Journal of the Marine Biological Association of the United Kingdom, 2011, 91(1), 181–189.
doi:10.1017/S0025315410001402

Larval body size–mass relationships of barnacles common to the English Channel coast of the UK

E. MUXAGATA[1] AND J.A. WILLIAMS[2]

[1]Universidade Federal do Rio Grande—FURG, Laboratório de Zooplâncton, Instituto de Oceanografia, Avenida Itália, km8, Campus Carreiros, Caixa Postal 474–96201-900, Rio Grande, RS—Brazil, [2]School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, Southampton, European Way, SO14 3ZH, Southampton, United Kingdom

The study presents dry mass and body measurements of the larval stages of five common barnacle species occurring in meso-zooplankton catches of Southampton Water and the central Solent area of the south coast of the UK. Quantitative samples were collected with conventional 120-μm mesh plankton nets. Species-specific regression equations relating carapace width and total length with dry mass were obtained for stage II to stage VI nauplii and cyprids of Austrominius modestus, Amphibalanus improvisus, Balanus crenatus, Semibalanus balanoides *and* Verruca stroemia. *Width–dry mass and length–dry mass regressions obtained in the present study accounted for more than 98% of the variability for naupliar stages, and length–dry mass for 80% of the variability for cyprids. The dry mass of barnacle larvae predicted from carapace width equations determined here differed by only –6% from the measured dry masses of an independent data set, suggesting these first-reported equations of barnacle larvae are useful additions to zooplankton production studies.*

Keywords: body size–mass relationships, barnacle larvae, cirripedia, meroplankton, *Austrominius modestus*, *Amphibalanus improvisus*, *Balanus crenatus*, *Semibalanus balanoides*, *Verruca stroemia*

Submitted 23 December 2009; accepted 5 July 2010; first published online 27 September 2010

INTRODUCTION

The measurement of secondary production is one of the primary goals of zooplankton research (Runge & Roff, 2000), since such population level estimations are necessary for assessments of the total community productivity (Greze, 1978; Kimmerer, 1987), and are also the basis for the elaboration of general theories of biological productivity (Downing, 1984).

Several methods for the estimation of secondary production are available (Pechen *et al.*, 1971; Winberg *et al.*, 1971; Downing, 1984; Kimmerer, 1987; Omori & Ikeda, 1992), and the great majority of them require information on the biomass of the individuals. Zooplankton biomass can be measured using conventional volumetric or gravimetric methods as well as by biochemical approaches (Postel *et al.*, 2000), although gravimetric dry mass determination is one of the most widely used (Beers, 1966; Lovegrove, 1966; Omori, 1978; Hay, 1984; Giguère *et al.*, 1989; Bradford-Grieve *et al.*, 1998).

Dry mass determinations of zooplanktonic species is time consuming, involving the labour-intensive tasks of sorting, identification and accurately measuring the different developmental stages of the species present in the plankton. With sufficient material of a particular species and/or stage available, strong regression equations relating body measurements and mass can be established for easier assessment of biomass (Bird & Prairie, 1985).

Corresponding author:
E. Muxagata
Email: e.muxagata@gmail.com

Species specific length–dry mass relationships are available for several copepod species from a range of environments and geographical locations (Landry, 1978; Pearre, 1980; Uye, 1982; Uye *et al.*, 1983; McCauley, 1984; Middlebrook & Roff, 1986; Chisholm & Roff, 1990; Webber & Roff, 1995; Hopcroft *et al.*, 1998; Ara, 2001). No similar data are available, however, for barnacle larvae which are accepted to be a major component of the coastal meroplankton community, and adults of the species in this study, *Austrominius modestus* (Darwin), *Amphibalanus improvisus* (Darwin), *Balanus crenatus* Bruguière, *Semibalanus balanoides* (L.) and *Verruca stroemia* (O.F. Müller) are commonly found in the Solent and along the central English Channel coastline (Herbert, 2001; Herbert *et al.*, 2007; Herbert & Muxagata, 2009).

Barnacle larvae are, in fact, the second most abundant group within the zooplankton of Southampton Water, averaging 13% of the total zooplankton population, and accounting for up to 60–80% on some occasions (Muxagata *et al.*, 2004; Muxagata, 2005). The present study presents body mass and species-specific length–mass regression equations for the five most common barnacle larvae found in zooplankton catches within Southampton Water.

MATERIALS AND METHODS

Samples used in this study were collected at three fixed sites, marked by permanent shipping buoys within Southampton Water and the central Solent (Figure 1) in March 2001, April 2001, May 2001, June 2001, August 2001, April 2002

