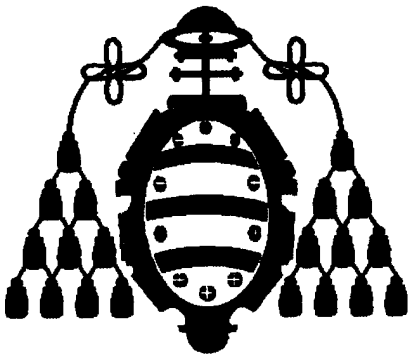

UNIVERSIDAD DE OVIEDO

Departamento de Biología de Organismos y Sistemas

Programa de Doctorado: “Biología aplicada a la sostenibilidad de recursos naturales (Mención de calidad)”

“Alcance teórico de la Ecología Metabólica”

“The theoretical scope of Metabolic Ecology”

TESIS DOCTORAL

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RESUMEN DEL CONTENIDO DE TESIS DOCTORAL

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RESUMEN (en español)

La Ecología Metabólica comprende las áreas del escalamiento biológico, alometría, bioquímica comparativa y fisiología, y considera al metabolismo como la fuerza motriz del flujo de energía y materiales a través de los distintos niveles de organización biológica: desde moléculas y células hasta ecosistemas. Por este motivo, para la Ecología Metabólica el metabolismo de los organismos determina el modo en que estos se relacionan con el medio ambiente, rigiendo por tanto su ritmo vital. Asimismo, la Teoría Metabólica de la Ecología propone una serie de relaciones, basadas en mecanismos químicos y físicos básicos, que describen la relación del metabolismo con la temperatura y el tamaño corporal. Estas relaciones permiten establecer puntos de partida para analizar los efectos de la temperatura y el tamaño corporal en distintas variables ecológicas, pero también para delimitar la capacidad de la fisiología para explicar las desviaciones de las pautas generales de determinados grupos de especies, o grupos funcionales. En esta tesis se intenta determinar cual es el alcance de la fisiología para explicar distintas variables ecológicas, y por tanto cómo influyen otros marcos teóricos (como las historias de vida, o las estrategias reproductivas) a la hora de determinar la ecología de los organismos.

El análisis del alcance teórico de las premisas de la Ecología Metabólica se hace desde dos puntos de vista: *entre* distintos niveles de complejidad biológica estudiados y *dentro* del nivel individual de complejidad biológica. El análisis considerando distintos niveles de complejidad biológica se lleva a cabo en el Capítulo 1, al estudiar variables ecológicas medidas al nivel de individuos y poblaciones. El alcance teórico de la Ecología Metabólica se estudia dentro del nivel individual en todos los capítulos, aumentando progresivamente la complejidad de las variables ecológicas estudiadas en cuanto a su relación con distintas estrategias reproductivas o de historias de vida. El Capítulo 1 estudia la propagación de la curvatura de la tasa metabólica basal a otras variables ecológicas tales como la tasa metabólica de campo, o la productividad, observándose que la dispersión de los datos en las variables más complejas se alejan más del patrón predicho por la Ecología Metabólica que en las variables más simples en términos de historias de vida. En el Capítulo 2 se estudia la necesidad de acompañar el modelo para el tiempo de desarrollo de organismos propuesto por la Ecología Metabólica, por una serie de relaciones basadas en optimizaciones de historias de vida. Al considerar ambas perspectivas, la predicción del modelo es

universal y describe el balance existente entre el tiempo de desarrollo y el número de descendientes producidos. De igual modo, en el Capítulo 3 se integran los efectos de la fisiología y los de las distintas estrategias de crecimiento seguidas por las larvas planctónicas de organismos bentónicos marinos para describir la duración del periodo larvario. Lo que se observa es que el escalamiento entre la duración del periodo larvario y la masa de la larva depende de muy diversos factores y no es negativa, como tradicionalmente se ha modelado. En el Capítulo 4 se analiza la dispersión de larvas planctónicas microscópicas en el eje costa-océano. Lo que se pone de manifiesto es que las distribuciones observadas de las larvas no siguen los patrones esperados si estas se comportan como partículas inertes, sino que parecen más bien estar sujetas a fenómenos de agregación activa, describiendo distribuciones normales y relacionadas con su fisiología. Finalmente, el Capítulo 5 analiza la influencia de la capacidad de dispersión larvaria en el tamaño del rango geográfico ocupado por organismos marinos bentónicos, y por tanto la influencia de las variables fisiológicas y de estrategias de vida relacionadas en la duración del periodo larvario en el tamaño del rango geográfico.

RESUMEN (en Inglés)

The Metabolic Ecology comprises the areas of biological scaling, allometry, comparative biochemistry and physiology, and considers the metabolism of individuals as the engine of the flow of energy and materials, through the different levels of biological organisation. In other words, for the Metabolic Ecology, the metabolism of organisms determines the way in which they relate with their environment, being hence the main driver of the pace of life. The Metabolic Theory of Ecology suggests specific relationships based on simple chemical and physical principles to describe the relationship between metabolism and temperature and body size. These relationships establish base-lines to analyse the effect of temperature and body size on different ecological variables, but also to delimit the ability of physiology to explain the deviation of given groups of species, or functional groups, from the general trends predicted. This Doctoral Thesis attempts to determine the theoretical scope of physiology to explain different metabolic-based ecological traits, and hence, the influence of other theoretical frameworks (such as Life History Theories) to determine the ecology of organisms.

The analysis of the theoretical scope of Metabolic Ecology is made from two different perspectives: *among* and *within* different levels of biological organisation. The analysis considering different levels of biological complexity is shown in Chapter 1, by studying different ecological variables measured at the individual and population levels. The theoretical scope of Metabolic Ecology within the individual level is addressed in the rest of chapters. Hence, through the 5 chapters of the thesis, the level of complexity of the ecological variables under study increases progressively from the point of view of reproductive strategies and life histories. In Chapter 1, the propagation of the curvature of the metabolic rate to other ecological traits such as field metabolic rate or productivity is studied. The results show that the more complex variables are farther to fit the premises of the Metabolic Ecology than the simple variables. In Chapter 2 it is analysed the necessity to provide the model for developmental time based on the premises of the Metabolic Ecology, with some relationships based on life history optimisation. Considering both points of view, the prediction of the model is universal, and describes the trade-off between the offspring developmental time and the offspring

number. Similarly, in Chapter 3, the effects of physiology and the different growth strategies followed by planktonic larvae of benthic marine organisms are integrated on the same model for the duration of planktonic development. What is found is that the scaling relationship between the duration of planktonic development and the size of larvae depends on diverse factors and is not negative, as traditionally modeled. In Chapter 4 the dispersion of microscopic planktonic larvae in the coastal ocean is modeled. The distribution of larvae does not follow the expected patterns if they behave as passive particles, rather, it looks like they have aggregation active mechanisms, what explains the shape of the distributions, related to physiology. Finally, in Chapter 5, the influence of the dispersal ability of larvae on the geographic range size of marine benthic organisms is analysed, and hence, the influence of the physiology and life histories related to the duration of the platonic phase on the geographic range size.

SR. DIRECTOR DE DEPARTAMENTO DE ORGANISMOS Y SISTEMAS

Aos meus pais, Gil e Elisa

Pero nosotros, que comprendemos la vida, nos burlamos de los números.
Le Petit Prince, Antoine de Saint-Exupéry

Contents

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Resumen

La Ecología Metabólica comprende las áreas del escalamiento biológico, alometría, bioquímica comparativa y fisiología, y considera al metabolismo como la fuerza motriz del flujo de energía y materiales a través de los distintos niveles de organización biológica: desde moléculas y células hasta ecosistemas. Por este motivo, para la Ecología Metabólica el metabolismo de los organismos determina el modo en que estos se relacionan con el medio ambiente, rigiendo por tanto su ritmo vital. Asimismo, la Teoría Metabólica de la Ecología propone una serie de relaciones, basadas en mecanismos químicos y físicos básicos, que describen la relación del metabolismo con la temperatura y el tamaño corporal. Estas relaciones permiten establecer puntos de partida para analizar los efectos de la temperatura y el tamaño corporal en distintas variables ecológicas, pero también para delimitar la capacidad de la fisiología para explicar las desviaciones de las pautas generales de determinados grupos de especies, o grupos funcionales. En esta tesis se intenta determinar cual es el alcance de la fisiología para explicar distintas variables ecológicas, y por tanto cómo influyen otros marcos teóricos (como las historias de vida, o las estrategias reproductivas) a la hora de determinar la ecología de los organismos.

El análisis del alcance teórico de las premisas de la Ecología Metabólica se hace desde dos puntos de vista: *entre* distintos niveles de complejidad biológica estudiados, y *dentro* del nivel individual de complejidad biológica. El análisis considerando distintos niveles de complejidad biológica se lleva a cabo en el Capítulo 1, al estudiar variables ecológicas medidas al nivel de individuos y poblaciones. El alcance teórico de la Ecología Metabólica se estudia dentro del nivel individual en todos los capítulos, aumentando progresivamente la complejidad de las variables ecológicas estudiadas en cuanto a su relación con distintas estrategias reproductivas o de historias de vida. El Capítulo 1 estudia la propagación de la curvatura de la tasa metabólica basal a otras variables ecológicas tales como la tasa metabólica de campo, o la productividad, observándose que la dispersión de los datos en las variables más complejas se alejan más del patrón predicho por la Ecología Metabólica que en las variables más simples en términos de historias de vida. En el Capítulo 2 se estudia la necesidad de acompañar el modelo para el tiempo de desarrollo de organismos propuesto por la Ecología Metabólica, por una serie de relaciones basadas en optimizaciones de historias de vida. Al considerar ambas perspectivas, la predicción del modelo es universal y describe el balance existente entre el tiempo de desarrollo y el número de descendientes producidos. De igual modo, en el Capítulo 3 se integran los efectos de la fisiología y los de las distintas estrategias de crecimiento seguidas por las larvas planctónicas de organismos bentónicos marinos para describir la duración

del periodo larvario. Lo que se observa es que el escalamiento entre la duración del periodo larvario y la masa de la larva depende de muy diversos factores y no es negativa, como tradicionalmente se ha modelado. En el Capítulo 4 se analiza la dispersión de larvas planctónicas microscópicas en el eje costa-océano. Lo que se pone de manifiesto es que las distribuciones observadas de las larvas no siguen los patrones esperados si estas se comportan como partículas inertes, sino que parecen más bien estar sujetas a fenómenos de agregación activa, describiendo distribuciones normales y relacionadas con su fisiología. Finalmente, el Capítulo 5 analiza la influencia de la capacidad de dispersión larvaria en el tamaño del rango geográfico ocupado por organismos marinos bentónicos, y por tanto la influencia de las variables fisiológicas y de estrategias de vida relacionadas en la duración del periodo larvario en el tamaño del rango geográfico.

General Introduction

Metabolic Ecology

Metabolism (the "fire of life") is the set of biochemical reactions through which organisms turn the energy and materials obtained from their environment into energy and substances valid for the construction and maintenance of body structures, growth, survival and reproduction. The sum of these metabolic reactions, known as the basal metabolic rate (B), represents the amount of energy needed to sustain the basic functioning of organisms. Knowledge on B and the factors ruling the energetic demands of organisms are needed to understand the way in which organisms interact with their environment.

The idea that metabolism rules the relationship between individuals and environment has been supported by observations of biological patterns found at multiple levels of organisation (from molecules and cells to populations, communities and ecosystems) attributable to surprisingly simple and general principles (Enquist et al., 2003). These observations, and the development of a mathematical framework based on well established principles of physics, chemistry and biology constituted the basis for the development of the Metabolic Theory of Ecology (Brown et al., 2004). According to these authors, the central pillars of the Metabolic Theory of Ecology are: 1) to characterise the effects of body size and temperature on the metabolism of individual organisms, and 2) to describe the effect of the metabolism of individual organisms on the pools and flows of energy and matter at higher levels of biological organisation. Following these premises, the metabolism of individual organisms becomes a fundamental variable in ecology that connects the processes occurring at different levels of biological organisation and, furthermore, allows to make predictions of ecological processes occurring at the population, community and ecosystem levels. In summary, to understand the whole complexity, and the mechanisms underpinning this flow of energy and materials, it is needed first to identify the variables ruling the metabolism of individuals.

The study of the body size effects on metabolism began in 1883, when the German physiologist Max Rubner described the relationship between basal metabolic rate, and body size, M, in the form $B = aM^{\beta}$ (where a is a normalisation constant and β is a scaling exponent) (Rubner, 1883). This power law between B and M have captured the attention of ecologists for many years and fed a warm debate on the value -and universality- of β (Dodds et al., 2001; White and Seymour, 2003; Glazier, 2005, 2006; Banavar et al., 2010; White, 2010). However, the Metabolic Theory of

Ecology assumed a general value of $\beta = 3/4$ (and multiples of $1/4$ for associated rates, biological times, and mass-specific rates) considering the fractal-like distribution network of resources, from cells to organisms (West et al., 1999). On the other hand, the effect of temperature on B is also well understood. Temperature governs metabolism through its effect on the velocity of biochemical reactions, and hence, its influence can be described using the Arhenius-Boltzmann's factor, $e^{(-E/kT)}$, where T is the absolute temperature (in degrees K), E is the activation energy, and k is the constant of Boltzmann ($8.62x10^{-5}eVK^{-1}$). This way to describe the influence of temperature on metabolism is valid within the range of biologically relevant temperatures between approximately 0^o and 40^oC.

Combining the effect of body size and temperature, the basal metabolic rate of organisms can be expressed as:

$$B = B_0 e^{-E/kT} M^{3/4} \tag{1}$$

being B_0 a normalisation coefficient. The Metabolic Theory of Ecology uses Eq. 1 to tests predictions about the effect of body size and temperature on the energy flow between organisms and environment. The Metabolic Ecology however, is not limited to a specific idealised model for the effects of temperature and body size on metabolic rate, but it attempts to be a more general metabolic framework for ecology, with broader applications. The theoretical background of the Metabolic Ecology presumably applies to any kind of organism and ecosystem. In this thesis, the physiological effects of body size and temperature on the different ecological variables under study will be analysed using Eq. 1. Using this relationship as a mathematical backbone, it will be possible to separate the effects of physiology, life histories, and other kind of factors ruling different ecological traits of a wide diversity of organisms.

Life history theories and environmental constraints

The view that body size and temperature (through their effect on the metabolism and physiology of organisms) rule the ecology of individuals, populations and other levels of organisation, seems to be too rigid to cope with the many evolutionary strategies present amongst organisms. This idea constitutes the basis of this thesis and, testing it is a way to explore the theoretical limits of the Metabolic Ecology. The basis of the evolution of species is the adaptation of organisms to their environment, what entails an enormous variety of life histories among and within species (Roff, 2002). But this diversity can not be explained solely by the effect of physiology (Harte, 2004; O'Connor et al., 2007*b*). Hence, despite Eq. 1 has been successfully applied to describe the basal metabolic rate for a wide diversity of organisms, there is a residual variation that can not be explained by body size and temperature. The same happens when analysing the inter-specific variation of

metabolic-based traits at different levels of biological organisation (e.g. individuals, populations, communities, etc.). The central hypothesis of this thesis is that, when analysing metabolic-based traits, the residual variation from the predictions of MTE will increase when analysing traits at higher than individual level of organisation, or when analysing complex traits subject to optimisation by Life History theories.

To model the effect of body size on metabolic-based traits, the Metabolic Ecology and Life History theories also have different points of view. Hence, for the Metabolic Ecology, body mass is considered a cause (independent variable) ruling metabolism because of its influence on the distribution of resources in a fractal-like system of vessels. However, for life history theories, body size is a consequence (dependent variable) of the evolutionary history of organisms and, through processes of optimisation, it constraints metabolism.

On the other hand, environmental factors can also play important roles on the performance of individual organisms. These external factors force organisms to permanently adapt to their environment and constitutes the natural mechanism through which badly fit individuals are removed from populations. The consequence is that the performance of individuals can be abruptly modified and the ecological patterns expected to be found can be drastically distorted. In this thesis, traits at different levels of biological organisation will be analysed. As we will see, some of them can be strongly influenced by environmental factors that will mask the ability of Metabolic Ecology and Life Histories to explain the observed inter-specific variability.

Thesis organisation

Along the different chapters of this thesis, the ability of Metabolic Ecology and Life Histories to explain different metabolic-based traits and ecological patterns will be analysed. To do so, and in order to mark out the limits of predictability of the Metabolic Ecology, in each chapter the complexity of the traits (in terms of the number of involved variables and the level of biological organisation considered) will be increased.

Hence, in the first chapter the principal tenet of the Metabolic Ecology will be tested. To do so we will apply the recent finding of Kolokotrones et al. (2010) that the metabolic rate of mammals do not follow a straight line when plotted against body size in a logarithmic axis. Hence, demonstrating that the curvature of metabolism can be found at different levels of biological organisation, constitutes a strong evidence for the validity of the theoretical roots of the Metabolic Ecology, and hence that metabolism of individuals rules the ecology of populations and communities, as well as other traits at the individual level. Other important characteristic of the the study in Chapter 1 is that different metabolic-based traits are analysed within the individual level of biological organisation. This study is outstanding and broadly

summarises the corollary of this thesis so, the next chapters will be more focused on specific traits or levels of biological organisation

In Chapter 2 the ability of metabolic rate to explain a more complex biological variable from the physiological point of view is analysed: the duration of development of organisms from the fecundation of the ovocyte until the end of maternal cares or energetic resources. The growth rates of organisms are ultimately controlled by physiology and the velocity of metabolic reactions. But, on the other hand, ecologists have long recognised that maternal reproductive strategies can affect many life history traits, including offspring size and development. Having into account the different life histories and reproductive strategies, the ability of the model for developmental time of West et al. (2001) can be improved, quantitatively diminishing the residual variance in developmental time for a wide diversity of organisms, from zooplankton to mammals and birds.

In Chapter 3, the complexity of the variable under study increases from the point of view of the interaction of individuals with more selective pressures: the planktonic larval duration (PLD) of marine benthic organisms. Larvae considered in this study are absolute planktotrophic, what means that they do not depend on maternal cares or energetic stores to complete the development. This implies that PLD is subject to more external variables than the duration of development described in Chapter 2, sustained exclusively on maternal resources. The existence of different strategies of larval growth responds to the interaction of species with their environment and constitute, together with temperature, the major forces driving PLD.

In Chapter 4, the biological and environmental variables ruling the dispersal of larvae of intertidal crustaceans across the shelf are analysed. The position of a small crustacean larvae (several microns) in the marine environment has been traditionally assumed as passive and mediated exclusively by ocean currents (Siegel et al., 2003; White et al., 2009*b*). For this reason, it would be expected that larvae would be uniformly distributed in the along-shore axis. But this hypothesis entails a controversy: how are larvae able to recruit back in adult populations if they act as passive particles? This question motivated the study of Chapter 4 consisting on the analysis of larval distributions and its relationship with different environmental and biological variables.

Finally, in Chapter 5, the determinants of the geographic range size in benthic marine organisms are analysed. The geographic range size is an important variable in ecology and biogeography, given its implications on the ability of species to face environmental changes. For marine organisms, different biological and environmental traits have been indicated as possible mechanisms ruling geographic range size. The results have been diverse and, sometimes, contradictory. Of them, the effect of dispersal ability has attracted the bulk of the attention, although its role is still not clear and seems to be influenced by other variables acting at different ecological levels. This chapter goes a step farther in the complexity of the trait analysed because the influence of larval dispersal on such a complex trait, in terms of the many

environmental variables involved, is analysed.

The ability of Metabolic Ecology to capture the inter-specific variability of different metabolic-based ecological traits will be analysed from two points of view: first, within a given level of biological organisation, by increasing the complexity of the traits in terms of reproductive strategies, or trade-offs imposed by life histories; and secondly, by increasing the level of biological organisation.

Objectives

The main objective of this thesis is to delimit the scope of Metabolic Ecology regarding the different levels of biological organisation and the complexity of the ecological traits studied. Each chapter of the thesis will be focused on specific ecological traits, being the level of biological complexity increased gradually, from Chapter 1 to Chapter 5. Here are resumed the particular objectives of each chapter:

- Chapter 1
  - To test the validity of the main tenet of Metabolic Ecology: that the metabolism of individual organisms rules other metabolic-based traits at different levels of biological organization.
  - To analyse the influence of the level of biological organisation on the ability of individual metabolism to explain the inter-specific variability of different ecological traits.
  - To explore the effects of the intra-specific variation in inter-specific analysis of ecological traits.
- Chapter 2
  - To introduce the effects of reproductive strategies into a model for developmental time based on the Metabolic Ecology.
  - To understand the relationship between the offspring number and the offspring development time.
- Chapter 3
  - To understand the determinants of the duration of the planktonic period of larvae of marine benthic organisms.
  - To include the effect of different larval growth strategies into a model based on larval size and temperature.
- Chapter 4
  - To elucidate if models of larval dispersal (assuming passive particles) can be improved by considering larval physiology and behaviour.

  - To analyse, from a physiological point of view, the determinants of the distribution of larvae in the along-shore axis.

- Chapter 5
  - To test the influence of larval dispersal on the geographic range size of benthic marine organisms.
  - To investigate the effect of the number of broadcasted particles on the geographic range size of benthic marine organisms

Chapter 1

Scaling up the curvature of mammalian metabolism

Contents

1.1 Introduction

Metabolic Ecology (ME) views metabolism as the backbone of ecology, driving the relationship between the biology of individual organisms and the ecology of populations, communities and ecosystems Brown et al. (2012). The Metabolic Theory of Ecology (MTE) Brown et al. (2004) is a specific framework within ME based on a central equation that attempts to summarise in a single model the effects of body size and temperature on metabolic rate:

$$B = B_o M^{\beta} e^{-E/kT} \tag{1.1}$$

where B is basal metabolic rate, B_0 is a normalisation constant, M is body mass, β is the allometric exponent, and $e^{-E/kT}$ is the Boltzmann's factor describing the temperature dependence of metabolic processes (where E is the activation energy of metabolic processes, k is Boltzmann's constant, and T is the absolute temperature in K). According to West et al. (1999) β takes a constant value of 0.75, while E is close to $0.65eV$ for aerobic processes (Gillooly et al., 2002).

The mass scaling term in the MTE central equation was first described in 1883 by the German physiologist Max Rubner in the form $B = B_0 M^{\beta}$ (Rubner, 1883). This power law between B and M captured the attention of ecologists for decades, feeding an intense debate on the exact value of β (Heusner, 1982; Hayssen and Lacy, 1985; West et al., 1999; Dodds et al., 2001; White and Seymour, 2003; Savage et al., 2004*b*). Taking logarithms, the model of Rubner is rewritten as:

$$\ln(B) = \beta_0 + \beta * \ln(M) + \varepsilon \tag{1.2}$$

with β_0 being the logarithm of B_0 and ε the error term that includes both experimental error and variability in metabolic rate not explained by body size. According to Eqs. 1.1 and 1.2, the slope of the relationship between $\ln(B)$ and $\ln(M)$ is the constant value β. However, in the last years, different works have pointed to the nonlinearity of this relationship (Dodds et al., 2001; Packard and Birchard, 2008; Savage et al., 2008; White et al., 2009*a*; Banavar et al., 2010; Kolokotrones et al., 2010; Ehnes et al., 2011). Kolokotrones et al. (2010) provide a general analysis of the curvature of metabolism, giving an overview of its causes and consequences. These authors show that, for mammals, the basal metabolic rate describes a curve in response to body size and that a quadratic polynomial model of the form:

$$\ln(B) = \beta_0 + \beta_1 * \ln(M) + \beta_2 * (\ln(M))^2 + \varepsilon \tag{1.3}$$

accounts for a higher amount of variance than a linear model. This implies that in a plot of $\ln(B)$ versus $\ln(M)$ the slope is $\beta_1 + 2 * \beta_2 * \ln(M)$, a non-constant value that increases with body size. In consequence, the increase in metabolic rate with body size is sharper for large mammals than for smaller ones. This curvilinear relationship questions the form of the central equation of MTE (Eq. 1.1) and suggests that it should take the form of :

$$B = B_o M^{\beta_1} M^{\beta_2 * \ln(M)} e^{-E/kT} \tag{1.4}$$

where the allometric exponent β_1 can be viewed as a scale dependent coefficient (Mackay, 2011; Deeds et al., 2011), while the exponent β_2 is a measure of the degree of curvilinearity.

The goal of this work is to explore the consequences of the curvature of metabolism on the scaling of other life history traits. Assuming Eq. 1.1 and the central tenet of ME as valid, MTE predicts that body size and temperature should rule

Table 1.1: Body size and metabolic scaling for different ecological traits/phenomena. The proposed scalings show the expected proportionality between each trait and metabolic rate together with the predicted scaling from the linear model and the expected scaling from the curvilinear model using the simple proportionalities. Note that if the ontogenetic growth model is used to derive these scalings the values of β_1 and β_2 would change between traits. Column curvature indicates the convexity/concavity of the theoretical curve described by the trait in a log-log plot versus body mass.

Phenomenon	**Proposed scalings**	**MTE**	**Curvilinear scaling**	**Curvature**
Whole organism rates B, FMR, Ingestion rate, Productivity	$Trait \propto B$	$B = B_0 * M^{3/4}$	$B = B_0 * M^{\beta_1} * M^{(\beta_2 * \ln(M))}$	Concave
Mass specific rates Locomotion costs, Population growth rate	$Trait \propto B/M$	$R = R_0 * M^{-1/4}$	$R = R_0 * M^{(\beta_1 - 1)} * M^{(\beta_2 * \ln(M))}$	Concave
Biological times Life span	$Trait \propto M/B$	$T = T_0 * M^{1/4}$	$T = T_0 * M^{(1-\beta_1)} * M^{(-\beta_2 * \ln(M))}$	Convex
Pop. carrying capacity Pop. density	$Trait \propto 1/B$	$K = K_0 * M^{-3/4}$	$K = K_0 * M^{-\beta_1} * M^{(-\beta_2 * \ln(M))}$	Convex

the ecology of individuals and populations. This central Eq. 1.1, linear on a log-log scale, has been applied to different phenomena and levels of organisation (Brown et al., 2004; Brown and Sibly, 2012). A persuasive model (West et al., 1999) suggests that the mass scaling allometry then takes some value multiple of 1/4 depending on the phenomenon under consideration (Table 1.1). Whole organism rates should scale with body mass with a 3/4 allometry, while mass-specific rates should scale with a mass exponent of $-1/4$. Biological times should show a 1/4 mass scaling while measures of ecosystem carrying capacity such as maximal population density should scale as the $-3/4$ power of body mass (Brown et al., 2012). Tests of the coincidence of the observed body-size scaling coefficients with these predictions have been used to support (e.g. Savage et al. (2004*b*); Ernest (2003); Economo et al. (2005)) or reject (i. e. Duncan et al. (2007)) MTE.

To make predictions on the scaling of developmental times (Gillooly et al., 2002) and rates at the population level (Savage et al., 2004*b*; Duncan et al., 2007), MTE incorporates Eq. 1.1 in a growth model (West et al., 2001; Moses et al., 2008; Hou et al., 2008) that balances energy uptake and maintenance costs during ontogeny. An important, often overlooked, assumption in this general ontogenetic growth model is that the metabolic rate during ontogeny scales with the same allometric coefficient observed across adult animals of different species (Makarieva et al., 2009; Zuo et al., 2009). So ontogenetic growth is modeled as:

$$\frac{dm}{dt} = am^{\beta} - bm \tag{1.5}$$

where m is the mass of the organism as a function of time (t), and a and b are parameters related to fundamental cellular properties (Gillooly et al., 2002; West

et al., 2001; Moses et al., 2008).

Integrating Eq. 1.5 from t = birth to t = maturity, yields the prediction that developmental time should scale interspecifically with an exponent equal to $\beta - 1$ (Gillooly et al., 2002). MTE then uses demographic theory to make predictions at the population level (i. e. Savage et al. (2004*b*); Duncan et al. (2007); Jetz et al. (2004); White et al. (2007)).

If we follow the same steps, but instead of using Eq. 1.1 we use the curvilinear Eq. 1.4, we reach the equation:

$$\frac{dm}{dt} = am^{\beta_1+\beta_2 \ln(m)} - bm \tag{1.6}$$

whose integral cannot be solved analytically to make predictions on the exact curvilinear scaling of biological times (and hence rates at the population level) with body mass. Intuitively, however, the increasing slope in the allometry of mammalian metabolism should translate in a curvature in the size scaling of other metabolic-mediated traits such as life span, population density or population growth rate. If these curvatures exist they should be perceived as concave for whole organism and mass specific rates, and as convex for biological times and population carrying capacities (Table 1.1).

In this work we demonstrate the propagation of the curvature of metabolism through different mammalian life-history traits, both at the individual and population level. We will first show the existence of curvatures in the different life history traits evaluated; then, we will show that the type of curvature in terms of concavity/convexity is different for each trait as expected according to the proportionality between the scaling of each trait and metabolic rate. Because the allometric coefficients change with body size, the existence of such curvilinear relationships prevents any attempts to test MTE on the basis of comparison of linear log-log scaling coefficients unless the ranges of body mass considered by all data sets are the same. Given that the number of species for which all traits have been measured is very low, we will compare the body size scaling of each trait with the size scaling of metabolism for the same subset of species. Finally we will try to solve the differential Eq. 1.6 numerically to understand how the curvature of metabolism should affect the scaling of other biological traits. As explained above, the differential Eq. 1.6 is based on the assumption that interspecific and intraspecific metabolic scalings should be equal, here we will explore the consequences of the relaxation of this assumption on the curvilinear scaling of metabolic rate.

