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Latitudinal variation in maternal investment traits of the kelp crab *Taliepus dentatus* along the coast of Chile

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Abstract

Maternal investment (MI), the energy allocated by mothers to offspring, has important effects on the life-history traits of marine organisms. Variation in such traits shows strong correlation with latitude for several marine taxa (Thorson's rule). Large-scale latitudinal variation in MI within a single species suggests population genetic divergence, while temporal changes in MI, rather, reflect plasticity. At higher latitudes (i.e., colder waters), traits associated with MI (brood weight, fecundity, egg volume, and energy content) increase. To identify phenotypic plasticity along a latitudinal gradient in MI traits (brood weight, egg volume, density number, and egg lipid composition), five populations of the kelp crab *Taliepus dentatus* along the coast of Chile (30°S–42°S) were investigated during the summer (December–February) and winter months (June–August) of 2015–2016. Despite this wide latitudinal range, the sea surface temperature (SST) difference between the northernmost and the southernmost sites was only approximately 2.0 °C in winter and 5.5 °C in summer. In summer, when latitudinal variation in SST was highest, brood weight, egg density, fecundity, and egg lipids increased with latitude, while egg volume decreased. No trends in MI were observed in winter when the SST gradient was almost non-existent. These results suggest that the relationship between MI and latitude is shaped by temperature rather than being site-specific. The seasonality of latitudinal MI traits also suggests a trade-off between the costs of female maintenance and/or brooding behaviours and MI. When investigating latitudinal and temporal variation in marine brooder MI, the effect of temperature on life-history traits and the associated costs of female brooding should be quantified.

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Introduction

The type and amount of maternal resources allocated to offspring is an important biological trait with critical ecological and evolutionary implications (Vance 1973; Smith and Fretwell 1974; Marshall and Keough 2007; Marshall and Uller 2007). Maternal investment (MI) is the energy that mothers allocate to reproduction including the energy assigned to produce more or larger eggs, increased egg reserves, or extended parental care of eggs and young (Thiel 1999; Laptikhovsky 2006; Vogt 2013). The energy allocated by mother to offspring, however, is limited, leading to a trade-off between quality and quantity of offspring (Smith and Fretwell 1974). Moreover, such energy investment must sometimes balance conflicting trade-offs between a mother's fitness and the fitness of her offspring. This can make it difficult to identify the evolutionary drivers of spatial or temporal variation in MI (Marshall and Uller 2007).

In the marine realm, MI has been shown to affect egg size, larval developmental rates and success, larval morphology, size of larvae at hatching, and ultimately, adult

performance (Fox 1994; Emlet and Høegh-Guldberg 1997; Moran and Emlet 2001; Oliphant and Thatje 2013; Thatje and Hall 2016). Spatial (i.e., latitudinal) variation in traits associated with MI (e.g., egg size, brood weight, larval size, biochemical composition of eggs, and ventilation of egg brood) has been well documented for a wide range of marine taxa, including crustaceans (Thorson 1950; Christiansen and Fenchel 1979; Strathmann 1985; Lessios 1990; Moran 2004; Levitan 2006; Marshall and Keough 2007). Water temperature is undoubtedly one of the most important factors shaping MI because of its control on rates and energetic costs of most cellular and physiological processes (Schulte et al. 2011); in addition, it typically varies both spatially and temporally (Giménez 2006; Oliphant and Thatje 2013; Gonzalez-Ortegón and Giménez 2014). Specifically, temperature is negatively related to egg size, and this pattern has been well reported in marine organisms, mostly those with indirect development (i.e., taxa with a planktonic larval stage; Marshall et al. 2008; Collin and Salazar 2010). From the equator to the poles, many marine species show an increase in the per-offspring MI (sensu Thatje and Hall 2016), which is reflected in well-provisioned, larger but fewer eggs at higher latitudes (cooler temperatures) compared to related species living closer to the equator (warmer waters; Thorson 1950). Water temperature also influences the biochemical composition of eggs, particularly lipids and proteins (Dahlhoff 2004; Moran and McAlister 2009). The lipid content of embryos generally increases with decreasing temperatures in decapods (García-Guerrero et al. 2003; Tropea et al. 2015), generating a temperature-dependent latitudinal distribution of lipid content, with energy-rich lipids (i.e., triacylglycerols) being more abundant in embryos at higher latitudes (Clarke 1983; Graeve and Wehrtmann 2003).

Within a single species, spatial and temporal variation in MI traits is also common (Thorson 1950; Barnes and Barnes 1965; Urzúa et al. 2012). Spatial variation, especially over large scales, may suggest genetic divergence and/or local adaptation among populations (Lonsdale and Levinton 1985), while temporal variation usually reflects population phenotypic plasticity (Oliphant and Thatje 2013; Urzúa et al. 2012). For example, the distribution of the European anchovy over a wide latitudinal range (northern Europe to South Africa) strongly correlates with mtDNA variation (i.e., clade frequency), suggesting strong local adaptation and high correlation with the temperature difference over the whole species' range (Silva et al. 2014). For several marine invertebrates, temporal variation in the size of offspring has been demonstrated to occur between years and seasons, as well as within a single breeding season (Kattner et al. 1994; Oh and Hartnoll 2004; Urzúa et al. 2012).

