

Understory algae associations and predation risk influence broad-scale kelp habitat use in a temperate reef fish

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ABSTRACT: Habitat selection and predation are ecological processes that operate at small spatial scales. How these influence large-scale patterns in abundance and distribution of fauna remains to be resolved, especially in structurally complex systems such as kelp beds. In order to explain whether habitat selection, differential predation, or a combination of factors explain variation in fish abundance among sites, we conducted field surveys of abundance and microhabitat use of a temperate reef fish (Tripterygiidae, *Helcogrammoides cunninghami* Smitt, 1898) at sites of varying kelp cover and different understory algal assemblages. We observed variation in abundance among sites and, particularly, that sites with abundant kelp individuals have 4 times fewer fish. In order to explain these differences in habitat use and variation in abundance among sites, we conducted choice chamber experiments in the laboratory and tethering experiments in the field. In the laboratory, individuals tend to discriminate among options by selecting substrata with understory biogenic habitat (i.e. filamentous algae) and avoiding kelp. Finally, tethering experiments in the field evaluating *H. cunninghami* mortality rates in preferred habitat types compared to kelp beds confirmed an increase in predator richness and a 2-fold increase in predation rates inside kelp habitats. Together, these results suggest that multiple mechanisms that operate mainly at small spatial scales (predation and habitat selection) may influence the distribution and abundance of organisms over large areas.

KEY WORDS: Reef fish · Kelp forest · Habitat selection · Mortality rates

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INTRODUCTION

The role of small-scale processes in driving large-scale patterns of species abundance is a fundamental issue in marine ecology. Habitat selection and biotic interactions are processes that occur at small scales, yet these behaviors mediate how species interact with one another to determine assemblages of ecological communities and to maintain biodiversity (Robertson & Gaines 1986, Munday 2000, 2001, Wellenreuther et al. 2007, 2008, Efirid & Konar 2014).

In particular, habitat preference and availability of different habitat types influence species richness and distribution, population abundance and connectivity, and composition of local communities in several vertebrate taxa (Gregory & Gaston 2000, Munday 2002, Komyakova et al. 2013, Fulton et al. 2016). Empirical evidence suggests that patterns of habitat use are determined by the amount of suitable habitat available, which acts as a primary driver of species abundance and distribution (Venier & Fahrig 1996, Fulton et al. 2016). However, biotic interactions such as predation

are also often habitat-specific, and can thus ultimately affect the distribution of species across large areas (Werner et al. 1983, Gilliam & Fraser 1987).

Habitat associations tend to be more passive in early life stages, depending on reproductive strategies, stochastic processes, and parent body condition for successful settlement in an appropriate habitat (Almany et al. 2007, Harasti et al. 2014). Decision-making takes on a stronger role as individuals grow and successfully contribute to recruitment into a local population. In order to increase survival and reproductive success, individuals must sense and actively select preferred habitat characteristics (e.g. types of macroalgae and lithic elements of the surrounding environment: see Smith & Shima 2011). Non-random associations between organisms and surrounding habitat types can also be influenced by intra- and inter-specific interactions (Werner et al. 1983, Munday 2000, Rojas & Ojeda 2010). Negative interactions such as predation and competition can extirpate individuals from habitats that are presumably better for their fitness in terms of food and refuge availability (Lima & Dill 1990, Bay et al. 2001, Underwood et al. 2004). As such, demands are often in conflict, producing fitness trade-offs. This produces selection pressure on individuals of all size classes to choose amenable habitats and recognize their surroundings in order to mediate the negative effects of (1) density-dependent mortality (Shima 2001), (2) competition (Robertson 1996, Geange et al. 2013), and (3) predation (Turner 1996, Luttbeg & Sih 2004). The ability to identify the costs and benefits provided by different habitat types (i.e. one habitat may serve better for food while another for protection from predators; see Johnson 2007 for a review) comprises an important aspect of animal behavior. It is unclear how these decisions by individuals affect population abundances and species distributions.