1.2 Materials and methods

1.2.1 Evaluated life history traits

We have performed a bibliographic search on life history traits both at the organism and at population levels of organisation. The result of this compilation is presented in Appendix 1.A. Traits at the population level of organisation refer to traits varying at the population level for what we are using a species level average. We considered eight different traits (basal metabolic rate in $kJ\ h^{-1}$, field metabolic rate in $kJ\ h^{-1}$, offspring biomass production in $g\ d^{-1}$, ingestion rate in $kcal\ d^{-1}$, costs of locomotion in $mlO_2\ g^{-1}\ km^{-1}$, life span in d, population growth rate in $year^{-1}$ and population density in km^{-2}) using nine different bibliographic sources (see Table S1.1). If available, we obtained the data directly from tables but when tables were not provided we digitised the data from plots (Table S1.1). The offspring biomass production P was calculated using the clutch size C, the number of clutches produced per year N, and the mass of each individual offspring m, obtaining $P = CNm$. The data on ingestion rate refers both to carnivores and herbivores from the work of Farlow (1976) (Table S1.1).

To homogenise the species names of the different data sets, we followed the nomenclature provided in Fritz et al. (2009). Then, we constructed a database with the values of each trait reported for each mammalian species considered (Appendix 1.A). This compilation results in a total of 1365 species. Data on basal metabolic rate is available for 746 different species combining data from the data-bases of McNab (2008), Sieg et al. (2009), and Savage et al. (2004*b*). For those species with more than one data reported from the different data sets we calculated an arithmetic mean of the logarithms for B and body mass; these are the values used in the comparisons with the other traits in Fig. 1.2. Data on field metabolic rate is available for 116 species of which 84 have associated values of B. Data on offspring biomass productivity is available for 532 species of which data on B is available for 279 species. In the case of life span, we have data for 592 species of which 270 have a value of B. Data on population growth rate is available for 294 species of which we have values of B in the case of 162 species. Finally, for population density we have values for 553 different species, of which data for B is available for 245 species.

1.2.2 Analysis of the coincidence of the curvatures and measurement error

To compare the curvilinear fit of BMR and the curvilinear fits of the other life-history traits, and given that not all the traits follow 3/4 allometries, the values of the traits were transformed so that the expected scaling, based on MTE, would be 3/4 (see "Transformation" column in Table 1.1). To test the variation in the linear slopes we performed standard linear regressions of each trait and body size. The 95%

confidence intervals of these slopes are shown in Fig. S1.1 with the word "Slope". The curvatures of the different traits were analysed by fitting an orthogonal polynomial regression. This regression is of the form $Y = \alpha + \beta(X - \overline{X}) + \gamma(X_2 + aX - b)$; where $\overline{X}$ is the average of the X values, and a and b are chosen so that $\Sigma(X_2 + aX - b) = 0$ and $\Sigma X(X_2 - aX - b) = 0$. This method does not affect the estimate of γ and it makes the estimates of α, β and γ independent of each other. Additionally, this method is not affected by changes of scale, so the results are not dependent on the mass unit considered. To compare the coefficients of two orthogonal regressions the average of the X values (i.e. the average body masses) should be equal. For some species the average body mass was different in each trait database, what would make the average body sizes differ. To avoid this error in the calculation of the orthogonal regression coefficients we used an average body mass from the two datasets being compared.

To analyse the effect of measurement error and intraspecific variability in BMR, we performed a similar comparison but between BMR estimates reported by two different bibliographic sources for the same species. To create a BMR data set where the measurements for each species come from different sources, we removed from the work of McNab (2008) and Sieg et al. (2009) those species that had the same first author as the original data source (Appendix 1.A). To do that we performed an extensive search on the primary sources used by these studies on BMR. Quite often these sources were citations that compiled data from several sources, although a big effort was done to disentangle these sub-references, it was sometimes impossible to obtain the original data source. For example, although data on mass and BMR for the Chilean rock rat (*Aconaemys fuscus*) was exactly the same in the two data sets, the data sources (or sub-references we were able to obtain) were different. We included these species in our data set so our approach is conservative in the sense that some references considered here to be different could come from the same original source. In the case of the BMR data base of Savage et al. (2004*b*), it was not possible to analyse the bibliographic origin of the data, as the amount of sub-references was too high.

1.2.3 Analysis of the influence of the curvature of metabolism on the scaling of developmental time

To analyse the consequences of the curvature in metabolism in the scaling of developmental time, we tried to solve the growth model from Eq. 1.6. But, given that this equation cannot be solved analytically, we used numerical methods. To solve the differential growth Eq. 1.6 we used the solver for ordinary differential equations, switching automatically between stiff and non-stiff methods (lsoda; Petzold (1983)) using package "deSolve" in the R statistical package (R Development Core Team, 2011). The code used to run the simulations presented in Fig. 1.3 is provided in the Appendix 1.B.

1.3 Results

We have evaluated the propagation of the curvature of metabolic rate through seven different life history traits (see Materials and Methods and Table S1.1). The log-log plots of these traits versus body mass show a curvilinear response in most traits (Fig. 1.1, where the traits are ordered from the individual, upper panels, to the population level of organisation, lower panels). This visual perception of the curvatures is supported by the better fit of the quadratic model compared to the linear one and the significance of the quadratic term in Eq. 1.3 (Tables S1.2 and S1.3). Only for population density, where the variability explained by body size is small, the quadratic term is not significant (Table S1.3). In the cases where the curvature is significant, the convexity and concavity of these curvatures is coincident with the scalings proposed by MTE and shown in Table 1.1 (sign of β_2 in Table S1.3).

Tests on whether the curvature of each trait is coincident with the curvature found in basal metabolic rate cannot be based on the fits in Fig. 1.1 for two reasons. First, because the estimates of the coefficients for the quadratic term in a traditional least-squares polynomial regression are dependent on the estimates for the linear term, and second, because the body mass ranges in each data set are different (Table S1.1) and hence the expected fits for the linear term should not be the same. To solve these two problems we have established pairwise comparisons using only those species for which both data on each life history trait and basal metabolic rate were available (Fig. S1.1). We have then used orthogonal polynomial regression to test whether the first and second order polynomial terms coincide (i.e. whether the 95% confidence intervals overlap, see Materials and Methods for details on orthogonal polynomial regression). Although the confidence intervals for the second term of the polynomial fit overlap in all cases (indicating that the departure from linearity is similar in all cases), the estimates for the linear term (i.e. first term of the polynomial) only overlap with those for B in the case of field metabolic rate. For all the other traits analysed, the allometric scaling coefficients differ indicating that the body size scaling for most ecological traits is not the same as that of B.

This novel database with paired estimates of B and life history traits for each species lets us analyse the variance in metabolic rate not explained by body size. If a species has a metabolic rate different from that expected for animals of the same size (a difference measured by the residuals in a plot of metabolism *vs* body size), this difference should be perceived, following ME, in the residuals of the plots of other traits with body size for that same species. The analysis of the residuals of these body size relationships (Fig. 1.2) indicates that higher residuals in B translate into higher residuals of field metabolic rate, but not into higher residuals for the rest of traits considered. This is an indication that, once the effects of body size on metabolic rate have been accounted for, the remaining variance in metabolic rate does not have any perceptible effects on the other traits.

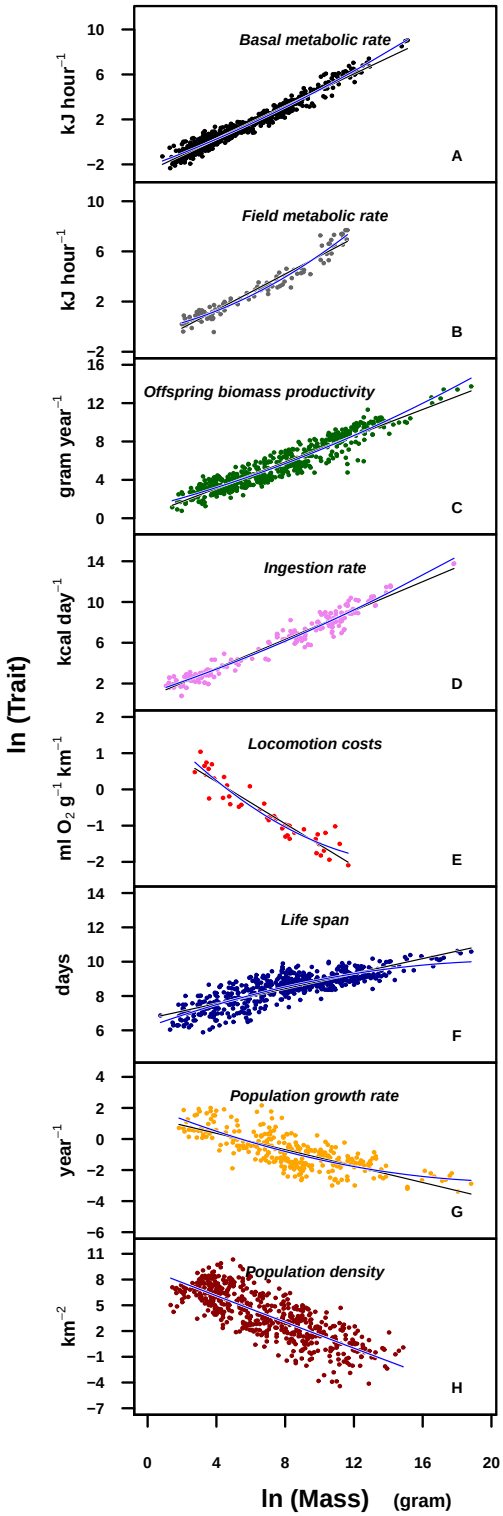

Figure 1.1: Plots of the different life history traits versus body mass in a log-log scale. Blue lines correspond to the fit of the quadratic model and black lines to the fit of a linear model. The upper panels correspond to individual level traits, while the lower panels to population level traits. See Appendix 1.A for the bibliographic sources used to construct each panel.

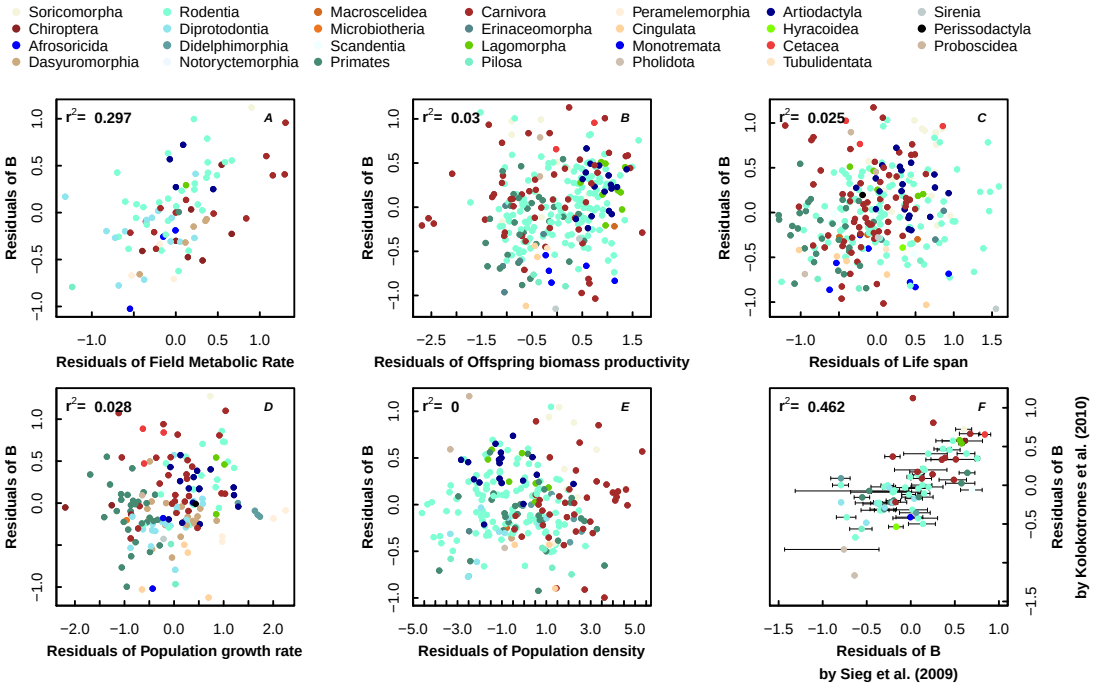

Figure 1.2: Relationships of the residuals of the linear regression fits of each evaluated trait and B.

To give a full interpretation to this result we need to know if the residuals in the metabolism *vs* body size relationship are an indication that a species has a different metabolic rate or is just the result of random or measurement error. As we pointed out in the introduction, the error term (ε) in Eqs. 1.2 and 1.3 includes both the experimental error and the variability not explained by body size. In an attempt to study the magnitude of this experimental error, we have compared two different data sets of basal metabolic rate (the one used by Kolokotrones et al. (2010) to describe the curvature of metabolism (McNab, 2008) and the data set of Sieg et al. (2009)), considering only those data coming from different bibliographic sources (Fig. 1.2, panel F, but see also Fig. S1.1 panels K and L). The degree of correlation between the residuals of B for each species in the two data sets is an indication of the relative importance of experimental error and true variability. An analysis of the residuals similar to the one applied above for other traits indicates a correlation between the residuals of both B data sets of 46.2%. In addition, the B estimates of these data sets for each species are the average of several measurements so intraspecific variability is not considered. Sieg et al. (2009) provided data on intraspecific variability measured as the standard deviation of B measurements for different individuals of the same species. For 34% of the species considered in the database used in Fig. S1.1 panel L, the intraspecific variability is larger than the residuals of the B *vs* body size plot. So, although the residuals of B *vs* body size hold some information, there is quite a lot of scatter introduced by intraspecific variation and measurement error.

Body size captures most of the variability in metabolic rate, in this comparison of B measured by different sources, body size explains 95.9% of the variance, while the B measured for the same species by a different author explains 96.7% (Fig. S1.2, panels A and B).

As we explained in the introduction, if the curvilinear scaling in B is accepted, the integral of Eq. 1.6 cannot be solved analytically to predict the exact scaling of developmental time and population rates with body size. The integral of Eq. 1.6 can be solved numerically (see simulations in Figs. 1.3A and 1.3B) to show that for a given curvilinearity in B, the resulting curvilinear relationship in developmental time does not have the same scaling coefficients (Appendix 1.B for the code used to solve the equations). In Fig. 1.3A we provide a numerical example of the prediction of MTE using a simple, linear allometry of B ($\beta_1 = 3/4$; $\beta_2 = 0$) resulting in the predicted linear scaling of developmental time ($\gamma_1 = 1/4$; $\gamma_2 = 0$). But, following the same approach using the curvilinear model for B (Table S1.3; $\beta_1 = 0.5593$; $\beta_2 = 0.0123$), the resulting scaling of developmental time has a $\gamma_1 = 0.4746$ and a $\gamma_2 = -0.0061$ (Fig. 1.3B). Hence, if there is a curvilinear scaling of B with body size, following MTE we reach the counter-intuitive result that the scaling of developmental time should be curvilinear but with different scaling coefficients.

1.4 Discussion

Kolokotrones et al. (2010) have shown that the curvature in metabolic scaling is not against the principles of MTE and that the mechanistic model of West et al. (1999) can be extended to meet the premises of the quadratic equation. Our work is based on the premise that if the scalings suggested by MTE, and more generally by ME, are correct (Brown et al., 2004; Economo et al., 2005; Enquist et al., 2003), the curvature should be perceived in other ecological traits. In consequence, the fact that most traits considered show a curvature (Fig. 1.1) coincident with the predicted convexity or concavity as expected from MTE, can be viewed as a support for ME.

The nonlinearity of different life history traits with body size has been previously described. Silva and Downing (1995) have considered the relationship between population density and body size for different groups of mammals. These authors found a negative relationship between population density and body mass, but with a more pronounced slope for smaller animals than for larger organisms. In their study they considered data on population density regardless of whether this was maximal so the energetic equivalence rule (Damuth, 1981) is not expected to hold (Isaac et al., 2011). In addition, the shape of the relationship between population density and body mass remains controversial and some authors argue that it could be triangular instead of linear, with medium sized species attaining a higher density (Marquet et al., 1995). We have chosen to analyse the data set of Damuth (1993) because it considers only the size range for which maximal population density decreases with

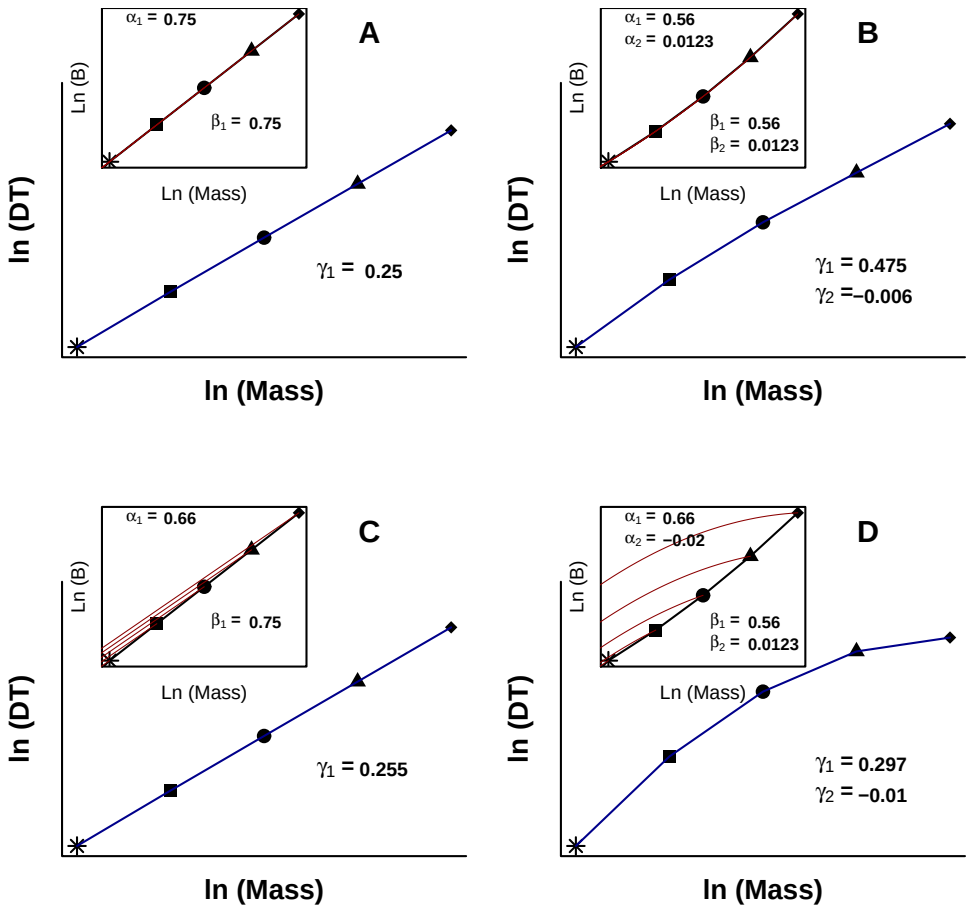

Figure 1.3: Numerical solutions for Eq. 1.6. The inset in each panel represents the interspecific (black line) and ontogenetic (red lines) scalings of B *vs* body size. The different symbols represent hypothetical adult body sizes of different species. The blue lines show the scaling of developmental time (DT, defined as the moment in which the organism reach an arbitrary fraction of adult body size) with body mass. The coefficients shown correspond to the models $\ln(B_{ontogenetic}) = a_{onto} + \alpha 1 * \ln(m) + \alpha 2 * \ln(m)^2$; $\ln(B_{interspecific}) = a_{inter} + \beta 1 * \ln(M) + \beta 2 * \ln(M)^2$ and $\ln(DT) = a_3 + \gamma 1 * \ln(M) + \gamma 2 * \ln(M)^2$; where m is the mass of the organism during growth and M is the asymptotic adult mass of the species. In panels A and B, the ontogenetic and interspecific scalings are coincident; in panel C they are different and linear, and in panel D they are different and curvilinear. See Appendix 1.B for further details on the mathematical background and the R code to solve the model.

body size and the energetic equivalence rule should hold.

Charnov and Ernest (2006) studied the allometry of reproductive trade-offs and explored the relationship between the number of offspring produced (corrected for the female mass) and the offspring size. They found a slight curvature or break at a neonate size around 1,000 g. Using these data, as well as the number of offspring per clutch and the clutches per year (see Materials and Methods) we obtain the curvature in Fig. 1.1C. The relationship between offspring biomass productivity and body size describes a concave curve that, following MTE, agrees with the concave curvature in B, suggesting that the break found by Charnov and Ernest (2006) could have a metabolic origin. The nonlinearities described in these studies lacked a general theoretical explanation and were considered as consequences of other ecological factors adding noise to the relationships.

Tests on the difference between the allometric scaling of different traits and the scalings predicted by MTE, based on the linear Eq. 1.2, have been used to refute (i. e. Duncan et al. (2007)) or accept (i. e. Savage et al. (2004*b*)) MTE. The existence of curvilinear scalings, however, invalidates to some extent all these attempts. The linear (in a log-log scale) coefficients depend on the body mass range considered, so a trait would have a scaling coefficient different or similar to 3/4 depending on the body mass range of the database under consideration. A way to correctly make these comparisons is, for each trait, to construct a database of B and trait measurements for the same species. Because in such a database the body masses coincide, the linear fits of B and the given trait should be the same if MTE is correct. For the traits considered, such comparisons (Fig. S1.1) lead to the conclusion that the linear fits for all traits (except field metabolic rate) differ.

But the existence of a curvature in metabolism introduces further uncertainties in the comparison of scaling coefficients. If Eq. 1.3 is accepted as valid, it is not possible to analytically reach the prediction on the expected scalings for developmental time and traits at the population level. But Eq. 1.6 can be integrated numerically to show that when the scaling of B is curvilinear, the resulting scaling in developmental time is also curvilinear but with a different degree of curvilinearity. Furthermore, Eq. 1.6 is reached after assuming that during ontogeny the scaling of B with body mass parallels interspecific scaling (Moses et al., 2008; Hou et al., 2008), a coincidence that has been focus of some debate and is unlikely to be met (Makarieva et al., 2009; Zuo et al., 2009; Glazier, 2005). We can use our numerical model to test the resulting interspecific scaling of developmental times (and hence traits at the population level) if the assumption of equal ontogenetic and interspecific metabolic scalings is relaxed (see the Supplementary Information for the equations used).

Figs. 1.3C and 1.3D show two scenarios where the allometry of B during ontogeny is different to the allometry of the interspecific scaling of B. The most simple case is one where both scalings are linear on a log-log scale but ontogenetic B takes an allometric slope lower than interspecific allometric scaling. This reflects the commonly observed phenomenon that a juvenile of a species has a higher B than

an adult individual of another species with the same body mass (Makarieva et al., 2009). In Fig. 1.3C, we run a simulation where the slope of ontogenetic scaling is 2/3 and the interspecific scaling 3/4. The result of this simulation is a linear scaling of developmental time with body size, with an interspecific scaling coefficient 0.255. From these simulations we can conclude that the interspecific scaling in B has more importance in the resulting interspecific scaling in developmental time. Fig. 1.3D shows another simulation where ontogenetic and interspecific scalings are different, both are curvilinear and each has a different degree and sign of curvilinearity. In this simulation, the scaling of B is concave between species but convex during ontogeny. The convex curvature of B during ontogeny introduces variability but the scaling of developmental time is still convex as expected from the interspecific concave scaling of B. These simulations suggest that it is not possible to refute MTE if the scaling coefficients of ecological traits are different to that of B. This conclusion imposes important constraints in the evaluation of MTE.

A possible way to test ME would be to analyse the residuals of the relationship between B and body size. If a species has a B different than expected for its body size, it should have an influence on its ecology and be reflected in the residuals of other life history traits for this species. We have attempted such analysis as presented in Fig. 1.2. For example, for field metabolic rate we can see that species that have a B higher than predicted from body mass (positive B residuals) tend to have higher field metabolic rates (positive field metabolic rate residuals), but even for this trait the correlation is very low ($r^2 = 0.297$). For the rest of traits considered there is no relationship between the residuals of the B relationship with body size and the residuals of other traits. MTE has focused on the scaling of body mass and temperature to other traits with little attention paid to the scaling of the residuals of these relationships. Our analysis show that the residuals do not scale in accordance with MTE, suggesting that the principal tenet of ME could be wrong.

But, do the residuals hold ecological information or are they the result of random and experimental noise? Although some phylogenetic groups have been shown to fall above the B *vs* mass regression line (McNab, 2008; Capellini et al., 2010), and despite a phylogenetic signal in the linear term of the B scaling exponent has been detected (Isaac and Carbone, 2010; Capellini et al., 2010), these differences are not reflected in the other traits analysed (Fig. 1.2). But it is hard to ascertain to what extent these differences are influenced by common experimental errors due to the use of different protocols to measure B for each group or species, and hence to what extent these deviations should be reflected in the scaling of other traits. We have attempted to assess this experimental error creating a database where each species has two B measurements each one coming from a different original bibliographic source. If experimental error is very low compared to ecological effects we would expect a good correlation between the two B measurements. The relatively low correlation ($r^2 = 0.462$, Fig. 1.2F) between the residuals of each B data set indicates that the measurement error of B is considerable. We cannot quantify the magnitude of the measurement error in the values of the other traits considered but it is likely

to be, at least, similar to that of B. This suggests that, to some extent, the lack of correlation in the plots of Fig. 1.2 could be due to the influence of experimental or random error (White et al., 2012). In addition, intraspecific variability within traits should be considered. Intraspecific variability is larger than the residuals of the B *vs* body size plot for 34% of the species in our database. Because B and each trait are measured on different sets of individuals this introduces further uncertainty in the comparison of residuals.

In summary, our analysis leaves an uncertain scenario on the acceptance of MTE as a general macroecological theoretical framework. We have shown that testing MTE on the basis of comparison of regression slopes is not a valid approach and that the analysis of residuals has important uncertainties introduced by intraspecific and experimental error. The pervasive effect of body size on B, explaining a similar amount of variance than B measured in another set of individuals of the same species, makes difficult to analyse the residual variance. Studies measuring B and other ecological traits on the same set of individuals with sample sizes large enough to reduce experimental error are needed to fully evaluate MTE. In any case, the curvatures of the traits, in agreement with the concave/convex scaling expected by ME, point to a regularity in the curvilinear scaling of many different life history traits which could have a metabolic origin.

1.5 Acknowledgements

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1.6 Supplementary Information

1.6.1 Background for analytically solving differential equations of growth

In the Appendix 1.B, we describe the R (R Development Core Team, 2011) code used to solve numerically Eq. 1.6 of the main text. The models used allow us to modify and simulate different coefficients for the interspecific and ontogenetic scalings of B with body size. Hence, we will refer as B_{inter} for the interspecific scaling of B vs body size, and as B_{onto} for the scaling of B with body size during ontogeny.

The models considered are hence in the form:

$$B_{inter} = a_{inter} * M^{\beta_1+\beta_2*ln(M)} \tag{1.7}$$

$$B_{onto} = a_{onto} * m^{\alpha_1+\alpha_2*ln(m)} \tag{1.8}$$

where M is the asymptotic adult mass, m is the mass of the organism at any given moment of development, and a_{inter} and a_{onto} are constants. Note that when β_2 or α_2 are zero, these models follow a linear relationship in a log-log scale, otherwise, they are curvilinear.

When a growing organism reaches the asymptotic adult size, the ontogenetic scaling of B is:

$$B_{onto} = a_{onto} * M^{\alpha_1+\alpha_2*ln(M)} \tag{1.9}$$

In this moment, the ontogenetic scaling should be equivalent to the interspecific scaling, letting us to relate the constants a_{onto} and a_{inter}:

$$a_{onto} * M^{\alpha_1+\alpha_2*ln(M)} = a_{inter} * M^{(\beta_1+\beta_2*ln(M))} \tag{1.10}$$

$$a_{onto} = a_{inter} * M^{(\beta_1+\beta_2*ln(M))-(\alpha_1+\alpha_2*ln(M))} \tag{1.11}$$

This approach is different to that of Moses et al. (2008) in that the coefficient a is allowed to vary during ontogeny and hence interspecific and ontogenetic scalings are not forced to be the same. This relationship allows to rewrite B_{onto} in terms of a_{inter}:

$$B_{onto} = a_{inter} * M^{(\beta_1+\beta_2*ln(M))-(\alpha_1+\alpha_2*ln(M))} * m^{\alpha_1+\alpha_2*ln(m)} \tag{1.12}$$

Knowing the scaling of basal metabolic rate and following the work of West et al. (2001), at any given time t, the change in total body mass m of a growing organism, can be expressed as:

$$\frac{\delta m}{\delta t} = a_{inter} * M^{(\beta_1+\beta_2*ln(M))-(\alpha_1+\alpha_2*ln(M))} * m^{\alpha_1+\alpha_2*ln(m)} - b * m \tag{1.13}$$

where b is a constant related to the energetic costs of maintenance of the existing tissues (West et al., 2001). The increment in body mass equals zero when the organism reaches the adult mass, allowing to express b in terms of M, a_{inter}, β_1 and β_2:

$$0 = a_{inter} * M^{(\beta_1+\beta_2*ln(M))-(\alpha_1+\alpha_2*ln(M))} * M^{\alpha_1+\alpha_2*ln(m)} - b * M \tag{1.14}$$

$$b = \frac{a_{inter} * M^{(\beta_1+\beta_2*ln(M))}}{M} \tag{1.15}$$

Following these steps and nomenclature for the variables in the models, we have constructed the code in Appendix 1.B allowing to solve analytically Eq. 1.13. The coefficients of interspecific scaling (β) and the coefficients of ontogenetic growth scaling (α) are combined to describe the growth rate of any organism, allowing to infer the body size scaling of developmental time. The solution of the model depends on the value of a_{inter} which has to be arbitrarily selected since we lack experimental data to fit its value. Because a_{inter} has units of mass (to some exponent) and time, its value should be selected within a given range in accordance with the time steps used in evaluating the model. For our model parametrisation these values should range between 0.1 and 10 (i. e. for different values of a_{inter} the time steps at which the model is solved should be changed). Tests of sensitivity of numerical simulations to the value of a_{inter} did not have an effect on the conclusions reached.

