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SHORT REPORT

Inshore spawning grounds of the squid *Doryteuthis gahi* suggest the consistent use of defoliated kelp *Lessonia trabeculata* in Central Chilean waters

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**ABSTRACT**

Coastal spawning grounds of the squid *Doryteuthis gahi* were identified for the first time at three sites in Central Chile during 2014 and 2015. A total of 15 egg masses were collected from between 10 and 15 m depth and brought to the laboratory for evaluating capsular, embryonic and when possible, paralarval characters. Egg capsules from all spawning areas were similar in size (∼25 mm in length) and number of embryos per capsule (∼15). Egg-laying patterns, in addition to field observations, suggest that relatively small *D. gahi* may be using shallow waters in semi-protected environments to reproduce and spawn. Additionally, the differential use of healthy versus defoliated kelp *Lessonia trabeculata* suggests that egg-laying females selectively choose substrata that limit mechanical damage to the fragile egg capsules and that also allow for adequate water flow, which could be reduced in a mass of kelp fronds. These findings highlight the opportunistic behaviour of *D. gahi* which use overgrazed *L. trabeculata*, a condition that is widespread in areas with high herbivory pressure.

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Introduction

Understanding how ecologically and economically important coastal marine species cope with anthropogenically induced environmental changes such as overfishing, increasing temperatures and/or habitat loss is critical for evaluating the synergistic effects of fisheries and climate change on marine ecosystems (Harley et al. 2006). Identifying responses to ecosystem perturbations generally requires long-term datasets in long-lived species of commercial and ecological value (e.g. coastal reef fishes; Hsieh et al. 2009; Field et al. 2010). Nonetheless, responses of short-lived species (invertebrates) to environmental changes have also provided important insights into their ecological functioning under deleterious conditions (see Pörtner 2002; Byrne 2011).

Among invertebrates, cephalopods have a unique suite of life history traits (i.e. semelparity, short generation time, low adult mortality, high food conversion and elevated growth rates; see Arkhipkin 2013). These traits, in addition to the high spatiotemporal heterogeneity of the physical environment observed in the Humboldt Current System (HCS) (Camus 2001; Thiel et al. 2007), provide a valuable model for evaluating how ecosystem changes mediate short-term responses to variable environmental conditions. Nonetheless, for most of the cephalopod species inhabiting this particular environment, ecological and demographic consequences of their early life history traits are as yet unknown (but see Carrasco et al. 2012; Uriarte et al. 2012; Pardo-Gandarillas et al. 2015). For example, the widely distributed long-finned squid *Doryteuthis gahi* (d’Orbigny, 1835), is the only loliginid species that spawns in cold waters of around 5°C (Arkhipkin et al. 2000; Barón 2002; Cinti et al. 2004) and the only one that attaches egg-capsules to ecologically and economically important substrates such as the brown macroalgae *Lessonia* spp. and *Macrocystis pyrifera* (Linnaeus) C. Agardh (Arkhipkin & Middleton 2003; Rosenfeld et al. 2014). Although spawning areas have been previously reported from San Lorenzo Island, Perú (Cardoso et al. 2005; Argüelles et al. 2008), the Falkland (Malvinas) Islands (Arkhipkin et al. 2000) and the Magellanic channels of Southern Chile (Rosenfeld et al. 2014), no other formal records (i.e. *in situ* observations) have provided additional spawning locations throughout the species’ geographic range.

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The supplementary material for this article (Video Clip S1) can be accessed at [https://www.youtube.com/watch?v=y5epnb7cYxs](https://www.youtube.com/watch?v=y5epnb7cYxs)

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Temperate subtidal habitats along the southeast Pacific coast (habitat of D. gahi) are dominated by lush monospecific kelp beds of the brown macroalga Lessonia trabeculata Villouta & Santelices, providing suitable reproduction and feeding grounds for many species of fish and invertebrates inhabiting coastal habitats (Angel & Ojeda 2001; Pérez-Matus et al. 2007; Villegas et al. 2008). Within this particular environment, however, some coastal areas lack protection from fishing (i.e. open access sites), have lower abundances of fish predators and higher abundances of herbivorous grazers (Gelich et al. 2010, 2012), resulting in a significant impact on kelp condition by transforming kelp beds into defoliated forests (i.e. kelp with few or no stipes remaining; Figure 1a,b). Species-specific responses to these small-scale habitat changes in kelp forest ecosystems along the HCS still remain unexplored.

Since this variation in habitat traits may be directly related to a series of abiotic and biotic factors, which in turn may modulate species’ behaviour (see Werner & Peacock 2003; Shears et al. 2008; Ling et al. 2010), habitat for egg deposition in the coastal squid was collected from inshore spawning grounds (i.e. kelp and (2) morphologically characterize the egg-masses in turn may modulate species related to a series of abiotic and biotic factors, which systems along the HCS still remain unexplored.

