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Seasonal and developmental variation in the fatty acid composition of *Mysis mixta* (Mysidacea) and *Acanthostepheia malmgreni* (Amphipoda) from the hyperbenthos of a cold-ocean environment (Conception Bay, Newfoundland)

NICOLE B. RICHOUX*†, DON DEIBEL, RAYMOND J. THOMPSON AND CHRISTOPHER C. PARRISH

OCEAN SCIENCES CENTRE, MEMORIAL UNIVERSITY, ST. JOHN'S, NEWFOUNDLAND AND LABRADOR, CANADA A1C 5S7

†PRESENT ADDRESS: DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY, PO BOX 94, RHODES UNIVERSITY, GRAHAMSTOWN, EASTERN CAPE PROVINCE 6140, SOUTH AFRICA

*CORRESPONDING AUTHOR: n.richoux@ru.ac.za

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Fatty acid composition in different life-history stages of Mysis mixta (Crustacea, Mysidacea) and Acanthostepheia malmgreni (Crustacea, Amphipoda) from Conception Bay, Newfoundland, was examined throughout 1999 and 2000. The primary aim was to relate the seasonal fatty acid dynamics to each species' life cycle and to published information on the occurrence and quality of the annual phytoplankton bloom. Divergent patterns in fatty acid composition and specific fatty acid marker ratios reflected different life styles, diets and critical periods of energy accumulation and utilization in M. mixta and A. malmgreni. Changes in fatty acids reflected the sequence of plankton taxa during and following the spring bloom, starting with diatoms and dinoflagellates and ending with copepods. Immature mysids exhibited a particularly rapid accumulation of diatom-associated fatty acids at the start of the spring bloom, probably owing to the high degree of motility of M. mixta and the broad range of prey types available to this species. In contrast, immature amphipods did not begin to accumulate significant amounts of phytoplankton fatty acids until after the spring bloom material had settled to the hyperbenthos in May. Differences in fatty acid composition indicated that A. malmgreni was restricted to a lower quality diet than was M. mixta and that the trophic connection between A. malmgreni and production in the euphotic zone was weaker.

INTRODUCTION

Previous examination of population and lipid class dynamics in *Mysis mixta* Lilljeborg (Mysidacea) and *Acanthostepheia malmgreni* Goës (Amphipoda) indicated a close coupling between the species' life-history and energy cycles and seasonal production in the euphotic zone of Conception Bay, Newfoundland (Richoux *et al.*, 2004a,b,c,d). Despite the importance of hyperbenthic populations in the energetics of marine systems (Mees and Jones, 1997), little is known about species inhabiting the hyperbenthos. The aim of this research was to determine the seasonal fatty acid composition of *M. mixta* and *A. malmgreni*, particularly in relation to the changes in reproductive cycles, foraging strategies and diets resulting from variations in productivity within the euphotic zone.

Populations of *M. mixta* and *A. malmgreni* in Conception Bay are both abundant and lipid rich (Richoux *et al.*, 2004a,b,c,d). These species protect spawned eggs within a brood pouch following fertilization; larvae are brooded for ~5 months, and brood release occurs in April and May while the spring bloom material is settling to the

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hyperbenthos (Richoux *et al.*, 2004a,c). In Conception Bay, the life span of females is 2.5 years (spawning to death), of which 2 years of development are normally required before reproduction occurs (Richoux *et al.*, 2004a,c). *Mysis mixta* is an opportunistic omnivore that undergoes ontogenetic shifts in its diet (Viherluoto and Viitasalo, 2001; Richoux *et al.*, 2004a). *Acanthostepheia malmgreni* appears more limited to a carnivorous feeding mode, although juveniles feed on small particles including phytoplankton and detritus (Sainte-Marie and Brunel, 1985; Richoux *et al.*, 2004c). Both species are potentially important links to higher trophic levels, as they are prey for fish and a variety of invertebrates (Mauchline, 1980; Sainte-Marie and Brunel, 1985). Some members of the *M. mixta* population migrate from the hyperbenthos to shallower waters at night (Rudstam *et al.*, 1989), although there is no evidence that *A. malmgreni* undergoes such migrations in Conception Bay. Observations in the laboratory indicate that *A. malmgreni*, although capable of rapid bursts of swimming, is generally less motile than *M. mixta* (N. B. Richoux, unpublished results). These differences in behaviour, diet and motility in the two populations are expected to be reflected in their seasonal fatty acid composition.

The extent to which *M. mixta* and *A. malmgreni* assimilate and store organic material produced during and following the annual spring phytoplankton bloom was of particular interest in this study. Chlorophyll *a* (Chl *a*) and total fatty acid concentrations in phytoplankton vary with environmental conditions and algal physiology (Reuss and Poulsen, 2002). Furthermore, there are clear relationships between algal fatty acid composition and taxonomy, providing an opportunity for tracing trophic paths to the primary producers within a food web (Sargent and Falk-Petersen, 1988). Phytoplankton produce essential polyunsaturated fatty acids (PUFA) that are necessary for proper membrane structure and function. Some heterotrophic protozoans are also able to produce PUFA from shorter chain dietary fatty acids and thereby improve the quality of seston available to consumers in some environments (Klein Breteler *et al.*, 2003). PUFA are particularly important in cold-water organisms because cell membranes must remain sufficiently fluid despite the tendency for increased rigidity at low temperatures (Hall *et al.*, 2000). As water below 80-m depth in Conception Bay remains near 0°C year-round (Richoux *et al.*, 2004a), temperature is not considered a highly influential variable in this study.

In 1999 and 2000, the spring bloom in Conception Bay began in late March and reached a maximum in late April to mid-May (Chl *a* maximum 2.22 μg L^{-1} in 1999 and 3.64 μg L^{-1} in 2000; Richoux *et al.*, 2004a). Settling of the material occurred in May each year, and a secondary bloom appeared in July 1999 (Richoux *et al.*, 2004a). As is typical for Newfoundland fjords, the upper 50 m of Conception Bay is characterized by a successional pattern of plankton each year. Large diatoms generally dominate the plankton biomass early in the spring, whereas flagellates, bacteria and meso- and microzooplankton flourish in late summer/early autumn (Parrish *et al.*, 2000; Tian *et al.*, 2003). Consequently, hyperbenthic and benthic organisms experience a seasonal shift in food availability and quality. The dense diatomaceous material produced during the bloom is quickly transferred to the bottom, and high concentrations of essential PUFA have been found in benthic organisms from Conception Bay (Parrish *et al.*, 1996). Input of organic matter to the hyperbenthos decreases following the bloom, primarily because the increased dominance of the microbial food web results in retention of organic carbon within the upper mixed layer (Tian *et al.*, 2003). By August, calanoid copepods that have accumulated lipid stores within the euphotic zone descend to begin diapause (Davis, 1982; D. Deibel *et al.*, unpublished results). The downward migration of lipid-rich late copepodites provides an added food source for deep-living organisms in autumn and winter.

The relatively few comprehensive studies involving ontogenetic and seasonal changes in fatty acid composition of zooplankton in the field have focussed primarily on copepods (mainly *Calanus* spp.) or euphausiids (Tande and Henderson, 1988; Kattner *et al.*, 1994; Hagen and Auel, 2001). In polar and temperate regions, ontogenetic variation in the fatty acid composition of zooplankton has been associated with changes in lipid biosynthesis, behaviour, diet, seasonal environmental productivity, or a combination of these factors. In this study, determination of the fatty acid composition of developing *M. mixta* and *A. malmgreni* will demonstrate the ecological link between hyperbenthic species and the annual phytoplankton bloom.

METHOD

Study site and sample collection

Hyperbenthic zooplankton were collected approximately monthly between October 1998 and November 2000 from the depositional zone at 240-m depth in Conception Bay, Newfoundland, using an epibenthic sled. Organisms were retained by a 500-μm mesh net that tapered to a closed cod end. Tows commenced at 47°30.5′ N, 53°07.5′ W and ended near 47°32.5′ N, 53°07.0′ W, with collection distance ranging from 620 to 930 m and water volume filtered per tow from 87 to 196 m^3. All tows were completed between 1100 and

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1400 h, a time when zooplankton that undergo diel migrations aggregate in the hyperbenthos (Rudstam *et al.*, 1989). Data on phytoplankton bloom start times (when Chl *a* concentrations reached 1 μg L^{-1} in the spring) and bloom material settling times (Chl *a* concentrations between 0.5 and 0.8 μg L^{-1} extending to the benthos following each bloom event), in addition to detailed information on sampling methodology in Conception Bay, are presented elsewhere (Richoux *et al.*, 2004a).

Specimens

Depending on availability, one to five replicate individuals of all life-history stages of *M. mixta* and *A. malmgreni* were analysed following each sampling day. Life-stage categories and measurements of live specimens, in addition to sample storage protocol for all lipid samples, are described in detail elsewhere (Richoux *et al.*, 2004b,d). The dry mass (DM) of each sample was calculated from body length (*M. mixta*, rostrum tip to telson tip; *A. malmgreni*, frontal edge of the eyes to telson tip; separate allometric relationships were applied to each life stage), and the DM of each brood was calculated from brood size (Richoux *et al.*, 2004a,c). Lipids were extracted from each sample using a modified Folch procedure, and total lipid (TL) was determined by summing all lipid classes following thin-layer chromatography and flame-ionization detection (Parrish, 1999; Richoux *et al.*, 2004b). Fatty acid composition of each extract was determined by gas chromatography (GC) analysis (Omegawax 320 column, Varian Model 3400) of fatty acid methyl esters prepared by transmethylation in the presence of boron trifluoride (85°C for 1 h) (Budge and Parrish, 1998). Fatty acid methyl esters were identified by comparison of retention times with known external standards (Supelco; identifications confirmed using a Varian 2000 GC/mass spectrometer), and quantified by comparing peak areas with the area under an internal standard [23:0, at a concentration of ~10% total identified fatty acids (TFA)]. Values of a lipolysis index (LI), LI (%) = [(free fatty acids + alcohols)/(total acyl lipids + alcohols)] × 100, calculated from all samples to assess degradation, remained <10% indicating adequate storage and processing protocols (Parrish *et al.*, 2000).

