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Sharks in the forest: relationships between kelp physical-complexity attributes and egg deposition sites of the red-spotted catshark

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ABSTRACT: Foundational organisms, such as corals, mangroves, and kelps, form structurally complex habitats in multiple coastal ecosystems of the world. However, habitat complexity comprises several interrelated attributes, such as number, size, and spatial arrangement of complexity-forming elements. Understanding the roles of these attributes in determining how associated organisms use biogenic habitats remains an elusive task. Here, we assessed the relationships between several structural-complexity attributes of the kelp *Lessonia trabeculata* and the abundance and distribution of egg depositions by the red-spotted catshark *Schroederichthys chilensis*. Over 1 yr, we conducted seasonal SCUBA surveys (i.e. ca. every 10 wk) of egg capsule depositions across individual and patch scales. The number of eggs per kelp plant was modeled as a function of kelp maximum frond length, holdfast diameter, number of stipes, percentage cover, plant density, and plant aggregation. The analysis of zero-inflated generalized linear models and second-order Akaike's information criterion indicated that the models incorporating maximum frond length and percentage cover consistently showed the best balance between fit and complexity. In general, these attributes were positively, but not necessarily linearly, linked to egg counts. The presence of egg capsules in advanced developmental stages at the end of the year indicated a high temporal persistence of eggs, particularly those occurring in taller, thicker kelps. These findings suggest that catsharks select for taller, physically stable, and thicker kelps to deposit egg capsules. Moreover, our results allow us to enhance the accuracy of the definition of shark nursery grounds, a central concept for shark conservation.

KEY WORDS: Nursery ground · Essential fish habitat · Reproduction · Scyliorhinidae

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1. INTRODUCTION

Habitat complexity is central for fundamental and applied ecology (reviewed by Kovalenko et al. 2012). This concept becomes even more relevant in the context of species conservation and the current scenario of global change. For example, habitat destruction can be an important element in predicting local extinction probabilities (Fahrig 1997, Brooks et al. 2002). Habitat modification is a major cause of ex-

tingtion of reptiles (Gibbons et al. 2000), mammals (Schipper et al. 2008), and invertebrates (Parker & Mac Nally 2002, Richman et al. 2015). In coastal environments, the alteration of biogenic habitat can have significant repercussions on the life history of associated species (Castro 1993, Jennings et al. 2008, Chapman et al. 2009). Egg-laying behavior is a life history trait that might well be sensitive to alterations of habitat structure (e.g. see Sheaves et al. 2015). Thus, understanding how variations in the structural

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complexity of biogenic habitats relate to the development of associated populations is necessary for conservation and management decisions.

Habitat complexity consists of different structural dimensions or attributes (Tokeshi & Arakaki 2012). Thus, the study of habitat complexity should consider different structural attributes (complexity per se) instead of just the number of structural components (known as 'heterogeneity'; McCoy & Bell 1991). Consequently, 5 interrelated attributes have been suggested to characterize habitat complexity: (1) scale of complexity, (2) diversity of complexity-generating elements, (3) spatial arrangement of elements, (4) size of elements, and (5) abundance/density of elements (Tokeshi & Arakaki 2012). Considering these criteria will provide a more accurate view of how scale-dependent habitat complexity is related to relevant biological processes of natural populations.

Kelp forests constitute a structurally complex type of habitat that supports the assemblage of highly diverse communities (Mann 1973, Graham 2004). Kelp canopies provide (1) protection against mechanical stress produced by waves and currents, (2) proximity to a food supply, (3) improved physical conditions (e.g. reduction in temperature variation), and (4) lower predation risk and competitive exclusion, among other resources (Parsons & Hoffmayer 2007, Rosman et al. 2013). For example, some vertebrate and invertebrate species use complex biogenic habitats as nursery areas where early life stages develop until maturity (Springer 1967, Boehlert & Mundy 1988, Gruber et al. 1988, Bustos et al. 2008, Knip et al. 2010, Almanza et al. 2012, Carrasco & Pérez-Matus 2016). In oviparous species (e.g. sharks), these areas are categorized as primary and secondary nursery areas. Primary nursery areas are those where females give birth or lay their eggs, while the secondary areas are those used later by juveniles until maturity (Bass 1978). Kelp forest architecture provides primary nursery grounds for many pelagic and benthic organisms (reviewed by Steneck et al. 2002). Moreover, structural complexity of kelps can be scale dependent, such that spatial patterns of complexity that are evident at certain levels of resolution can disappear at others (e.g. Davenport et al. 1996, Tokeshi & Arakaki 2012). Yet, our understanding of how kelp complexity determines the way in which

associated species use these habitats is still limited (Loher & Armstrong 2000, Kovalenko et al. 2012).

