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Global macroecological patterns of larval size in decapods are governed by temperature and dissolved oxygen

José M. Landeira¹*, Diego Deville², Effrosyni Fatira¹, Zhixin Zhang³, Yuanning Li⁴, Sven Thatje⁵

¹*Department of Biology, Norwegian University of Science and Technology, Norway*

²*Onagawa Research Field Center, Tohoku University, Japan*

³*State Key Laboratory of Tropical Oceanography, Guangdong Provincial Key Laboratory of Applied Marine Biology, South China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou, China*

⁴*Institute of Marine Science and Technology, Shandong University, China*

⁵*Centro Austral de Investigaciones Científicas y Técnicas, Argentina*

*Corresponding author: jose.landeira.sanchez@ntnu.no

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ABSTRACT

Macroecological patterns of life history traits, such as larval size, are fundamental to understanding the biogeography and diversity of marine invertebrates. The long-established Thorson's Rule hypothesizes an increase in maternal energy allocation per offspring with increasing latitude, primarily as an adaptation to offset slower development in cold, food-limited waters. Here, we conduct the largest analysis to date on decapod crustaceans using the size of the first larval instar as a proxy for per offspring investment, to test whether reproductive and developmental patterns are governed by environmental factors on an evolutionary timescale. Our results confirm a strong phylogenetic signal in larval size and reveal that it systematically increases with latitude and greater water depth. This pattern aligns with ambient habitat conditions of lower temperature and higher dissolved oxygen. As expected, we found a strong inverse relationship between larval size and the number of larval stages, confirming that larger, provisioned offspring undergo abbreviated development. In addition, our findings support the hypothesis that increased per offspring investment and larval abbreviation represent a conservative, bet-hedging evolutionary strategy to minimize the vulnerable planktonic duration in cold, high-latitude and deep-sea environments. The deep-sea trend is, therefore, a conceptual extension of the latitudinal gradient into the vertical dimension. This study consolidates the notion that temperature, oxygen and developmental constraint, are the overriding global drivers of offspring investment strategies in decapod crustaceans, shaping their evolutionary pathways and global macroecological patterns.

KEY WORDS: Offspring investment, Larval development, biogeography, distribution, depth, latitudinal patterns.

INTRODUCTION

Macroecological patterns of life history traits influence the biogeography and biodiversity of marine invertebrates on both ecological and evolutionary timescales [1-3]. One of the most widely recognized patterns is the increase in per offspring investment with latitude, often accompanied by a shift from planktotrophic (feeding) to lecithotrophic (nonfeeding) larval

development at higher latitudes. The Danish ecologist, Gunnar Thorson, was the first to study latitudinal trends in marine invertebrate reproduction by examining larval developmental modes and maternal energy investment in species from the North-East Atlantic and the Arctic Ocean [4-6]. Thorson proposed that species inhabiting high latitudes produce fewer but larger offspring with greater maternal investment. He suggested that this reproductive strategy represents an adaptation to the mismatch between prolonged developmental times and the short seasonal periods of food availability at high latitudes. Under such conditions, larvae that depend on external food sources are at a selective disadvantage [4,6].

Evidence for this latitudinal trend was mainly documented in molluscs and caridean shrimps from high-latitude environments and became known as “Thorson’s Rule” [7]. Later, it has also been referred to as the “Thorson-Rass Rule” or “Rass-Thorson-Marshall Rule,” acknowledging the contributions of Rass and Marshall, who described similar latitudinal trends in egg size of teleost fishes [8-10]. Since then, these observations have developed into one of the most influential concepts in marine ecology.

More current studies have found that not all taxa conform to this macroecological trend, with exceptions found in Arctic and Antarctic echinoderms [11-13,3]. Further, increasing records of pelagic larvae in polar regions have been used to dismiss Thorson’s rule [11,12,14,1]. These examples highlight species-specific life history traits in response to environmental factors, and hint at the difficulties when defining generalised ‘rules’ from ecological patterns and observations [15].

Thorson distinguished between planktotrophic (pelagic) and lecithotrophic (benthic) larvae only. Today, we know that aquatic invertebrates develop through a diverse array of larval developmental modes and nutritional states. There are planktic/planktonic, swimming, larvae that are obligate feeders from hatching, as well as those that do not feed and utilise maternal yolk provisions for development (lecithotrophs). There are also many intermediate developmental forms. These include facultative feeders, which partially rely on maternally derived energy, as well as species with encapsulated development that depend on nurse eggs for nutrition [16, 17].

Current data indicate that the distribution of larval development modes is not homogenous within the oceans. Instead, it forms a macroecological pattern across latitudinal gradients. The proportion of species with lecithotrophic (nonfeeding) larvae increases at high latitudes [4-7,18, 19,1,10,2,3]. Coupled with this trend is a latitudinal decrease in maternal fecundity and an increase in resource allocation per offspring, allowing for larval development independent of external nutrition [6,1,3].

Recent studies have found that both temperature and food availability govern maternal offspring investment and larval developmental modes. Probably best studied in decapod crustaceans, there is intriguing evidence for a cline in per offspring investment (POI) with decreasing temperatures towards higher latitudes as well as with increasing water depth, as shown in anomuran and brachyuran crabs [20,21,22,17,23]. An increase of egg size – often used as a proxy for POI – occur with increasing latitude in caridean shrimps. This pattern also involves changes in egg biochemistry and often reduced fecundity [24,25,26,27,28,19]. Plasticity in development, too, is observed in carideans [29,30], presenting an increase of larval size, as well as an abbreviation of the larval cycle (fewer instars) at higher latitudes [19]. Recently, and at an intraspecific level, the influence of internal nutritional resources available to a larva has been experimentally demonstrated to affect developmental mode and larval instar number [31,32,33]. Higher POI enables caridean crustacean larvae to develop more rapidly through fewer, and larger larval instars. This has been demonstrated under a range of salinity, temperature, and nutritional conditions [31,34,32]. It is also expected that other variables like oxygen concentration can influence offspring size. For example, oxygen can become a limiting resource at higher temperatures, where the demand for oxygen increases [35]. These latitudinal patterns driven by environmental parameters can translate on macroecological scales over evolutionary periods of time.