Calculations and statistics

Each major fatty acid (μg individual^{-1}; defined as >1% TFA) was regressed against TL per individual, regardless of sex, season, stage or cohort, to determine its relative contribution to lipid accumulation (Hagen and Kattner, 1998). Accumulation rates for the 6 most abundant fatty acids and the main fatty acid groups were estimated from slopes of linear sections of the regression lines relating the fatty acid content to time (μg month^{-1}). Cohorts and life-history stages were regressed in groups according to pre- and post-bloom periods (*M. mixta*) or pre- and post-bloom sedimentation periods (*A. malmgreni*). The Durbin–Watson statistic was calculated to detect temporal autocorrelation in the regressions, and the Cochrane–Orcutt procedure was used to correct any autocorrelations (Neter *et al.*, 1996). Biomarkers (16:1ω7 + 16:1ω5)/16:0, 22:6ω3/20:5ω3, ΣPUFA/Σsaturates, ΣC16/ΣC18 (ratio of C_{16} to C_{18} fatty acids) and 18:1ω9/18:1ω7 were calculated in all cohorts. Data are reported as means ± one standard deviation (SD). The relationship between 16:1ω7 and 18:1ω7 was established by regression analysis. Areal concentrations of PUFA were estimated from population densities, determined within 1 m of the bottom (Richoux *et al.*, 2004a,c), multiplied by mean PUFA content per individual on each date (Arts *et al.*, 1992).

RESULTS

Fatty acids in *M. mixta*

Forty-three fatty acids were identified in *M. mixta* (Tables I and II). The major saturated fatty acids (SFA) in all life-history stages were 14:0 and 16:0. The principal monounsaturated fatty acids (MUFA) were 16:1ω7, 18:1ω9, 18:1ω7, 20:1ω9(11) and 22:1ω11, and the principal PUFA included 18:2ω6, 18:4ω3, 20:4ω6, 20:5ω3 and 22:6ω3.

In general, the fatty acids in juveniles were dominated by 20:5ω3, 22:6ω3, 16:0 and 18:1ω9, typical components of phospholipids. As the juveniles increased lipid storage while maturing (Richoux *et al.*, 2004b), concentrations of these four fatty acids remained high and 16:1ω7 and 14:0 increased in DM (Tables I and II). Of all the major fatty acids (μg individual^{-1}) regressed against TL (μg individual^{-1}), these 6 (in decreasing order quantitatively: 20:5ω3, 18:1ω9, 16:1ω7, 16:0, 14:0 and 22:6ω3) had the greatest slopes, confirming their overall contribution to lipid accumulation in *M. mixta* (data not shown; slopes > 0.0235, $P < 0.0001$, $r^2 > 0.446$).

Four cohorts (C1, C2, C3 and C4) were distinguished during 2 years (Fig. 1). Mysids from C2 collected between December 1998 and February 1999 were not sexed and were pooled in an 'undifferentiated immatures' category, whereas mysids from C1, C3 and C4 were differentiated throughout development. The concentrations (% DM) of SFA, MUFA and PUFA varied within and among cohorts (Tables I and II). PUFA, dominated by 20:5ω3 and 22:6ω3, were generally the

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Table I: Major fatty acids (>1% total identified fatty acids), dry mass and total lipid in mature males and females from C1, C2 and C3 of Mysis mixta

Cohort	C1	C2	C3	C3	C1	C2	C3	C1	C2
Stage	Mature females (n = 8)	Mature females (n = 13)	Mature female (early spawner) (n = 1)	Mature females (n = 4)	Males (n = 4)	Males (n = 6)	Males (n = 8)	Spent females (n = 3)	Spent females (n = 4)
Period	December 1998 to March 1999	September 1999 to March 2000	March 2000	November 2000	December 1998 to March 1999	May to September 1999	August to September 2000	May 1999	March to April 2000
Fatty acids	% DM ± SD (% TFA)								
14:0	0.97 ± 0.76	0.88 ± 0.51	0.26	0.94 ± 0.30	0.06 ± 0.02	0.36 ± 0.25	0.63 ± 0.33	0.95 ± 0.21	0.24 ± 0.14
16:0	1.41 ± 0.63	1.52 ± 0.39	0.98	1.47 ± 0.42	0.34 ± 0.09	0.93 ± 0.37	1.11 ± 0.32	1.81 ± 0.85	0.70 ± 0.22
ΣSFA	2.51 ± 1.41 (22)	2.51 ± 0.92 (27)	1.33 (66)	2.52 ± 0.76 (22)	0.43 ± 0.12 (19)	1.37 ± 0.66 (24)	1.82 ± 0.67 (19)	2.93 ± 1.13 (24)	1.01 ± 0.38 (44)
16:1ω7	1.29 ± 1.02	0.98 ± 1.00	0.03	1.42 ± 0.50	0.06 ± 0.05	0.63 ± 0.57	1.42 ± 0.79	1.64 ± 0.28	0.17 ± 0.12
18:1ω9	1.60 ± 1.10	1.31 ± 0.70	0.16	1.88 ± 1.02	0.27 ± 0.03	0.74 ± 0.31	1.01 ± 0.32	1.34 ± 0.63	0.25 ± 0.19
18:1ω7	0.32 ± 0.16	0.22 ± 0.14	0.02	0.30 ± 0.11	0.05 ± 0.01	0.15 ± 0.07	0.24 ± 0.07	0.31 ± 0.14	0.04 ± 0.03
20:1ω9,11	0.67 ± 0.48	0.56 ± 0.39	0.05	0.75 ± 0.27	0.11 ± 0.05	0.35 ± 0.11	0.60 ± 0.27	0.43 ± 0.04	0.07 ± 0.05
22:1ω11	0.34 ± 0.32	0.30 ± 0.23	0.02	0.38 ± 0.14	0.05 ± 0.04	0.18 ± 0.06	0.33 ± 0.17	0.14 ± 0.15	0.03 ± 0.02
ΣMUFA	4.43 ± 3.20 (39)	3.52 ± 2.46 (38)	0.29 (15)	4.93 ± 1.67 (42)	0.59 ± 0.17 (26)	2.13 ± 0.95 (35)	3.76 ± 1.63 (40)	4.01 ± 0.99 (33)	0.60 ± 0.37 (26)
18:2ω6	0.18 ± 0.12	0.16 ± 0.12	0.02	0.22 ± 0.07	0.02 ± 0.01	0.11 ± 0.07	0.24 ± 0.10	0.27 ± 0.03	0.03 ± 0.02
18:4ω3	0.26 ± 0.18	0.22 ± 0.18	0.01	0.31 ± 0.15	0.01 ± 0.00	0.07 ± 0.07	0.18 ± 0.12	0.03 ± 0.02	0.04 ± 0.03
20:4ω6	0.05 ± 0.02	0.04 ± 0.01	0.01	0.05 ± 0.02	0.05 ± 0.02	0.07 ± 0.03	0.10 ± 0.02	0.07 ± 0.03	0.01 ± 0.01
20:5ω3	1.72 ± 0.72	1.32 ± 0.78	0.12	1.90 ± 0.78	0.46 ± 0.11	1.17 ± 0.73	1.51 ± 0.48	2.41 ± 1.32	0.28 ± 0.21
22:6ω3	1.30 ± 0.47	0.92 ± 0.33	0.10	1.02 ± 0.51	0.59 ± 0.17	0.89 ± 0.42	1.19 ± 0.16	1.33 ± 1.26	0.17 ± 0.18
ΣPUFA	4.09 ± 1.79 (36)	3.15 ± 1.75 (34)	0.31 (16)	4.15 ± 1.74 (35)	1.20 ± 0.31 (53)	2.61 ± 1.46 (39)	3.66 ± 1.11 (39)	4.96 ± 2.78 (41)	0.67 ± 0.48 (29)
ω3	3.54 ± 1.46 (31)	2.69 ± 1.38 (29)	0.26 (13)	3.52 ± 1.54 (30)	1.09 ± 0.28 (48)	2.25 ± 1.21 (34)	3.03 ± 0.82 (32)	4.10 ± 2.63 (34)	0.53 ± 0.42 (23)
TFA	11.24 ± 6.38	9.33 ± 5.15	1.99	11.74 ± 3.84	2.26 ± 0.56	6.20 ± 3.09	9.40 ± 3.43	12.12 ± 4.83	2.32 ± 1.11
Bacterial	0.28 ± 0.11 (3)	0.20 ± 0.12 (2)	0.11 (6)	0.19 ± 0.07 (2)	0.06 ± 0.01 (3)	0.13 ± 0.09 (2)	0.20 ± 0.08 (2)	0.27 ± 0.13 (2)	0.07 ± 0.06 (3)
Copepod	1.08 ± 0.84 (9)	0.91 ± 0.65 (9)	0.08 (4)	1.16 ± 0.43 (10)	0.17 ± 0.09 (7)	0.56 ± 0.07 (11)	0.98 ± 0.47 (10)	0.62 ± 0.17 (6)	0.11 ± 0.08 (4)
Terrestrial	0.26 ± 0.16 (2)	0.22 ± 0.15 (2)	0.02 (1)	0.33 ± 0.11 (3)	0.03 ± 0.01 (1)	0.12 ± 0.08 (2)	0.27 ± 0.12 (3)	0.31 ± 0.04 (3)	0.04 ± 0.03 (2)
Dry mass (mg ± SD)	56.95 ± 9.85	51.10 ± 7.45	27.57	60.80 ± 10.00	35.60 ± 3.88	34.59 ± 2.31	34.56 ± 1.28	47.33 ± 5.17	43.52 ± 5.04
Total lipid (mg ± SD)	19.99 ± 5.97	19.14 ± 5.78	4.40	31.32 ± 4.62	1.70 ± 0.51	3.16 ± 0.60	6.29 ± 2.26	7.02 ± 3.10	2.75 ± 0.60