Along the south-central coast of Chile, the red-spotted catshark *Schroederichthys chilensis* (Guichenot 1848) uses fronds and stipes of the subtidal kelp *Lessonia trabeculata* Villouta & Santelices 1986 as anchoring structures for egg-capsule deposition (Miranda Brandt 1980, Fariña & Ojeda 1993, Hernández et al. 2005, Reyes & Hüne 2012). Primarily during summer, red-spotted catsharks anchor their egg capsules by tying the tendrils and filaments of the ovisac to vertical structures (Fig. 1). Egg capsules are deposited in an early stage of development (i.e. extended oviparity; Wourms et al. 1988, Compagno 1990), followed by an incubation period of around 7 mo (Castro et al. 1988, Fariña & Ojeda 1993, Hernández et al. 2005, J.E. Trujillo pers. obs.). Accordingly, complex vertical physical structures (e.g. fronds and stipes) are likely fundamental as anchoring sites and as protection for *S. chilensis* egg capsules. Therefore, increased occurrences of egg capsules in taller and thicker kelps, as well as in areas with greater densities and plant aggregations, could be predicted. In addition, the selection of appropriate physical structures should result in better protection, and thus increased temporal persistence of eggs (Pihl & Van der Veer 1992).

In this study, we tested the hypothesis that the structural complexity of kelp habitats is positively related with the abundance and persistence of *S. chilensis* egg capsules. Hence, we predicted that (1)

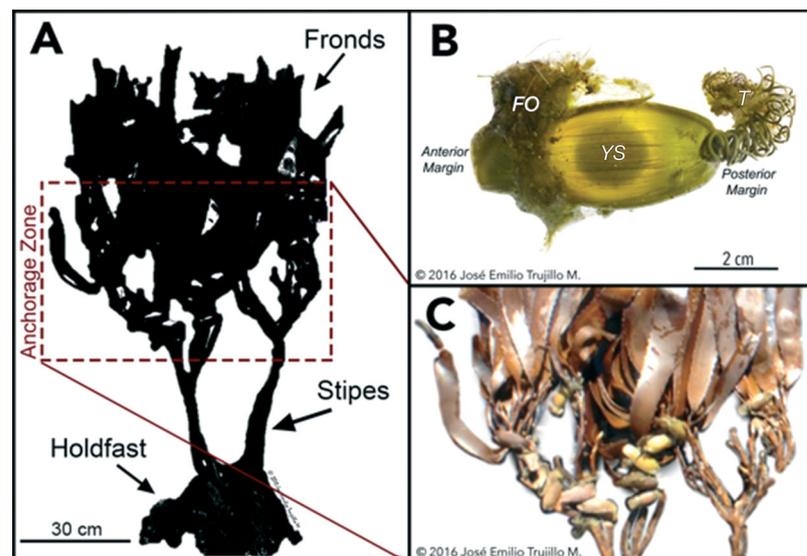


Fig. 1. (A) *Lessonia trabeculata*. (B) Morphology of a 1 d old *Schroederichthys chilensis* egg capsule (alive). FO: filaments of the ovisac. YS: yolk sac, T: tendrils. Egg capsules are ca. 5 cm length. (C) Close-up of kelp anchorage zone, showing attached egg capsules



the number of stipes, percentage cover, and maximum frond length will be important attributes accounting for the distribution pattern of egg depositions, (2) a positive and saturating relationship between egg count and these attributes will be observed, and (3) a temporal persistence of egg capsules will be evident, as most of them will be in advanced stages of development by the end of the sampling period. These predictions were tested through an observational study in which the number of egg capsules of the red-spotted catshark was monitored for 1 yr and modeled as a function of multiple structural attributes of *L. trabeculata*.

2. MATERIALS AND METHODS

2.1. Study sites and sampling design

This work was conducted at 2 sites along the coast of south-central Chile, Huiro (39° 57' 24" S, 73° 38' 33" W) and Morro Gonzalo (39° 51' 8" S, 73° 27' 51" W), characterized by a maximum depth of 12 m and a substratum consisting of boulders and large rocks. Both sites contain *Lessonia trabeculata* forests of around 500 m². Previous observations demonstrated *Schroederichthys chilensis* egg capsule deposition at both sites.

At each site, SCUBA divers permanently moored mid-water buoys randomly distributed within the same kelp forest. Within a 7 m² area around each buoy (hereafter referred to as 'patches'), we marked and identified every individual of *L. trabeculata* (ca. 5 plants patch⁻¹) with plastic fasteners (Codiplas CP2318). Patch size was kept constant across all buoys.

2.2. Estimation of kelp structural variables and catshark egg counts

Measures of structural complexity were quantified at 2 observational scales (i.e. centimeter and meter scales, respectively): (1) Individual-scale variables were number of stipes (NE), plant height (maximum frond length, MFL), and holdfast diameter (HD). (2) Patch-scale variables were percentage cover (PC), density (ind. m⁻², p) and aggregation (mean distance to nearest neighbor, R ; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/mxxxxpxxx_supp.pdf). The aggregation index R is a measure of spatial relationships, with values ranging from 0 to 2.1491, where 0 means maximal possible aggregation of

patches, 1 indicates a random distribution, and 2.1491 shows uniformity (Clark & Evans 1954). Therefore, the lowest values of R would indicate higher structural complexity. Percentage cover (PC) was calculated as:

$$PC = [(\sum A_i) / A_p] \times 100 \quad (1)$$

where A_i is the individual area occupied by alga i , and A_p is the total area of the patch (ca. 7 m²; see Fig. S1B).

