SPRFMO
South Pacific Regional Fisheries Management Organisation

13th MEETING OF THE SCIENTIFIC COMMITTEE

8 to 13 September 2025, Wellington, New Zealand

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Peru

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INSTITUTO DEL MAR DEL PERU
CIENCIA Y TECNOLOGIA

When hatching fails: A bioenergetic approach to the early life stages of jumbo flying squid (*Dosidicus gigas*)

by

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1 Introduction

Cephalopods are invertebrate animals that have spread to almost all marine ecosystems and show diversity in their life histories, from species that spawn only once and then die, to species that experience more than one reproductive event (Robin *et al.*, 2014).The ecology of these organisms undergoes a transition from the egg stage to the adult stage (Vidal & Shea, 2023), with some species exhibiting ontogenetic migrations (Alegre *et al.*, 2014). Within the Humboldt Current System, the jumbo flying squid (*Dosidicus gigas*) is a species of particular interest due to its ecological and economic importance (Tam *et al.*, 2008), with annual catch volumes of approximately half a million tons since 2009 (PRODUCE, 2022).

The jumbo flying squid, like other species of ommatrephids, thrives in diverse environmental conditions that vary in time and space. These conditions are normally associated with oceanographic upwelling regimes, also known as upwelling systems (Anderson & Rodhouse, 2001). The California Current System and the Humboldt Current System contain the most representative populations in terms of biomass (Rodhouse, 2008; Argüelles & Tafur, 2010). However, these large fisheries have not been immune to collapse (Argüelles *et al.*, 2001; Frawley *et al.*, 2019). Then, the species' high resilience has enabled its recovery following adverse periods, particularly those associated with significant temperature increases, such as El Niño events (Ibáñez *et al.*, 2015).

Dosidicus gigas, the largest and most abundant squid species in the neritic zone of the ocean, is a notable example. Its maximum mantle length is 1.2 meters and its total weight is approximately 65 kilograms (Ibáñez *et al.*, 2015; Csirke *et al.*, 2018). This species exhibits sexual dimorphism, with up to three size ranges/groups recognized according to sex and maturity (Nigmatullin *et al.*, 2001). *Dosidicus gigas* is a fast-growing predator with high energy demands; it is a species associated with highly productive water masses, such as upwelling systems. The average life expectancy of these organisms is one year, at which point they reach their maximum level of maturity during the spawning process. At this stage, the organism's accumulated energy is derived from a single reproductive event. Subsequently, the organism perishes, thus meeting the definition of a semelparous organism (Nigmatullin *et al.*, 2001; Rocha *et al.*, 2001). The largest individuals have been observed to extend their life cycle to two years (Nigmatullin *et al.*, 2001). It has been observed that variations in temperature and food availability over space and time could potentially explain changes in population dynamics, including maturation, growth rates, and migration patterns. This phenomenon could result in individuals maturing earlier and reaching smaller sizes in warm conditions, and subsequently maturing later and reaching larger sizes with more extensive migration ranges in cold conditions (Keyl *et al.*, 2008; Tafur *et al.*, 2010).

The variable size until reaching maturity, the temporary decoupling between females and males in the formation of reproductive tissue to manage their energy, and changes in the sex ratio are the characteristics that enable the giant squid to adapt to the environmental variability in which it develops. The reproductive strategy of the species is characterized by the release of successive spawning pulses throughout the year, with a total of 10 to 14 batches. The highest number of releases occurs during the spring months, and the reproductive potential of the largest females is estimated to reach 32 million oocytes. This phenomenon is directly related to the length of the mantle, with females exhibiting a dominance ratio of up to 24:1 compared to males. The fact that only large individuals have been found south of the colder Humboldt Current System thus far lends further support to the hypothesis that maturity size is linked to water masses, i.e., temperature and food availability (Tafur *et al.*, 2010).