ω3, sum of ω3 fatty acids; bacterial, sum of odd chain fatty acids (iso and ante-iso forms); copepod, Σ(22:1 + 20:1); DM, dry mass; ΣMUFA, sum of monounsaturated fatty acids; *n*, sample size; ΣPUFA, sum of polyunsaturated fatty acids; ΣSFA, sum of saturated fatty acids; terrestrial, Σ(18:2ω6 + 18:3ω3); TFA, total identified fatty acids.
Data are grand means for stages collected within the indicated periods. Fatty acids found in trace amounts: 15:0, 15:0i, 15:0ai,16:0i, 16:0ai, 17:0, 17:0i, 17:0ai, 18:0, 16:1ω5, 18:1ω5, 20:1ω7, 22:1ω9, 24:1, 16:2ω4, 18:2ω4, 20:2ω6, 16:3ω4, 18:3ω6, 18:3ω4, 18:3ω3, 20:3ω6, 20:3ω3, 16:4ω3, 16:4ω1, 18:4ω1, 20:4ω3, 22:4ω6, 21:5ω3, 22:5ω6, 22:5ω3.

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Table II: Major fatty acids, dry mass and total lipid in juveniles and immatures from C2, C3 and C4 of Mysis mixta

Cohort	C2	C3	C4	C2	C2	C3	C3	C3	C3
Stage	Juveniles (n = 16)	Juveniles (n = 5)	Juveniles (n = 20)	Immature females and immature males (n = 11)	Immature females and immature males (n = 6)	Immature females (n = 13)	Immature females (n = 20)	Immature males (n = 15)	Immature males (n = 17)
Period	December 1998 to February 1999	July 1999	June to November 2000	March to April 1999	May 1999	September 1999 to February 2000	March to September 2000	September 1999 to February 2000	March to July 2000
Fatty acids	% DM ± SD (% TFA)								
14:0	0.42 ± 0.20	0.17 ± 0.06	0.47 ± 0.24	0.44 ± 0.13	1.35 ± 0.39	0.41 ± 0.27	0.94 ± 0.34	0.39 ± 0.15	1.00 ± 0.35
16:0	1.14 ± 0.45	0.78 ± 0.16	1.15 ± 0.26	1.06 ± 0.22	2.55 ± 0.78	0.91 ± 0.31	1.47 ± 0.41	1.03 ± 0.24	1.59 ± 0.40
ΣSFA	1.67 ± 0.63 (22)	1.04 ± 0.23 (57)	1.74 ± 0.49 (23)	1.59 ± 0.34 (22)	4.11 ± 1.15 (23)	1.41 ± 0.58 (45)	2.52 ± 0.77 (23)	1.51 ± 0.56 (25)	2.71 ± 0.77 (22)
16:1ω7	0.44 ± 0.22	0.08 ± 0.09	0.55 ± 0.30	0.49 ± 0.17	2.53 ± 0.76	0.23 ± 0.25	1.81 ± 0.82	0.40 ± 0.21	1.99 ± 0.85
18:1ω9	0.95 ± 0.36	0.15 ± 0.16	0.88 ± 0.30	0.84 ± 0.22	1.84 ± 0.58	0.31 ± 0.32	1.20 ± 0.43	0.77 ± 0.33	1.22 ± 0.28
18:1ω7	0.18 ± 0.07	0.05 ± 0.05	0.23 ± 0.08	0.16 ± 0.04	0.40 ± 0.12	0.05 ± 0.06	0.27 ± 0.11	0.15 ± 0.07	0.26 ± 0.06
20:1ω9,11	0.23 ± 0.10	0.05 ± 0.04	0.56 ± 0.43	0.19 ± 0.05	0.47 ± 0.17	0.12 ± 0.16	0.40 ± 0.20	0.24 ± 0.47	0.41 ± 0.13
22:1ω11	0.08 ± 0.04	0.01 ± 0.01	0.31 ± 0.30	0.07 ± 0.04	0.19 ± 0.07	0.05 ± 0.06	0.19 ± 0.11	0.10 ± 0.08	0.20 ± 0.08
ΣMUFA	1.99 ± 0.80 (26)	0.35 ± 0.35 (19)	2.67 ± 0.99 (35)	1.85 ± 0.43 (26)	5.65 ± 1.57 (32)	0.80 ± 0.89 (26)	4.01 ± 1.59 (35)	1.76 ± 1.12 (28)	4.24 ± 1.30 (35)
18:2ω6	0.10 ± 0.04	0.02 ± 0.02	0.13 ± 0.06	0.11 ± 0.03	0.39 ± 0.11	0.04 ± 0.05	0.26 ± 0.09	0.09 ± 0.04	0.29 ± 0.11
18:4ω3	0.15 ± 0.09	0.02 ± 0.04	0.17 ± 0.10	0.11 ± 0.05	0.32 ± 0.10	0.07 ± 0.08	0.32 ± 0.16	0.12 ± 0.08	0.34 ± 0.11
20:4ω6	0.07 ± 0.03	0.06 ± 0.12	0.06 ± 0.02	0.07 ± 0.03	0.10 ± 0.04	0.04 ± 0.08	0.05 ± 0.01	0.06 ± 0.48	0.07 ± 0.02
20:5ω3	1.47 ± 0.58	0.10 ± 0.13	1.13 ± 0.43	1.66 ± 0.34	3.82 ± 1.35	0.24 ± 0.29	2.12 ± 0.73	1.04 ± 0.84	2.21 ± 0.51
22:6ω3	1.46 ± 0.59	0.07 ± 0.09	1.13 ± 0.40	1.20 ± 0.35	2.09 ± 0.95	0.21 ± 0.23	1.07 ± 0.36	1.15 ± 0.86	1.15 ± 0.37
ΣPUFA	3.63 ± 1.38 (49)	0.36 ± 0.29 (20)	3.00 ± 0.81 (40)	3.53 ± 0.79 (49)	7.78 ± 2.70 (43)	0.79 ± 0.83 (25)	4.59 ± 1.52 (41)	2.75 ± 2.84 (45)	4.89 ± 1.11 (41)
ω3	3.27 ± 1.27 (44)	0.23 ± 0.27 (13)	2.61 ± 0.78 (35)	3.12 ± 0.71 (44)	6.50 ± 2.38 (36)	0.63 ± 0.68 (20)	3.71 ± 1.23 (33)	2.46 ± 1.99 (39)	3.92 ± 0.88 (33)
TFA	7.49 ± 2.82	1.83 ± 0.84	7.56 ± 2.00	7.15 ± 1.55	17.80 ± 5.30	3.12 ± 2.26	11.29 ± 3.84	6.16 ± 4.52	12.04 ± 2.99
Bacterial	0.24 ± 0.09 (3)	0.12 ± 0.04 (7)	0.21 ± 0.07 (3)	0.21 ± 0.06 (3)	0.35 ± 0.09 (2)	0.13 ± 0.06 (5)	0.21 ± 0.06 (2)	0.18 ± 0.18 (3)	0.25 ± 0.06 (2)
Copepod	0.34 ± 0.16 (5)	0.06 ± 0.05 (3)	0.90 ± 0.72 (11)	0.29 ± 0.10 (4)	0.75 ± 0.29 (4)	0.19 ± 0.24 (5)	0.62 ± 0.32 (5)	0.36 ± 0.88 (6)	0.64 ± 0.23 (5)
Terrestrial	0.16 ± 0.07 (2)	0.03 ± 0.03 (1)	0.19 ± 0.08 (3)	0.14 ± 0.04 (2)	0.44 ± 0.12 (3)	0.07 ± 0.07 (2)	0.31 ± 0.11 (3)	0.14 ± 0.06 (2)	0.34 ± 0.11 (3)
Dry mass (mg ± SD)	20.19 ± 2.73	4.30 ± 1.70	9.39 ± 4.17	25.68 ± 4.81	32.74 ± 5.03	16.32 ± 5.10	38.97 ± 12.54	14.49 ± 5.73	26.97 ± 6.39
Total lipid (mg ± SD)	2.58 ± 0.59	0.36 ± 0.15	1.11 ± 0.66	3.28 ± 0.96	8.78 ± 1.41	1.80 ± 1.00	8.32 ± 4.43	1.58 ± 0.81	5.54 ± 2.42

ω3, sum of ω3 fatty acids; bacterial, sum of odd chain fatty acids (iso and ante-iso forms); copepod, Σ(22:1 + 20:1); DM, dry mass; ΣMUFA, sum of monounsaturated fatty acids; n, sample size; ΣPUFA, sum of polyunsaturated fatty acids; ΣSFA, sum of saturated fatty acids; terrestrial, Σ(18:2ω6 + 18:3ω3); TFA, total identified fatty acids.
Data are grand means for stages collected within the indicated periods. Immatures from C2 were pooled, but C3 males and females were separated owing to their divergent profiles. C2 and C3 immatures were divided into high lipid versus low lipid periods corresponding to pre- and post-bloom start periods. Fatty acids found in trace amounts: 15:0, 15:0i, 15:0ai,16:0i, 16:0ai, 17:0, 17:0i, 17:0ai, 18:0, 16:1ω5, 18:1ω5, 20:1ω7, 22:1ω9, 24:1, 16:2ω4, 18:2ω4, 20:2ω6, 16:3ω4, 18:3ω6, 18:3ω4, 18:3ω3, 20:3ω6, 20:3ω3, 16:4ω3, 16:4ω1, 18:4ω1, 20:4ω3, 22:4ω6, 21:5ω3, 22:5ω6, 22:5ω3.