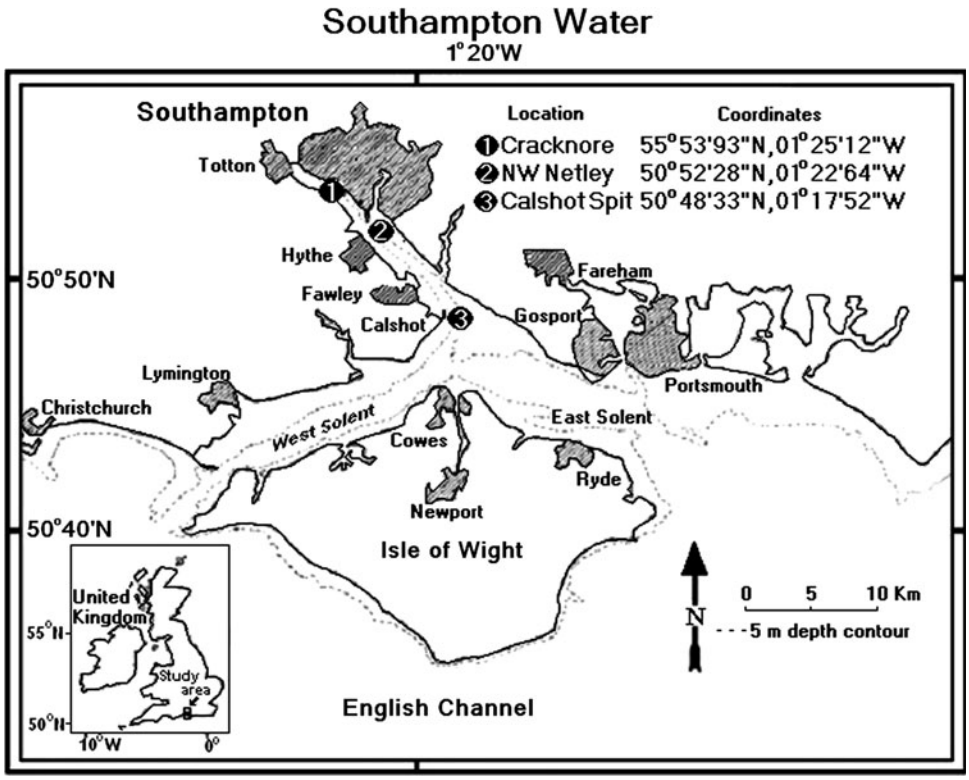

Fig. 1. The Southampton Water study area, with indication of sampling sites during 2001–2002.

Table 1. Number (N) of nauplii and cyprids from a particular sampling site and date of collection that were used in each biomass determination, with rep. indicating the number of replicates made for each determination.

Stages	*Austrominius modestus* (16 July 2002) Cracknore		*Balanus crenatus* (9–25 April 2002) Calshot		*Amphibalanus improvisus* (16 July 2002) Cracknore		*Semibalanus balanoides* (4–10 April 2001) north-west Netley		*Verruca stroemia* (4–10 April 2001) Calshot	
	N	rep.	N	rep.	N	rep.	N	rep.	N	rep.
N II	1000	4	1000	4	1000	2	700	3	1000	2
N III	800	4	500	4	800	2	265	2	356	2
N IV	500	4	200	4	500	3	142	2	240	1
N V	200	4	100	4	200	4	100	4	90	1
N VI	100	4	100	4	100	2	100	4	25	1
Cyprid	100	2	50	2 + 2*	25	1*	50	4 + 1*	–	–

Note: the + sign indicates that replicates with cyprids with two different sizes were utilized due to relatively larger individuals found through the season (see different sizes in Table 3); *, for *B. crenatus* cyprids from 22 June 2001 from Calshot and 9–25 April 2002 from north-west Netley were used; for *S. balanoides* cyprids from 23 March 2001, 4–10 April 2001 and 18 May 2001 from Cracknore and north-west Netley were used; for *A. improvisus* cyprids from 20 August 2001 were used.

and July 2002 as part of a wider study focused on zooplankton secondary production (Muxagata, 2005). The stations were sampled during the extended 2–3 hour period of slack water around high tide, characteristic of Southampton Water, previous studies (Mujica, 1999) having established that barnacle larvae were more common in the water column during slack-ebb tide. Samples from quantitative, oblique tows of ~50 m^3 performed with a conventional 120-μm mesh cod-end plankton net were collected and preserved in 4% formaldehyde–seawater buffered with borax (Steedman, 1976). No significant differences were noted in the pattern of carapace width (CW) and total length (TL) measured at each site (Muxagata, 2005), and data presented in this study are from single site samples.

Cirripedia were identified to species level (Bassindale, 1936; Pyefinch, 1948, 1949; Knight-Jones & Waugh, 1949; Jones & Crisp, 1954; Crisp, 1962; Lang, 1980; Branscomb & Vedder, 1982; Lee *et al.*, 1998), and were sorted to larval stage in accordance with the definitions presented in Lang (1979). Additional information on the study area and collection/processing protocols can be found in Muxagata *et al.* (2004), Muxagata (2005) and Williams & Muxagata (2006).

For dry mass (DM) determinations, between 25 cypris and up to 4000 nauplii of a particular size/stage (Table 1), were sorted from the samples after at least 1 year of preservation to allow necessary time for the individuals to reach equilibrium volume and weight (Ahlstrom & Thrailkill, 1963; Beers, 1976, 1981). Pre-counted batches of 25–1000 nauplii,

https://doi.org/10.1017/S0025315410001402 Published online by Cambridge University Press

Table 2. Comparison of dry masses (μg) of fresh and preserved (4% borax buffered formaldehyde solution) late stages larvae of *Austrominius modestus*.

Stage	N fresh/ preserved	Average mass (μg) DM ± SD (n)		% dry mass loss
		fresh material	preserved	
V	200/200	1.29 ± 0.08 (5)	1.01 ± 0.09 (4)	21.67%
VI	100/100	2.08 ± 0.11 (6)	1.88 ± 0.07 (4)	9.59%
Cypris	50/100	3.68 ± 0.31 (5)	2.83 ± 0.19 (2)	23.21%

DM, dry mass; SD, standard deviation; N, number of organisms utilized in each replica; n, number of replicates.

from a single day or from consecutive samples in the same month (Table 1) and 25–100 cypris of similar sizes from different days (Table 1) were concentrated and pipetted, together with 200–400 μl of the preserving fluid, into 4 ml of de-ionized water for dilution of salts and preserving fluids. After repeating the dilution procedure a second time, the sample was then pipetted into pre-weighed and ashed aluminium vessels of ±200 μl. After the animals settled, as much of the surrounding liquid was removed as possible with a fine pipette. Each sample was oven dried for 16–24 hours at 60°C, and transferred to silica gel desiccators for cooling (Lovegrove, 1966; McCauley, 1984) before weighing on a Mettler MT 5 (±1 μg) balance to determine the DM. Weighing was repeated until reaching stable readings.

Blanks were made with ±200 μl of the last dilution solution of four different batches, and they averaged ±9.2% of the sample mass. Since the amount of surrounding liquid on each determination was variable, but always less than 200 μl, it was decided not to apply any correction. To estimate the effect of preservation on dry mass, the same procedure was applied to freshly-caught, late-stage larvae of *A. modestus*,

Table 3. Mean mass values (μg) of the naupliar stages II to VI + cypris stages of cirripedes, together with the % of ash considered for each stage, and the averaged body measurements of each larval stage used in the biomass analysis.

