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Temperature effect on survival, growth, and triacylglycerol content during the early ontogeny of *Mytilus edulis* and *M. trossulus*

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ABSTRACT: Temperature is a major factor contributing to the biogeography of intertidal poikilotherms. The population dynamics of intertidal invertebrates like mussels are strongly dependent on larval supply and larval mortality. Unlike adults, which are resistant to fluctuating environmental conditions, larvae are highly sensitive to the physicochemical conditions of the pelagic zone. The effects of rearing temperature on larval and post-larval performance of 2 coexisting mussels species, *Mytilus edulis* and *M. trossulus*, were examined in this study. In the first experiment, larvae of both species were reared separately at constant temperatures of 10, 17, and 24°C from D-larvae to the dissoconch stage. In the second experiment, pediveligers were reared under the same experimental conditions as the larvae for 2 wk. Survival, growth, and lipid composition (triacylglycerol [TAG] and sterol [ST] contents) were used to compare the performance of both species. The first experiment showed a species-specific thermal tolerance range, reflecting the biogeography of the species. *M. trossulus* larvae showed a preference for water at 10 and 17°C, corresponding to the more northerly distribution of this species, whereas *M. edulis* preferred temperatures of 17 and 24°C. Moreover, the TAG content in larvae of both species varied with temperature, supporting the hypothesis of a positive correlation between energy reserve content and the survival of mussel larvae. In contrast, the species-specific characteristics of thermal tolerance were not observed during post-larval development, suggesting that the selective effect of temperature on mussel species occurs during early ontogeny.

KEY WORDS: Thermal adaptation · Bivalve mollusk · Selection · Biogeography · Lipid · Larval ecology

INTRODUCTION

The distribution patterns of organisms are generally constrained by temperature (Sarver & Foltz 1993, Jones et al. 2009). Thus, in moving from lower to higher latitudes, species replacement patterns are ubiquitous and may involve the substitution of a species by a congener. Temperature affects essentially every aspect of an organism's physiology, particularly in ectothermic animals (Hochachka & Somero 2002, Fields et al. 2006). For example, temperature alters rates of chemical and enzymatic reactions, rates of diffusion, membrane fluidity, and protein structure. Therefore, each species occupies a particular thermal niche within which it functions well, but outside of which it may fail to survive (Hochachka & Somero 2002).

Blue mussels of the genus *Mytilus* are eurythermal suspension-feeding bivalve molluscs of the temperate regions of both the northern and southern hemispheres (Hutchins 1947, Gosling 1992). Along the Atlantic coast of North America, this genus is represented by the species *M. edulis* and *M. trossulus* (Koehn et al. 1984, Varvio et al. 1988, McDonald et al. 1991). *M. edulis* extends from Newfoundland and Labrador (Canada) to North Carolina (USA), while *M. trossulus* is restricted to sub-polar areas; the southern distribution limit for this species is the Gulf of Maine (e.g. Rawson et al. 2001). Populations of both

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species coexist in the Gulf of St. Lawrence (Varvio et al. 1988, Mallet & Carver 1995, Comesaña et al. 1999, Innes & Bates 1999, Moreau et al. 2005) and along the east coast of Maine, USA (Rawson et al. 2001).

The mussel *Mytilus trossulus* is traditionally considered to be a cold-water species due to its more northern distribution, whereas *M. edulis* is believed to prefer warmer habitats (Koehn 1991). However, the effect of temperature per se on the survival and growth of *M. edulis* and *M. trossulus* has rarely been investigated. The only information available from the scientific literature suggests that temperature is likely to explain the biogeographical distribution of these 2 mussel species, reflecting physiological adaptation. For example, adult *M. trossulus* are more tolerant to low temperatures than *M. edulis* and the closely related *M. galloprovincialis*, as evidenced by the capacity of *M. trossulus* for sustaining heart rate activity at low temperatures (Braby & Somero 2006). In addition, adult *M. trossulus* and its southern congener *M. galloprovincialis* acclimated to laboratory conditions at 13°C exhibit different levels of ubiquitinated proteins and amounts of endogenous heat shock proteins (hsp70), and display variations in the induction of stress-protein synthesis (Hofmann & Somero 1996). These results provide evidence that these 2 mussel species are physiologically different with respect to temperature.