For each plant in each patch and site, we registered the number of complete egg capsules. Decaying (e.g. incomplete, empty) egg capsules were not counted in order to exclude old egg capsules remaining from previous months and years. The same observer counted the egg capsules at every sampling time with the aid of 2 divers who searched for egg capsules. The 3 divers looked at the same kelp plant simultaneously. To estimate development of egg capsules, we used *in situ* ovoscopy with a diving flashlight of 400 lumens (Underwater Kinetics SL4 eLED L1). Egg capsules were classified according to Hernández et al. (2005) as follows: Stage 1 egg capsules comprised those in which we observed an ovum with a small translucent embryo with gill filaments (equivalent to stages I, II, III, and IV in Hernández et al. 2005); in stage 2 egg capsules, the embryo was no longer translucent, but gill filaments were still present and the embryo adopted the final morphology of development with an evident yolk sac (equivalent to stage V); finally, stage 3 egg capsules included a developed embryo without gill filaments and small yolk sac, an embryo with its tail flexed 180°, or egg capsules with the anterior margin opened (indicative of hatching, see Smith & Griffiths 1997). Recently laid egg capsules with embryos in the first stages of development presented opaque green coloration, whereas advanced stages were dark brown (see Fig. S2). Egg capsules in marked *L. trabeculata* were monitored every 2 to 3 mo from austral fall to late spring of 2016 (i.e. April, June–July, September–October, and November–December). Egg capsule developmental stages were reassessed during each survey.

2.3. Statistical analysis

Separate, independent models were computed for each survey and for the individual and patch scales, respectively. This was done to deal with the repeated measures in our data, and to prevent analytical issues derived from auto-correlation of errors. Total egg

count was analyzed as the response variable, and the structural variables measured at each scale were the predictors. Appropriate error distribution (either Poisson or negative binomial) was determined through visual inspection of errors, distribution of residuals, and likelihood ratio tests (Harrison et al. 2018). For the individual scale, negative binomial models showed a better fit than Poisson models (Table S1). At the patch scale, Poisson models showed better distributions of residuals than negative binomial models (Fig. S3). We assessed zero-inflation by visually inspecting errors and using model selection procedures (Zuur et al. 2009; see the explanation of model selection in the next paragraph). The individual scale showed an excess of zeros in egg counts while the patch scale did not (Fig. S4). Hence, zero-inflated negative binomial models (ZINBs) showed a better fit at the individual scale compared to a negative binomial generalized linear model (ZINB Akaike weight $[\omega_i] = 0.83$; difference of Akaike's information criterion corrected for small sample sizes with the best model $[\Delta AICc] = 3.21$). Zeros were modeled as coming from 2 processes, the binomial (false zeros vs. the rest of the data) and the negative binomial (counts vs. true zeros). False zeros would occur when an egg capsule was present, but the observer did not count it (observer error; we adjusted our sampling design to minimize this issue, see above) or when there is no egg capsule even though the habitat is appropriate (Zuur et al. 2009). This feature lets us model the probability of underestimating egg counts (i.e. probability of measuring a false zero over the rest of the data; binomial process), independently of the total number of egg capsules per plant (negative binomial process). Conversely, as we considered there was no zero-inflation at the patch scale, we used a generalized linear model (GLM) with a Poisson distribution of errors to analyze this scale of observation. We assessed goodness-of-fit of all models by visually inspecting partial residual and residuals vs. fitted plots (Zuur et al. 2009). Parameter estimation was done through maximum likelihood. Partial-residual plots showed a perfect fit between each variable and the partial residuals in the individual-scale models (Fig. S5). Equally spread residuals in the patch-scale residuals vs. fitted plots indicated a small proportion of unexplained patterns in the data after fitting the model (see Fig. S3).

We used a second-order AICc to test the first prediction, i.e. that the number of stipes, percentage cover, and maximum frond length account for the variation in egg count. The highest value of Akaike weight (ω_i) was used as a decision rule for selecting

between 2 competing models (Burnham & Anderson 2002, Wagenmakers & Farrell 2004, Burnham et al. 2011). Therefore, all variables included in the optimal model were considered to be significant and as evidence supporting our first prediction. Positive coefficients from the final models were then considered supporting evidence for a positive relationship between egg count and the selected physical attributes (second prediction).

All analyses were conducted in the R statistical environment version 3.4.0 (R Core Team 2017). We used 'zeroinfl' and 'glm' functions in 'pscl' and 'stats' R-packages (Zeileis et al. 2008), respectively, to compute the statistical models. The 'model.sel' function in the 'MuMIn' R-package was used for the model selection process (Barton 2009).

