



Body condition and energy content of shore crab *Carcinus maenas* in a temperate coastal system: temporal variability

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ABSTRACT: The body condition of the shore crab *Carcinus maenas* in a temperate coastal system (western Dutch Wadden Sea) was followed over 14 mo. Fulton's condition factor K , dry weight condition and the percentage of dry weight were determined as indirect indices, while bomb calorimetry was applied to obtain the energy density and total energy, as direct biochemical measures of condition. General linear models identified sex, size and season as relevant regressors explaining observed variance in crab condition, whereas colour morphotype effect was negligible. The seasonal pattern was consistent with the natural cycling in temperature and expected food availability, but the peak in body condition differed depending on the type of measure used: energy peaked in autumn, while morphometric condition was at its highest in winter, uncovering different latencies in the response of direct and indirect indices. Concordant with higher energy investment in reproduction, body condition and energy content of non-ovigerous females were higher than those of males, and egg-bearing females always had the lowest condition values. Energy content of adult females ranged from 16.37 ± 1.30 (winter 2013) to 19.83 ± 0.54 kJ g⁻¹ ash-free dry weight (AFDW) (autumn 2013), attaining 18.77 ± 1.22 kJ g⁻¹ AFDW prior to the onset of reproduction in 2012, while maximum energy density of ovigerous females (eggs excluded) was 16.49 ± 0.64 kJ g⁻¹ AFDW. Besides low correlation between indirect and direct indices, fluctuations were more pronounced in the energetic data. Therefore, the morphometric measures seem weak surrogates to estimate energy density of these crabs.

KEY WORDS: Fulton's K · Condition indices · Energy density · Calorimetry · Energy allocation · Wadden Sea

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1. INTRODUCTION

Temperate intertidal systems are harsh environments for organisms inhabiting them due to their strong fluctuations in environmental conditions which, besides tidal and diel variations, typically present pronounced seasonal variations mainly related to the

cyclic pattern of geophysical factors, temperature and day length. Only a few species can cope with such difficult conditions, which require extensive flexibility in their physiology and behaviour. That is the case for the shore crab *Carcinus maenas*, one of the most common and abundant species in estuaries and shallow coastal systems in its native north-eastern Atlantic

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distribution (Crothers 1968), and more recently, in invaded systems worldwide (Cohen et al. 1995, Darling et al. 2008). European populations of the shore crab are consistently highly abundant, reflecting great reproductive success and physiological plasticity: adult crabs can withstand salinities from 4 to 52‰ (Cohen & Carlton 1995), have a wide thermal tolerance (Cohen & Carlton 1995, Freitas et al. 2007) and are voracious opportunistic omnivores with an extensive list of prey species (Ropes 1968, Elner 1981, Cohen et al. 1995, Baeta et al. 2006). The key role of *C. maenas* in soft sediment habitats has motivated a wealth of studies providing comprehensive information on various aspects of the biology, ecology and life history of crabs, summarized in a recent review (Young & Elliott 2020). However, assessments of the physiological state, particularly the energetic state, of shore crabs are lacking. The physiological state of an animal can provide indications of past foraging success and its ability to cope with environmental pressures (Jakob et al. 1996), and can greatly affect population dynamics.

Simple condition indices have long been used to express the nutritional or health status of animals (Jakob et al. 1996, Stevenson & Woods 2006), often applied to fishes (Grant & Brown 1999, Froese 2006, Ovegård et al. 2012), and less often to crustaceans (Kennish 1997, Moore et al. 2000, Pinheiro & Fiscarelli 2009, Martínez-Calderón et al. 2018). A morphological condition index, such as Fulton's condition factor K , is a whole-animal indicator which relates the weight to the length of the organism. A higher index reflects a healthier animal, as the extra weight is assumed to be related to storing extra reserves to allow for normal healthy physiological condition, growth and reproduction (Kennish 1997, Martínez-Calderón et al. 2018). In contrast, a low or poor morphological condition indicates fewer available energy reserves that may be due to adverse environmental conditions (e.g. food limitation, suboptimal temperature) (Rätz et al. 2000). Adverse biological effects on condition can also occur (Rätz et al. 2000). In soft sediment areas, the shore crab is itself a source of hard substrate for colonization by sessile species such as barnacles; the epibiotic load represents an extra cost expectedly reducing condition in crabs. Parasite infection (e.g. by the rhizocephalan *Sacculina carcini*) can also affect crab condition. Nevertheless, knowledge on the extent of epibiosis and parasitism effects require clear baseline information on natural variations in healthy condition.

Besides morphological indices, physiological or somatic (e.g. hepatosomatic, gonadosomatic indices) and biochemical indices can be determined. These

are more time-consuming and lethal methods, and, in the case of biochemical measurements, require more sophisticated laboratory analyses of the proximate composition of the whole body or certain tissues or organs (e.g. hepatopancreas, gonads, muscle). These methods have been used to describe the nutritional state and welfare of marine animals (Fukuda et al. 2001, Stevenson & Woods 2006), including crustaceans (Kennish 1997, Lucić & Erben 2005, Bonilla-Gomez et al. 2012, Brodie et al. 2017). Standard biochemical indices include measurements of nutrient content, energy density and nucleic acid content such as the RNA:DNA ratio (Houlihan et al. 1990, Suthers 1998, Moore et al. 2000, Fukuda et al. 2001, Hufnagl et al. 2010). A combination of methods is advised, as the response of the various indices to environmental conditions may differ (Craig et al. 2000, Gilliers et al. 2004, Amara et al. 2007), although they are expected to be correlated (Suthers 1998, Fukuda et al. 2001, Amara et al. 2007).

This paper is based on a comprehensive investigation of shore crab body condition in the largest coastal wetland system in Europe, the western Dutch Wadden Sea. The present study focussed on assessing which intrinsic and extrinsic factors influence patterns of change in energy content over time. The intrinsic factors here refer to individual-level attributes, including colour morphotype, size, sex and reproductive state, whilst the extrinsic factors refer to environmental conditions, i.e. natural cycles in temperature and food availability. Other extrinsic factors such as infection by *S. carcini* and epibiosis will be dealt in the following 2 studies. The objective of the present study was to provide basic information for future comparisons by calculating standard indirect indices, i.e. Fulton's K , dry weight condition and the percentage of dry weight as morphometric indices, and direct condition indices, i.e. body energy, a biochemical measure, determined here by direct bomb calorimetry, for shore crabs to (1) examine seasonal trends in condition, (2) examine the sensitivity of morphological condition indices to changes in energy condition and (3) identify factors contributing to the variation in these indices.