As is the case with the vast majority of marine species, the early life stages (i.e., eggs and paralarvae) are subject to elevated levels of natural mortality due to environmental conditions. Furthermore, experiments involving artificial fertilization with specimens captured in the Humboldt Current System have demonstrated that in conditions of warmth equivalent to or greater than 25°C, the hatching mechanism is compromised (Yatsu *et al.*, 1999; Staaf *et al.*, 2011), thereby indicating that the inadequate recruitment subsequent to extreme environmental events is associated with their intensity and duration. However, in the northern hemisphere, the weak recruitment following extreme environmental events is associated with their intensity and duration. The hatching mechanism is known to malfunction at temperatures of 29°C (Camarillo-Coop *et al.*, 2011), thereby suggesting a correlation between the intensity and duration of extreme environmental events and weak recruitment. However, in the northern hemisphere, paralarvae have been reported in temperatures as high as 29°C. The impact of environmental variability on their early life stages, particularly the availability of food (i.e., zooplankton) (Csirke *et al.*, 2018), suggests a medium vulnerability of this species in Peru (Ramos *et al.*, 2022). Also, the observation of phenotypic plasticity indicates the potential for survival in adverse environmental conditions (Ferreri, 2014). Given that, akin to other cephalopods, they incur high energy expenditures for vital processes such as maintenance, growth, and reproduction, this information is instrumental in formulating hypotheses concerning the impact of the environment on individual organisms (Wells & Clarke, 1996). The dynamic energy budget (DEB) theory stands as a prominent model in the representation of the life cycle of numerous species and possesses the capacity for integration with other ecosystem models (Kooijman, 2009).

Therefore, it is imperative to define the concepts related to the life cycle of Dosidicus gigas in order to formulate the appropriate inquiries regarding the mechanisms that can be evaluated at each stage. It is widely accepted that cephalopods undergo the following stages: embryo, paralarva, juvenile, subadult, and adult (Vidal & Shea, 2023).

- Embryo: Commences with fertilization and culminates in hatching. Cephalopods are known to produce vitellus, a structure that is rich in proteins, carbohydrates, and lipids. This vitellus is contained within an egg, which is a specialized structure that allows for the development of the cephalopod offspring.

- Paralarva: Begins with the hatching of the egg and ends when the individual loses its adaptations for planktonic life. In this phase, the individual differs morphologically from adults.

- Juvenile: This phase culminates when all the morphological traits that define the species (with the exception of those related to sex or size) are fully manifested, although the morphological proportions may deviate from those observed in the adult phase. At this stage, ontogenetic development is considered to be complete.

- Sub-adult: The organism has reached the final adult stage of development. While it has not yet attained its maximum size, the specimen begins to develop sexual organs and increase its mass.

- Adult: The development of these organisms reaches its zenith with the capacity to spawn and release gametes at the culmination of their life cycle.

In this research, the planktonic phase of the species will be the focal point. During this phase, the organism is incapable of assimilating food and is influenced by ocean currents and temperature in order to successfully reach the hatching process.

2 Methods

2.1 3D Lagrangian model

An Individual-Based Model (IBM) is a mathematical representation of a population or community. It simulates the behavior of individuals and their characteristics (state variables) to create a dynamic and complex system. The based IBM utilized in this study was the Lagrange tool, designated as Ichthyop, which was developed by Lett *et al.* (2008) in version 3.2. A protocol was developed by Grimm *et al.* (2006, 2010) for this type of IBM, as described by Grimm, with the objective of investigating the dynamics of embryonic development and hatching success of *Dosidicus gigas* eggs.

Purpose

Evaluate the effect of ocean currents and temperature on the dispersion and embryonic development of Dosidicus gigas within the Peruvian Exclusive Economic Zone (EEZ).

Entities and state variables

The model included two types of entities: the environment and individuals (virtual particles). The environment was represented by biogeochemical simulations of Coastal and Regional Ocean COmmunity model (CROCO, Hilt *et al.* (2020); Shchepetkin & McWilliams (2005), which provide the physical forcing: ocean currents (ms^{-1}). Individuals were characterized by the following state variables: age (d), position (longitude, latitude, depth), and the DEB model variables (Reserve, E; Structure, V; maturity, E_H).

The hydrodynamic model configuration extended from 22°S to 5°N in latitude and from 96°W to 70°W in longitude, with a horizontal resolution of 10 km and 32 vertical levels. The bathymetry was obtained from the $STRM30$ database (Becker *et al.*, 2009). The simulation covered the period from 1980 to 2000.