The range of thermal tolerance is often narrowest in the early stages of development for a large variety of marine species (Bayne 1965, 1976). During the early ontogeny of *Mytilus edulis* and *M. trossulus*, Hayhurst & Rawson (2009) observed that the mortality of *M. trossulus* is generally higher compared to *M. edulis* when exposed to a temperature of 20°C, therefore reflecting the biogeographical distributions of these 2 species. Yaroslavtseva & Sergeeva (2006) applied various temperature challenges during the development of *M. trossulus* from the blastula to veliger stages. They noted that only 12.5‰ of larvae developed to the veliger stage at 4°C and that the best development and growth rates were observed at 20°C. Nevertheless, they suggested that the high phenotypic variability of morphological characteristics observed at 20°C represented strong evidence that this temperature was not optimal for *M. trossulus* larvae. Their experiment on larval temperature preference in a stratified column supported these observations, showing a concentration of veliger larvae in water layers with temperatures below 15°C (Yaroslavtseva & Sergeeva 2003).

We investigated the effect of temperature on survival, growth, and lipid composition of *Mytilus edulis* and *M. trossulus* during their early ontogeny and post-larval stages. Specimens of the 2 species were reared in the laboratory at constant temperatures of 10, 17, and 24°C from D-larvae to post-larvae. The selected temperatures are threshold values for both mussel species. Indeed, 10°C represents the minimum at which larvae of *M. edulis* grow (Bayne 1965), and 17°C is an optimal temperature for rearing *M. edulis* larvae. Also, it has been noted that *M. trossulus* is sensitive to temperatures higher than 16°C (Hofmann & Somero 1995), while no stress responses for *M. edulis* at 20°C were observed in Newfoundland (Thompson & Newell 1985). Finally, at temperatures higher than 18°C, the growth rate of *M. edulis* larvae decreases compared to that of animals maintained at lower temperatures, and at 25°C, the development of veligers is arrested (Bayne 1976). We chose to work on larvae because they are highly sensitive to their environment, and larval tolerance to water characteristics can be species-specific (e.g. Qiu et al. 2002). Moreover, mussel population dynamics are strongly influenced by larval supply (Gaines & Roughgarden 1985, Caley et al. 1996, Dudas et al. 2009). Thus, environmental stress, larval dispersal, and biotic interactions, all of which affect larval supply, influence the structure and dynamics of mussel communities. We focused our study on changes in lipid classes. On one hand, bivalve larvae generally store large amounts of triacylglycerol (TAG) as the primary endogenous energy reserve to fuel basal metabolism and growth (Holland 1978, Gallager et al. 1986). The TAG level is also a predictor of survival in bivalve larvae (Pernet et al. 2004). On the other hand, *M. edulis* and the oyster *Crassostrea virginica*, 2 bivalve species with different temperature optima, show a contrasting use of TAG at low temperatures (Pernet et al. 2007).

Based on the biogeographical distribution of the 2 mussel species, we predicted that the survival of *Mytilus trossulus* would be lower at warm temperatures than that of *M. edulis*. We also hypothesized that growth, survival, and TAG content would vary with interspecific differences due to thermal adaptation at 10, 17, and 24°C.

MATERIALS AND METHODS

Rearing procedure. Eighty-five adult mussels (52 ± 1.3 mm, mean ± SE) were collected in May 2006 from nearly monospecific populations (Moreau et al. 2005) and transferred to the marine station of the Institut des Sciences de la Mer de Rimouski. Specimens of *Mytilus trossulus* were from the intertidal zone of Rivière-au-Renard (Québec, Canada; 48° 00′ N, 65° 20′ W, a location where *M. edulis* represents less than 20% of the mussel population), and specimens of *M. edulis* were obtained from a mussel farm located at House Harbour, Iles de la Madeleine, Canada (47° 25′ N, 61° 50′ W, where *M. trossulus* account for less than 4% of the mussel population, see Moreau et al. 2005). Mus-