3. RESULTS

The total egg counts were 341, 193, 160, and 93 units in fall, winter, early spring, and late spring, respectively. We estimated that 90.03, 69.43, 38.10, and 48.39% of these counts were new depositions (i.e. stage 1 egg capsules) in fall, winter, early spring, and late spring, respectively. Therefore, the highest oviposition activity of *Schroederichthys chilensis* likely occurred during summer. New egg depositions observed across the 4 sampling periods agreed with previous records in central Chile (Fariña & Ojeda 1993). Advanced stages of development (i.e. stage 2 and stage 3 egg capsules) increased from fall to early spring (indicative of temporal persistence) but decreased in late spring (Fig. 2). Hence, most hatches occurred during early spring (i.e. September–October).

Each plant housed between 0 and 35 eggs (1.68 ± 5.55 , mean \pm SD) in Huiro and between 0 and 38 eggs (5.35 ± 8.69) in Morro Gonzalo. In addition, we observed no egg capsules outside *Lessonia trabeculata* kelp forests (i.e. in *Macrocystis pyrifera* forests or on rocks). At Huiro, the tallest fronds were on average 85.37 ± 24.17 cm in length, the average number of stipes was 14.00 ± 8.31 units ind.^{-1} , and holdfast diameters were on average 26.90 ± 8.18 cm. At Morro Gonzalo, these averages were 131.59 ± 31.76 cm, 8.85 ± 6.86 units ind.^{-1} , and 30.82 ± 6.51 cm, respectively. The kelp forest at Huiro had an average density of 0.48 ± 0.17 ind. m^{-2} , an average aggregation of 0.71 ± 0.23 , and an average percentage cover of $25.49 \pm 13.78\%$. The Morro Gonzalo kelp forest had the same density of 0.48 ± 0.12 ind. m^{-2} , but an average aggregation of 0.46 ± 0.20 and an average percentage cover of $58.15 \pm 18.71\%$.

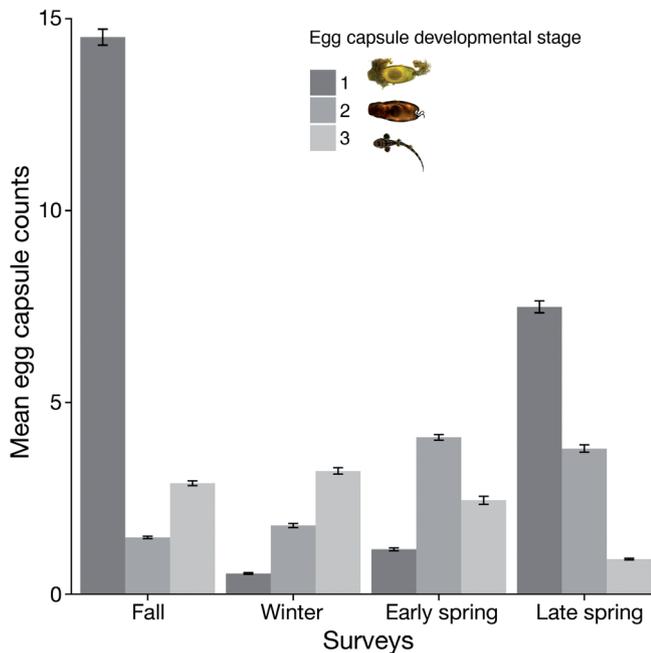


Fig. 2. Mean counts of *Schroederichthys chilensis* egg capsules for each developmental stage during 1 yr of monitoring (2016). Bars represent 95 % confidence intervals obtained by bootstrapping. Stage 1: recently spawned egg capsules, light green in color and very small embryo; Stage 2: small translucent embryo, egg capsules dark brown in color; Stage 3: well developed embryo with small yolk sac and empty egg capsules with anterior margin opened (indicative of successful hatching)

3.1. Model selection

Selected models differed between the 4 sampling periods at both scales of observation (i.e. individual and patch scales). In general, the first 2 models had a ΔAIC lower than 2 points. However, ω_i values were high for the first models in the 4 sampling periods (Table 1). Hence, selected models had a high probability of being the models with greater contribution of information despite their low ΔAIC . In the individual scale, we observed that maximum frond length was included in the optimal models consistently over 3 sampling periods (i.e. fall, winter, and early spring). Holdfast diameter (HD) was included once (i.e. late spring), but the number of stipes (NE) was dropped from the models across the 4 sampling periods. At the patch scale, percentage cover (PC) was included in the optimal models estimated across the 4 sampling periods. However, plant density (p) and aggregation (R) were included 3 times—the former was selected in the optimal models of fall, winter, and early spring, and the latter in fall, early spring, and late spring (Table 1).