2. MATERIALS AND METHODS

2.1. Sampling

A monthly sampling programme was carried out from August 2012 to March 2014 (except in September 2012 and 2013, October 2013, and January and

February 2014, due to weather constraints) at 3 sites in the Marsdiep tidal basin in the western Dutch Wadden Sea (Fig. 1), along a very slight salinity gradient (Table 1) to guarantee that all population traits (colour morphotype, gender, reproductive state) were represented in the samples. A 2 m beam trawl (single tickler chain, 1 × 1 cm mesh size) was towed by boat at a speed of approximately 60 m min⁻¹. Each haul covered a surface area of at least 900 m². All catches were sorted immediately, and the shore crabs were transported alive to the lab.

2.2. Laboratory procedures

The total carapace width (CW) of sampled shore crabs was measured to the nearest mm with a digital calliper. Shore crabs were sexed according to the sexual dimorphism traits described by Squires (1990) (male: triangular abdomen, third to fifth somites fused; female: subtriangular laterally rounded abdomen, somites not fused). Each individual was classified as 1 of 2 colour morphotypes, green or red, based on the predominant colour of the thoracic sternum (McKnight et al. 2000), and inspected for reproductive condition (presence of eggs in females). The crabs were checked for the presence of epibiont fouling and external parasites such as *Sacculina carcini* and its scars, and fouled as well as infected crabs were excluded from the analysis to avoid bias due to the effects of parasites and epibiosis on shore crab condition.

Each month, about 10 crabs of each sex, colour and size (considering 10 mm CW size classes) were randomly selected for subsequent morphometric and calorimetric analyses. The wet weight of each crab was recorded to the nearest 0.0001 g. All animals were eviscerated and weighed immediately after, to avoid mixing of stomach content in the calorimetry analysis. Shore crabs (whole body excluding stomach and eggs) were dried to a constant dry weight (DW) (for 10 d, at 60°C) and its percentage was calculated (%DW). Two morphological indices were determined: Fulton's condition index K , obtained by dividing the wet weight by CW³; and the DW condition (DWK), obtained by dividing the DW by CW³.

2.3. Calorimetry

The energy density was determined for a subsample of the shore crabs (total 476, Table 2) using an IKA C2000 Basic Calorimeter. After maceration of

each dried crab, the powder sample was pressed in a mortar to build a pellet, and taken into the calorimeter, where it was combusted and analysed for caloric content (cal g⁻¹ DW). The resulting ash was weighed. Complete combustion of samples with ash content higher than 30% is not guaranteed (Cummins & Wuycheck 1971). In *Carcinus maenas*, the inorganic material consists largely of calcium (Adelung 1971), and corresponds to about 40% of the DW, affecting

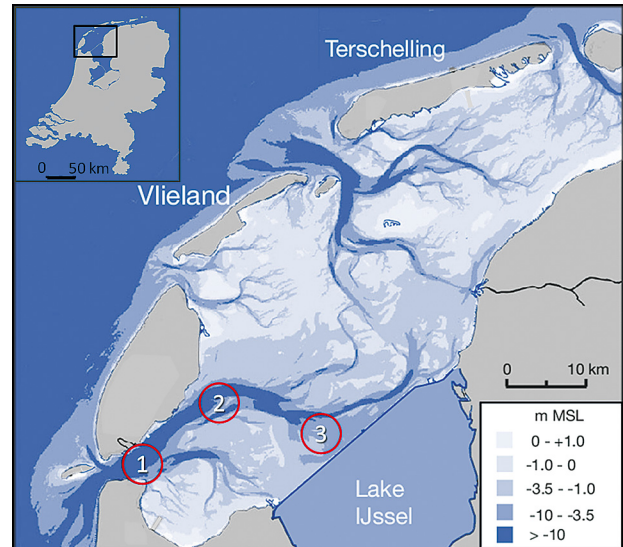


Fig. 1. Sampling locations in the western Dutch Wadden Sea. (1) Gat van der Stier (52° 57.27' N, 4° 55.73' E); (2) Texelstroom (53° 02.03' N, 5° 03.37' E); and (3) Kornwerderzand (53° 04.52' N, 5° 16.55' E). Insert shows the sampling area in the Netherlands (adapted from van Katwijk & Hermus 2000)

Table 1. Summary of observations at each sampling site: mean ± SD salinity; *Carcinus maenas* total abundance and fraction of total catch; percentage relative to total catch of red morphotype crabs, females and ovigerous females; and carapace size (width) range and mean ± SD

	Gat van de Stier	Texel- stroom	Kornwerder- zand
Salinity	24.50 ± 3.31	24.17 ± 2.37	22.63 ± 2.59
Total abundance	1541	2071	3112
Fraction of total catch (%)	22	30	48
Red morpho- type (%)	20	6	2
Female (%)	9.8	14.8	14.8
Ovigerous females (%)	3.6	1.2	0.3
Size range (mm)	9.25–88.59	8.86–90.29	4.23–89.69
Average size (mm)	48.19 ± 13.59	41.63 ± 13.88	30.51 ± 13.94

Table 2. Number (and percentage of total sample in parentheses) of *Carcinus maenas* analysed for morphological and energetic condition, by sex (F: female; Fe: ovigerous females; M: males), colour morphotype (G: green; R: red) and season