Variation in temperature also affects oxygen concentration in seawater, which partially shapes MI traits in marine organisms by affecting adult performance (Strathmann and Strathmann 1995; Fernández et al. 2002; Baeza and Fernández 2002; Deutsch et al. 2015). Among brachyuran crabs, oxygen demand of embryos triggers active and costly brooding behaviours (i.e., ventilation through abdominal flapping) to assure oxygen delivery to the embryo (Naylor et al. 1999; Baeza and Fernández 2002; Fernández and Brante 2003). Brooding behaviour and oxygen demand of brooding females increase with temperature (Brante et al. 2003), and there is a trade-off between the size of egg masses and costs of ventilation in several decapods, including brachyuran crabs (Brante et al. 2003; Reinsel et al. 2014). In the crab *Cancer setosus*, a positive relationship between egg ventilation and temperature as well as a concomitant increase in brood size with latitude (Brante et al. 2003) both suggest that latitudinal changes in temperature may affect female brooding behaviour and brood size. Therefore, the interpretation of latitudinal (temperature) variation in traits associated with MI among populations of marine invertebrates is complex, and needs to consider the effect of predictable variation in environmental factors (e.g., seasons), particularly under a scenario of global warming.

The Chilean coast has a broad latitudinal range in the South Pacific, offering the opportunity to investigate latitudinal variation in ecologically important traits, such as those associated with MI. Over this range, water temperature varies spatially and temporally due to latitudinal and seasonal variation in solar radiation and the intensity of upwelling favourable winds (Strub et al. 1998; Letelier et al. 2009; Tapia et al. 2014). The subtidal kelp-dominated rocky shores of Chile are inhabited by the kelp crab *Taliepus dentatus,* which is reported to have an extensive distribution, from central Peru (11.90°S) to the Chilean Patagonia (51.00°S; Fagetti and Campodonico 1971). Females of *T. dentatus* brood embryos year-round with no clear seasonality in reproduction, although spring/summer has the highest egg production (Fagetti and Campodonico 1971; pers obs). Experimental studies show that the thermal performance of larvae of *T. dentatus* varies significantly with latitude, suggesting local adaptation (Storch et al. 2009). The widespread distribution of *T. dentatus* along the latitudinal cline and the temperature-dependent performance of its larvae allow us to hypothesise that traits associated with MI respond to changes in temperature and may be fixed at extremes of the gradient. Experiments have also shown that females *T. dentatus* (Baldanzi et al. unpubl.) ventilate the egg mass, as do other brachyurans (Naylor et al. 1999; Baeza and Fernández 2002; Fernández and Brante 2003). Thus, oxygen availability to embryos may also be a limiting factor modulating kelp crab MI, as the cost of ventilating egg masses depends on temperature (Brante et al. 2003). Since there is marked seasonal temperature fluctuation along the latitudinal gradient and thus seasonal differences in the costs of brooding, one might expect plastic rather than fixed

MI responses. Since this species is reproductive year-round (Fagetti and Campodonico 1971), it offers an opportunity to examine whether latitudinal patterns in traits associated with MI persist when one of the main environmental drivers weakens or disappears.

We investigated latitudinal and seasonal variation in several MI traits in *T. dentatus* (brood dry weight, egg volume, egg number, egg density, and egg lipid composition), which are expected to differ in response to variation in environmental conditions encountered along this latitudinal cline. We tested the hypothesis that higher mean annual SST at lower latitudes leads to changes in brood attributes (i.e., brood dry weight, egg density, egg number, and lipid composition) due to trade-offs associated with increasing costs of oxygen delivery to brooded embryos (e.g., ventilation) at higher temperatures (Brante et al. 2003; Fernández et al. 2006). If the costs associated with brooding embryos underlie latitudinal/temperature-driven MI patterns (i.e., greater brood weight, denser eggs, and higher lipid content at higher latitudes), we expect such latitudinal trends to weaken or disappear in winter, when SST and the consequent costs of oxygen delivery are more homogeneous, showing phenotypic plasticity in traits associated with MI.

Materials and methods

Sampling area and kelp crab collection

The sampling area ranged between 30°S and 42°S. Locations north of 30°S–33°S were not sampled because of the difference in the upwelling regime (Tapia et al. 2014). Two northern locations were surveyed at 23°S and 20°S, respectively, but no crabs were found among kelp forests. Locations south to 42°S were not surveyed for logistical reasons. Within our sampling area, five locations were chosen based on: (a) Euclidean distance (spacing) to represent a substantial part of the large latitudinal gradient (Fig. 1), (b) general accessibility, (c) presence of kelp forest, and (d) similarity in coastal upwelling conditions (weak upwelling, see Wieters et al. 2003; Narváez et al. 2004; Navarrete et al. 2005; Tapia et al. 2009). From north to south, the sites were: El Frances (FR, S 29.95), Punta de Tralca (PT, S 33.41), Los Cuervos (LC, S 36.73), Los Molinos (LM, S 39.85), and Ancud (AN, S 41.83). At these locations, upwelling is less frequent or never occurs (e.g., upwelling shadows), causing generally warmer surface waters and a stronger seasonal signal. For instance, FR and PT are in "upwelling shadow" areas (Wieters et al. 2003; Tapia et al. 2009), while CU, LM, and AN are in areas where coastal topography and satellite images suggest there is no active upwelling (Atkinson et al. 2002). Across the study area, the trend of decreasing SST with increasing latitude is stronger in summer than winter, a