1.6.2 Supplementary tables and figures

Table S1.1: The different phenomena or life history traits considered in the study, with their respective bibliographic sources. The traits are ordered by increasing level of organisation, following the same criterion used to construct the figures of the main text. In the case of basal metabolic rate, the average values of basal metabolic rate and body mass reported by the three sources have been considered. Column *Sp.number* shows the number of species considered for each trait and used for the fit of the different models. The column *Digitised* shows the sources from where data were obtained digitising graphics instead of directly from tables. For these cases we lack the species names so the pairwise comparisons can not be performed. Column *Mass.range* refers to the whole body size range in grams, comprised by the data set.

Trait	**Sp.number**	**Digitised**	**Source**	**Mass.range, g**
Basal Metabolic Rate	746	No	McNab (2008) Sieg *et al.* (2009) Savage *et al.* (2004)	2.35 - 3,672,000
Field Metabolic Rate	116	No	Capellini *et al.* (2010)	7.3 - 111,400
Offspring biomass productivity	532	No	Ernest *et al.* (2003)	4.15 - 149,000,000
Ingestion rate	171	Yes	Farlow (1976)	2.90 - 55,050,690
Locomotion costs	46	Yes	Fedak & Seeherman (1979)	15.52 - 116,507
Life span	592	No	Ernest *et al.* (2003)	2.10 - 149,000,000
Population growth rate	294	No	Duncan *et al.* (2007)	6.16 - 147,910,800
Population density	564	No	Damuth (1993)	3.80 - 2,860,000

Table S1.2: Fit of the data in Fig. 1.1 using a linear ($ln(Trait) \sim \beta_0 + \beta ln(M)$) model. "Trait" is each one of the analysed life history traits and "M" the body size values associated to each value of "Trait".

Trait	**Parameter**	**Estimate**	**St. Error**	**p-value**	$\mathbf{r^2}$
Basal metabolic rate	β_0	-2.6205	0.0335	$< 2 * 10^{-16}$	0.9574
	β	0.7223	0.0055	$< 2 * 10^{-16}$	
Field metabolic rate	β_0	-1.5607	0.1091	$< 2 * 10^{-16}$	0.9454
Capellini et al. 2010	β	0.7191	0.0162	$< 2 * 10^{-16}$	
Productivity	β_0	0.3642	0.0897	$5.69 * 10^{-5}$	0.8853
Ernest et al. 2003	β	0.6859	0.0107	$< 2 * 10^{-16}$	
Ingestion rate	β_0	0.6404	0.0797	$3.65 * 10^{-14}$	0.9563
Farlow 1976	β	0.7097	0.0094	$< 2 * 10^{-16}$	
Locomotion costs	β_0	1.3746	0.1180	$4.95 * 10^{-15}$	0.8832
Fedak & Seeherman 1979	β	-0.2901	0.0159	$< 2 * 10^{-16}$	
Life span	β_0	6.6789	0.0535	$< 2 * 10^{-16}$	0.688
Ernest et al. 2003	β	0.2187	0.0060	$< 2 * 10^{-16}$	
Population growth rate	β_0	1.4209	0.1216	$< 2 * 10^{-16}$	0.5693
Duncan et al. 2007	β	-0.2639	0.0134	$< 2 * 10^{-16}$	
Population density	β_0	9.16203	0.1890	$< 2 * 10^{-16}$	0.6319
Damuth 1993	β	-0.7644	0.0248	$< 2 * 10^{-16}$	

Table S1.3: Fit of the data in Fig. 1.1 using a linear ($ln(Trait) \sim \beta_0 + \beta_1 ln(M) + \beta_2 (ln(M))^2$) model. "Trait" is each one of the analysed life history traits and "M" the body size values associated to each value of "Trait".

Trait	**Parameter**	**Estimate**	**St. Error**	**p-value**	$\mathbf{r^2}$
Basal metabolic rate	β_0	-2.1872	0.0669	$< 2 * 10^{-16}$	0.9603
	β_1	0.5593	0.0226	$< 2 * 10^{-16}$	
	β_2	0.0123	0.0016	$3.72 * 10^{-13}$	
Field metabolic rate	β_0	-0.3712	0.2209	0.0956	0.9585
Capellini et al. 2010	β_1	0.2712	0.0763	0.00054	
	β_2	0.0337	0.0056	$2.76 * 10^{-8}$	
Productivity	β_0	1.1397	0.1790	$4.23 * 10^{-10}$	0.8905
Ernest et al. 2003	β_1	0.4615	0.0463	$< 2 * 10^{-16}$	
	β_2	0.0135	0.0027	$9.07 * 10^{-7}$	
Ingestion rate	β_0	1.0122	0.1238	$1.38 * 10^{-14}$	0.9587
Farlow 1976	β_1	0.5592	0.0400	$< 2 * 10^{-16}$	
	β_2	0.0104	0.0027	0.000145	
Locomotion costs	β_0	2.0385	0.2986	$2.29 * 10^{-8}$	0.897
Fedak & Seeherman 1979	β_1	-0.5130	0.0941	$2.30 * 10^{-6}$	
	β_2	0.0160	0.0067	0.0209	
Life span	β_0	6.1929	0.0961	$< 2 * 10^{-16}$	0.7061
Ernest et al. 2003	β_1	0.3585	0.0239	$< 2 * 10^{-16}$	
	β_2	-0.0083	0.0013	$3.17 * 10^{-9}$	
Population growth rate	β_0	2.1311	0.2233	$< 2 * 10^{-16}$	0.5892
Duncan et al. 2007	β_1	-0.4489	0.0509	$< 2 * 10^{-16}$	
	β_2	0.0103	0.0027	0.000206	
Population density	β_0	9.2063	0.4112	$< 2 * 10^{-16}$	0.6319
Damuth 1981	β_1	-0.7788	0.1207	$2.46 * 10^{-10}$	
	β_2	0.00096	0.0079	0.904	

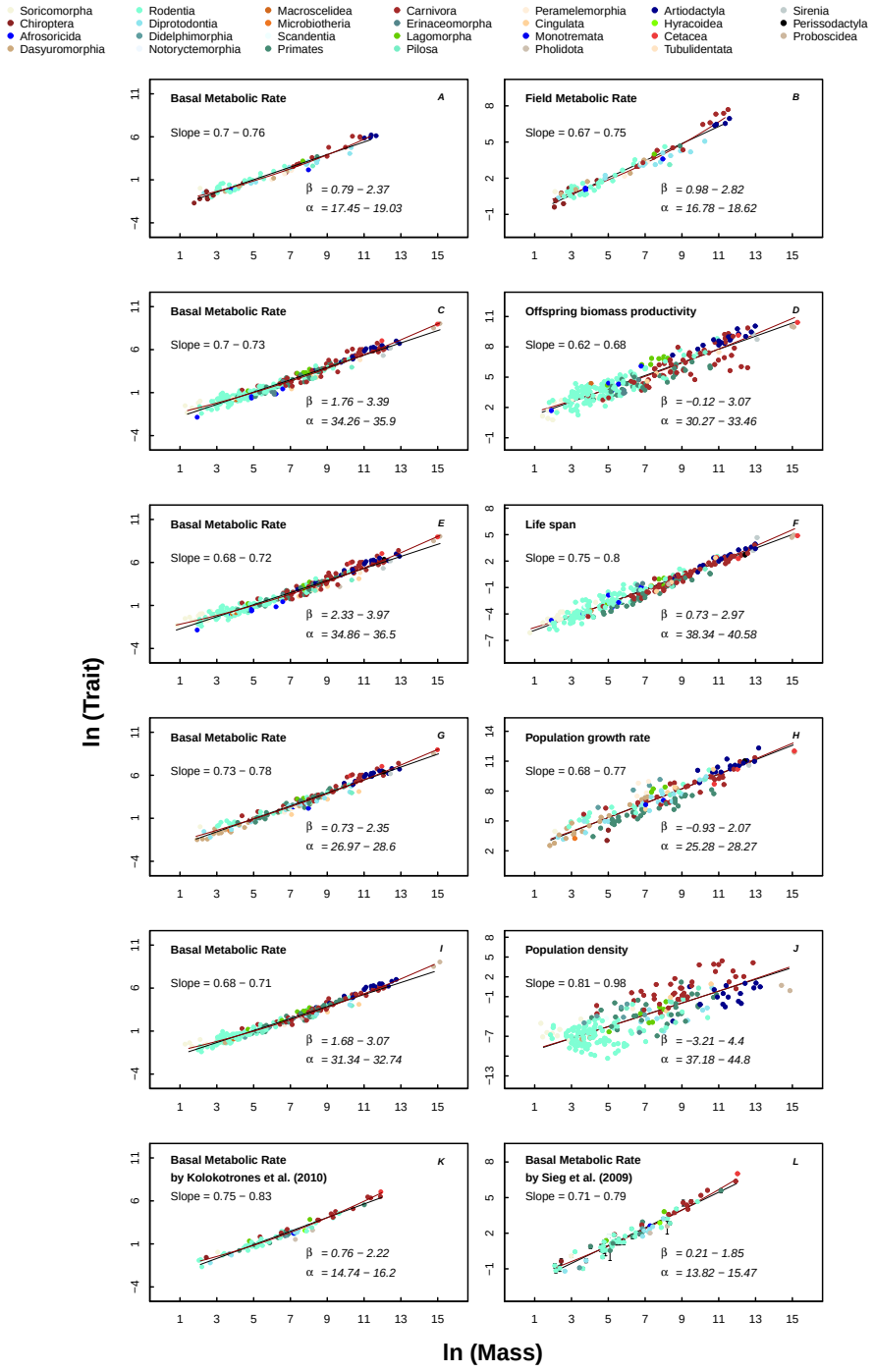

Figure S1.1: Analysis of the scalings of B and the different life history traits taking into account only those species for which data on both variables were available. Traits have been transformed to show a 3/4 allometry according to the predictions of MTE (Table 1.1 in main text). B values are the average value of the data reported in references (Savage et al., 2004*b*; Sieg et al., 2009; McNab, 2008). Two models are fit in left and right panels: a) a linear model whose slope's 95% confidence intervals are shown with the word "slope"; and b) an orthogonal polynomial regression of the form $Y = \alpha + \beta(X - \overline{X}) + \gamma(X^2 + aX - b)$ (see Analysis of the coincidence of curvatures section in the Methods section of the main text) whose 95% confidence intervals for α and β are shown.

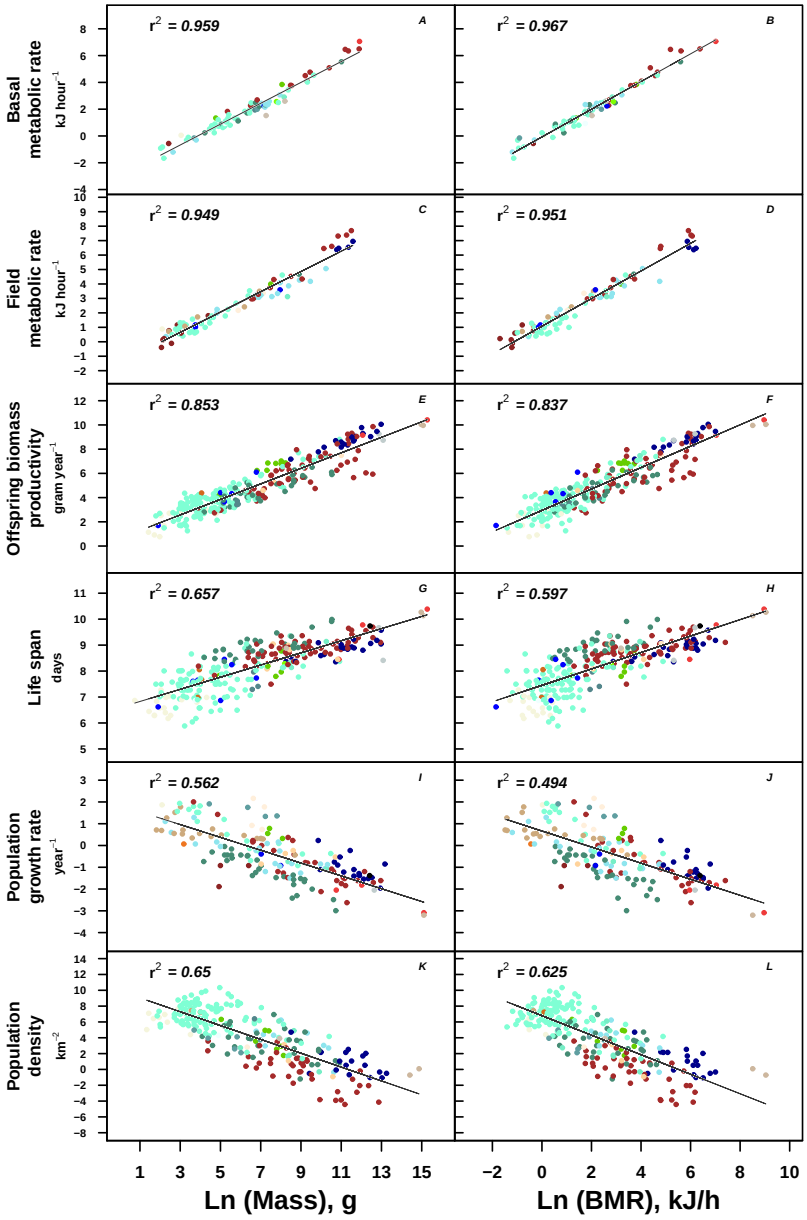

Figure S1.2: Does B explain more variability in ecological traits than body mass?. This figure shows the amount of variation in each trait explained by body size (left column) and basal metabolic rate (B, right column). These comparisons have been made taking into account only those species for which data on the evaluated trait and B were available. B are the average of the data reported in the databases of McNab (2008), Sieg et al. (2009) and Savage et al. (2004*a*). It should be noted that, as explained in the Methods section of the main text, B might have been measured in individuals of the same species but with different body mass, what might partly explain why the variance explained by B is lower than that explained by body mass. The colour legend is the same than in Fig S1.1. For basal metabolic rate in panels A and B, we compare the percentage of the variance in B from McNab (2008) explained by body mass (Fig. S1.1A) to that explained by the B measured by a different author (Sieg et al., 2009).

1.A Appendix 1.A

http://www.repositorio.ieo.es/e-ieo/handle/10508/1578

1.B Appendix 1.B

http://www.repositorio.ieo.es/e-ieo/handle/10508/1579

Chapter 2

The offspring-development-time/offspring-number trade-off

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Contents

2.1 Introduction

Developmental time determines how fast populations grow and reproduce (Savage et al., 2004*a*), so the interest in understanding developmental time transcends the limits of individual energetics and biology. In animal populations, the elapsed time from fertilisation of the oocyte to the birth of the new individual is therefore an important life history trait subject to optimisation depending on reproductive and life history strategies (Stearns, 1992; Roff, 2002; Kiørboe and Hirst, 2008), but it is also constrained by physiology as outlined by the Metabolic Theory of Ecology (MTE) (Gillooly et al., 2002).

A difference between the approaches of MTE and Life History Optimisation (LHO) is that MTE seeks to understand the effects of body size on developmental time, whereas LHO examines the evolutionary optimisation of body size. Body mass is considered a cause (independent variable) driving developmental time by MTE but a consequence (dependent variable) subject to optimisation by LHO theories. Ultimately, body mass can affect developmental time in two ways: first through allometric effects on metabolic rate controlling how fast an organism grows, and secondly through life history optimisations that set the relative body sizes at which transitions between developmental stages occur, and hence the duration of development.

Following the development of the MTE, Gillooly et al. (2002) developed a model that predicts a one-quarter power allometry between embryonic development time and newborn body mass. This general relationship holds for a wide diversity of organisms regardless of their life histories and taxonomy. The ability of newborn mass to describe developmental time relies on its capacity to capture in a single variable both the effect of the allometric constraints in the allocation of metabolic energy and the length of the trajectories along the ontogenetic growth curve until birth.

Here, we combine this general relationship between offspring size and developmental time with the classical trade-off between number and size of offspring (Smith and Fretwell, 1974; Charnov and Ernest, 2006) to show that, from a LHO perspective, there is a trade-off between the number of offspring and the duration of development.

Conceptually, our model is summarised in Fig. 2.1A, with some hypothetical combinations of offspring development time (ODT), offspring size (m_o), female mass (M) and the offspring production rate (C) of females. Fig. 2.1B shows the growth curves of these offspring and their size at birth, as well as their expected ODT, while Fig. 2.1C shows the resulting relationship between ODT and offspring mass. Females 1 and 2 and females 3 and 4 have the same maternal body size but different reproductive strategies. For example, while female 1 invests its reproductive potential in producing many small eggs, female 2 produces a few, larger offspring.

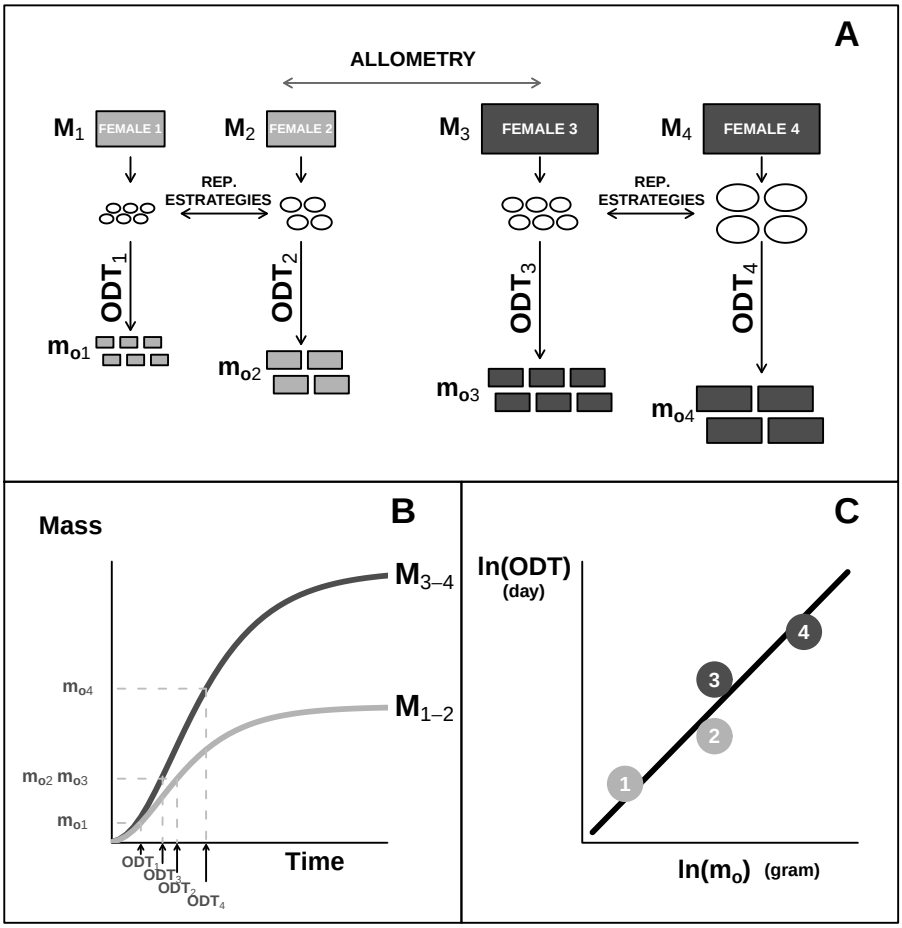

Figure 2.1: Schematics showing different combinations between adult size, M, offspring size, m_o and offspring development time, ODT. Panel A shows different scenarios where the differences in adult and offspring size between hypothetical species determine the length of their offspring development time. Pairs of females 1-2 and 3-4 have the same adult mass. The size ratio m_o/M is the same for pairs of females 1-3 and 2-4. Offspring from examples 2 and 3 have the same size m_o. Panel B schematises the sigmoidal growth curves of these species. Note that the ODT in each case is inferred from the mass of the offspring by projecting the ontogenetic curve to the time axis. Panel C represents an hypothetical plot of offspring development time versus offspring size in a log-log scale. The slope of the regression line drawn is 1/4. Each case is plotted according to the expected deviation from the predictions of MTE given the reproductive strategies followed.

The longer developmental time of the offspring of female 2 is mostly due to their longer ontogenetic trajectories compared to offspring of female 1, with the allometric constraints on metabolic rate having little effect on the difference in ODT. The allometric constraints on metabolism and growth rate play a major role, however, in the different developmental times of the offspring of small (cases 1 and 2) and large (cases 3 and 4) females. The resulting relationship between ODT and m_o therefore captures both reproductive and allometric constraints (Fig. 2.1C).

Our aim is to develop a model for offspring development time that explicitly parametrises these allometric and reproductive effects. To achieve this we will first extend Charnov and Ernest's (2006) model on the balance between offspring size and number in birds and ectotherms. These authors suggested that their model for the trade-off between offspring size and number in mammals could be applied more generally if the effects of temperature on maternal metabolic rates were considered. We therefore extend their model to include temperature as a control of reproductive investment, and we test this model with an extensive compilation of empirical data for ectotherms and endotherms demonstrating the universal generality of Smith and Fretwell's (1974) trade-off. We then put the resulting equation into Gillooly et al.'s (2002) model for embryo developmental time and generate a unifying model that captures the trade-off between offspring number and developmental time.

2.1.1 The model

We will introduce first the trade-off between size and number of offspring as presented by Charnov and Ernest (2006), and formulate the correction for temperature needed to compare endotherms and ectotherms. We will then briefly introduce the general ontogenetic growth model as developed by West et al. (2001) and the model for developmental time by Gillooly et al. (2002). Finally we will blend both theories in a unifying model.

2.1.1.1 LHO trade-offs

Life History Optimisation (LHO) theories view body mass as a trait that can be optimised and try to understand the trade-offs that lead to different relative body sizes at the transitions between ontogenetic periods. The classic life history optimisation model of Smith and Fretwell (1974) describes how the offspring production rate, C, is directly related to the amount of resources allocated to reproduction in a reproductive event, R, and inversely related to the allocation per offspring, I, ($C/R \propto 1/I$). Charnov and Ernest (2006) suggested that, in mammals, the investment per offspring is approximated well by the offspring mass (m_o) while the resources diverted to reproduction scale with adult mass (M) raised to 3/4. They showed that the relationship $C/M^{3/4} \propto m_o^{-1}$ was supported with data for mammals.

For ectotherms this relationship should be a bit more complex. The amount of resources allocated to reproduction (R) should be proportional to metabolic rate (B) and depend on body size and temperature following the general equation $R = C * m_o \propto B \propto M^{3/4} * e^{(-E/kT)}$, where $E \approx 0.62eV$ is the average activation energy for metabolic reactions (Gillooly et al., 2001) and k, in eV/K, is the Boltzmann's constant. Hence, the Smith and Fretwell's (1974) model for optimal offspring size can be expressed as $C * m_o = \lambda M^{3/4} e^{(-E/kT)}$ (where λ is a scaling constant). Rearranging terms we obtain:

$$\frac{C}{\lambda M^{3/4} e^{(-E/kT)}} = \frac{1}{m_o} \tag{2.1}$$

which represents the trade-off between offspring number (scaled for the effects of maternal body size and temperature) and offspring size. This model is equivalent to Charnov and Ernest's (2006) model but includes the effects of temperature on reproductive investment and captures the fact that as temperature increases there is an increase in metabolic rate that leads to faster biomass production and hence larger daily offspring production rate (C).

2.1.1.2 The MTE approach

At the basis of the Metabolic Theory of Ecology approach to modelling developmental time, and derived from the principles of allocation of metabolic energy at the cellular level, is the general model for ontogenetic growth (West et al., 2001; Hou et al., 2008), where growth rate is described as:

$$\frac{\delta m}{\delta t} = a m^{3/4} \left[1 - \left(\frac{m}{M} \right)^{1/4} \right] \tag{2.2}$$

where m is the organism mass at a given time t, M is the asymptotic adult mass and a is a variable related to fundamental cell properties. The parameter a includes the effect of temperature (T in K) on metabolic rate through the Arrhenius - Boltzmann's factor, $a = a_0 e^{(-\frac{E}{kT})}$, where a_0 is a normalisation constant independent of temperature.

This equation parametrises the classical sigmoidal ontogenetic growth curve present in many organisms (West et al., 2001). The term $1 - (m/M)^{1/4}$ represents the growth efficiency G (the proportion of energy devoted to growth) that is highest at the beginning of development.

Eq. 2.2 is usually simplified assuming that the growth efficiency during embryo development is maximal ($1 - \left(\frac{m}{M}\right)^{1/4} \approx 1$) (Gillooly et al., 2002; Moses et al., 2008) leading to:

$$\frac{\delta m}{\delta t} = a m^{3/4} \tag{2.3}$$

Integrating Eq. 2.3 from $t = 0$ to $t =$ end of offspring development, we obtain Gillooly et al.'s (2002) formulation for offspring development time (ODT)

$$ODT = \left(\frac{4}{a_0 e^{(-E/kT)}}\right) m_o^{1/4} \tag{2.4}$$

2.1.1.3 The balance between offspring development time and offspring number

The relationship between offspring number and developmental time is obtained first solving Charnov-Ernest relationship as described in Eq. 2.1 for $m_o^{1/4}$:

$$m_o^{1/4} = \lambda^{1/4} \frac{M^{3/16} e^{(-E/4kT)}}{C^{1/4}} \tag{2.5}$$

and substituting this expression in Eq. 2.4 for offspring development time:

$$ODT = \lambda^{1/4} \left(\frac{4}{a_0}\right) \frac{M^{3/16} e^{(3E/4kT)}}{C^{1/4}} \tag{2.6}$$

This equation expresses offspring development time in maternal terms and shows that developmental time is mainly ruled by temperature, adult mass and the offspring production rate. It shows that there is a trade-off between the number of offspring that can be produced and the offspring development time.

2.2 Materials and Methods

We first carried out a bibliographic search in order to test the major prediction of the Charnov and Ernest's (2006) model for optimal clutch size (Eq. 2.1) for endotherms and ectotherms. We compiled data on offspring production rate and the temperature at which this variable was measured for 1985 species (Appendix 2.A). Secondly, we also made a literature search to test the relationship between ODT and mass and temperature, resulting in a database of 2252 species with a wide diversity of life histories (Appendix 2.B). Finally, we combined both data-sets to study the balance between ODT and offspring production rate predicted by Eq. 2.6. Data on ODT and fecundity rarely come from the same reference (Appendixes 2.A and 2.B), and usually each variable was measured at different temperatures. To correct this source of uncertainty we used the exponential correction of temperature to obtain an estimate of fecundity at the same temperature at which ODT was measured:

$$C' = C * e^{E/k(1/T_C - 1/T_{ODT})} \tag{2.7}$$

where C' is the estimated fecundity at the temperature at which ODT was measured T_{ODT} , C is the fecundity for that species and T_C is the temperature at which C was measured (see Appendix 2.A).

2.3 Results

2.3.1 The offspring-size/clutch-size trade-off in endotherms and ectotherms.

Charnov and Ernest (2006) demonstrated an energetic trade-off between the number and size of offspring in mammals. Here we demonstrate that this balance also holds for a wider diversity of organisms, including both endotherms and ectotherms. A plot of temperature corrected offspring biomass production versus adult mass in a log-log scale yields a slope of 0.76, not significantly different from 3/4 ($p-value$ of a t-test of slope different than $0.75 = 0.104$, Fig. 2.2A, $r^2 = 0.97$) in accordance with the postulates of MTE. The effect of temperature on offspring production rate also fits the prediction of MTE. The value of the slope in Fig. 2.2B represents the activation energy, E, of the relationship between mass corrected offspring biomass production and temperature. According to Gillooly et al. (2001), the theoretical value should be $0.62eV$, and our result ($0.67eV$) is not significantly different ($p - value = 0.201$.)

Finally, the universal trade-off between number and size of offspring is corroborated by the inverse isometrical relationship between the mass of the offspring (m_o) and the offspring production rate as predicted by Eq. 2.1 (Fig. 2.2C, $r^2 = 0.98$). The slope of this relationship is -0.986 only marginally significantly different from -1 ($p - value = 0.026$).