Sex	Colour	Total	2012				2013			2014
			Spring	Summer	Autumn	Winter	Summer	Autumn	Winter	Spring
F	G	161 (34)	39	4	28	36	33	4	12	5
Fe	G	12 (3)	4	0	2	3	1	0	2	0
M	G	151 (32)	14	14	29	30	26	7	21	10
All	G	324 (68)	57	18	59	69	60	11	35	15
F	R	41 (9)	4	0	14	18	5	0	0	0
Fe	R	79 (17)	42	0	4	33	0	0	0	0
M	R	32 (7)	0	1	7	21	1	0	0	2
All	R	152 (32)	46	1	25	72	6	0	0	2

the calorimetric result since calcium reaction in the calorimeter is endothermic (Topley et al. 1928), i.e. absorbs heat. Therefore, the ash was re-burned at 900°C in a muffle furnace to remove the minerals that could not be removed during the calorimetric burning, and the remaining was weighed again to determine the ash-free dry weight (AFDW). The difference was used to calculate the percentage of calcium, which was then used to correct the energy content values, considering 1.4 cal g⁻¹ as the caloric value of carbonate calcium in calorimetric reactions (Paine 1964). Finally, caloric values were converted to kJ g⁻¹ DW (hereafter E_{DW}) and kJ g⁻¹ AFDW (hereafter E_{AF}). Total energy content (E_{tot}, kJ) was obtained multiplying E_{DW} by the DW of the crab.

2.4. Data analysis

Multiple linear regression analyses were used to assess how shore crab condition (K , DWK , %DW), energy density (E_{AF}, E_{DW}) and total energy (E_{tot}) are affected by (1) colour morphotype (green and red); (2) body size (i.e. CW); and (3) sex and reproductive state (ovigerous females, non-ovigerous females, males), as intrinsic factors; and (4) season/year, as extrinsic factors. Given the observed temperature patterns, months were aggregated into seasons as follows: April–June were defined as spring, July and August as summer, October and November as autumn and December–March as winter (see Fig. 2). Exploratory data analysis showed that relationships between shore crab morphometric condition and energy and body size (the only continuous variable in the model) were curvilinear. Therefore, a quadratic term for shore crab size was added to the model. Next to the full model (with all variables), a parsimonious model was computed using a backward stepwise pro-

cedure. In each step, each model term was tested for significance (likelihood-ratio test), and non-significant terms were removed, starting with the least significant, until all remaining model terms were significant. Besides examining the significance level, the model regressor was considered 'negligible' when the variance explained was <2%.

Given that variables are usually not all independent of each other, sharing some variance and/or interfering with each other, the amount of variance explained by each variable, or regressor, depends on the regressors already present in the model, i.e. on the regressor order in the model formulation. The relative importance of the regressors in the linear model was therefore assessed through the 'lmg' metric (calculated using the R package 'relaimpo'; Gromping 2006), which provides a decomposition of the model-explained variance into non-negative contributions, with the R² partitioned by averaging over orders (as in Lindeman et al. 1980, Gromping 2006).

For the description of the influence of size, 4 size classes were defined as follows: individuals with CW ≤25 mm: juveniles; 25–40 mm: adults A1; 40–55 mm: adults A2; >55 mm: adults A3.

To estimate the sensitivity of the indirect indices (morphological) to variations in the direct ones (energy content), the relationships between them were analysed using correlation tests. Given that none of the variables was normally distributed (Shapiro-Wilk normality test), Spearman correlations and correlation tests between morphological (K , %DW, DWK) and energy variables (E_{AF}, E_{DW}, E_{tot}) were evaluated. A linear model was applied to the variables which had a (highly significant) correlation coefficient higher than 0.800, i.e. E_{AF} in relation to E_{DW}, and DWK in relation to K .

Data analyses were performed with the R statistical software package version 3.5.3 (R Core Team 2019).

3. RESULTS

3.1. Sampling conditions

Water temperature varied significantly during the study ($F=3.97$, $p < 0.05$), from $2.70 \pm 0.60^\circ\text{C}$ (mean \pm SD) in February 2013 to $21.76 \pm 0.35^\circ\text{C}$ in July 2013, following similar patterns at the 3 sites (Fig. 2). Salinity differed between sites ($F = 0.08$, $p < 0.01$), with significantly lower salinities at Kornwerderzand than at Gat van de Stier ($p < 0.01$, Tukey test) (Fig. 2, Table 1). The majority of the sampled shore crabs (6724 in total)

were green males (53.4%), followed by green females (27.7%). Red females (12.0%) were twice as abundant as red males (5.6%); females with eggs represented 5.0% of the total catch (13.0% of all females).

3.2. Generalized linear models

The full linear regression models and the models excluding non-significant variables are presented in Table 3. Total variance explained by most models was 26–34%, except for the %DW for which the model

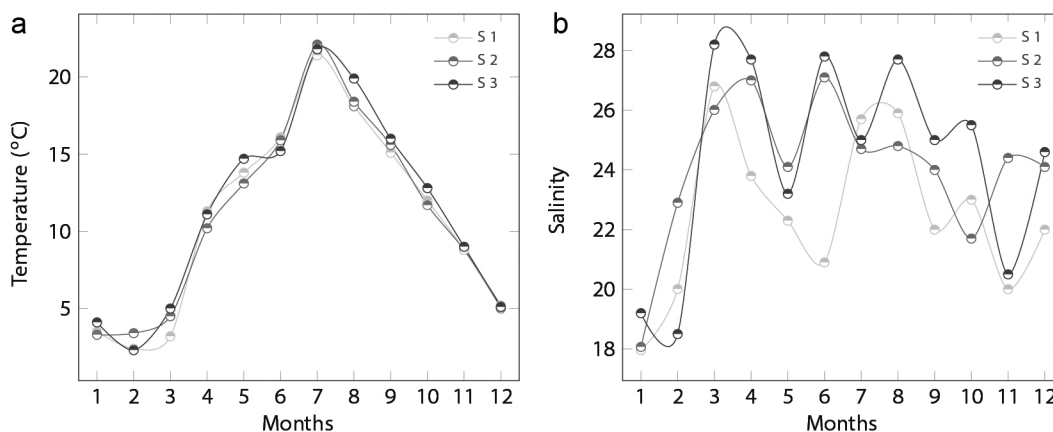


Fig. 2. Mean (a) water temperature ($^\circ\text{C}$) and (b) salinity per month and sampling location in the western Dutch Wadden Sea during 2013. S1, Gat van der Stier; S2, Texelstroom; S3, Kornwerderzand (see Fig. 1)