Temperate rocky reefs comprise heterogeneous subtidal landscapes that vary in complexity and quality (i.e. biological versus lithic substrata) (Connell & Irving 2008). Kelp forests occur in patches along open, high-energy coasts, and are characterized by abundant low-diversity kelps and highly diverse understory species (Graham et al. 2007, Villegas et al. 2008). While kelps provide the primary 3-dimensional structure and greatly influence the local physical environment (Dayton 1985), understory benthic species are an important source of food and habitat (Holbrook et al. 1990, Prado & Castilla 2006). The mosaic distribution of kelp stands and open spaces dictates large-scale habitat availability, influencing the distribution and local abundance of asso-

ciated species. For instance, patterns of habitat use by kelp-forest fishes may be determined by differences in kelp density, understory algal species and other biogenic benthic habitat types (i.e. mussel beds, amphipod reefs) (Palma & Ojeda 2002, Pérez-Matus et al. 2007) and/or by patterns of human use (Gelcich et al. 2008). In particular, some species may prefer the fringe of kelp forests or more open habitats, taking advantage of the open space near established beds and avoiding dense stands and frond whiplash (Konar 2000). Predator distributions can also negate the potential prey refuge provided by biogenic habitat, such as when predators exhibit an aggregative response (Anderson 2001).

Our aims were to assess, for the temperate reef fish *Helcogrammoides cunninghami*: (1) the relationship between kelp density and fish abundance, (2) patterns of habitat selectivity under different kelp-dominated understory habitat conditions, and (3) rates of mortality due to predation across different habitat types. Due to our field observations, we hypothesized that preference for certain characteristics of understory microhabitats would influence large-scale patterns in the abundance of *H. cunninghami*. Additionally, we predicted that this preference would correlate with higher predation rates inside kelp stands, and that fish would actively seek out habitats where their predation risk was lowest.

MATERIALS AND METHODS

Study sites and biological system

The understory of Chilean kelp forests is primarily composed of patchily distributed crustose algae (*Lithothamnium* spp., *Hildenbrandia* sp.) (Pérez-Matus et al. 2007). Turf and foliose algae such as *Gelidium chilense*, *Cladophora* spp., and *Dictyota kuntii* comprise a smaller proportion of the understory community, presumably due to shading by the kelp canopy (Reed & Foster 1984, Flukes et al. 2014). Space is also shared with a diverse group of benthic suspension feeders including sea sponges (*Halichondria* spp., *Clionopsis platei*), polychaetes (*Phragmatopoma moerchi*), barnacles (*Austromegabalus psitacicus*, *Balanus* spp.), bivalves (*Perumytilus purpuratus*, *Semimytilus algosus*, *Choromytilus chorus*, and *Aulacomya ater*), and ascidians (*Pyura chilensis*) (Prado & Castilla 2006), which provide secondary substrate for associated organisms.

Studies were conducted in shallow subtidal boulder fields. Six of the 7 study sites were covered ex-

tensively (80%) with kelp *Lessonia trabeculata* and all were exposed to moderate wave action. The kelp understory at these sites was dominated by a diverse macroalgal assemblage composed of small corticated, foliose and filamentous algae (predominately *Gelidium chilense*, *Cladophora* spp.), sponges, and bryozoans (Fig. 1a,b). Only 1 site (Montemar) lacked kelp cover, where the substrate was dominated by filamentous green, calcareous, and non-calcareous crustose algae (Fig. 1a,c).