Inicialización

In each simulation (each year, each month), a total of 6,000 individuals were released at fixed positions, distributed evenly within 200 miles of the Peruvian coast (EEZ). Five spawning depths were set: ($5m$, $20m$, $35m$, $50m$, and $65m$), based on the vertical distribution of paralarvae samples. Although spawning at greater depths has been documented, it has not been taken into account in this study because the ocean is more stable at greater depths, which would not significantly affect dispersion patterns.

Transport model

To simulate particle transport, virtual individuals were advected using a trilinear interpolation scheme of the velocity fields derived from CROCO, in time and space, and using a numerical Euler forward scheme with horizontal diffusion as used by Peliz *et al.* (2007).

2.1.1 Growth model: embryonic development

The following description is a simplification of the *Dosidicus gigas* DEB model developed at *add_my_pet* since we only focus on the embryo stage, up to the moment before the individual begins to assimilate food. We implement these equations in the routines of the Lagrangian tool by Ichthyop (Lett *et al.*, 2008) to develop Ichthyop-DEB (Flores-Valiente *et al.*, 2023).

Forcing variables

T Temperature (K) is the temperature of the water surrounding the individual (modeled by CROCO-PISCES), expressed in Kelvin degrees.

Initial conditions of state variables (egg stage)

An individual's age starts at zero at the time of spawning.

Symbol	Value	Unit	Definition
$E0$	0.99	J	Initial Reserve
$V0$	0.000001	cm^3	Initial Structure
E_{H0}	0	J	Accumulated energy invested in development

Primary parameters

Primary parameters (rates are at reference temperature $T_1 = 293K$ $(= 20°C)$)

Symbol	Value	Unit	Definition
T_A	9000	K	Arrhenius temperature
T_L	279	K	Lower temperature limit
T_H	294	K	Upper temperature limit
T_{AL}	20000	K	Arrhenius temperature for the lower limit
T_{AH}	95000	K	Arrhenius temperature for the upper limit
E_H^b	0.0566	J	Maturity threshold at birth (first feeding)
L_b	0.0299	cm	Volumetric length at birth (estimated at $f = 1$)
$\{\dot{p}_{\text{Am}}\}$	1950.6	$J.cm^{-2}.d^{-1}$	Maximum surface-area-specific assimilation rate
$[E_G]$	5500	$J.cm^{-3}$	Structural costs by volume
$[\dot{p}_M]$	345.04	$J.cm^{-3}.d^{-1}$	Volume-specific somatic maintenance rate
κ	0.7354	-	Fraction of the mobilized reserve allocated to soma
$\dot{k}_J$	0.002	d^{-1}	Maturity maintenance rate coefficient
$\dot{v}$	0.02134	$cm.d^{-1}$	Energy conductivity

Temperature correction

Some parameters are corrected based on temperature according to the following equation (Kooijman, 2009).

$$C_T = exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)\left(\frac{1+exp\left(\frac{T_{AL}}{T_1}-\frac{T_{AL}}{T_L}\right)+exp\left(\frac{T_{AH}}{T_H}-\frac{T_{AH}}{T_1}\right)}{1+exp\left(\frac{T_{AL}}{T}-\frac{T_{AL}}{T_L}\right)+exp\left(\frac{T_{AH}}{T_H}-\frac{T_{AH}}{T}\right)}\right)$$

Where T_1 is the reference temperature (at which the parameters for energy flows were estimated), T_A is the Arrhenius temperature, and T_{AH}, T_{AH}, T_L, T_H are constants used to define the shape of the temperature correction curve.

$$\{\dot{p}_{\text{Am}}\}_T = C_T\,\{\dot{p}_{\text{Am}}\}_{T_1}$$

$$[\dot{p}_M]_T = C_T\,[\dot{p}_M]_{T_1}$$

Energy fluxes (Jd^{-1})

$$\dot{p}_{\text{A}} = f\,\{\dot{p}_{\text{Am}}\}_T\,V^{2/3}$$

Assimilation.

$$\dot{p}_{\text{M}} = [\dot{p}_M]_T\,V$$

Volume-related somatic maintenance.

$$\dot{p}_C = \frac{E\left([E_G]\frac{C_T\{\dot{p}_{\text{Am}}\}_T}{[E_m]}V^{-\frac{1}{3}}+[\dot{p}_M]_T\right)}{\kappa\left(\frac{E}{V}\right)+[E_G]}$$

Energy mobilization.