Fig. 1 Map of Chilean coast showing sampling locations for brooding female *Taliepus dentatus*. *FR* El Frances, *PT* Punta Tralca, *CU* Los Cuervos, *LM* Los Molinos, *AN* Ancud
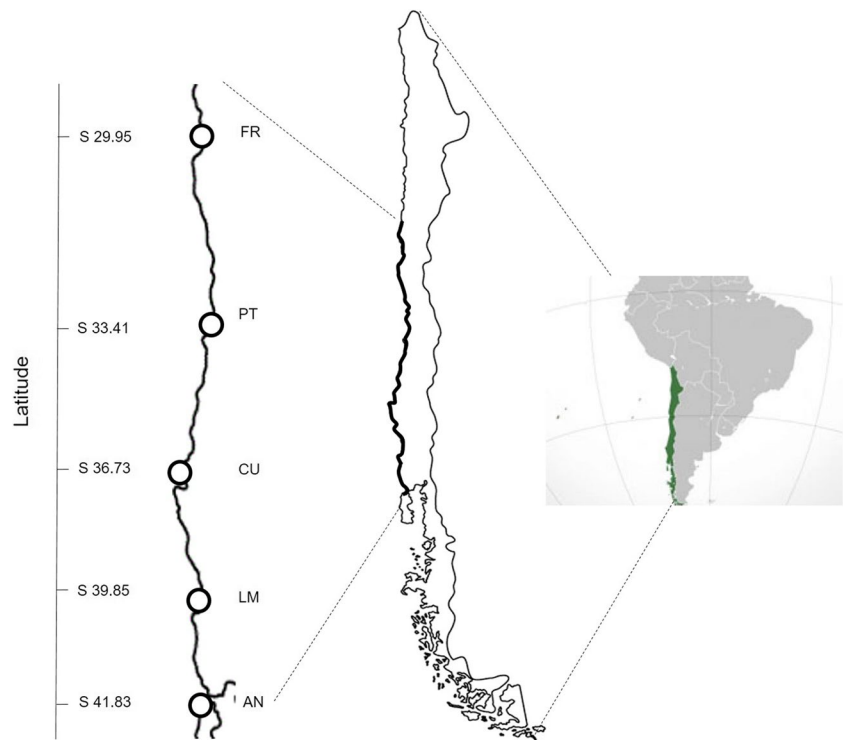
seasonal difference that weakens at sites directly affected by upwelling (Tapia et al. 2014). At each site, kelp crabs were collected by SCUBA divers at depths of 5–10 m, within forests or patches of the kelp *Lessonia trabeculata* (Laminariales, Phaeophyta).

A total of 125 brooding females (5–7 cm of carapace width, see table SUP MAT 1) were collected by hand. Sampling was conducted twice at each site, first during austral summer 2015–2016 (December, January, and February) and again during austral winter 2016 (June, July, and August). Ten females per site and season were haphazardly collected to measure egg volume, brood weight, and fecundity. We only collected females carrying early embryos (with homogeneous yolk, as defined by Vargas 1995) to examine the initial maternal investment (MI) (before the losses during development; Parichy and Kaplan 1992; Lorioux et al. 2012) and to avoid multiple stages of embryos. In summer 2016, five additional females per site were collected to examine egg lipid composition. Crabs were placed in an insulated, ice-filled container and taken to the laboratory within 24 h. In the laboratory, subsamples of about 100–150 mg of embryos were taken from 5 females per population for lipid analysis. The subsamples were placed in glass vials and stored at − 80 °C until further analysis. All other brooding females were stored at − 20 °C until processed (maximum storage time 1 month).

Sea surface temperature data

We obtained 8-day composite (4-km resolution) sea surface temperature (SST) data for all sites from satellite imagery (freely available at ftp://podaac.jpl.nasa.gov/OceanTemperature/modis/L3/aqua) for the respective summer 2015–2016 and winter 2016 seasons. Google Earth (http://www.google.com/earth/download/ge/) was used to select a point 4 km from the coast at each site, around which 9 pixels were used to obtain winter and summer SST averages. The point was chosen by drawing a circle of 4-km radius (using the circle tool in Google Earth) excluding land (Zhang et al. 2007).

Female morphometrics and maternal investment

In the laboratory, four female morphometric traits were measured: carapace length (CL), carapace width (CW), abdomen length (AL), and abdomen width (AW). Following Brante et al. (2004), the whole embryo mass was removed, and females and egg masses were wet-weighed. To obtain dry weights (24 h at 100 °C), we processed the female bodies minus the embryos (female dry weight, FDW) using a microbalance, precise to the nearest 0.0001 g. A few embryos were removed from the egg mass and examined under a stereoscope to confirm the early developmental stage (Vargas 1995).

We used four traits to describe MI: brood dry weight (BDW, g), fecundity (F, number of eggs), egg volume (V, mm^3), and egg density (D, g mm^{-3}). Egg masses were placed individually into 150-mL glass bowls with filtered seawater and stirred thoroughly. Then, three random subsamples of eggs (precisely 0.05 g of egg wet weight, about 200–300 eggs) were taken to estimate egg volume and the total number of eggs (see below). Subsamples were individually placed in a 250-μm mesh, washed with seawater to separate eggs (Tuset et al. 2011), and transferred to a petri dish where eggs were further separated from each other using a fine needle. Each subsample was photographed using a digital camera (CANON PowerShot SX40) installed perpendicularly to the petri dish at a fixed focal distance. Egg volume was obtained from the egg diameter measured in photographs and calculated using the formula for a sphere (see Brante et al. 2004 for the congeneric species *Taliepus marginatus*). For each female, an average of the volume of the eggs was then calculated from the three subsamples and expressed as mm^3 egg^{-1}. The number of eggs in each subsample was counted and used to estimate fecundity (see below). Images were analysed using the software Image-J (developed at the US National Institute of Health and available online at http://rsb.info.nih.gov/ij/).

After photographing, egg subsamples and the remaining egg mass were dried at 100 °C for 24 h and then weighed on a microbalance to the nearest 0.0001 g to estimate total BDW for each female. The fecundity of each female (total number of eggs) was estimated by extrapolating the relationship between number of eggs and dry weight of the subsample to the BDW. The density of the egg mass was calculated using the estimate of female condition (corrected by FDW, see below) and egg volume by simply dividing BDW and egg volume. Density is, therefore, expressed in g mm^{-3}. Density of egg mass has been proposed as a good estimate of body condition and egg quality (Moya-Laraño et al. 2008; Baldanzi et al. 2015).