The focal species

The fish species studied was the triplefin *Helcogrammoides cunninghami*, locally known as trombolito tres aletas (Fig. 1d). This is a cryptic species,

abundant on rocky reefs of coastal Chile, and has no commercial value; therefore, it is amenable to field studies since it has 'natural' abundances and no perceivable escape response to divers. This small, territorial, cryptic, microcarnivorous fish inhabits the shallow subtidal zone to a maximum depth of 35 m (A. Pérez-Matus pers. obs.). Individuals can reach up to 63 mm in total length (TL) and the species occurs from Lima, Peru (12° S) to Southern Chiloe, Chile (47° S) (Williams & Springer 2001). This triplefin species is also found in Puerto Madryn in the Atlantic Ocean (Castillo & Pequeño 1998). Stomach analyses of individuals at our study sites showed that small crustaceans such as amphipods, harpacticoid copepods, barnacles, cumaceans, and small mollusks (e.g. bivalves) constitute the bulk of the triplefin diet, but with variation among sites (M. Goicoechea, N. Winkler

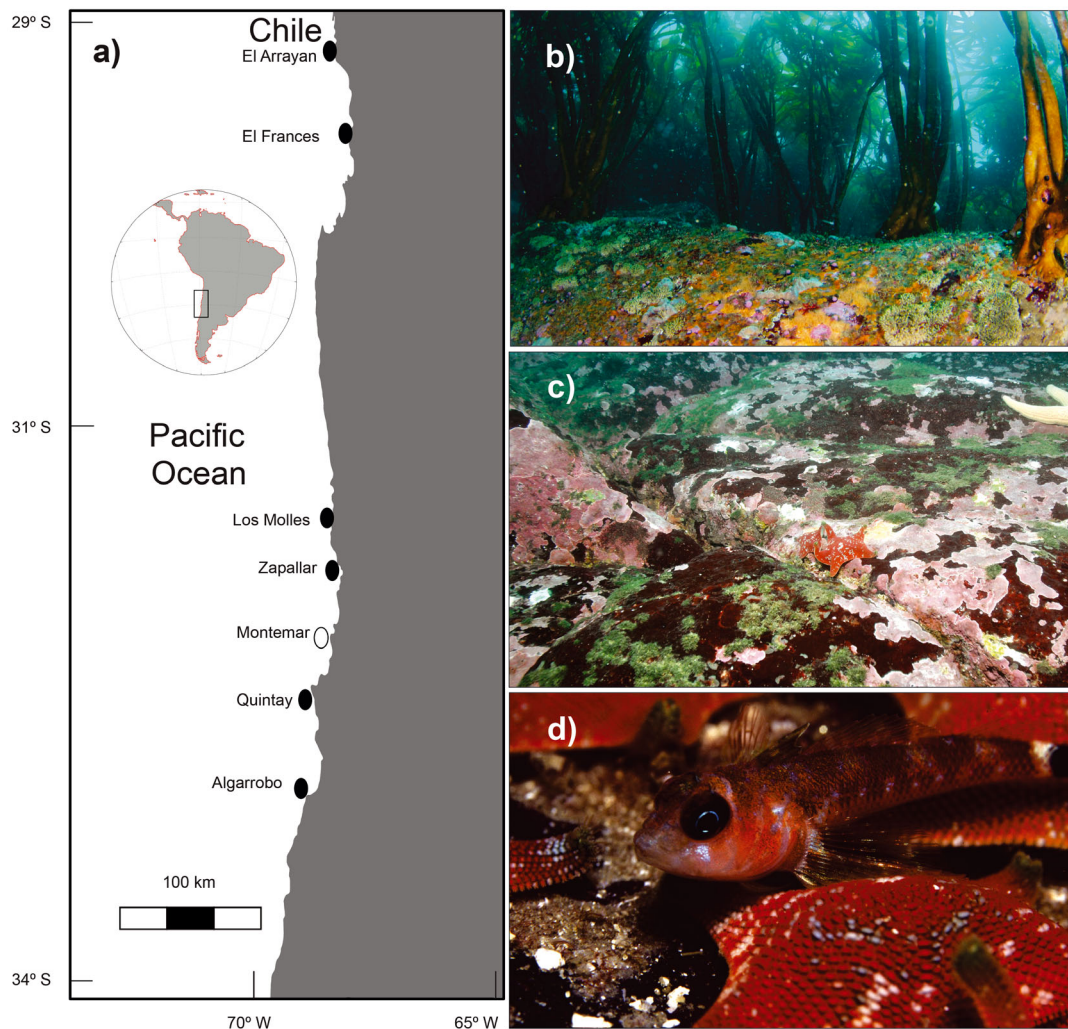


Fig. 1. (a) Study sites including surveys in kelp-dominated *Lessonia trabeculata* sites (●) and 1 non-kelp dominated site (○); (b) kelp understory with several species of crustose algae and bryozoans; (c) dominant non-kelp understory species including several crustose and filamentous algae and lithic substrate; and (d) focal species *Helcogrammoides cunninghami*

& A. Pérez-Matus unpubl. data). As with most benthic species, this triplefin recruits to the subtidal benthos during December to February after approximately 3 mo in the pelagic environment (Mansur et al. 2014).

Population size, habitat availability, and habitat use of *H. cunninghami*

The 7 sites were surveyed in austral fall (March to April) to characterize mesoscale spatial variation in triplefin population size and habitat use. At each site, we used two 100 m transects, within which 10 recording stations were established at discrete kelp beds separated by a distance of 10 m. Transects were placed perpendicular to the shoreline and were separated by 200 m from each other. Studies conducted on a member of the same family (Tripterygiidae, *Forsterygion lapillum*) in temperate reefs indicated that home ranges are considerably small (i.e. home ranges $<0.5 \text{ m}^2$) (Mensink & Shima 2015). Based on the size of the focal species and potential home range size, we reasoned that recording stations every 10 m could be considered as truly independent replicates for estimating abundance. At each