Table 1. Summary of model selection for 2 scales of observation (i.e. kelp individual and patch). Models are sorted according to Akaike's information criterion corrected for small samples (AICc). The degrees of freedom (df), log-likelihood function (logLik), the difference of AICc with the best model (ΔAIC), and Akaike weights (ω_i) are included for each model. EC: egg capsule counts, MFL: maximum frond length, NE: number of stipes, HD: holdfast diameter, PC: percentage cover, p : density, R : aggregation

Models	df	logLik	AICc	ΔAIC	ω_i
Individual scale					
Fall					
MFL	5	-137.58	285.81	0.00	0.49
MFL + NE	7	-136.09	287.4	1.59	0.22
Null	3	-141.62	289.49	3.68	0.08
Winter					
MFL	5	-90.2	191.61	0.00	0.28
MFL + NE	7	-87.67	191.67	0.06	0.27
HD + MFL + NE	9	-85.22	192.35	0.74	0.19
Early spring					
MFL	5	-69.19	150.10	0.00	0.50
MFL + NE	7	-66.84	151.08	0.98	0.31
HD + MFL + NE	7	-67.96	153.31	3.21	0.10
Late spring					
HD	5	-59.39	130.44	0.00	0.41
MFL	5	-59.92	131.5	1.06	0.22
Null	3	-62.9	132.42	2.00	0.15
Patch scale					
Fall					
PC + p + R	4	-175.06	360.79	0.00	0.52
PC + p	3	-177.28	362.07	1.28	0.28
PC	2	-179.28	363.27	2.48	0.15
Winter					
PC + p	3	-102.82	213.64	0.00	0.50
PC + p + R	4	-101.08	213.80	0.16	0.46
PC	2	-107.13	219.17	5.53	0.03
Early spring					
PC + p + R	4	-66.78	145.56	0.00	0.82
PC + R	3	-70.20	148.58	3.02	0.18
PC	2	-77.76	160.51	14.96	0.00
Late spring					
PC + R	3	-89.32	187.04	0.00	0.58
PC	2	-91.78	188.64	1.61	0.26
PC + p + R	4	-89.06	190.57	3.53	0.10

3.2. Relationships between attributes of habitat complexity and egg counts

Zero-inflated models with binomial distribution showed that the probability of measuring a false zero decreased by 2, 4.4, and 1.1 % per cm of maximum frond length in fall, winter, and early spring, respectively. Similarly, there was a decrease of 9 % per cm of holdfast diameter in late spring. In general, the sub-estimation of *S. chilensis* egg capsules decreased

in relation with increasing values of the structural attributes of *L. trabeculata* (see Fig. S6).

According to the zero-inflated models with Poisson distribution, the number of egg capsules increased by 1.2, 0.03, and 2% per cm of frond length in fall, winter, and early spring, respectively (Fig. 2). On the other hand, the number of egg depositions increased by 19% per cm of holdfast diameter in late spring. The relationships between egg count and individual-scale physical attributes were positive and linear during winter, but non-linear during fall, early spring, and late spring (Fig. 3).

At the patch scale, we observed an increase in the number of egg capsules by 2, 2.8, 2.5, and 1% per

unit of percentage cover in fall, winter, early spring, and late spring, respectively. The number of eggs increased by 342, 357, and 725% per unit of density in fall, winter, and early spring, respectively. Egg counts also increased per unit of aggregation by 44, 86, and 65% in fall, early spring, and late spring, respectively (Fig. 4).

4. DISCUSSION

In this work, we determined positive relationships between multiple components of kelp-forest habitat complexity and the abundance of egg capsules of