Egg lipid composition

Eggs in pre-weighed 12-mL glass vials were weighed with a microbalance to the nearest 0.0001 g. Lipid extraction was performed following the process detailed in Folch et al. (1959). One hundred microliters of 23:0 standard solution and 6 mL of dichloromethane/methanol solution (V 2:1) were added. Vials were then placed in an ultrasonic bath for about 60 min at 20–25 °C until egg tissue had completely broken. Thereafter, samples were washed with 2 mL of KCl (0.88%) and centrifuged at 2000 rpm for 5 min; the lipid-containing phase was isolated and transferred in 8-mL pre-weighed glass vials. This step was repeated twice. Subsequently, the organic phase was evaporated under a gentle stream of nitrogen and vials were

weighed with a microbalance to the nearest 0.0001 g. Lipids were resolved in 100 μL of chloroform and transferred to 2-mL glass vials suitable for liquid chromatography. The lipid classes were separated and identified according to Graeve and Janssen (2009) on a monolithic silica column (Chromolith®Performance-Si) using high-performance liquid chromatography (HPLC, LaChromElite HPLC system) with an evaporative light scattering detector (ELSD). Total lipid content in terms of percent dry mass was calculated using the sum of neutral and polar lipids according to Lu et al. (2008).

Data analysis

SST 8-day composite data were averaged for the two sampling seasons, providing an average SST for each site and season. Latitudinal trends in SST were examined using ordinary least square (OLS) linear regressions for winter and summer seasons. Slopes from these regressions measured the rate of linear change in temperature per degree of latitude, and were considered estimates of the magnitude of the SST latitudinal trend. Quadratic polynomials were used to examine whether the trend was non-linear across the region. In all cases, linear trends provided better fits to SST data (see "Results").

As expected, the different morphometric variables (FDW, CW, CL, AL, and AW) were linearly or non-linearly (power) related among themselves and, therefore, any of these alternatives can likely be used to account for the effect of female body size on brood size. We chose FDW as the most representative variable of female size, as it has been used before for several other brachyuran species (Hines 1986; Brante et al. 2004). Strong and significant linear relationships between FDW and BDW ($R^2 = 0.28$; $p < 0.0001$) and between FDW and F ($R^2 = 0.19$; $p < 0.0001$) suggest that dividing these variables by FDW effectively removes the potentially confounding effect of female size on latitudinal patterns.

To characterise latitudinal trends in traits associated with MI, we plotted all variables against latitude for each sampling season and fitted both linear and quadratic regressions using OLS. In this manner, emphasis was placed on the spatial trends for different seasons rather than on the individual sites chosen for the study. The Akaike information criterion (AIC) was used to evaluate which type of regression (linear vs. quadratic) best fitted our data. Separate analyses of covariance (ANCOVAs) were performed for all MI traits (BDW, F, V, and D), with season and latitude as a fixed factor and covariate, respectively.

Lipid classes were obtained from chromatography following Graeve and Jenssen (2009). Six major lipid classes were found (see "Results"), and their concentration in gram corrected by egg dry weight, and, therefore, lipid abundance

was expressed in non-dimensional units. The contribution of each lipid class was then expressed as percentage of total lipids. Based on their molecular characteristics, lipid classes were pooled into polar and neutral lipids (PL and NL, respectively; see "Results"). Latitudinal trends in these lipid fractions per egg were examined through linear and quadratic regressions as explained above for other variables. An analysis of covariance (ANCOVA) was used to compare trends in the concentration of PL versus NL lipid fractions.

Results

Mean SST was negatively related to latitude in both sampling seasons (Table 1, Fig. 2a), but the rate of increase toward lower latitudes more than doubled in summer (0.48 °C/°latitude) than in winter (0.20 °C/°latitude; Table 1 and SUP MAT 1). The seasonal change (ΔSST) was higher at lower latitudes (Fig. 2), which resulted in a significant negative relationship between ΔSST and latitude ($R^2 = 0.81$; $p < 0.05$, data not shown). Seasonal change at the northernmost location (FR) was 4.6 °C and only 1.1 °C at the southernmost location (AN) (SUP MAT 1).

In summer, significant positive linear relationships were found between brood dry weight, fecundity, and density versus latitude; that is, these MI traits increased toward higher latitudes (Table 1, Fig. 3a, c, g). In contrast, there was a significant negative linear relationship between latitude and egg volume (Table 1, Fig. 3e). In winter, none of the MI traits

Table 1 Linear regression analyses (OLS) of sea surface temperature (SST) and MI traits of *Taliepus dentatus* over 12° latitude for summer 2015–2016 and winter 2016

Variables	n	Slope	Intercept	R^2	p values
Summer 2015–2016					
SST	5	− 0.493	32.84	0.97	**0.0017**
BDW	43	0.002	0.023	0.28	**0.0002**
F	43	52.77	591.5	0.11	**0.0318**
V	43	− 0.001	0.287	0.11	**0.0311**
D	43	0.008	0.117	0.32	**0.0001**
NL	19	0.014	0.192	0.42	**0.0023**
PL	19	− 0.002	0.177	0.11	0.1570
Winter 2016					
SST	5	− 0.22	19.73	0.87	**0.0206**
BDW	40	0.001	0.081	0.01	0.4774
F	40	5.589	1761	0.00	0.8023
V	40	0	0.214	0.00	0.9800
D	40	− 0.003	0.394	0.02	0.4244