2.3.2 The effects of offspring size and temperature on offspring development time

Following Eq. 2.4, once ODT is corrected for the effects of temperature, offspring size explains part of the remaining variability found across taxa (Fig. 2.3A). As predicted by MTE, the slope of this relationship is not significantly different from 1/4 ($p - value = 0.458$). Similarly, a plot of ODT corrected for the effect of mass versus temperature (Fig. 2.3B) has a slope of 0.54, significantly different but close to the predicted activation energy for the metabolic reactions proposed by Gillooly et al. (2001) ($p - value = 1.7 * 10^{-5}$).

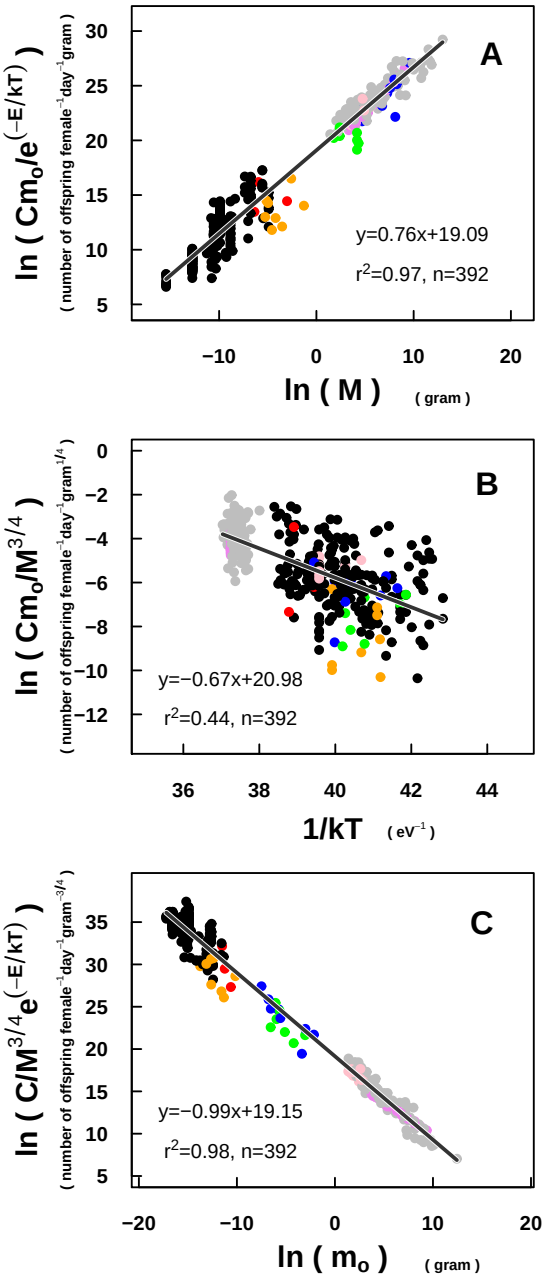

Figure 2.2: The offspring-size/clutch-size trade-off relating offspring production rate, C, adult mass, M, offspring mass, m_o, and the exponential term including the effect of temperature on offspring production, $e^{-E/kT}$. (A), relationship between the temperature-corrected offspring biomass production and adult mass. (B), effect of the temperature on the offspring biomass production once corrected for the effects of female size. (C), inverse isometrical relationship between the offspring production rate corrected for the effects of female mass and temperature and the offspring size. Colours represent each group in the data-set: mammals (gray), non-procellarid birds (pink), procellarids (violet), amphibians (green), fish (blue), univoltine insects (orange), multivoltine insects (red) and zooplankton (black).

2.3.3 The trade-off between offspring development time and offspring number

The direct corollary of Eq. 2.6 is the existence of a trade-off between offspring development time and offspring production rate. This trade-off is the result of different reproductive strategies of resource allocation between many-small or few-big offspring. In consequence, once corrected for the effect of temperature and adult body mass, a plot of the offspring development time versus the offspring production

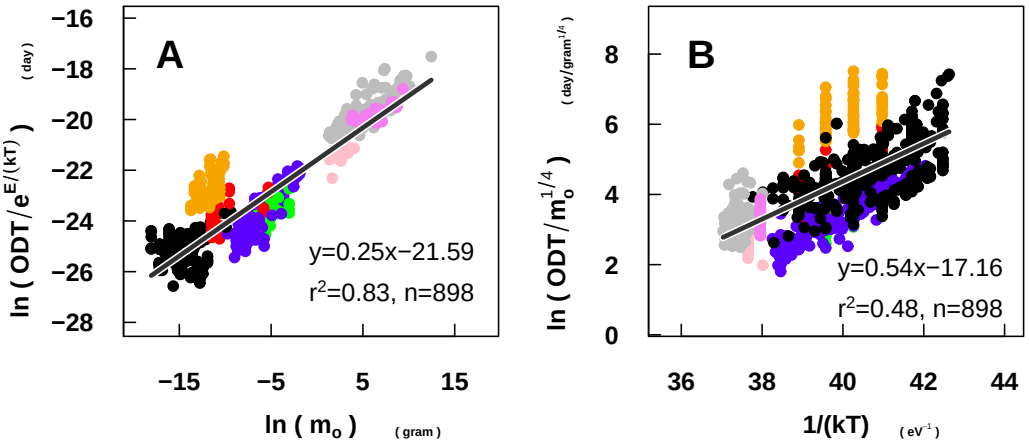

Figure 2.3: Model for offspring development time from Eq. 2.4. Panel A shows the relationship between the temperature corrected ODT versus offspring mass. Panel B represents the logarithm of ODT corrected for the effects of offspring mass versus the logarithm of $e^{E/kT}$. Colour legend as in Fig. 2.2.

rate shows an inverse relationship (Fig. 2.4, $r^2 = 0.78$). But the estimation of the allometric exponent of offspring production rate on offspring development time using this relationship is not correct because we are already assuming a $3/4$ scaling allometry when correcting ODT by $M^{3/16}$. In fact, considering Fig. 2.4, the resulting slope -0.34 is significantly different from the expected $-1/4$ ($p-value = 2.2*10^{-16}$). To correctly evaluate the allometric exponent a non-linear multiple regression is needed. Taking logarithms in Eq. 2.6 and given an allometric exponent α and activation energy E we obtain the formula:

$$ln(ODT) = \beta - \alpha * ln(C) + (1-\alpha)\alpha * ln(M) + (1-\alpha)E/kT \qquad (2.8)$$

where β is a scaling intercept. This equation can be fitted through non-linear least squares with α, β and E as parameters to be estimated. The values obtained by this procedure are close to the predictions of MTE: $\alpha = 0.269$ with 95% confidence intervals of 0.250 to 0.288 and $E = 0.480$ with 95% confidence intervals between 0.382 and 0.584.

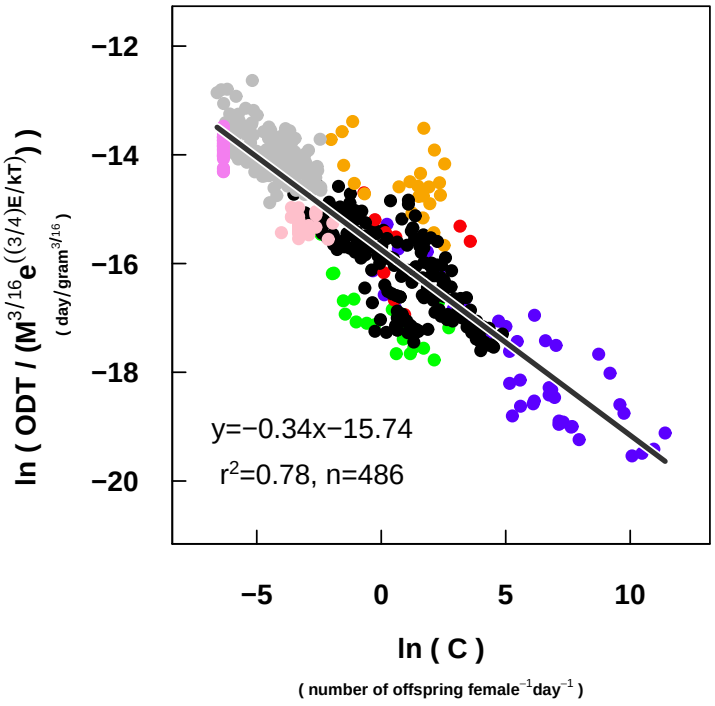

Figure 2.4: The trade-off between offspring development time and offspring number. According to Eq. 2.6, there is a balance between ODT and the number of offspring produced by female per unit time. See main text for interpretation on the regression slope. Colour legend as in Fig. 2.2.

2.4 Discussion

2.4.1 Effects of body size and temperature on developmental time

The Metabolic Theory of Ecology (MTE) is grounded on the laws of physics and biochemical kinetics. It states that metabolic rate forms the backbone of ecology driving many other ecological properties at higher levels of organisation (West et al., 2001; Gillooly et al., 2002; Brown et al., 2004; Hou et al., 2008). This view of biology as ruled by the laws of physics and thermodynamics is often seen as too rigid to satisfactorily explain the many evolutionary strategies present amongst organisms (Harte, 2004; O'Connor et al., 2007*b*) and clashes with the perception by life-history theorists that most biological traits are subject to fitness optimisation. Combining MTE with offspring size-number theory we have shown that it is possible to reconcile these two approaches.

Offspring development comprises the processes of growth and transformation leading from the fertilised zygote to the independence of the offspring. According to MTE, the time required for offspring development is mostly determined by the offspring size and the developmental temperature. These effects are explained as a direct consequence of the faster rates of metabolism of smaller organisms and of animals with warmer body temperatures (Brown et al., 2004). This explanation, however, downplays the fact that larger newborns usually take longer to develop not only due to their slower metabolism but because they have to develop to a larger size and hence have a longer ontogenetic trajectory to follow. That is, two species with the same metabolic rate, which hence grow equally fast, can have very disparate developmental times due to optimisation of their mass at birth (cases 1 and 2 Fig. 2.1).

Gillooly et al. (2002) showed that newborn mass explained much of the variability in embryo development time, and we corroborate this result for ODT (Fig. 2.3). In our analysis we include also an extensive data compilation on marine birds from the order *Procellariformes* (such as petrels, albatrosses and shearwaters) and mammals, known to follow very specific reproductive strategies. By doing so and introducing the notion of offspring development time, which includes the complete maternal investment per offspring, we extend the universality of the model of Gillooly et al. (2002).

2.4.2 Growth efficiency and the simplified ontogenetic growth model

Offspring size captures in a single variable two effects, both of which lead to longer developmental times: slower metabolism with increasing adult asymptotic size (differences between cases 1-2 and 3-4 in Fig. 2.1) and longer ontogenetic growth trajectories with larger mass at birth (differences between cases 1 and 2 or 3 and 4). The only situation not explained by Gillooly et al.'s (2002) simplified model and Eq. 2.3 is the differences in developmental time between offspring 2 and 3 in Fig. 2.1.

The simplification in Eq. 2.4 is usually considered valid (Gillooly et al., 2002; Moses et al., 2008) on the basis that growth efficiency during embryo development is maximal ($1 - \left(\frac{m}{M}\right)^{1/4} \approx 1$). That is, on the assumption that mass at birth is minimal compared to adult mass and hence growth efficiency is well approximated by 1. However, the assumption of $1 - (m/M)^{1/4} \approx 1$ is not always valid and hence the simplification should be adopted carefully. For instance, using data from our data-set, we have found organisms with growth efficiencies close to 0.50 at birth (some species of zooplankton and mammals). Integrating the complete ontogenetic growth model from Eq. 2.2, from $t = 0$ to $t =$end of maternal care, and assuming that the mass of the embryo at $t = 0$ is negligible, we obtain the complete model for ODT:

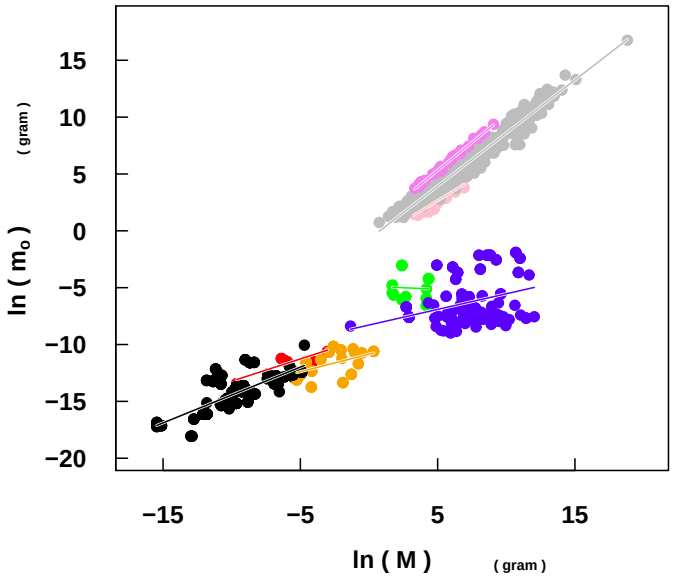

Figure 2.5: Relationship between offspring and adult size for the groups considered in our database. This relationship varies strongly depending on the group considered. The slope of the relationship is for 0.93 for mammals, 0.73 for non-procellarid birds, 0.98 for procellarid birds, 0.27 for fishes, -0.05 for amphibians, 0.30 for univoltine insects, 0.39 for multivoltine insects and 0.40 for zooplankton. Colour legend as in Fig. 2.2.

$$ODT = -\left(\frac{4}{a}\right) M^{1/4} ln\left[1-(m_o/M)^{1/4}\right] \tag{2.9}$$

where ODT is driven by temperature, adult mass and the growth efficiency of offspring by means of a size ratio logarithmic term, $SR = -ln\left[1-(m_o/M)^{1/4}\right]$. Fig. 2.1A shows the ability of this model to describe offspring development time.

There are, however, some cases where even if mass at birth is not negligible compared to adult mass the approximation of Eq. 2.9 by Eq. 2.4 is correct. For example, most mammals in our data-set have mass at birth close to 30% percent adult mass so growth efficiency at birth considerably departs from 1. But the fact that there is a nearly isometrical scaling between adult and offspring mass (Fig. 2.5) implies that the growth efficiency term $\left(1-\left(\frac{m}{M}\right)^{1/4}\right)$ is invariant across mammalian species, and hence the simplification in Eq. 2.3 is still correct because the term $ln\left[1-(m_o/M)^{1/4}\right]$ is a constant.

On the other hand, other groups do not show invariance in the offspring size - adult size ratio (Fig. 2.5). For example in fishes, offspring size seems to be very constant across taxa and independent of adult size. So the quotient m_o/M

varies with adult mass and the offspring growth efficiency is different across species. Nevertheless, in this group the mass of the offspring is very small compared to adult mass, what means that their growth efficiency at birth is close to 1. For this reason, the model in Eq. 2.4 is valid to describe their developmental time.

We could not find any cases in our data-set to illustrate the situation exemplified by offspring 2 and 3 in Fig. 2.1. For these cases, however, a complete model for developmental time derived from Eq. 2.2 would be able to account for the differences in offspring development time, and the trade-off between ODT and offspring production rate (C) will still hold (Supplementary Information).

2.4.3 The offspring-size/offspring-number trade-off in endotherms and ectotherms.

Offspring mass is a life history attribute that can be optimized and that can be subject to trade-offs. The balance between the size of the newborns and the number of offspring is a central principle of life-history theory (Smith and Fretwell, 1974). We have shown that this trade-off can be universally formulated by Eq. 2.1 with a striking similarity in how viviparous and oviparous species fall along the same mass and temperature corrected trade-off axis (Fig. 2.3). Interestingly, regardless of the taxonomy, reproductive strategies or body size, a nearly constant fraction of the assimilated energy is allocated to production of offspring biomass for the wide diversity of organisms considered here. This finding of constant reproductive allocation is in agreement with the results of Meiri et al. (2012) for different species of lizards.

Charnov and Ernest's (2006) model for mammals effectively showed that the resources available for reproduction are not constant across taxa and that the normalization of offspring production rate by the allometric scaling of energy allocation with adult mass is needed. We have shown that maternal body temperatures also affect reproductive potential, with increased reproductive output with increasing temperature. The consideration of the temperature dependence of metabolism has allowed us to successfully apply Charnov and Ernest's (2006) model to birds, fish, amphibians and invertebrates.

2.4.4 The trade-off between offspring development time and offspring number

Our analysis should reconcile LHO theorists with MTE as it shows that body mass effects include both metabolic scaling and life-history optimizations. By introducing the Smith and Fretwell's (1974) trade-off between offspring size and number in the MTE-based model for ontogenetic development of Gillooly et al. (2002) we reach a synthetic approach to model developmental time based on a two-fold perspective of

allometry and life history optimization. Our model captures both the physiological effects on offspring development time (the effects of temperature and body mass on metabolic rate) and the life-history optimization effects through the offspring production rate. There are still differences between groups that might be due to different stoichiometries and the growth rate hypothesis (Gillooly et al., 2002) or to further evolutionary effects not explained by our model.

The interpretation of developmental time as modeled in Eq. 2.6 can have important implications for population fitness. This implies that for viviparous species, there could be a trade-off between the number of offspring that can be produced and the duration of parental care. For broadcasting oviparous species, such as many fish, egg development takes place in the water column. This life-stage represents an important period for population connectivity while the embryos remain as propagules in the water. The balance between the number of broadcasted eggs and the time spent as a propagule links the trade-off described here with the field of population connectivity and genetic flow (Mitarai et al., 2008).

Gillooly et al.'s (2002) model is at the basis of many higher order predictions of MTE (Brown et al., 2004; Savage et al., 2004*a*). The integration of metabolic theory and life-history evolution can provide a synthetic theory of population energetics (Economo et al., 2005). Our model is a step in this direction and shows that both theories play a major role in controlling developmental time.

2.5 Acknowledgements

This work was partially funded by Theme 6 of the EU Seventh Framework Program through the Marine Ecosystem Evolution in a Changing Environment (MEECE No. 212085) and project CONSOLIDER Malaspina 2010 funded by Spanish National I+D+I Plan. J. B. is a recipient of a PhD fellowship from the Instituto Español de Oceanografía. We thank Jan Heuschele, Drew Kerkhoff and an anonymous reviewer for useful comments.

2.6 Supplementary Information

2.6.1 Growth efficiency and the ontogenetic growth model

Fig. S2.1A shows the validity of Eq. 2.9 to describe offspring development time. To validate the allometric exponents of Eq. 2.6 using Fig. 2.4, the use of the 1/4 allometry in both adult mass and the SR term interferes the assessment of exponents by means of plots as the one in Fig. S2.1A. In consequence we have followed the same procedure described in the results section for ODT, by fitting a non-linear model

$$ln(ODT) = -\gamma + E/kT + \alpha ln(M) + \beta ln\left[ln(1-(m_o/M)^{\alpha})\right] \tag{2.10}$$

with with α, γ and β and E as parameters to be estimated[1]. The values obtained are close to the statements of MTE: $\alpha = 0.2189$ with 95% confidence intervals of 0.207 to 0.230, $\beta = 1.09 \pm 0.05$ and $E = 0.547\pm$ with 95% confidence intervals between 0.489 and 0.605.

Following a similar procedure described for the simplified model, we can introduce the Smith and Fretwell's (1974) trade-off between size and number of offspring in the ontogenetic growth model of West et al. (2001). Solving Charnov and Ernest's (2006) relationship for $M^{1/4}$ we obtain the expression $M^{1/4} = C^{-1} * M/m * e^{(-E/(kT))}$, that incorporated to the complete model for developmental time in Eq. 2.9 gives:

$$ln(ODT) = -\frac{1}{C} * \frac{1}{\mu} * ln(1-\mu^{1/4}) \tag{2.11}$$

with $\mu = m_o/M$ and C the offspring production rate.

Fig. S2.1 represents the validity of this synthetic model to describe offspring development time using the complete ontogenetic growth model of West et al. (2001) and the Smith and Fretwell's (1974) trade-off between offspring size and number.

2.6.2 Supplementary figures

[1] To fit this model, we removed the group of procellarid birds from the data-set. Their offspring is bigger than the adult before leaving the nest, so an infinity is obtained when trying to calculate the logarithm in Eq. 2.10.

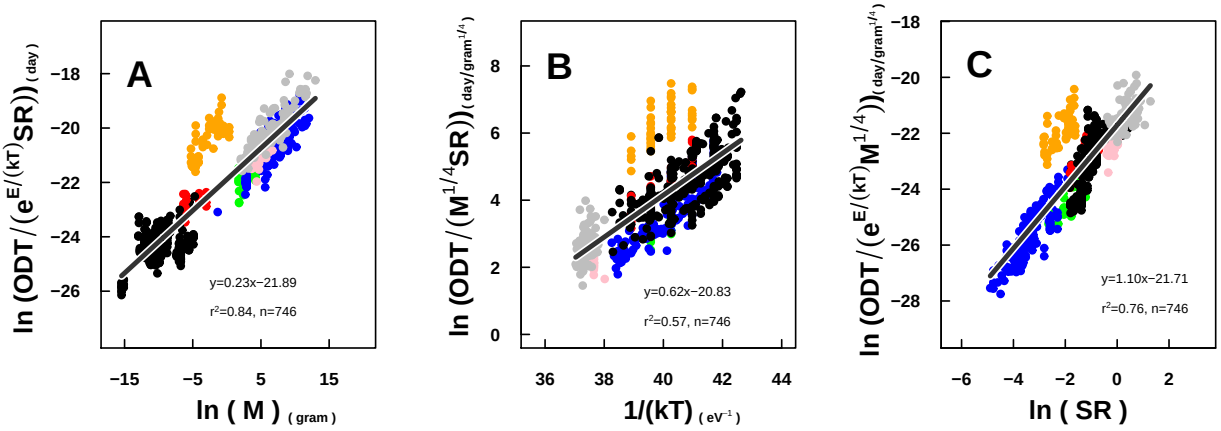

Figure S2.1: The complete model for developmental time. A, relationship between the offspring development time, ODT, and female mass, M, once the former is corrected for the effects of temperature through the exponential factor $e^{E/kT}$, and the size ratio logarithmic term SR. B, Effect of temperature on the offspring development time corrected for the effects of female size and the SR term. C, the SR term explains some of the remaining variance in ODT when it is corrected for the effects of female size and temperature. Colour legend as in Fig. 2.2.

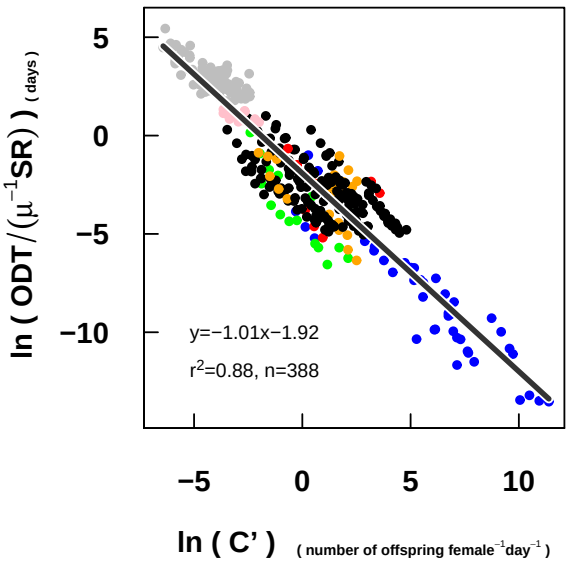

Figure S2.2: The trade-off between offspring-development time and offspring-number using the complete model for developmental time in Eq. 2.11. The offspring production rate shows an inverse scaling isometry with offspring development time once it is corrected for the effect of mass.

2.A Appendix 2.A

http://www.repositorio.ieo.es/e-ieo/handle/10508/1580

2.B Appendix 2.B

http://www.repositorio.ieo.es/e-ieo/handle/10508/1581

Chapter 3

Planktotrophic modes of larval growth and their consequences on the scaling of development time and fecundity

Contents

3.1 Introduction

Many benthic marine organisms spend a period of time as free-swimming planktonic larvae after hatching. The duration of this planktonic phase (hereafter PLD, from Planktonic Larval Duration) determines the dispersive ability of individuals

and hence the connectivity and survival of metapopulations (Scheltema, 1971; Kinlan and Gaines, 2003; Weersing and Toonen, 2009; Planes et al., 2009). As any other biological time, PLD is ruled by temperature and body size (Gillooly et al., 2002; O'Connor et al., 2007*a*), but for it has also been shown to be linked to the larval feeding strategy adopted (Todd, 1981; Havenhand, 1993; Herrera et al., 1996; Marshall and Keough, 2008; Oyarzun and Strathmann, 2011). For planktotrophic larvae, which feed actively after hatching, the classic work of Vance (1973*b*) predicts that the longer duration of the embryonic prefeeding period for organisms with larger eggs causes the shortening of the post-embryonic active-feeding period. Vance (1973*a*) proposed the fecundity-time hypothesis which states that benthic organisms that lay many small eggs have longer planktotrophic larval durations than organisms that lay few larger eggs.

This prediction contrasts with the fecundity-offspring developmental time relationship proposed by Bueno and López-Urrutia (2012). Bueno and López-Urrutia (2012) have shown that the ODT, defined as the elapsed time from the fertilisation of the ovocyte until the end of maternal cares or energetic stores, increases with egg size in accordance with metabolic scaling theories. Combined with the classical trade-off between the size and the number of offspring (Smith and Fretwell, 1974), they concluded that there is a trade-off between fecundity and ODT. These authors showed that species with larger offspring have longer ODT but at the cost of being able to produce fewer offspring. For lecithotrophic larvae the end of development is coincident with the end of the maternal energetic stores (although some exceptions occur (Emlet and Hoegh-Guldberg, 1997)), so ODT equals egg development time plus PLD.

Albeit Vance's model has been profoundly debated in terms of reproductive efficiency (Strathmann, 1977; Podolsky and Strathmann, 1996; Levitan, 2000; McEdward, 1997; McEdward and Miner, 2003; Nybakken and Bertness, 2004; Kupriyanova, 2013), little attention has been paid to its underlying assumption that the size of larvae at metamorphosis must be independent of the size of larvae at hatching (but see Emlet and Hoegh-Guldberg (1997)). Fig. 3.1 is a conceptual diagram showing two scenarios where the final size of larvae is independent of the initial size of larvae (Vance's hypothesis, upper panels), or dependent (lower panels). In panel A, which summarises Vance's model, an increase in the initial larval size causes a shortening of PLD because the larval size at the end of development is more or less constant among species.

On the other hand, in panel D larval size at the end of the planktotrophic periods scales isometrically with embryo size. Panels B and E use the ontogenetic growth curve of West et al. (2001) as a tool to visualise the expected developmental time (x-axis) taken for each larval growth increment (note that larval size in the y-axis is expressed relative to adult mass) through ontogeny. Following Vance's model (panel B), PLD is determined by the initial larval size, because small larvae have to grow longer in the curve to reach a similar size. This causes a negative scaling

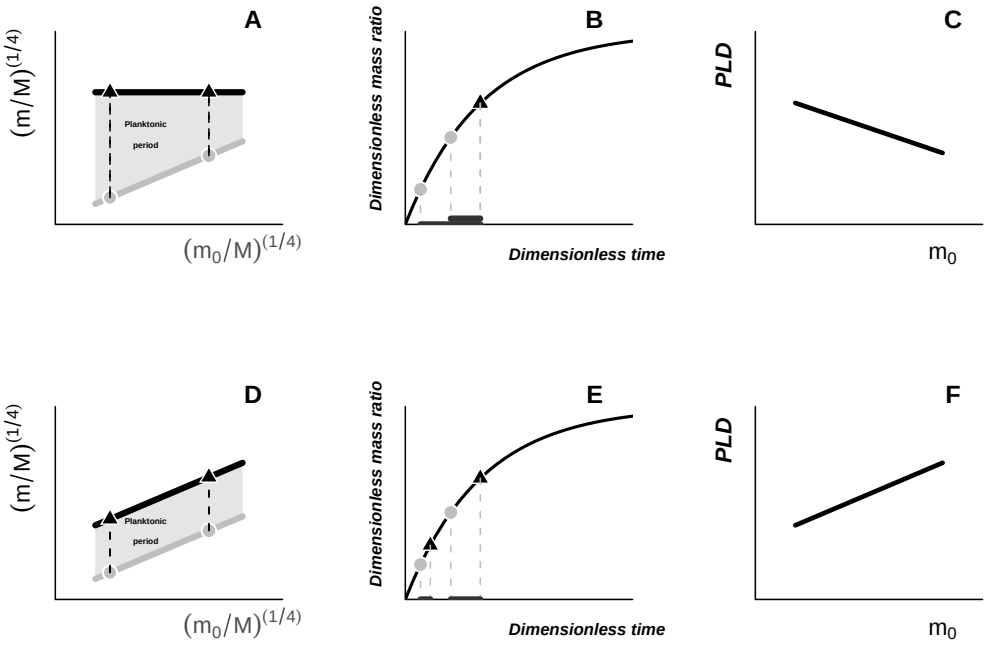

Figure 3.1: Hypothetical scenarios of larval growth. Black triangles represent the size of larvae (relative to adult size) at the end of growth and grey circles the size of larvae at hatching. In panel A the final size of larvae is unrelated to the initial size of larvae (the assumption made by Vance (1973*b*)), while in Panel D larger larvae at hatching develop reaching larger size at metamorphosis. Panels B and E use the universal growth curve of West et al. (2001) to represent the time required to develop by larvae in scenarios A and D respectively (note the influence of the differences in growth efficiency ($G = 1-[(m/M)^{1/4}]$)). Panels C and F show the expected scaling relationship between PLD and the initial size of larvae, according to the scenarios in panels A and D respectively.

relationship between initial larval size and PLD (panel C). However, if the final larval size is related to the initial larval size, the larger the larva the longer the time it will take to develop, due to its smaller growth efficiency (panel E) (West et al., 2001; Moses et al., 2008; Bueno and López-Urrutia, 2012). This situation causes a positive scaling relationship between PLD and larval size (panel F).