Here, we hypothesise that the decapod crustaceans follow Thorson’s rule and test whether environmental variables, such as temperature, salinity, oxygen, and food availability do govern life history patterns globally and on evolutionary time scale. We test whether reproductive patterns occur across latitude and water depth, and we discuss observed patterns in relation to infraorder-specific early ontogeny and evolutionary history.

MATERIAL AND METHODS

Species list and collection of size data

Our initial attempt aimed to compile a comprehensive dataset on egg size across Decapoda. However, this effort did not yield sufficiently complete and consistent coverage across taxa to support robust macroevolutionary analyses in maternal energy investment. As a result, we instead focused on the size of the first larval instar (named nauplii in Dendrobranchiata and zoea in Pleocyemata [36]) as a more consistently available proxy for early life-history investment across decapod groups. This approach is supported by evidence that egg size is

proportional to the size of the first post-embryonic instar [37,38,39]. Carapace length (CL) was used as the standard measure as it is regarded as the most reliable metric for decapod crustaceans. The carapace being a rigid and well-defined part of the exoskeleton, remains relatively stable across moulting stages, unlike the abdomen, which may vary in flexibility and proportions. This consistency enables researchers to obtain reproducible allometric relationships across different life stages [40].

Data were obtained from published descriptions in which the morphology of the larva was illustrated using drawings or photographs (see [41] for full list of references). We extracted the CL data measuring from the anterior margin (or the base of the rostral spine when present) to the posterior dorsal margin of the carapace as described by [42]. We used our own collection of published taxonomic descriptions to gather data regarding “number of larval stages” and “size of the first larval instar”. To expand the dataset, published information was added from the Institute for Scientific Information Web of Knowledge using the search terms “larva” AND “development” AND “Decapoda” AND “description”. Moreover, taxonomic journals (e.g. Zootaxa, Crustaceana, Journal of Crustacean Biology, etc.) were individually searched for extra datasets. We were careful to include only studies following the taxonomic standard propositions by [42] updated by [43]. To avoid misidentifications, we only used descriptions based on larvae obtained from laboratory-reared ovigerous decapods or collected in the field and identified by DNA barcoding. Moreover, those descriptions with low quality drawings/photographs, and/or without scale were discarded. Following these criteria, abstracts and figures were screened to select appropriate studies. In some cases, we extracted carapace size data directly from published tables or scatter plots (e.g. [44]) using the free online app PlotDigitalizer (<https://plotdigitizer.com>). Our dataset of larval size includes a total of 647 species across Decapoda: 48 Achelata, 135 Anomura, 8 Astacidea, 14 Axiidea, 293 Brachyura, 113 Caridea, 20 Dendrobranchiata, 11 Gebiidea, 1 Polychelidea, 3 Stenopodidea [41]. Species names and phylogenetic position of all decapods were updated using the World List of Decapoda [45]. In addition to CL, we gathered data on the feeding mode (lecithotrophic or planktotrophic) of the first larval instar, and number of stages required to complete the larval phase, when the information was available.

Environmental data collection

For each species, we retrieved its opportunistic occurrence records and distribution depth from widely-used online biodiversity repositories, including Ocean Biodiversity Information System

(OBIS; <https://obis.org/>), Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>) and [45]. For those species with limited distribution data, we performed literature review and extracted occurrence records from scientific papers. Occurrence records from biodiversity databases are prone to sampling bias and/or errors [46,47]. To reduce uncertainties associated with these issues, we (1) determined species-specific distributional range based on literature/database and removed records outside species known range, (2) excluded invalid occurrences (e.g., zero coordinates, absence of distribution depth), and (3) avoided clustered records by leaving one occurrence per 5 arcmin grid cell (i.e., the spatial resolution of marine predictors). To confirm the reliability of our analyses, we only considered species with over 5 records.

We characterised environmental requirements of decapod crustacean species using marine data layers from the Bio-ORACLE database version 2.0 (<https://www.bio-oracle.org>) [48]. Apart from latitude and depth, we selected ecophysiological predictors based on empirical evidences [36], including temperature (°C), salinity (PSU), dissolved molecular oxygen ($\text{mmol}\cdot\text{m}^{-3}$), and chlorophyll ($\text{mmol}\cdot\text{m}^{-3}$) as a proxy of food availability following the methodology applied in previous similar analyses [49,50,51]. Given the pelagic nature of most crustacean larvae, we used environmental data exclusively from the sea surface layers, as the preferred spawning depth is unknown for the majority of species in our dataset [49,50]. For each species, we extracted environmental information from the filtered occurrence records and used the corresponding median and mean values to characterize its environmental requirements.

Phylogenetic reconstruction

Analyses were performed in R v. 4.3.3 [52]. The Open Tree of Life interface (rotl package, [53]) was employed to match 646 species with morphological and environmental information with their respective identifiers. In March 2024, eight species did not have identifiers; thus, a phylogenetic tree of 638 species and *Euphausia superba* as outgroup was retrieved from the synthetic tree. Branch lengths were estimated using the computation of Grafen, whereby branch lengths are the difference between the height of the nodes after counting the number of leaves originated from each node and scaling them to the root [54]. Two pruned trees were generated from the retrieved tree. The first contained 617 species with information on all the environmental variables, while the second included only 406 species with information on the number of larval stages. These trees contained 102 and 62 polytomies, respectively.

Phylogenetic comparative analyses

The *fastAnc* function (phytools package [55]) was used to reconstruct the ancestral states of log-transformed CL in the pruned trees of 617 and 406 species. The reconstructed states and bar plots indicating the square-rooted values of maximum depth distribution of adults and number of larval stages [55]. The phylogenetic signal was estimated for maximum depth distribution, latitude, and number of stages considering the λ Pagel estimator [56]. This estimator scales the correlations between species based on the expected correlation according to Brownian evolution. The λ Pagel estimator was chosen because it provides a non-inflated estimate of phylogenetic signal in the presence of polytomies [57].