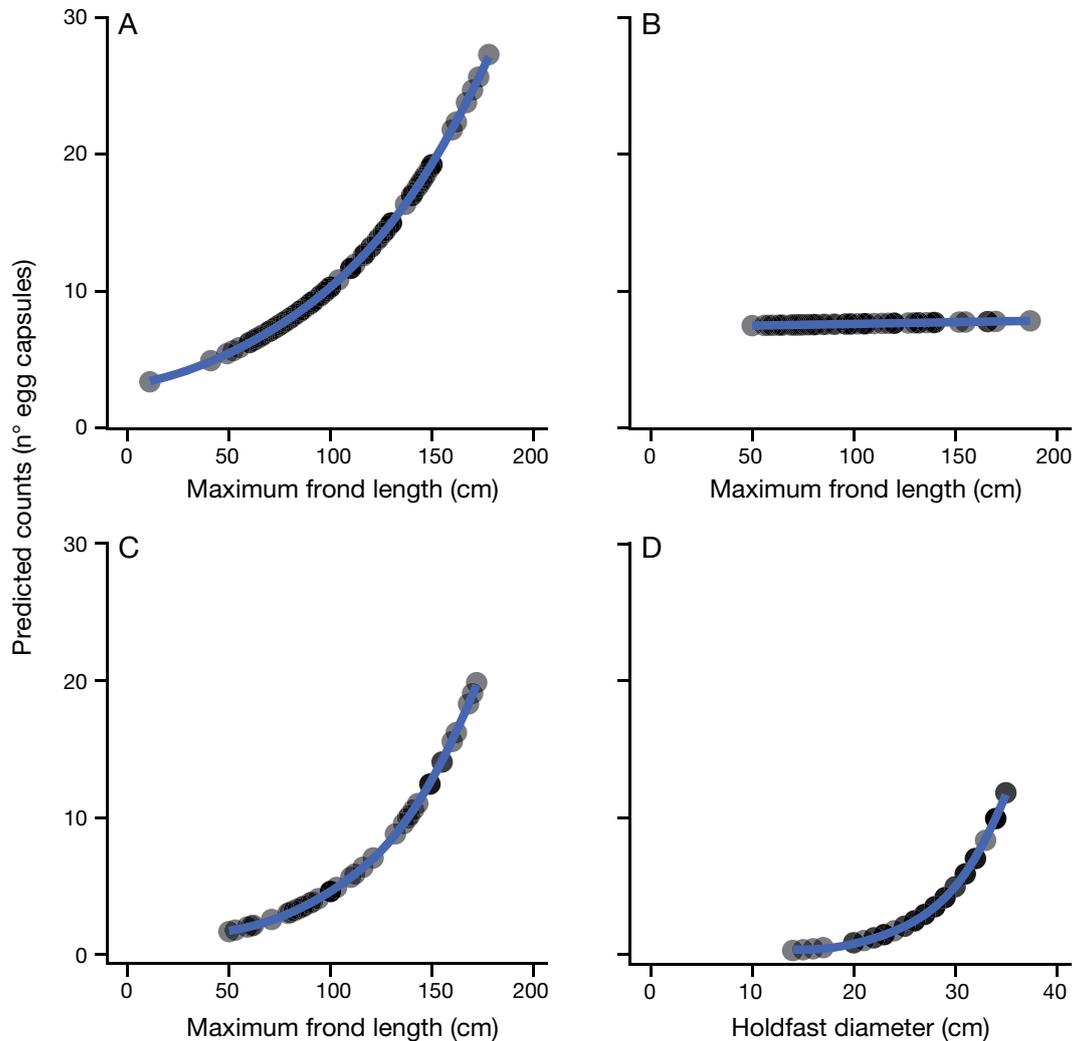


Fig. 3. Predicted smoothed curves from Poisson zero-inflated generalized linear models fitted to individual-scale data from four periods in 2016: (A) April (fall); (B) June–July (winter); (C) September–October (early spring); (D) November–December (late spring). Gray dots are estimated egg capsule counts (μ_i). Blue lines were plotted by means of locally (weighted) scatterplot smoothing (LOESS). The following were not selected through AICc procedures, and so are not presented here: holdfast diameter for Apr, Jun–Jul and Sep–Oct; maximum frond length for Nov–Dec; and no. of stipes for all 4 periods

the red-spotted catshark at 2 sites in southern-central Chile. Predictions of egg counts were consistent over 4 sampling periods during 2016 (i.e. fall, winter, early spring, and late spring). Specifically, the models that included maximum frond length and percentage cover consistently showed the best balance between fit and complexity (Burnham & Anderson 2002), hinting at a significant effect of these variables on egg count. The other variables, i.e. holdfast diameter, density, and aggregation, were included in the models on one or two occasions, which implied a temporally variable contribution of information to the models. In general, our analyses showed a greater number of egg capsules in kelp forests with higher values of measured attributes. Hence, attributes of kelp forests' structural complexity (e.g. frond length), at individual and patch scales, are of fundamental importance as a primary nursery ground for *Schroederichthys chilensis*.