sels used for spawning showed typical *M. edulis* and *M. trossulus* shell shape (McDonald et al. 1991, Mallet & Carver 1995). Species identities were confirmed using the nuclear DNA PCR-based marker Glu-5′ (Rawson et al. 1996). Mussels from each population were kept in separate 180 l tanks with flow-through seawater at 11.8 ± 1.3°C and 27.8 ± 0.7 salinity for 14 d before spawning. Mussels were continuously fed a 1:1:1 mixture (v/v/v) of *Isochrysis galbana*, *Pavlova lutherii*, and *Nannochloropsis occulata* at a total concentration of ~40 cells µl^{-1} (Cocktail-TMN, Nutrocean; see www.nutrocean.com/fr/produits-micro-algues.html). Spawning was individually induced by thermal shock from ~11 to 25°C. Gametes began to be released after 15 min, and adult mussels were transferred to 18°C filtered (1 µm) seawater to improve oocyte or sperm release. Gametes from 10 to 15 individuals of the same species were mixed at a ratio of 20 spermatozoids oocyte^{-1}, and the fertilized eggs were left undisturbed at 18°C for 12 h in 180 l tanks at densities of 30 × 10^6 eggs tank^{-1}. Trochophore larvae were then gently siphoned into another 180 l tank and maintained in the water column with light aeration. After 2 d, 80% of the larvae had reached the D-larva stage and were collected on a 20 µm mesh screen. Larvae were kept at a density of 20 ind. ml^{-1} in 1 µm filtered seawater treated with UV. Water was gently aerated with 0.2 µm filtered air, and water and food were renewed every 2 to 3 d. Larvae were fed with the same microalgae mixture used for adults at a concentration ~30 cells µl^{-1}. A stock of D-larvae was used for the first experiment. The remaining D-larvae were cultured at 18.7 ± 0.6°C and 28.1 ± 1.1 salinity to obtain the pediveliger larvae for the second experiment. Separate sets of experimental materials were used for each species to avoid any potential cross-contamination.

Experimental design. ***Expt 1:*** Mussel larvae were maintained at 10 ± 1.1°C, 17 ± 0.1°C, and 24 ± 1.3°C from D-stage until the dissoconch stage. Each temperature treatment was applied to two 37 l water bath aquaria that contained nine 1 l jars. Water bath aquaria for a given temperature contained either 4 jars with *Mytilus edulis* and 5 jars with *M. trossulus* or vice versa. Each aquarium had its own filtration, aeration, and temperature control unit (6-Pack Arctic model, Aquabiotech). Temperature was monitored continuously, salinity was maintained constant at 28 ± 1.3, and the natural photoperiod was followed.

Mussel larval growth and survival were measured in each jar every 5 d. Lipid class composition was measured first, prior to the experiment on eggs, and then 3 times on animals from 3 jars for each combination of species and temperature. The 3 jars were randomly selected from the 2 aquaria. The entire content of each jar was filtered onto Whatman GF/C filters pre-combusted at 450°C and stored in lipid-free amber glass vials with Teflon-lined caps under nitrogen in 1 ml dichloromethane at −80°C for a maximum of 3 mo. The 3 ages for lipid analyses were 280, 500, and 600 degree days (dd), which corresponded to the veliger, pediveliger, and dissoconch developmental stages, respectively (Table 1).

Expt 2: Pediveliger larvae of *Mytilus edulis* and *M. trossulus* originating from the 180 l tanks were transferred for settlement and metamorphosis to 24 sieves that were placed in 6 aquaria (4 sieves aquarium^{-1}, 12 sieves species^{-1}). Aquaria were maintained at 10 ± 0.9°C, 17 ± 0.3°C, and 24 ± 1.4°C in duplicate for 2 wk. Each sieve (8 cm in height, 4 cm in diameter) had a base of 132 µm Nitex mesh and contained 5000 larvae. Growth, survival, and lipid class composition were measured in larvae within each sieve at the end of the experimental period following the same methods used in Expt 1.

Survival and growth. Shell length (SL; greatest anterior–posterior dimension) and percent survival (number in sample/initial number × 100) were monitored at each water renewal. Each batch was concentrated to 100 ml and gently homogenized. A 1 ml subsample was removed and placed into a well to determine the concentration of live larvae using an Olympus SZ61 binocular microscope. Afterwards, formaldehyde (4%) was added and SL measured at 400× using an Olympus BX41 microscope coupled with a color camera (Evolution VF, MediaCybernetics) equipped with Image-Pro express V5.1 software (Media Cybernetics). At least 30 larvae aquarium^{-1} were measured at each sampling date. These data were used to determine mean (±SD) SL for each sample.