Table 3. Linear regression model results, presenting the full models (full) and models excluding non-significant (ns) predictor variables through a backward stepwise selection (step); the relative importance of each predictor variable (as % of explained variance, according to the 'lmg' metric) and its significance (p-value, comparing the models with and without that variable through ANOVA), and the total variance explained by each model is given. CW: carapace width; DW: dry weight; DWK: dry weight condition index; K : Fulton's K condition index; E_{DW} : caloric value converted to kJ g^{-1} DW; E_{AF} : caloric value converted to kJ g^{-1} ash-free dry weight (AFDW); E_{tot} : total energy content

Response variable	Model		Predictor variable					Total
			Season/year	Sex	Colour	CW	CW ²	
%DW	Full	%	8.33	3.24	1.50	0.36	0.45	13.89
		p	<0.0001	0.0001	0.0085	ns	ns	<0.0001
DWK	Step	%	8.40	3.07	1.83			13.29
		p	<0.0001	0.0001	0.0023			<0.0001
K	Full	%	2.92	3.54	1.01	12.05	8.00	27.52
		p	0.0047	0.0015	0.0009	<0.0001	<0.0001	<0.0001
E_{DW}	Full	%	2.86	2.05	0.88	14.55	9.77	30.12
		p	0.0017	0.0138	0.0106	<0.0001	<0.0001	<0.0001
E_{AF}	Step	%	7.66	20.04	4.10	1.07	1.27	34.13
		p	<0.0001	<0.0001	ns	0.0005	0.0004	<0.0001
E_{tot}	Full	%	8.04	23.46		1.05	1.26	33.81
		p	<0.0001	<0.0001		0.0008	0.0005	<0.0001
E_{tot}	Step	%	6.78	15.56	1.96	0.85	1.13	26.27
		p	0.0006	<0.0001	ns	0.0135	0.0046	<0.0001
E_{tot}	Full	%	7.08	17.12		0.90	1.15	26.26
		p	0.0005	<0.0001		0.0116	0.0043	<0.0001
E_{tot}	Step	%	7.04	8.04	1.25	31.24	37.01	84.58
		p	<0.0001	<0.0001	0.0048	<0.0001	<0.0001	<0.0001

explained about 14% (and was then considered a poor descriptor of crab condition), and E_{tot} for which the model explained near 85% of the variance. Overall, colour was the least relevant factor: it was either non-significant or resulted in a negligible effect (<2% of the explained variance); season, sex and body size were the most relevant regressors. Size was particularly relevant for E_{tot} , explaining more than 68% of the variance (both the linear and quadratic term of CW have to be considered), and for K and DWK , explaining about 24 and 20%, respectively. In contrast, for the energy density measures E_{DW} and E_{AF} , being standardized for size (by dividing by crab weight), size influence was negligible, explaining less than 1.5% of the variance. Shore crab sex was particularly influential for E_{DW} and E_{AF} , representing more than 20 and 15% of the explained

variance, respectively, and almost negligible for the 3 morphometric indices. Season explained between 2.9 and 8.4% of the variance and was a significant regressor in all models.

3.3. Intrinsic and extrinsic differences in condition

Table 4 presents the range and mean values of the condition indices per colour morphotype, size and sex, while seasonal trends are described separately per gender in Fig. 3. Although 'colour' morphotype, when significant, explained less than 1.5% of the variance, red shore crabs had lower condition values than green ones (mean K of green crabs: 1.41 ± 0.24 , 1.18 ± 0.23 , 1.34 ± 0.33 ; mean K of red crabs: 1.33 ± 0.21 , 1.15 ± 0.38 , 1.30 ± 0.13 , respectively for females,

Table 4. Statistics (minimum, maximum, mean and SD) of the morphological (%DW: % dry weight; DWK: DW condition index; K : Fulton's condition index) and energy (E_{DW} : caloric value converted to kJ g^{-1} DW; E_{AF} : caloric value converted to kJ g^{-1} ash-free dry weight [AFDW]; E_{tot} : total energy content) condition indices of *Carcinus maenas* in relation to significant and non-negligible regressors (sex, colour and size), overall, by sex (F: females; Fe: ovigerous females; M: males), colour (G: green; R: red) and size (juv: juveniles ≤ 25 mm carapace width; A1–A3: adults of 25–40, 40–55 and >55 mm, respectively)

Sex	Colour	%DW				E_{DW}				E_{AF}			
		Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD
F	G	17.46	42.34	32.79	5.00	6.63	15.27	12.07	1.72	10.66	22.66	18.00	1.53
F	R	24.84	41.12	36.58	3.38	7.70	15.75	12.53	2.04	14.58	26.84	18.67	2.03
F	Both			33.59	4.95			12.17	1.79			18.14	1.66
Fe	G	29.15	38.48	33.93	3.16	8.82	11.97	10.56	0.93	15.61	17.56	16.68	0.64
Fe	R	13.47	53.32	31.63	3.85	7.61	11.74	9.48	0.94	14.77	18.74	16.22	0.67
Fe	Both			31.91	3.83			9.62	1.01			16.28	0.68
M	G	15.21	55.18	32.58	4.73	7.70	15.72	11.57	1.50	14.98	23.16	17.64	1.25
M	R	31.52	42.12	35.75	2.36	7.80	14.23	10.93	1.64	14.44	19.84	17.14	1.30
M	Both			33.13	4.57			11.46	1.54			17.55	1.27
All	G			32.73	4.80			11.78	1.63			17.79	1.41
All	R			33.76	4.14			10.61	1.95			17.08	1.65
Total		13.47	55.18	33.07	4.62	6.63	15.75	11.41	1.82	10.66	26.84	17.56	1.53
Sex	Size class	DWK				K				E_{tot}			
		Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD
F	Juv	0.35	2.02	0.66	0.38	1.19	2.21	1.72	0.25	3.20	26.99	9.49	5.88
F	A1	0.30	1.27	0.50	0.13	1.10	2.50	1.46	0.18	7.43	58.49	24.45	11.61
F	A2	0.17	0.63	0.44	0.10	0.80	1.60	1.28	0.17	17.85	125.19	54.60	23.23
F	A3	0.21	0.56	0.39	0.10	0.59	1.46	1.15	0.22	39.71	199.37	98.06	48.61
F	All			0.49	0.18			1.39	0.24			39.41	30.96
Fe	A1	0.30	1.53	0.49	0.25	0.93	2.56	1.46	0.48	10.03	34.31	20.75	6.91
Fe	A2	0.12	0.88	0.35	0.11	0.37	1.91	1.06	0.25	15.26	66.21	33.50	10.92
Fe	A3	0.25	0.37	0.30	0.04	0.83	1.10	0.96	0.10	52.64	89.27	64.62	11.12
Fe	All			0.38	0.17			1.16	0.36			33.56	15.90
M	Juv	0.36	1.34	0.64	0.29	1.43	3.03	1.74	0.47	5.58	39.01	9.77	9.29
M	A1	0.21	1.10	0.49	0.13	0.70	3.04	1.50	0.34	6.59	64.02	21.26	10.74
M	A2	0.29	0.85	0.44	0.09	1.01	1.70	1.30	0.15	23.57	105.29	60.73	21.24
M	A3	0.14	0.60	0.40	0.10	0.60	1.98	1.19	0.20	40.65	293.78	131.48	57.87
M	All			0.45	0.14			1.33	0.30			78.87	66.02
Total				0.45	0.17			1.32	0.30			53.44	50.30