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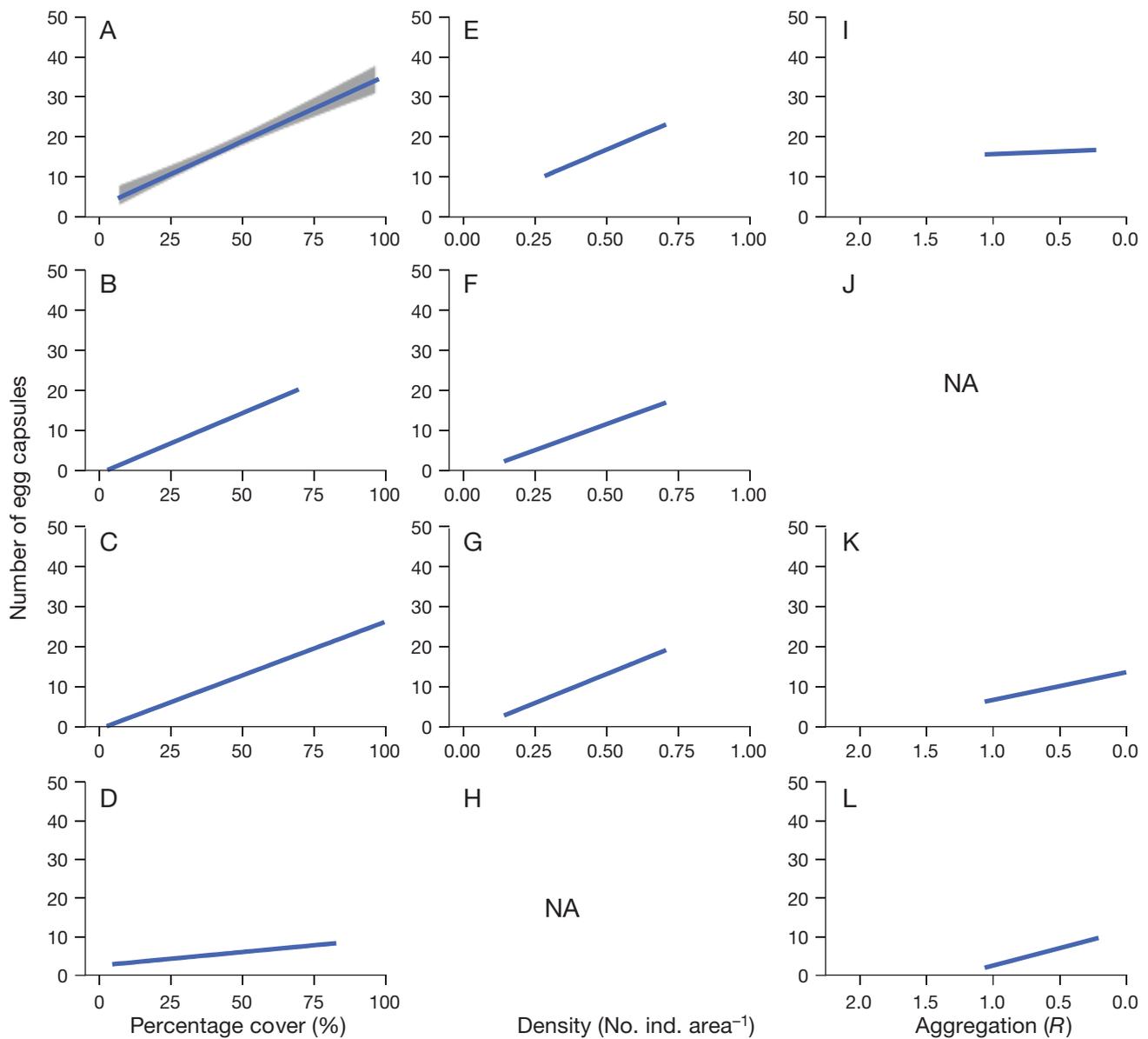


Fig. 4. Predicted curves (blue lines) from Poisson GLMs fitted to patch-scale data from 4 periods in 2016. Gray dots are served egg capsule counts and gray bands are 95% confidence intervals. Panels are sorted according sampling time: (A, April (fall)); (B,F,J) June–July (winter); (C,G,K) September–October (early spring); (D,H,L) November–December (late spring). Note that the x-axes in the aggregation plots (panels I, K, and L) are **inverted** to indicate higher complexity with decreases values of R . NA: variable was not selected in that specific time of year

4.1. Structural complexity: mechanisms involved in the use of kelps for oviposition by red-spotted catsharks

The number of egg capsules of the red-spotted catshark had a positive (but weak) relationship with kelp frond length. Subtidal forests of *Lessonia trabeculata* provide a 3-dimensional habitat (Villegas et al. 2008), increasing substratum vertical dimension in the sense of maximum frond length. The female catshark circles around vertical structures to tie the tendrils of the egg capsule (e.g. see Castro et al. 1988). This anchoring technique may help to pull the egg capsules out of the uterus. In contrast, laying the egg capsules on a horizontal surface requires sudden movements and contractions of the pelvic region to expel the capsules (Luer & Gilbert 1985). In addition, an egg case hanging vertically may experience increased passive ventilation, reducing the high metabolic cost of active ventilation (i.e. continuous movements of embryos, Tullis & Peterson 2000, Flam-mang et al. 2007). Consequently, anchoring the egg capsules to a vertical structure can have a high adaptive value in terms of reproductive investment for the red-spotted catshark.

Besides reducing the energy costs, anchoring egg capsules in taller kelps can decrease predation risk by reducing the access of potential predators. In fact, egg clusters were separated 36.2 ± 8.02 cm (mean \pm SD, $n = 12$) from the rocky bottom where a variety of predators may be found. Moreover, predator avoidance of eggs can be further enhanced by passive ventilation (see above), as seen in other elasmobranchs (Sisneros et al. 1998, Kempster et al. 2013). However, elasmobranch egg capsules are preyed on by several species, including gastropods, echinoderms, and elasmobranchs (Bor & Santos 2003, Lucifora & García 2004, Powter & Gladstone 2008, Hoff 2009). In addition, the majid crab *Taliepus dentatus* (H. Milne Edwards 1834) could be a potential predator of *S. chilensis* eggs at the study sites (J.E. Trujillo unpubl. data). *T. dentatus* can climb the fronds of *L. trabeculata*, and adults can be commonly seen hanging from these subtidal kelps (J.E. Trujillo pers. obs.). It is still necessary to determine more accurately the predation pressure operating upon the red-spotted catshark egg capsules. Nevertheless, the results presented herein suggest that the vertical dimension of kelp forests is an important characteristic that reduces predation risk in this shark species.