The offspring size and number trade-off (Vance, 1973*b*; Smith and Fretwell, 1974) links the scenarios presented in Fig. 3.1 with the fecundity of organisms. If the trade-off between offspring size and number is valid, a negative relationship between PLD and larval size (Vance's hypothesis, Fig. 3.1C) translates into a positive relationship between fecundity and PLD (the fecundity-time hypothesis (Vance, 1973*a*)). However, if the final size of larvae is determined by their initial size, the fecundity - time relationship should be opposite (Fig. 3.1F) and with the same pattern as the offspring developmental time - offspring number trade-off of Bueno and López-Urrutia

(2012).

In summary, the relationship between the initial and final size of larvae influences the scaling of PLD, larval size, and fecundity. In this work we will explore this relationship for a wide variety of benthic marine organisms with planktotrophic development, analysing their effect on reproductive trade-offs and life history traits.

3.2 Materials and Methods

3.2.1 Data compilation

We performed a literature search for experimental studies rearing pelagic larvae of marine benthic organisms at different constant temperatures (Appendix 3.A). The compilation comprised 109 species from 11 taxonomic groups. PLD was considered the time between hatching and settlement of larvae. In the case of PLD measured by rearing cohorts of embryos, PLD was assumed to finish when the 50% of the cohort settled. Additionally, when the studies analysed the effect of different factors (such as salinity or food limitation) on developmental time, we considered only the values under optimal rearing conditions. Given that we perform phylogenetic analysis (see below) it is not possible to have replicated data (coming from experiments measuring PLD at different temperatures) for a given species. Hence we calculated average PLD values using the mean temperature of the experiments for each species (see Appendix 3.B).

We also compiled the larval sizes at the beginning and at the end of the planktonic phase. Larval size was estimated as the individual biovolume approximating larval shape to geometrical figures and assuming a density of 1 gml^{-1}. The biovolume of the first larva was sometimes assumed as a sphere of the diameter of the egg, given that we consider negligible the yolk content of planktotrophic eggs. The different figures and combination of figures used are summarised in Appendix 3.A. When possible, we used the same bibliographic sources for developmental time and larval size (Appendix 3.A). When we lacked data on different larval dimensions, we calculated them from real zooplankton samples. These samples were obtained on board the José de Rioja within the RADIALES project of the Instituto Español de Oceanografía (transect off Gijón, N Spain). Hence, in Appendix 3.A the reference "This work" indicates that abdomen length and width were assumed to be a fixed fraction of the carapace length and width. Additionally, in the cases of *Liocarcinus depurator* and *Necora puber* we estimated the carapace length of the initial and final larvae from 20 individuals of each species, obtained from the zooplankton samples mentioned above.

Similarly, we compiled data on the adult stage of organisms. Appendix 3.C reports the adult body dimensions, with their respective bibliographic sources and the geometrical figures used for biovolume calculations, assuming a density of 1

gml^{-1}. We compiled also data on the fecundity of these species (Appendix 3.C, see next).

3.2.2 Phylogenetic analysis

The shared evolutionary history of the different species considered in this work implies a correlation between the data that must be considered when analysing functional relationships between traits (Butler and King, 2004). The Phylogenetic General Least Square regression (PGLS regression) (Felsenstein, 1985) allows to evaluate these kind of relationships when a phylogenetic signal exists between the data. The correlation must be introduced in the PGLS regression through a phylogenetic tree with known branch lengths. To construct this tree we considered the data base from the World Register of Marine Species (Boxshall et al., 2013) and considered the length branch between consecutive nodes to be 1 (Fig. S1.1). Then, we performed the regressions using the ape and mle packages in R (R Development Core Team, 2011), following the methodology described in (Kolokotrones et al., 2010).

3.2.3 Fecundity estimations

Fecundity in marine organisms is usually reported as the number of eggs per clutch. However, since the number of egg clutches produced per year also varies across species, this estimation of fecundity is not valid to accommodate the effect of life histories to the models for development time (Bueno and López-Urrutia, 2012). In consequence, we estimated daily fecundity rates using the mean number of eggs in a clutch and the average number of clutches per year (Appendix 3.C).

The temperature at which fecundity is measured rarely coincides with the temperature at which PLD is measured (see Appendix 3.C for references). To account for this source of uncertainty, we corrected the daily offspring production rate (C) using the Boltzmann's factor ($C/e^{(E/(k*T_c))}$) considering T_c as the temperature at which C was measured. In some cases, fecundity was reported without any reference to the temperature at which it was measured. In these cases we obtained an annual average temperature for the area of the study or for the geographical area of the species, using objectively analysed annual mean temperatures from the World Ocean Atlas (Locarnini et al., 2010).

3.2.4 Empirical approximation of the activation energy of metabolic reactions.

Using the Boltzmann's factor, the relationship between PLD and T takes the form $PLD \sim e^{(E/kT)}$. Taking logarithms and rearranging terms we have that the slope

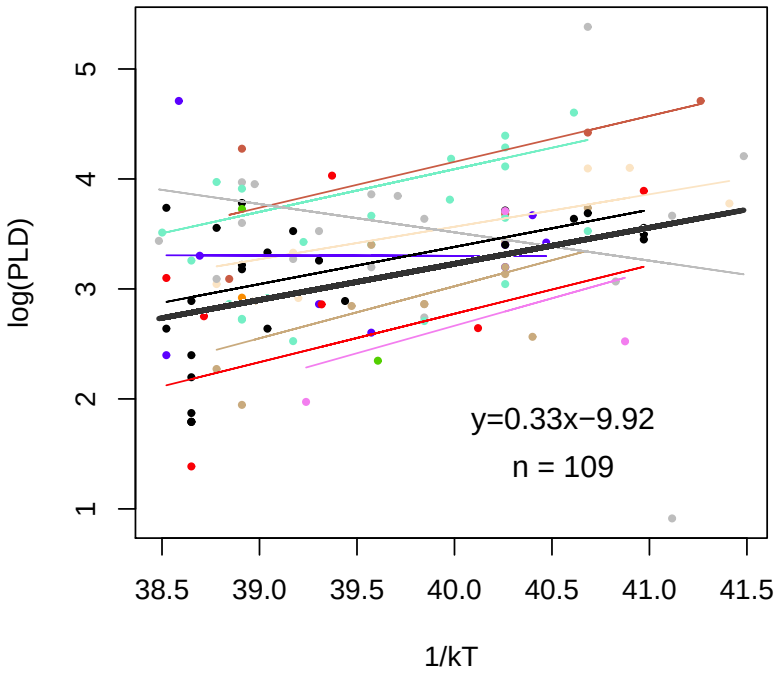

Figure 3.2: Relationship between planktonic larval duration (PLD) and temperature (T) using the Boltzmann's factor (see Methods section). See colour legend in Fig. 3.3A.

of the plot $ln(T)$ *vs* $1/kT$ (Fig. 3.2 and Table S1.1) is an empirical approximation of the value of the activation energy of metabolic reactions (E). The value obtained (0.3286) is used to construct the Figs. 3.3 and 3.4.

3.3 Results

There is a significant positive relationship between the size of larvae at hatching and at metamorphosis when the data for the different groups is considered together (Table 3.6 and Fig. 3.3A, $p.val << 0.001$, $n = 109$). The slope of this relationship is not isometrical (0.79), what indicates a lower proportional size increment of big larvae during PLD, and hence situates our data in an intermediate position between the one described in Fig. 3.1A and the one in Fig. 3.1D. Analysing each group separately, this relationship is significant and positive only for gastropods, barnacles (Cirripedia) and decapod carideans (shrimps) (Table 3.6), with slopes higher than 1 for carideans and gastropods and smaller than 1 for barnacles. As explained in the introduction, the relationship between the initial and final larval size influences the

larval mass scaling of PLD. In consequence, the hypothesis that PLD is inversely related to egg size (Vance's hypothesis) is expected to hold for all the groups except of gastropods and carideans, which should show a positive relationship given that the slope of the relationship between initial and final larval size is higher than 1.

To evaluate the relationship between PLD and the initial size of larvae for echinoid echinoderms, Levitan (2000) plotted a temperature-corrected development time (using a Q_{10} between 3.0 and 3.6) *vs* egg volume, obtaining a significant negative relationship even when the phylogeny of the groups was taken into account. Following a similar methodology, we corrected PLD for temperature using the Boltzmann's factor with the estimate of E (0.3286) obtained in Fig 3.2. We then represented it *vs* the size of larvae at hatching. In agreement with the finding of Levitan (2000), this relationship seems to be slightly negative considering all the taxa together (Table 3.6 and Fig. 3.3B, $p.val = 0.1868$, Akaike Information Criterion = 233.88). Only for decapod carideans, gastropods, and anomurans it is positive (but not significant, Table 3.6), in concordance with the hypothesis presented before.

Fig. 3.3C shows how a steeper slope in the relationship between initial and final larval size translates into steeper slope in the relationship between temperature-corrected PLD and larval size. In fact, we can observe that fish and echinoids are the only two groups with negative relationships both between initial and final larval size, and between PLD and initial larval size (the only two significant; Tables 3.6 and 3.6).

The corollary of the work of Vance (Vance, 1973*a*) and the subsequent works using his theoretical framework is that organisms producing more offspring have also longer planktonic developmental periods (the fecundity-time hypothesis). However, as we have explained before, this idea depends ultimately on the relationship between initial and final larval size. According to the results shown in Fig. 3.3, we expect the fecundity-time hypothesis to hold for all the groups except for carideans and gastropods, for which big initial larvae grow proportionally more than small larvae.

In order to test the validity of the fecundity-time hypothesis for the different groups, we evaluated first if the offspring-size/clutch-size trade-off described by Charnov and Ernest (2006) holds for the groups considered (see methods for the correction of temperature) (Fig. 3.4A). Despite we were not able to obtain enough fecundity data to obtain reliable trends, it is possible to appreciate that in general, the classic offspring-size/clutch-size trade-off holds, what means that organisms producing larger offspring produce smaller clutch sizes and viceversa (Table 3.6).

We then evaluated the relationship between the temperature-corrected PLD and the daily offspring production rate (C) (Fig. 3.4B). The result is that when considering all the groups together, the relationship between PLD and fecundity can not be perceived. We can observe also a strong variability among groups, although none of them show a significant relationship due to the low number of data available (Table 3.6). Hence, the relationship is positive for brachyuran crabs, barnacles, and

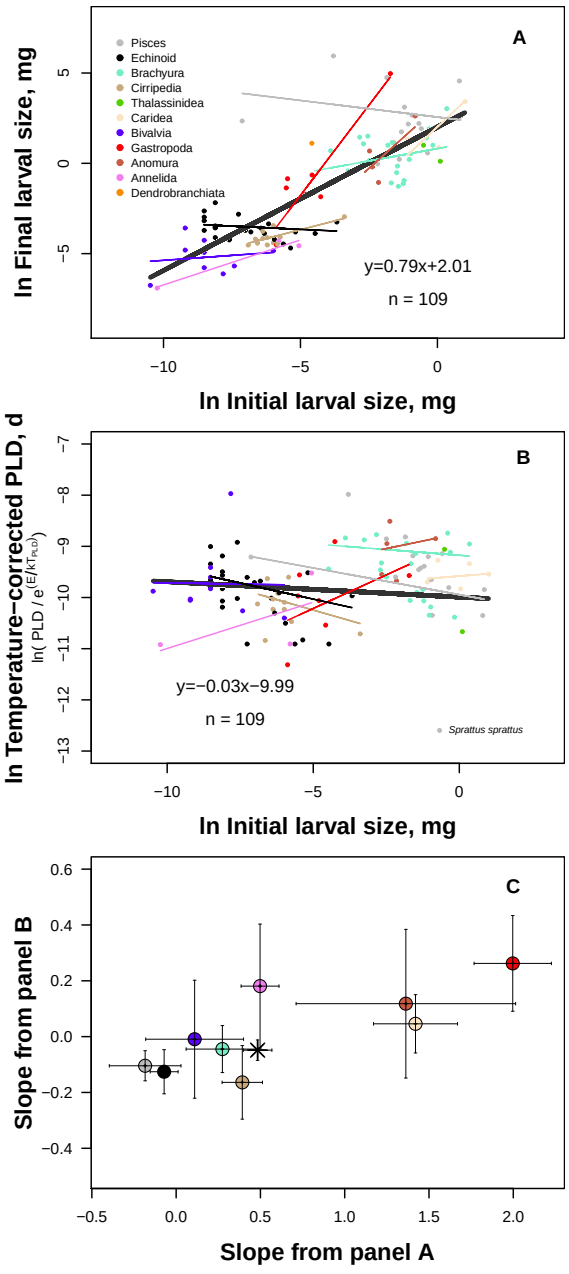

Figure 3.3: The relationship between initial and final larval sizes, and its consequences on the mass scaling of PLD. Panel A shows the relationship between egg size and the size of larvae at the end of development. Panel B represents the relationship between temperature-corrected PLD and egg size. And panel C shows how the slopes of the relationship obtained in panels A and B are related for the different groups considered. The asterisk represents the slopes of the overall relationship considering all taxa. All the regressions shown are calculated by phylogenetic least squares regression (see methods).

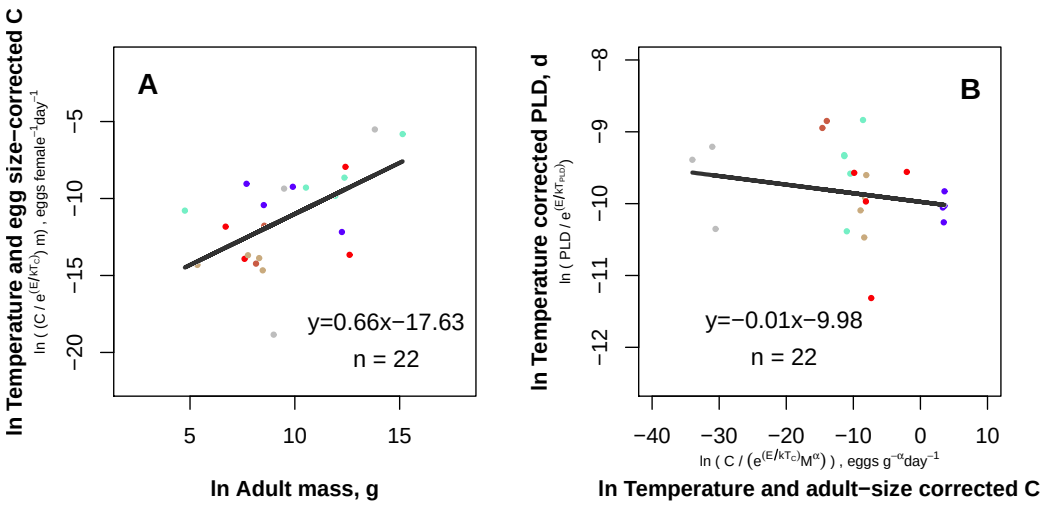

Figure 3.4: The trade-offs between offspring size and fecundity, and PLD and fecundity. Panel A shows the offspring size/clutch size trade-off for the organisms considered, using the Boltzmann's factor as a temperature correction. Panel B represents the relationship between the temperature-corrected PLD and fecundity. Colour legend as in Fig. ref3.3A.

bivalvs, while it is negative for the whole diversity of taxa, fish, and gastropods. Unfortunately, the low number of data prevented us to obtain reliable trends, and the negative slope of gastropods is not consistent enough to conclude that the effect of the relationship between initial and final larval size is not important to determine the effect of fecundity on PLD.

3.4 Discussion

3.4.1 The consequences of the relationship between the initial and final larval size

We have found that larval size at the end of development is related to initial larval size when considering a wide diversity of benthic marine organisms (Fig. 3.3A). This implies that small larvae at hatching reach the competent stage for settlement at smaller size than large larvae. However, this relationship is not isometrical (slope of 0.79) and hence, the proportional size increment is smaller for big larvae. Previous works have reported negative relationships between the initial and final larval size (Hart, 1995; Herrera et al., 1996; Levitan, 2000; Allen and Pernet, 2007; McAlister and Moran, 2012) but they are mainly focus on echinoderm echinoids and, as we have seen, the relationship can be negative when considering the groups independently (Table 3.6).

Then, we have shown that this relationship between the initial and final larval size determines the scaling relationship between PLD and egg size. According to our results, only for decapod carideans and gastropods we would expect PLD to increase with egg size because there is a significant and positive relationship between initial and final larval size with slope higher than 1 (Table 3.6). The analysis of the temperature-corrected PLD *vs* initial larval size (Fig. 3.3B) shows that considering the whole diversity of taxa, the relationship is almost unexisting (slope = -0.0484, $p.val = 0.1868$, Table 3.6). However, although none of the groups analysed shows a significant positive relationship, it is noteworthy that the two groups with a significant positive (higher than 1) relationship between initial and final larval size (carideans and gastropods) show a positive relationship between PLD and larval size (Table 3.6). This is an evidence of the dependence of Vance's model on the relationship between the initial and final larval size.

Many of the works studying the evolutionary forces modelling egg size (Vance, 1973*b*; Strathmann, 1977; Levitan, 2000; Allen, 2012) lay on the basic assumptions that larval mortality rate is constant over time in the plankton, and that egg size is inversely related to PLD (Nybakken and Bertness, 2004). However, the interspecific variability of this relationship demonstrates that it is dependent on the relationship between the larval size at the beginning and at the end of PLD. Some authors pointed in this direction previously. Hence, Strathmann (1977), emphasised the importance of the variation in size at metamorphosis to explain the fails in Vance's model for optimal egg size. Similarly, Underwood (1974) pointed out some limitations in the model of Vance by analysing a compilation of data from the literature. He concluded that energetic considerations alone are not able to explain the distribution of the different modes of development at different latitudes and depths. He also pointed out that life history traits governing the life and dispersion type of larvae should be taken into account to explain the variability in PLD among organisms.

It is worthwhile to note also that the temperature dependence of PLD (the slope of the relationship between $ln(PLD)$ and $1/kT$ shown in Fig. 3.2) has an activation energy (E) of 0.33 eV, which can be approximated to a Q_{10} of 1.6379 (Gillooly et al., 2001). This value is lower than the value of 3-3.6 used by Levitan (2000) (which correspond to activation energies between 0.73 and 0.85 eV respectively). There are, however, previous evidences for a high variability in empirical measurements of E for ectotherm animals (Gillooly et al., 2001; Irlich et al., 2009; Zuo et al., 2011), with values between 0.15 and 1.21 eV.

3.4.2 The relationship between fecundity and PLD

Bueno and López-Urrutia (2012) have recently proposed a model in which offspring development time (ODT) can be expressed in terms of offspring production rate, body size and temperature. This model captures the effect of the partition of reproductive resources between many small or few large offspring on developmental

time for a wide diversity of organisms. The basis of their theory is that the offspring size and number trade-off (Smith and Fretwell, 1974) holds until the end of maternal cares, allowing to substitute the offspring/adult size ratio by the offspring production rate (C) in models for developmental time. However, for the postembryonic period, the relationship between maternal investment in reproduction and the length of this period is not clear. Hence, in the case of lecithotrophic larvae ODT equals the sum of PLD and egg development time, so the offspring size and number trade-off (Bueno and López-Urrutia, 2012) should hold. But in the case of strict planktotrophic larvae, maternal cares and energetic stores end at hatching and PLD is fuelled by the active energy acquisition of larvae (Anger, 2001). The result is that the relationship between PLD and offspring production rate is harder to predict because PLD depends also on selective forces acting during the larval phase.

The fecundity-time hypothesis of Vance (1973*b*) predicts that species with higher fecundity are expected to have longer PLD. The grounds of this theory are in the smaller amount of maternal energetic resources devoted per offspring as fecundity increases (Vance, 1973*b*; Smith and Fretwell, 1974). Hence, as smaller embryos have fewer maternal resources for development within the egg, hatching occurs earlier extending the postembryonic active-feeding period (PLD). A condition for this hypothesis to hold is that the final size of larvae should be independent of the initial size (or have a slope lower than 1 in the relationship between initial and final larval size). If that condition happens, by bringing forward the moment of hatching, PLD will be extended because settlement is not brought forward (Fig. 3.1). In consequence, there would be a negative relationship between PLD and fecundity. According to our results (Table 3.6), we would expect the fecundity-time hypothesis to hold for all the groups except for gastropods and decapod carideans (relationship between initial and final larval size significant with slope higher than 1, Table 3.6). The relationship between the temperature-corrected PLD and fecundity is slightly negative for the general diversity of taxa considered, in disagreement with the fecundity-time hypothesis (Fig. 3.4B and Table 3.6). Also in the case of gastropods it seems to be negative, although it is not significant and the regression is based only in four data. Unfortunately, we lack enough fecundity data to properly test the validity of the fecundity-time hypothesis

In summary, we have shown that the mode of larval growth rules the duration of PLD with consequences on the scaling of PLD and body size. Furthermore, we have established the theoretical basis to explain the relationship between fecundity and PLD. Hence, when the slope of the relationship between initial and final larval size is equal or higher than 1, high fecundity should translate into short PLD, in opposition to the fecundity-time hypothesis of Vance (1973*a*). In conclusion, knowledge of the environmental forces governing the end of the planktonic phase of benthic marine organisms are critical to understand the trade-offs ruling their reproductive biology and ecology, and should be considered also by models based on Vance's hypothesis.

3.5 Acknowledgements

This work was partially funded by Theme 6 of the EU Seventh Framework Program through the Marine Ecosystem Evolution in a Changing Environment (MEECE No. 212085) and project CONSOLIDER Malaspina 2010 funded by Spanish National I+D+I Plan. J. B. is a recipient of a PhD fellowship from the Instituto Español de Oceanografía. We would like to thank Antonina dos Santos for her useful comments on the identification of decapod larvae and the access to bibliographic sources. S. Sal, L. Arbesú, D. Sousoni and M. Louzao helped us to obtain difficult bibliographic sources. This work is dedicated to the memory of Jesús Cabal.

3.6 Supplementary tables and figures

Table S3.1: Relationship between PLD and temperature.Phylogenetic least squares regressions of the relationship between PLD and 1/kT, shown in Fig. 3.2 of the main text. Column "n" shows the number of data on which the fit is calculated and "p.val" the p-value of the relationship. Fish* is the fit of the data of fishes without considering the outlier *Sprattus sprattus*.

Group	**n**	**p.val**	**slope**
All	109	00.00	0.328621
Brachyura	22	0.0059	0.3885
Caridea	6	0.0266	0.2952
Anomura	5	0.00	0.4170
Fish	17	0.0955	−0.2573
Fish*	17	0.1658	0.1872
Cirripedia	12	0.0101	0.4732
Bivalvia	9	0.9880	−0.0036
Gastropoda	7	0.1158	0.4402
Annelida	3	0.6969	0.4990
Echinoidea	25	0.0096	0.3380

Table S3.2: Relationship between the initial and final larval sizes. Phylogenetic least squares regression of the relationship between the initial and the final larval size shown in Fig. 3.3A. Column names as in Table 3.6.

Group	**n**	**p.val**	**slope**
All	109	00.00	0.7944
Brachyura	22	0.2173	0.2742
Caridea	6	0.0047	1.4199
Anomura	5	0.1274	1.3628
Fish	17	0.4000	−0.1841
Cirripedia	12	0.0083	0.3923
Bivalvia	9	0.7170	0.1095
Gastropoda	7	$3 * 10^{-4}$	1.996
Annelida	3	0.1414	0.4977
Echinoidea	25	0.3977	−0.0714

Table S3.3: Relationship between temperature-corrected PLD and larval size. Phylogenetic least squares regressions of the relationship shown in Fig. 3.3B. Column names as in Table 3.6.

Group	n	p.val	slope
All	109	0.1868	−0.0484
Brachyura	22	0.6017	−0.0446
Caridea	6	0.6826	0.0459
Anomura	5	0.6877	0.1180
Fish	17	0.0493	−0.1786
Cirripedia	12	0.2417	−0.1638
Bivalvia	9	0.9663	−0.0092
Gastropoda	7	0.1862	0.2623
Annelida	3	0.0718	−0.1044
Echinoidea	25	0.125	−0.1258

Table S3.4: The offspring size/offspring number trade-off. Phylogenetic least squares regression of the relationship shown in Fig. 3.4A. Column names as in Table 3.6.

Group	n	p.val	slope
All	48	00.0068	0.6633
Brachyura	5	00.00	0.3521
Caridea	0		
Anomura	2		
Fish	3	0.3859	2.1492
Cirripedia	4	0.8996	0.0304
Bivalvia	4	0.3220	−0.5347
Gastropoda	4	0.6167	−0.0351
Annelida	0		
Echinoidea	0		

Table S3.5: Relationship between PLD and daily offspring production rate. Phylogenetic least square regression of the relationship shown in Fig. 3.4B. Column names as in Table 3.6.

Group	n	p.val	slope
All	22	0.4958	−0.0119
Brachyura	5	0.4818	0.1991
Caridea	0		
Anomura	2		
Fish	3	0.7204	−0.1305
Cirripedia	4	0.2928	0.7567
Bivalvia	4	0.6930	0.5427
Gastropoda	4	0.1104	−0.4249
Annelida	0		
Echinoidea	0		

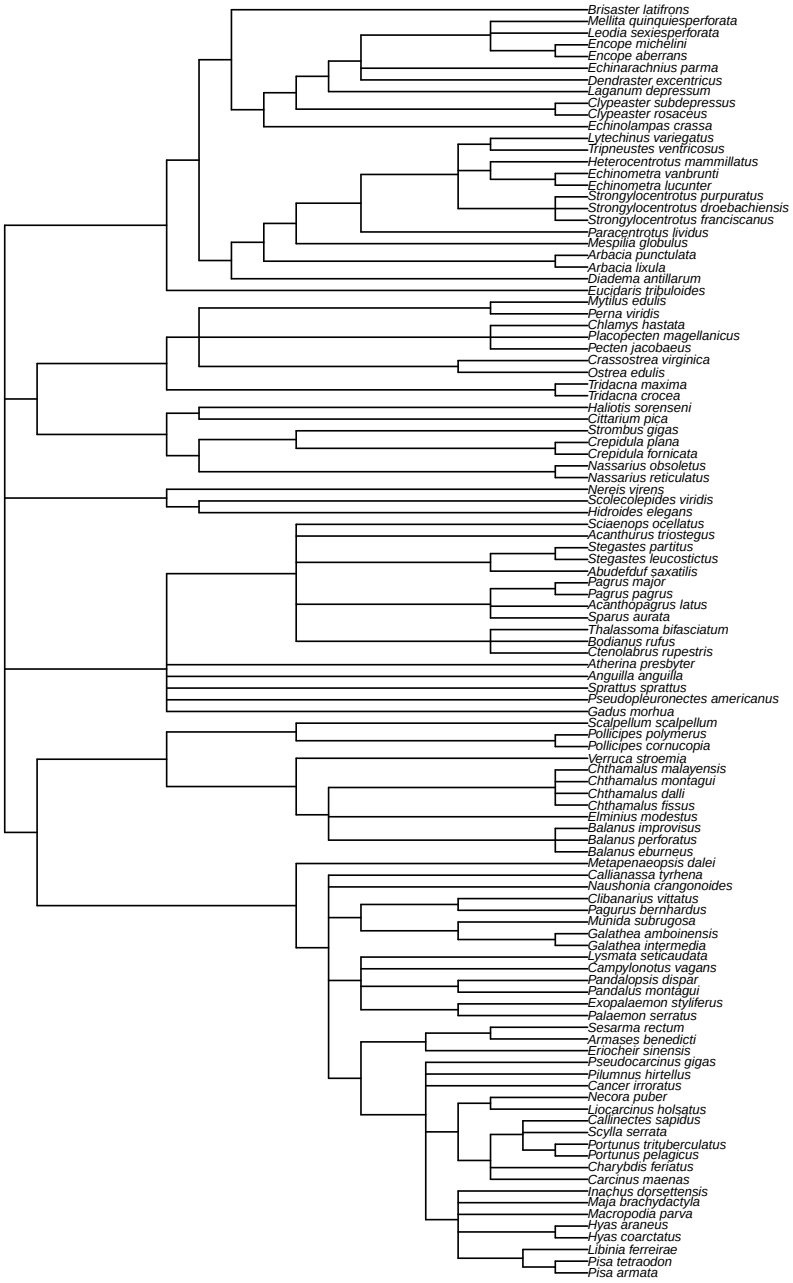

Figure S3.1: In order to incorporate the correlation of the data due to a shared evolutionary history, we constructed a phylogenetic tree for the taxa considered. This tree was constructed with data from the Boxshall et al. (2013) assuming an inter-node branch length of 1 (see methods section in the main text).