Phylogenetic generalised least squares (PGLS) were respectively fitted to evaluate the correlation between CL and square-rooted maximum depth distribution, absolute latitude, temperature, salinity, oxygen, and number of larval stages while accounting for the phylogenetic relatedness of species (caper package [58]). Outliers were removed before performing PGLS models using the λ Pagel estimator to account for phylogenetic influence on the models. Again, the λ Pagel estimator was chosen because it provides more accurate estimates and better-fit effects than the other models when polytomies are included in the reference phylogenetic tree [59]. Additionally, thirty-two multiple generalised models were fitted to evaluate the combined effects of various predictors on the CL of the 406 species with information on the number of larval stages. For these models, multicollinearity of variables was avoided by excluding temperature and oxygen, which had variance inflation factors higher than 10 [60]. The model with the lowest Akaike information criterion [61] was chosen as the model that best fitted the data.

RESULTS

Dendrobranchiate had the lowest mean CL (0.29 ± 0.11 mm), with the sergestid species *Acetes americanus* displaying the smallest CL value (0.19 mm). The largest mean CL was observed in Astacidea (1.17 ± 0.14 mm) followed by Anomura (1.26 ± 0.10 mm) where the eurybathic lithodid crab *Lithodes maja* exhibited the longest CL (4.60 mm) of the entire dataset (**Fig. 1**). Note that carapace length data were collected only for the first larval instar.

The ancestral reconstruction of CL showed that the estimated means for each infraorder are consistent within, except for Caridea, Anomura, and Achelata (**Fig. 2**). In this sense, Anomura

exhibited a wide range of variability in CL across families (Galatheidae: 0.43 mm; Lithodidae: 2.29 mm). Similarly, Caridea displayed high variability of CL, with Processidae showing a mean CL of 0.43 mm and Campylonotidae reaching 2.03 mm. In contrast, Brachyura, represented by 50 families, showed less pronounced variations in CL, ranging from 0.29 mm in Dotillidae to 1.22 mm in Cymonomidae (**Fig. 1**). This CL variation pattern across and within infraorders was reflected in high levels of phylogenetic signal ($\lambda = 0.936$, P value < 0.0001). The phylogenetic tree did not display clear patterns of variation in CL regarding maximum distribution depth nor latitude (**Fig. 2**). However, the PGLS models revealed that CL increased systematically with higher latitudes and greater water depths. With respect to environmental variables, models showed that larger larvae tend to occur in lower temperature and more oxygenated waters (**Fig. 3, Table S1**). Food availability (measured as mean Chl-a) and salinity did not show any significant relationship with larval size. Regarding reproduction strategies, the PGLS model revealed a strong negative relationship between larval size and number of stages required to complete larval development. Specifically, species with smaller first larval instar required an extended larval development (more larval stages) to complete development compared to species producing larger larvae at hatching (**Fig. 3, Table S1**). The multiple generalised model best fitting the data included latitude, depth, and number of larval stages as significant predictors ($CL \sim 0.0327 + 0.0168*\text{sqrt.Latitude} + 0.0032*\text{sqrt.Depth} - 0.0409*N\text{stages}$) (**Table S2**). A similar model including Chl-a was the second best fitting the data ($\Delta AICc = 0.765$) (**Table S2**) ($CL \sim 0.0215 + 0.0209*\text{sqrt.Latitude} + 0.0029*\text{sqrt.Depth} - 0.0205*\text{Chl-a} - 0.0408*N\text{stages}$).

Despite the limited dataset on feeding mode, we found a significant association of both developmental traits (larval size and number of larval stages) and environmental factors (**Fig. 4**). In Anomura, Brachyura, and Caridea (the infraorders with the most feeding mode data available), species producing larvae with some degree of lecithotrophy in the first instar tend to be larger and develop through abbreviated development in fewer stages. Additionally, these species with lecithotrophic strategies are more frequent at higher latitudes and/or inhabit greater water depths, which are associated with colder habitats and/or more oxygenated waters.

Table S1. Parameters of the phylogenetic generalised least squares (PGLS) analyses modelling log-transformed carapace length on environmental variables and number of larval stages.^(a) square-rooted values. N, indicates the number of species used for the PGLS models. Bold values indicate significant relationships between the variables. and lambda “ Λ ” is the estimated Pagel’s parameter scaling branch lengths in each PGLS analysis.

Variables	N	Slope	<i>P</i> value	Λ
Maximum depth ^(a)	615	0.0056	<0.001	0.932
Latitude ^(a)	617	0.0227	<0.001	0.931
Temperature	607	-0.0042	<0.001	0.928
Oxygen	610	0.0009	<0.001	0.927
Chlorophyll-a	610	-0.0058	0.7043	0.937
Salinity	606	0.0006	0.8487	0.937
Larval stages	406	-0.0414	<0.001	0.905

Table S2. Fit of the 32 multiple generalised models assessed for carapace length. The number of explanatory variables, differential of the Akaike information criterion (Δ AICc), and lambda “ Λ ” estimator of Pagel are shown for each model. CL = carapace length; Chla = Chlorophyll a.