Interestingly, there was also a positive relationship between the holdfast diameter and the number of eggs oviposited. The greater physical stability pro-

vided by larger holdfast diameter may facilitate increased pulling force when entangling the capsules. This could be provided by algae with broader holdfasts (but see Friedland & Denny 1995, Milligan & DeWreede 2000) and stiffer stipes (Villouta & Santelices 1986), which may explain the higher occurrences of egg capsules in kelps with larger holdfasts observed in our study. Moreover, shallow-water currents can be strong in the area in association with a seasonal upwelling center located south of the sampling sites (Letelier et al. 2009), which confers more relevance to the physical stability of *L. trabeculata* kelps. In contrast, *Macrocystis pyrifera*, which has comparatively smaller holdfasts than *L. trabeculata*, is not used by *S. chilensis* as an anchoring structure (Dayton et al. 1984, Seymour et al. 1989, Hobday 2000), even though *M. pyrifera* provides an important vertical dimension, and is significantly taller than *L. trabeculata* (Kain 1982). A high stability of anchoring structures will have long-term implications, since it guarantees the persistence of egg capsules in a restricted area with adequate physical (e.g. temperature and salinity; Ward-Paige et al. 2015) and predator-sheltered conditions (Wharton & Mann 1981, Steele 1999, Hinojosa et al. 2015).

At the forest scale, kelps with high density and percentage cover will provide a greater number of anchoring structures for the egg capsules of *S. chilensis*, a species that forms aggregations near-shore during oviposition (Miranda Brandt 1980). Egg capsules are deposited in an early stage of development (i.e. extended oviparity; Wourms et al. 1988, Compagno 1990) and the incubation period is at least 7 mo before completing full development. During this period, *S. chilensis* egg capsules undergo a tanning process in contact with seawater (Krishnan 1959), exhibiting similar colorations to kelps (see Fig. 1C and Fig. S2). Therefore, kelp forests with high densities, percentage cover, and aggregations offer a suitable habitat to hide the egg capsules from visual predators, as has been shown elsewhere (Nafus et al. 2015). In fact, we observed more egg capsules in an advanced stage of development in the last sampling periods (suggesting increased persistence) in patches with high values of these attributes.

Despite the large amount of evidence suggesting the importance of kelp forests, these ecosystems, and their associated species, face a number of threats. Worldwide, kelp deforestation can result from local factors such as excessive herbivory by sea urchins, coastline urbanization, or direct harvesting of canopies (Steneck et al. 2002, Connell et al. 2008, Krumhansl et al. 2016), and from global factors like ENOS (Fernández



dez et al. 1999, Vásquez et al. 2008). According to this scenario, the need to improve our ability to predict the ecological consequences of the multiple stressors that threaten kelp forests is evident.

4.2. Kelp forests fulfill the role of nursery ground for sharks

Early studies have recognized the use of certain habitats for oviposition or parturition by a variety of organisms, and most have assumed that protection of early developmental stages was the primary determinant in the selection of these habitats (e.g. Springer 1967, Bass 1978, Branstetter 1990). Nevertheless, the majority of these studies fail to provide evidence that such areas have a nursery role, which is problematic when making conservation decisions about these habitats (Heupel et al. 2007). Proximity to an appropriate food supply, physical conditions (e.g. temperature and salinity) that support individual growth and development, and reduced biological interactions (e.g. predation and competition) have been used as criteria to classify an area as a nursery ground (sensu Parsons & Hoffmayer 2007). Furthermore, Beck et al. (2001) established that one should encounter greater (1) densities, (2) growth, (3) survival of juveniles, and (4) movement to adult habitats within a nursery ground. In the case of *S. chilensis*, although the egg capsule protects the embryo (Knight et al. 1996), the fact that these capsules are vulnerable to predation (e.g. Bor & Santos 2003) underscores the importance of the oviposition habitat to ensure survival of the developing embryo. In this study, we highlighted the adaptive value of various habitat physical attributes (i.e. second criterion of Parsons & Hoffmayer 2007) in determining the occurrence of a greater number of egg capsules in general (i.e. first criterion of Beck et al. 2001) and in determining the occurrences of egg capsules in advanced stages of development (i.e. second criterion of Beck et al. 2001). Thereby, forests of the subtidal kelp *L. trabeculata* would be an important refuge for the early stages of development of *S. chilensis*, guaranteeing a contribution of juveniles to the environment (i.e. hatched egg capsules). The evidence presented here supports the idea of a nursery role by complex kelp forests.

5. CONCLUSIONS

In summary, physical attributes of kelp that account for vertical anchoring structures and temporal

stability of red-spotted catshark egg capsules were relevant elements of the structural complexity of these foundation species. These attributes, and their patterns of variation across spatial scales, would therefore be key for the establishment of kelp forests as nursery grounds of *S. chilensis*. Future manipulative and observational studies are needed to determine the strength of predation pressure in relation to the structural complexity of kelps. Besides identifying *L. trabeculata* forests as important shark nursery grounds, our results give practical nursery-value information to managers on how to protect these ecosystems. Habitat complexity should therefore be included in future models and criteria defining nursery grounds, in order to improve our ability to manage and conserve natural ecosystems facing multiple anthropogenic threats.

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