Lipid analyses. Prior to lipid extraction, samples were ultrasonicated as described by Pernet et al. (2003a). Lipid extraction was based on the modified

Table 1. *Mytilus edulis* and *M. trossulus*. Summary of the sampling dates and experimental designs used for Expts 1 and 2

Expt	Degree days	Stage	Temperature (°C)			
			10	17	24	18.7
1	0	Spawning				9 June
	78	Beginning of treatment				14 June
	280	Veliger	5 July	26 June	23 June	
	500	Pediveliger	26 July	9 July	2 July	
	600	Dissoconch	6 August	15 July	6 July	
2	0	Spawning				9 June
	450	Pediveliger				4 July
	680	Juvenile	27 July	18 July	14 July	

Folch method (Folch et al. 1957) as described by Parrish (1987). Extracted lipids were spotted onto S-III Chromarods (Iatron Laboratories) for thin layer chromatography (Parrish 1987). Chromarods were scanned by a flame ionization detection system (FID; Iatroscan Mark-VI, Iatron Laboratories). Integration software (Peak Simple version 3.2, SRI) was used to analyze chromatograms of each lipid class as described by Parrish (1999).

Data analysis. ***Expt 1:*** Differences in SL and larval survival between 2 species and among 3 temperature treatments were tested with 3-way split-split plot analyses of variance (ANOVAs). The main plot was temperature level, subplot was species, and sub-subplot was age. The effects of temperature and species on TAG and sterol (ST) content were analyzed for different ontogenic stages (veliger, pediveliger, dissoconch) with 3-way split-plot ANOVAs. The main plot was temperature level, and subplots were species and ontogenic stage.

Expt 2: Differences in biometric parameters and lipid contents between the 2 species and among 3 temperature treatments were tested with 2-way split-plot ANOVAs. Residuals were tested using Shapiro-Wilk and Kolmogorov-Smirnov tests (Sokal & Rohlf 1997). Homogeneity of variance was graphically assessed. When necessary, data were log (x + 1) transformed to achieve normality of residuals and homogeneity of variances. Where differences were detected, least-square means multiple comparison tests were used to determine which means were significantly different. Analyses were carried out using the mixed procedure in SAS 9.1.3 (SAS Institute).

Table 2. *Mytilus edulis* and *M. trossulus*. Results of the 3-way split-split plot analyses of variances (ANOVAs) examining the effects of temperature and age on survival rate and shell length of mussel larval stages. Independent variables were temperature (Temp: 10, 17, and 24°C), mussel species (Sp.: *M. edulis* and *M. trossulus*), and age (8 dates between 16 June and 2 August 2006). Significant p-values ($p < 0.05$) are shown in **bold**

Source of variation	Larval survival df	*F*	p	Shell length df	*F*	p
Main plot analysis						
Temp	2	1434.8	**<0.001**	2	1.2	0.397
Error A	3			3		
Subplot analysis						
Sp.	1	31.6	**<0.001**	1	3.3	0.074
Sp. × Temp	2	698.7	**<0.001**	2	2.1	0.133
Error B	45			45		
Sub-subplot analysis						
Age	8	998.1	**<0.001**	7	261.4	**<0.001**
Age × Temp	14	55.0	**<0.001**	14	3.5	**<0.001**
Age × Sp.	8	3.8	**0.001**	7	1.9	0.062
Age × Temp × Sp.	14	30.5	**<0.001**	12	1.4	0.160
Error C	275			275		

RESULTS

Expt 1

Temperature, species, and age showed interactions in their effects on mussel larval survival (Table 2, Fig. 1). At 24°C, *Mytilus edulis* survival was consistently higher than that of *M. trossulus*. At 17°C, survival of both species was similar until 270 dd, when *M. edulis* showed a slightly higher survival than *M. trossulus*. Finally, at 10°C, the survival of *M. edulis* was lower than that of *M. trossulus* for the entire experiment.

For *M. edulis*, 17°C was the optimal temperature of the 3 tested. Indeed, the final survival of *M. edulis* at 17°C was 74% compared to <46% in the other temperature treatments. In contrast, the highest survival of *M. trossulus* was observed at both 17 and 10°C. *M. trossulus* survival was the lowest at 24°C (19% by the end of the experiment).