SST sea surface temperature, *BDW* brood dry weight, *F* fecundity, *V* eggs' volume, *D* density, *n* number of samples, R^2 coefficient of determination

p values in bold are significant ($p < 0.05$)
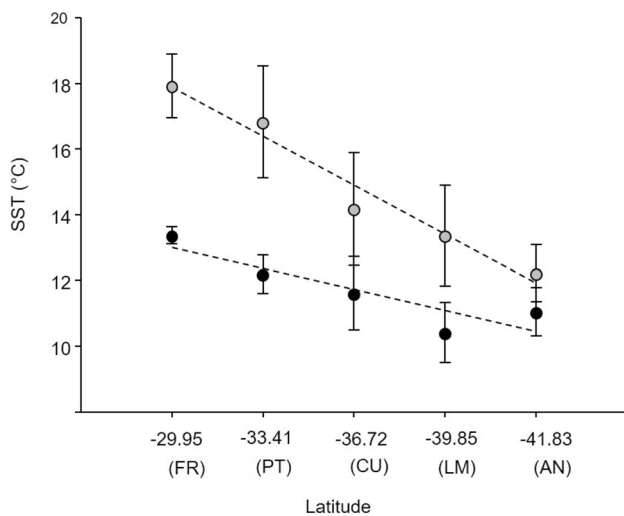
Fig. 2 SST data (mean ± SD) from summer 2015–2016 (grey circles) and winter 2016 (black circles) for each location. Dotted line indicates linear regressions between SST and latitude

were related to latitude (Fig. 3b, d, f, h). Quadratic regressions highlighted a slightly different pattern, with brood dry weight and density being significantly related to latitude in both seasons (SUP MAT 2). In summer, volume and fecundity showed significant and marginally non-significant relationships with latitude, respectively, while, in winter, no relationships were found (SUP MAT 2). Consequently, ANCOVA showed significant interactions between season and latitude (heterogeneous slopes) for brood dry weight and egg density, indicating that the latitudinal change in these proxies occurred only, or primarily, in the summer (Table 2, Fig. 3). Although the same general pattern (i.e., linear relationship with latitude) was observed for fecundity and egg volume (Fig. 3c, d, e, f), the interactions between latitude and season were non-significant for both traits (Table 2), probably because the trend in summer was weaker than for the other MI traits.

Many lipid classes were detected via high-performance liquid chromatography (HPLC), but only the most abundant, present in all samples (total of 6 classes), are shown. Major lipid classes (Table 3) were: triacylglycerols (TAG), cholesterol (Chol), monoacylglycerols (MAG), phosphatidylethanolamine (PE), phosphatidylserine (PS), and phosphatidylcholine (PC). TAG was the most abundant lipid class (FR: 62%; PT: 65%; CU: 70%; LM: 71%; AN: 74%), followed by PC (FR: 25%; PT: 21%; CU: 18%; LM: 15%; AN: 13%) and MAG (FR: 6%; PT: 6%; CU: 7%; LM: 10%; AN: 9%). Other lipid classes were less abundant (Fig. 4). The neutral lipid (NL) (TAG, Chol, and MAG) and polar lipid (PL) (PE, PS, PC) composition followed the north-to-south trend, with NL higher at higher latitudes (FR: 70%; PT: 73%; CU: 79%; LM: 82%; AN: 84%) with a concomitant decrease of PL (FR:

30%; PT: 27%; CU: 21%; LM: 18%; AN: 16%) (Fig. 5a). The abundance of NL increased significantly from lower to higher latitudes, while a non-significant relationship was found for PL (Table 1, Fig. 5b). Consequently, ANCOVA showed significant interactions between lipid fraction and latitude (heterogeneous slopes), indicating that change in lipids occurred only in the neutral fraction (NL, Table 2 and Fig. 5b).

Discussion

Our results showed that most traits associated with maternal investment in the kelp crab *Taliepus dentatus* exhibited significant latitudinal variation in the summer when the temperature gradient between northern and southern locations was stronger. These latitudinal trends disappeared in the winter months, when the latitudinal gradient in SST weakens, indicating that MI is largely driven by the environmental temperature during gonadal maturation and egg production. Thus, the relationship between maternal investment and latitude appears to be a plastic response controlled primarily by temperature, rather than a site-specific, fixed trait of populations. In this study, however, we had no measure of genetic variability among populations, and, therefore, cannot rule out some genetic differentiation and possible local adaptation. A temporal shift in the latitudinal distribution of MI, however, was evident, suggesting plasticity over time in these traits (Urzúa et al. 2012). In particular, brood dry weight and egg density showed a strong positive association with lower SST at higher latitudes, while egg volume increased with higher SST at lower latitudes. Fecundity was weakly and inversely correlated with temperature, yet it was greater at higher latitudes. We suggest that the bigger brood dry weight and egg density toward the south in summer and the absence of latitudinal variation in winter are related to the higher maintenance and brooding cost to females at higher temperatures, leaving less energy to invest in eggs. This is further suggested by greater egg lipid content (particularly storage lipids) at colder summer temperatures in southern populations. Unfortunately, we did not assess whether this trait is also seasonally plastic.