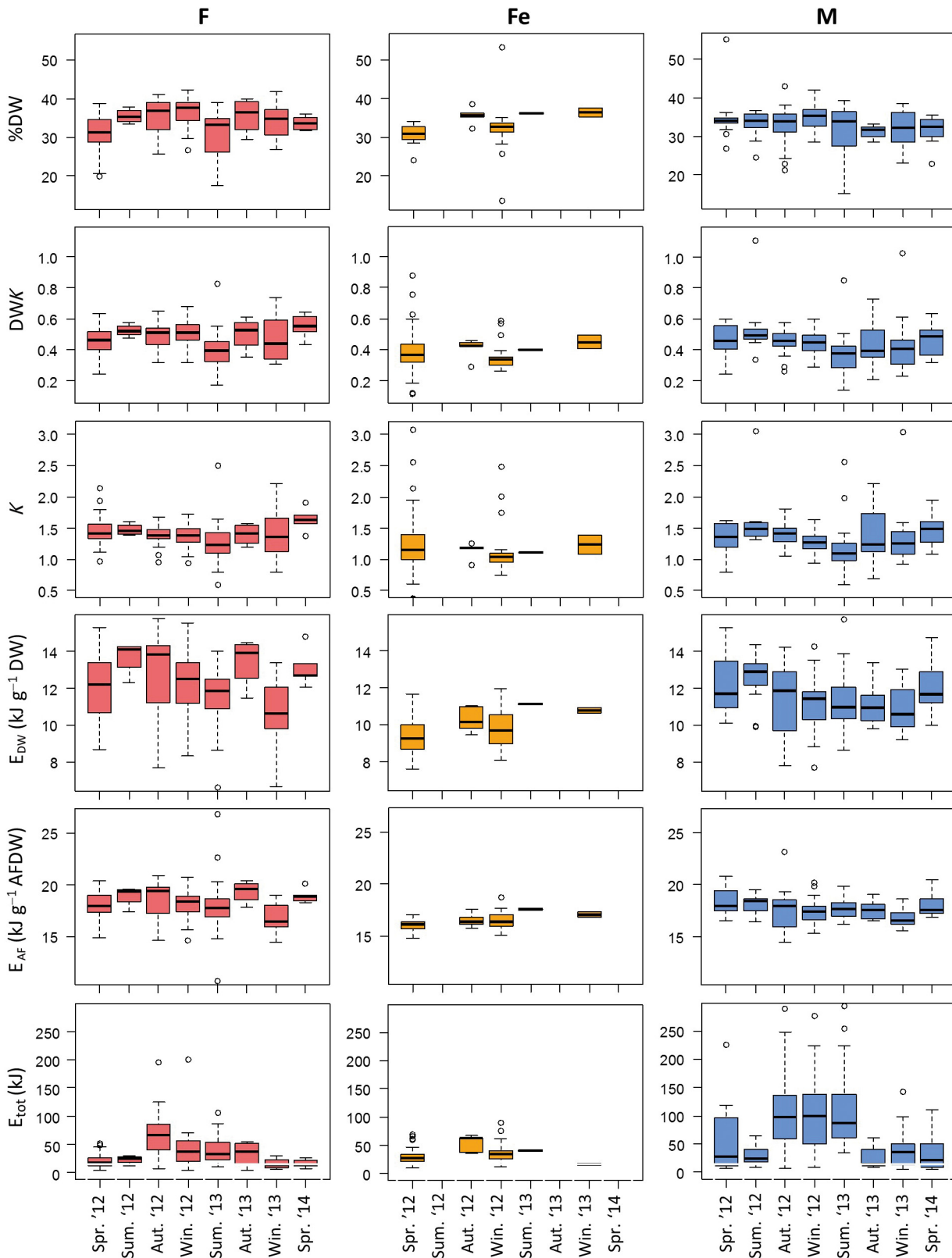


Fig. 3. Seasonal fluctuations in the morphological (%DW: % dry weight; DWK: dry weight condition index; K : Fulton's K condition index) and energy (E_{DW} : caloric value converted to kJ g⁻¹ DW; E_{AF} : caloric value converted to kJ g⁻¹ ash-free dry weight [AFDW]; E_{tot} : total energy content) condition of *Carcinus maenas* by sex (F: females; Fe: ovigerous females; M: males). The line represents the median value, the box is the interquartile range (IQR), comprising the second and third quartiles, the whiskers extend to 1.5× the IQR (though limited by the data range), and the circles are outliers (observations that exceed 1.5× the IQR). The number of animals per season is given in Table 2

ovigerous females and males), except for E_{tot} , female %DW and energy indices, and male DWK and %DW. As expected, E_{tot} increased with increasing size over time reflecting growth, while Fulton's K and DWK decreased; the other indices had inconsistent trends resulting in negligible effect of body size in the models. Although mean E_{tot} of females was half of that of males, overall mean condition of females was higher than that of males (4.3% in K , 1.4% in DWK, 8.2% in %DW, 5.8% in E_{DW} , 7.3% in E_{AF} ; Table 4), and the condition of egg-bearing females was always lower than that of non-ovigerous females and males, both considering the morphometric (up to 6.5% in K , 2.4% in DWK, 5% in %DW) and the energetic indices (up to 21.0% in E_{DW} , 10.3% in E_{AF} , 57.0% in E_{tot}), reflecting the differential investment in reproduction.

