

## Potential for production of ‘mini-mussels’ in Great Belt (Denmark) evaluated on basis of actual and modeled growth of young mussels *Mytilus edulis*

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**Abstract** The present study is a first step towards evaluation of the potential for line-mussel production in the Great Belt region between the Kattegat and Baltic Sea, Denmark. We present experimental results for actual growth rates of juvenile/adult mussels *Mytilus edulis* in suspended net bags in terms of shell length and dry weight of soft parts during extended periods (27–80 days) in the productive season in the first 6 series of field experiments, including 4 sites in Great Belt and 2 sites in Limfjorden, Denmark. Data were correlated and interpreted in terms of specific growth rate ( $\mu$ , % day<sup>-1</sup>) as a function of dry weight of soft parts ( $W$ , g) by a previously developed simple bioenergetic growth model  $\mu = aW^{-0.34}$ . Results were generally in good agreement with the model which assumes the prevailing average chlorophyll *a* concentration at field sites to essentially account for the nutrition. Our studies have shown that *M. edulis* can grow from settlement in spring to 30 mm in shell length in November. We therefore suggest line farming of 30 mm ‘mini-mussels’ during one growth season, recovering all equipment at the time of harvest and re-establishing it with a new population of settled mussel larvae at the beginning of the next season, thus protecting the equipment from the damaging weather of the Danish winter season. The growth behavior during the fall–winter season was recorded in an additional 7th series of mussel growth experiments on farm-ropes to show the disadvantage of this period.

**Keywords** Energy budget · Bioenergetic growth model · Specific growth rate · Doubling time · Chl *a* · Pelagic biomass · Line-mussels

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## Introduction

Bivalve aquaculture is of increasingly economic importance, and about 50 % of the annual worldwide harvest of mussels comes from Europe where the main yields of the Atlantic blue mussel (*Mytilus edulis*) and the Mediterranean mussel *M. galloprovinciales* are from Spain, France, The Netherlands, and Denmark (Smaal 2002; Buck et al. 2010). In Denmark, the mussel production mainly comes from fishery on wild stocks of *M. edulis* in Limfjorden with annual landings of 80,000–100,000 t in the 1990's (Kristensen 1997; Dolmer and Frandsen 2002), resulting in overfishing and a subsequent reduction of the mussel stock (Kristensen and Hoffmann 2004; Dolmer and Geitner 2004), and in 2006–2008, the mussel fishery declined to about 30,000 tons per year (Dinesen et al. 2011) which led to restrictions and a national policy that aims at developing a sustainable production of cultured mussels in balance with the extensive fishery of mussels (Dinesen et al. 2011). In recent years, the total annual Danish mussel harvest has been around 35,000 tons, with 70 % coming from Limfjorden (data available at [http://naturerhvrv.fvm.dk/landings-\\_og\\_fangststatistik.aspx?ID=24363](http://naturerhvrv.fvm.dk/landings-_og_fangststatistik.aspx?ID=24363)). Because eutrophication and seasonal oxygen depletion cause high mortality of bottom-living wild mussels during late summer, especially in the central parts of Limfjorden, line-mussel farming has recently been introduced to increase the production of mussels and to mitigate the temporary habit disturbance of mussel dredging (Dolmer et al. 1999; Ahsan and Roth 2010; Dinesen et al. 2011). An alternative solution to the problems with mussel dredging and farming in the eutrophicated Limfjorden and other shallow Danish fjords may be the use of more open and deeper marine areas for cultivation of mussels. Thus, the aim for the MarBioShell project (2008–2012) has been to evaluate the potential of the Great Belt region between the Kattegat and the Baltic Sea as a new line-mussel cultivation site to relieve some of the pressure on the vulnerable Limfjorden and to cover an increasing demand for blue mussels. Deeper water and faster current speeds in the Great Belt are likely to prevent the environmental problems encountered in Limfjorden, although a mean salinity in the Great Belt, being approximately half of that in Limfjorden, may reduce the growth of mussels. The wild blue mussels in the Great Belt have never been commercially exploited (no official landing statistics) and the mussel stocks have not been assessed. The present study is a first step towards evaluation of the potential for mussel production in the Great Belt region based on field experiments analyzed and interpreted by a bioenergetic growth model (BEG) introduced by Clausen and Riisgård (1996) and further developed by Riisgård et al. (2012a, 2013a) and Larsen et al. (2013). In addition an important by-product of the present study has been the consequent further testing of the bioenergetic growth model because it could assist in evaluating the growth potentials at different locations in the Great Belt and other Danish waters. Further, because the growth model assumes that the prevailing average chlorophyll *a* (chl *a*) concentration accounts for the nutrition, the possible role of heterotrophic plankton (without chl *a*) as supplementary diet has been evaluated.

## Methods

### Bioenergetic growth model

The growth (production) of a mussel may be predicted from the difference between assimilated food energy and metabolic energy expenses, here limited to the seasonal growth ignoring energy loss due to spawning. Thus, equating the rate of net intake of

nutritional energy to the sum of various rates of consumption, the energy balance for the growing organism may be written as (see earlier development by Clausen and Riisgård 1996; Riisgård et al. 2012a, 2013a; Larsen et al. 2013),

$$G = [(F \times C \times AE) - R_m] / a_0 \tag{1}$$

where  $F$  is the filtration rate (= clearance, assuming 100 % retention),  $C$  the algal concentration,  $AE$  the assimilation efficiency ( $AE = 1 - \text{excretion/ingestion}$ , excretion: feces + urine, e.g. Jørgensen 1990),  $R_m$  the maintenance respiratory rate. The constant  $a_0$  (=1.12) follows from the experience that the metabolic cost of growth (i.e., synthesis of new biomass) constitutes an amount of energy equivalent to 12 % of the growth (biomass production) (Clausen and Riisgård 1996). Because the filtration rate ( $F$ ,  $l\ h^{-1}$ ) of *Mytilus edulis* can be estimated from the dry weight of soft parts ( $W$ , g) according to  $F = a_1 W^{b_1}$ , ( $a_1 = 7.45$ ;  $b_1 = 0.66$ , Møhlenberg and Riisgård 1979) and the maintenance respiratory rate ( $R_m$ ,  $ml\ O_2\ h^{-1}$ ) can be estimated according to  $R_m = a_2 W^{b_2}$ , ( $a_2 = 0.475$ ;  $b_2 = 0.663$ , Hamburger et al. 1983), the growth rate may now be expressed as,

$$G = (C \times AE \times a_1 - a_2) W^{b_1} / a_0 = a W^{b_1}, \tag{2}$$

where  $b_1 \approx b_2 = 0.66$  has been used. Thus, the resulting semi-empirical BEG for weight-specific growth rate ( $\mu = G/W = aW^{b_1}/W$ ) may now be expressed as

$$\mu = aW^b, (a = 0.871 \times C - 0.986; b = -0.34), \tag{3}$$

where units are  $\mu$  in  $\% \text{ day}^{-1}$ ,  $W$  in g dry weight of soft parts, and  $C$  in  $\mu\text{g chl } a\ l^{-1}$ .

The constants in Eq. (3) are obtained from use of the cited formulas above for filtration and respiration, assuming the value of  $AE = 80\ \%$  (although  $75\ \%$  has been suggested by Rosland et al. 2009, Table 1 therein), and use of the following conversion factors: (a)  $1\ ml\ O_2 = 19.88\ J$ ; (b) energy of *Rhodomonas salina*, equivalent to  $1.75\ \mu\text{J cell}^{-1}$  (Kiørboe et al. 1985); (c)  $1\ mg$  dry weight of soft parts of *M. edulis* =  $20.51\ J$  (Dare and Edwards 1975); (d)  $1\ \mu\text{g chl } a\ l^{-1} = 1/(1.251 \times 10^{-3}) = 799\ Rhodomonas\ salina\ cells\ ml^{-1}$  (Clausen and Riisgård 1996).

### Equations of data analysis

The condition index (CI) of the mussels at given times during growth was calculated from the dry weight of soft parts ( $W$ , mg) and the shell length ( $L$ , cm) according to the formula:

$$CI = W/L^3 \tag{4}$$

According to the definition,  $dW/dt = \mu W$ , this may be integrated assuming a constant average value  $\mu_a$  ( $\text{day}^{-1}$ ) of weight-specific growth rate,

$$W_t = W_0 \exp(\mu_a t), \tag{5}$$

or

$$\mu_a = (\ln W_t - \ln W_0) / t \tag{6}$$

Therefore, considering a particular size group of mussels, the mean value of  $\mu$  for growth from  $W_0$  to  $W_t$  during period  $\Delta t = t - 0$  equals the slope of the linear regression line to a plot of  $\ln W$  versus  $t$ , or according to Eq. (5), as the coefficient in the exponent of an exponential regression to a plot of  $W$  versus  $t$  for  $\mu$  constant over the time period. Given

**Table 1** Coordinates of mussel growth sites, Danish national environmental monitoring stations, water depth, and distance/direction of monitoring stations relative to growth sites for mussels in net bags (Series #1 to #6) or on farm-ropes (Series #7)