Stage	CW ± SD (n)	TL ± SD (n)	Average mass (μg)		%ash ±SD	Species
			*DM± SD (n)	**AFDM ± SD (n)		
I	—	—	—	—	—	
II	156 ± 8.4 (10)	364 ± 15.8(10)	0.29 ± 0.01 (4)	0.24 ± 0.01 (4)	17.03 ± 6.25	
III	180 ± 0.0 (10)	390 ± 14.0(10)	0.49 ± 0.05 (4)	0.40 ± 0.04 (4)	17.88 ± 4.00	*Austrominius modestus*
IV	216 ± 8.4 (10)	428 ± 14.0(10)	0.77 ± 0.70 (4)	0.65 ± 0.06 (4)	15.25 ± 6.82	
V	262 ± 6.3 (10)	478 ± 22.0(10)	1.20 ± 0.09 (4)	1.03 ± 0.08 (4)	13.61 ± 6.41	
VI	314 ± 9.7 (10)	537 ± 13.8(10)	2.23 ± 0.05 (4)	1.90 ± 0.04 (4)	14.57 ± 7.74	
Cypris	—	530 ± 10.5(10)	3.34 ± 0.04 (2)	3.30 ± 0.05 (2)	1.06 ± 0.74	
I	—	—	—	—	—	
II	164 ± 8.4 (10)	438 ± 11.4(10)	0.46 ± 0.01 (4)	0.41 ± 0.01 (4)	11.03 ± 6.27	
III	196 ± 8.4 (10)	486 ± 25.0(10)	0.74 ± 0.05 (4)	0.63 ± 0.05 (4)	14.13 ± 3.68	
IV	250 ± 10.5 (10)	580 ± 16.3(10)	1.48 ± 0.04 (4)	1.18 ± 0.03 (4)	20.30 ± 1.97	*Balanus crenatus*
V	316 ± 12.6 (10)	682 ± 14.8(10)	2.70 ± 0.04 (4)	2.21 ± 0.03 (4)	18.02 ± 4.73	
VI	396 ± 15.8 (10)	800 ± 29.8(10)	5.47 ± 0.58 (4)	4.27 ± 0.45 (4)	21.90 ± 9.59	
Cypris	—	854 ± 14.0(10)	11.49 ± 0.20 (2)	11.15 ± 0.20 (2)	3.01 ± 2.82	
	—	650 ± 42.4(10)	6.50 ± 0.01 (2)	6.19 ± 0.0 (2)	4.73 ± 3.61	
I	—	—	—	—	—	
II	144 ± 8.4 (10)	318 ± 14.8(10)	0.27 ± 0.03 (2)	0.20 ± 0.02 (2)	25.05 ± 3.85	
III	180 ± 0.0 (10)	354 ± 19.0(10)	0.46 ± 0.00 (2)	0.36 ± 0.00 (2)	20.46 ± 0.01	*Amphibalanus improvisus*
IV	222 ± 6.3 (10)	416 ± 15.8(10)	0.76 ± 0.03 (3)	0.62 ± 0.02 (3)	18.90 ± 4.00	
V	294 ± 13.5 (10)	493 ± 14.9(10)	1.42 ± 0.06 (4)	1.18 ± 0.05 (4)	17.12 ± 0.75	
VI	380 ± 0.0 (10)	600 ± 0.0 (10)	2.87 ± 0.25 (2)	2.34 ± 0.21 (2)	18.44 ± 4.34	
Cypris	—	530 ± 0.0 (10)	4.90 (1)	3.88 (1)	20.69	
I	—	—	—	—	—	
II	196 ± 8.4 (10)	472 ± 19.3(10)	0.69 ± 0.02 (3)	0.56 ± 0.02 (3)	18.23 ± 2.29	
III	230 ± 10.5 (10)	557 ± 21.1(10)	1.11 ± 0.06 (2)	0.86 ± 0.05 (2)	22.37 ± 4.13	
IV	313 ± 16.4 (10)	678 ± 19.9(10)	2.47 ± 0.15 (2)	2.01 ± 0.12 (2)	18.97 ± 1.02	*Semibalanus balanoides*
V	398 ± 35.8 (10)	798 ± 61.4(10)	5.56 ± 0.51 (4)	4.49 ± 0.42 (4)	19.22 ± 5.42	
VI	505 ± 33.1 (10)	1008 ± 37.9(10)	10.41 ± 0.23 (4)	8.51 ± 0.18 (4)	18.31 ± 2.39	
Cypris	—	797 ± 18.9(10)	9.79 ± 0.37 (4)	9.21 ± 0.35 (4)	5.93 ± 2.47	
	—	930 ± 49.2(10)	23.19 (1)	21.80 (1)	6.01	
I	—	—	—	—	—	
II	180 ± 0.0 (10)	408 ± 10.3(10)	0.33 ± 0.03 (2)	0.25 ± 0.03 (2)	25.17 ± 6.76	
III	204 ± 15.8 (10)	452 ± 27.0(10)	0.49 ± 0.02 (2)	0.37 ± 0.01 (2)	23.20 ± 2.17	*Verruca stroemia*
IV	242 ± 17.5 (10)	468 ± 23.5(10)	0.79 (1)	0.55 (1)	30.00	
V	297 ± 16.3 (10)	545 ± 15.8(10)	1.32 (1)	1.15 (1)	12.94	
VI	360 ± 18.9 (10)	660 ± 18.9(10)	3.06 (1)	2.50 (1)	18.18	
Cypris	—	—	—	—	—	

DM, dry mass; AFDM, ash free dry mass; CW, carapace width (μm); TL, total length (μm);
SD, standard deviation; —, not available; n, number of organisms measured/or replicates (the number of larvae utilized for each dry mass replica in this work can be seen in Table 1); *, DM values are corrected values by 18.15% due to formalin preservation; **, AFDM were obtained subtracting the measured % of ash from corrected DM values.

https://doi.org/10.1017/S0025315410001402 Published online by Cambridge University Press