station, we placed two 1 m^2 quadrats on each side of the transect (separated by 1 m from each other) and counted the number of individuals per quadrat. Additionally, in order to have an estimate of kelp abundance at each study site, a second observer counted the number of *L. trabeculata* individuals in each plot, following standardized protocols (see Pérez-Matus et al. 2007, Villegas et al. 2008). A third observer on the same monitoring station estimated abundance and composition of available microhabitats. We used random point contact (RPC) to record percent cover of all sessile organisms occurring within two 0.5 m quadrats placed on either side of the transect at each recording station ($n = 40$ per site). We then standardized the data to an area of 1 m^2 . The depth of each station was also recorded. Data were obtained using SCUBA, and were taken by the same observer for each of the 3 metrics in order to ensure standardized visual sampling. We averaged the abundance of fish, kelp, and percent cover of sessile specimens of both quadrats per station (due to proximity of both quadrats along the monitoring station within the transect). All sites were sampled once during the austral fall season from March 27 through April 11, 2012.

Microhabitat types were grouped into one of the following 7 categories: ascidians, bryozoans, sponges, corticated algae, foliose algae, encrusting algae, and

bare substrate (i.e. cobbles, boulders) (following Steeneck & Dethier 1994). To estimate the habitat use of *H. cunninghami* among different types of microhabitats, we first calculated Manly's selectivity index (α_{ij} ; Manly et al. 1972, Chesson 1978, Pledger et al. 2007), which measures the likelihood of finding a fish within a habitat under the null hypothesis of random distribution based on the following:

$$\alpha_{ij} = \frac{\frac{F_i}{H_i}}{\sum_{j=1}^n \frac{F_j}{H_j}} \quad (1)$$

where habitat selection is evaluated separately for each habitat type in each replicate sampling unit (quadrat). H is the proportion of surveyed habitat (i.e. percent cover) of a given type, and F is the proportion of surveyed habitat of the censused fish on a given habitat type. A value of $\alpha_{ij} = 1$ indicates exclusively using habitat type j . We converted the α_{ij} values to electivities (ε_{ij}) to estimate the preference for a particular habitat. Electivity is an index ranging from -1 , which represents a habitat that is never used, to $+1$, an exclusively used habitat. A value of 0 indicates neutral association. Electivity was calculated as follows:

