.02	1.2±0.1	0.7±0.1
20:5n-3	11.6±1.4^{a}	18.1±0.9^{b}	33.8±4.5^{b}	36.4±2.7^{b}	3.9±1.0^{a}	6.1±0.5^{ab}	7.8±0.8^{ab}	8.2±1.9^{b}
22:4(n-9)13t	0.2±0.03	0.2±0.02	0.3±0.1	0.2±0.04	0.6±0.1	0.6±0.02	0.7±0.1	0.5±0.1
22:6n-3	6.8±0.6^{a}	5.6±0.4^{a}	13.2±2.2^{b}	12.6±1.1^{b}	4.5±0.8	4.7±0.3	6.0±0.4	6.0±0.9
TMTD	1.05±0.1^{a}	1.2±0.1^{a}	2.0±0.2^{b}	2.1±0.2^{b}	1.4±0.3^{a}	2.8±0.2^{b}	1.4±0.2^{a}	1.7±0.2^{a}
Σ NMID	0.2±0.04	0.1±0.02	0.1±0.07	0.1±0.02	0.2±0.04	0.3±0.01	0.3±0.02	0.3±0.1
Σ SAT	21.0±1.52^{a}	25.0±1.5^{a}	39.4±4.9^{b}	38.9±3.9^{b}	4.5±0.8	6.9±1.1	7.3±1.1	8.1±2.3
Σ MUFA	9.9±0.8^{a}	12.0±0.6^{a}	18.3±2.1^{b}	18.4±1.97^{b}	1.5±0.3	2.3±0.5	2.5±0.51	3.2±1.0
Σ PUFA	33.3±3.0^{a}	41.2±1.6^{a}	86.7±12.7^{b}	90.1±7.3^{b}	13.0±2.6	16.6±1.3	20.7±2.0	22.4±4.7
Total	65.7±1.2^{a}	79.7±0.7^{a}	148±4.4^{b}	151±3.0^{b}	20.5±0.9	28.7±0.6	32.1±0.8	35.6±1.8

See table 1 for abbreviations.

Table 3. Muscle acid concentrations (µmol/g, w/w) and percentage (in parenthesis) in neutral and polar fractions of *Nodipecten subnodosus* scallops sampled from December 1999 to June 2000. Unifactorial ANOVA followed by Tukey post-hoc analyses were applied to assess differences among means. Means sharing different superscript in a row were significantly different ($P < 0.05$). Neutral and polar fractions were analyzed separately (n=5).