Morphometric indices and energetic measures displayed seasonal fluctuations (Fig. 3). Variation in Fulton's K was more pronounced in males, but the general trend was similar in both genders: decreasing from summer 2012 to the following summer, and increasing to peak in spring 2014. The seasonal trends showed some consistency between E_{DW} and E_{AF} . In females, E_{AF} slightly increased from spring to autumn 2012, with a second peak in the autumn 2013, reaching the lowest values in the following winter. Values of energy density of adult females ranged from 16.37 ± 1.30 (mean \pm SD, winter 2013) to 19.83 ± 0.54 kJ g^{-1} AFDW (autumn 2013). Adult females had 18.77 ± 1.22 kJ g^{-1} AFDW in summer 2012 prior to the onset of reproduction (autumn). For adult males, highest values of E_{AF} were recorded in spring/summer 2012 (18.48 ± 1.39 kJ g^{-1} AFDW) and also decreased up to the winter 2013 (min 16.82 ± 0.93 kJ g^{-1} AFDW). Egg-bearing females always had lower E_{AF} (and E_{DW}) values than the other females and males. Maximum E_{AF} of females with eggs was recorded in autumn/winter 2012 (16.49 ± 0.64 kJ g^{-1} AFDW) and summer 2013, with minimum values observed in spring 2012. The same general trends were observed in the E_{DW} . The interannual pattern of E_{tot} differed, with higher values observed from autumn 2012 to summer 2013 in males, prolonging to autumn 2013 in females.

3.4. Correlation between morphometric and energetic indices

Correlations between the studied variables are presented in Table 5. While E_{tot} was only slightly correlated with the other energy variables, the 2 energy density variables (E_{DW} and E_{AF}) and the 2 morphometric variables (K and DWK) were highly positively

correlated. In contrast, the energy variables were not correlated with K and only slightly correlated with DWK. All regression equations between the condition variables had $r^2 < 20\%$, except the equation relating E_{AF} and E_{DW} , which is useful to compare with previous publications where E_{AF} is seldom determined: $E_{\text{AF}} = 6.793 + 0.944 \times E_{\text{DW}}$ ($r^2 = 0.79$, $p < 0.0001$, $N = 476$), and the equation relating DWK and K : $\text{DWK} = 0.022 + 0.315 \times K$ ($r^2 = 0.85$, $p < 0.0001$, $N = 476$).

4. DISCUSSION

The present work demonstrated fluctuations in the morphological and physiological condition of *Carcinus maenas* from the temperate western Wadden Sea population. These fluctuations were related to environmental conditions, reflected in important seasonal changes, and in differences related to intrinsic biological traits of the shore crabs (sex, size and colour morphotype). Since the energy content is directly related to the nutritional status of an animal and responds more pronouncedly to stressors, it constitutes a better metric to analyse fluctuations in shore crab body condition than indirect morphometric indices.

4.1. Morphometric indices as surrogates of energy content

Even though morphometric and energetic indices were positively correlated, the correlation was very weak, indicating that the former, which are more easily determined, are not good predictors of the energy density of shore crabs. The correlation between the %DW and the energy indices was slightly higher, but their models were the worst in explaining the observed variance. The other 2 morphometric indices (K and DWK) showed identical trends, and hence a single one can be used; the same can be said in relation to the 2 energy density indices (E_{DW} and E_{AF}). Nevertheless, the amplitude of the fluctuations was more pronounced in the energetic condition, suggesting a higher sensitivity to the factors tested in the models. This emphasises the advantage of combining morphometric information with biochemical or physiological metrics, for a deeper insight on the condition of natural populations.

Fulton's K of the shore crabs from the western Wadden Sea was mostly over 1.00, the value expected for healthy crustaceans assuming isometric growth (Hartnoll 1978); the dry weight condition was

Table 5. Correlation matrix for the morphological and energy variables (abbreviations as in Table 4). Spearman correlations and respective significance test results are given (** $p < 0.001$, ** $0.001 \leq p < 0.01$, * $0.01 \leq p < 0.05$, ns: $p \geq 0.05$), $N = 476$

	K	E_{DW}	E_{AF}	E_{tot}	%DW
E_{DW}	0.089 ns				
E_{AF}	0.087 ns	0.887***			
E_{tot}	-0.147**	0.128**	0.107*		
%DW	-0.009 ns	0.401***	0.383***	0.330***	
DWK	0.921***	0.249***	0.236***	-0.031 ns	0.360***

about one-third of Fulton's K , which is in line with the expectations of about 70% of water content. Although isometry is common in decapods after settlement (Martínez-Calderón et al. 2018), significant changes in the allometry of various parts of the *C. maenas* body have been documented (Crothers 1967, Hartnoll 1974, 1978), including the stomach size (Griffen et al. 2018), and with special reference to the chelae (e.g. Hartnoll 1978, Souza et al. 2019). In contrast, observed energy density values (ranging from 16.2 to 18.7 kJ g⁻¹ AFDW) were in the lower limit of the large range reported for other crustaceans, i.e. from 16.5 to 28.0 kJ g⁻¹ AFDW (Bally 1994, Company & Sarda 1998, Romero et al. 2006, Janas & Brusca 2010), though not as low as 12.7 kJ g⁻¹ AFDW found in the mud crab *Rhithropanopeus harrisi* (Wiszniewska et al. 1998). In the shore crab, the weight of the calcified exoskeleton represents nearly half of the body (about 40%) (Crothers 1967). In this work, the carapace was included in the energy measurements to obtain an overall value of the energy density, assuming that the maintenance of the exoskeleton also requires energy. However, it is expected that the carapace comprises a low energy density (Zwarts & Blomert 1990), justifying the relatively low energy values obtained in the present study. In moulting *C. maenas* (i.e. hard exoskeleton excluded), the energy density is higher (23.0 kJ g⁻¹ DW, ~29.5 kJ g⁻¹ AFDW) (Klein Breteler 1975a).