Many studies have documented latitudinal variation in reproductive traits in a wide variety of taxa, confirming the generality of Thorson's rule (Marshall and Keough 2007); in the present study, we showed that the majid crab, *Taliepus dentatus*, along Chile's coast is no exception. In the summer, most MI traits in the five local populations changed predictably with latitude (i.e., increasing towards higher latitudes), as reported for other brachyurans of the same region (Lardies and Castilla 2001; Brante et al. 2004). However, given that we only sampled a small part of the species' range, it is possible that surveys over a greater range would reveal
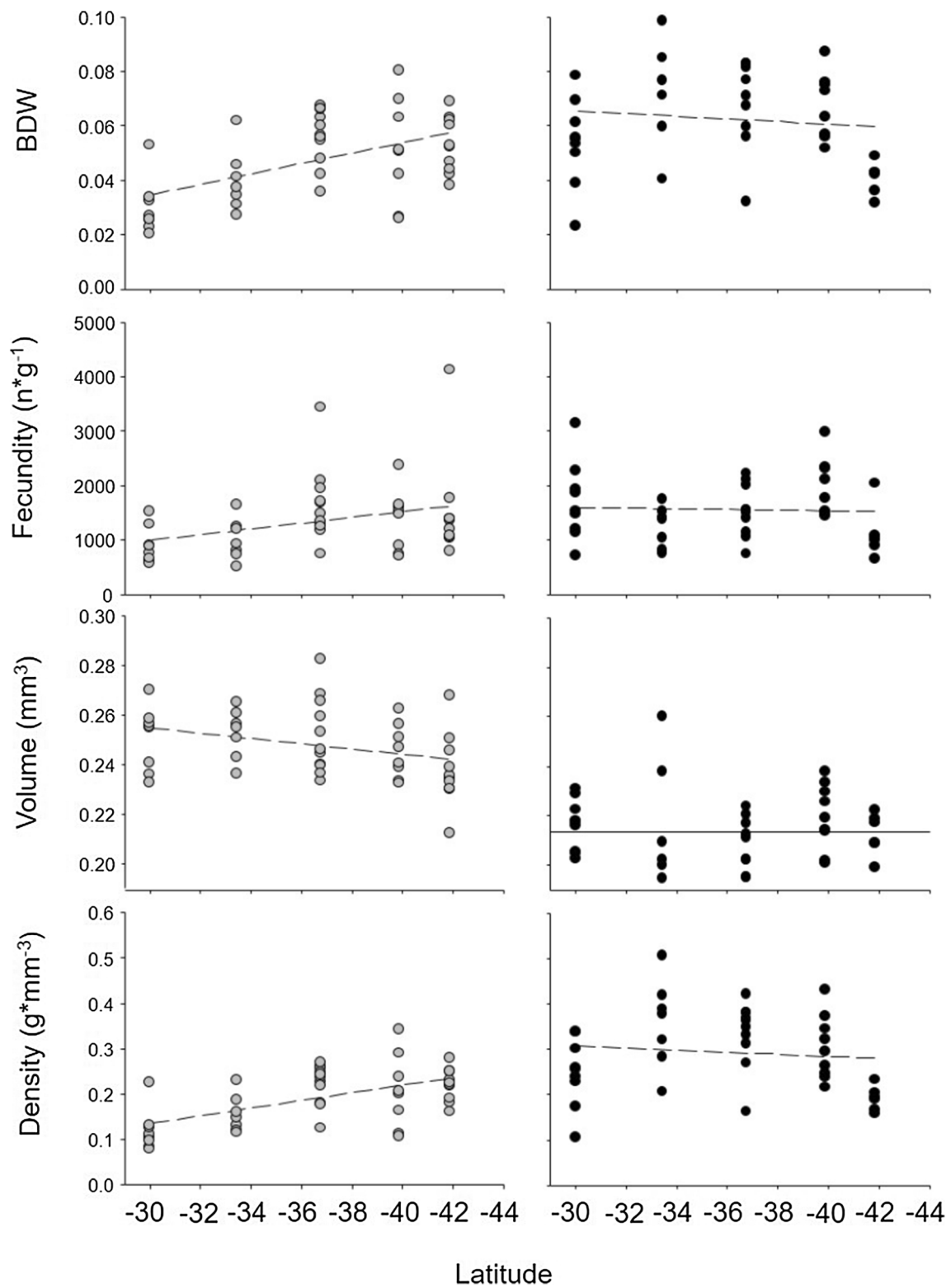
Fig. 3 Brood dry weight (**a**, **b**), fecundity (**c**, **d**), egg volume (**e**, **f**), and egg density (**g**, **h**) of females from different latitudes. Summer (grey circles) and winter (black circles). Dotted lines indicate linear regressions (see supplementary material for quadratic fit). Each data point represents a female ($n = 10$ females for each site and season)

Table 2 Analyses of covariance (ANCOVAs) for the BDW, F, V, D, and egg lipids

MI proxies	df	MS	F	p value
BDW				
Season	1	2.99E−03	1.14E+01	**0.001**
Season × latitude	2	1.53E−03	5.84E+00	**0.004**
Res	81	2.62E−04		
F				
Season	1	8.34E+05	2.09E+00	0.152
Season × latitude	2	1.28E+06	3.20E+00	**0.077**
Res	81	3.99E+05		
V				
Season	1	1.50E−03	7.06E+00	**0.009**
Season × latitude	2	4.12E−04	1.94E+00	0.167
Res	81	2.12E−04		
D				
Season	1	6.84E−02	1.27E+01	**0.001**
Season × latitude	2	2.97E−02	5.52E+00	**0.006**
Res	81	5.38E−03		
Lipids				
Fraction	1	1.55E−02	5.50E+00	**0.025**
Fraction × latitude	2	3.18E−02	1.13E+01	**0.000**
Res	34	2.82E−03		

BDW brood dry weight, *F* fecundity, *V* eggs volume, *D* density, *Res* residuals, *df* degree of freedom, *MS* mean sums of squares

Significant *p* values are highlighted in bold

a more permanent differentiation (fixed response) at the extremes. Our results cannot be generalized to the evolution of the crab's reproductive mode, but our evidence for variation in MI traits across a relatively large area is useful in understanding ecological and evolutionary pressures in this species.