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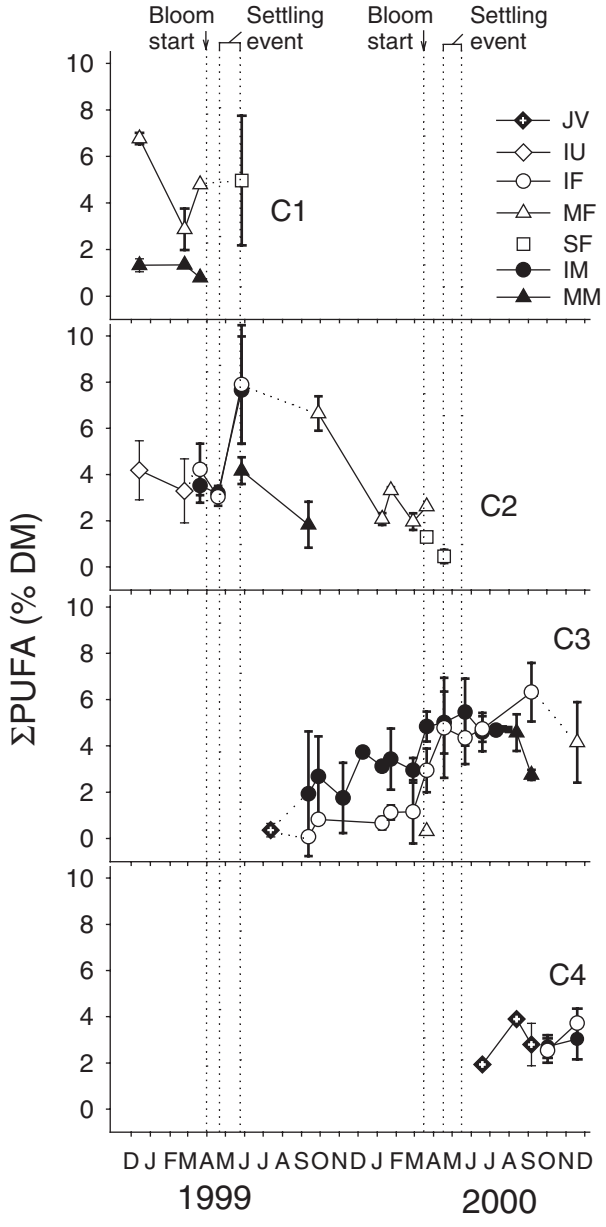

Fig. 1. *Mysis mixta*. Changes in sum of polyunsaturated fatty acids (ΣPUFA) [% dry mass (DM)] in four cohorts (C1, C2, C3 and C4). JV, juveniles; IU, immatures undifferentiated; IF, immature females; MF, mature females (includes brooded embryos); SF, spent females; IM, immature males; MM, mature males. Dotted lines within a cohort represent transition periods between stages; vertical dotted lines are bloom start and settling times; error bars are SD around the mean.

most prevalent fatty acids in most juveniles, immatures, spent females and mature males, whereas MUFA were dominant in most mature females (Tables I and II). SFA concentrations varied, but were commonly lower than those of PUFA and MUFA.

The highest PUFA concentrations occurred in immature C2 females (8% DM; Fig. 1), and minimal changes were observed in PUFA in immature mysids before the spring bloom. Rapid accumulation of PUFA, mainly 20:5ω3, occurred once the bloom started in March, particularly in immature females (Fig. 1; Table III). Mysids showed increases in SFA and MUFA throughout development, and accumulation was often most pronounced in females (Tables I, II and III). Significant amounts of PUFA, SFA and MUFA were utilized by mature C2 females during the 5-month brooding period (no significant utilization of PUFA in mature C1 females; Table III), resulting in low levels of all fatty acids in spent females (Table I). Mature females utilized MUFA faster than PUFA or SFA (Table III), and an early-spawning female from C3 had very low concentrations of all fatty acids (Table I). Mature males showed either no change or significant decreases in fatty acid concentrations before death (Fig. 1; Table III). Juveniles from C4 exhibited fatty acid accumulation rates similar to those in C3 juveniles, although there were no pre-bloom data available for comparison because C4 juveniles were released during the spring bloom in 2000 (Fig. 1; Table III).

Dietary markers

The diatom marker (16:1ω7 + 16:1ω5)/16:0 increased rapidly in immature mysids beginning in March each year and reached 1.5 after the bloom material had settled to the hyperbenthos (Fig. 2A). At other times the ratio remained <1.0 except in some C1 females. The trend in the dinoflagellate marker 22:6ω3/20:5ω3 was opposite to that of the diatom marker, with values fluctuating near 1.0 during non-bloom times and then dropping rapidly once the bloom had started (Fig. 2). PUFA/SFA ratios [proposed as an index of carnivory; (Cripps and Atkinson, 2000)] increased with development in C3 mysids; otherwise, the ratios fluctuated near 2.0 and were largely independent of the bloom (data not shown). In C2 and C3, 18:1ω9/18:1ω7 (carnivory marker; Graeve *et al.*, 1997) peaked at 8.0 and then returned to ~5.0 before the bloom (Fig. 3A). Ratios of ΣC16/ΣC18 exhibited no patterns (data not shown; marker indicates dominance of diatoms or dinoflagellates; Claustre *et al.*, 1989). The fatty acid 18:1ω9 (% DM; associated with marine animals) and Σ(20:1ω9 + 22:1ω11) fatty acids (% DM, marker for calanoid copepods; Sargent and Falk-Petersen, 1988) increased in developing mysids after the onset of the bloom, similar to the changes in total PUFA (Figs 1 and 3B; plot of 18:1ω9 not shown). Unlike PUFA, concentrations of 18:1ω9 and Σ(20:1 + 22:1) continued to increase after the bloom material had settled. As a result, mature females early in their brooding period contained high concentrations of both markers in midwinter

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Table III: Within-cohort rates of accumulation or utilization of major fatty acids, sums of polyunsaturated fatty acids (PUFA), saturated fatty acids (SFA), monounsaturated fatty acids (MUFA) and copepod marker (20:1 + 22:1) (μg month^{-1}; rates produced from regression slopes) in Mysis mixta and Acanthostepheia malmgreni

Cohort	Stages	Time period	Bloom status	20:5ω3	22:6ω3	PUFA	14:0	16:0	SFA	18:1ω9	16:1ω7	20:1 + 22:1	MUFA	*n*
Mysis mixta														
C1[a]	MF	December 1998 to March 1999	Not applicable	0.00	0.00	0.00	–305**	0.00	–508*	–429**	–417***	–339**	–1280**	8
C1	MM	December 1998 to March 1999	Not applicable	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4
C2[a]	IU, IM and IF	December 1998 to March 1999	Pre	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	21
C2[a]	IM	March 1999 to May 1999	Post	349**	0.00	710**	152**	251**	422**	180**	313**	–89.0**	634**	9
C2	IF	March 1999 to May 1999	Post	397*	0.00	762*	147*	257*	424*	0.00	337**	–61.7*	607*	8
C2	MM	May 1999 to September 1999	Not applicable	0.00	0.00	0.00	–40.5*	–60.6*	–107*	–107*	0.00	0.00	0.00	6
C2	MF	September 1999 to March 2000	Not applicable	–174***	–63.5**	–391****	–109***	–73.4***	–189***	–143**	–174**	–123**	–541****	12
C3[a]	JV and IM	July 1999 to March 2000	Pre	39.9***	32.5****	103****	17.2****	26.5****	43.7****	25.5****	22.3**	12.3****	60.4****	24
C3[a]	JV and IF	July 1999 to March 2000	Pre	19.5**	0.00	0.00	16.7***	26.3****	45.1****	14.9***	13.5*	9.51**	41.4**	21
C3[a]	IM	March 2000 to July 2000	Post	80.1*	0.00	0.00	0.00	0.00	0.00	43.0*	169***	27.7**	237**	16
C3	IF	March 2000 to September 2000	Post	215****	119****	444****	75.7****	107****	190****	127****	141**	87.9****	425****	20
C3	MM	August 2000 to September 2000	Not applicable	–355**	–124**	–829**	–229*	–223*	–473**	–202*	–512*	0.00	–934*	8
C4[a]	JV, IM and IF	June 2000 to November 2000	Post	27.0*	43.4*	79.3***	23.2*	32.2**	58.6*	26.9**	0.00	43.3**	88.2***	20
Cohort	Stages	Time period	Bloom status	20:5ω3	22:6ω3	PUFA	16:0	SFA	18:1ω9	18:1ω7	16:1ω7	20:1 + 22:1	MUFA	*n*
Acanthostepheia malmgreni														
C1	MF	December 1998 to May 1999	Not applicable	0.00	0.00	0.00	–126*	–199*	–173*	–115**	–76.5*	–92.3**	–477**	16
C1[a]	NS	October 1998 to May 1999	Not applicable	269**	0.00	0.00	112*	143*	155*	70.2*	0.00	0.00	315*	20
C2	JV	February 1999 to July 1999	Not applicable	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4
C2	JV and IF	Jul 1999 to Nov 1999	Not applicable	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3
C3	JV	September 1999 to April 2000	Pre	24.9****	18.8****	52.0****	8.53****	11.4****	9.44****	6.49****	2.27***	4.52***	24.0****	27
C3	IM	May 2000 to November 2000	Post	41.7**	25.1**	97.8***	22.5**	39.5**	24.1***	18.9**	23.2**	21.9**	97.1**	22
C3	IF	May 2000 to Nov 2000	Post	50.8****	26.1****	101****	22.8****	35.5****	31.6****	21.6****	22.3****	22.4****	103****	23

IM, immature males; IF, immature females; IU, immatures undifferentiated; JV, juveniles; MM, mature males; MF, mature females; NS, non-sexed (includes mature male and non-reproductive female amphipods); MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; SFA, saturated fatty acids. Subgroups of *Mysis mixta* were created to establish rates before (pre) and after (post) the start of the bloom, although bloom status was not assigned to mature males/females. Subgroups of *Acanthostepheia malmgreni* were formed according to development stage and correspond roughly to before and after sedimentation of the bloom material. Spent females were not included in analyses. A rate of 0.00 μg month^{-1} was assigned when a regression was not significant ($P > 0.05$).