	Neutral fraction				Polar fraction			
	Dec. 99	**Feb. 00**	**Apr. 00**	**Jun. 00**	**Dec. 99**	**Feb. 00**	**Apr. 00**	**Jun. 00**
14:0	0.05±0.01	0.03±0.01	0.04±0.01	0.04±0.01	0.1±0.01	0.3±0.1	0.3±0.02	0.2±0.03
16:0	0.2±0.03^{ab}	0.1±0.01^{a}	0.3±0.04^{b}	0.3±0.02^{b}	1.7±0.23	2.6±0.51	2.7±0.21	2.1±0.3
18:0	0.1±0.01^{a}	0.1±0.01^{a}	0.2±0.03^{b}	0.2±0.03^{b}	0.9±0.1	1.1±0.2	1.0±0.1	0.8±0.1
16:1n-7	0.06±0.01	0.04±0.01	0.05±0.01	0.06±0.01	0.1±0.02	0.3±0.07	0.2±0.02	0.2±0.1
18:1n-9	0.04±0.01^{ab}	0.03±0.01^{a}	0.05±0.01^{b}	0.06±0.01^{b}	0.2±0.01	0.2±0.04	0.2±0.02	0.2±0.02
18:1n-7	0.04±0.01^{a}	0.03±0.01^{a}	0.08±0.01^{b}	0.10±0.01^{b}	0.3±0.04	0.4±0.1	0.5±0.04	0.4±0.1
20:1n-x	0.02±0.01^{ab}	0.01±0.01^{a}	0.06±0.01^{b}	0.07±0.01^{b}	0.3±0.02	0.4±0.1	0.3±0.01	0.3±0.02
18:2n-6	0.02±0.004	0.01±0.001	0.02±0.003	0.02±0.002	0.1±0.01	0.2±0.03	0.2±0.01	0.1±0.02
18:3n-3	0.02±0.01^{ab}	0.01±0.01^{a}	0.03±0.01^{b}	0.02±0.01^{ab}	0.1±0.01	0.2±0.03	0.2±0.01	0.2±0.04
18:4n-3	0.05±0.01	0.03±0.01	0.08±0.02	0.08±0.02	0.1±0.03^{a}	0.5±0.1^{ab}	0.6±0.04^{b}	0.7±0.2^{b}
20:4n-6	0.06±0.02^{a}	0.02±0.01^{a}	0.11±0.03^{b}	0.13±0.02^{b}	0.6±0.01^{ab}	0.8±0.2^{a}	0.6±0.03^{ab}	0.4±0.03^{b}
20:5n-3	0.2±0.04^{a}	0.1±0.01^{a}	0.5±0.1^{b}	0.6±0.1^{b}	2.0±0.4	3.8±0.7	4.2±0.3	3.3±0.6
22:4(n-9)13t	0.02±0.01	0.01±0.001	0.03±0.001	0.04±0.02	0.3±0.01	0.3±0.04	0.3±0.02	0.2±0.03
22:6n-3	0.4±0.1^{a}	0.2±0.1^{a}	0.8±0.1^{b}	0.8±0.1^{b}	3.9±0.4	5.3±1.1	4.7±0.3	3.5±0.3
TMTD	0.01±0.002	N.D.	0.01±0.002	0.01±0.002	N.D.	N.D.	0.03±0.01	0.03±0.01
Σ NMID	0.01±0.01	0.01±0.01	0.01±0.01	0.01±0.01	0.09±0.01^{ab}	0.11±0.02^{a}	0.07±0.01^{ab}	0.05±0.01^{b}
Σ SAT	0.4±0.1^{ab}	0.2±0.1^{a}	0.5±0.1^{bc}	0.6±0.1^{c}	3.0±0.3	4.2±0.8	4.2±0.3	3.2±0.5
Σ MUFA	0.2±0.04^{ab}	0.1±0.01^{a}	0.3±0.04^{bc}	0.3±0.03^{c}	0.9±0.1	1.4±0.3	1.28±0.1	1.1±0.2
Σ PUFA	0.8±0.2^{ab}	0.4±0.1^{a}	1.7±0.3^{bc}	1.9±0.2^{c}	8.3±0.9	12.4±2.5	12.1±0.8	9.5±1.3
Total	1.4±0.3^{ab}	0.7±0.1^{a}	2.5±0.4^{b}	2.8±0.3^{b}	12.3±1.3	18.1±3.5	17.6±1.2	13.9±1.9

See table 1 for abbreviations.

Table 4. Mantle acid concentrations (µmol/g, w/w) and percentage (in parenthesis) in neutral and polar fractions of scallops sampled from December 1999 to June 2000. Unifactorial ANOVA followed by Tukey post-hoc analyses were applied to assess differences among means. Means sharing different superscript in a row were significantly different ($P < 0.05$). Neutral and polar fractions were analyzed separately (n=5).