Series	Growth site	Abbreviation	Coordinates	Monitoring station	Coordinates	Depth	Distance, direction
#1, #7	Kerteminde Bugt	GB-K	55°25.56N, 10°44.20E	ST53, close to Romsø (St. 1)	55°30.46N, 10°51.72 E	32 m	12.0 km, NE
#2	Musholm Bugt	GB-M	55°28.74N, 11°03.12E	ST53, close to Romsø (St. 1)	55°30.46N, 10°51.72E	32 m	12.3 km, W
#3	Svendborg Sund	GB-S	55°00.31N, 10°40.83E	Langelandssundet (St. 2)	53°03.96N, 10°48.12E	8.8 m	10.3 km, NE
#4	Karrebeksminde Bugt (Bisserup)	GB-B	55°07.36N, 11°29.13E	Karrebeksminde Bugt (St. 3)	55°06.87N, 11°41.16E	9.0 m	13.0 km, E
#5	Risgård Bredning (Hvalpsund)	L-H	56°42.63N, 09°12.15E	Løgstør Bredning (St. 4)	56°57.24N, 09°03.75E	7.1 m	28.2 km, N
#6	Salling Sund (Glyngøre)	L-G	56°45.03N, 08°51.60E	Salling Sund (temp./sal.) (St. 5)	56°44.56N, 08°50.58E	5.5 m	1.4 km, SW
				Nissum Bredning (chl <i>a</i> ) (St. 6)	56°36.05N, 08°24.89E	6.2 m	32.0 km, SW

several size classes of mussels at a given site, such  $\mu$ -values referred to corresponding average sizes  $W_{\text{avg}} = (W_0 \times W_t)^{1/2}$  leads to an experimentally determined relation of form:

$$\mu_a = a' W_{\text{avg}}^{b'} \quad (7)$$

which may be compared to Eq. (3) for growth according to the model. Finally, given  $\mu_a$  the time to double the size in terms of dry weight is obtained from Eqs. (5) or (6) for  $W_t/W_0 = 2$ ,

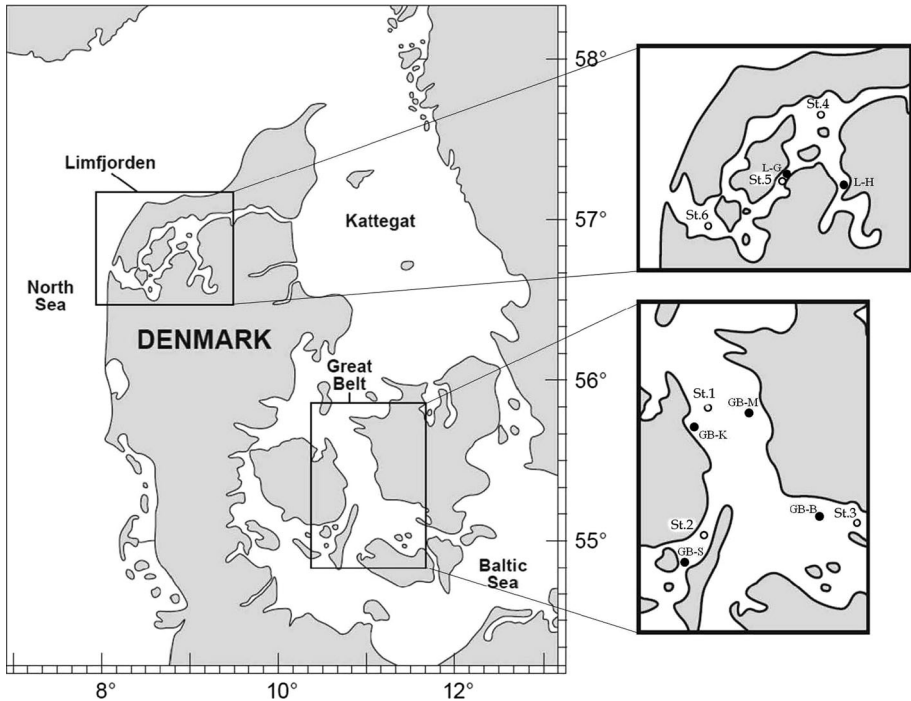
$$\tau_2 = \ln 2 / \mu_a \quad (8)$$

## Study areas

Main focus of the present study was on field growth experiments with mussels in net bags in the Great Belt (Denmark), but in order to evaluate the bioenergetic growth model and the potential for line-mussel farming in this area, it was found useful to conduct similar growth experiments in Limfjorden where the environmental conditions are rather different with regard to levels and changes in salinity, water current speeds, and chl *a* concentrations as it appears from the following two sections.

*Great Belt* is one of the Danish Straits that form the transition between the tidal North Sea and the non-tidal Baltic Sea (Fig. 1). The prevailing depths are 10–25 m along the sides of the deep (up to 70 m) winding main channel. The water exchange between the Baltic Sea and the open sea is driven both by the river run off and by the meteorological conditions over the North Sea–Baltic Sea area (Kullenberg and Jacobsen 1981). The freshwater supply to the Baltic Sea generates an outgoing brackish water surface current of less density than the more saline water from the Kattegat, and therefore, the Straits are permanently stratified. Thus, the surface salinity in the southeast Kattegat is low, less than 20 psu, whereas the salinity beneath the halocline at about 15 m depth is high, about 30–34 psu. Due to shifting winds, the water level difference between Kattegat and the western Baltic Sea is highly variable causing an oscillating flow through the Straits (Møller 1996). In the Great Belt, the salinity therefore varies according to changing flow situations. Outflow of water from the Baltic Sea gives salinities down to less than 10 psu, whereas inflow to the Baltic Sea gives salinities up to 27 psu in the upper layer of the Great Belt (Jürgensen 1995). The tides cause current speed in the surface layer on the order of 20–40 cm s<sup>-1</sup> and sea level fluctuations of about ±10–30 cm within a 12-h period. A combination of tides, wind, and atmospheric pressure causes the currents in the Great Belt which can be described as pulsating movements of the same body of water which does not, over a period of days or weeks, result a net transportation of water through the Great Belt. Normally, the actual current speed through the Great Belt is about 50 cm s<sup>-1</sup> (Funen 1991, p. 132 therein). The annual mean (±SD) chl *a* concentration measured in the period 2000 to 2010 at 1 m depth in the northern Great Belt was  $2.8 \pm 2.4 \mu\text{g l}^{-1}$ . For the same area from April to November (without including spring peaks and winter periods) the mean annual concentration was  $2.5 \pm 1.2 \mu\text{g chl } a \text{ l}^{-1}$ . There were between 35 and 50 sampling days distributed throughout the years. (Data supplied by Environmental Centre Odense, Danish Ministry of the Environment).

*Limfjorden* is a shallow water system that connects the North Sea in the west with the Kattegat in the east (Fig. 1). The mean water depth is about 4.5 m, the tidal amplitude is 10–20 cm, and vertical mixing is mainly wind driven. Westerly wind causes inflow of North Sea water in the west, whereas easterly wind results in inflow of Kattegat in the east.



**Fig. 1** Map of Denmark showing the locations for field growth experiments with *Mytilus edulis* hung up in net bags at different localities in Great Belt (Kerteminde Bugt = GB-K, Musholm Bugt = GB-M, Svendborg Sund = GB-S, Karrebæksminde Bugt = GB-B), and in Limfjorden (Risgård Bredning (Hvalpsund) = L-H, Salling Sund (Glyngøre) = L-G). Coordinates for mussels growth sites (*closed symbol*) and environmental monitoring stations (*open symbols*, St. 1–6) are presented in Table 1

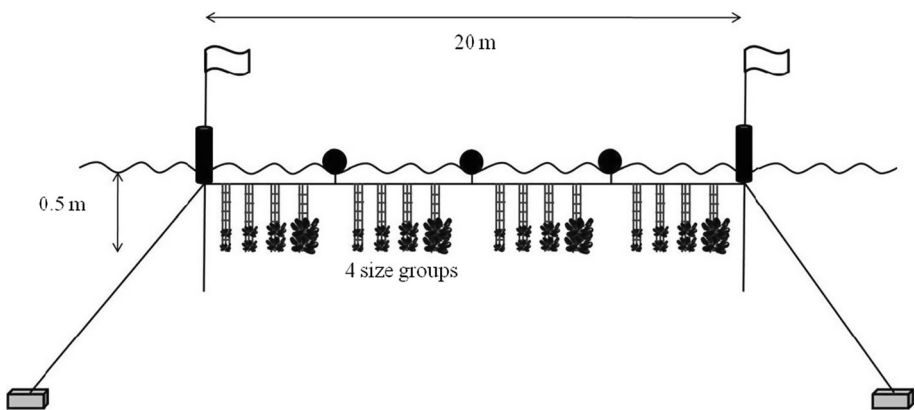
Between the west and east boundaries, there is a permanent horizontal salinity gradient having a salinity of 32–34 psu at the connection to the North Sea and 19–25 psu at the connection to the Kattegat (Wiles et al. 2006; Hofmeister et al. 2009). Limfjorden is eutrophic, receiving nutrient from the catchment area which is dominated by agriculture. The western part of Limfjorden is less eutrophicated and less stratified than the central northern part with intermediate stratified and eutrophic conditions, while the inner central southern part is strongly stratified and eutrophic which frequently results in oxygen depletion in the near-bottom water. The key factor determining the extent of oxygen depletion is the weather conditions during the summer months July through September where high temperatures coupled with low wind cause severe oxygen depletion, especially in areas with dense mussel beds (Jørgensen 1980; Dolmer et al. 1999; Møhlenberg 1999; Møhlenberg et al. 2007; Møller and Riisgård 2007; Maar et al. 2010; Dinesen et al. 2011). The water currents in Limfjorden are driven by horizontal water density gradients and the wind. The water current velocity 1 m above the bottom varies typically between <math><1</math> and \pmSD) chl *a* concentration in the period 1982–2006 in the central northern part of Limfjorden (Løgstør Bredning) was

depth on station was 7.3 m. (Data supplied by Environmental Centre Ringkøbing, Danish Ministry of the Environment).