Age and temperature interacted in their effect on SL (Table 2, Fig. 2). From 200 dd until the end of the experiment, mussel larvae grew in similar patterns regardless of the temperature. High mortalities for *Mytilus edulis* larvae exposed to 10°C forced the end of the experiment before 400 dd for these samples. As shown in previous studies (e.g. Bayne 1976), growth rate of both mussel species was positively correlated with temperature: 7 µm d^{-1} at 24°C, 5 µm d^{-1} at 17°C, and 3 µm d^{-1} at 10°C.

Temperature and development stage interacted in their effect on TAG content (Table 3, Fig. 3A). TAG concentration increased during ontogeny, except that it did not vary significantly throughout larval development at 24°C. TAG contents for pediveliger and dissoconch larvae exposed to 10°C and for veligers reared at 24°C were similar to levels observed in eggs. Moreover, the correlation between TAG concentration and temperature was positive for veligers and negative for pediveligers while the TAG content remained constant for dissoconch larvae at all temperatures. The temperature × species interaction was also detected for larval TAG content (Table 3, Fig. 3B). At 10 and 17°C, there was no difference between the TAG content of both species. In contrast, the TAG concentration of *Mytilus edulis* at 24°C was 4.1 times higher than that of *M. trossulus*.

ST content was only influenced by larval stage, regardless of temperature or species (Table 3). Overall, mean (±SD) ST content was 0.5 ± 0.3 ng $veliger^{-1}$, 1.4 ± 0.3 ng $pediveliger^{-1}$, and 2.0 ± 0.3 ng $dissoconch^{-1}$.

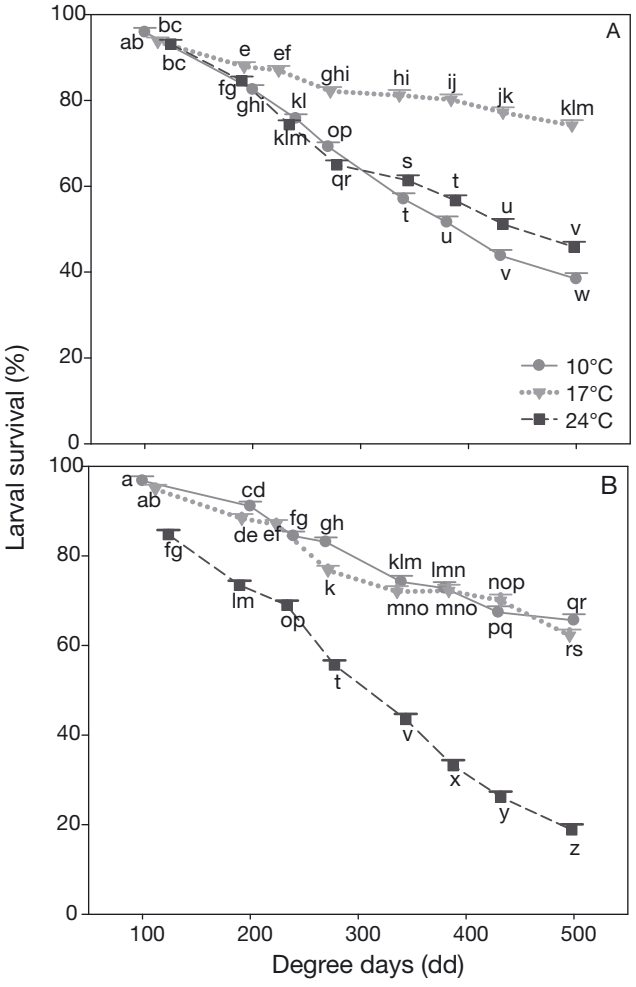

Fig. 1. *Mytilus edulis* and *M. trossulus*. Survival rate of (A) *M. edulis* and (B) *M. trossulus* larvae as a function of temperature and age in degree days. Different letters indicate significant differences. Data are mean ± SD between jars (n = 3)