$\dot{p}_G = \kappa \dot{p}_C - \dot{p}_\mathrm{M}$ Energy directed toward structural growth.

$\dot{p}_J = V \frac{(1-\kappa)}{\kappa} [\dot{p}_M]_T$ Maturity maintenance.

Hatching test

if $E_H b \geq E_H$ If the energy threshold for the first feed is exceeded.

$hatched = 1$ The individual hatched successfully.

Differential equations

$\frac{dE}{dt} = \dot{p}_\mathrm{A} - \dot{p}_C$ Reserve Dynamics.

$\frac{dV}{dt} = \frac{\dot{p}_G}{[E_G]}$ Structural Dynamics.

Integration

$$E(t+\Delta t) = E(t) + \frac{dE}{dt}\Delta t$$

$$V(t+\Delta t) = V(t) + \frac{dV}{dt}\Delta t$$

Con $\Delta t = 0.083d\,(= 2horas)$

Simulations

Each simulation lasted 60 days. An hatching test was performed at each time step.

3 Results

3.1 Temporal variability in hatching success

Hatching success, defined as the percentage of individuals that exceed the energy threshold $E_H^b = 0.0566\ J$ (prior to the first feeding), was calculated for each year and each month (Fig. 1). The El Niño effect (92/93 and 97/98, temperatures above 25 °C) had a clear negative effect on embryonic development and hatching in Dosidicus gigas. The 82/83 event caused low hatching rates, with only 40% hatching success, while in the 97/98 event, rates were as low as 25%. It was also observed that in years that did not experience an extraordinary El Niño, hatching rates were above 80%.

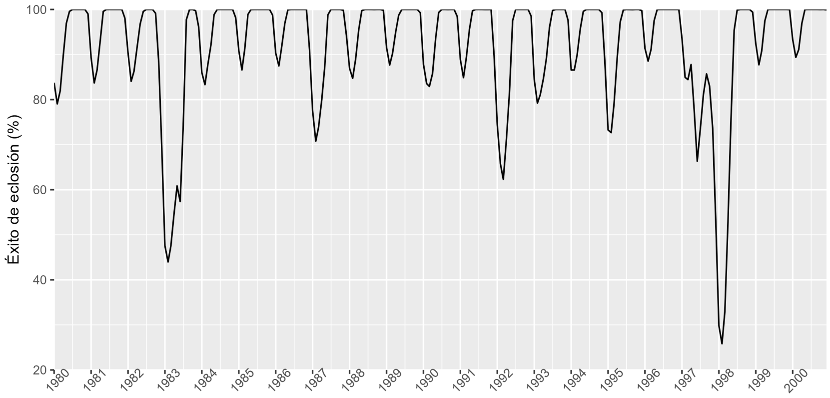

Fig. 1: Hatching success rate (%) of Dosidicus gigas embryos, simulated by Ichthyop-DEB, between 1980 and 2000.

Spawning depth played an important role in hatching success (Fig. 2). Individuals spawned in shallow layers (5 meters) experienced low hatching rates, with no apparent additional effect from El Niño. Those individuals spawned at depths greater than 20 meters showed higher hatching rates and the negative effect of El Niño. It was observed that at spawning depths greater than 50 meters, a minimum of 50% hatching success could be assured.

The distance to the coast (in km) did not show a significant effect on hatching success (Fig. 3). However, it was sensitive to the effect of the El Niño event.