3.A Appendix 3.A

http://www.repositorio.ieo.es/e-ieo/handle/10508/1582

3.B Appendix 3.B

http://www.repositorio.ieo.es/e-ieo/handle/10508/1583

3.C Appendix 3.C

http://www.repositorio.ieo.es/e-ieo/handle/10508/1584

Chapter 4

Environmental and biological determinants of larval dispersal across the inner shelf

Contents

4.1 Introduction

The larval phase of coastal benthic organisms constitutes an important component of the plankton in terms of abundance and number of species (Highfield et al., 2010). Dispersal of these early stages in the pelagic environment is a key feature in conservation ecology as for many organisms they are the unique link between isolated adult populations of sessile or reduced motility animals. Thus, processes affecting larval dispersal can determine the structure and even the persistence of a whole metapopulation (Cowen and Sponaugle, 2009). The emerging science of marine reserves design uses larval dispersal parameters to infer the main characteristics that protected areas must present to be effective, such as their location along the coast, size, spacing and the percentage of no take zones within them (Botsford et al., 2001, 2003; Largier, 2003; Lubchenko et al., 2003; White, 2010).

Dispersion parameters used to set the spatial characteristics of marine protected areas were usually obtained under a simple assumption: larvae may drift with the currents. Due to their little size, larvae and plankton in general have been traditionally conceived as passive drifters. However, this consideration has led to a paradox, especially evident for the planktonic stages of intertidal invertebrates: inert particles may be exported offshore by Ekman transport induced by alongshore winds (Roughgarden et al., 1992). During upwelling, upward currents may transport larvae to the surface Ekman layer that is being displaced seawards; during downwelling, larvae may sink with the prevalent downward flow to the bottom layer, which is moving offshore. Thus, wind forcing dynamics may cause the wash out of the larval population at coastal waters away from their recruitment sites, a theoretical prediction that does not allow the replenishment of adult populations. Similar paradoxes apply to the persistence of populations under the forcing of strong, unidirectional currents along the coast (Largier, 2003; Shanks and Brink, 2005). The search for mechanisms that may prevent this wash out or at least may transport larvae back to the shore has promoted the progressive inclusion of active behaviour in theories regarding the dispersal processes. Eventually, as the first hundreds of meters from the shore were surveyed in search of larvae, the relationship between Ekman and larval transport became less evident: most larvae and coastal plankton in general were found to remain nearshore regardless of wind forcing dynamics (Poulin et al., 2002; Shanks and Brink, 2005; Shanks, 2009). Genin et al. (2005) showed that swimming against the vertical flow may enable larvae to remain at the surface in downwelling and at the bottom in upwelling thus concealing offshore export.

Due to the multiple evidences of Ekman transport active avoidance supported by research in the field, larval behaviour is starting to be considered as an essential component to model dispersal in space and time. Recent models incorporating mesoscale hydrography but also different vertical patterns of migration show that these types of synchronised movements significantly reduce theoretical dispersal distances in agreement with field observations (Robins et al., 2013). In addition, the

Metabolic Theory of Ecology (MTE, Brown et al. (2004)) arose in the last years as an important tool to understand the relationships between the ecology of individuals, populations and communities and their environment (Enquist et al., 2003; López-Urrutia et al., 2006). This theoretical field may be used for the integration of biological characteristics in models of particle dispersal for a wide range of organisms in combination with hydrodynamic studies. More precisely, MTE allows the calculation of key parameters such as planktonic larval duration (PLD) and swimming speed based mainly on larval size and water temperature (Gillooly et al., 2002; Huntley and Zhou, 2004). The potential of MTE to obtain relatively complex biological features from simple bio-physical properties has been poorly explored in larval ecology. Hence, albeit in this work we include a metabolic approach to obtain estimates of PLD in a model for larval dispersal, understanding the physiological determinants of swimming ability, remain a crucial task to establish a theoretical link between larval physiology and dispersal.

Although the role of behaviour is acquiring great importance in models explaining net larval advection, little is known about how it affects diffusion or aggregation. Extremely patchy distributions of many zooplankters are difficult to explain if larvae were strictly passive in the light of the highly stochastic nature of flow in the ocean (Knysh et al., 1993; Largier, 2003). More likely, larvae may actively reduce environmental diffusion probably by facing the currents in the vertical or even in the horizontal plane (Shanks, 1995; Natunewicz and Epifanio, 2001). Aggregation capacity of meroplankters in the coastal ocean may influence timing and spatial patterns in settlement (Pineda and Hare, 2007) and dense larval patches are actively preyed on by fish which may also aggregate in turn (Turner et al., 2001). Despite its importance, the magnitude of diffusive distances in real spatial distributions has been neither appropriately measured nor linked with the biological characteristics of larvae.

In this work we want to address the following questions:

- Do fine-scale, across shore larval distributions respond to classical advection-diffusion models?

- Are the parameters of these models, with emphasis on diffusion, defined by the evolution of a passive system, or is larval biology playing a role?

4.2 Materials and Methods

4.2.1 Physical sampling methods

The field work for this study took place in Cudillero, located on the north coast of Spain (Fig. 4.1), on board of the Research Vessel *José de Rioja* and consisted of 4 daily cruises (13^{th} March, 17^{th} April, 7^{th} August and 15^{th} September) with 11 stations along a transect perpendicular to the coast. The spatial resolution of each transect was higher towards the coast. Hence, the separation between the 6 more coastal stations was 200 m, but 500 m between the 5 more oceanic. The length of the transect was approximately 4 km and its seaward end overlapped with station E1 of the time-series project RADIALES (Llope et al., 2006) which has been monitored since 1993. In every station, a vertical profile of temperature, oxygen concentration and fluorescence was obtained with a CTD SBE 25. Fluorescence values were transformed to chlorophyll-a concentrations by using a calibration linear fit based on previous monthly surveys at E1 from January 2007 to November 2008 where water samples were taken at 10 m intervals from 0 to 50 m depth with Niskin bottles. These 200 ml water samples were filtered onto 0.2 μm filters which were frozen, their chlorophyll contents extracted following Yentsch and Menzel (1963) procedure and then measured with a Turner Designs 10 fluorometer. The calibration fit was obtained by regressing the measurements from the fluorometer to their corresponding CTD fluorescence values (n=120, r^2=0.74, p<0.0001).

An Acoustic Doppler Current Profiler (ADCP) placed 400 m off Cudillero (43º 34.18'N, 6º 8.43'W) measured the magnitude and direction of the currents throughout the water column (until 20 m in depth) every 30 minutes during the spring/summer of 2009. The spatial resolution of these measurements, or cell size, was 1 m in the March and April samplings, and 2 m in the August and September ones. Due to tides, waves and the refractory behaviour of the surface, the measures of the shallowest cell (x-0 m) were removed and replaced with the previous cell (x1-x2 m) (Kirincich et al., 2005).

4.2.2 Biological sampling methods

The zooplankton was collected throughout the whole water column with a 40 cm mouth diameter and 100 μm mesh size triple WP2 net. That mesh size allows a correct sampling of small barnacle nauplii larvae and it is appropriate for sampling in coastal waters with abundant phytoplankton (Sameoto et al., 2000). These samples were preserved in a 4% buffered formaldehyde seawater solution and larvae were then identified and counted in the laboratory under a dissecting scope.

In the laboratory, each sample was washed free of formaldehyde on an 80 μm sieve, transferred to a 250 ml beaker, and made up to 200 ml. The sample was homogenised by vigorous haphazard stirring, and a 10% and 50% of the sample

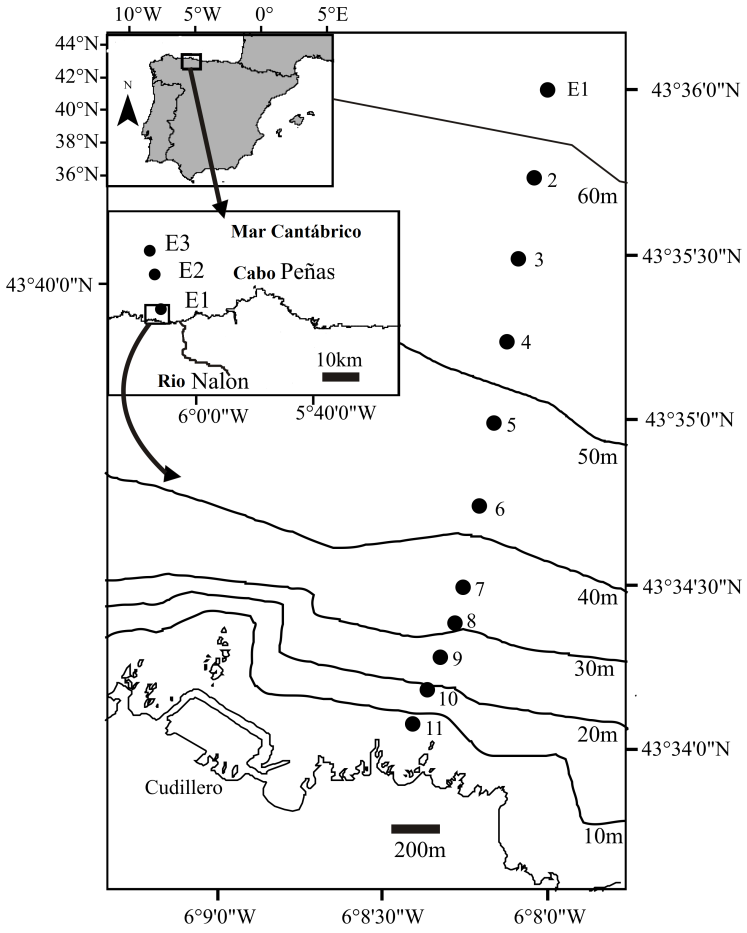

Figure 4.1: Geographical location of the nearshore cruises. In the main figure, the crossed circle sets the position of the ADCP Doppler current meter. Mesoscale topographic features and stations E1, E2 and E3 for the long term monitoring time series are represented in the left small panel.

was sorted for the species of intertidal barnacles and decapods, respectively. We considered these percentages to minimise the intrinsic error associated with the sample processing. To test this, we compared the total number of larvae with the number of larvae counted in the subsamples for two samples in which different taxa and stages seemed to be present at different densities. The percentage of error decreased with the number of larvae observed in the subsample, following very similar exponential functions in barnacles and decapods (data not shown). The minimum number of larvae counted in an aliquot to get an admissible error (<30%) is 3 individuals for both groups, which gives abundances of 234 $ind\ m^{-2}$ and 48 $ind\ m^{-2}$ for barnacles and decapods, respectively.

4.2.3 Statistics: dependent variables

The distribution of passive particles in the sea has been described traditionally on the basis of advection-diffusion models that result in a normal probability density function or PDF (Siegel et al., 2003; White, 2010). Real abundance distributions would match Gaussian PDFs only if larvae are emitted at the same time from a unique, known and spatially fixed source. To comply with these premises, we analysed distributions of larvae of intertidal organisms at different stages across the shelf. Thus, we can assume that larvae belonging to the same developmental stage are also in the same age class and were emitted approximately at the same time from a unique and fixed source at the coast. Spawning from the intertidal along the shore or from different depths across the shore may imply multiple, unknown release locations. Thus, species selection was made according to the adult depth distribution, considering only species with a depth range of distribution shallower than 20 m according to the underwater topography of the study area. With the aim of testing whether the observed spatial across-shore distribution patterns corresponded with theoretical Gaussian bell-shape functions, larval abundances ($ind\ m^{-2}$) were regressed to distance to the coast by using these Gaussian fits. Taxa considered for this analysis were those whose maximum abundance in a given transect reached the minimum essential to reduce error rates below 30%. The mathematical function is expressed as follows:

$$N = A * e^{\left(\frac{-(D-D_A^2)}{2*D_D^2}\right)} \tag{4.1}$$

where N represents larval abundance, A is the amplitude of the normal curve or maximum abundance and D is the distance to coast in meters. DA and DD are the advective and diffusive distances, respectively, and the parameters which define the shape of the Gaussian bell. DA is the average distance where the larval population is located in relation to the coast, which approximately overlaps with the distance of the maximum A (Siegel et al., 2003). We will consider the variance explained by the PDF functions (the coefficient of determination of these regressions, R^2) as a good

Table 4.1: Acronyms and abbreviations of the main environmental and biological parameters and variables.

Variable	Acronym or abbreviation
BV	Biovolume
CHLA	Chlorophyll-a concentration
D_A	Advective distance
$D_A CHLA$	Adevective distance, chlorophyll-a
D_D	Difussive distance
$D_D CHLA$	Difussive distance, chlorophyll-a
H	Shanon's entropy
O_2	Oxygen concentration
PLD	Planktonic larval duration
Q	Larval relative speed
R^2	Goodness of fit to a Gaussian function
T	Mean water temperature
μ	Flow velocity
v	Larval absolute speed

measure of the similarity of the organisms' observed distributions to a Gaussian spatial pattern.

As another variable to characterise cross shore spatial patterns, Shannon´s entropy H of the distributions was inferred (Shannon, 1948). H measures the average degree of uncertainty when predicting the value of the dependent variable (distance offshore) for a randomly chosen individual taken from the population. It is calculated as:

$$H = -\Sigma p_i * \frac{ln(p_i)}{ln(2)} \tag{4.2}$$

where p_i is the probability of a given value i of the dependent variable.

4.2.4 Statistics: independent variables

We took into consideration 3 variables as possible predictors of the distribution patterns in the coast-ocean axis: the biovolume (BV, see Table 4.2.4 for acronyms and abbreviations of the variables), the planktonic larval duration (PLD) and the larval speed-current speed ratio (Q). The size of the organism can affect its ability to disperse, so we estimate its biovolume obtaining measurements and morphological proportions from different bibliographical sources, and then equating the morphology of the larvae to simple geometric figures assuming a density of 1 g/cm^3 (Appendix 4.A, and methods section in Bueno and López-Urrutia (2012).

We estimated the time spent by larvae in the pelagic environment using a bibliographic compilation of PLD of larvae reared under controlled conditions at constant

temperatures (Appendixes 4.B and 4.C). As described in the Supplementary Information, we followed the model of Gillooly et al. (2002) assuming an allometric exponent for larval size of 1/4 and an activation energy of metabolic reactions of 0.65 Ev. Our estimates of PLD are hence depending on larval biovolume, but also on the average temperature of the water for each one of the 4 transects measured with the CTD. As shown in Fig. S4.1, the obtained estimates of PLD are reasonably accurate.

The third variable considered is swimming ability, which determines if larval behaviour may potentially conceal the environmental flow and in turn influence spatial distributions, or on the contrary, larvae may act as passive particles following the flow. This ability is given as the larval speed - current speed quotient (Q). As larval sampling consisted in vertically integrated tows, to know the exact position of larvae through the water column and in turn the flow at that specific depth may not be possible. This is an important limitation of our study and we can only infer a rough estimate based on the dynamic vertical structure during larval development. To determine the mean current speed to which larvae were exposed, we estimated the average velocities for each depth within the time interval that larvae remained in the water column. This period goes from the theoretical time of larval releasing to the time we sampled (sampling date at 10:00 am), the first one being calculated by subtracting the PLD to the sampling time. These values were plotted against depth to infer the hydrographic structure of the water column experienced during the pelagic life. Thus, we establish the depth and thickness of the water layers which flow northward and which can cause larval exportation to open ocean if larvae passively follow the streamlines. If those layers are shallow, upwelling is supposed to be the normal condition during the larval development and the organism would tend to stay on the surface because of the prevailing upwards flow. On the contrary, if those layers are deep in the water column, downwelling was supposed to occur and the flow would advect the organisms downward and northward, under the same assumption of passive transport. In the absence of any layer moving offshore, vertically uniform downwelling prevailed and larvae were supposed to be located within the lower half of the water column. Once the theoretical vertical position has been determined and a layer assigned (upper, middle or bottom), we calculated its mean current speed averaged over the larval period (μ) as a proxy to the environmental flow experienced by larvae. On the other hand, the larval velocity in the water (v), was estimated from the biovolume using the equation in Huntley and Zhou (2004):

$$v = a * BV^b \tag{4.3}$$

where v is the swimming velocity in m/s, a is a constant with value 0.483, BV is the organisms biovolume in Kg, and b is an allometric exponent with value 0.275. Once μ and v are obtained, it is possible to estimate the quotient Q ($Q = v/\mu$). This variable indicates the magnitude of larval speed with respect to that of the currents and may be an easy approach to estimate the potential ability of the animal to avoid

passive transport.

Environmental variables measured with the CTD sensor through the water column were used to plot contour profiles but also as potential predictors of larval distributions. Thus, mean values of temperature (T), oxygen (O_2) and chlorophyll-a (CHLA) concentrations for each month were added to the regression models.

4.2.5 Regression models

Every one of the dependent variables which characterise the distribution of the different larvae (DA, DD, R^2, H) was matched up to the independent variables group (BV, PLD, Q, O_2, T, CHLA) using multiple linear regressions. To achieve homokedascity and improve linearity, both dependent and independent variables were log-transformed with the exception of R^2 and H, which is already calculated on the logarithm of probabilities. We followed the backwards regression procedure till all non-significant variables were removed. Due to the fact that some independent variables were used to calculate others, and to avoid multicolinearity, those models incorporating predictors which significantly correlate were not considered. The Akaike´s Information Criterion (AIC) was used to account for the variance explained, even though it penalises complexity (number of predictor variables), aiming to choose the best model for each dependent variable.

4.3 Results

4.3.1 Physical structure

The four cruises presented contrasting hydrographical features which responded to the marked seasonality typical of the Cantabrian Sea. No thermal stratification occurred during both spring cruises (Fig. 4.2) although in April higher O_2 and chlorophyll-a concentrations reveal an ongoing phytoplankton bloom (Fig. 4.2). In August a clear summer thermocline and subsurface chlorophyll maximum were present. Temperatures reached maximum values at the surface (>20ºC). In September thermal stratification was weaker but still conspicuous and mean O_2 concentrations reached their minimum values for the four cruises (Fig. 4.2). However, surface chlorophyll-a concentrations were relative high pointing to an autumn phytoplankton bloom, probably caused by wind driven coastal upwelling.

Complex patterns in vertical dynamic stratification arise when analysing cross shore currents measured by the ADCP current meter integrated over the planktonic life of different larvae. Two layers were apparent in both spring cruises even though thermal stratification did not occur. In the upper water column the flow trended onshore pointing to a downwelling regime (Table 4.3.1). In contrast, offshore surface transport typical of upwelling prevailed during the larval development of most of

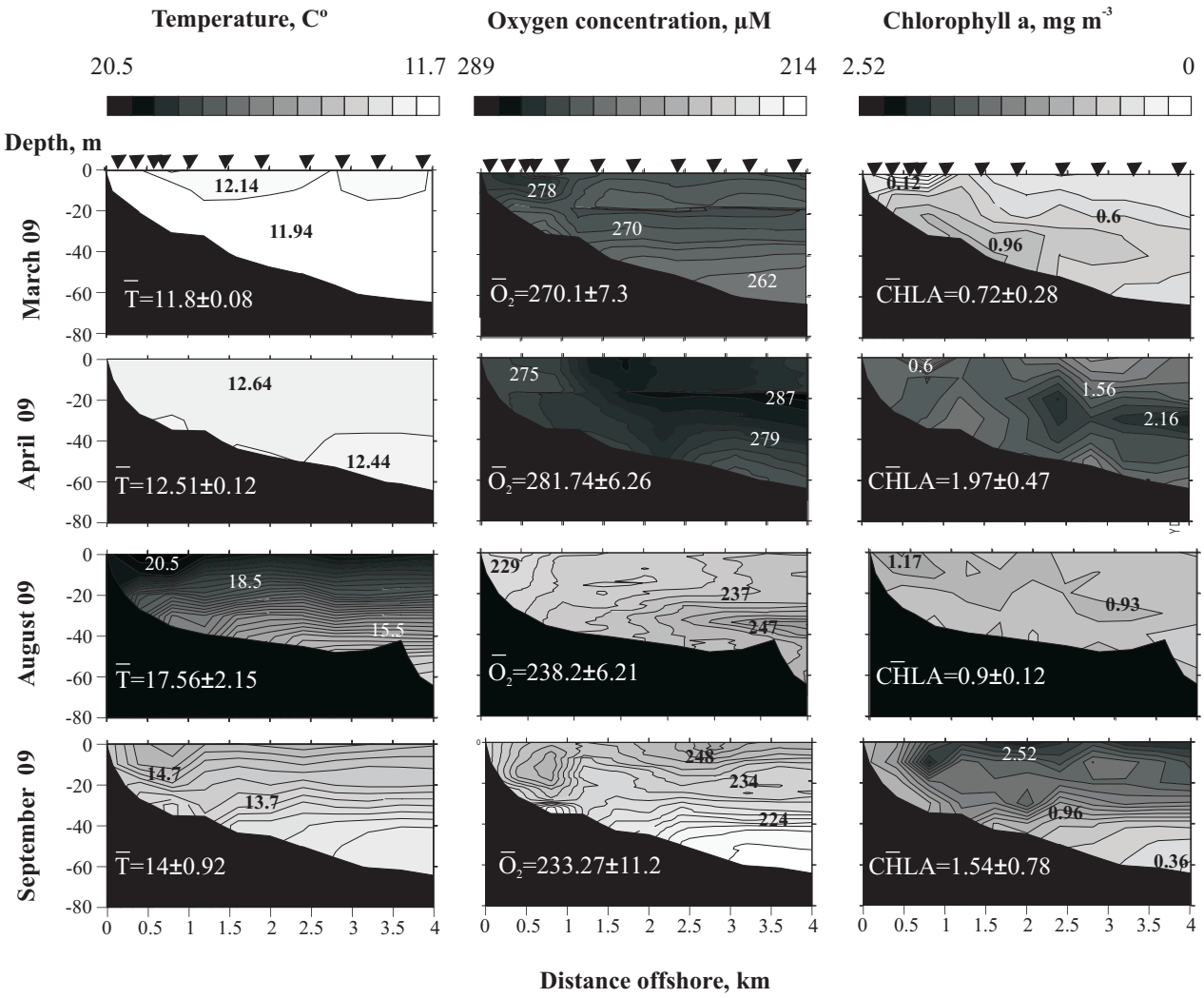

Figure 4.2: Cross shore contour profiles of temperature, oxygen and chlorophyll a for the 4 coastal cruises. Mean values for each variable are also shown.

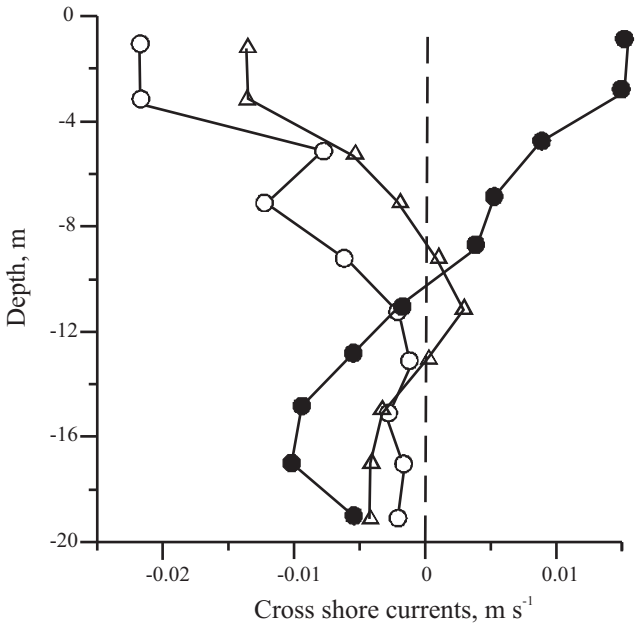

Figure 4.3: Three examples of different patterns in the dynamic stratification of the water column. In the X axis, positive and negative values stand for seawards and landwards currents, respectively, with a discontinuous line positioned at cross shore flow equal to 0. Black circles represent a typical upwelling flow pattern in two layers for *Popllicipes pollicipes* II in August 09; white triangles show a three layer transitional phase for *Diogenes pugilator* III in September 09; and white dots show a uniform one layer downwelling pattern for *P. perforatus* II in September 09.

every the taxa in August (Table 4.3.1, Fig. 4.3). A more complex circulation pattern was present during the larval development of most of the species in September: three layers were apparent, the upper and bottom ones moving onshore while currents at mid depths were directed offshore (Table 4.3.1, Fig. 4.3). However, currents moving onshore through the whole water column prevailed for nauplii II of both *C. montagui* and *Perforatus perforatus* (Table 4.3.1, Fig 4.3).

4.3.2 Larval distributions and characteristics

The larval stages of common intertidal crustaceans in the Cantabrian Sea were identified and counted for the four cruises. Six different species fulfilled the minimum abundance criteria to perform further statistical analyses: among the barnacles, *Perforatus perforatus*, *Chthamalus montagui*, *Chthamalus stellatus* and *Pollicipes pollicipes*; among the decapods the hermit crab *Diogenes pugilator* and the hairy crab *Pilumnus sp.* Regarding the hairy crab, the distribution of the different species within this genus remains relatively unknown in the southern Bay of Biscay, to the point that d'Udekem d'Acoz (1999) identified one new very coastal species in the region. Thus, we have considered *Pilumnus sp.* larvae for the analyses although

Table 4.2: Biological and environmental parameters for all the taxa and stages analysed (see Table 4.2.4 for acronyms and abbreviations). The dynamic stratification of the water column is also indicated by reporting the number of water layers and the Ekman transport phase: UPW and DOWN stand for upwelling and downwelling, respectively.

Cruise	Taxa	Dyn. stratif.	D_A, m	D_D, m	R^2	H	BV, mm^3	PLD, d	v, m/s	μ m/s	Q
March 09	P. perf II	Down, 2 layers	0.00	206.68	89.12	1.64	0.0069	10.06	0.0027	0.0031	0.8677
	P. perf III	Down, 2 layers	0.00	1890.26	53.16	3.24	0.0141	12.05	0.0034	0.0057	0.5989
	P. perf IV	Down, 2 layers	620.50	106.37	86.73	2.25	0.0149	12.20	0.0034	0.0057	0.5979
	P. perf VI	Down, 2 layers	1056.29	39.41	71.79	2.00	0.0706	18.01	0.0052	0.0048	1.0768
April 09	P. perf II	Down, 2 layers	0.00	163.58	98.52	1.12	0.0069	9.43	0.0027	0.0024	1.1206
	C. stell III	Down, 2 layers	3643.00	174.22.	91.69	1.61	0.0113	10.68	0.0032	0.0031	1.0380
August 09	P. perf II	Up, 2 layers	1385.07	1544.17	16.18	3.09	0.0069	5.99	0.0027	0.0077	0.3506
	P. perf III	Up, 2 layers	1516.19	1413.63	16.67	2.78	0.0141	7.17	0.0033	0.0085	0.3887
	P. perf IV	Up, 2 layers	2671.55	845.41	68.33	2.47	0.0149	7.26	0.0034	0.0076	0.4461
	C. mont II	Up, 2 layers	2513.21	341.24	52.22	2.79	0.0039	5.19	0.0023	0.0090	0.2562
	C. stell II	Up, 2 layers	1079.10	534.70	34.35	3.02	0.0052	5.59	0.0025	0.0097	0.2567
	P. polli II	Up, 2 layers	2169.07	1281.95	6.64	2.99	0.0091	6.42	0.0030	0.0097	0.3098
	D. pugi I	Up, 2 layers	1451.70	791.94	47.53	2.98	0.0621	10.38	0.0050	0.0062	0.8075
	D. pugi II	Up, 2 layers	1602.40	509.75	49.78	2.82	0.1273	12.42	0.0061	0.0031	1.9456
	D. pugi III	Up, 2 layers	2489.64	707.40	97.14	2.61	0.2068	14.02	0.0070	0.0058	1.2097
	D. pugi IV	Up, 2 layers	2517.46	444.27	84.76	2.46	0.3369	15.84	0.0080	0.0042	1.8827
	Pil sp. I	Up, 2 layers	840.95	284.14	64.29	1.56	0.0831	11.16	0.0055	0.0050	1.0903
	Pil sp. II	Up, 2 layers	1741.82	860.56	83.03	3.08	0.1415	12.75	0.0063	0.0069	0.9133
	Pil sp. III	Up, 2 layers	2382.07	320.07	77.54	2.27	0.2997	15.39	0.0078	0.0046	1.6958
	Pil sp. IV	Up, 2 layers	1896.20	564.61	73.74	1.89	0.3837	16.37	0.0083	0.0037	2.2294
Sept 09	P. perf II	Down, 1 layer	857.05	262.36	97.5	2.33	0.0069	8.21	0.0027	0.0019	1.3923
	P. perf III	Down, 3 layer	993.52	252.93	95.39	2.29	0.0141	9.83	0.0034	0.0039	0.8798
	C. mont II	Down, 1 layer	591.18	161.91	98.19	2.01	0.0039	7.12	0.0023	0.0031	0.7536
	C. mont III	Down, 1 layer	886.40	458.00	99.00	0.76	0.0066	8.13	0.0027	0.0020	1.3239
	P. polli II	Down, 3 layer	2694.00	1267.19	53.90	2.90	0.0091	8.81	0.0030	0.0005	5.4828
	D. pugi I	Down, 3 layer	1522.98	526.25	67.77	2.17	0.0621	14.24	0.0050	0.0020	2.4740
	D. pugi II	Down, 3 layer	2244.81	199.34	64.9	2.13	0.1273	17.04	0.0061	0.0013	4.7747
	D. pugi III	Down, 3 layer	2056.27	436.58	86.25	1.66	0.2068	19.24	0.0070	0.0014	5.0798
	Pil sp. I	Down, 3 layer	2721.03	684.27	88.66	2.41	0.0831	15.32	0.0055	0.0014	3.8333

the available identification keys do not allow for exclusion of other offshore species within this same genus.