4.2. Intrinsic variability: influence of sex, size and colour

C. maenas colour morphs display differences in behaviour and physiology, which result in a higher resilience to environmental extremes and a competitive advantage in green morphs (Reid & Aldrich 1989, Reid et al. 1997, Souza et al. 2019) and thus, large differences were expected. However, results were

counter-intuitive: on one hand, red crabs are generally heavier than green crabs (Crothers 1968); as such, Fulton's K was expected to be higher in red shore crabs than in green ones, contrary to the present observations. On the other hand, red crabs have a thicker carapace and heavier chelae (Kaiser et al. 1990), suggesting a lower energy density, because the exoskeleton has less energy density than other softer body parts (Zwarts & Blomert 1990), which was not confirmed in females (see Table 4). Red shore crabs tend to inhabit subtidal areas, and are less abundant in the high intertidal or salt marshes, while green crabs tend to be less restricted (McGaw et al. 1992). Consequently, green morphs are more prone to migrate and forage over more extensive areas (Smallegange et al. 2009), and therefore might have a higher feeding success than red morphs, justifying their higher energetic condition. In fact, red morphs are considered to be dedicated to reproduction (Wolf 1998, Lee et al. 2003), contrasting with green morphs, which allocate more energy to actively moult and grow (Aldrich 1983, Young et al. 2017). Red morphs have a higher metabolic rate (Reid & Aldrich 1989), which increases the energy requirements, in addition to the extra demand for energy to sustain increased aggressiveness in relation to green morphs (Kaiser et al. 1990), and to osmoregulate, as they are inefficient osmoregulators (McGaw et al. 1992, Lee et al. 2003). Thus, the 2 indices presented a differential sensitivity to colour effects. Differences in condition between colour morphotypes, however, were not sufficient to explain the observed variance.

A large influence of size on crab condition was expected, as some traits suggest a correlation between condition and growth (e.g. ontogenetic changes in diet and spatial distribution). In fact, E_{tot} of the crabs increased as they grew larger (in CW): larger animals have higher biomass and hence higher energy content in total. Regarding energy density (both in relation to dry weight, E_{DW} , and to ash free dry mass, E_{AF}), the 2 variables were, by definition, standardized for weight and hence, to a certain extent also standardized for size, resulting in a weaker size influence on their variation. This suggests that energy storage (in density) is relatively independent of size and of size increase (growth), while for Fulton's K , the influence of size may again be related with growth, with the increase in biomass being different than the increase in CW.

For all condition variables considered, significant differences were found between sexes, and were again more pronounced in the direct condition indices. The overall differential investment in repro-

duction in females and males was evident, even though only the reproductive state of females was assessed, and therefore the influence of gonad maturation in males cannot be determined. Regardless of the index, condition was always higher for non-ovigerous females, followed by that of males, and was always lower for egg-bearing females. The intermediate energy density (and morphometric condition) of males was not surprising: on one hand, males were considered together irrespective of their reproductive state, and, on the other hand, higher energy density in females is common in other crustaceans (Cummins & Wuycheck 1971, Wiszniewska et al. 1998), and ovigerous females tend not to feed (Ropes 1968, Baeta et al. 2006, Young et al. 2017). The energy allocated into gonads usually differs between genders because sperm production requires less energy than oogenesis (Lucić & Erben 2005). In *C. maenas*, clutch sizes can be on the order of 10^6 eggs (Broekhuysen 1936, Warner 1977, Audet et al. 2008, Griffen 2014), the production of which is energetically demanding. Furthermore, females carry and nurse the eggs during the first months of development, ranging from 1 to 3 mo (Best et al. 2017), depending on temperature (Broekhuysen 1936, Crothers 1967, Gehrels et al. 2016), with additional energy expenditure. Therefore, females must spend a considerably larger energy share in reproduction than males. This suggests that the condition of crabs responds to the energy investment in reproduction, at least in females.

Prior to reproduction, females must take up and store large amounts of energy which will be transferred to the eggs. The difference in energy density between the highest values of adult females before the beginning of the reproductive season (18.77 kJ g^{-1} AFDW in summer) and the lowest values of similar sized egg-bearing females with the eggs' energy excluded (16.49 kJ g^{-1} AFDW in autumn/winter), could be considered a proxy of the energy females allocate to reproduction, if we assume similar maintenance energy costs, and is on the order of 2.28 kJ g^{-1} AFDW. However, egg mass energy density can range between 13.23 and 29.91 kJ g^{-1} AFDW, corresponding to a total energy ranging between 1.24 and 20.77 kJ (mean \pm SD $E_{\text{DW}} \approx E_{\text{AF}} = 24.87 \pm 5.21 \text{ kJ g}^{-1}$ AFDW, mean $E_{\text{tot}} = 12.30 \pm 7.39 \text{ kJ}$, $N = 9$; authors' unpubl. data). This is far more than the difference in energy density observed in adult females before and after reproduction, which is natural, as energy is probably allocated into reproduction throughout the previous seasons and not suddenly from one season (summer) to the next (autumn).