[a]some regressions in these subgroups were corrected for temporal autocorrelation using the Cochrane–Orcutt procedure.

*: $P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; $^{****}P < 0.000$.

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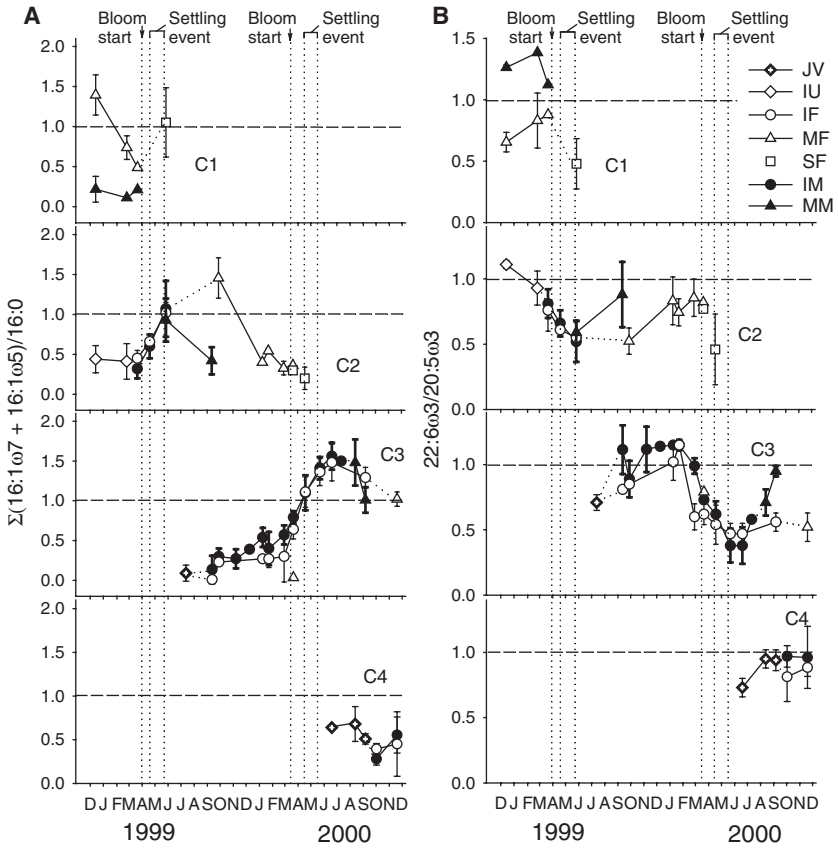

Fig. 2. *Mysis mixta*. Changes in the diatom marker Σ(16:1ω7 + 16:1ω5)/16:0 (**A**) and the dinoflagellate marker 22:6ω3/20:5ω3 (**B**) in cohorts 1–4. Dashed horizontal lines are reference lines for between-panel comparisons only (additional details as in Fig. 1).

(Fig. 3B; Table I). Bacterial (odd and branched chain fatty acids; <7% TFA) and terrestrial plant [sum of 18:2ω6 + 18:3ω3 in coastal Newfoundland regions (Budge and Parrish, 1998); <3% TFA] marker proportions were relatively low; therefore, material of bacterial and terrestrial plant origin were not considered important sources of nutrition for *M. mixta*.

Fatty acids in *A. malmgreni*

Forty-three fatty acids were identified in *A. malmgreni* (Table IV), with 14:0, 16:0 and 18:0 the major SFA in all stages. The MUFA fraction was dominated by 16:1ω7, 18:1ω9, 18:1ω7, 18:1ω5, 20:1ω9(11) and 20:1ω7, and the PUFA fraction by 18:2ω6, 20:4ω6, 20:5ω3, 22:5ω3 and 22:6ω3.

The most abundant fatty acids in juveniles were 20:5ω3, 22:6ω3, 16:0, 18:1ω7 and 18:1ω9. These five fatty acids remained dominant while *A. malmgreni* matured and accumulated lipid stores (Richoux *et al.*, 2004d; Table IV), and quantities of 16:1ω7 increased with developmental stage. Of those regressed against TL (μg individual^{-1}), 20:5ω3, 18:1ω9, 22:6ω3, 16:0, 18:1ω7 and 16:1ω7 (in the order of decreasing abundance) had the greatest slopes (slopes > 0.0129, $P < 0.0001$, $r^2 > 0.401$) and were the major contributors to lipid accumulation in *A. malmgreni*.

The concentrations (% DM) of SFA, MUFA and PUFA changed with development in the cohorts (C1, C2, C3 and C4) of *A. malmgreni* (Table IV). PUFA, consisting mainly of 20:5ω3 and 22:6ω3, were predominant in all stages, followed by MUFA and SFA (Table IV). Maximum PUFA concentrations occurred in immature C3 males (3.4 ± 1.0% DM; Fig. 4). PUFA accumulation rates in immature C3 amphipods were low before the bloom but increased once the bloom material had settled in April/May. Accumulation rates were similar in immature males and females (Fig. 4; Table III). Only a few amphipods from C2 were collected, therefore data from this cohort are less informative than are data derived from the larger cohorts. Immature C3 amphipods accumulated MUFA at rates similar to PUFA accumulation rates, whereas SFA accumulation rates were generally much lower (Table III). Mature females utilized significant amounts of SFA and MUFA during the brooding period, although PUFA concentrations

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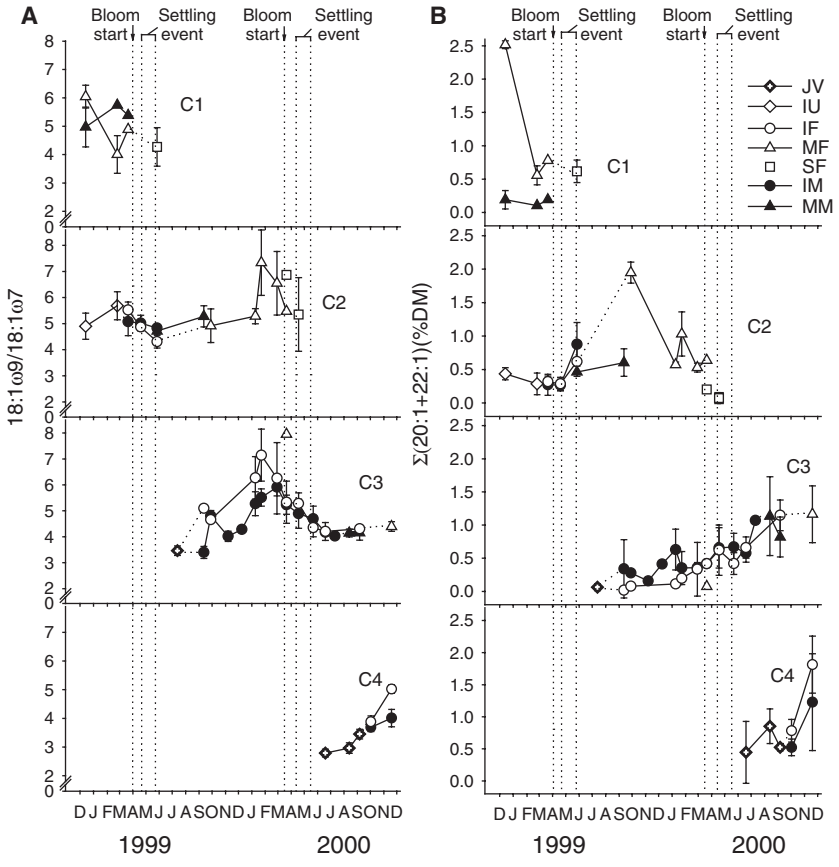

Fig. 3. *Mysis mixta*. Changes in the carnivory marker 18:1ω9/18:1ω7 (**A**) and in the calanoid copepod marker Σ(20:1 + 22:1) [% dry mass (DM)] (**B**) in cohorts 1–4 (additional details as in Fig. 1).

remained at ~2% DM (Table III). Spent females contained half the amount of PUFA, SFA and MUFA as did mature females (Table IV). The non-sexed group in C1, consisting of mature males and large non-reproductive females, showed significant increases in all three fatty acid types before it disappeared after May 1999 (Fig. 4; Table III). Variation in fatty acid composition was high within this group, presumably because it was composed of more than one life-history stage.

Dietary markers

The diatom marker (16:1ω7 + 16:1ω5)/16:0 was normally <0.6 and increased rapidly to 1.0 only in immature C3 amphipods following the settling event (Fig. 5A). Changes in ΣC16/ΣC18 (data not shown) mirrored the patterns in (16:1ω7 + 16:1ω5)/16:0. The dinoflagellate marker 22:6ω3/20:5ω3 was highly variable within cohorts, with values approaching 1.0 before and during the bloom and then decreasing to ≤0.6 following sedimentation (Fig. 5B). Ratios of PUFA/SFA increased before the bloom in C1, C2 and C3 (data for only one sample from C4), peaked above 4.0 in March/April, and then decreased to <3.0 in the summer (Fig. 6A). The carnivery marker 18:1ω9/18:1ω7 did not fluctuate far from 1.4 in C2 and C3 amphipods, although ratios in the large C1 individuals varied considerably and exceeded 2.2 in the spring (data not shown). Trends in 18:1ω9 (% DM) and Σ(20:1 + 22:1) (% DM) were similar to those of PUFA (i.e. the markers increased in developing amphipods following settling of bloom material, decreased in mature females during brooding, and varied substantially within C1; Figs 4 and 6B). Highest concentrations (% DM) of 18:1ω9, Σ(20:1 + 22:1) and PUFA were reached during winter in C1, C2 and C3 individuals (Figs 4 and 6B; Table IV). As in *M. mixta*, accumulation of bacterial and terrestrial plant markers was minimal (Table IV).