Independent predictors inferred from larval biological characteristics matched those extracted from the literature. BV ranged from 0.004 for small chthamalid nauplii to 0.4 mm^3 for late stages of *Pilumnus sp.* (Table 4.3.1), reminiscent of those values found in Ingle (1992) and in Anger (2001). PLD was in the order of several days-a few weeks (Table 4.3.1 and Appendix 4.A), values which correspond to periods obtained in the laboratory (Anderson, 1994; Anger, 2001; dos Santos and González-Gordillo, 2004; Guerao et al., 2008). We also assessed the goodness of the prediction of PLD by calculating theoretical PLD's for larvae in Appendixes 4.B and 4.C (see Supplementary Information and Fig. S4.1). Eventually, our calculations gave theoretical swimming speeds of few $mm\ s^{-1}$ (Table 4.3.1), in accordance with typical velocities found for marine invertebrate larvae (Chia et al., 1984; Mileikovsky, 1973). Note that the PLD-averaged across shore flow measured with the ADCP current meter was of the same magnitude, which leads to values of the velocity ratio Q around unity (Table 4.3.1). Nauplii II of *Pollicipes pollicipes* in September 09 were able to swim up to 5 times faster than currents, while at the other end, the same taxa was 3 times slower in August 09 (Q=0.3, Table 4.3.1).

Twenty three out of the 29 larval distributions analysed were found to significantly fit a normal distribution across the inner shelf (Fig. 4.4). In 13 cases,

Table 4.3: Regression models for the parameters characterising larval distributions. Best models, ordered by Akaike´s Information Criterion (AIC), are highlighted in bold. The sign of the correlation is the sign of the std. coefficient. Ln stands for natural logarithm, see Table 4.2.4 for acronyms and abbreviations. For the *p.values*: $*<0.05$, $**<0.01$, $***<0.001$.

Variable	N model	N of var.	AIC	Overall R^2	Predictor	p value	R^2	Std. coef.
lnD_A	1	1	122.139	0.409	lnO_2	***	0.409	-0.639
	2	1	127.055	0.299	lnT	**	0.299	0.547
lnD_D	1	1	71.6	0.28	lnT	**	0.28	0.529
	2	1	74.986	0.191	lnO_2	*	0.191	-0.437
R^2	1	3	267.357	0.435	lnT	**	0.225	-0.491
					$lnBV$	*	0.108	0.373
					$lnCHLA$	*	0.102	0.335
	2	2	267.889	0.363	$lnPLD$	*	0.196	0.436
					$lnCHLA$	*	0.167	0.373
	3	2	268.722	0.345	lnT	*	0.225	-0.387
					lnQ	*	0.12	0.357
	4	1	270.874	0.225	lnT	**	0.225	-0.475
	5	1	271.653	0.204	lnQ	*	0.204	0.452
	6	1	271.953	0.196	$lnPLD$	*	0.196	0.442
	7	1	272.757	0.173	$lnCHLA$	*	0.173	0.416
H	1	2	51.699	0.33	$lnCHLA$	**	0.21	-0.512
					lnO_2	*	0.12	-0.351
	2	1	53.781	0.21	$lnCHLA$	*	0.21	-0.458
	3	1	54.155	0.2	lnT	*	0.2	0.447
	4	2	55.295	0.242	lnQ	*	0.118	-0.419
					lnO_2	*	0.124	-0.360

Gaussian functions explained more than 80% of the total variance of the abundance pattern with distance offshore (Table 4.3.1), these values being unusually high for spatial planktonic distributions. DA varied from 0 to 3643 m offshore while DD ranged from 39 to 1890 m around the centre of the normal distribution. Shannon´s entropy H ranged from 0.76 to 3.24 (Table 4.3.1).

4.3.3 Regression models

Models resulting from the multiple linear regressions carried out for the 4 parameters which characterised larval spatial distributions (D_A, D_D, R^2 and H) explained significant amounts of variability (Table 4.3.3). Both D_A and D_D significantly decrease with mean oxygen concentrations and temperature along the transects, suggesting that larvae remain onshore and aggregated in cool, well oxygenated waters (Table 4.3.3, Fig. 4.5). The fit to a normal distribution R^2 improves with chlorophyll a concentrations, body size and the ability of the larvae to face environmental currents, but decreases with water temperature and developmental time (Table 4.3.3, Fig. 4.5). Regarding H, it significantly decreases with both CHLA and O_2, which implies that less chaotic, more predictable spatial distributions are found in oxygenated waters with higher concentrations of potential food (Table 4.3.3, Fig. 4.5). In a lesser extent, entropy also decreases with larval relative speed and increases in warmer waters (Table 4.3.3, Fig. 4.5).

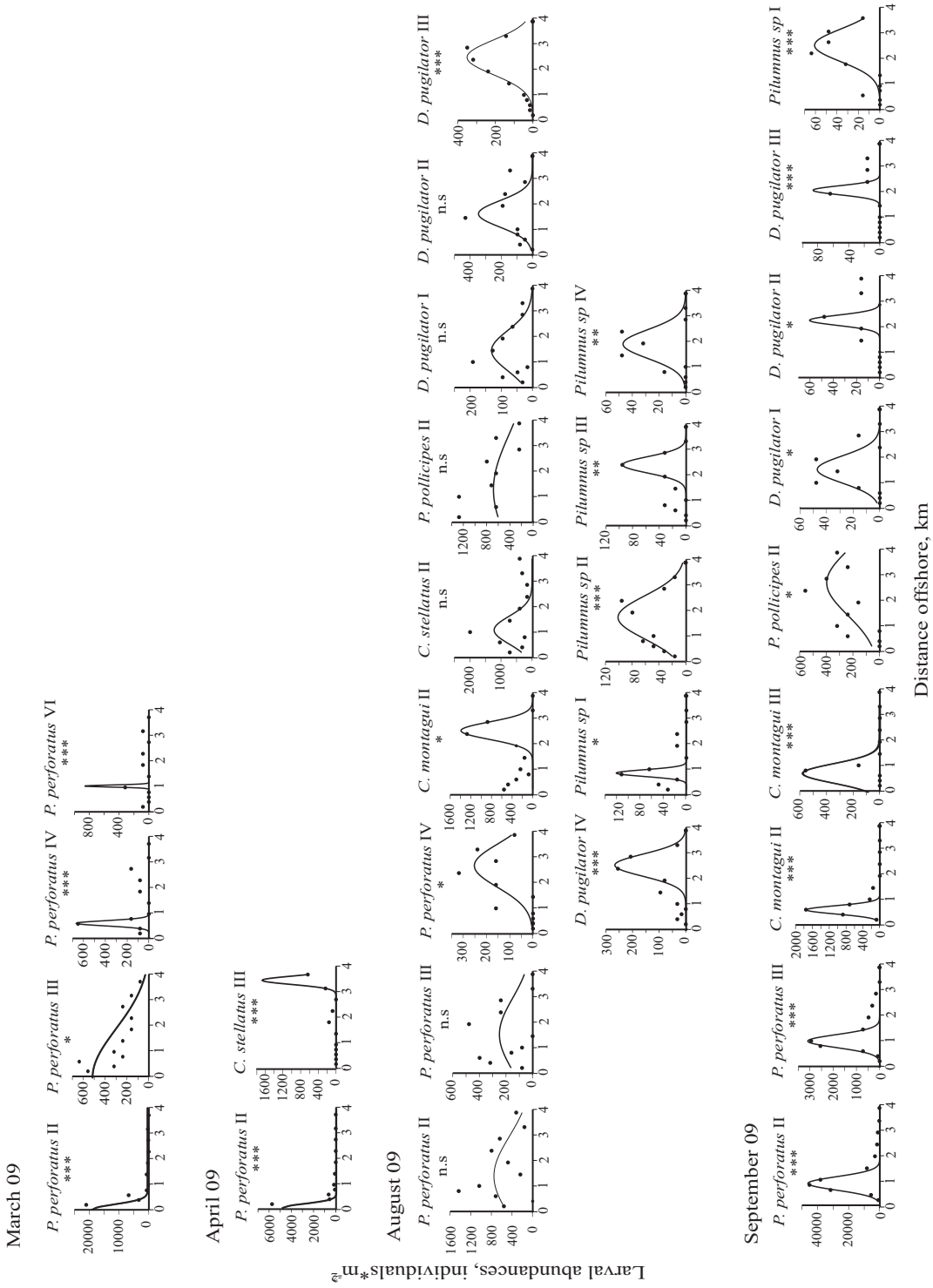

Figure 4.4: Cross shore patterns in abundance for all the larvae analysed with their respective Gaussian fit (n.s=non significant,*<0.05, **<0.01, ***<0.001). See Table 4.3.1 for R^2 values.

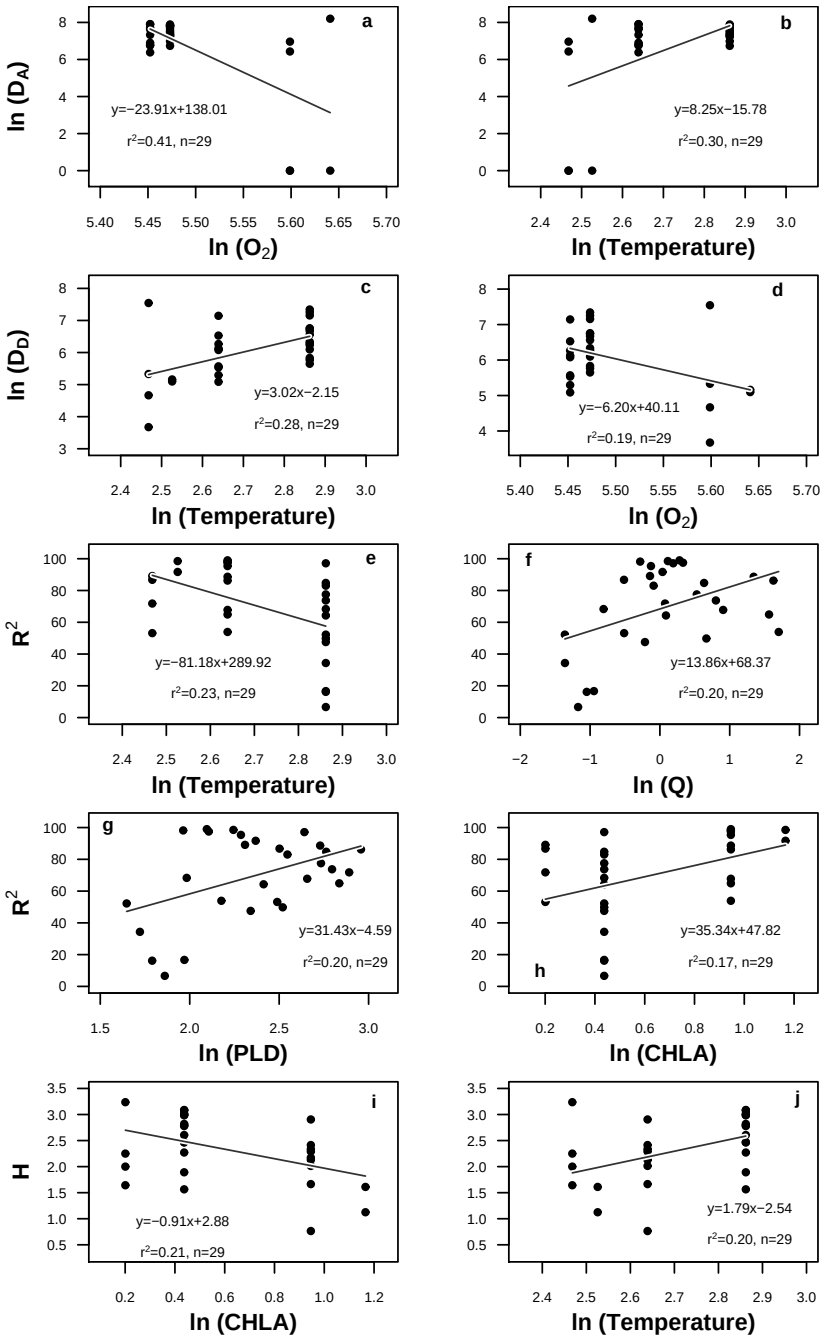

Figure 4.5: Simple linear regression representing the significant one-variable-models for each larval distribution parameter with N=29 for all of them (see Table 4.2.4 for acronyms). Panels a and b represent the relationship between DA and 02 and T respectively. Panels c and d show the relationship between DD and T and 02 respectively. Panels e, f, g, and h depict the relationship between R^2 and T, Q, PLD and chlorophyll-a concentration, while panels i and j the relationship of H with chlorophyll-a concentration and T. With the exception of R^2 and H, both predictors and parameters are represented in a natural logarithm scale. See Table 4.3.1 for the percentage of variance explained and statistical significance of each model.

4.4 Discussion

4.4.1 Variability in the water column structure.

Our first striking result is that organisms collected at the same time experienced different hydrographic conditions in the case of our late summer sampling in September (Table 4.3.1, Fig. 4.3). Most likely these differences obeyed rapid changes in the Ekman transport regime which are characteristic of the study region. Summer wind driven coastal upwelling in the Cantabrian Sea is far from being continuous along the season as upwelling favourable winds usually weaken after 3-4 d and turn into westerly winds prone to downwelling (Varela et al., 2005). The typical PLDs of several days we have estimated for our taxa may be long enough to integrate these short-scale reversals in Ekman transport. Specifically, we interpret the three layered structure apparent for some larval taxa as a transitional state between upwelling and downwelling periods (Table 4.3.1, Fig. 4.3). This high hydrographical variability imposed on different planktonic organisms collected simultaneously calls into question the reliability of the traditional methodology employed to test cross-shelf transport of larvae under different wind regimes, at least for the region of our study. Usually, both upwelling and downwelling phases are defined a priori by the researcher on the basis of the present hydrographical data available just before sampling (Shanks et al., 2002; Shanks and Brink, 2005). This approach may be correct only in systems where Ekman transport is constant and predictable, like off the coast of California and Western Iberia. However, as the Cantabrian Sea is located at the fringe of an upwelling system these conditions do not apply and the upwelling/downwelling phase cannot be set beforehand. On the contrary, under the forcing of short time scale wind shifts it is the taxa-specific planktonic larval duration that defines the sign of the prevalent Ekman transport experienced by a given species. According to this statement, mean distances offshore for different, simultaneously collected larvae in our study area were found to correlate only with the upwelling index averaged over their specific PLD (Weidberg et al., 2013).

4.4.2 Passive *vs* active mechanisms.

Our results suggest that PLD affects larval distributions indirectly by defining the flow at which larvae may be exposed along their pelagic life. However, in light of our regression models, PLD´s direct effects on across shelf patterns in abundance do not follow the dynamics expected for time-dependent passive processes. If larvae were inert particles, we may expect D_D and D_A to correlate with PLD as in theory both variables increase with time (Largier, 2003; Siegel et al., 2003; White, 2010), but that was not the case. The same assumptions apply to H: within a system, entropy is supposed to increase with elapsed time (Shannon, 1948), but we did not observe that relationship for this data set (Table 4.3.3). Therefore, the functioning and evolution of the system may not be passive but may be influenced by the characteristics of the

larvae. This hypothesis is supported by our statistical models, as the goodness of fit to a normal function correlates with PLD but in the opposite way to the passiveness assumption: the more the time spent in the pelagic environment, the better the fit to a well-defined, bell-shaped distribution (Table 4.3.3, Fig. 4.5). In addition, the relative swimming speed Q, significantly explained the spatial patterns of larvae (Table 4.3.3, Fig. 4.5). Distributions were less chaotic when larvae were faster in relation to the environmental flow (Table 4.3.3). Moreover, the Gaussian nature of these distributions may also depend on the organisms´ swimming performance as R^2 significantly increases with Q (Table 4.3.3, Fig. 4.5).

Swimming ability has been found to successfully explain planktonic distributions in the field. Gallager et al. (2004) calculated the ratio Mn (swimming speed/turbulent velocity) and related it to significant plankton aggregations over the Georges Bank. Similarly, the ratio Q explained the degree of accumulation of some invertebrate larvae at very nearshore fronts (Weidberg, 2012). Natunewicz and Epifanio (2001) concluded that the spatiotemporal scales at which the larval patches of the blue crab *Callinectes sapidus* developed did not match those of aggregative physical forces in the sea. Although these studies suggest that the ability to be independent of the currents affects spatial patterns in abundance, little is known about the exact active behaviours which may reduce environmental advection and especially diffusion. In some theoretical models, an attractive biological force proportional to the swimming speed of the organism was added to account for plankton patchiness (Okubo and Anderson, 1984; Yamazaki, 1993), see also Metaxas (2000) for review. According to these models, animals would be able to detect the edge of the plankton swarm and turn back. In experimental tanks, Price et al. (1988) found that krill responded to decreasing algal concentrations in a very similar way, thus remaining within potential food patches. This active aggregative behaviour requires high swimming performance in the horizontal plane which can be applied to krill and probably to the decapod larvae collected in our cruises, but not to much slower barnacle nauplii. Early larval stages of barnacles may be able to actively modify their position through the water column swimming against the much weaker vertical flow (Genin et al., 2005). This behaviour may enhance plankton patchiness close to the coast (Franks, 1992; Genin et al., 2005).

The advantages of active aggregation have been widely studied in terrestrial systems: high prey densities reduce predators´ efficiency and increase the individual survival probability (O'Dowd and Gill, 1984; Turchin and Kareiva, 1989). This strategy could be of greater importance at the time of recruitment at the parental intertidal habitat where predation rates are much higher than in the plankton (Johnson and Shanks, 2003).

4.4.3 Physiological, metabolically driven effects on spatial patterns.

One can hypothesise that if swimming ability to face the currents affects larval distributions, then those factors acting on locomotion, such as food supply, oxygen saturation and temperature, among others, may also play a role. Our results suggest that actually these variables contributed to explain across shore abundance patterns: note that factors potentially influencing organismal physiological condition were selected for the best regression models (Table 4.3.3, Fig. 4.5).

The effect of increasing chlorophyll-a concentration in the water resulted in less chaotic distributions of larvae, with better fits to normal distributions (Table 4.3.3, Fig. 4.5). Folt and Burns (1999) pointed out the importance of food concentration as a determinant of zooplankton patchiness, with three main processes underlying this relationship: physical mechanisms of dispersion (assuming food and larvae as passive particles), zooplankton behaviour, and enhanced growth. Our analyses show that the effect of chlorophyll-a concentration in R^2 and H are accompanied by the effects of temperature, larval size or oxygen concentration, suggesting additional physiological mechanisms for larval aggregation.

Higher 0_2 concentrations led also to more aggregated, less chaotic distributions with the core of the larval population closer to the parental habitats at the shore (Table 4.3.3, Fig. 4.5). Again, the fact that onshore retention was more effective in oxygenated waters seems to relate this result with the effect of larval physiology, probably because retention depends on oxygen dependent-swimming performance. Larvae could not remain aggregated close to the coast if their active vertical or even horizontal positioning fails (Poulin et al., 2002; Shanks and Brink, 2005; Genin et al., 2005). However, the question remains if the relative small decrements in O_2 concentrations observed in our coastal cruises ($<$50 μM, Fig. 4.3) would be theoretically enough to limit swimming performance and in turn affect larval spatial distributions. Swimming against the environmental flow would require metabolic rates falling between routine and active levels, that is, between minimum and maximum motor activity (Prosser, 1961). For zooplankton, those rates are substantially higher than the basal metabolism required for organismal maintenance: 2.6 and 6 times higher for krill and copepods, respectively (Torres and Childress, 1983; Buskey, 1998). Thus, decays in oxygen concentrations would affect swimming performance much before being lethal. Lethal O_2 concentrations for the megalopae of the crab *Cancer irroratus* attained 70.5 μM at 15ºC (1.58 $ml\ O_2\ L^{-1}$, Vargo and Sastry (1977)), so our field values (between 233 and 270 μM, Fig. 4.2) could already limit active metabolism and in turn swimming behaviour in similar larvae.

In the sea, the potential of oxygen to be a limiting factor is mainly a function of temperature. By reducing dissolved oxygen availability (Benson and Krause, 1984) and enhancing metabolic demands (Gillooly et al., 2001), increments in temperature strongly affect organismal physiology. In fact, usually the effect of both variables on

the metabolism cannot be separated and it is said that a given organism presents a certain oxygen- limited thermal tolerance (Pörtner and Knust, 2007; Pörtner, 2010). Similarly, our statistical analyses do not allow for any differentiation, but temperature contributed to explain the main parameters in larval distributions in the same way as oxygen concentration did. Thus, more chaotic and less aggregated distributions displaced offshore were found in warmer waters (Table 4.3.3, Fig 4.5), indicating less swimming efficiency in order to keep onshore retention and spatial patchiness. Little is known about how temperature-mediated oxygen limitations act on planktonic swimming speeds. In the case of krill, the same increment in swimming velocity may require significantly higher oxygen consumption rates at higher temperatures (Torres and Childress, 1983). Storch et al. (2011) studied the thermal tolerance windows for the larvae of the kelp crab *Taliepus dentatus* and found that swimming performance may be constrained just above the thermal range at which the organism is not limited by oxygen supply ("pejus" temperature). Such a thermal window is really narrow and kelp crab larvae may often be exposed to temperatures which can drastically limit their ability to swim (Storch et al., 2011).

The possibility that collateral, physiological effects of temperature on larval swimming ability could be translated to the population level has been poorly explored, even in the actual context of climate change. However, this could actually be happening: preliminary data suggest that, in the case of kelp crabs, not only is locomotion negatively affected above the "pejus" temperature (17^oC), but so are recruitment rates on the shore (Navarrete, personal communication). In our study we show indirect evidence of temperature effects on larval distributions within a relatively small thermal range consistent with the normal seasonality in the region ($11.8\text{-}17.56^oC$, Fig. 4.2). Given the high inter-annual thermal variability in marine systems, populations may cope with such effects alternating high with low recruitment seasons (Sinclair, 1987; Planque and Fox, 1998). Nevertheless, populations´ capacity to buffer temporal variability in recruitment may fail in warming seas where temperatures constraining motor activity could become pervasive in the long term. Increments in surface sea temperature around $0.05^oC\ year^{-1}$ have been reported for the Cantabrian Sea (Koutsikopoulos et al., 1998; Llope et al., 2006). Thus, future scenarios in which larvae of intertidal invertebrates may become inert particles unable to remain onshore and recruit for long periods must be considered to better forecast the effects of climate change in the coastal ocean.

This study presents obvious methodological limitations which could be surpassed with further analysis of more detailed physical data sets. Specially, biological samplings at different water layers, instead of our vertically integrated tows, would allow a better characterisation of the physical conditions experienced by larvae. In addition, temperature, oxygen and chlorophyll CTD data are just instantaneous measurements taken at the time we were sampling. However, the means for each cruise may be representative of the yearly seasonality in the region. On the other hand, environmental flow averages come from detailed, time-integrated data sets from the ADCP current meter, but just at one single location (Fig. 4.1). Despite

this lack of spatial coverage for flow data, current measurements at this nearshore site were found to correlate with the flow recorded at other meteorological stations (Weidberg, 2012) and to appropriately describe inter-annual patterns in Ekman transport (Rivera et al., 2013). Thus, uncertainties coming from our methodological constraints may not invalidate our results.

4.5 Conclusions

Our results may provide answers to the initial questions we wanted to address with this study. Cross shore larval distributions can be characterised by Gaussian fits predicted by classical advection-diffusion models. However, the parameters of these models may not be defined by the evolution of a passive system but by larval swimming ability and its physiological determinants, mainly oxygen and temperature.

New questions arise from the outcomes of this study: metabolically driven decays in individual performance may result in changes of whole spatial patterns in abundance across the shelf, but would those changes significantly impact larval supply to the adult habitat? Could populations cope with those changes in a context of global warming? Studies capable of examining in detail recruitment success in conjunction with larval physiological performance may allow the identification of sensitive populations and species.

4.6 Acknowledgements

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4.7 Supplementary Information

To calculte the time spent by larvae in the pelagic environment (PLD), we followed the model presented by Gillooly et al. (2002):

$$PLD = \frac{4}{a_0} * e^{E/kT} * BV^{\alpha} \tag{4.4}$$

where $4/a_0$ is a constant, E represents the activation energy of metabolic reactions ($\sim 0.65eV$), k is the Boltzmann constant, T is the temperature of water in Kelvin, and α is the allometric exponent (0.25). This equation shows how an increase in the water temperature reduces the duration of the larval period and how larger organisms have longer developmental times.

Using a bibliographic compilation (see Appendix 4.B and 4.C) we obtained constant-temperature laboratory measures of PLD for decapod and cirripedian larvae. These data allow us to estimate a value for the constant $4/a_0$, needed to apply Eq. 4.4 and obtain expected PLD's for the plankton from the samples, depending on BV and the average temperature of the water for each one of the 4 transects measured with the CTD. Hence, correcting PLD by the effect of temperature and body size ($log(PLD/(e^{(0.65/kT)} * BV^{1/4}))$), we calculated a mean value of $1.1240 * 10^{-10}$for $4/a_0$, which is used in Appendix 4.A to infer PLD.

In order to test the goodness of our estimation of PLD, we have calculated the expected PLD of the larvae in Appendix 4.B and 4.C ("Predicted PLD") and plotted it against the PLD reported by the literature ("Observed PLD") (Fig. S4.1).

4.8 Supplementary figure

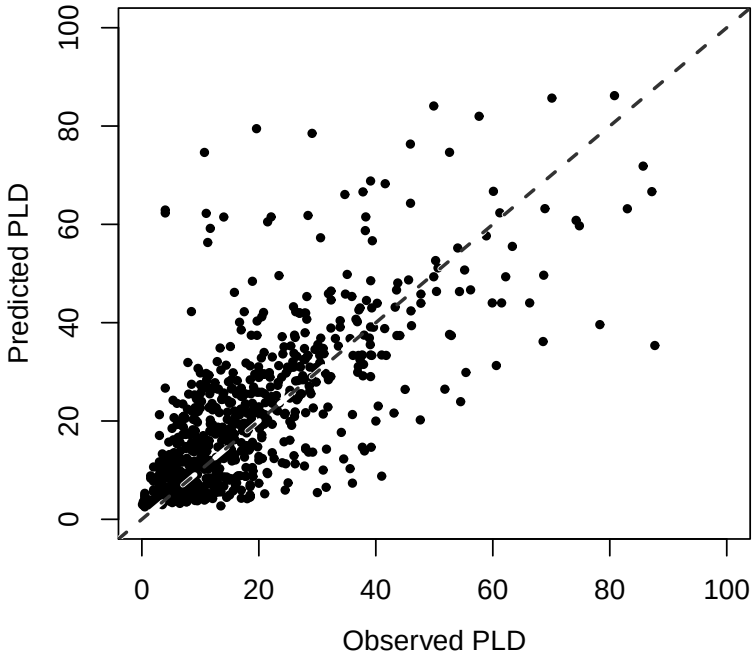

Figure S4.1: Predicted against observed values of PLD for decapod and barnacle larvae in Appendixes 4.B and 4.C. The dashed line indicates the 1:1 relationship.

4.A Appendix 4.A

http://www.repositorio.ieo.es/e-ieo/handle/10508/1585

4.B Appendix 4.B

http://www.repositorio.ieo.es/e-ieo/handle/10508/1586

4.C Appendix 4.C

http://www.repositorio.ieo.es/e-ieo/handle/10508/1587

Chapter 5

The effect of the relationship between planktonic development time and fecundity on the geographic range size of marine benthic organisms

Contents

5.1 Introduction

The geographic range size (GRS) of species is related to the availability of space and nutritional resources (Gaston, 2003). Hence, species with large GRS are expected to be exposed to more diverse environments than species with small GRS, what is a sign of adaptability to environmental changes (Brown et al., 1996). For this reason, GRS is considered a fundamental variable in ecology and biogeography, used to characterise the risk of extinction of endangered species, and in the management of wild populations. Numerous factors have been proposed to rule GRS, although the role of dispersal, with implications in colonising new regions or facing the reduction of suitable habitats, comprises the bulk of the research (Gaston, 2009). In the case of marine benthic organisms, dispersal is usually restricted to a planktonic larval phase that drifts with ocean currents. Albeit there have been many attempts to relate GRS with the duration of the planktonic larval phase (PLD) (Paulay and Meyer, 2006; Lester et al., 2007; Mora et al., 2012), other kind of factors such as body size and behavioural traits of adults and larvae, have also been demonstrated to play an important role (Luiz et al., 2013).

Larval dissemination in the benthic marine environment is usually modelled by generating probability curves of larval settlement termed "larval dispersal kernels". Considering a unique point of larval emission, dispersal kernels constitute a useful way to quantify the average probability distribution of propagules in the along shore axis. According to this, larval dispersal kernels have been applied to infer the genetic connectivity between metapopulations of benthic coastal organisms (Siegel et al., 2003; Aiken et al., 2007), being PLD the most important factor defining the amplitude of the kernel and also, the genetic structure of populations (Siegel et al., 2003; Rivera et al., 2013).