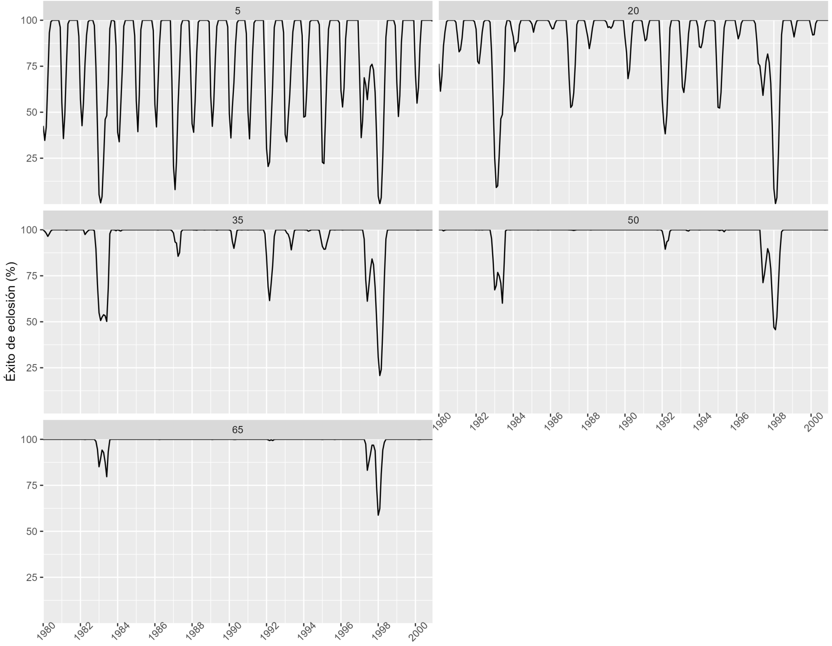

Fig. 2: Hatching success rate (%) of Dosidicus gigas embryos, simulated by Ichthyop-DEB, between 1980 and 2000 at different spawning depths (in meters).

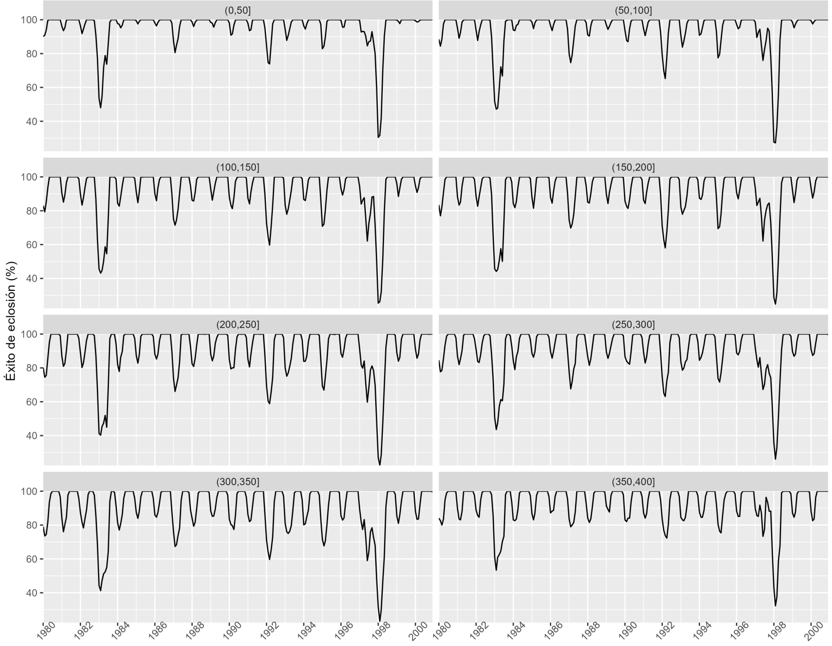

Fig. 3: Hatching success rate (%) of Dosidicus gigas embryos, simulated by Ichthyop-DEB, between 1980 and 2000, depending on distance from the coast (in km).

3.2 Spatial (latitudinal) variability of hatching success

Latitudinally, the hatching success of Dosidicus gigas was negatively affected by El Niño events, with values close to zero during 82/83 and 97/98 from 3° to 20° S (Fig. 4).