### Experimental mussels and growth sites

Blue mussels, *M. edulis*, were collected in Limfjorden (Skive Fjord) and in the Great Belt (Kerteminde Bugt) (Fig. 1) about 2 weeks before the onset of 6 (Series #1 to #6) field growth experiments with different size groups of mussels in net bags transferred to various localities with different chl *a* concentration levels. In Great Belt, 4 locations: Kerteminde Bugt (Series #1), Musholm Bugt (Series #2), Svendborg Sund (Series #3), and Karrebæksminde Bugt (Series #4) (Fig. 1) were chosen for growth experiments with mussels from Kerteminde Bugt between slightly variable periods from 20 July to 8 October depending on location (Table 1). In Limfjorden, Risgård Bredning and Salling Sund (Fig. 1) were chosen, and on these locations, growth experiments with locally collected mussels were carried out during two periods: (Series #5) July 29 to August 25, 2010 and (Series #6) July 29 to September 21, 2010 (Table 1).

Before sorting of mussels in size groups, these were kept in aerated 1000-l tanks with running seawater from the inlet to Kerteminde Fjord (18–22 psu). Mussels were then cleaned, total shell length measured with a vernier gauge, sorted into 4 size groups (each with near identical shell length  $\pm 0.4$ –1.3 mm), and put into net bags (Go Deep International Inc.) before they were transferred to the field location and hung up in a buoy system (Fig. 2). The net bags were made of polypropylene fibers and cotton strings that rot away after about 1 week which result in an increase in mask width. This system enables mussels to settle firmly, and the subsequent disappearance of cotton strings ensure that the shell opening of the mussels does not become restricted. The widths of the masks for small mussels (20.8–31.0 mm shell length) were  $10 \times 10$  mm, and for larger mussels ( $>40.0$  mm shell length) were  $10 \times 15$  mm. The net bags were 50 cm long and placed approximately 1 m apart to avoid entanglement. Subsamples were subsequently collected with about 14 days interval from the buoy systems and transported to the Marine Biological Research Centre, Kerteminde, for analysis. Shell length was measured with a vernier gauge, soft parts removed from the shells, wet weight measured, and then drying



**Fig. 2** Buoy system with mussels (Series #1 to #6) in net bags used at 4 locations in Great Belt and 2 locations in Limfjorden (see Fig. 1)

**Table 2** *Mytilus edulis* (Series #1 to #6)

Series location period	$\Delta t$ (day)	Chl <i>a</i> ( $\mu\text{g l}^{-1}$ )	Temp. ( $^{\circ}\text{C}$ )	Salinity (psu)	$L_0$ (mm)	$L_g$ (mm day $^{-1}$ )	$W_0$ (mg)	$\mu$ (%day $^{-1}$ )	$W_{\text{avg}}$ (mg)	$\tau_2$ (day)
Series #1, GB-K Kerteminde Bugt 28 Jul to 7 Oct 2010	71	3.1 $\pm$ 0.7	16.0 $\pm$ 3.5	14.2 $\pm$ 3.4	20.8	0.149	41.2	3.3	138	21.0
					25.8	0.116	79.9	2.5	182	27.7
					30.8	0.104	91.6	2.6	231	26.7
					39.1	0.067	242.5	2.0	465	34.7
Series #2, GB-M Musholm Bugt 20 Jul to 8 Oct 2010	80	3.1 $\pm$ 0.7	16.0 $\pm$ 3.5	14.2 $\pm$ 3.4	21.0	0.123	41.7	2.9	98	23.9
					26.0	0.070	69.2	2.0	152	34.7
					30.8	0.060	115.6	1.7	230	40.8
					39.0	0.040	233.7	1.3	352	53.3
Series #3, GB-S Svendborg Sund 26 Jul to 13 Sep 2010	49	3.0 $\pm$ 2.8 <sup>a</sup>	17.5 $\pm$ 3.5	15.4 $\pm$ 1.8	21.2	0.183	41.2	3.6	111	19.3
					25.9	0.135	75.4	2.8	160	24.8
					31.0	0.129	105.1	2.9	234	23.9
					39.2	0.095	194.2	2.5	368	27.7
Series #4, GB-B Karrebæksmønde Bugt (Bisserup) 24 Jul to 7 Oct 2010	75	2.8 $\pm$ 2.1	17.1 $\pm$ 3.9	10.7 $\pm$ 1.1	21.3	0.125	42.9	2.4	71	28.9
					25.9	0.063	69.2	1.8	108	38.5
					30.6	0.060	102.3	1.8	168	38.5
					40.0	-0.003	203.2	1.1	259	63.0
Series #5, L-H Risgård Bredning (Hvalpsund) 29 Jul to 25 Aug 2010	27	3.6 $\pm$ 1.6	18.8 $\pm$ 1.5	26.9 $\pm$ 0.8	21.1	0.266	41.2	5.2	84	13.3
					25.9	0.215	74.9	4.0	129	17.3
					30.8	0.174	108.6	3.7	180	18.7
					39.4	0.100	199.8	2.8	292	24.8



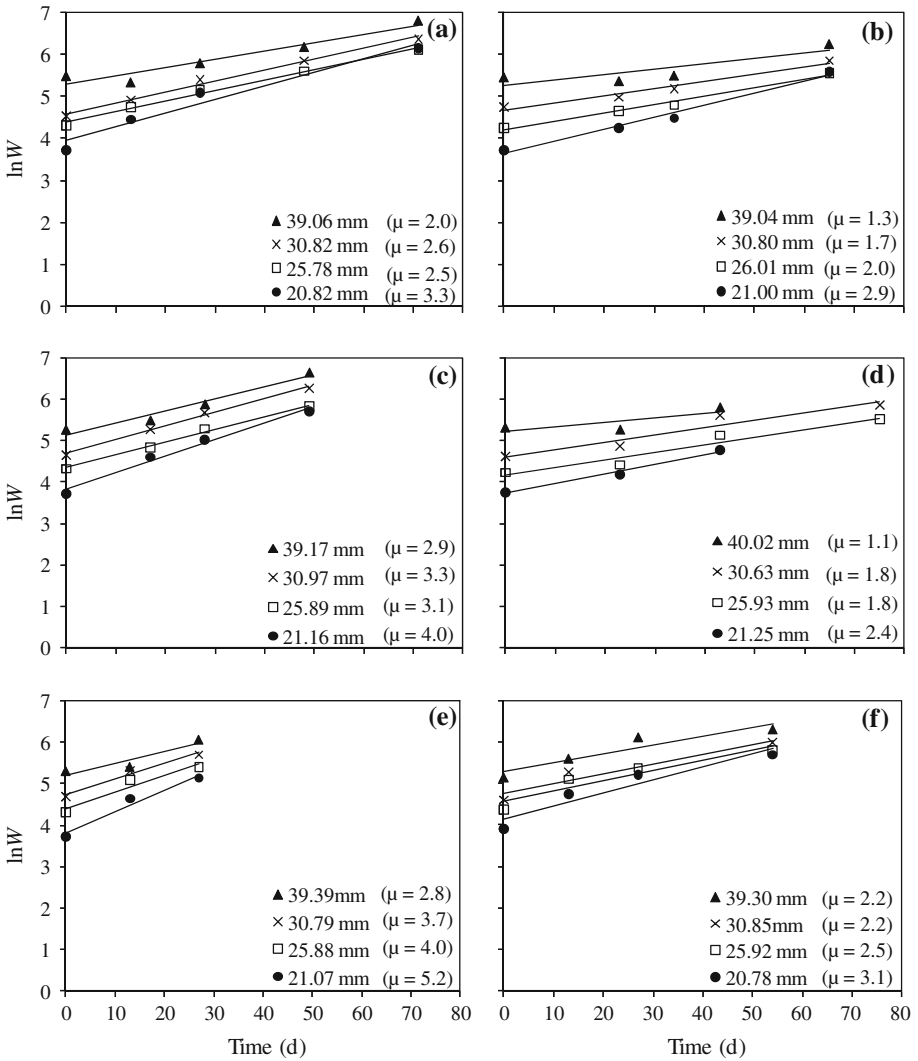
**Table 2** continued

Series location period	$\Delta t$ (day)	Chl $a$ ( $\mu\text{g l}^{-1}$ )	Temp. ( $^{\circ}\text{C}$ )	Salinity (psu)	$L_0$ (mm)	$L_g$ (mm day $^{-1}$ )	$W_0$ (mg)	$\mu$ (%day $^{-1}$ )	$W_{\text{avg}}$ (mg)	$\tau_2$ (day)
Series #6, L-G Salling Sund (Glyngøre) 29 Jul to 21 Sep 2010	54	$3.2 \pm 1.7^b$	$19.0 \pm 1.9$	$29.4 \pm 1.0$	20.8	0.225	49.7	3.1	121	22.4
					25.9	0.221	79.6	2.5	163	27.7
					30.9	0.185	99.9	2.2	200	31.5
					39.3	0.122	173.2	2.1	310	33.0

<sup>a</sup> Data are mean ( $\pm$ SD) concentration of chl  $a$  in the period 2000–2009 as no chl  $a$  data from this location were available for 2010

<sup>b</sup> chl  $a$  data are from Nissum Bredning because no chl  $a$  data from Salling Sund exist for this period

Overview of locations, periods, and duration ( $\Delta t$ ) of mussel growth in Great Belt (GB-K, GB-M, GB-S, GB-B) and Limfjorden (L-H, L-G) in 2010. Mean ( $\pm$ SD) values of chlorophyll  $a$  (chl  $a$ ), temperature, salinity, initial shell length ( $L_0$ ) and body dry weight ( $W_0$ ), average daily increase in shell length ( $L_g$ ), average body dry weight ( $W_{\text{avg}}$ ), average weight-specific growth rate ( $\mu$ , slopes in Fig. 3), and doubling time ( $\tau_2$ ). Chlorophyll  $a$  data were supplied by Environmental Centre, Ringkøbing, Danish Ministry of the Environment. Mean  $\pm$  SD are based on data collected on the locations at a depth of 1 m between 5 and 11 times distributed throughout the experimental periods



**Fig. 3** *Mytilus edulis* (Series #1 to #6: figures a–f, see Table 1). Natural logarithm ( $\ln$ ) of dry weight of soft parts ( $W$ , mg) as a function of time (days) of 4 size classes of mussels. The slope  $\mu$  ( $\% \text{ day}^{-1}$ ) denotes the weight-specific growth over the period

both shells and soft parts on pieces of tin foil in an oven for 24 h at 90 °C to obtain also the dry tissue weight.