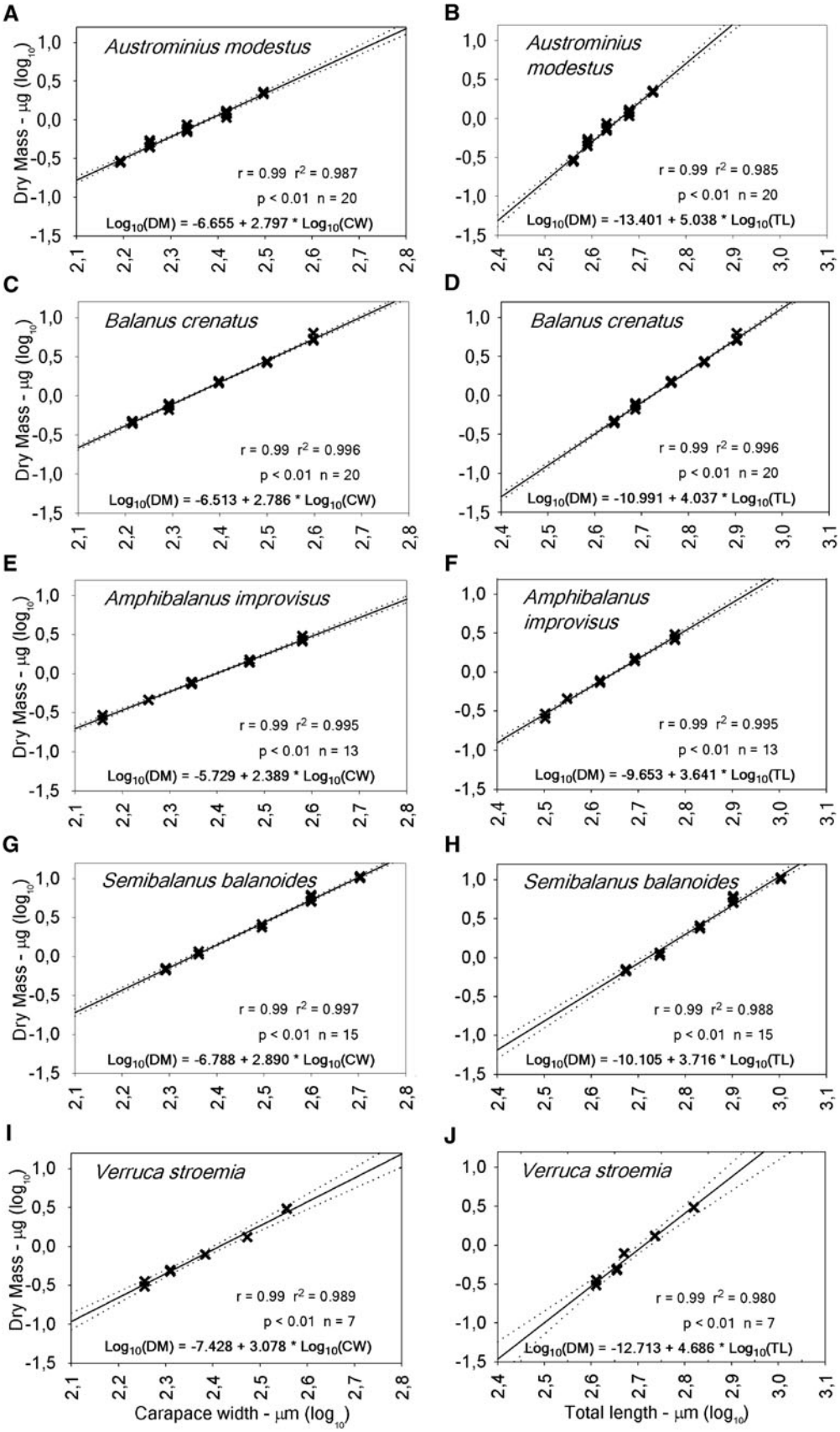

Fig. 2. Simple regression analysis between dry mass values with carapace width (left) and also with total length (right) measurements for naupliar stages (II to VI) of the 5 barnacle species considered. Regression equations are also shown. DM, dry mass (µg individual^{-1}); CW, carapace width (µm individual^{-1}); TL, total length (µm individual^{-1}); r, correlation coefficient; r^2, coefficient of determination; p, significance level; n, number of data points. Solid line indicates the resulting equation and broken line indicates 0.95 confidence interval.

https://doi.org/10.1017/S0025315410001402 Published online by Cambridge University Press

specifically naupliar stages V and VI and cypris of the same sampling day of the preserved specimens and compared with preserved values.

After DM determination, samples were ashed at 500°C (Beers, 1976, 1981), for ±4 hours (Kimmerer & McKinnon, 1987) then placed in silica gel desiccators and weighed on a Mettler MT 5 (±1 μg) balance for ash mass (AM) determination. This procedure was repeated until reaching stable readings. The ash free dry mass (AFDM) of samples was determined after subtracting the % of AM from DM.

For each species, measurements of TL and CW using a micrometric scale (±20 μm), were taken from 10 individuals of each stage prior to DM determination. The relationship between TL and CW with DM of barnacle larvae can be expressed as:

$$DM = aL^b$$

where DM = dry mass, a and b are constants and L is a morphometric measurement, either TL or CW. To stabilize the variance of the data, all three measurements were $\log_{10}$ (x) transformed before analysis (Prepas, 1984; Zar, 1999) resulting in the linearized equation:

$$\mathrm{Log}_{10}(DM) = a + b\mathrm{Log}_{10}(\mathrm{TL\ or\ CW}).$$

Naupliar stage I of all 5 barnacle species, as well as cyprids of *Verruca stroemia* were not considered in analysis as insufficient numbers for DM determinations were obtained. There are no previous DM–length or width relationships for any of those species.

RESULTS

The averaged DM of freshly-caught naupliar stages V and VI and cyprids of *A. modestus* compared with those preserved more than 1 year, indicated losses of 9–23% with an average of 18.15% (±7.46) (Table 2).

Dry mass, AFDM and ash content of each naupliar stage, of the five species considered, after the correction factor of 18.15% was applied, are presented in Table 3.

On a general basis, the DM of the naupliar stages of all five species increased logarithmically with increasing CL and TL, with both measurements strongly positively correlated with DM values (Figure 2). The data used in the species-specific regression equations for naupliar stages were pooled in order to obtain a regression equation for all species considered (Figure 3A, B). This same approach was also used for the cyprids stages (Figure 3C).