One assumption usually found in works on the determinants of geographic range size is that PLD is critical to determine GRS in marine organisms (Shanks et al., 2003; Lindsay, 2012). Considering the relationship between PLD and the amplitude of larval dispersal kernels shown by Siegel et al. (2003), the previous assumption should be equivalent to say that the maximal larval dispersal (MLD), or the amplitude of kernels, determines GRS. So, if these premises are true, and larval dispersal ability actually rules GRS, the effect of other variables with influence on MLD should also be perceived on GRS. In this work we will analyse the effect of the number of broadcasted planktonic propagules (H) on the maximal distance that they can reach from the emission point. Then, considering this relationship, we will study the joint influence of H and PLD on GRS. Our results should throw some light on the influence that dispersal ability has on GRS in the marine environment.

5.2 Results and Discussion

As shown in Fig. 5.1, considering a fixed PLD, the number of broadcasted particles, H, does not modify the kurtosis of kernels. Furthermore, H does not have any effect on the average dispersal distance (the mode of the distribution). Instead, H increases or diminishes the probability of larvae to settle at any given point. Considering the MLD predicted by these kernels, increasing H also increases the probability of larvae to reach the extremes of the probability distribution what means that larvae will reach farther distances from the emission point.

To study how the joint effect of PLD and H influences MLD, we have generated dispersal kernels from random particle tracks constructed following the equations of Siegel et al. (2003). According to these authors, the spread of the kernels are mainly dependent on PLD and the competency period established (the time after which particles are able to settle). To introduce the effect of H in the model, we simulated the dispersal of a given number (10^1, 10^2, 10^3, 10^4, 10^5, 10^6) of particle tracks for each of the different PLD considered (5, 12, 21, 36, 56, 75, 100, 125, 150, 175 and 200 d, with a competency period of three quarters of PLD). Defining GRS as the maximal settlement distance reached by simulated tracks, we demonstrate that both PLD and H exert a positive influence on MLD.

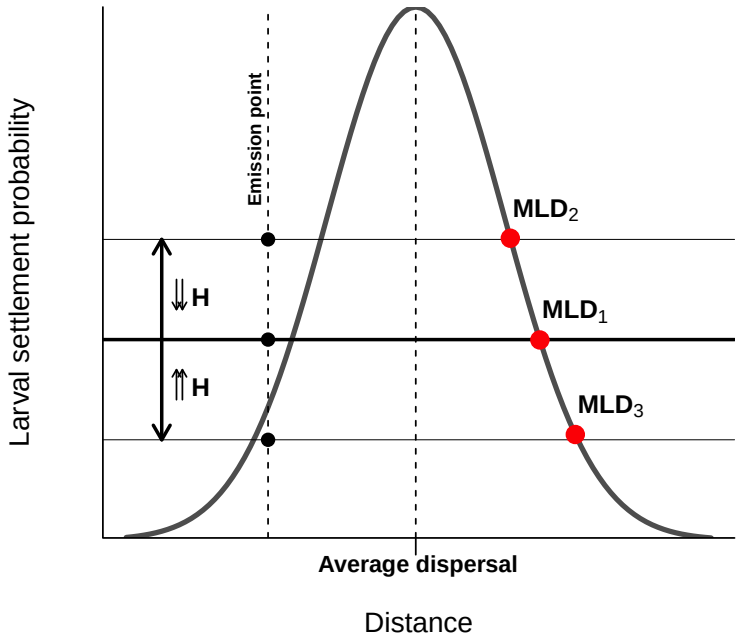

Figure 5.1: Influence of the number of broadcasted particles (H) on the maximal geographic distance reached at a fixed PLD, according to the model of Siegel et al. (2003). Dispersal kernels represent the probability of larvae to settle at a given distance from the emission point, but also show the maximal distance travelled by larvae (MLD). Here we show that increasing H, for a fixed PLD, elevates the probability of particles to reach farther distances from the emission point ($MLD_3 > MLD_1$), and viceversa ($MLD_1 > MLD_2$).

As stated above, if MLD is a valid mechanism ruling GRS, the influence of H and PLD should be perceived also in GRS. However, it is difficult to quantify the population offspring production rate (H) in the field. As a proxy we will use the daily offspring production rate (C) of the population albeit we acknowledge that adult population size would also be an additional determinant of GRS. To analyse the relationship between C, PLD, and GRS we have compiled data for PLD, GRS and the daily offspring production rate (C) of benthic marine organism (Appendix 5.A). GRS was obtained from the Ocean Biogeographic Information System (OBIS), following the methodology in Luiz et al. (2013). PLD and C were obtained from the bibliographic references found in Appendix 5.A.

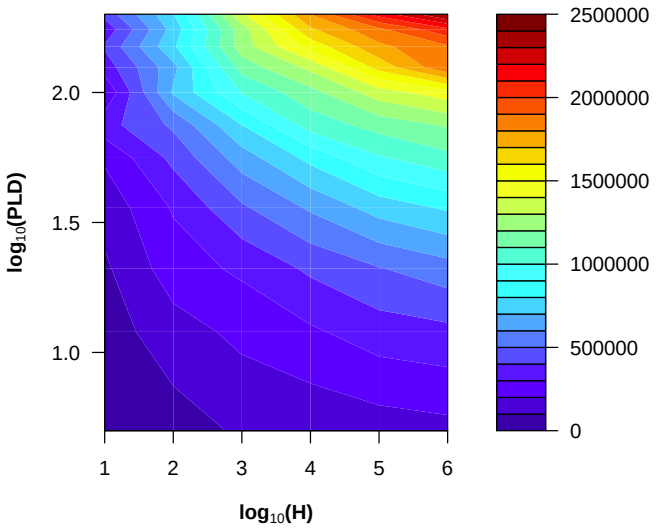

Figure 5.2: The model presented by Siegel et al. (2003) allows to calculate the maximal dispersal distance travelled by particles from the emission point (MLD), as a function of the time that particles are drifted by currents (PLD). By modifying the number of particles simulated, we can analyse the effect of H on MLD. This figure shows the joint positive effect of both PLD and H on MLD.

We have obtained a positive and significant ($p.val = 0.0494$) relationship between GRS and the daily offspring production rate (C) of organisms (Fig. 5.3A). The relationship between PLD and GRS is negative, although it is not significantly different than zero ($p.val = 0.918$). The finding that PLD and GRS are not related is in opposition to the recent work of Luiz et al. (2013), but other previous studies have already reported a weak relationship between both variables (Paulay and Meyer, 2006; Mora et al., 2012), with influence also of the scale of study (Lester et al., 2007). On the other hand, as far as we know, this is the first time that the relationship between the fecundity of species (as a proxy of the number of broadcasted particles) and GRS is studied.

The model of Siegel et al. (2003) that we have used to obtain the dispersal kernels of larvae has been successfully used to explain the genetic distance between metapopulations of shore organisms in the along-shore axis (Rivera et al., 2013). According to our Fig. 5.2, besides any other environmental factors, PLD and H are the main drivers of the propagation of larvae from a given point in the coast. This result is in agreement with the work of Selkoe and Toonen (2011), who used empirical data to describe the relationship between PLD and the connectivity between

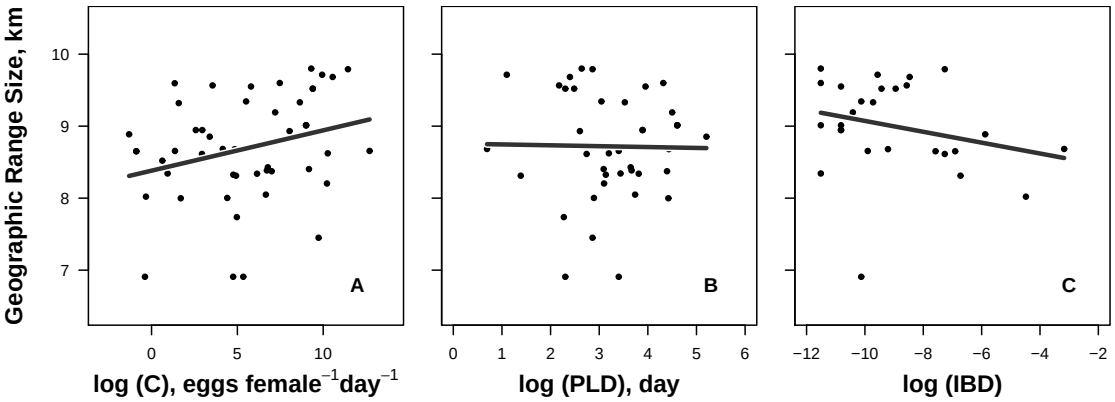

Figure 5.3: Relationship between Geographic Range Size (GRS) and: A) the daily offspring production rate (C); B) the Planktonic Larval Duration (PLD); C) the Isolation by Distance (IBD) slope.

populations, assuming a stepping stone model of dispersion of individuals. However, given that the average dispersal distance is the parameter of the distribution that determines the connectivity among populations, and that the offspring production rate does not affect the displacement of the dispersal kernel, we do not expect C to affect the population connectivity.

Considering that species with large GRS are good colonisers with high spreading capacity, the existence of a relationship between population connectivity and GRS would give support to the hypothesis that larval dispersal is an effective mechanism underpinning the geographic extension of species. Given the difficulty to track individual larvae in the marine environment, population connectivity is usually compared to the genetic structure between populations. The "isolation-by-distance" (IBD) slope (Wright, 1943) is a commonly used genetic metric of dispersal that represents the genetic connectivity among neighbour populations in relation to the distance. In our data set, IBD data were compiled from the work of Selkoe and Toonen (2011), and it has been used to test the relationship between the genetic connectivity among populations and GRS (Fig. 5.3C). Although the scatter in the data is high and there is no significant correlation ($p.val = 0.197$), interestingly, the relationship between these variables is negative, suggesting that populations of species with large GRS are better connected than species with a more restricted range of occurrence. This finding suggests that the dispersive capacity of benthic marine organisms might be linked to the GRS of the species. The previous work of Lester et al. (2007) has reported a weak relationships between GRS and IBD only found at small scales of study, such as small geographical areas and/or within certain taxonomic groups. This result, together with our findings, points to the existence of the relationship between population connectivity and GRS but, probably, the effect of the many environmental factors ruling both IBD and GRS masks the appearance of a clear pattern.

In conclusion, our results point to a role of larval dispersal on the GRS of benthic marine organisms. We should note however that, despite the model in Fig. 5.2 shows a positive influence of both PLC and H on the dispersion of larvae from a given point, when analysing empirical data the sign of the relationship of these variables with GRS is opposite (Fig. 5.3A and 5.3B). This result could be caused by the complex relationship between PLD and fecundity in benthic marine organisms (Chapter 3). Hence, the existence of a trade-off between PLD and fecundity imposes a limit in the dispersive ability of planktonic larvae. In this manner, organisms with short PLD are able to broadcast a high number of propagules, but when PLD is increased the number of propagules should decrease. Aiming to analyse if the effect of H and PLD can be considered independently on GRS, we corrected it dividing GRS by C ($GRS * C^{-1}$). Again, we did not find a significant relationship between this variable and PLD ($p.val = 0.560$), what suggests the influence of other factors except of larval dispersal to define GRS.

As pointed out by Mora et al. (2011), the hypothesis that PLD rules GRS in benthic marine species with planktonic larvae is intuitively attractive. However, despite many works have tried to find a relationship between both variables, the results have been contradictory, and still it has not been demonstrated a clear positive influence of PLD on GRS. The explanations to this lack of relationship are varied, from a question of scale of study and the influence of a pool of variables adding noise to the relationship (Lester et al., 2007), to the existence of a strong network of larval connectivity mediated by ocean currents, which allows species with short PLD to reach very distant points in the ocean (Mora et al., 2011). This work has shown other possible cause of lack of a clear relationship between PLD and GRS based on a trade-off between PLD and fecundity. According to the results presented in Chapter 3, the relationship between these variables could be quite complex and variable among marine taxa, but in general, species with long PLD tend to have a lower number of broadcasted particles. For the organisms considered in this study, despite we could not correct both variables for the effect of temperature, it seems to be a negative, but not significant, relationship between PLD and C. This trade-off could explain the lack of a relationship between PLD and GRS, as it is hard to disentangle the effects of PLD and C. In any case, it seems that PLD is not the unique factor determining the dispersal ability of larvae from a given point of the coast (Fig. 5.2) and hence, works on the relationship between larval dispersal and GRS in marine organisms should not only consider PLD, but also the offspring productivity of populations as a proxy of the number of planktonic propagules. Finally, we would like to highlight that the complexity of GRS makes hardly difficult to analyse the effect of a single variable on it, and even more considering that some of the variables can be correlated or traded-off. For this reason, despite we have presented some non-significant relationships, we believe that the patterns found are consistently pointing to the influence of larval dispersal on GRS. In conclusion, the influence of the number of particles released (which could be traded-off with PLD), should be further considered in works on the determinants of GRS.

5.3 Acknowledgements

This work was partially funded by Theme 6 of the EU Seventh Framework Program through the Marine Ecosystem Evolution in a Changing Environment (MEECE No. 212085) and project CONSOLIDER Malaspina 2010 funded by Spanish National I+D+I Plan. J. B. was funded with a PhD fellowship from the Instituto Español de Oceanografía.

5.A Appendix 5.A

http://www.repositorio.ieo.es/e-ieo/handle/10508/1588

General Discussion

Contents

5.2 The validity of the Metabolic Ecology

As it has been shown through the different chapters of this Thesis, the Metabolic Ecology uses scaling relationships based on elemental principles of physics and chemistry to make predictions about the flow of energy and materials trough ecological systems. This predictions allow ecologists to model the role of organisms and their interaction with the environment, as well as to understand the functioning of populations, communities or ecosystems when integrating the metabolic requirements of individual organisms at higher levels of biological organisation. Albeit the predictions made by the Metabolic Ecology are still focus of debate (e.g. Makarieva et al. (2004); Glazier (2006); Duncan et al. (2007); Isaac and Carbone (2010)), and despite the objectives of this dissertation seem to point to the opposite direction, this Thesis aims to reveal its wide usefulness and validity. Hence, in this work, there have been several results in agreement with the theoretical ground of Metabolic Ecology that should be mentioned.

One of the most outstanding results presented here giving support to the Metabolic Ecology is that the curvature of most of the traits analysed in Chapter 1 is coincident with the curvature found for the basal metabolic rate by Kolokotrones et al. (2010). Taking into account the very different sources of data used in this chapter and the variety of traits analysed, it can not be a chance result that the only two convex curvatures shown in Fig. 1.1 correspond to the two traits expected to have convex curvatures according to the Metabolic Ecology: life span and population density. The curvature of some of these traits have already been mentioned or discussed before (Damuth, 1981; Charnov and Ernest, 2006), but this is the first time that it is explained using a mechanistic approach.

It is worth to mention also that the pervasive quarter-power scaling exponents predicted by the Metabolic Theory of Ecology have been found repeatedly through the different chapters of the Thesis. Hence, the slopes of the traits considered in Chapter 1 are extremely close to the 1/4 multiples predicted by the Metabolic Theory of Ecology (see Table S1.1 for comparison of expected and observed slopes). Additionally, when considering the developmental time of organisms in Chapter 2, the 1/4 exponent appears in the relationship between the temperature-corrected ODT and the offspring mass (Figs. 2.2A and S2.1A). Similarly, the effect of temperature, the other main responsible of the metabolic demands of organisms, is also captured by the Boltzmann's factor in the way predicted by the Metabolic Theory of Ecology (Fig. 2.2B and Fig. 3.2). These relationships show the effect of temperature on traits corrected by body size. Using logarithmic plots, the slopes of these relationships are estimates of the value of the activation energy for metabolic reactions (E), all of them falling close to the theoretical predicted value of 0.62 eV (Gillooly et al., 2001).

In conclusion, this Thesis provides new evidences to support the statements of the Metabolic Ecology in general, and the Metabolic Theory of Ecology in particular. The match between the theoretical predictions and the observed ecological patterns demonstrates that the Metabolic Ecology can be used as a tool to infer many ecological responses of organisms to environmental changes (Duarte, 2007). This is specially important in the present scenario of fast climate change, where the responses of organisms to the global warming are hard to unpredict. Changes in the behaviour, physiology, life histories, reproductive strategies, inter-specific relationships, etc. are expected to occur amongst organisms subject to these environmental characteristics. Understanding the way in which organisms interact with their environment and how the environmental changes influence their biology is the best way to predict the functioning of ecosystems and forecast future ecological scenarios. For these reasons, and according to the results presented here, the field of Metabolic Ecology should be considered as a valuable tool allowing to predict, at least in part, the evolution of ecosystems under changing conditions.

5.3 The limits of Metabolic Ecology

Along the chapters of this Thesis, it has been demonstrated the validity and accuracy of the predictions made by the Metabolic Ecology. As commented in the introduction, these predictions provide base lines from which to measure the effect of factors ruling the final performance of organisms in their environment. The variation observed makes possible to identify specific functional groups or phylogenetic lineages that do not match the general patterns of energy usage, and analyse hence the reasons for these exceptions. The existence of organisms that do not match these patterns indicates the impossibility of physiology to explain all the variation found in comparative analysis, establishing the limits of predictability of Metabolic

Ecology. In this sense, through the different chapters of this Thesis, it has been observed that the scatter of the data of ecological traits was more different from the predictions of Metabolic Ecology in two scenarios: when the level of biological organisation increased, and when the level of complexity of the analysed trait increased in terms of life histories or environmental effects.

5.3.1 The influence of the level of biological organisation on the predictability of Metabolic Ecology

The effect of the level of biological organisation on the match of the data to the predictions of Metabolic Ecology has been considered in Chapter 1. In this analysis of the transmission of the curvature of metabolism (Kolokotrones et al., 2010) to other different traits, eight different metabolic-based traits were considered, six of them measured at the individual and two (population growth rate, and population density) at the population level of biological organisation. Through a visual analysis of the capacity of body size to explain the inter-specific variability in these traits (Fig 1.1) it is obvious that the scatter of the points of the traits at the population level (panels G and H) are higher than for the traits analysed at the individual level (see the drop of the coefficient of determination, r^2, in Table S1.2). Additionally, the curvature of metabolism is noticeable at all the traits except of population density, where it resulted to be not significant (Table S1.3). The specific reasons for what population density should be considered carefully in scaling analysis are discussed in Chapter 1, but this result is indicative of the increase of scatter of the data when evaluating traits at higher level of biological organisation.

Several works have investigated the propagation of metabolic scaling laws from molecules to ecosystems with positive results (e.g. Enquist et al. (2003); Ernest et al. (2003); Savage et al. (2004*a*); Economo et al. (2005)). These works are in agreement with the principal statement of Metabolic Ecology and demonstrate that the mechanisms ruling the scaling of metabolism at the individual level are the same than those ruling the scalings of populations and ecosystems. However, it should be noted that the number of factors involved in the ecology of traits measured at higher levels of biological organisation is higher than that of traits measured on individuals. Hence, the network of interactions between selective pressures, life histories, environmental constraints, etc. occurring at higher levels of organisation complicates the measurements of traits such as population growth rate or population density, being easier to measure traits at the individual level such as life span, or the heart rate. The difficulty to measure different traits should influence also the variability of data reported by different data sources on the same trait. This is not a minor topic in comparative ecology that has been considered in Chapter 1. Here, it has been shown that this variation can be considerable even for a relatively easy-to-measure trait such as basal metabolic rate. Considering that the variability of the measurements should theoretically increase with the complexity of the traits, it

is worth to note that measurements of traits at high levels of biological organisation should be considered carefully in comparative analysis.

5.3.2 The scope of Metabolic Ecology through the effect of life histories

Other phenomenon observed through the different chapters of this Thesis is that, within the individual level of biological organisation, the Metabolic Ecology looses part of its predictive capacity when the complexity of the evaluated traits increases in terms of life histories or environmental factors. As mentioned before, this observation determines part of the scope of Metabolic Ecology, and is the reason for what the five chapters of the Thesis are organised by increasing complexity in terms of life histories and involved environmental factors. In this sense, Chapter 1 represents by its own a good example of the importance of the complexity of the traits in terms of life histories. Given that this analysis is based on mammals, no temperature correction is needed for the evaluated traits, and all the variation due to physiology is expected to be captured by body size. For this reason, the amount of inter-specific variance in basal metabolic rate and field metabolic rate explained by body size is very high (Figs. 1.1A and 1.1B) but becomes weaker to explain the inter-specific variation at other traits such as life span or productivity (Tables S1.2 and S1.3). The effect of the variable difficulty to measure the different traits could be in part responsible for the worst fit of the data to the expectations of Metabolic Ecology. However, it seems to be obvious also for traits that are easy to measure such as life span.

The ability of Metabolic Ecology to explain the duration of development of any living organism was tested in Chapter 2. The duration of development, is considered here as the elapsed time from the fertilisation of the ovocyte to the end of maternal cares or resources for the offspring (yolk exhaustion in fish, weaning in mammals). In consequence, this trait is ruled by physiology but also by the many different reproductive strategies of the organisms considered (from zooplankton to fish and mammals) (Fig. 2.1). The corollary of this work is that introducing the relationship between size and number of offspring described for mammals by Charnov and Ernest (2006), with a correction for the temperature in ectotherm animals, the relationship between offspring development time and body size falls close to a single universal straight line. This result evidences that considering the effect of the different life histories present among organisms, it is possible to account for the deviations of specific groups from the premises of the Metabolic Ecology.

The same conclusion is obtained for the duration of the planktonic larval phase (PLD) in Chapter 3. As we mention before, the offspring development time studied in Chapter 2 is considered the period until the end of maternal cares or resources. These maternal cares diminishes the interaction of individuals with environmental pressures, what decreases the importance of environmental factors ruling PLD.

However, in the case of the planktonic phase of benthic marine organisms, organisms are subject to many environmental pressures that have originated the many different larval forms existing through the evolution. For this reason, PLD is considered a more complex trait than offspring development time in terms of life histories. This complexity, and the many evolutionary forces acting on PLD made the scaling between PLD and larval size a recurrent topic in the field of marine ecology. The sign of this relationship is controversial, being positive from the point of view of Metabolic Ecology, and negative according to the work of Vance (1973*b*)). As shown in Chapter 3, this controversy can be explained taking into consideration the different larval growth strategies present among organisms. In this case, these factors are able to mask or hide the expected scalings of organisms predicted by Metabolic Ecology, what demonstrates again the importance of accounting for the effect of the life histories in comparative analysis of metabolic-based traits.

In conclusion, knowledge on the life histories and the main environmental factors acting on organisms is crucial when analysing scaling relationships based on physiology. This information can be critical to explain deviations of the data from the predictions of Metabolic Ecology, and could help to understand the performance of specific phylogenetic or functional groups. Accounting for information from both theoretical frameworks makes possible to obtain universal patterns such as the offspring-development-time/offspring-number trade-off described in Chapter 2.

5.3.3 The importance of physiology on complex ecological traits

As we have mentioned before, the metabolism of individuals determines the pace of life and hence, the way in which organisms relate to their environment. For this reason, even when considering traits with no apparent relationship with metabolism, some general patterns predicted by the Metabolic Ecology seem to hold and explain a considerable amount of inter-specific variance. These are the cases shown in Chapters 4 and 5, where it has been demonstrated that the effect of larval physiology must not be neglected when evaluating traits where metabolism in not directly involved. In fact, the dispersion of larvae in the marine environment (Chapter 4) is usually modelled as the dispersion of passive particles drifted by ocean currents (Siegel et al., 2003). Considering the findings in Chapter 4 and some recent literature pointing to the direction that planktonic larvae are able to modify their position by active swimming (Genin et al., 2005), new theoretical models for larval dispersal should be defined. These new models should consider the physiology of larvae within individual based models incorporating the effect of larval behaviour and the strength and direction of ocean currents. Little is known yet on the ability of larvae to swim and face the oceanic currents. Hence, for example, if swimming is fed by metabolism, it should have a temperature and size dependence on the position of larvae in the water. In the work presented in Chapter 4, the ability to swim of planktonic larvae is calculated based on larval size following the equations

of Huntley and Zhou (2004). However, the effect of temperature or oxygen concentration on the motility of plankton on the water column has not been studied to the date. Considering the premises of the Metabolic Ecology, high temperatures increase the metabolism of organisms, what could benefit the motility of plankton. However, the increase of temperature reduces the oxygen concentration of water, what could have an opposite effect on the movement of zooplankton. In order to develop feasible models for larval dispersal in the ocean, these considerations need to be more profoundly analysed, with validations *in situ* and laboratory experiments considering the physiological responses of larvae to environmental changes.

5.4 Phylogenetic analysis

The necessity to perform phylogenetic comparative analysis in studies of metabolic scaling is controversial, with authors claiming the necessity to provide these analysis (Blackburn and Gaston, 1998; Garland et al., 1999) and others questioning their validity or utility (Ricklefs and Starck, 1996; Björklund, 1994; McNab, 2008). Supporters consider that accurate statistical testing in comparative ecology needs to account for phylogenetic information, because closely related species share characteristics that generates non-independence of the data and hence, individual species cannot be regarded as independent data points. In this way, some simulations have shown that ignoring the "phylogenetic signal" of the data can lead to erroneus conclusions (Martins and Garland, 1991). However, these phylogenetic comparative analsys are also subject to criticism, specially for two reasons: first because if the variation of a character through some phylogenetically-related species is related to the phylogeny, this is irrelevant given that closely related species will tend to occupy similar ecological niches (Freckleton et al., 2002). And second, because the most commonly used method of evolution is based on a constant rate of variability through the different branches of the phylogeny. This constant-variance process is known as "Brownnian motion" and the results obtained are hence subject to the validity of this model of evolution, which is not always appropriate. The phylogenetic analysis performed in this Thesis are presented in order to replicate previous analysis from the literature (e.g. Kolokotrones et al. (2010); Levitan (2000)) or because a phylogenetic signal (λ) was detected in the evaluated traits (λ between 0 and 1).

Conclusiones

1. El tamaño corporal, como aproximación de la tasa metabólica de mamíferos, explica buena parte de la variabilidad inter-específica observada al evaluar distintas variables ecológicas al nivel individual o poblacional de organización biológica.

2. La curvatura del metabolismo de los mamíferos es percibida en otras variables ecológicas tanto al nivel individual como poblacional de organización biológica. Este resultado refuerza los principios teóricos de la Ecología Metabólica, que considera al metabolismo como la fuerza motriz de los recursos individuales a través de los distintos niveles de organización, determinando por tanto la interacción entre los organismos y su medio.

3. Al aumentar el grado de complejidad biológica de las variables estudiadas, la capacidad del tamaño corporal de explicar la variabilidad inter-específica disminuye. Esto sugiere, que a mayor grado de complejidad biológica, otros factores distintos de la fisiología cobran importancia para determinar la ecología de especies y poblaciones.

4. Al considerar variables ecológicas medidas al nivel individual de organización biológica, la capacidad del tamaño corporal de explicar la variabilidad inter-específica en mamíferos también parece disminuir cuando la complejidad de las variables, en términos de historias de vida, aumenta.

5. El modelo basado en la Ecología Metabólica para el tiempo de desarrollo no es capaz por si solo de explicar las diferencias en tiempo de desarrollo existentes entre grupos animales con distintas estrategias reproductivas. Sin embargo, un modelo conjunto que considera también el balance entre el número y el tamaño de la prole es capaz de capturar esa la variabilidad. Al incorporar el efecto de las diferentes historias de vida a las premisas de la Ecología Metabólica, la desviación de algunos grupos filogenéticos o funcionales de los patrones generales esperados en función de su fisiología disminuye, obteniendo patrones que parecen cumplirse de forma general.

6. Uno de los patrones generales observados al incorporar el efecto de las estrategias reproductivas al modelo basado en la Ecología Metabólica para el tiempo de desarrollo es que organismos que producen mucha descendencia tardan menos en desarrollarse que organismos que producen poca descendencia.

7. El tiempo de desarrollo larvario en organismos bentónicos está determinado

por factores tanto fisiológicos (masa larvaria y temperatura) como de estrategias de vida (distintas estrategias de crecimiento larvario).

8. El escalamiento alométrico existente entre el tiempo de desarrollo larvario y la masa de la larva es dependiente de las estrategias de crecimiento seguidas por las larvas en función de las historias de vida y el ambiente que las rodea.

9. A pesar de su aparente no relación con distintas variables ecológicas, las predicciones de la Ecología Metabólica pueden resultar de gran ayuda al describir estados basales fisiológicos de los organismos. Algunas de estas variables ecológicas resultan por tanto relacionadas con la temperatura o el tamaño corporal de los organismos de manera similar a lo predicho por las leyes de la Ecología Metabólica, y por tanto estas relaciones pueden ser usadas como base para establecer modelos (o complementar otro tipo de modelos ya existentes) para esas variables ecológicas.

10. La dispersión de larvas microscópicas en el océano está mediada en parte por la capacidad de movimiento activo de las mismas. Así, además de la dirección y fuerza de las corrientes oceánicas, la concentración de alimento, la temperatura o la concentración de oxígeno parecen influir en el grado de agrupación de las larvas en el eje costa-oceáno. Conociendo por tanto la fisiología de las larvas y su relación con las variables físicas del medio supone una mejora de los modelos clásicos de dispersión larvaria basados en partículas inertes.

11. El rango de dispersión geográfico de las especies bentónicas marinas parece estar ligado a la capacidad dispersiva de las larvas, lo cual a su vez está determinado por la duración del periodo larvario y el número de propágulos liberados. Este resultado refleja la importancia de la fisiología y las estrategias de vida en una variable ecológica poco relacionada, en principio, con la fisiología de las especies.

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