Environmental data

Data on chl *a*, salinity, and temperature for the actual mussel growth periods were obtained from 6 stations monitored by Environmental Centre Ringkøbing (Limfjorden), Environmental Centre Odense, and Environmental Centre Roskilde (Great Belt). Temperature and

salinity were measured with a CTD at heights spaced 0.2 m apart, from 0.8 m below the surface down to about 0.3 m above the bottom. Oxygen concentrations were measured in the top and bottom layers using the Winkler method. Chl *a* was determined from water samples taken from a depth of 1 m and subsequently analyzed at an authorized laboratory according to Danish national standards. The water depths at the 6 monitoring stations and distance to the mussel growth sites are summarized in Table 1. Current velocity data were supplied by DHI.

#### Growth of mussels on farm-ropes (Series #7)

From September 2010 to March 2011, 7 samples of 1-m-long pieces of rope with mussels were collected 1 m below the water surface at the experimental mussel farm run by the MarBioShell project in Kerteminde Bugt (Fig. 1, location GB-K). The farm-ropes were made of long 15-cm-width bands cut out of fishing net (3 mm nylon, 5 × 5 cm mesh; Hvalpsund Net A/S). The rope samples were transported to the nearby Marine Biological Research Centre, Kerteminde, and stored in a freezer until analysis could take place. For analysis, the rope samples were allowed to defreeze and representative segments of 5 cm (small mussels) or 10 cm (larger mussels) from the middle of the ropes were cut out with a scalpel, the mussels removed, counted, and thoroughly mixed in a container where after about 100 mussels were randomly sampled with a spoon. The density (number of mussels per cm rope), mean shell length, and wet and dry weight of soft parts were subsequently determined.

#### Pelagic biomass in Limfjorden and the Great Belt

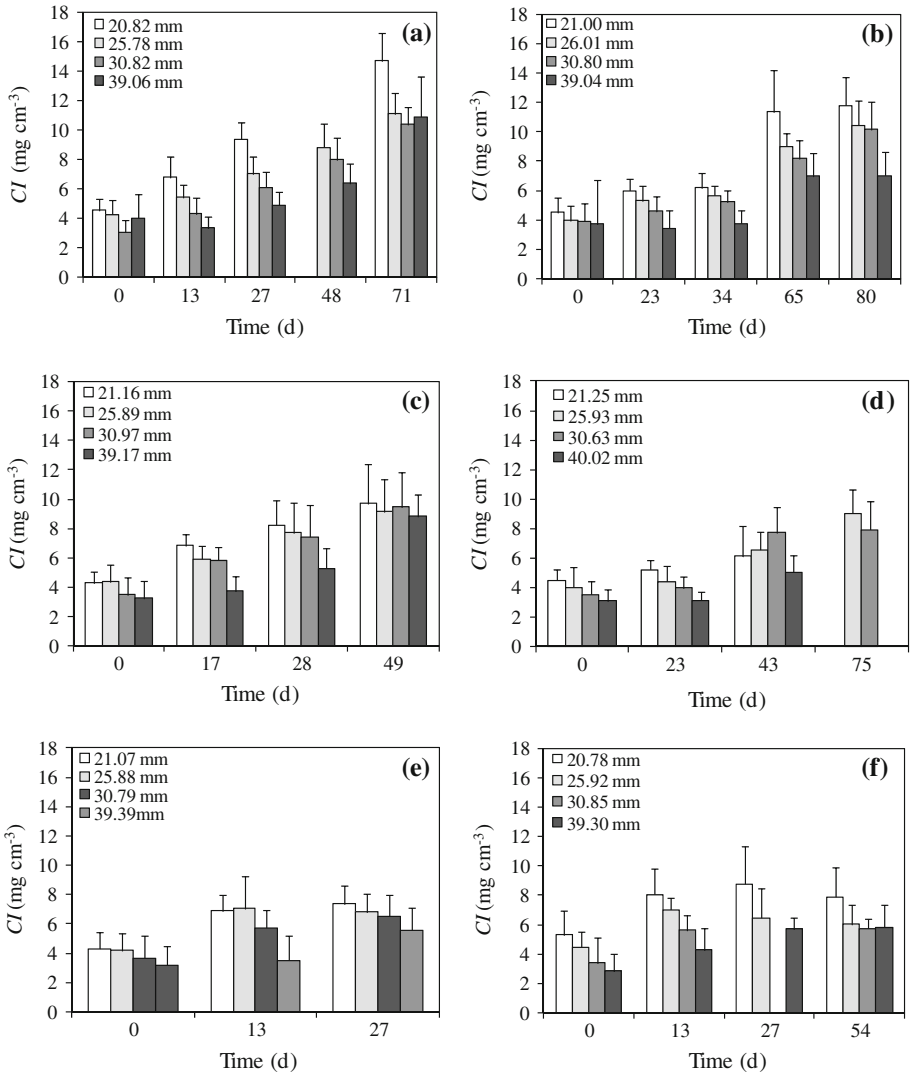
Data on pelagic biomass of autotrophic and heterotrophic plankton in the Great Belt and Limfjorden were obtained from the Danish National Environmental Research Institute (<http://www.dmu.dk/en/water/marinemonitoring/mads/plankton/>) and the Danish Ministry of the Environment, Nature Agency, respectively.

## Results

The field studies involve 6 sites (Series #1 to #4 in Great Belt, and Series #5 & #6 in Limfjorden) with measurement of growth of mussels in net bags in the productive summer season (Tables 1, 2; Figs. 3, 4, 5, 6), and one site (Series #7, close to that of Series #1) with growth measurement of mussels settled on farm-rope, covering fall and winter seasons (Tables 3, 4; Figs. 7, 8).

#### Actual growth and average weight-specific growth rates (Series #1 to #6)

The recorded data on field growth of 4 size classes of mussels at each of the 6 sites are presented in Fig. 3 in terms of the natural logarithm of dry weight ( $\ln W$ ) versus time with the slope of linear regression lines giving the average weight-specific growth rate ( $\mu$ ) over the period, according to Eq. (5). These  $\mu$ -values, for 4 size groups at each site, are shown in Fig. 5 versus the corresponding values of average dry weight ( $W_{\text{avg}}$ ) along with power law regression lines approximations of form Eq. (7),  $\mu_a = a' W_{\text{avg}}^{b'}$ . For comparison, model predictions from Eq. (3) for indicated values of chl *a* concentrations are shown as dashed



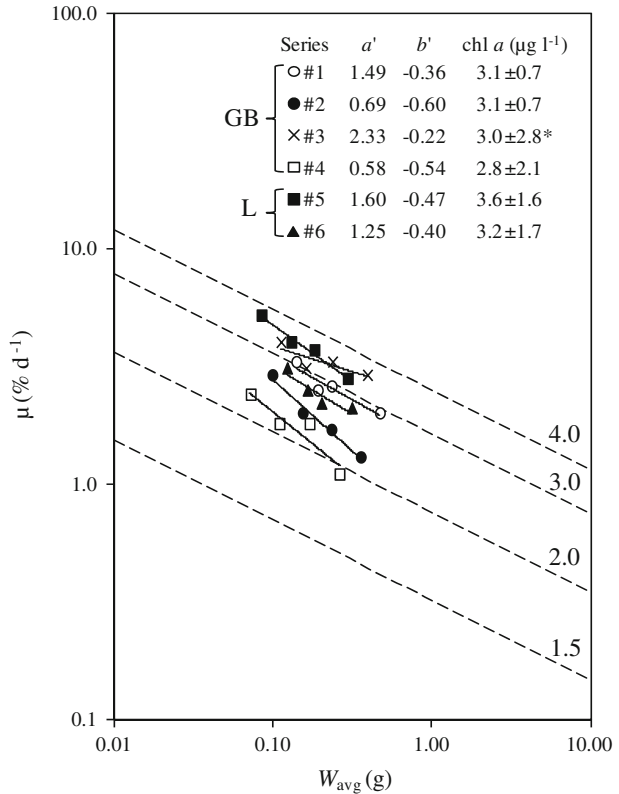
**Fig. 4** *Mytilus edulis* (Series #1 to #6: figures a–f). Condition index (CI,  $\text{mg cm}^{-3}$ , mean  $\pm$  SD) as a function of time (days) of 4 size classes of mussels

lines in Fig. 5. Growth data in terms of the condition index (CI) are presented in Fig. 4, showing generally increasing CI for almost all classes during the period.