$$\varepsilon_i = \frac{n\alpha_{ij} - 1}{(n-2)\alpha_{ij} + 1} \quad (2)$$

where n is the number of habitat types within each quadrat. We calculated both indices at each site using the microhabitat availability values averaged across the 2 quadrats at each monitoring station. Mean electivity was then calculated within transects. We reported the mean ($\pm 95\%$ CI) electivity per site accounting for the variability within stations ($n = 2$ quadrats) and within transects ($n = 10$ stations). We considered individuals to show a significant association (or aversion) of a habitat type if 95% confidence intervals did not overlap zero.

Site and depth (m) differences in the abundance of *H. cunninghami* and kelp were tested using generalized linear models (GLMs) due to the nature of the response variable (visual counts), which had unequal variances and non-normally distributed errors (Crawley 2007). For this GLM, we specified Poisson distribution errors with a log-link function to evaluate the influence of both site and depth (as continuous variables) on variation in abundance based on counts, contrasting each site and depth interaction. Data were overdispersed for counts of fish abundance only (residual deviance model = 377 on 126 degrees of freedom) and were corrected using a quasipoisson error distribution (Crawley 2007). In order

to determine the influence of the different biotic elements (percent cover of sessile species and kelp abundance) and abiotic parameters (depth) on the focal fish species, we conducted a series of Spearman's rank correlations using fish abundance as the response variable. Additionally, we performed Spearman's rank correlations in order to understand best correlates between understory species and kelp abundance. Using both fish and kelp abundance as response variables, we conducted these analyses at 2 different scales: (1) at the quadrat level (by averaging the 2 quadrats per station, $n = 10$ per transect) and (2) at the site level by averaging all monitoring stations along the transect ($n = 2$ per site). This was designed to evaluate how variation in habitat features affect the abundance of reef fish and kelp at small scales (monitoring station) and at coarse scales (site-level variation) to determine if a certain habitat influences broad-scale patterns in abundance of kelp and fish (see Supplement at www.int-res.com/articles/suppl/m559p147_supp.pdf).

Laboratory choice experiment

Microhabitat preferences were evaluated in the laboratory using a choice chamber (see McDermott & Shima 2006) during June and July of 2012 in seawater. Individual triplefins of similar size (3 to 5.5 cm TL) were offered the choice of multiple natural habitats commonly observed in our field study: (1) corticated foliose algae (mainly *Gellidium* sp.), (2) crustose algae (*Lithothamnium* spp. and *Hildenbrandia* spp.) with small patches of algae, (3) juvenile kelp *L. trabeculata* of 30 cm height and 15 cm holdfast attached with transparent cable ties to a small 1 kg lead, and (4) lithic substrate composed of small cobbles and boulders (40 cm). These natural substrates were laid on top of small boulders (30 to 35 cm) and all associated epifauna/potential prey were removed. The proportions of habitat types were standardized to have similar biomass of habitat among the treatments within the choice chamber, thus adjusting for potential differences in encounter rates.

Fish for all experiments were collected using a hand net at Montemar (Fig. 1). Upon collection, individuals were immediately transported to the laboratory and allowed to acclimate for 24 h in 1000 l indoor aquaria with continuous aeration and seawater flow. All assays were conducted during daylight between 12:00 and 18:00 h. At the start of the assay, an individual fish was introduced to the center of the choice chamber and held within a plastic tube with holes

for 2 min, after which the tube was lifted by a controlled system of pulleys so as to standardize and minimize interference. Upon release, we continuously observed fish behavior and movements until the individual settled to rest (i.e. ceased activity) or until a maximum time of 5 min. This limit was chosen because preliminary tests indicated this time was appropriate for the fish to select a treatment (McDermott & Shima 2006). The substrate upon which the individual settled was recorded. If after 5 min an individual remained active or outside a particular habitat, it was noted as no choice. At the end of the trial, the fish was removed from the choice chamber, measured, and released back to the catch site. Individuals were used only once and treatments were randomly repositioned within the choice chamber. After completion of 10 replicates, we allowed water to circulate within the choice chamber for 5 min to completely replace the water in the chamber. These procedures were taken to minimize the potential for non-independence of the trials (e.g. individuals may tend to follow scent trails left by previous trials). A total of 75 replicate trials were run.