DISCUSSION

Despite the potential changes in DM due to formalin preservation, the use of freshly caught material for DM analysis during this work was impractical. The counting and identification of the individuals required for replicate DM measurements from preserved samples often took more than a single day to obtain, and for some stages, weeks were required to obtain numbers necessary for a single replicate.

There is a large body of literature concerning the effects of formalin preservation on zooplanktonic organisms, suggesting that DM losses are most likely to occur depending on the fixative fluid, rinsing method, species composition and

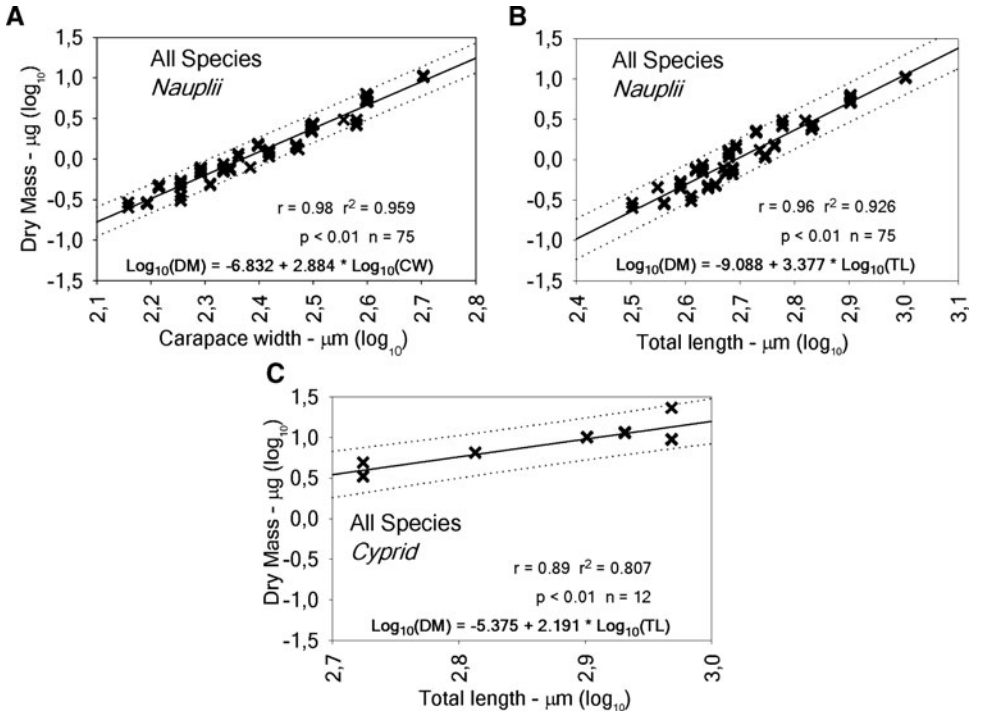

Fig. 3. Simple regression analysis between dry mass values with carapace width (A) and also with total length (B) measurements of naupliar stages (II to VI) of the 5 barnacle species pooled and the simple regression analysis between dry mass values with total length measurements of all cypris stages of the barnacle species pooled (C). Regression equations are shown on each figure. DM, dry mass (μg individual^{-1}); CW, carapace width (μm individual^{-1}); TL, total length (μm individual^{-1}); r, correlation coefficient; r^2, coefficient of determination; p, significance level; n, number of data points. Solid line indicates the resulting equation and broken line indicates 0.95 confidence interval.

https://doi.org/10.1017/S0025315410001402 Published online by Cambridge University Press

Table 4. Mean carapace width (μm) and mass values (μg) of the naupliar stages II to VI and cyprids of *Austrominius modestus* cultured in laboratory at given temperatures and salinities of 30–33 (Harms, 1986, 1987) and the resulting predicted dry mass (DM) values generated using nauplii carapace width equations for *A. modestus* (Figure 2A) and total cypris length equations (Figure 3C) on Harms (1986, 1987) data, together with the % difference to average DM predicted from carapace width (CW) or total length (TL) in this study.

Austrominius modestus							
Stage	**T (°C)**	**(Harms, 1986)[a] CW (μm) ± SD(n)**	**(Harms, 1987) DM(μg) ± SD(n)**	**(Harms, 1986) predicted DM (μg)**	**Difference %**	**Present study CW (μm) average**	**Present study predicted DM (μg) average (% difference)**
I	—	—	—	—	—		—
	6	175 ± 3***	—	0.42*	—		
	9	176 ± 4***	—	0.42*	—	156	0.30* (+3.45%)
II	12	175 ± 4***	0.39 ± 0.03 (27)	0.42*	+7.69%		
	18	179 ± 4***	0.41 ± 0.03 (27)	0.44*	+7.31%		
	24	173 ± 4***	0.39 ± 0.03 (26)	0.40*	+2.56%		
	6	209 ± 4***	—	0.68*	—		
III	9	210 ± 3***	—	0.69*	—	180	0.45* (−8.16%)
	12	209 ± 5***	0.71 ± 0.04 (19)	0.68*	−4.23%		
	18	204 ± 6***	0.75 ± 0.07 (13)	0.64*	−14.67%		
	24	210 ± 3***	0.70 ± 0.14 (8)	0.69*	−1.43%		
	6	252 ± 6***	—	1.15*	—		
IV	9	247 ± 5***	—	1.09*	—	216	0.75* (−2.60%)
	12	264 ± 6***	1.20 ± 0.08 (20)	1.31*	+9.17%		
	18	257 ± 9***	1.47 ± 0.15 (13)	1.22*	−17.01%		
	24	260 ± 5***	1.06 ± 0.10 (15)	1.26*	+18.87%		
	6	317 ± 12***	—	2.19*	—		
V	9	313 ± 8***	—	2.11*	—	262	1.28* (+6.67%)
	12	327 ± 7***	2.45 ± 0.16 (23)	2.39*	−2.45%		
	18	314 ± 9***	2.62 ± 0.18 (20)	2.13*	−18.70%		
	24	311 ± 6***	2.33 ± 0.17 (19)	2.08*	−10.73%		
	6	403 ± 18***	—	4.29*	—		
VI	9	393 ± 11***	—	3.99*	—	314	2.13* (−4.48%)
	12	392 ± 10***	4.27 ± 0.17 (60)	3.97*	−7.03%		
	18	390 ± 9***	5.19 ± 0.18 (39)	3.91*	−24.66%		
	24	367 ± 7***	4.39 ± 0.75 (10)	3.30*	−24.82%		
	6	566 ± 32***	—	4.53**	—		
	9	597 ± 36***	—	5.10**	—	530	3.93** (−17.37%)
Cypris	12	567 ± 14***	4.56 ± 0.48 (20)	4.55**	−0.22%		
	18	583 ± 39***	5.81 ± 0.27 (22)	4.84**	−16.70%		
	24	542 ± 12***	4.38 ± 0.28 (28)	4.12**	−5.94%		