#### Mussels on farm-ropes (Series #7)

The growth as a function of time of the biggest 5-mm-size group of mussels (1–5 mm longer than the other mussels) on farm-rope samples collected during the period September 1, 2010 to March 2, 2011 has been shown in Figs. 7 and 8 along with data for chl *a*, temperature, and salinity in the same period. The growth period can be divided into two: Period I = September 1, 2010 to November 16, 2010, where the increase in shell length is

**Fig. 5** *Mytilus edulis* (Series #1 to #6). Experimental data for average weight-specific growth rate ( $\mu = a'W_{avg}^{b'}$ , cf. Eq. 7), derived from slope of regression lines in Fig. 3 as a function of average body dry weight ( $W_{avg}$ ) of all size classes of mussels (GB = Great Belt, L = Limfjorden. Constants  $a'$  and  $b'$  equal coefficient and exponent in power law regression lines shown, and chl  $a$  from Table 2. Predictions (dashed lines, slope  $b = -0.34$ ) from growth model at different constant levels of chl  $a$  (from 1.5 to 4.0  $\mu\text{g l}^{-1}$ ) calculated according to Eq. (3). \*Mean concentration at 1 m depth for the period 2000–2009, because chl  $a$  was not measured on this location (GB-S, see Table 2) in 2010



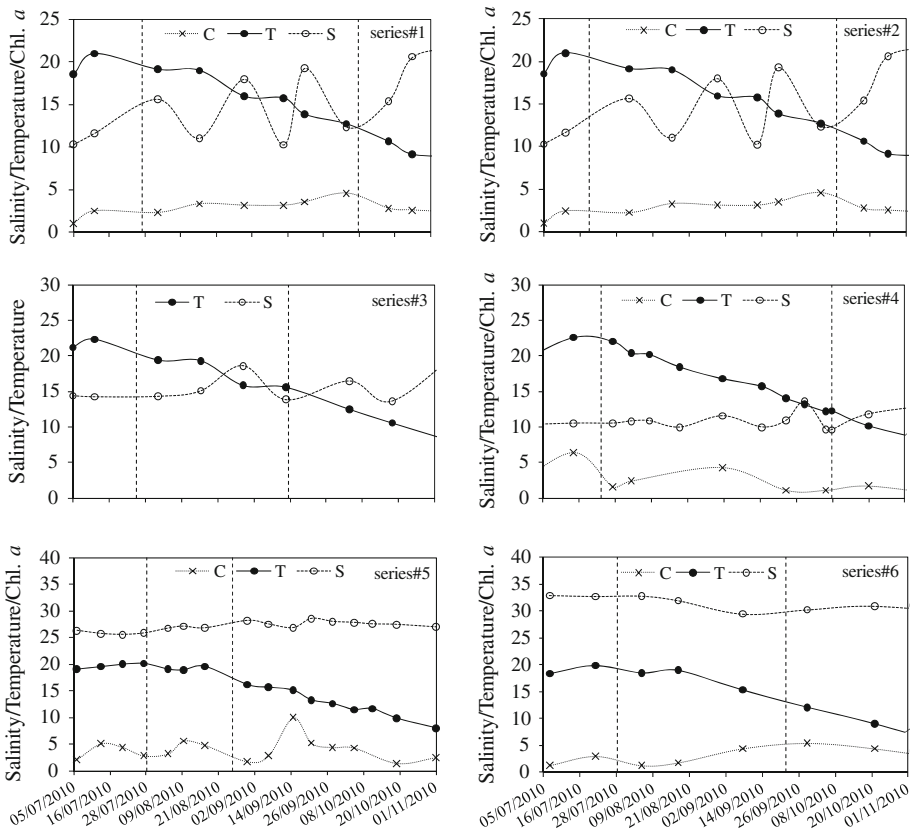
0.277 mm day<sup>-1</sup>, and Period II = November 16, 2010 to March 2, 2011 with loss of weight (Fig. 8) but essentially without increase in shell length (Fig. 7b; Table 3). Further details on weight loss during Period II are given Table 4.

**Pelagic biomass**

The biomass of autotrophic and heterotrophic plankton in the Great Belt in 1997 and in Limfjorden in 2010 when also mixotrophic species were quantified are shown in Tables 5 and 6. It appears that the heterotrophic biomass in the Great Belt in 1997 was  $3.4 \pm 3.3 \%$  of the total pelagic biomass, whereas the heterotrophic and mixotrophic biomass were  $23.7 \pm 24.5 \%$  of the total in Løgstør Bredning and  $5.9 \pm 6.7 \%$  in Skive Fjord, respectively. Although the heterotrophic fraction of the total plankton biomass available for filter-feeding mussels may at times be relatively high, it seems safe to conclude that the autotrophic plankton, which can be quantified by measurement of the chl  $a$  concentration, generally dominates the pelagic microplankton.

**Discussion**

In the present work, we first present experimental data on the growth of mussels during the productive summer season and also test to what degree the observed weight-specific



**Fig. 6** Chlorophyll *a* (C,  $\mu\text{g l}^{-1}$ ), temperature (T,  $^{\circ}\text{C}$ ), and salinity (S, psu) in Kerteminde Bugt (Series#1), Musholm Bugt (Series#2; same as for Series #1), Svendborg Sund (Series#3), Karrebæksminde Bugt (Series#4), Risgård Bredning (Series#5), and Salling Sund (Series#6) during growth periods. Dashed vertical lines mark the beginning and end of mussel growth period. No chl *a* data are available for Svendborg Sund (Series#3) in 2010. Data supplied by Environmental Centre Odense, Danish Ministry of the Environment

growth rate as a function of mussel dry weight can be related to the model expressed by Eq. (3). We suggest that deviations from either the expected exponent of  $b = -0.34$  or the constant  $a$  expressing the magnitude of growth for the prevailing chl *a* concentration level indicate suboptimal growth conditions, although more precise interpretations may not be possible without supplementary studies.

Figure 5 shows that field data from 6 different sites fall in the general area of prediction according to the bioenergetic growth model. But in regard to predicted levels of growth rates for the theoretical and the measured chl *a* concentrations near the growth sites, there are some differences. Series #1, #5, and #6 appear close to the model, Series #2 and #4 appear suboptimal, while Series #3 appears to grow faster than predicted by the theory for the measured chl *a* concentration near the site.

The reasons for suboptimal growth in Series # 2 and #4 despite high chl *a* levels may be suggested by examination of Eq. (1)–(3). Thus, if the  $b$ -exponent is essentially that of the model, this implies  $b_1$ - and  $b_2$ -exponents to be near identical ( $\approx 0.66$ ), and this leaves the constants  $a_1$ ,  $a_2$ , AE, and  $a_0$  as sources of suboptimality (or deviations from prerequisites

**Table 3** *Mytilus edulis* (Series #7)

Date	Day	Rope (cm)	$n_{tot}$	Density (ind. $cm^{-1}$ )	$n_s$	$L_s$ (mm)	$n_{big\ 5}$	$L_{big\ 5}$ (mm)	$W_{sp}$ (mg)	CI (mg $cm^{-3}$ )	$W_{shell}$ (mg)	WC (%)	$\mu$ (% $day^{-1}$ )
01-09-2010	0	5.0	1123	225	162	4.4 ± 1.6	22	7.4 ± 1.5	3.3 ± 2.7	7.3 ± 1.5	16.1 ± 11.1	67.7 ± 7.6	
18-09-2010	17	4.5	831	185	81	7.0 ± 3.2	24	11.2 ± 0.9	11.1 ± 3.6	7.7 ± 1.4	40.8 ± 11.0	76.2 ± 3.0	7.1
07-10-2010	36	10.0	1683	68	91	11.6 ± 4.7	17	18.1 ± 2.4	53.4 ± 26.3	8.7 ± 1.4	185.2 ± 78.5	78.1 ± 2.0	8.3
16-11-2010	76	10.0	1145	115	155	14.4 ± 6.8	10	28.1 ± 2.1	197.3 ± 21.6	7.0 ± 0.6	700.0 ± 69.8	79.8 ± 1.3	3.3
05-01-2011	126	9.7	1066	110	124	13.0 ± 7.1	9	27.9 ± 2.6	171.9 ± 28.6	6.6 ± 1.4	884.5 ± 110.9	81.4 ± 1.3	-0.3
02-03-2011	182	10.5	1468	140	198	11.6 ± 6.5	8	29.1 ± 2.4	146.9 ± 37.9	5.1 ± 1.3	896.9 ± 132.8	84.2 ± 1.3	-0.3

Overview of growth parameters for farm-rope mussels collected in the period September 1, 2010 to March 2, 2011.  $n_{tot}$  = total number of mussels on rope segment sample;  $n_s$  = number of randomly collected mussels in sample for shell length measurement;  $n_{big\ 5}$  = number of mussels from biggest 5-mm-size group in  $n_s$ ;  $L_s$  = shell length of mussels in  $n_s$ ;  $L_{big\ 5}$  = shell length of mussels in  $n_{big\ 5}$ ;  $W_{sp}$  = dry weight of soft parts; CI = condition index;  $W_{shell}$  = dry weight of shells; WC = water content = % water in body soft parts. Mean ± SD are shown. Weight-specific growth rate ( $\mu$ ) calculated from Eq. (6) for each specific subsample of farm-rope mussels (see also Fig. 8)