	Neutral fraction				Polar fraction			
	Dec. 99	**Feb. 00**	**Apr. 00**	**Jun. 00**	**Dec. 99**	**Feb. 00**	**Apr. 00**	**Jun. 00**
14:0	0.02±0.003	0.03±0.01	0.04±0.01	0.04±0.01	0.1±0.01^{a}	0.2±0.01^{b}	0.2±0.02^{b}	0.2±0.03^{b}
16:0	0.1±0.02	0.2±0.03	0.4±0.04	0.3±0.04	0.9±0.04^{a}	1.1±0.1^{ab}	1.5±0.2^{b}	1.5±0.1^{b}
18:0	0.1±0.01^{a}	0.1±0.01^{a}	0.3±0.03^{b}	0.2±0.02^{b}	0.7±0.03^{a}	0.9±0.1^{ab}	1.1±0.1^{b}	1.2±0.1^{b}
16:1n-7	0.03±0.01	0.04±0.01	0.04±0.01	0.04±0.01	0.07±0.01^{a}	0.12±0.02^{ab}	0.11±0.01^{ab}	0.14±0.02^{b}
18:1n-9	0.03±0.01^{a}	0.03±0.01^{a}	0.06±0.01^{b}	0.04±0.01^{ab}	0.1±0.01	0.2±0.02	0.2±0.02	0.2±0.02
18:1n-7	0.02±0.01^{a}	0.02±0.01^{a}	0.05±0.01^{b}	0.05±0.01^{b}	0.16±0.01^{a}	0.21±0.02^{ab}	0.28±0.03^{bc}	0.35±0.04^{c}
20:1n-x	0.02±0.01^{ab}	0.01±0.01^{a}	0.05±0.01^{b}	0.04±0.01^{ab}	0.2±0.01	0.2±0.01	0.2±0.01	0.2±0.01
18:2n-6	0.01±0.01^{a}	0.01±0.01^{ab}	0.02±0.01^{ab}	0.02±0.01^{b}	0.1±0.01	0.1±0.01	0.1±0.01	0.1±0.02
18:3n-3	0.01±0.001	0.01±0.003	0.03±0.01	0.01±0.003	0.03±0.002	0.04±0.004	0.04±0.01	0.05±0.01
18:4n-3	0.01±0.002^{a}	0.03±0.01^{ab}	0.04±0.01^{ab}	0.05±0.01^{b}	0.06±0.01^{a}	0.11±0.02^{a}	0.15±0.02^{ab}	0.29±0.06^{b}
20:4n-6	0.10±0.03^{a}	0.07±0.01^{a}	0.28±0.04^{b}	0.23±0.03^{b}	0.8±0.1	0.9±0.1	0.9±0.1	0.8±0.1
20:5n-3	0.09±0.02^{a}	0.12±0.04^{a}	0.36±0.05^{b}	0.32±0.04^{b}	0.8±0.04^{a}	1.3±0.1^{ab}	1.8±0.2^{b}	1.8±0.3^{b}
22:4(n-9)13t	0.04±0.02^{a}	0.01±0.01^{a}	0.11±0.02^{b}	0.10±0.02^{b}	0.5±0.04	0.6±0.1	0.6±0.1	0.6±0.1
22:6n-3	0.3±0.2^{a}	0.2±0.1^{a}	1.2±0.1^{b}	0.9±0.1^{b}	2.7±0.2	3.4±0.4	4.1±0.5	4.1±0.4
TMTD	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
Σ NMID	0.01±0.01^{a}	0.01±0.01^{a}	0.07±0.02^{b}	0.05±0.01^{b}	0.1±0.02	0.2±0.03	0.2±0.02	0.2±0.03
Σ Saturated	0.3±0.03^{a}	0.3±0.04^{a}	0.6±0.1^{b}	0.6±0.1^{b}	1.8±0.1^{a}	2.3±0.2^{ab}	3.0±0.3^{b}	3.0±0.3^{b}
Σ MUFA	0.10±0.02^{a}	0.11±0.02^{ab}	0.21±0.03^{b}	0.19±0.02^{ab}	0.6±0.02^{a}	0.7±0.1^{ab}	0.8±0.1^{ab}	0.9±0.1^{b}
Σ PUFA	0.6±0.3^{a}	0.5±0.2^{a}	2.4±0.3^{b}	1.9±0.2^{b}	5.8±0.4	7.4±0.9	8.8±0.9	8.9±1.0
Total	1.1±0.3^{a}	0.9±0.3^{a}	3.2±0.4^{b}	2.7±0.3^{b}	8.3±0.4^{a}	10.6±1.1^{ab}	12.8±1.3^{b}	13.1±1.4^{b}

See table 1 for abbreviations.

Table 5: Gonad development in *Nodipecten subnodosus* from December 1999 to June 2000 (adapted from Racotta et al., 2003)

	Nov. 99	**Dec. 99**	**Jan. 00**	**Feb. 00**	**Apr. 00**	**Jun. 00**
GSI (%)	3.7	2.4	2.9	3.7	6.4	7.0
Immature (%)	68	73	100	53	6.7	0
Maturing (%)	6.2	0	0	40	0	0
Mature (%)	26	13	0	6.7	67	100
Spawned (%)	0	13	0	0	27	0
Oocyte diameter (µm)	24	13	8	12	48	36

GSI = Gonadosomatic index; for maturation stages, the proportion of individuals within each maturation stage assessed by histology is indicated (for more details see Racotta et al., 2003).