Variables	Model	Δ AICc	Λ
0	CL ~ 1	84.530	0.922
1	CL ~ 1 + Stages	10.995	0.905
	CL ~ 1 + Salinity	86.474	0.921
	CL ~ 1 + Chla	86.480	0.922
	CL ~ 1 + Depth	78.386	0.909
	CL ~ 1 + Latitude	79.106	0.909
2	CL ~ 1 + Salinity + Stages	12.945	0.904
	CL ~ 1 + Chla + Stages	12.995	0.905
	CL ~ 1 + Chla + Salinity	88.318	0.921
	CL ~ 1 + Depth + Stages	4.194	0.888
	CL ~ 1 + Depth + Salinity	79.841	0.905
	CL ~ 1 + Depth + Chla	80.385	0.909
	CL ~ 1 + Latitude + Stages	4.356	0.888

	CL ~ 1 + Latitude + Salinity	80.942	0.910
	CL ~ 1 + Latitude + Chla	78.272	0.907
	CL ~ 1 + Latitude + Depth	75.103	0.898
3	CL ~ 1 + Chla + Salinity + Stages	14.919	0.904
	CL ~ 1 + Depth + Salinity + Stages	5.642	0.883
	CL ~ 1 + Depth + Chla + Stages	6.135	0.887
	CL ~ 1 + Depth + Chla + Salinity	81.687	0.905
	CL ~ 1 + Latitude + Salinity + Stages	6.132	0.889
	CL ~ 1 + Latitude + Chla + Stages	3.911	0.887
	CL ~ 1 + Latitude + Chla + Salinity	80.095	0.905
	CL ~ 1 + Latitude + Depth + Stages	<0.001	0.873
	CL ~ 1 + Latitude + Depth + Salinity	77.085	0.897
	CL ~ 1 + Latitude + Depth + Chla	75.531	0.897
4	CL ~ 1 + Depth + Chla + Salinity + Stages	7.620	0.883
	CL ~ 1 + Latitude + Chla + Salinity + Stages	5.834	0.886
	CL ~ 1 + Latitude + Depth + Salinity + Stages	1.994	0.873
	CL ~ 1 + Latitude + Depth + Chla + Stages	0.765	0.874
	CL ~ 1 + Latitude + Depth + Chla + Salinity	76.940	0.893
5	CL ~ 1 + Latitude + Depth + Chla + Salinity + Stages	2.363	0.870

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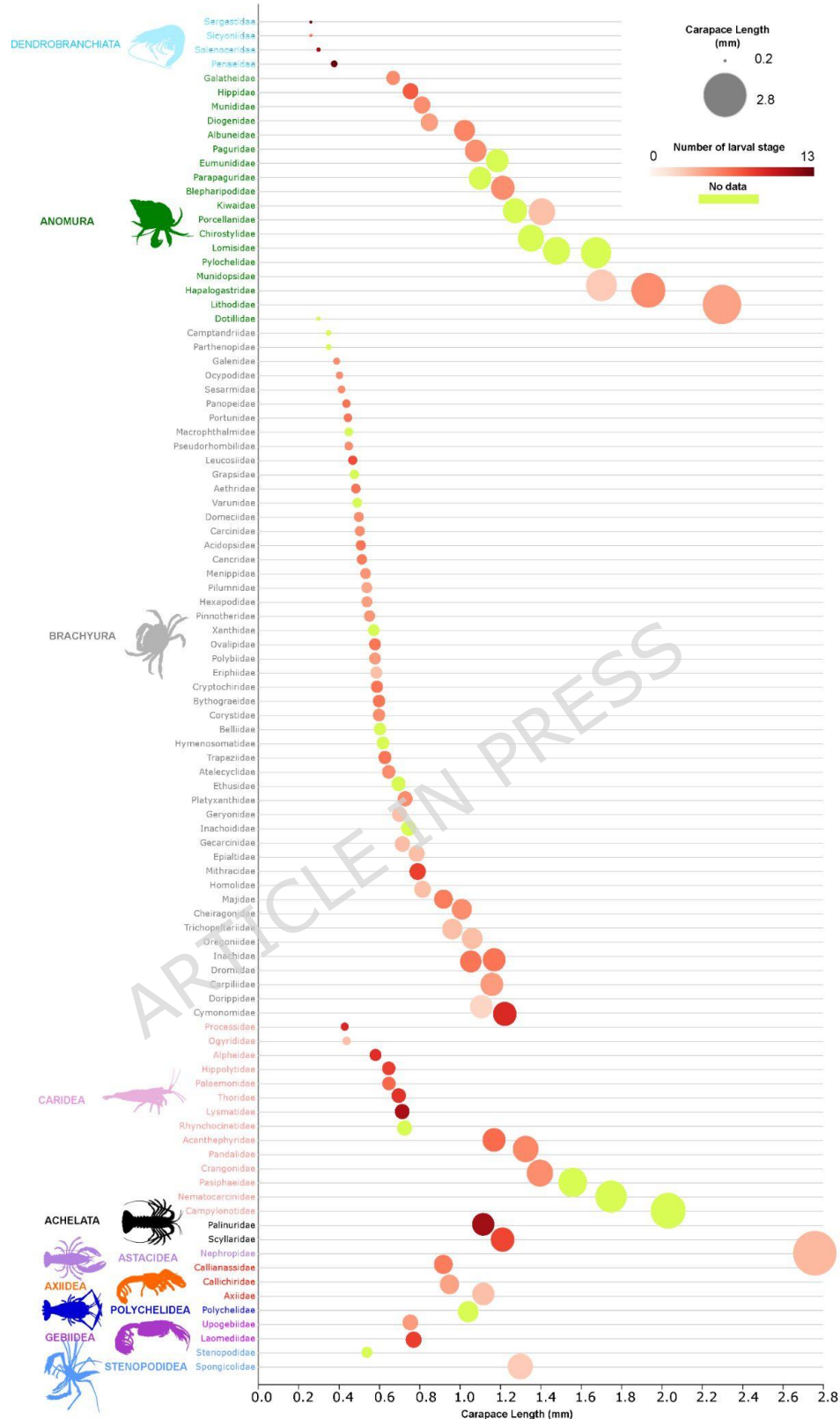


Figure 1. Dot plot showing the mean carapace length (mm) for each family across Decapoda. The size of each dot represents the carapace length, while the dot color (red gradient in the scale bar) indicates the mean number of larval stages. Families without larval stage data are represented in light green. Note that carapace length data were collected only for the first larval instar.