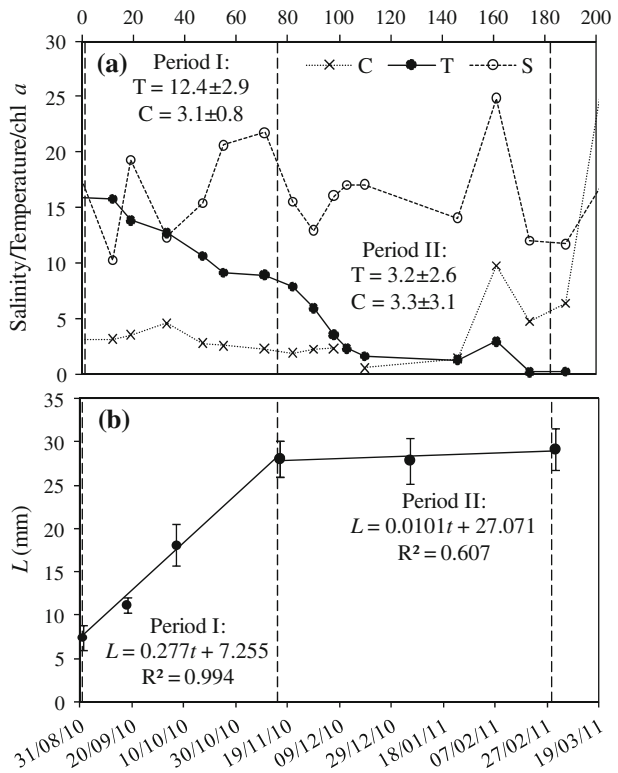
**Table 4** *Mytilus edulis* (Series #7)

Date	Time (day)	W (mg)	$\Delta W_{\text{period}}$ (mg)	$\Delta W_{\text{act}}$ (mg day <sup>-1</sup> )	$R_m$ (ml O <sub>2</sub> h <sup>-1</sup> )	$\Delta W_{\text{est}}$ (mg day <sup>-1</sup> ) <sup>a</sup>
16-11-2010	0	197.3			0.162	-3.8
05-01-2011	50	171.9	-25.4	-0.508	0.148	-3.4
02-03-2011	106	146.9	-25.0	-0.446	0.133	-3.1

<sup>a</sup>  $\Delta W_{\text{est}}$  (mg day<sup>-1</sup>) =  $(R_m \times 24 \text{ h day}^{-1} \times 19.88 \text{ J h}^{-1}) / (20.51 \text{ J mg}^{-1})$

Mean dry weight of soft parts (W) of mussels in the biggest 5-mm-size group of mussels sampled from farm-ropes in the winter-starvation period, November 11, 2010 to March 2, 2011 (Fig. 8). Loss of dry weight in period between sampling ( $\Delta W_{\text{period}}$ ) and actual daily weight loss ( $\Delta W_{\text{act}}$ ) is shown along with estimated weight loss ( $\Delta W_{\text{est}}$ ) calculated from the maintenance respiratory rate ( $R_m$ , see text)

**Fig. 7** **a** Chlorophyll *a* (C,  $\mu\text{g chl } a \text{ l}^{-1}$ ), temperature (T, °C), and salinity (S, psu) from September 1, 2010 to March 2, 2011. **b** *Mytilus edulis* (Series #7). Mean ( $\pm$ SD) shell length (L, mm) as a function of time (t, d) of the biggest 5-mm-size group of mussels (1–5 mm longer than the other mussels) on farm-rope samples collected during this period. The growth period is divided into two: Period I = September 1, 2010 to November 16, 2010, Period II = November 16, 2010 to March 2, 2011 (see Table 3)

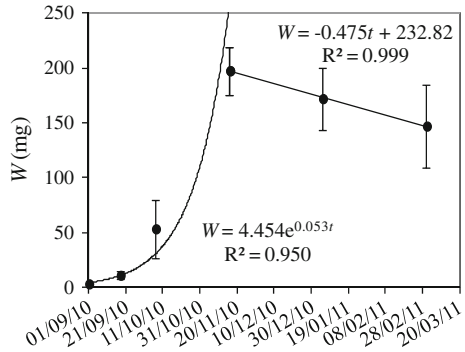


for the growth model) associated with the level of growth. The most obvious candidate for low level of growth is some degree of reduced filtration rate for the full size range (i.e., smaller  $a_1$ ) or increased respiration rate due to, e.g., stress caused by varying salinity (i.e., larger  $a_2$ ) (e.g., Strickle and Sabourin 1979; Riisgård et al. 2012b).

The case of Series #3, showing higher growth rates than predicted for the chl *a* concentration measured nearby, could be explained by the rather large experimental uncertainty of data, notably  $3.0 \pm 2.8 \mu\text{g l}^{-1}$ , or by the availability of other sources of nutrition



**Fig. 8** *Mytilus edulis* (Series #7). Mean ( $\pm$ SD) dry weight of soft parts ( $W$ , mg) as a function of time of farm-rope samples collected in the period September 1, 2010 to March 2, 2011 (Table 3). The weight-specific growth rate ( $\mu$ , % day<sup>-1</sup>) during the period September 1, 2010 to November 16, 2010 (76 days) was 5.3 % day<sup>-1</sup>



**Table 5** Total pelagic biomass ( $\mu\text{g C l}^{-1}$ ) of autotrophic plankton (phytoplankton), heterotrophic plankton (microzooplankton), and percentage heterotrophic biomass of total biomass of plankton in the Great Belt during 1997

Date 1997	Autotrophic	Heterotrophic	Total	% Heterotrophic
1 Jan	13.7	0.6	14.3	4.1
13 Jan	11.6	0.3	11.9	2.4
27 Jan	10.4	0.2	10.6	2.0
10 Feb	1115.5	15.2	1130.7	1.3
24 Feb	95.1	1.7	96.7	1.7
10 Mar	219.1	4.1	223.2	1.8
24 Mar	59.7	14.3	74.0	19.4
7 Apr	16.6	3.7	20.2	18.1
21 Apr	12.5	0.2	12.7	1.8
6 May	21.4	0.5	21.9	2.3
26 May	35.5	2.6	38.1	6.8
9 Jun	295.7	1.9	297.6	0.6
24 Jun	50.7	9.4	60.1	15.6
3 Jul	35.4	3.3	38.7	8.6
21 Jul	28.7	3.2	31.9	10.1
4 Aug	302.4	3.6	306.0	1.2
18 Aug	159.9	1.6	161.4	1.0
2 Sep	339.8	9.4	349.3	2.7
16 Sep	134.8	35.5	170.3	20.8
22 Sep	164.8	9.7	174.5	5.6
6 Oct	143.7	13.4	157.0	8.5
20 Oct	181.1	6.3	187.4	3.3
3 Nov	516.8	2.5	519.3	0.5
17 Nov	63.6	0.1	63.7	0.2
1 Dec	18.8	0.4	19.2	2.2
15 Dec	76.2	1.5	77.6	1.9
Mean	158.6	5.6	164.2	3.4
$\pm$ SD	232.7	7.7	235.0	3.3

**Table 6** Total biomass of autotrophic (Nostocophyceae, Chrysophyceae, Euglenophyceae, Prasinophyceae, Cryptophyceae, Diatomophyceae, Dinophyceae, and other undetermined species), mixotrophic (Dinophyceae, Crysofhyceae, and Prymnesiophyceae), and heterotrophic (Dinophyceae, Cryptophyceae, ciliates, pelagic bacteria, flagellates other microzooplankton species, but not including copepods, and other mesozooplankton species) plankton in Løgstør Bredning and Skive Fjord in 2010

	5 Mar		15 Mar		29 Mar		6 Apr		12 Apr		4 May		26 May		7 Jun		22 Jun		6 Jul		21 Jul		5 Aug		17 Aug		7 Sep		21 Sep		28 Sep		19 Oct		1 Nov		22 Nov		Mean ± SD
	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr	Mar	Apr			
Autotrophic	548.7	1.1	375.8	198.2	98.4	4.8	61.8	120.0	208.8	36.2	421.0	201.6	130.9	136.4	81.2	96.7	17.4	21.8	13.6	146.0 ± 152.7																			
Mixotrophic	0.4	0.2	4.0	2.0	14.8	0.4	2.2	18.8	0.4	0.0	3.6	4.2	6.6	9.0	9.8	11.8	1.7	0.2	3.1	4.9 ± 5.5																			
Heterotrophic	18.2	14.3	32.1	47.9	35.5	58.3	54.5	59.7	75.6	129.3	61.6	38.9	31.7	340.1	95.5	82.6	61.7	44.2	28.1	68.9 ± 71.4																			
% mixo + hetero	3.3	92.9	8.1	12.9	18.7	12.6	17.6	18.0	22.9	45.6	12.3	15.1	20.1	46.5	53.5	46.2	75.1	60.2	39.3	23.7 ± 24.5																			
Skive Fjord	2	6	12	4	26	7	22	5	20	4	16	6	28	18	25	Mean ± SD																							
Autotrophic	690.4	503.5	78.6	64.7	72.4	58.4	40.0	96.0	373.2	379.0	197.0	1150.7	15.8	66.5	5.9	252.8 ± 322.0																							
Mixotrophic	0.5	0.0	3.1	25.5	0.0	0.4	3.7	5.0	0.0	0.0	3.8	2.5	0.1	0.4	0.0	3.0 ± 6.5																							
Heterotrophic	1.2	15.8	30.5	3.8	28.6	2.8	0.8	6.4	19.9	4.0	61.4	8.9	0.1	7.8	2.7	13.0 ± 16.6																							
% mixo + hetero	0.2	3.0	29.9	31.2	28.3	5.2	10.1	10.6	5.1	1.0	24.9	1.0	1.3	11.0	31.4	5.9 ± 6.7																							