Areal PUFA calculations

Maximum areal concentrations of PUFA in the hyperbenthic populations of *M. mixta* (14.6 mg m^{-2}) and *A. malmgreni* (5.77 mg m^{-2}) occurred in August 2000

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Table IV: Major fatty acids, dry mass and total lipid in C1, C2, C3 and C4 of Acanthostepheia malmgreni

Cohort	C1	C1	C1	C2	C3	C4	C2	C3	C3
Stage	Mature females (n = 16)	Spent females (n = 4)	Non-sexed (n = 22)	Juveniles (n = 4)	Juveniles (n = 37)	Juvenile (n = 1)	Immature females (n = 2)	Immature females (n = 16)	Immature males (n = 17)
Period	December 1998 to May 1999	April to May 2000	October 1998 to May 1999	February to July 1999	September 1999 to April 2000	September 2000	September to November 1999	May to November 2000	May to November 2000
Fatty acids	% DM ± SD (% TFA)								
14:0	0.10 ± 0.07	0.03 ± 0.04	0.10 ± 0.07	0.05 ± 0.04	0.05 ± 0.03	0.08	0.08 ± 0.02	0.17 ± 0.08	0.21 ± 0.11
16:0	0.61 ± 0.29	0.29 ± 0.26	0.64 ± 0.41	0.32 ± 0.15	0.42 ± 0.16	0.35	0.47 ± 0.10	0.63 ± 0.20	0.71 ± 0.31
18:0	0.06 ± 0.03	0.02 ± 0.02	0.05 ± 0.03	0.04 ± 0.02	0.05 ± 0.02	0.03	0.05 ± 0.00	0.06 ± 0.02	0.07 ± 0.04
ΣSFA	0.85 ± 0.43 (17)	0.38 ± 0.36 (16)	0.86 ± 0.53 (18)	0.44 ± 0.23 (21)	0.58 ± 0.22 (18)	0.50 (18)	0.65 ± 0.13 (15)	0.93 ± 0.31 (17)	1.06 ± 0.49 (18)
16:1ω7	0.26 ± 0.17	0.09 ± 0.13	0.24 ± 0.21	0.06 ± 0.04	0.08 ± 0.05	0.28	0.18 ± 0.05	0.49 ± 0.23	0.58 ± 0.33
18:1ω9	0.80 ± 0.36	0.34 ± 0.26	0.71 ± 0.50	0.24 ± 0.05	0.39 ± 0.15	0.30	0.58 ± 0.26	0.58 ± 0.26	0.60 ± 0.27
18:1ω7	0.45 ± 0.23	0.20 ± 0.19	0.39 ± 0.22	0.16 ± 0.03	0.28 ± 0.11	0.17	0.34 ± 0.13	0.42 ± 0.17	0.46 ± 0.22
18:1ω5	0.07 ± 0.03	0.03 ± 0.03	0.06 ± 0.04	0.02 ± 0.00	0.04 ± 0.02	0.02	0.05 ± 0.02	0.06 ± 0.03	0.07 ± 0.04
20:1ω9,11	0.18 ± 0.10	0.07 ± 0.09	0.14 ± 0.10	0.05 ± 0.02	0.10 ± 0.05	0.05	0.14 ± 0.05	0.19 ± 0.10	0.23 ± 0.12
20:1ω7	0.09 ± 0.06	0.04 ± 0.05	0.09 ± 0.05	0.03 ± 0.01	0.06 ± 0.03	0.02	0.07 ± 0.03	0.11 ± 0.05	0.13 ± 0.08
ΣMUFA	1.90 ± 0.94 (38)	0.81 ± 0.77 (33)	1.68 ± 1.10 (36)	0.57 ± 0.04 (28)	0.99 ± 0.41 (31)	0.86 (31)	1.40 ± 0.52 (33)	1.94 ± 0.85 (36)	2.20 ± 1.11 (37)
18:2ω6	0.10 ± 0.04	0.05 ± 0.05	0.07 ± 0.04	0.03 ± 0.00	0.05 ± 0.02	0.05	0.06 ± 0.02	0.13 ± 0.05	0.14 ± 0.07
20:4ω6	0.11 ± 0.04	0.08 ± 0.05	0.11 ± 0.08	0.06 ± 0.03	0.08 ± 0.04	0.06	0.10 ± 0.02	0.10 ± 0.03	0.11 ± 0.05
20:5ω3	1.01 ± 0.39	0.54 ± 0.43	0.93 ± 0.65	0.46 ± 0.20	0.73 ± 0.33	0.75	1.06 ± 0.41	1.17 ± 0.40	1.22 ± 0.50
22:5ω3	0.07 ± 0.03	0.04 ± 0.04	0.07 ± 0.06	0.03 ± 0.01	0.05 ± 0.02	0.03	0.07 ± 0.03	0.08 ± 0.03	0.09 ± 0.06
22:6ω3	0.64 ± 0.20	0.40 ± 0.22	0.69 ± 0.53	0.34 ± 0.20	0.52 ± 0.27	0.37	0.66 ± 0.20	0.73 ± 0.20	0.78 ± 0.30
ΣPUFA	2.13 ± 0.75 (43)	1.22 ± 0.87 (50)	2.06 ± 1.41 (44)	0.99 ± 0.44 (48)	1.59 ± 0.68 (50)	1.39 (50)	2.12 ± 0.74 (50)	2.46 ± 0.80 (46)	2.63 ± 1.09 (44)
ω3	1.81 ± 0.64 (36)	1.03 ± 0.73 (42)	1.77 ± 1.25 (38)	0.85 ± 0.40 (41)	1.36 ± 0.62 (43)	1.20 (43)	1.86 ± 0.66 (43)	2.09 ± 0.67 (39)	2.22 ± 0.91 (37)
TFA	4.97 ± 2.01	2.45 ± 2.02	4.72 ± 2.83	2.05 ± 0.23	3.20 ± 1.18	2.77	4.28 ± 1.35	5.39 ± 1.97	5.97 ± 2.69
Bacterial	0.16 ± 0.10 (3)	0.08 ± 0.06 (3)	0.18 ± 0.11 (4)	0.08 ± 0.02 (4)	0.09 ± 0.04 (3)	0.05 (2)	0.16 ± 0.03 (4)	0.12 ± 0.05 (2)	0.14 ± 0.07 (2)
Copepod	0.31 ± 0.17 (6)	0.13 ± 0.16 (4)	0.27 ± 0.17 (6)	0.09 ± 0.04 (5)	0.18 ± 0.09 (6)	0.10 (4)	0.25 ± 0.07 (6)	0.37 ± 0.18 (7)	0.46 ± 0.26 (8)
Terrestrial	0.12 ± 0.05 (2)	0.06 ± 0.06 (2)	0.09 ± 0.06 (2)	0.04 ± 0.01 (2)	0.06 ± 0.03 (2)	0.05 (2)	0.07 ± 0.02 (2)	0.15 ± 0.07 (3)	0.17 ± 0.09 (3)
Dry mass (mg ± SD)	127.23 ± 17.60	100.21 ± 14.39	108.96 ± 31.26	31.44 ± 9.67	5.08 ± 5.46	6.03	79.31 ± 26.57	51.49 ± 20.31	49.29 ± 19.27
Total lipid (mg ± SD)	28.79 ± 8.58	3.14 ± 1.89	9.86 ± 5.33	1.39 ± 0.71	0.45 ± 0.31	0.27	8.86 ± 4.61	4.36 ± 2.30	4.30 ± 2.67

ω3, sum of ω3 fatty acids; bacterial, sum of odd chain fatty acids (iso and ante-iso forms); copepod, Σ(22:1 + 20:1); DM, dry mass; ΣMUFA, sum of monounsaturated fatty acids; n, sample size; ΣPUFA, sum of polyunsaturated fatty acids; ΣSFA, sum of saturated fatty acids; Terrestrial, Σ(18:2ω6 + 18:3ω3); TFA, total identified fatty acids.

Data are grand means for stages collected within the indicated periods (non-sexed C1 group includes mature males and some large immature or non-reproductive females). Fatty acids found in trace amounts: 15:0, 15:0i, 15:0ai,16:0i, 16:0ai, 17:0, 17:0i, 17:0ai, 16:1ω5, 18:1ω5, 22:1ω9, 22:1ω11, 24:1, 16:2ω4, 18:2ω4, 20:2ω6, 16:3ω4, 18:3ω6, 18:3ω4, 18:3ω3, 20:3ω6, 20:3ω3, 16:4ω3, 16:4ω1, 20:4ω3, 22:4ω6, 21:5ω3, 22:5ω6.