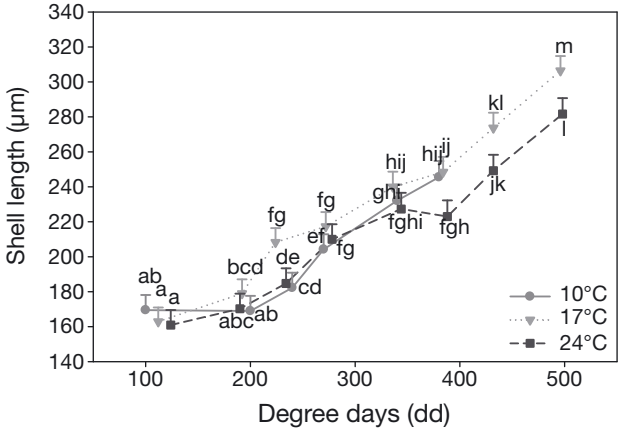

Fig. 2. *Mytilus edulis* and *M. trossulus*. Shell length of mussel larvae as a function of temperature and age in degree days. Different letters indicate significant differences. Data are mean ± SD between jars (n = 3). At least 30 individuals were measured in each jar when possible

Table 3. *Mytilus edulis* and *M. trossulus*. Results of the 3-way split-plot analyses of variances (ANOVAs) examining the effects of temperature, species, and age on triacylglycerol (TAG) and sterol (ST) contents (ng larva^{-1}) of larval stages. Independent variables were temperature (Temp: 10, 17, and 24°C), mussel species (Sp.: *M. edulis* and *M. trossulus*), and ontogenic stage (veliger, pediveliger, and dissoconch). Significant p-values ($p < 0.05$) are shown in **bold**. The data were log ($x + 1$) transformed to achieve homogeneity of variances

Source of variation	df	TAG		ST	
		F	p	*F*	p
Main plot analysis					
Temp	2	3.1	0.187	5.8	0.094
Error A	3				
Subplot analysis					
Sp.	1	0.4	0.511	0.4	0.559
Stage	2	5.6	**0.009**	5.1	**0.013**
Sp. × Stage	2	2.7	0.083	0.3	0.770
Temp × Sp.	2	4.0	**0.030**	0.8	0.472
Temp × Stage	4	3.7	**0.015**	0.9	0.491
Temp × Sp. × Stage	4	<0.1	0.999	0.8	0.542
Error B	27				

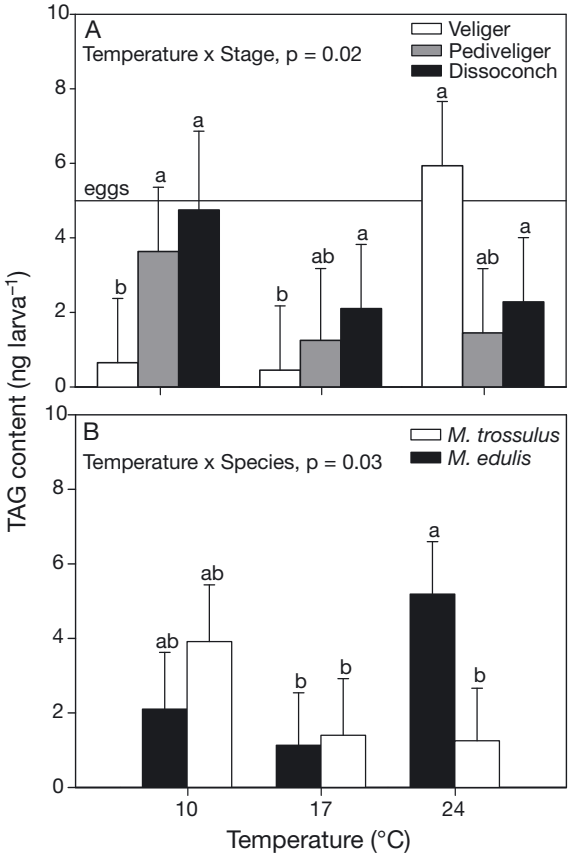

Fig. 3. *Mytilus edulis* and *M. trossulus*. Triacylglycerol (TAG) content of mussel larvae as a function of (A) temperature × stage and (B) temperature × species. Different letters indicate significant differences. Data are mean ± SD between aquaria (n = 3). The reference line in (A) represents the initial level of TAG content observed in eggs

Expt 2

Temperature × species interactions were observed for SL in post-larvae (Table 4, Fig. 4). The shell size of *Mytilus edulis* was ca. 1.2 times smaller than that of *M. trossulus* except at 17°C, where they were similar. Moreover, *M. trossulus* showed differences in SL among temperatures (354 ± 11 µm at 10°C and 383 ± 14 µm at 24°C), while the SL of *M. edulis* was the same at all temperatures.