**Table 7** Maximum, minimum, and mean ( $\pm$ SD) current speeds at the 4 mussel growth sites in the Great Belt during the growth periods (Fig. 1, Table 1)

Location	Max speed (cm s <sup>-1</sup> )	Minimum speed (cm s <sup>-1</sup> )	Mean speed (cm s <sup>-1</sup> )	% >25 cm s <sup>-1</sup>	% >50 cm s <sup>-1</sup>	S (2010) (psu)	S (2008–2010) (psu)
Kerteminde Bugt	0.66	0	0.20 $\pm$ 0.14	34.2	3.6	15.4 $\pm$ 3.8	16.5 $\pm$ 4.2
Musholm Bugt	0.87	0	0.27 $\pm$ 0.20	46.2	15.5	15.4 $\pm$ 3.8	16.5 $\pm$ 4.2
Svendborg Sund	0.12	0	0.04 $\pm$ 0.02	0	0	15.4 $\pm$ 3.2	16.7 $\pm$ 3.9
Karrebæksmide Bugt	0.12	0	0.04 $\pm$ 0.03	0	0	11.6 $\pm$ 1.7	11.9 $\pm$ 1.8 <sup>a</sup>

<sup>a</sup> No data available for 2009 (mean of 2008 and 2010)

Additionally, the current speed above 25 and 50 cm s<sup>-1</sup> in % of total time is shown. Mean current speeds at the two northernmost stations (Kerteminde Bugt and Musholm Bugt) and two southernmost stations (Svendborg Sund and Karrebæksmide Bugt) were 0.77 and 0.12 cm s<sup>-1</sup>, respectively. Mean  $\pm$  SD salinities (S, psu) in 2010 and in the 3-year period (2008–2010) for the 4 mussel growth locations in Great Belt

**Table 8** Mean chlorophyll *a* (chl *a*), minimum, maximum, and average temperature (*T*), and salinity (*S*) in the northern part of Great Belt (Fig. 1, St #1) in 2000–2010. Additionally, the frequency of salinity changes of more than 9 psu are shown along with the corresponding changing rate expressed as psu day<sup>-1</sup> and psu h<sup>-1</sup>

Year	Chl <i>a</i> (µg l <sup>-1</sup> )	<i>T</i> <sub>min</sub> (°C)	<i>T</i> <sub>max</sub> (°C)	<i>T</i> <sub>avg</sub> (°C)	<i>S</i> <sub>min</sub> (psu)	<i>S</i> <sub>max</sub> (psu)	<i>S</i> <sub>avg</sub> (psu)	Freq Δ <i>S</i> >9 psu	Amplitude (psu)	Δ <i>t</i> (day)	Change (psu day <sup>-1</sup> )	Change (psu h <sup>-1</sup> )
2000	2.6	2.43	17.11	9.77	10.98	27.14	17.16	2	13.41	21	0.64	0.03
2001	2.3	2.15	19.80	9.76	10.20	22.57	16.30	0	12.42	14	0.89	0.04
2002	2.4	2.41	20.17	10.08	9.57	24.76	16.09	1	9.95	10	1.00	0.04
2003	2.4	0.66	19.13	9.21	9.93	25.59	17.15	7	10.52	20	0.53	0.02
									11.01	43	0.26	0.01
									12.49	14	0.89	0.04
									9.90	35	0.28	0.01
									10.26	14	0.73	0.03
									11.60	28	0.41	0.02
									10.20	14	0.73	0.03
2004	2.8	1.72	18.79	10.06	10.66	24.15	17.41	2	10.01	24	0.42	0.02
									11.89	38	0.31	0.01
2005	2.7	1.02	18.29	10.42	10.50	25.34	15.99	2	12.63	34	0.37	0.02
									10.41	24	0.43	0.02
2006	3.8	0.84	19.57	11.06	10.06	24.10	16.65	3	10.83	36	0.30	0.01
									10.47	14	0.75	0.03
									9.49	29	0.33	0.01
2007	3.5	3.01	18.50	10.94	10.80	23.18	16.44	1	12.31	27	0.46	0.02
2008	2.3	3.36	18.29	10.22	9.38	25.22	16.80	5	10.46	56	0.19	0.01
									13.41	51	0.26	0.01
									11.97	34	0.35	0.01
									9.38	17	0.55	0.02
									10.01	21	0.48	0.02

**Table 8** continued

Year	Chl <i>a</i> ( $\mu\text{g l}^{-1}$ )	$T_{\text{min}}$ ( $^{\circ}\text{C}$ )	$T_{\text{max}}$ ( $^{\circ}\text{C}$ )	$T_{\text{avg}}$ ( $^{\circ}\text{C}$ )	$S_{\text{min}}$ (psu)	$S_{\text{max}}$ (psu)	$S_{\text{avg}}$ (psu)	Freq $\Delta S > 9$ psu	Amplitude (psu)	$\Delta t$ (day)	Change (psu day $^{-1}$ )	Change (psu h $^{-1}$ )
2009	3.1	2.15	19.05	11.12	10.48	24.36	17.60	3	10.55	23	0.46	0.02
									10.62	61	0.17	0.01
									11.07	21	0.53	0.02
2010	2.7	-0.48	20.98	8.23	10.23	22.44	15.42	3	9.70	29	0.33	0.01
									9.04	7	1.29	0.05
									9.42	38	0.25	0.01

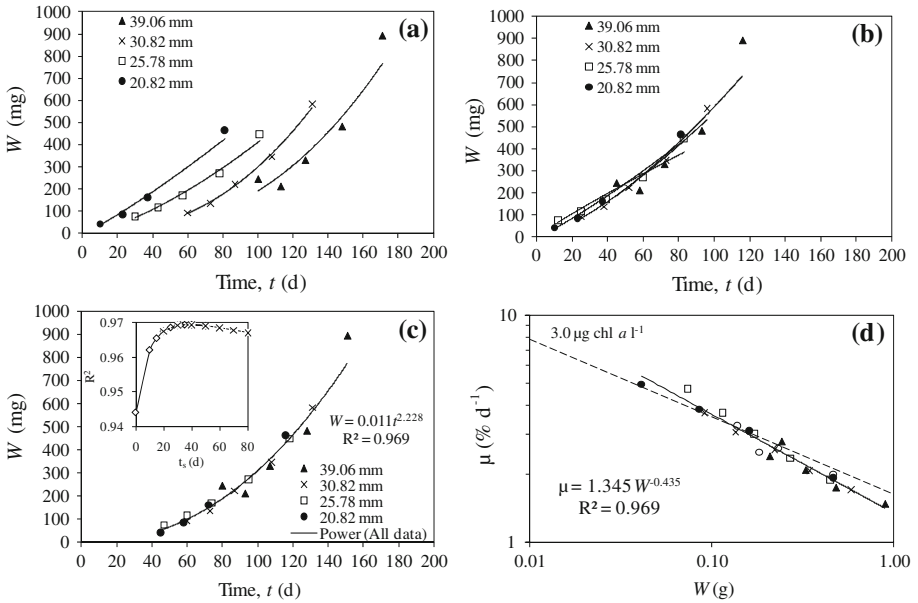
than phytoplankton, e.g., heterotrophic flagellates, ciliates, and other microzooplankton that may form part of the in situ diet of mussels (Nielsen and Maar 2007), and further that mesozooplankton in turbulent water may be ingested by filter-feeding mussels (Davenport et al. 2000). Thus, growth rates higher than estimated from an energy budget based solely on chl *a* may express a possible supplementary ingestion of heterotrophic food.

In case of Series #6, showing growth rates somewhat lower than predicted for the growth model, a probable explanation is the generally high current speeds at this growth site in Great Belt (Musholm Bugt). Here, the current speed was higher than 0.25 and 5 cm s<sup>-1</sup> for 46.2 and 15.5 % of the time, respectively (Table 7), and according to Wildish and Miyares (1990) flow-induced inhibition of the filtration rate of blue mussels takes place in flume flows above 6 cm s<sup>-1</sup>, and at flows between 25 and 38 cm s<sup>-1</sup>, the filtration rate was reduced to only about 12 % of that measured at 6 cm s<sup>-1</sup>.

Secondly, we study mussel growth during the fall–winter season. Here, the growth of mussels on farm-ropes (Series #7) shows that the weight-specific growth rate (about 5 % day<sup>-1</sup> at about 3–4 µg chl *a* l<sup>-1</sup>, Fig. 8) followed model prediction during Period I, thus suggesting density independent growth of the biggest 5-mm-size group of mussels, but in Period II when both the chl *a* concentration and temperature became very low (Fig. 7a), the mussels were losing weight (Fig. 8), a scenario which is beyond the parameter range covered by the model. As it appears from Table 4, the actual daily weight loss is significantly lower (about 7 times) than the estimated weight loss calculated from the maintenance respiration rate assuming this were at the normal level of a fully open mussel. This indicates that the mussels during Period II may have been partially closed and thus saving energy by the reduced respiration rate (Jørgensen et al. 1986).