4.3. Extrinsic variability: influence of season

Seasonal fluctuations in condition were more pronounced in the energy data, as has commonly been reported in other species (Encina & Granado-Lorencio 1997, Gilliers et al. 2004, Amara et al. 2007), again reflecting a higher sensitivity to the environment than morphometric indices. Seasonality in *C. maenas* dynamics is common throughout the temperate regions in the native geographic range of this species (Klein Breteler 1975b, Aagaard et al. 1995, Baeta et al. 2006, Bessa et al. 2010). Patterns corresponded well to the expected fluctuations in prey availability linked to the temperature cycle (Hislop et al. 1991, Pedersen & Hislop 2001). Spring and summer are periods of prey abundance (Honkoop & Beukema 1997), and these were seasons when the shore crab showed an active weight increase and accumulation of somatic energy, increasing body condition, although energy storage prolonged towards autumn. In contrast, in winter, when crab weight increase is compromised and somatic energy is depleted, food availability and quality are lower due to decreases in abundance and biomass of macrozoobenthic prey species (Zwarts 1991, Beukema & Dekker 2014). Studies in the Dutch Wadden Sea with shorebirds, preying on similar invertebrate prey as crabs, have clearly shown that the seasonal variation in harvestable prey biomass is even larger, due to changes in burial depth (accessibility) and energy content (profitability) of prey in winter (Zwarts & Wanink 1993). Similar seasonal patterns in morphological and energetic condition are commonly reported (Wiszniewska et al. 1998, Yamaguchi 2003, Martínez-Calderón et al. 2018). Yet, the response of the 2 types of indices displayed different latencies. The high energetic condition in the autumn reflects a certain latency in the response, as prey availability is expected to be lower than during summer (Suthers 1998, Gilliers et al. 2004). Fulton's K and DWK displayed a larger response latency, as they were still relatively high in periods of food shortage, as in winter 2013. A time lag in the readjustment of the metabolic rate as a response to abrupt changes in food ingestion has been observed in other species (Grant & Brown 1999).

The shore crab is an opportunistic omnivore, with a very wide diet, preying on organisms from at least 158 genera, including bivalves, gastropods, crustaceans and various fish species (Crothers 1968, Cohen et al. 1995, Baeta et al. 2006). Shore crabs become more carnivorous with age, with adults showing a strong preference for bivalves such as the highly

caloric mussel *Mytilus edulis* (Ropes 1968). Although animals in poor nutritional condition are more likely to actively forage, because they are in greater energy need (Ovegård et al. 2012), the foraging activity of shore crabs can be 15–20 times higher in summer and autumn than in winter (Aagaard et al. 1995). Despite energy costs of migration, part of the *C. maenas* population moves to deeper areas to overwinter (Crothers 1968, Hunter & Naylor 1993, Smallegange et al. 2009), which might have masked differences (e.g. between colour morphs) that were not uncovered in the models. The energy expenditure during feeding is itself a major factor in the energy budget (Houlihan et al. 1990). Yet, it is still not entirely resolved if the preference of crab predation follows the optimal foraging model (Enderlein et al. 2003).

Discontinuous growth complicates the interpretation of nutritional indices in crustaceans. Moulting or ecdysis, i.e. shedding the exoskeleton and forming a new carapace, requires a relevant share of energy (d'Udekem d'Acoz 1993, Sánchez-Paz et al. 2007). This process typically includes the intake of seawater which is later replaced by organic tissue and causes the enlargement of the body. Therefore, the dry weight of the animals changes considerably during the intermoult. The next moult will take place only after achieving a minimum of tissue growth (Adelung 1971). Crabs with low reserves during winter may be inhibited from moulting and growing (Crothers 1967), and severe food limitation restricts the moult increment (Adelung 1971). In contrast, ecdysis is accelerated when conditions are favourable for growth (spring and summer) and condition is higher. During the intermoult, the increase in weight may be partly due to the storage of reserves (Adelung 1971), while the hardening and thickening of the exoskeleton may increase the morphological condition to a still unknown extent. Feeding activity increases prior to periods of moulting, and ceases immediately before and after ecdysis (Ropes 1968, Phlippen et al. 2000). Seasonal fluctuations in temperature are expected to influence the moulting frequency by affecting the rate of the metabolic processes.

As the reproductive state is correlated with season, seasonal trends in condition can also be related with gonad maturation, and may reflect different stages of sexual maturity of an individual, or different energy investment, storage and allocation strategies as frequently observed between genders (Färber-Lorda et al. 2009). The presence of egg-bearing females suggests that the reproductive period of the shore crab extended from autumn to late spring,

confirming previous results for the same area (Broekhuysen 1936). Females as small as 26 mm CW were found with eggs, which is in the minimum size reported for sexual maturity (starting at 26–34 mm) (Mohamedeen & Hartnoll 1989, d'Udekem d'Acoz 1993). The seasonal fluctuations in energy allocation to reproduction of the shore crab may then diverge from the pattern of food availability, as the presence of ovigerous females occurred in periods of expected food scarcity, including winter. Winter was the period of lowest condition (depletion of energy reserves). Despite this divergence, spawning in this period is advantageous for crab broods because it ensures that larvae will hatch at a time (spring and summer) of abundant food and favourable temperatures promoting faster growth. Therefore, most likely a combination of food supply, energy storage and other factors such as salinity or photoperiod, in addition to temperature, are involved in the timing of reproduction of shore crabs, as in other marine invertebrates from temperate latitudes (Starr et al. 1990). Poor condition has been associated with reduced reproductive success and increased natural mortality (Ovegård et al. 2012). Nutrient and energy storage in the hepatopancreas during periods when food is nutritionally rich and most abundant may not guarantee reproductive success, but may be a prerequisite (Kennish 1997). It is not clear if crabs cease feeding during the reproduction period, but both ovigerous females and actively mating *C. maenas* have been found with empty stomachs, suggesting that they do not feed while sexually active (Ropes 1968). Therefore, the shore crab combines features of a 'capital breeder' which stores energy prior to the onset of reproductive activity, with that of an 'income breeder' which acquires most energy from active feeding during the spawning season.

In conclusion, seasonal fluctuations in crab condition were better described through energetic indices, and were in accordance with expected natural food availability and patterns of growth. In contrast, reproductive timing seems not to follow the same pattern, as the energetic investment in reproduction culminates when prey abundance is usually scarce (winter/early spring), although differences in body and energetic condition between ovigerous and non-ovigerous females reflected well the energy investment in reproduction. Further studies are needed on the contribution of seasonality in food quality and abundance to the energy density fluctuations in crabs, which may further explain inter-annual variations.

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