CW, carapace width; DM, dry mass; SD, ± 1 standard deviation; n, number of replicates;*, predicted using equation $Log_{10}(DM)$, $-6.655 + 2.797*Log_{10}(CW)$;**, predicted using equation $Log_{10}(DM)$, $-5.375 + 2.191*Log_{10}(TL)$;***, n not given; cypris values are total length; [a], only measurements on salinity 30 of table 2 of Harms (1986) were considered.

even stage of development (Beers, 1976; Omori, 1978; Böttger & Schnack, 1986; Giguère *et al.*, 1989; Postel *et al.*, 2000). Giguère *et al.* (1989), in an extensive compilation, reported changes of 37 to 43% for total zooplankton, while Buskey (1993) applied a correction factor of 25%. In contrast, Dumont *et al.* (1975) reported losses of only 5 to 10% for a selection of Copepoda, Cladocera and Rotifera, while Chisholm & Roff (1990) did not observe any loss for a selection of tropical copepods. Omori (1978) attributes DM changes primarily to the loss of stored lipids. Based on these reports, a simplistic value for overall loss of ~25% could be argued when using formalin-preserved samples.

The present study's correction factor of 18.15%, determined from comparisons between preserved and freshly caught *A. modestus* larvae of the same size (Table 2) falls within the lower limits of the reported values from literature and close to the 'hypothetical' 25% loss. When the average corrected DM values for each *A. modestus* larvae obtained in this study (Table 3) were compared with the averaged values of laboratory-cultured larvae (Table 4), dry masses between 24 and 57% lower were observed. This could be interpreted to suggest that the correction factor of 18.15% was, in fact, an underestimation of preservation losses. Comparing the Harms (1986, 1987) data with the field values measured in the present study, however, it is clear that the larval DM and CW values of natural populations of *A. modestus* from Helgoland (North Sea) cultured at 6, 9, 12, 18 and 24°C and salinity of 30 under excess food conditions, were usually greater than values from individuals measured in the present study (Tables 3 & 4) that were collected from Cracknore on 16 July 2002 at 18.3°C and salinity of 31.6 (Muxagata *et al.*, 2004). The 24 to 57% DM difference in nauplii is therefore essentially a reflection that the smaller and lighter nauplii found in this study may be simply 'food limited' compared with individuals from laboratory rearing experiments with excess food (Harms, 1986, 1987).

https://doi.org/10.1017/S0025315410001402 Published online by Cambridge University Press

When the DM–width and/or length equations derived in the present study were applied to the Harms data shown in Table 4, differences ranging from +19 to −25% were found, assuming that the width data of each nauplius stage presented in Harms (1986) is linked with the mass data published in Harms (1987). Therefore, an overall averaged difference of −6% could be assumed between the present weight values and the relatively higher values of Harms (1987).

Larval width and length obtained in the present study were measured as accurately and precisely as possible to minimize potential error (McCauley, 1984). The high R^2 values obtained in this study confirm that more than 98% of the variability of DM was accounted for by the morphometric measurements considered for naupliar stages (Figure 2), and more than 80% was accounted for by length measurement of cyprids (Figure 3C). Like the findings of Pearre (1980) for copepods, our predicted dry mass values of all barnacle stages/species (shown in Figures 2 & 3C) from width equations gave slightly better results than those predicted from length.

It is clear that seasonal patterns in environmental parameters and the comparisons of field (food-limited) versus laboratory-reared larvae could have some impact on the differences in biomass identified in this study. Muxagata (2005) reported a 'seasonal' pattern in naupliar TL and CW, with a decrease in measured size toward summer. Regression analysis indicates a clear inverse relationship with temperature only in *A. (Elminius) modestus*, *B. crenatus* and *A. (Balanus) improvisus*. In general, an inverse pattern with temperature and salinity and a positive relationship with chlorophyll were noted in some naupliar stages of all species. An earlier study by Geary (1991) describing the isomorphic growth pattern between *A. modestus* naupliar dry weight and total length also recognized the potential impact of environmental factors on larval size and growth. The study determined a 'condition index' relating dry weight to total length, based on an index for copepod growth (Durbin & Durbin, 1978). The index was seasonally stable, showing that increasing size was matched by increased biomass, but the absolute value of the index was suggested to show an interannual difference, although not statistically tested, reflecting phytoplankton species availability.

Following Chisholm & Roff (1990), the accuracy of the estimates using the equations presented here were checked against the measured values. Predicted DM values of nauplii using width equations differed from measured values on average for all species by −0.02%, while the equations of length differed on average by −2.29% for nauplii and −9.12% for cyprid, and by an average of −6% against the independent data set (Table 4).

While accepting the variability inherent in field-based data, we propose the first-reported, field-based equations generated in this study can be considered accurate, reproducible and valuable as first-step biomass estimates for the larvae of those barnacle species common to English Channel waters, and possibly useful for species with similar carapace widths and lengths in other temperate waters.

ACKNOWLEDGEMENT

E.M. acknowledges the support from Conselho Nacional de Desenvolvimento Científico e Tecnológico CNPq, Brazil with grant 200797/98-0.

REFERENCES

Ahlstrom E.H. and Thrailkill J.R. (1963) Plankton volume loss with time of preservation. *California Cooperative Oceanic Fisheries Investigations Reports* 9, 57–73.