Testing whether the observed patterns represent fixed, genetically determined adaptive differences among local populations would require common garden experiments where geographically distant populations of *T. dentatus* (e.g., FR and AN) are exposed to similar laboratory conditions. These experiments are difficult to perform as they require a number of controls and maintenance of large individuals under controlled temperature for long periods of time, but they would stimulate further research on this species. We have shown that the small latitudinal differences in temperature in the winter did not result in spatial difference in MI (brood dry weight, lipids, and density of the eggs). In contrast, the twofold increase in latitudinal SST gradient (between FR and AN) seems to underlie the large differences in MI. These results can guide future experimental research.

Regarding egg volume, we found a weak negative relationship with latitude, which was the inverse of the "typical" trend of higher egg volume in colder waters. Indeed, several studies in other decapods have found latitudinal differences in egg volume with larger and fewer eggs in colder regions (Clarke 1991; Lardies and Castilla 2001; Wehrtmann and Lopez 2003; Brante et al. 2003). However, Brante et al. (2004) had already reported a similar pattern to the one observed in this study for the congeneric species *Taliepus marginatus* (although only two sites were examined). This suggests a different pattern in kelp crabs compared to other decapods. The trend in our study was only marginally significant and should be examined further with a larger sample size. We offer a potential explanation related to food availability. Higher availability of new kelp tissue (i.e., *Lessonia trabeculata*), the main food source of kelp crabs, occurs in the summer, when the kelp grows more rapidly (Murúa et al. 2013). This could explain the bigger volume of eggs at lower latitudes. It should also be noted that quadratic regressions seem to better explain the relationship between egg volume and latitude in summer, suggesting more complex relationships. A unimodal or saturation relationship may reflect the higher costs of production and maintenance of larger eggs at lower latitudes. Females of *T. dentatus* may invest in larger eggs at lower latitudes up to a point where the costs of greater egg size become too high.

A trade-off between number and size of eggs is a well-documented pattern among marine invertebrates (Marshall

Table 3 Lipid class concentrations (mean ± SD) for the five locations in summer 2015–2016

Site	TAG	CHOL	MAG	PE	PS	PC	NL	PL
FR	0.233 ± 0.072	0.006 ± 0.004	0.024 ± 0.017	0.015 ± 0.012	0.007 ± 0.002	0.090 ± 0.013	0.279 ± 0.093	0.111 ± 0.028
PT	0.247 ± 0.051	0.007 ± 0.001	0.023 ± 0.005	0.017 ± 0.002	0.005 ± 0.002	0.081 ± 0.020	0.277 ± 0.057	0.103 ± 0.024
CU	0.235 ± 0.027	0.006 ± 0.002	0.024 ± 0.015	0.008 ± 0.005	0.005 ± 0.003	0.061 ± 0.015	0.265 ± 0.029	0.073 ± 0.018
LM	0.344 ± 0.067	0.006 ± 0.001	0.047 ± 0.023	0.011 ± 0.004	0.004 ± 0.002	0.070 ± 0.013	0.408 ± 0.058	0.089 ± 0.010
AN	0.359 ± 0.069	0.006 ± 0.005	0.047 ± 0.040	0.016 ± 0.010	0.003 ± 0.002	0.067 ± 0.038	0.412 ± 0.081	0.086 ± 0.050

Lipid concentrations are given in grams

Refer to main text and Fig. 1 for site abbreviations

TAG triacylglycerols, *Chol* cholesterol, *MAG* monoacylglycerols, *PE* phosphatidylethanolamine, *PS* phosphatidylserine, *PC* phosphatidylcholine, *NL* neutral lipids, *PL* polar lipids
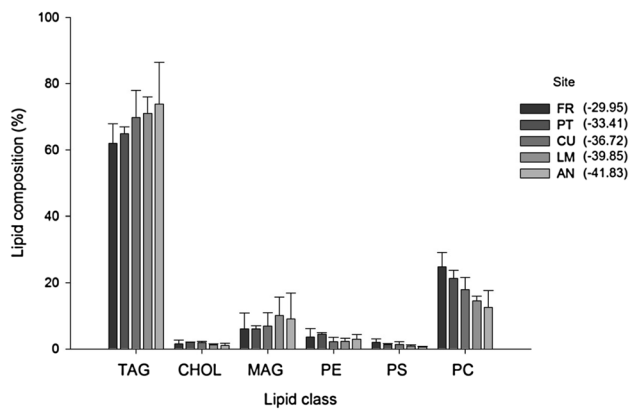
Fig. 4 Barplots showing the composition (% ± SD) of each lipid class for all the five locations. The legend on the top right shows the colour code for each location. *FR* El Frances, *PT* Punta Tralca, *CU* Los Cuervos, *LM* Los molinos, *AN* ancud, *TAG* triacylglycerols, *Chol* cholesterol, *MAG* monoacylglycerols, *PE* phosphatidylethanolamine, *PS* phosphatidylserine, *PC* phosphatidylcholine

and Keough 2007), and is explained by the fact that the energy that mothers allocate to reproduction is limited (Smith and Fretwell 1974). Linear regressions between fecundity and latitude and between egg volume and latitude in *T. dentatus* seem to support this hypothesis, by showing a latitudinal increase in fecundity with a concomitant decrease in volume. This trade-off in the latitudinal trends between fecundity and egg volume only appeared in summer, when temperature differences along the cline were greater. MI traits—particularly fecundity—are also related to maternal size (Baldanzi et al. 2015). Our measurements of MI (i.e., brood dry weight and fecundity) were, indeed, related to female size, with larger females producing more eggs and larger broods. Our samples consisted of only ten brooding females of similar size per site, so we cannot say anything about latitudinal patterns in female size.