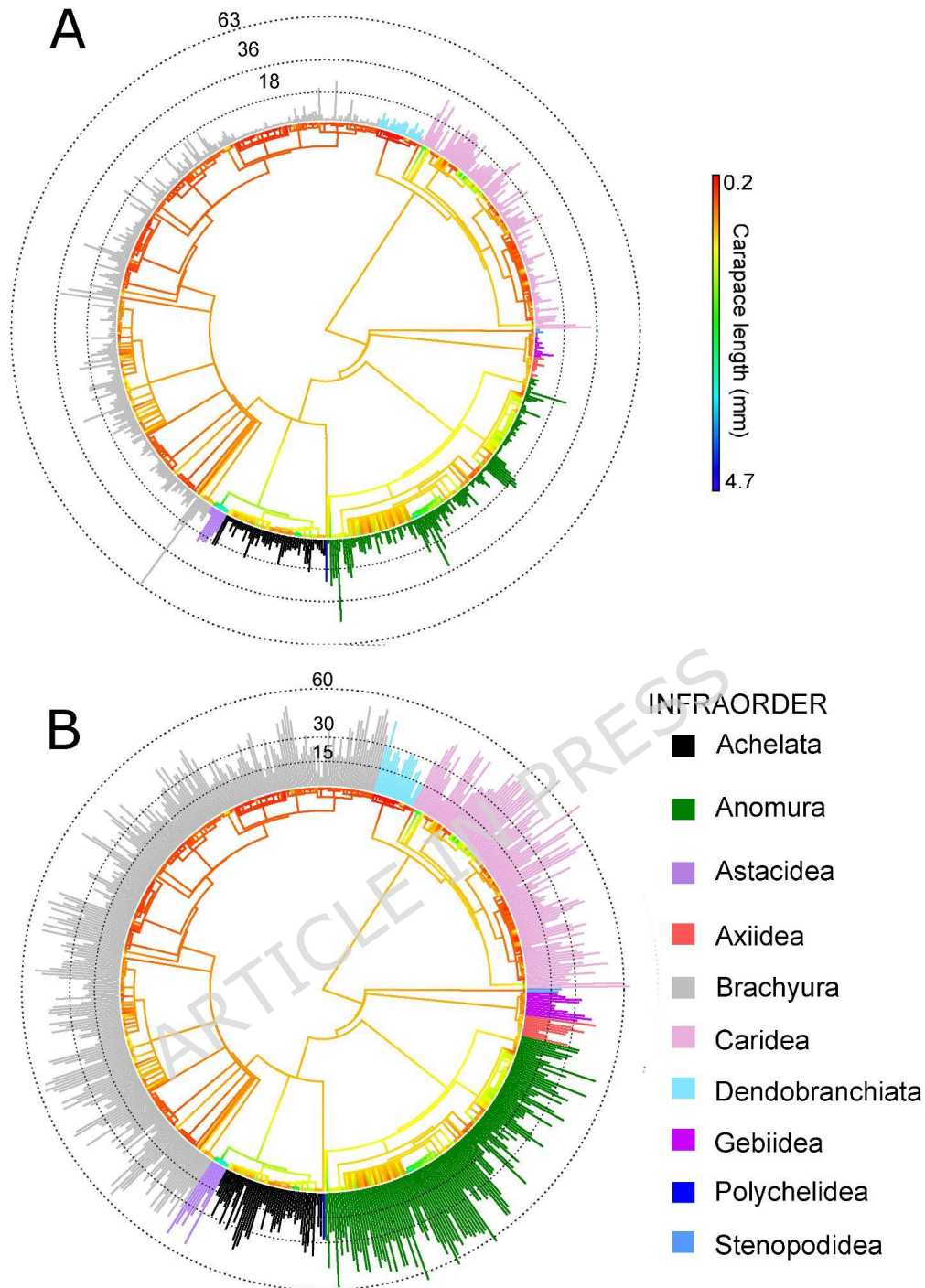


Figure 2. Carapace length in decapod crustaceans across a single synthetic tree retrieved from the Tree of Life interface. Ancestral state reconstruction of carapace length estimated from the tree of 617 species, in which the bar plots around the tips indicate the square-rooted maximum depth distribution of adults (A) and absolute latitudinal distribution (B). Trees with barplots were plotted using functions of the phytools package [55]. Barplots were colored to facilitate the distinction of each infraorder. Scales of reference for the barplots are represented by dotted circles around them. The scale of reference for the reconstructed states of carapace length is also added. Note that carapace length data were collected only for the first larval instar.