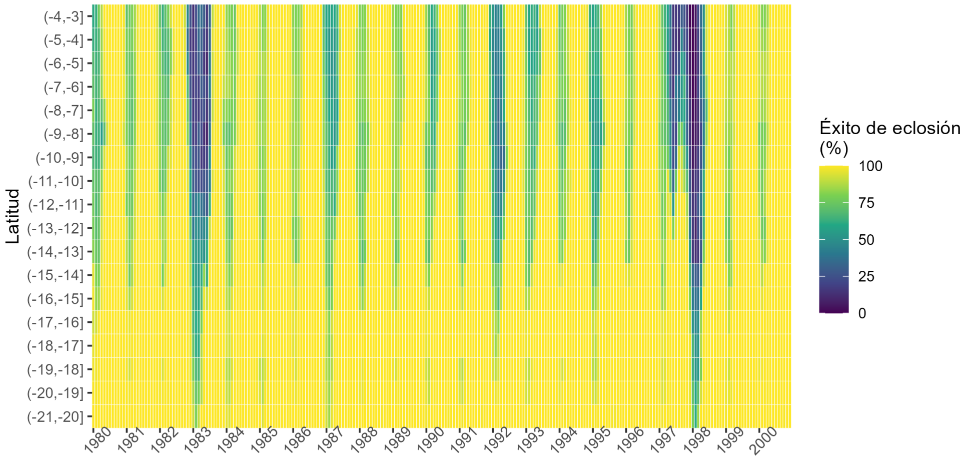

Fig. 4: Hovmöller diagram of the hatching success rate (%) of Dosidicus gigas embryos, simulated by Ichthyop-DEB, between 1980 and 2000 as a function of latitude.

By including spawning depth, we can see that at depths of 50 meters or more, hatching success could be assured in southern Peru. However, in northern Peru, hatching success would be affected during El Niño events (Fig. 5).

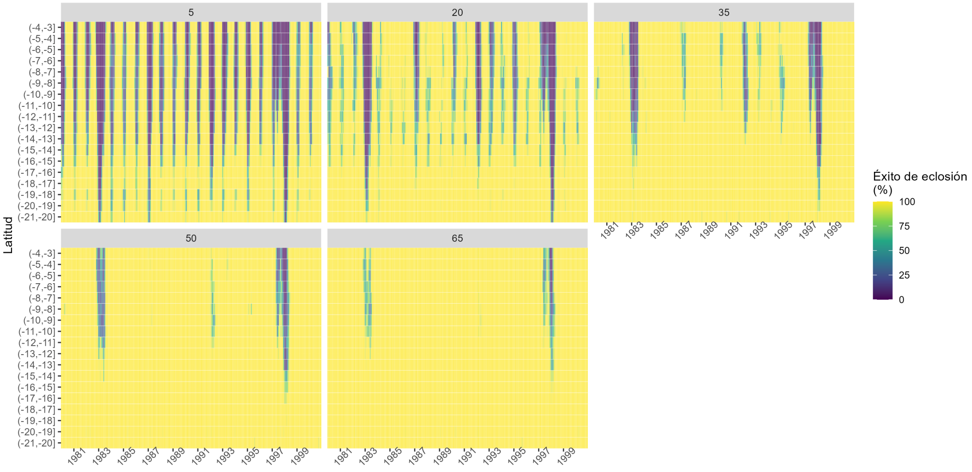

Fig. 5: Hovmöller diagram of the hatching success rate (%) of Dosidicus gigas embryos, simulated by Ichthyop-DEB, between 1980 and 2000 as a function of latitude and at different spawning depths.

4 Conclusions

- According to the literature, temperatures above 25 °C would cause problems in embryonic development, which would subsequently result in hatching failure. Using Lagrangian simulations and a temperature-dependent growth model, we conducted a hatching success test for Dosidicus gigas.

- Hatching success is highly influenced by the extraordinary El Niño event, whose temperatures exceeded 25 °C for several consecutive months, especially in northern Peru.

- The negative effect of El Niño on hatching was particularly evident in the surface layers (5 and 20 meters). On the other hand, distance from the coast did not show a significant effect.

5 Future work

The next step is to complete the simulation time series up to 2024 to assess the effect of El Niño 2023/2024 on giant squid egg hatching.

Subsequently, temperature-dependent growth and food availability during the early life stages of Dosidicus gigas (eggs and paralarvae) will be included.

This section is part of the scientific research for the SPRFMO (South Pacific Regional Fisheries Management Organization), which is 50% complete. IMARPE actively participates each year in the SPRFMO Scientific Meeting, and since 2024, it has taken a special interest in the study of early life stages, not only in giant squid, but also in other species of interest within the framework of the SPRFMO. It is hoped that this work will be complemented in the coming months through a scientific publication.

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