Materials and methods

Egg masses of the squid Doryteuthis gahi were collected during eight field surveys carried out from May 2014 to January 2015 at three areas with open access management regimes (i.e. fishing is unregulated) in central Chile: Valparaiso Harbor (33°02'25''S, 71°36'31''W), Canelillo (33°21'54''S, 71°41'27''W) and Punta de Tralca (33°25'29''S, 71°42'19''W) (see Table I). The former corresponded to a recreational wharf dominated by a sandy bottom (no kelp) and sunken fishing objects such as concrete moorings and ropes, whereas the latter two corresponded to hard-bottom, kelp-dominated habitats where healthy and overgrazed patches of Lessonia trabeculata intermix (see Figure 1a,b, respectively). All samples were hand-collected by scuba diving at depths between 10 and 15 m, where bottom temperatures ranged between 12 and 13°C. In all cases samples were transported in seawater to the laboratory and each egg mass placed separately in 500 ml plastic containers with constantly flowing fresh seawater at ambient temperature (12.4 ± 1.6°C; mean ± SD). The stage of embryonic development in each egg mass was determined according to Arnold et al. (1974) and Guerra et al. (2001). All observations were conducted at the laboratory, Estación Costera de Investigaciones Marinas (ECIM).

Once in the laboratory, the number of capsules per egg mass and the relationship between capsule length (L, mm) and the number of encapsulated embryos were evaluated in all samples collected. Egg masses containing more than 30 capsules were partially analysed (i.e. 50% of the total amount of capsules; see Table I for details). In all cases, total capsule length was measured using a vernier caliper to the nearest 0.05 mm and encapsulated embryos were counted and photographed under a dissecting scope at 20× magnification (Olympus SZ61). In order to characterize the inshore spawning grounds of D. gahi in Central Chile, differences in capsule size among sites were evaluated using a one-way Analysis of Variance (ANOVA), and the relationship between capsule size vs number of embryos encapsulated was evaluated using Pearson’s product-moment correlation.

Results

In the field, egg masses consisted of a clump of elongated, gelatinous and translucent capsules firmly attached to the substrata at its basal end. Egg masses were predominantly collected from heavily grazed stipes (i.e. no blades; see Figure 1b) of the brown macroalga Lessonia trabeculata (Canelillo and Punta de Tralca), but also from man-made substrata such as rope moorings (Valparaiso). Field-collected capsules (Figure 1c) usually contained embryos at intermediate stages of development (i.e. stage 16–17; Figure 1d,e); however, an egg mass containing embryos in advanced stages (i.e. 27–28; Figure 1f) was also found in Valparaiso.

The size and number of capsules in the sampled egg masses was variable, with Valparaiso (no kelp site)
having the largest egg capsules compared with Canelillo and Punta de Tralca (kelp-dominated sites) (one-way ANOVA, df = 2, \( F = 84.9, P < 0.05 \); Figure 2a). The total number of eggs in the sampled egg masses (i.e. a female’s estimated fecundity) ranged from 118 to 930 eggs. The specific locations, dates and egg mass characteristics are presented in Table I.

Despite the variability in egg mass traits, inshore spawning grounds of *Doryteuthis gahi* in Central Chile were generally characterized by small egg capsules with an average length of 23 ± 0.4 mm (mean ± SE; \( n = 210 \)) and an average of 15 ± 0.3 (mean ± SE) embryos per capsule. When data from all spawning sites were pooled, capsule length and number of embryos per capsule were significantly and positively correlated, with larger capsules containing more embryos (\( t = 12.4, \text{df} = 115, P < 0.05 \); Figure 2b). Further, encapsulated eggs had an average maximum diameter of 2.4 ± 0.02 mm (mean ± SE; \( n = 159 \); Figure 1d). Development lasted around 35 days at 12–13°C, and newly hatched paralarvae were on average 2.8 ± 0.02 mm in size (dorsal mantle length [DML]; mean ± SE; \( n = 100 \); Figure 1g).

**Discussion**

From these field surveys it was possible for the first time to identify spawning grounds of the coastal squid *Doryteuthis gahi* located in relatively protected bays in central Chile. All egg masses were collected at depths of around 12 m and were consistently attached to defoliated (i.e. overgrazed) stipes of the ecologically and economically important brown macroalga *Lessonia trabeculata* (Canelillo and Punta de Tralca), but also to artificial structures such as rope moorings (Valparaíso). These findings suggest that *D. gahi* females may selectively avoid healthy *L. trabeculata* (i.e. blades in all seaweed stipes) for egg deposition, possibly because of the potential damage to egg capsules by mechanical disturbance of fronds (i.e. whiplash) and/or the reduced flow in highly frondose kelp. These findings agree with previous studies that have highlighted the use of short, solitary kelp stipes of both *Lessonia* spp. and *Macrocystis pyrifera* by egg-laying females of *D. gahi* in the Falkland Islands and in the Magellanic channels of the sub-Antarctic ecoregion (see Arkhipkin et al. 2000; Arkhipkin & Middleton 2003; Rosenfeld et al. 2014).