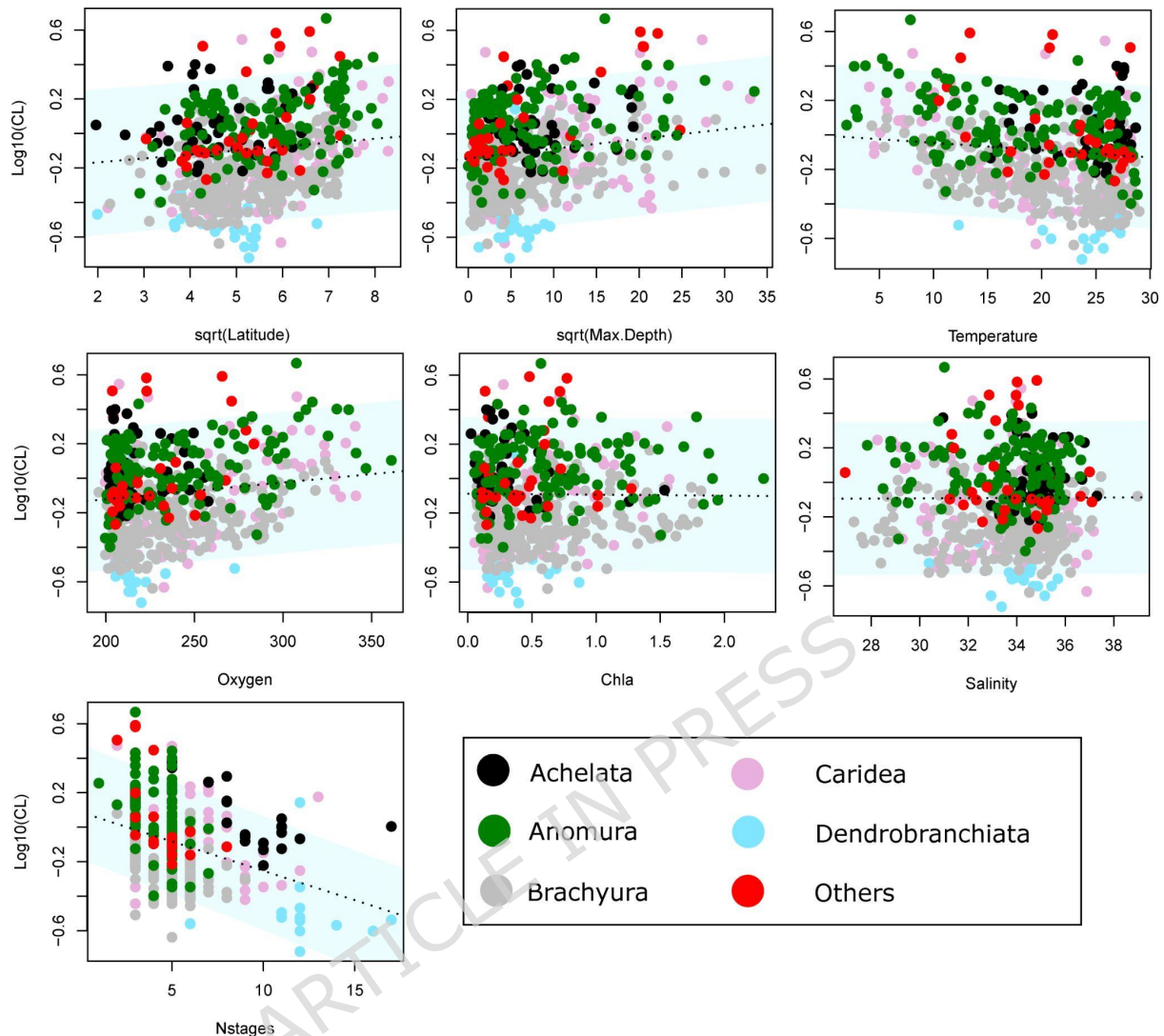


Figure 3. Phylogenetic generalized least square models of carapace length on variables. The fitted models and their confidence intervals are represented as dotted lines and sky-blue shaded areas, respectively. Points were coloured to facilitate distinction of the five infraorders with more species in the analyses. Note that carapace length data were collected only for the first larval instar.