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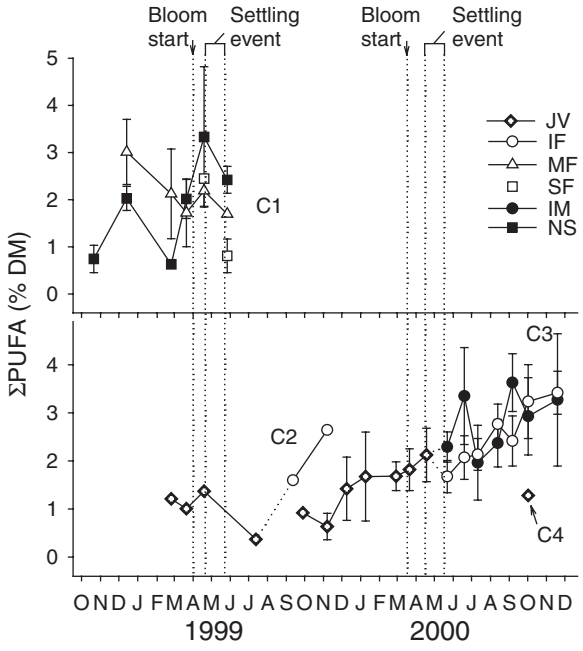

Fig. 4. *Acanthostepheia malmgreni.* Changes in sum of polyunsaturated fatty acids (ΣPUFA) [% dry mass (DM)] in four cohorts. JV, juveniles; IF, immature females; MF, mature females (includes brooded embryos); SF, spent females; IM, immature males; NS, non-sexed. Dotted lines within a cohort represent transition periods between stages; vertical dotted lines represent spring bloom start and settling times; error bars are SD around the mean.

(Fig. 7). Areal concentrations in *M. mixta* during 1999 were less than half those in 2000 (up to 6.36 mg m^{-2} in 1999), with lowest concentrations in June. *Acanthostepheia malmgreni* exhibited similar maximum areal concentrations of PUFA in both years (5.57mg m^{-2} in 1999), and a prolonged period of low concentrations was apparent throughout 1999 (Fig. 7). Variation in population density was the primary determinant of the interannual differences in areal PUFA concentration in each population.

DISCUSSION

Analyses of fatty acids and marker ratios in this study indicate that sexual maturation in one-year-old *M. mixta* and *A. malmgreni* is fuelled primarily by phytoplankton production in the upper water column during and following the spring bloom. The disparities between pre- and post-bloom rates were less pronounced in *A. malmgreni* than in *M. mixta*; marked increases in fatty acid concentrations in the amphipod population did not begin until after the bloom material had settled in May. These differences in accumulation rates of fatty acids in the two species suggest that energy cycles in the *M. mixta* population are more tightly coupled to primary production in the euphotic zone of Conception Bay. Overall, depletion of fatty acids occurred only in mature post-spawned males and females in each species, therefore overwintering was not accompanied by the food shortages typical of other cold-ocean regions (e.g. Arctic; Auel *et al.*, 2002).

To place the seasonal and developmental changes in the fatty acid composition of *M. mixta* and *A. malmgreni* in an ecological context, it is useful to understand the type and quality of food available throughout an annual cycle. Recent studies have provided information on the taxonomy and fatty acid composition of seston in Conception Bay and nearby systems (Budge and Parrish, 1998; Ramos *et al.*, 2003; Parrish *et al.*, 2005). Ramos *et al.* (Ramos *et al.*, 2003) observed that several biomarkers

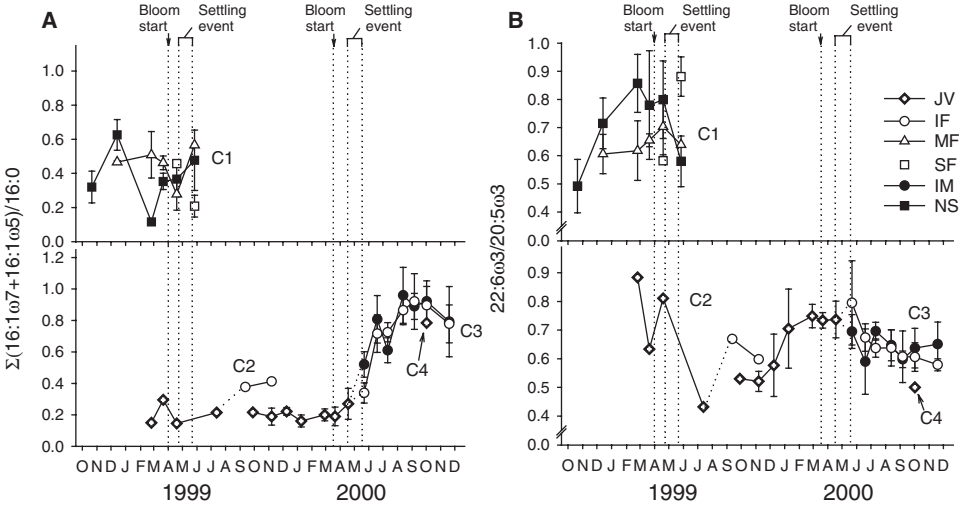

Fig. 5. *Acanthostepheia malmgreni.* Changes in the diatom marker Σ(16:1ω7 + 16:1ω5)/16:0 (**A**) and the dinoflagellate marker 22:6ω3/20:5ω3 (**B**) in cohorts 1–4 (additional details as in Fig. 4).

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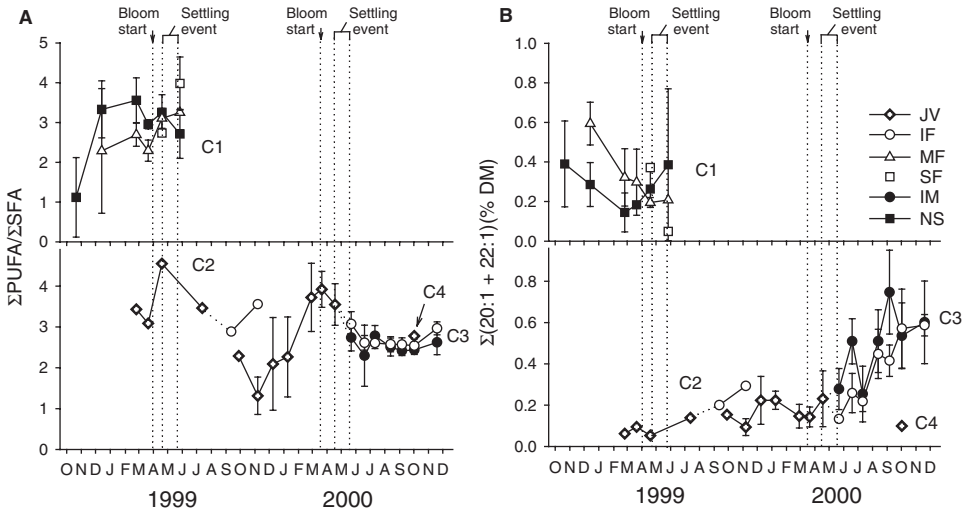

Fig. 6. *Acanthostepheia malmgreni*. Changes in the carnivory marker sum of polyunsaturated fatty acids/sum of saturated fatty acids (ΣPUFA/ΣSFA) (**A**) and the calanoid marker Σ(20:1 + 22:1) [% dry mass (DM)] (**B**) in cohorts 1–4 (additional details as in Fig. 4).

reflected the shift in phytoplankton from diatoms to dinoflagellates during the 1996 bloom in Conception Bay. In particular, Σ16:1/16:0, ΣC16/ΣC18 and 16:4ω1 indicated the dominance of diatoms in the seston from the start of the spring bloom in March, as well as in the sediment traps 2 weeks after the onset of the bloom, and 22:6ω3/20:5ω3 reflected the increase in dinoflagellates as the bloom waned in June and July (Ramos *et al.*, 2003). In Trinity Bay, a nearby fjord with similar physical and biological characteristics as Conception Bay, changes in phytoplankton composition in the 1996 bloom were also reflected in the seston fatty acids

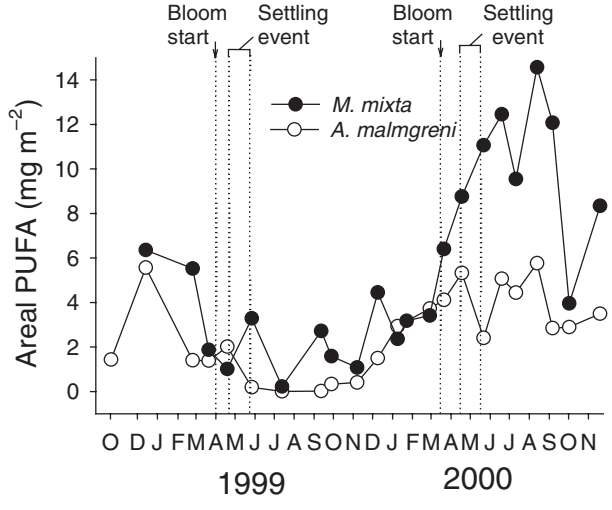

Fig. 7. *Mysis* mixta and Acanthostepheia *malmgreni*. Areal polyunsaturated fatty acids (PUFA) concentrations within the hyperbenthic populations in Conception Bay. Vertical dotted lines represent spring bloom start and settling times.

(Budge and Parrish, 1998). Higher amounts of the same PUFA noted in Conception Bay (18:4ω3, 20:5ω3 and 22:6ω3) coincided with the spring bloom, and fatty acid markers were consistent with the dominance of diatoms *Thalassiosira* sp. and *Chaetoceros* sp. from late March and of the dinoflagellate *Ceratium tripos* after the bloom had subsided in June (Budge and Parrish, 1998).

In this study, the succession of the dominant plankton was exhibited by changes in the fatty acid composition and in several marker ratios in the hyperbenthic species, particularly in *M. mixta*. High concentrations of 16:1ω7 and 20:5ω3, with 16:1ω7 increasingly prevalent in older life-history stages, suggest the importance of diatoms as a source of nutrition (possibly indirectly through consumption of herbivorous prey) in both *M. mixta* and *A. malmgreni* (Tables I, II and IV). The diatom-associated fatty acid 16:4ω1 occurred in only trace amounts in both species despite its frequent occurrence in seston and sediment trap material throughout the spring bloom in Conception Bay (Parrish *et al.*, 2005). The diatom marker Σ16:1/16:0 increased rapidly in *M. mixta* and *A. malmgreni* after the bloom onset each year (Figs 2A and 5A), and a second diatom marker ΣC16/ΣC18 exhibited a clear pattern in *A. malmgreni*, comparable to the changes in Σ16:1/16:0. Eighteen-carbon fatty acids are present in high concentrations in a variety of flagellates, and an increase in C18 fatty acids can be observed when dinoflagellates become dominant (Kattner *et al.*, 1983; Claustre *et al.*, 1989). Surprisingly, there was no discernible pattern of ΣC16/ΣC18 in *M. mixta*, perhaps indicating that ontogenetic processes are more influential than dietary factors in some instances.