In contrast to measurements of SL, TAG and ST contents as well as survival in post-larvae were not influenced by temperature and/or species (Table 4). Overall, TAG concentration was 2.4 ± 0.4 ng ind.$^{-1}$, ST content was 1.3 ± 0.2 ng ind.$^{-1}$, and the average survival rate was 84 ± 1%.

DISCUSSION

Our study suggests that the thermal tolerance range of mussel larvae is species-specific. *Mytilus trossulus* had lower survival than *M. edulis* at 24°C, the warmest temperature we tested. In contrast, *M. trossulus* showed higher survival than *M. edulis* at 10°C, the lowest temperature in these experiments. These survival patterns that varied as a function of temperature reflect the distribution of *M. trossulus* and *M. edulis* in the field. *M. trossulus* in the North Atlantic region is restricted to the cooler waters of the Labrador Current and the Baltic Sea, whereas it is found from southern Alaska to central California on the Pacific coast of North America (Varvio et al. 1988, McDonald et al. 1991, Gosling 1992, Rawson et al. 2001). Although the northern distribution limit of *M. edulis* has never been well established, it appears that this species occurs at more southern latitudes compared to *M. trossulus* (Rawson et al. 2001). Therefore, the species-specific adaptation to temperature that we observed in larval survival rates conforms to predictions based on the biogeography of the species.

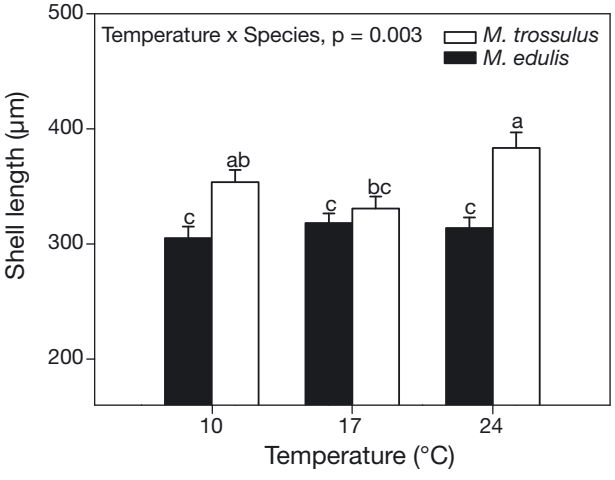

Fig. 4. *Mytilus edulis* and *M. trossulus*. Shell length of mussel post-larvae as a function of temperature and species. Different letters indicate significant differences. Data are mean ± SD between sieves (n = 5). At least 30 individuals were measured in each sieve

Our results also indicate that temperature influences mussel mortality during the larval stage but not during post-larval development. Consequently, the selective pressure of temperature on mussel populations likely acts predominantly during early ontogeny. This result agrees with the observations of Bayne (1965, 1976) concerning temperature effects on development quality. Similarly, Qiu et al. (2002) observed that a species-specific response to hyposaline stress occurred mostly during larval stages while juveniles and adults were less sensitive. For the first time, we show that temperature, one of the most important factors contributing to the biogeography of sessile marine species, acts during the early ontogeny of *Mytilus edulis* and *M. trossulus* while later ontogenic stages seem to be more resistant.

At 24°C, *Mytilus trossulus* showed low TAG levels compared to *M. edulis,* which survived better at this temperature. This observation supports the hypothesis of a positive correlation between energy reserve contents and survival of mussel larvae. Several authors have suggested that the lipid content of bivalve larvae may be an indicator of physiological condition and of the potential for successful metamorphosis, since lipid is the primary endogenous energy reserve fuelling

Table 4. *Mytilus edulis* and *M. trossulus*. Results of the 2-way split-plot analyses of variances (ANOVAs) examining the effects of temperature, species, and age on survival, shell length, and triacylglycerol (TAG) and sterol (ST) contents on post-larval stages (ng ind.$^{-1}$). Independent variables were temperature (Temp: 10, 17, and 24°C) and mussel species (Sp.: *M. edulis* and *M. trossulus*). Significant p-values ($p < 0.05$) are shown in **bold**. For biochemical analyses, the data were log ($x + 1$) transformed to achieve a normal distribution