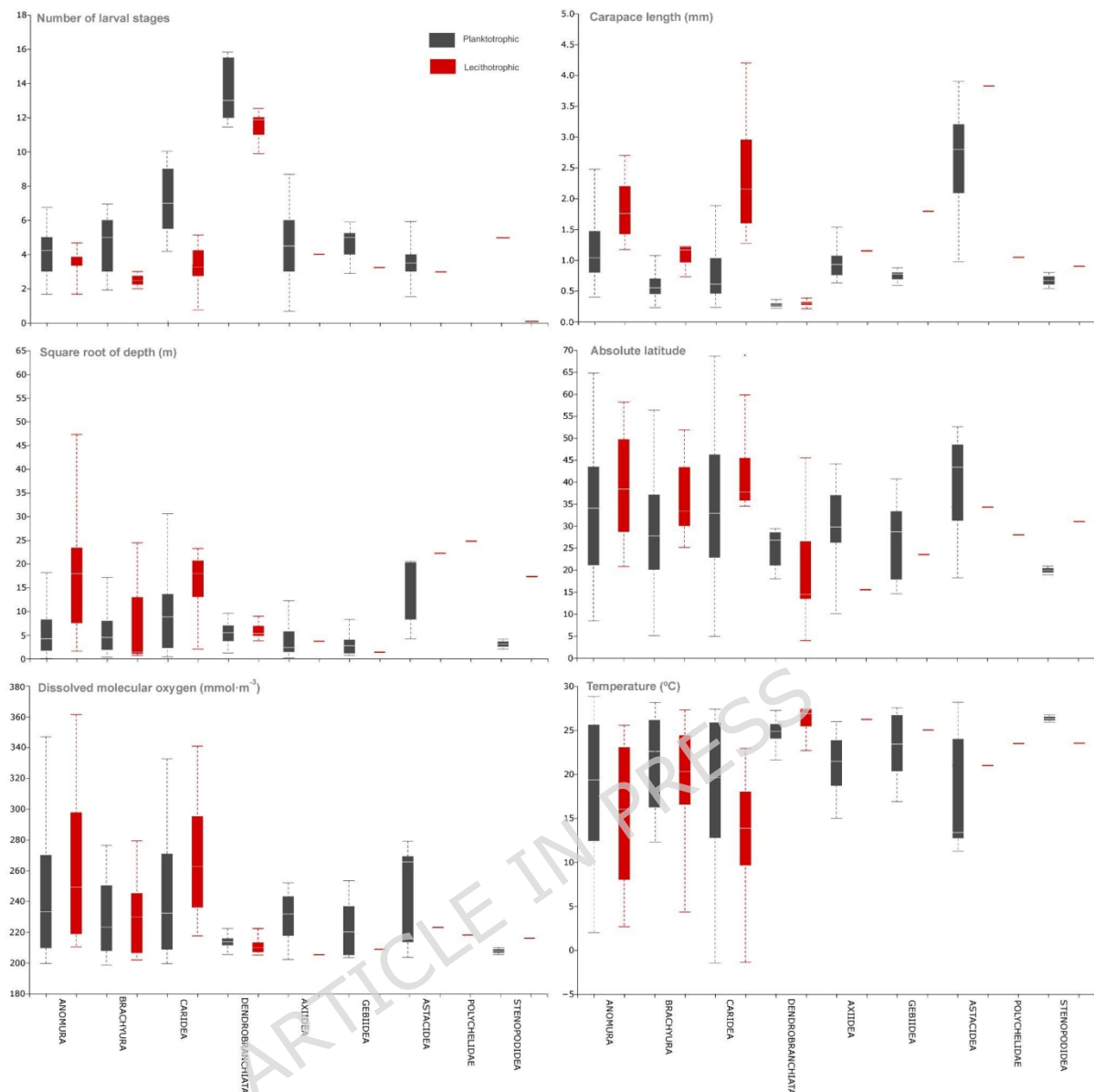


Figure 4. Box and whiskers plots representing the number of larval stages, carapace length of the first instar (mm), square-rooted maximum depth (m), absolute latitudinal distribution, dissolved molecular oxygen concentration ($\text{mmol}\cdot\text{m}^{-3}$), and sea surface temperature ($^{\circ}\text{C}$) conditions of the habitat during adult stage. The data include only those infraorders with known lecithotrophic (obligate or facultative) feeding mode during the first instar. Note that carapace length data were collected only for the first larval instar.

DISCUSSION

This study offers new perspectives on the variation in larval size and the corresponding POI in relation to environmental conditions and developmental strategies in decapod crustaceans across both latitudinal and bathymetric gradients. Our results largely align with established macroecological hypotheses [6,3] while also revealing significant variability within infraorders. This highlights the intricate interplay of evolutionary and ecological factors shaping reproductive strategies in these marine organisms. Our dataset includes a total of 617 species, which, although far from representing the full diversity within Decapoda [45], falls within the range of similar studies on macroecological patterns of marine life histories (e.g., $n = 288$ fish species in [50]; $n = 800$ marine invertebrate species in [49]). The fact that some taxonomic groups (e.g., Dendrobranchiata or Gebiidea), as well as lecithotrophy at the first instar, are under-represented in the database due to insufficient data introduces an obvious bias; however, this did not prevent us from characterizing consistent global patterns in decapod life-history traits, particularly larval size.

Environmental drivers

The robust negative relationship between temperature and larval size, both latitudinally and bathymetrically, confirms its status as overriding environmental driver. It is well known that lower temperatures lead to slower progression of developmental stages in marine ectotherms [62] such as decapod crustaceans [71]. This general slowdown potentially increases the risk of mortality from predation and advective loss. Therefore, selection acts strongly to favour strategies that compress the developmental period by reducing the number of vulnerable planktonic steps [63]. In this sense, increased POI serves as the primary strategy to achieve this larval abbreviation. This investment provides a buffer against the slow-down effect of cold water by supplying a greater endogenous energy reserve (lecithotrophy). This reserve facilitates the reduction of instars, a defining characteristic of abbreviated development [64]. By producing fewer and larger offspring, decapods effectively reduce the number of critical transition periods (molts) in the plankton, thereby significantly reducing the overall vulnerable pelagic duration. This strategy with higher POI is essential in cold and food-limited environments like those at high-latitude but also at deep-sea. The depth trend observed in this study is thus conceptually an extension of the latitudinal trend into the vertical dimension as observed in fishes [51]. For example, in the deep-water genus *Sclerocrangon*, species have suppressed the planktonic phase and produce a lecithotrophic and well-developed first larval

instar, which are brooded under the pleon, e.g. *Sclerocrangon rex* [65]. Evidence for protracted and lecithotrophic larval development in deep-waters have been found in the yeti squat lobster *Kiwa tyleri* from hydrothermal vents [66] and in the stenopodidean shrimps *Spongicola japonicus* [67]. However, it is worth noting that we only used environmental data collected at the sea surface. Therefore, further studies that consider the preferred spawning depths of each species could more accurately determine the relationship between depth, environmental conditions, and larval size/POI [10].

While our results confirm that temperature defines the fundamental structure of development, dissolved oxygen also emerges as a key environmental factor. It is known that embryos of many decapods generally exhibit some capacity for oxyregulation, whereas early larval stages are typically unable to maintain oxygen uptake under declining dissolved oxygen concentrations [68]. However, studies indicate that oxyregulatory capacity tends to recover during the later developmental stages [35]. Since oxygen diffusion efficiency decreases as volume increases, small-size offspring may be favoured in those tropical regions with elevated temperatures and lower dissolved oxygen levels.

Interestingly, we found no relationship between larval size and Chlorophyll a, our proxy for food availability. This result, while seemingly contradictory to Thorson's original hypothesis [6], highlights the fact that evolution has fixed the developmental mode as an adaptation to predictable resource scarcity and temporal mismatch, as observed in fishes [50,51]. The observed pattern may reflect a strategy that decouples larval success in decapod crustaceans from immediate external food availability in the water column. Nevertheless, our results indicate a tendency toward lecithotrophy at higher latitudes, where food availability exhibits strong seasonal variations, as proposed by [69]. The macroecological pattern of producing large, well-provisioned, abbreviated larvae, is a conservative bet-hedging strategy [70], that minimizes the risk of mismatch between phytoplankton bloom and planktonic larval duration. By increasing the energy allocation and reducing the number of feeding stages of the offspring the mother ensures greater chance of settlement success during the brief feeding window [3].