Ara K. (2001) Length–weight relationships and chemical content of the planktonic copepods in the Cananéia Lagoon estuarine system, São Paulo, Brazil. *Plankton Biology and Ecology* 48, 121–127.

Bassindale R. (1936) The developmental stages of three English barnacles, *Balanus balanoides* (Linn.), *Chthamalus stellatus* (Poli), and *Verruca stroemia* (O.F. Muller). *Proceedings of the Zoological Society of London* 106, 57–74.

Beers J.R. (1966) Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea of Bermuda. *Limnology and Oceanography* 11, 521–528.

Beers J.R. (1976) II—Determination of zooplankton biomass. In Steedman H.F. (ed.) *Monographs on oceanographic methodology No 4.—zooplankton fixation and preservation*. Paris: UNESCO Press, pp. 35–84.

Beers J.R. (1981) Determinación de la biomasa del zooplancton. In Boltovskoy D. (ed.) *Atlas del Zooplancton del Atlántico Sudoccidental y métodos de trabajo con el zooplancton marino*. Mar del Plata, Argentina: INIDEP, pp. 133–141.

Bird D.F. and Prairie Y.T. (1985) Practical guidelines for the use of zooplankton length–weight regression equations. *Journal of Plankton Research* 7, 955–960.

Böttger R. and Schnack D. (1986) On the effect of formaldehyde fixation on the dry weight of copepods. *Meeresforschung* 31, 141–152.

Bradford-Grieve J.M., Murdoch R., James M., Oliver M. and McLeod J. (1998) Mesozooplankton biomass, composition, and potential grazing pressure on phytoplankton during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. *Deep-Sea Research* 45, 1709–1737.

Branscomb E.S. and Vedder K. (1982) A description of the naupliar stages of the barnacles *Balanus glandula* Darwin, *Balanus cariosus* Pallas, and *Balanus crenatus* Bruguière (Cirripedia, Thoracica). *Crustaceana* 42, 83–95.

Buskey E.J. (1993) Annual pattern of micro- and mesozooplankton abundance and biomass in a subtropical estuary. *Journal of Plankton Research* 15, 907–904.

Chisholm L.A. and Roff J.C. (1990) Size–weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. *Marine Biology* 106, 71–77.

Crisp D.J. (1962) The planktonic stages of the Cirripedia *Balanus balanoides* (L.) and *Balanus balanus* (L.) from north temperate waters. *Crustaceana* 3, 207–221.

Downing J.A. (1984) Assessment of secondary production: the first step. In Downing J.A. and Rigler F.H. (eds) *A manual on methods for the assessment of secondary productivity in fresh waters (IBP Hand Book 17)*. London: Blackwell Scientific Publications, pp. 1–18.

Dumont H.J., Van de Velde I. and Dumont S. (1975) The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* 19, 75–97.

Durbin E.G. and Durbin A.G. (1978) Length and weight relationships of *Acartia clausi* from Narragansett Bay, R.I. *Limnology and Oceanography* 23, 958–969.

Geary A.P. (1991) *Aspects of the population dynamics and production of cirripede larvae in Southampton Water, with particular reference to* Elminius modestus *(Darwin)*. MSc thesis. University of Southampton, Southampton, U.K.

https://doi.org/10.1017/S0025315410001402 Published online by Cambridge University Press

Giguère L.A., St Pierre J.F., Bernier B., Vézina A. and Rondeau J.G. (1989) Can we estimate the true weight of zooplankton samples after chemical preservation? *Canadian Journal of Fisheries and Aquatic Science* 46, 522–527.

Greze V.N. (1978) Production in animal populations. In Kinne O. (ed.) *Marine ecology—volume IV—dynamics*. New York: John Wiley and Sons, pp. 89–114.

Harms J. (1986) Effects of temperature and salinity on larval development of *Elminius modestus* (Crustacea, Cirripedia) from Helgoland (North Sea) and New Zealand. *Helgoländer Meeresuntersuchungen* 40, 355–376.

Harms J. (1987) Energy budget for the larval development of *Elminius modestus* (Crustacea: Cirripedia). *Helgoländer Meeresuntersuchungen* 41, 45–67.

Hay D.E. (1984) Weight loss and change of condition factor during fixation of Pacific herring, *Clupea harengus pallasi*, eggs and larvae. *Canadian Journal of Fisheries and Aquatic Science* 25, 421–433.

Herbert R.J.H. (2001) *Testing hypotheses related to changes in abundance and distribution of warm-temperate invertebrates on rocky shores along the south coast of England*. PhD thesis. University of Southampton, Southampton, U.K.

Herbert R.J.H., Southward A.J., Sheader M. and Hawkins S.J. (2007) Influence of recruitment and temperature on distribution of intertidal barnacles in the English Channel. *Journal of the Marine Biological Association of the United Kingdom* 87, 487–499.

Herbert R.J.H. and Muxagata E. (2009) Barnacles (Crustacea: Cirripedia) of the Solent and Isle of Wight. *Proceedings of the Isle of Wight Natural History and Archaeology Society* 24, 42–56.

Hopcroft R.R., Roff J.C. and Lombard D. (1998) Production of tropical copepods in Kingston Harbour, Jamaica: the importance of small species. *Marine Biology* 130, 593–604.

Jones L.W.G. and Crisp D.J. (1954) The larval stages of the barnacle *Balanus improvisus* Darwin. *Proceedings of the Zoological Society of London* 123, 765–780.

Kimmerer W.J. (1987) The theory of secondary production calculations for continuously reproducing populations. *Limnology and Oceanography* 32, 1–13.

Kimmerer W.J. and McKinnon A.D. (1987) Growth, mortality, and secondary production of the copepod *Acartia tranteri* in Westernport Bay, Australia. *Limnology and Oceanography* 32, 14–28.

Knight-Jones E.W. and Waugh G.D. (1949) On the larval development of *Elminius modestus* Darwin. *Journal of the Marine Biological Association of the United Kingdom* 28, 413–428.