We analyzed the results of choice chamber preferences of *H. cunninghami* for different habitat types using a randomization test. We used Bray–Curtis distances (BCDs) between observed and expected values as our statistical test as follows:

$$BCD = \frac{\sum_n |\text{observed} - \text{expected}|}{\sum \text{observed} + \sum \text{expected}} \quad (3)$$

High values for BCD indicate a preference for any of the different treatments ($n = 5$ for experiments), and p-values were calculated by using the proportion of values in the null distribution (generated from 10 000 permutations of the data) that were greater than those estimated by BCD (we evaluated for significance using $\alpha = 0.05$).

Field-predation experiment

To determine if predation differed between kelp- and non-kelp-dominated sites (kelps were the least preferred habitat in the choice chamber experiments, see 'Results: Laboratory choice experiment'), we conducted a tethering experiment. Since changes in behavior and escape responses of tethered fish may result in vulnerability to predators, tethering experiments are only useful for quantifying relative predation rates (Aronson & Heck 1995). However, these artifacts presumably remained constant throughout the experiment. Along with field observations of po-

tential predators, we conducted this experiment to measure if triplefins were susceptible to predation under different circumstances of complex habitat features. Individual *H. cunninghami* were collected at Zapallar (kelp-dominated) and at Montemar (non-kelp-dominated) (Fig. 1) using hand nets and then maintained in the laboratory for 48 h. We transported each individual to each tethering site and we immobilized each fish using small doses of the anesthetic benzocaine (ethyl p-aminobenzoate). Each tether comprised a monofilament line (1.5 m long, 0.10 mm in diameter), one end being attached to the lower jaw of each fish individual with a small fishing hook (5 mm long, 0.20 mm in diameter) and the other end to a small lead weight (1 kg), which was placed at the bottom. Each tether was separated by more than 5 m from each other. We allowed fish to recover from anesthesia with each tether before placing them on the substrate. Preliminary experiments showed no mortality directly caused by the tether. We conducted the experiment using 6 replicates of 5 tethered fish in each habitat on 2 different dates ($n = 30$) between 10:00 and 15:00 h. At the kelp-dominated site (Zapallar), tethered individuals were placed under the kelp canopy. We recorded presence and absence of tethered individuals after 30 to 35 min (mortality rate) between 12 and 18 m depth. Some predatory fish that preyed upon the tethered triplefins became hooked,

in which case we recorded, identified, and then released when possible.

We used *t*-tests to examine differences in mortality rates (proportional mortality) for tethered individuals between the kelp and non-kelp habitat. Prior to the analysis, we improved homogeneity of variances by arcsine transformation (homogeneity of variance test, Fligner-Killeen, $df = 1$, $p = 0.049$). All statistical analyses were conducted using the R statistical software (R Core Team 2015).

RESULTS

Population size, habitat availability, and habitat use of *Helcogrammoides cunninghami*

The mean abundance of *H. cunninghami* ranged between 1.3 and 5.8 individuals per m^2 . We observed the highest densities at the non-kelp study site Montemar followed by Zapallar, Los Molles, Quintay, Algarrobo, El Arrayan, and El Frances, with statistically significant between-site differences (GLM; $df = 6$, $F = 4.39$, $p < 0.001$) (Fig. 2a). *H. cunninghami* tended to have higher abundances between 10 and 15 m depth at most sites, but no significant differences were detected among different depths. These site and depth differences in abundance of *H. cunninghami* led to a significant interaction of these 2 factors (GLM; $df = 6$, $F = 2.33$, $p = 0.03$), but particularly at Montemar, where this triplefin reached its highest abundances at deeper (>12 m) depths.