Local surveys have shown that defoliated (overgrazed) kelp *L. trabeculata* are significantly more abundant in open access management regime areas with little influence of coastal upwelling, where the abundances of invertebrate grazers, specifically the gastropod *Tegula tridentata* (Potiez & Michaud, 1838) increase by ~4-fold compared with areas where fishing is controlled or limited, i.e. Management and
Exploitation Areas for Benthic Resources (MEABR). These findings suggest that in open access sites where fishing is common, a lack of sub-tidal top predators (i.e., fish, crabs), in addition to low productivity, leads to outbreaks of herbivores that can modify the stipe to blade ratio of the kelp *L. trabeculata* (see Gelcich et al. 2012; see Figure 1a,b). Consequently, this change in local habitat may provide indirect benefits for opportunistic species such as the coastal squid *D. gahi* by increasing suitable habitats for egg-laying (i.e., the remaining holdfast and bladeless stipes of *L. trabeculata*). In the Falkland Islands, Arkhipkin et al. (2000) reported that this species generally uses the outer edge of kelp beds for egg deposition; however, our field observations suggest that adult squid are able to deposit egg capsules anywhere inside the kelp bed where defoliated *L. trabeculata* are available.

Interestingly, all the existing information may also suggest local adaptation for choice of egg deposition sites, as egg capsules of this species have also been recorded on sandy bottoms in Perú and Northern Chile (see Villegas 2001; Ibáñez et al. 2012). Although this pattern is well supported for Peruvian waters (San Lorenzo Island, Callao: Cardoso et al. 2005; Argüelles et al. 2008), there are no field studies supporting the presence of egg masses on sandy bottoms for Northern Chile. Further research is still needed in order to clarify the underlying mechanisms driving substrate selection, as in Peru and Northern Chile brown macroalgae (*M. pyrifera* and *L. trabeculata*, respectively) are present.

The encapsulation patterns recorded here are similar to those previously described along the distribution range of the species (Arkhipkin et al. 2000; Guerra et al. 2001; Arkhipkin & Middleton 2003; Barón 2003; Cinti et al. 2004; Cardoso et al. 2005; Argüelles et al. 2008; Rosenfeld et al. 2014; Table II). Nonetheless, we observed fewer and smaller capsules per egg mass and fewer encapsulated embryos, suggesting that small females (= low fecundity) may be responsible for these shallow water spawns (see Video Clip S1, supplementary material). The size of mature females varies seasonally, and the literature suggests that small females (i.e., 130 mm ML) may occur from December to January, increasing their sizes until April (i.e., 160 mm) and then decreasing again around June (see Arkhipkin et al. 2013). Although adult *D. gahi* have been sighted during several underwater surveys at the spawning sites, as well as in other locations in Northern-Central Chile (see Video Clip S1), to date no individuals have been collected in order to correlate adult size with female/male reproductive status (i.e., fecundity). Further fieldwork is currently underway in order to address this question.

Considering that all embryos within an egg mass were at similar developmental stages (i.e., all corresponding to one point on Arnold et al. 1974), it is likely that each of the collected egg masses corresponded to the reproductive output of a single female, agreeing with the total number of eggs reported in ‘single female spawns’ (400–1300) and also with the fecundity reported in maturing and mature females of the species (>2000 eggs) (see Arkhipkin et al. 2014). Interestingly, sizes of eggs and paralarvae were similar to those reported elsewhere (see Table II), suggesting an optimal range of egg and hatching sizes regardless of geographic differences and/or maternal attributes. Additional latitudinal comparisons need to be made in order to evaluate this assumption.

Taking into account all field and laboratory observations from this study, it is possible to infer that small-sized adult *D. gahi* are actively using kelp beds of *L. trabeculata* in coastal areas of Central Chile to reproduce and spawn. The uniqueness of squid life history, added to their high intrinsic capacity to transport significant amounts of biological resources (e.g., inorganic salts, proteins, carbohydrates, fats and vitamins; see Arkhipkin 2013), make *D. gahi* an important

![Figure 2](image_url)

Figure 2. (a) Boxplot showing differences in capsule size (mm) among the three spawning sites of *Doryteuthis gahi* in Central Chile: Canelillo and Punta de Tralca (kelp) and Valparaiso (no kelp), and (b) correlation between capsule length (mm) and number of embryos encapsulated by females at the three spawning sites. Boxplots next to the main axes indicate average values for each variable (n = 210 capsules).
nutrient vector in coastal ecosystems along the Humboldt Current System. Nonetheless, other life-history traits (e.g. reproductive biology, juvenile ecology) and/or trophic interactions of the species along the southeast Pacific still remain unexplored.

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**Disclosure statement**

No potential conflict of interest was reported by the authors.

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