Landry M.R. (1978) Population dynamics and production of a planktonic marine copepod, *Acartia clausii*, in a small temperate lagoon on San Juan island, Washington. *Internationale Revue Der Gesamten Hydrobiologie* 63, 77–119.

Lang W.H. (1979) Larval development of shallow water barnacles of the Carolinas (Cirripedia: Thoracica) with keys to naupliar stages. *NOAA Technical Report NMFS Circular* 421, 1–39.

Lang W.H. (1980) Cirripedia: balanomorph nauplii of the NW Atlantic shores. *Fiches d'Identification du Zooplancton, Fiche* 163, 1–6.

Lee C., Shim J.M., Jee Y., Ryu H.Y., Kim B. and Kim C.H. (1998) Larval development of a sessile barnacle *Balanus improvisus* Darwin (Cirripedia: Thoracica). *Journal of Fisheries Science and Technology* 1, 72–78.

Lovegrove T. (1966) The determination of the dry weight of plankton and the effect of various factors on the values obtained. In Barnes H. (ed.) *Some contemporary studies in marine science*. London: George Allen and Unwin Ltd, pp. 429–467.

McCauley E. (1984) The estimation of the abundance and biomass of zooplankton in samples. In Downing J.A. and Rigler F.H. (eds) *A manual on methods for the assessment of secondary productivity in fresh waters (IBP Hand Book 17)*. London: Blackwell Scientific Publications, pp. 228–265.

Middlebrook K. and Roff J.C. (1986) Comparison of methods for estimating annual productivity of the copepods *Acartia hudsonica* and *Eurytemora herdmani* in Passamaquoddy Bay, New Brunswick. *Canadian Journal of Fisheries and Aquatic Science* 43, 656–664.

Mujica C. (1999) *Position maintenance of barnacle larvae in Southampton Water*. MSc thesis. University of Southampton, Southampton, UK.

Muxagata E. (2005) *Seasonal and spatial distribution of the mesozooplankton of Southampton Water with particular reference to the contribution of copepods and barnacle larvae to pelagic carbon flux*. PhD thesis. University of Southampton, Southampton, UK.

Muxagata E., Williams J.A. and Sheader M. (2004) Composition and temporal distribution of cirripede larvae in Southampton Water, England, with particular reference to the secondary production of *Elminius modestus*. *ICES Journal of Marine Science* 61, 585–595.

Omori M. (1978) Some factors affecting on dry weight, organic weight and concentrations of carbon and nitrogen in freshly prepared and in preserved zooplankton. *Internationale Revue Der Gesamten Hydrobiologie* 63, 261–269.

Omori M. and Ikeda T. (1992) *Methods in marine zooplankton ecology*. Malabar: Krieger Publishing Company.

Pearre S. (1980) The copepod width–weight relation and its utility in food chain research. *Canadian Journal of Zoology* 58, 1884–1891.

Pechen G.A., Greze V.N., Shushkina E.A., Galkovskaya G.A. and Winberg G.G. (1971) Methods for estimating the production of populations with continuous reproduction. In Winberg G.G. (ed.) *Methods for the estimation of production of aquatic animals*. London: Academic Press, pp. 95–129.

Postel L., Fock H. and Hagen W. (2000) Biomass and abundance. In Harris R.P., Wiebe P.H., Lenz J., Skjoldal H.R. and Huntley M.E. (eds) *ICES zooplankton methodology manual*. London: Academic Press, pp. 83–192.

Prepas E.E. (1984) Some statistical methods for the design of experiments and analysis of samples. In Downing J.A. and Rigler F.H. (eds) *A manual on methods for the assessment of secondary productivity in fresh waters (IBP Hand Book 17)*. London: Blackwell Scientific Publications, pp. 266–335.

Pyefinch K.A. (1948) Methods of identification of the larvae of *Balanus balanoides* (L.), *B. crenatus* Brug. and *Verruca stroemia* O.F. Müller. *Journal of the Marine Biological Association of the United Kingdom* 27, 451–463.

Pyefinch K.A. (1949) The larval stages of *Balanus crenatus* Bruguière. *Proceedings of the Zoological Society of London* 118, 916–923.

Runge J. and Roff J.C. (2000) The measurement of growth and reproductive rates. In Harris R.P., Wiebe P.H., Lenz J., Skjoldal H.R. and Huntley M.E. (eds) *ICES zooplankton methodology manual*. London: Academic Press, pp. 401–454.

Steedman H.F. (1976) *Monographs on oceanographic methodology No. 4.—zooplankton fixation and preservation*. Paris: Unesco Press.

Uye S. (1982) Population dynamics and production of *Acartia clausi* Giesbrecht (Copepoda: Calanoida) in inlet waters. *Journal of Experimental Marine Biology and Ecology* 57, 55–83.

Uye S., Iwai Y. and Kasahara S. (1983) Growth and production of the inshore marine copepod *Pseudodiaptomus marinus* in the central part of the Inland Sea of Japan. *Marine Biology* 73, 91–98.

Webber M.K. and Roff J.C. (1995) Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. *Marine Biology* 123, 481–495.

Williams J.A. and Muxagata E. (2006) The seasonal abundance and production of *Oithona nana* (Copepoda: Cyclopoida) in Southampton Water. *Journal of Plankton Research* 28, 1055–1065.

Winberg G.G., Patalas K., Wright J.C., Hillbricht-Ilkowska A., Cooper W.E. and Mann K.H. (1971) Methods for calculating productivity. In Edmondson W.T. and Winberg G.G. (eds) *A manual on methods for the assessment of secondary productivity in fresh waters (IBP Hand Book 17)*. Oxford: Blackwell Scientific Publications, pp. 296–317.

and

Zar J.H. (1999) *Biostatistical analysis*. 4th edition. Upper Saddle River, NJ: Prentice-Hall.

Correspondence should be addressed to:
E. Muxagata
Universidade Federal do Rio Grande—FURG
Laboratório de Zooplâncton, Instituto de Oceanografia
Avenida Itália, km8, Campus Carreiros
Caixa Postal 474–96201-900, Rio Grande, RS—Brazil
email: e.muxagata@gmail.com

https://doi.org/10.1017/S0025315410001402 Published online by Cambridge University Press