Triplefin tended to prefer one particular microhabitat at most sites, but we observed substantial between-site variation in the type of preferred habitat. Corticated foliose algae were used preferentially in Los Molles, Zapallar, and Quintay, where the 95% CI did not overlap 0 (a significant use of this microhabitat type). Lithic substrata were used significantly more at Montemar while crustose algae were preferentially used at El Frances and bryozoans at Algarrobo. No preferred microhabitat was detected at El Arrayan, where a non-significant tendency to use crustose algae was observed but the 95% CI overlapped 0 (Fig. 3).

Lastly, there were significant associations between the abundance of

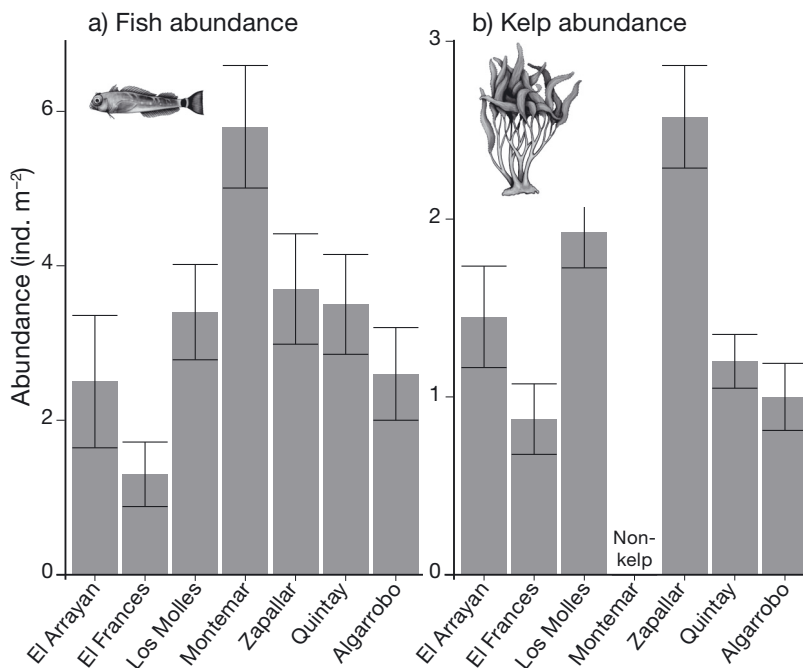


Fig. 2. Mean (\pm SE) abundance of (a) triplefin *Helcogrammoides cunninghami* and (b) kelp *Lessonia trabeculata* per sampling site, pooled by transects