Other fatty acids present in high quantities in Conception Bay seston that have been associated with

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dinoflagellates include 22:6ω3 and 18:4ω3 (Budge and Parrish, 1998; Reuss and Poulsen, 2002). The fatty acid 22:6ω3 was prevalent in both hyperbenthic species, whereas 18:4ω3 was abundant only in *M. mixta* (<1% TFA in *A. malmgreni*). As dinoflagellates are an extremely diverse group, 18:4ω3 and 22:6ω3 are not always reliable markers; the prevalence of these fatty acids in an ecosystem generally depends on the species composition and physiological status of the phytoplankton (Reuss and Poulsen, 2002). As 22:6ω3 alone is not a particularly useful biomarker, the ratio 22:6ω3/20:5ω3 appears to be the preferred index of the relative predominance of dinoflagellates over diatoms (Budge and Parrish, 1998). A marker ratio incorporating 18:4ω3 has not yet been established. Decreases in 22:6ω3/20:5ω3 corresponded with increases in Σ16:1/16:0 in both hyperbenthic populations, indicating the decreased dominance of dinoflagellates but continued abundance of diatoms in the diet (Figs 2 and 5). Consistent with reports for seston and sediment samples (Budge and Parrish, 1998), values of 22:6ω3/20:5ω3 in *M. mixta* were highest before the bloom and following settlement of the material, with a typical lag between the high abundance of dinoflagellates in June and the corresponding increase in the marker in the consumer (Fig. 2B). Neither Σ16:1/16:0 nor 22:6ω3/20:5ω3 reached 1.0 in *A. malmgreni*, whereas these ratios exceeded 1.5 at certain times of the year in *M. mixta*, thus supporting the hypothesis that *M. mixta* is more closely coupled to the upper mixed layer than is *A. malmgreni*.

The higher quantities of phytoplankton-derived fatty acids in *M. mixta* provide evidence that this species has more access to fresh algae through its nightly migrations towards the euphotic zone and is able to feed on a broader range of material, including phytoplankton, detritus and herbivorous zooplankton, than *A. malmgreni*. In contrast, due to its apparent confinement to the hyperbenthos and its prehensile feeding appendages, *A. malmgreni* probably derives the bulk of its essential PUFA indirectly from herbivorous and omnivorous prey, including copepods, available in the hyperbenthos. Stage V calanoids collected from Conception Bay during the winter contained relatively low levels of PUFA and high levels of 20:1ω9 and 22:1ω11 (Stevens, 2003). Owing in part to the high total fatty acid content of *M. mixta*, the calanoid copepod biomarker [Σ(20:1ω9 + 22:1ω11) (Sargent and Falk-Petersen, 1988)] was present at higher concentrations (% DM) in the mysids than in the amphipods (Figs 3B and 6B). Unlike PUFA concentrations, which stopped increasing shortly after the bloom material had settled in May, Σ(20:1 + 22:1) in *M. mixta* continued to rise in the autumn (Fig. 3B), possibly reflecting a dietary shift from phytoplankton to lipid-rich copepods and/or an ontogenetic shift in fatty acid utilization related to the reproductive cycle. Although Σ(20:1 + 22:1) concentrations (% DM) were generally lower in *A. malmgreni*, the rate of accumulation of Σ(20:1 + 22:1) after the bloom was similar to the accumulation rates of the major fatty acids found in this species, whereas accumulation of the major fatty acids in *M. mixta* often exceeded Σ(20:1 + 22:1) accumulation. These between-species differences in relative accumulation rates suggest that copepods become increasingly important as a dietary component, together with the phytoplankton, in maturing *A. malmgreni*. Furthermore, the lower concentrations of calanoid markers in *A. malmgreni* probably reflect the relatively lower total fatty acid content and a complex diet that may include mysids and chaetognaths (Richoux *et al.*, 2004c).

The monounsaturate 18:1ω9, often associated with animal prey (Sargent and Falk-Petersen, 1988) or detritus (Scott *et al.*, 2002), is a major component of the seston in Conception Bay (Parrish *et al.*, 2005) and the second most dominant fatty acid in *M. mixta* and *A. malmgreni*. Changes in 18:1ω9 resembled those in Σ(20:1 + 22:1) (Figs 3B and 6B), with increased accumulation after the spring bloom had started (*M. mixta*) or settled (*A. malmgreni*). Maximum concentrations of 18:1ω9 (%DM) occurred in mature female *M. mixta* during autumn, suggesting that in addition to copepod prey the mysids had access to other prey types. Differences in 18:1ω9/18:1ω7 can reflect alternative feeding behaviours and trophic levels. Graeve *et al.* (Graeve *et al.*, 1997) found increasing ratios from benthic suspension-feeders consuming freshly settled material (lowest ratio 0.1) to benthic predatory decapods and scavenging amphipods (highest ratio 3.6), with greater values associated with higher trophic levels. Significant regressions of 18:1ω7 on 16:1ω7 in both Conception Bay species [μg individual^{-1}; $P < 0.0001$, $r^2 > 0.8$, $n = 174$ (*M. mixta*), $n = 119$ (*A. malmgreni*)] supported the underlying premise of the ratio, i.e. that 18:1ω9 is derived from animal prey while 18:1ω7 is formed *in vivo* by chain elongation of diatom-produced 16:1ω7 (Graeve *et al.*, 1997). In *M. mixta*, the recurring peaks of 18:1ω9/18:1ω7 in midwinter each year may indicate the reliance of this species on a primarily non-phytoplankton diet before the bloom (Fig. 3A). In turn, the rapid decrease in the ratio with the onset of the bloom may represent the transition to a phytoplankton based diet. Less variable 18:1ω9/18:1ω7 ratios were observed in *A. malmgreni* (data not shown), possibly reflecting a more uniform diet year-round and less direct dependence on the spring bloom. Although high ratios have traditionally been associated with increased carnivory, the higher ratios in *M. mixta* may simply reflect a more varied diet and different lipid

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biosynthesis capabilities compared with *A. malmgreni*. The 18:1ω9/18:1ω7 marker also increases in starved zooplankton (Auel *et al.*, 2002), but lipid storage cycles in *M. mixta* and *A. malmgreni* indicate that adequate food is available year-round (Richoux *et al.*, 2004b,d).

High proportions of PUFA relative to SFA have been attributed to increased carnivory in antarctic krill fed an animal diet for 16 days (Cripps and Atkinson, 2000). The highest ratio measured in the carnivorous krill was 5, whereas krill fed with diatoms exhibited ratios of ~1 (Cripps and Atkinson, 2000). This ratio has not been a successful indicator of carnivory in all trophic studies, possibly due to differences in relative phospholipid content among zooplankton species and/or to regional differences in zooplankton feeding strategies and in phytoplankton taxonomy and fatty acid composition (Auel *et al.*, 2002; Stevens, 2003). Feeding strategies, phospholipid content (Richoux *et al.*, 2004b,d), and consequently PUFA/SFA ratios, differed between *M. mixta* and *A. malmgreni*. Ratios in *A. malmgreni* peaked around 5 during or before the phytoplankton bloom, indicating high levels of carnivery on animals other than calanoid cupepods and then decreased to ~2.5, consistent with a significant change in the diet after the bloom onset (Fig. 6A). In contrast, PUFA/SFA ratios in *M. mixta* did not coincide with periods of increased availability of non-calanoid animal prey. A high proportion of PUFA may indicate starvation (and preferential conservation of PUFA), but this was not the case here because triacylglycerol and PUFA content increased during the periods of high PUFA/SFA ratios in *M. mixta* and *A. malmgreni*.

Areal concentrations of PUFA were similar in *M. mixta* and *A. malmgreni* populations from December 1998 until March 2000, when concentrations in the former increased markedly and peaked in August (Fig. 7). Maximum areal PUFA in the *M. mixta* population represented 4.2% of the integrated input of seston PUFA to the hyperbenthos of Conception Bay [345 mg m^{-2}, measured from sediment trap material collected at 220 m during the 1996 bloom; (Parrish *et al.*, 2005)], whereas the highest areal PUFA concentrations in *A. malmgreni* represented 1.7% of integrated input. These disparate results are particularly interesting because areal concentrations of TL and triacylglycerol were remarkably similar in the two species, albeit with periods of rapid accumulation occurring at different times (Richoux *et al.*, 2004b,d). Lower areal concentrations of PUFA in the *A. malmgreni* population probably reflect the decreased PUFA content in partially decomposed organic material that had settled to the hyperbenthos, whereas *M. mixta* had access to PUFA-rich material and zooplankton prey higher in the water column.

This study represents the first comprehensive documentation of the seasonal and developmental changes in the fatty acid composition of *M. mixta* and *A. malmgreni* living in any environment. Although the majority of zooplankton fatty acid studies have focussed on trophic links within food webs, the ontogenetic changes in fatty acid composition of plankton have been largely overlooked. Nearly every marker examined in *M. mixta* and *A. malmgreni* varied in some manner during development. These results reiterate the need for increased emphasis on the life-history component, in addition to the environmental component, in trophic studies that utilise biomarkers. Comprehensive and multi-tiered studies are needed to put the observed variation in fatty acid composition in an ecological context.

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