Using lipid composition as a biochemical proxy for quality of maternal investment, we gained further valuable insights on female allocation of energy to eggs. In terms of total lipid content, we found greater investment at higher latitudes in summer 2016, which can be related to trends in brood dry weight and density. We found a north-to-south trend of an increasing proportion of neutral lipids with a concomitant decrease in polar lipids. Neutral lipids (mainly TAG) are the main energetic reserve for all marine crustacean embryos, while polar lipids (mainly phospholipids) are important for metabolic processes and the formation of cellular membranes (Anger 2001; Rey et al. 2016). At lower temperatures, developmental time of ectotherms is prolonged (Gillooly et al. 2001) and organisms need more energy to complete development (Geister et al. 2009). While energy stored in neutral lipids is needed in colder waters, towards the northern end of our sampling
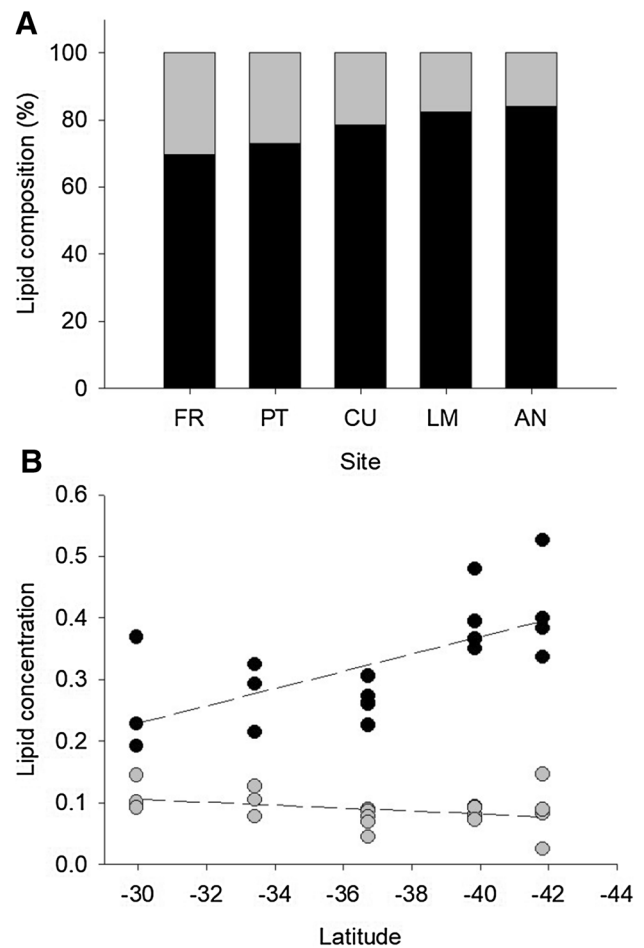
Fig. 5 Composition and concentration of neutral and polar lipids along the latitudinal cline. **a** Cumulative barplot of the composition (%) of polar (grey bars) and neutral lipids (black bars) along latitudinal cline. **b** Scattered plot of the lipid concentration of polar (grey dots) and neutral lipids (black dots) along latitudinal cline. Dashed lines represent linear regressions

region, eggs showed an increased proportion of polar lipids, mainly phosphatidylcholine (PC), which is a major component of biological membranes (Coutteau et al. 1997) and key in cell biochemistry and physiology (D'Abramo et al. 1982, 1985). Catabolism of PC may provide a secondary energy source when triacylglycerols are low in concentration (Sasaki et al. 1986). This could explain why PC was more abundant in northern than southern populations of *T. dentatus*. Longer embryo development at lower latitudes demands more molecules required to sustain high developmental rates (Jarošík et al. 2004). PCs are rich in EPA and DHA (eicosapentaenoic and docosahexaenoic acid, respectively), fatty acids required for cell differentiation and membrane formation during embryogenesis in brachyuran crabs (Fischer et al. 2009). Our biochemical analysis of MI, though limited to one sampling season (summer), suggested that temperature differences between

northern and southern locations induced different investments in the quality and energy allocation to the eggs.

The pattern found for brood dry weight and egg density in relation to temperature (latitudinal, seasonal) suggests a potential trade-off between MI and the cost of brooding (i.e., egg ventilation). We did not measure brooding costs, so this interpretation remains speculative, though the previous studies support such a hypothesis (Fernández et al. 2000; Baeza and Fernández 2002; Fernández and Brante 2003; Brante et al. 2003; Lucey et al. 2015). The cost of egg ventilation (estimated for brachyuran crabs, Brante et al. 2003) is higher when temperature rises (e.g., for individuals of this study at lower latitudes, summer). In this study, locations towards the south (i.e., LM and AN), which had the smallest temporal variation in SST, never showed seasonal differences in neither BDW, fecundity, nor egg density, suggesting that the difference in temperature between seasons was not sufficient to generate differences in the cost of brooding.

Conclusions

Our results partially support the hypothesis of greater MI towards higher latitudes for *T. dentatus*. While a latitudinal trend was found in the summer, with higher MI in colder waters, its absence in winter at higher latitudes highlighted a certain degree of plasticity, therefore, partially supporting Thorson's rule. This plastic response seems to be primarily induced by variation in temperature across latitudes and between seasons. Although a more extensive survey encompassing the entire geographic range of the species might shed more light on the plasticity and differentiation of MI among local kelp crab populations, our 12°-latitude study found consistency among several proxies for MI, including lipid composition. There may be a trade-off between the cost of maintenance and/or brooding and MI, although this should be experimentally tested. When investigating intraspecific latitudinal and temporal variation in maternal investment by brachyuran crabs (and for marine brooders in general), an estimate of the costs of MI should be included to provide a more comprehensive view of maternal and reproductive plasticity.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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