Importantly, there is solid evidence of strong variability within species/among populations. Thus, the ability to modulate larval size or number of instars during the development in response to environment is highly variable. Developmental plasticity is relatively common in caridean shrimps, and experimental studies have shown that increasing temperature can lead to an extended larval development (i.e., more instars), whereas a high POI results in developmental abbreviation (i.e., fewer instars) [33]. Moreover, maternal diet can

influence offspring size, as feeding at a higher trophic level has been observed to produce larger larvae [71]. In other decapod groups, such as brachyurans, variability in larval size among populations has been reported in response to contrasting environmental conditions. For instance, populations inhabiting colder regions produce larger first-stage zoeae in *Metacarcinus magister* [72], *Cancer setosus* [22] and *Chionoecetes opilio* [73]. In addition, there is mounting evidence in decapods that larger females confer a "bigger is better" advantage to their offspring through increased POI, directly affecting larval size [21,74]. This principle, also noted in fishes [75,76], emphasizes that maternal size affects offspring provisioning. Considering this, combined pressures of overfishing (which tend to remove large, high-POI females) and global warming (which reduces the protective advantages of large size by accelerating development and increasing stress) have significant implications for population dynamics as well as for conservation and resource management

Evolutionary drivers

Our study showed that CL patterns across and within infraorders are strongly influenced by phylogenetic signal. Dendrobranchiata produce the smallest first larval instar in Decapoda, the nauplius sensu lato, which hatches from free pelagic eggs. In contrast, Pleocyemata suppress the free nauplius stage, and larvae hatch from brooded eggs as larger and more developed zoeae [77,36]. These contrasting developmental modes reflect differences in parental care and distinct evolutionary pathways, as the nauplius represents an ancestral larval form already present in Upper Cambrian crustaceans [78], predating the divergence of Pleocyemata and Dendrobranchiata [79,80]. This pattern supports the "safe harbour" hypothesis [81], whereby parental care favours the evolution of larger offspring by reducing exposure to predation during development, as also observed in amphibians [82], fishes [51], and insects [83].

Within Pleocyemata, diversification was accompanied by the evolution of characteristic larval sizes and developmental strategies. The radiation of Caridea, Anomura, Achelata, and Brachyura during the Jurassic-Cretaceous coincided with the expansion of coral reefs [84], environments that likely favoured planktotrophic larvae with high dispersal potential. For example, ancestral palinurids possessed more phyllosoma stages than extant species [85]. Later, the evolution of Scyllaridae involved a reduction in larval stages and an increase in larval size [86,87], consistent with our results. In symbiotic reef species associated with patchily distributed hosts, larger larvae and abbreviated development may balance dispersal and local retention. This pattern occurs, for example, in the pinnotherid crab *Tunicotheres moseri*, which

lives associated with ascidians and develops through only two zoeal stages and one decapodid stage [88].

Our analyses also showed that species producing smaller offspring undergo longer larval development. Beyond developmental requirements, numerous larval instars may also function as an antiparasitic strategy. Molting enables crustaceans to shed damaged or infected exoskeletons [89], and frequent molting reduces parasite infection risk in other planktonic crustaceans [90]. In decapods, repeated molts during larval development may similarly reduce attachment time for ectoparasites and fungal-like pathogens. Supporting this idea, regions with higher parasite diversity and prevalence, such as tropical, coastal, and estuarine waters [91], tend to harbour species with more prolonged larval development and numerous stages.

Physiological and biogeographic constraints

Although environmental drivers explain global trends toward larger larval size at high latitudes, the absence of most reptant crabs (Brachyura) and true lobsters (Achelata, Nephropidae) from polar seas suggests additional phylogenetic constraints beyond ecophysiological limits.

Eco-physiologically, these decapod groups often lack the capacity for efficient osmoregulation and ion regulation at low temperatures, such as the requisite Mg^{2+} down-regulation [92,93] essential for coping with cold-water environments. From a developmental point of view, most larvae of these decapods show an inability to abbreviate the planktotrophic feeding phase to tune their development period with the short, seasonal primary production window characteristic of polar regions [19]. The combination of prolonged development time (due to cold) and the inability to buffer against acute food limitation excludes them from areas where the planktonic duration exceeds the short, high-quality feeding season. This constraint has been suggested to be a direct consequence of their evolutionary history [23]. The diversification and radiation of nearly 80% of modern Brachyuran groups occurred during the Cretaceous period when global oceans were substantially warmer, and polar temperatures were not prevalent [94,95,96]. This long evolutionary legacy in warm-temperate waters may have fixed life-history traits and physiological tolerances, making large-scale adaptation to the Cenozoic cooling and subsequent establishment in cold, high-latitude environments impossible for most clades [1].

The conquest of cold, high-latitude habitats by certain decapod clades highlights the strategic role of larval lecithotrophy in overcoming the coupled challenges of low temperature and food scarcity. This is most strikingly evident in Anomura, particularly the family Lithodidae, whose success in colonizing cold and deep-sea waters globally is directly linked to

a high maternal investment resulting in larval lecithotrophy plus large-size larvae [23]. In contrast, larval lecithotrophy is largely unknown or absent in the majority of Brachyura and in polar/sub-polar regions typically limited to partial lecithotrophy in only some caridean families like Pandalidae (e.g. *Pandalus japonicus* [97], and *Pandalus latirostris* [98]) and Campylonotidae (e.g. *Campylonotus vagans* [99]) where initial reserves supporting the first instar before external feeding is required. The striking absence of complete, or even facultative, lecithotrophy in these dominant infraorders reinforces the hypothesis of a phylogenetic constraint. This suggests that the evolutionary mechanism required to switch from planktotrophy to highly provisioned lecithotrophy may have been available, or more easily accessed, only in certain lineages (e.g., Anomura) and was fixed early in their cold-water radiation. In any case, further investigation into the phylogenetic origins of key decapod clades and their radiations across climate-dependent geological eras is warranted.

Overall, our study shows that larval size and developmental mode in decapod crustaceans result from interacting environmental, physiological, and evolutionary factors. The increase in larval size and abbreviated development at high latitudes and depths supports Thorson's Rule and highlights temperature and oxygen as key drivers of reproductive strategies. However, strong phylogenetic signals indicate that evolutionary history also constrains developmental flexibility in several lineages. Thus, macroecological patterns in larval traits reflect both present-day environmental pressures and deep evolutionary legacies.

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