Source of variation	df	Survival		Shell length		TAG		ST	
		F	p	*F*	p	*F*	p	*F*	p
Temp	2	0.1	0.942	2.1	0.267	1.5	0.353	1.2	0.417
Sp.	1	1.4	0.258	39.5	**<0.001**	0.2	0.629	0.6	0.446
Temp × Sp.	2	3.3	0.067	6.0	**0.003**	0.6	0.559	1.0	0.409

basal metabolism (Gallager et al. 1986, Fraser 1989). Furthermore, sea scallop survival at competency was partly explained by the efficiency of lipid recovery after embryogenesis (Pernet et al. 2003b). Therefore, our study is in good accordance with the existing scientific literature linking energetic reserves of TAG and survival in bivalve larvae. At 10°C, TAG levels in *M. edulis* were similar to those in *M. trossulus,* which survived better at this temperature. Therefore, in contrast to the observation made at 24°C, it seems that there is no relation between energetic reserves of TAG and survival between the 2 mussel species at this temperature. However, this apparently paradoxical result has to be tempered by the fact that there is a trend for TAG levels to be higher in *M. trossulus* than in *M. edulis*. Indeed, the average TAG content in *M. edulis* was 2.1 ± 1.5 ng larvae^{-1} compared to 3.9 ± 1.5 ng larvae^{-1} in *M. trossulus.*

Moreover, our results indicate that TAG content increased during the larval ontogeny of mussels maintained at 10 and 17°C, irrespective of the species. This result agrees well with other studies showing that TAG reserves are gradually accumulated during larval ontogeny prior to metamorphosis (Gallager et al. 1986, Delaunay et al. 1992, Pernet et al. 2006). Intriguingly, veligers maintained at 24°C showed higher TAG levels compared to those maintained at 10 and 17°C, and higher levels compared to later ontogenic stages. Although speculative, it is likely that mussels maintained at 24°C, which showed growth rates similar to those maintained at 10 and 17°C during their early development, displayed higher clearance and assimilation rates than mussels maintained at lower temperature regimes and thus their energetic reserves were higher. Although there is no comparative study on ingestion rates of *M. edulis* and *M. trossulus* reared at different temperatures, several studies on the physiology of bivalve larvae can be used to substantiate this speculation. For example, there is an increase in filtration rate of *M. edulis* larvae between 11 and 18°C with a Q_{10} of 3.2 (Bayne 1965). This was corroborated by Sprung (1984a,b), who show that temperature strongly influences ingestion, filtration, and growth between 6 and 12°C and to a lower extent between 12 and 18°C. More recently, it was reported that the ingestion rate of oyster larvae *Crassostrea gigas* increases with temperatures between 17 and 32°C (Rico-Villa et al. 2009).

Finally, our study showed that the growth rate of mussel larvae increased with temperature, as previously reported for post-larvae and adults (Almada-Villela et al. 1982, Pechenik et al. 1990). Moreover, the growth rates of *Mytilus edulis* and *M. trossulus* are similar irrespective of temperature. From an ecological standpoint, this result suggests that the 2 species spend the same amount of time in the water column. Thus, on one hand, the selective pressures that act on veliger larvae during the pelagic stage, such as predation, are the same. On the other hand, the dispersal potential could be similar for both species in the case of overlapping spawning periods in zones where the 2 species are found, contributing to their competition in the pelagic zone.

This similarity in growth rates irrespective of the temperature is not constant for all species of the *Mytilus* complex. Beaumont et al. (2004) observed faster growth for *M. galloprovincialis* larvae compare to *M. edulis* and their hybrids irrespective of the temperature tested (10, 14, and 20°C), while we observed no difference in the growth of *M. edulis* and *M. trossulus* for a comparable range of temperatures.

In conclusion, our study showed for the first time the selective effect of temperature on mussel larvae. *Mytilus edulis* and *M. trossulus* larvae had different survival rates that were related to temperature, whereas juveniles were not affected. This result suggests that the coexistence and competition of these species are driven by the effect of temperature during larval ontogeny. Although larvae of both species spend the same length of time as plankton, selection related to temperature will favor 1 species or the other. Thus not only is temperature an important factor in the distribution of benthic organisms (Sarver & Foltz 1993, Jones et al. 2009), but it also controls the dynamics of these communities even before the organisms have reached the benthic compartment.

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