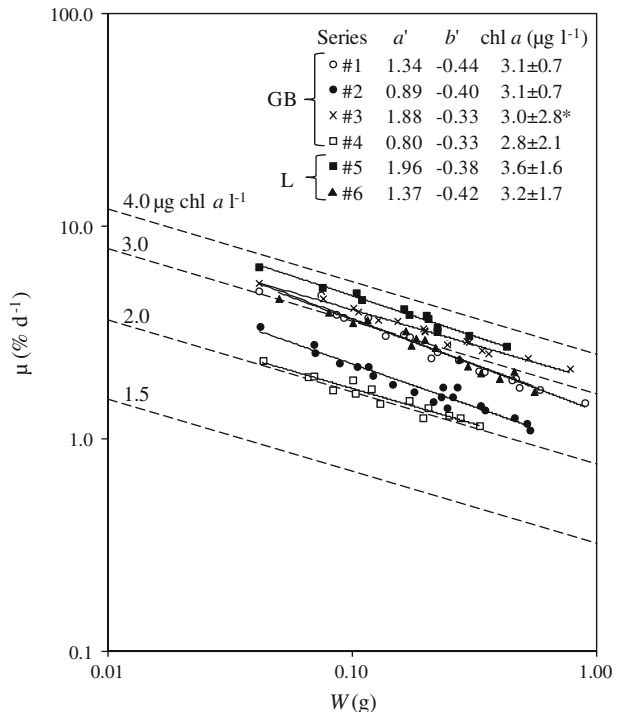
As to the general potential for mussel farming in Danish waters, it is noted that the variation in chl *a*, temperature, and salinity in the northern and southern part of Great Belt during a 10-year period, from beginning of 2000 to end of 2010, have been monitored by the Danish Nature Agency (Table 8), and the mean salinities in the study period 2008–2010 for the 4 mussel growth locations in Great Belt has been shown in Table 7. Based on the present study of actual growth of mussels in net bags and on farm-ropes in the field, it seems reasonable here to make a provisional evaluation of the potential for line-mussel farming in the Great Belt. The specific growth rates observed in Great Belt compare quite well with the growth in Limfjorden, although frequently high current speeds at certain sites in Great Belt may induce inhibition of feeding and thus growth. The observed variations in salinities, however, are not likely to influence the growth rate of mussels in Great Belt (Riisgård et al. 2012b, 2013b).

Thus, based on the present bioenergetic growth model and experimental approach, it is possible to evaluate the potential for optimal line-mussel growth in selected areas of special interest, especially if supplementary local field measurements of chl *a*, heterotrophic plankton, and current speeds were to be made to fine-adjust the growth model, all without the need for elaborate growth experiments. Regarding future mussel farming, our studies have shown that *M. edulis* can grow from settlement in spring to 30 mm in shell length in November. However, to reach the traditional consumer size of at least 45 mm, it will probably take about 18 months, as suggested by Dolmer and Frandsen (2002) for long line-mussels in Limfjorden, because of the winter period with weight loss and subsequent re-growth during the next season. It may therefore be suggested to consider a new approach of line farming of 30-mm mini-mussels during one growth season, from early spring to November, recovering all equipment at the time of harvest and re-establishing it at the beginning of the next season for a new population and thus protecting the equipment from the often damaging weather of the Danish winter season. The new, smaller-sized consumer

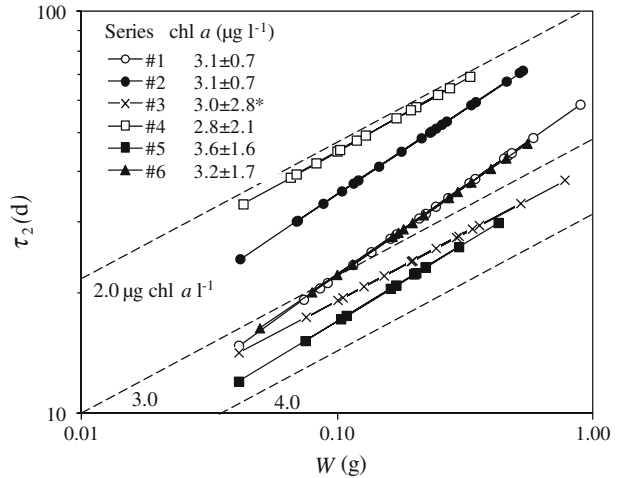


**Fig. 9** *Mytilus edulis* (Series #1). **a** 4 size groups separated by arbitrary shifts  $t_s = 10, 30, 60,$  and  $100$  days, respectively; **b** optimal overlap for shifts  $t_s = 10, 12, 25,$  and  $45$  days; **c** assembled time series shifted 30 days to start at  $t_s = 45$  days, giving maximal  $R^2$  (insert); **d** resulting relation  $\mu(W)$  calculated from Eq. (10) and compared to growth model at chl  $a$  of  $3 \mu\text{g l}^{-1}$  (dashed)

**Fig. 10** *Mytilus edulis* (Series #1 to #6). Weight-specific growth rates calculated from assembled and time-shifted data as explained in Fig. 9. See also legend to Fig. 5



**Fig. 11** *Mytilus edulis* (Series #1 to #6). Doubling time ( $\tau_2$ ) versus dry weight of soft parts of mussels ( $W$ ) from Eq. (12) based on regression lines to time series of experimental data with indicated chl  $a$  concentrations (solid lines) and growth model (dashed lines) calculated according to Eqs. (3) and (11) at constant levels of chl  $a$  (from 2 to 4  $\mu\text{g l}^{-1}$ )



product should be attractive in its own right—like the small French 40-mm ‘bouchot’ mussels for which there is a market (Prou and Gouilletquer 2002).

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**Appendix: Note on experimental time series**

If an extended time series of data  $W(t)$  is available, it is possible to obtain more detail in terms of how  $\mu$  varies with increasing size  $W$ . The first data point in an experimental time series is normally assigned the arbitrary value of  $t = 0$  at size  $W_0$ , but on a true time scale of mussel life this should be some time  $t_s > 0$ . We therefore shift the time series  $W(t)$  by  $t_s$  to  $W(t_s + t)$  and examine the  $R^2$  value of a power law regression to the time-shifted data to find the shift  $t_s$  that produces the maximal value of  $R^2$ . Denoting the power law fit

$$W = c(t_s + t)^d, \tag{9}$$

and using the definition  $\mu = (1/W) dW/dt$ , we obtain the estimate of  $\mu(W)$  as

$$\mu = (1/W)dc(t_s + t)^{d-1} = d(W/c)^{-1/d} = a'W^{b'}. \tag{10}$$

Comparing Eqs. (10)–(3) shows that growth follows the model provided  $a' \equiv dc^{1/d} = a$  and  $b' \equiv -1/d = b$ .

The time ( $\tau_2$ ) for doubling the dry weight of soft parts of any given size of mussel may be estimated by integrating Eq. (5) from  $W$  to  $2W$ , assuming a constant mean value of  $\mu$ , which yields  $\tau_2 = \ln 2/\mu$ , but this expression gives an underestimate for dry weight  $W$  since  $\mu$  decreases with increasing size. The correct value is obtained by use of Eq. (3) in the definition ( $\mu = (1/W) dW/dt$ ) which integrates to



$$\tau_2 = (2^{-b} - 1) (-baW^b)^{-1} = 0.782/\mu, \quad (11)$$

where  $\mu$  is now the model value at  $W$ . Similarly, for experimental data correlated by the power law of Eq. (10) integration yields

$$\tau_2 = \left(2^{1/d} - 1\right) (W/c)^{1/d}. \quad (12)$$

Also, the time ( $\tau_n$ ) to increase dry weight by an  $n$ -factor is obtained by replacing the number 2 by  $n$  in Eqs. (11) and (12).

### Weight-specific growth rates and doubling times from assembled time series

Noting the degree over overlap in dry weight among the 4 groups of data at each site, it is possible to construct one continuous time series covering the full range of sizes at each site. As explained for the data from Series #1 in Fig. 9, the procedure consists of first separating the 4 size groups by arbitrary time shifts to facilitate subsequent shifts for optimal overlap and finally shift the assembled time series to maximize the  $R^2$  value of a power law regression Eq. (9) through the data. Then, the weight-specific growth rate as a function of dry weight  $\mu(W)$  is calculated from Eq. (10). Such results are presented in Fig. 10 for the data of Series #1 to #6. The time ( $\tau_2$ ) to double the dry weight ( $W$ ) of a given mussel size calculated from Eq. (12) and based on the analytic equations for regression lines to time series of experimental data from Series #1 to #6 are shown in Fig. 11 and compared to the growth model (dashed lines) obtained from Eqs. (11) and (3) corresponding to constant levels of chl  $a$  (from 2 to 4  $\mu\text{g l}^{-1}$ ). As a result of the procedure, the data points fall exactly on the straight lines of the analytic solution but they are nevertheless shown to indicate the experimental size range corresponding to that of the data in Fig. 10.

Comparing the variation of slopes of regression lines of the size class data  $\mu(W_{\text{avg}})$  presented in Fig. 5 to those of the assembled time series  $\mu(W)$  in Fig. 10 suggests a beneficial smoothing effect of the latter procedure of data reduction. The experimental design of studying several (4) size groups simultaneously over a limited period of time to ensure overlapping size ranges is novel to our knowledge and is an efficient approach to obtain growth histories covering a large size range at the same relatively uniform environmental conditions.

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