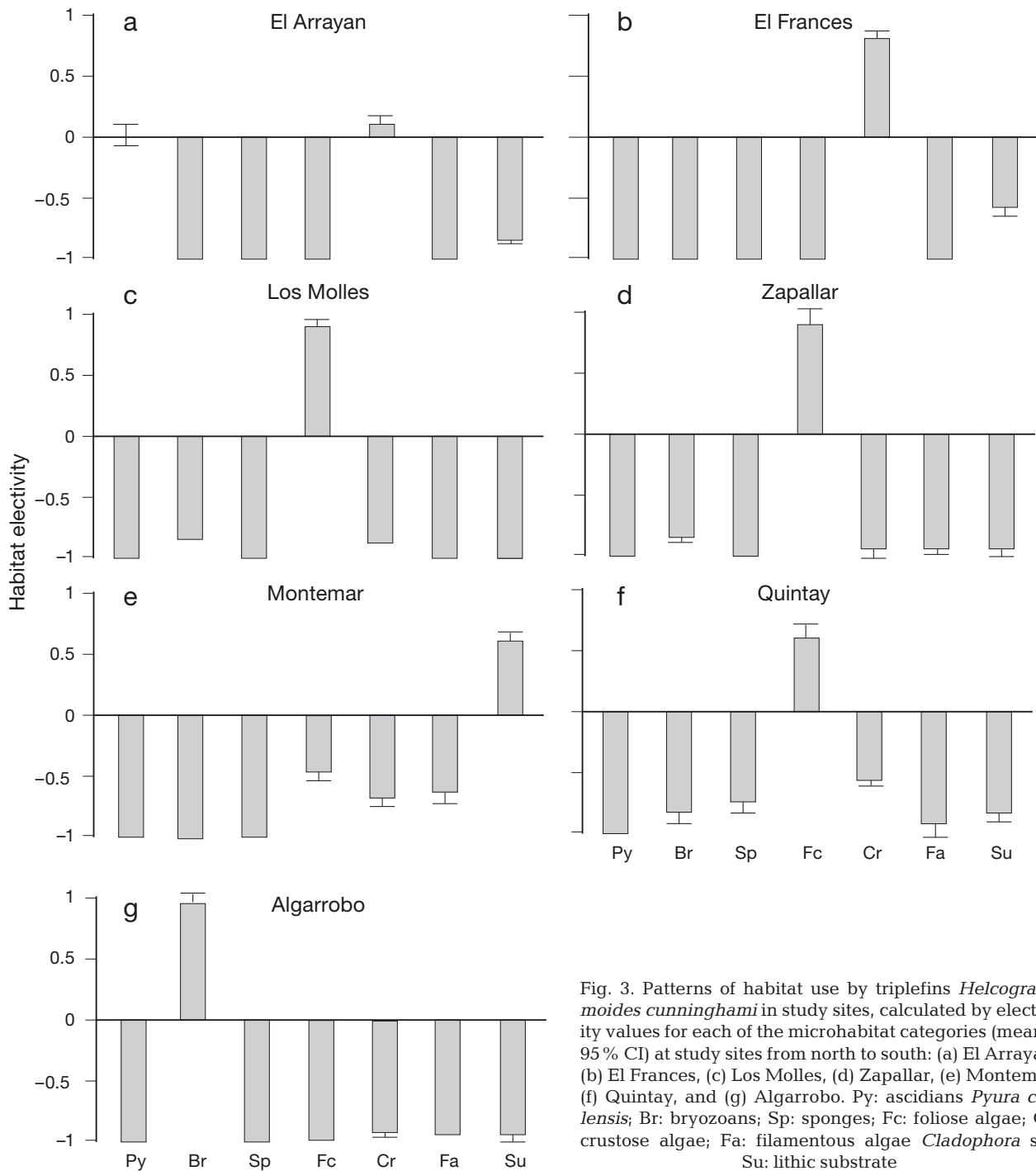


Fig. 3. Patterns of habitat use by triplefins *Helcogrammoides cunninghami* in study sites, calculated by electivity values for each of the microhabitat categories (mean \pm 95 % CI) at study sites from north to south: (a) El Arrayan, (b) El Frances, (c) Los Molles, (d) Zapallar, (e) Montemar, (f) Quintay, and (g) Algarrobo. Py: ascidians *Pyura chilensis*; Br: bryozoans; Sp: sponges; Fc: foliose algae; Cr: crustose algae; Fa: filamentous algae *Cladophora* sp.; Su: lithic substrate

triplefins and several habitat attributes at both transect and site levels. At the transect level, we detected significant positive associations between this fish and understory algae as well as bryozoans. A significant negative association was only observed between the abundance of this fish and the availability of bare substrata (empty rocks) (see Fig. S1a in the Supplement at www.int-res.com/articles/suppl

[/m559p147_supp.pdf](http://www.int-res.com/articles/suppl/m559p147_supp.pdf)). As occurred at the transect level, a significant negative association at the site level was only observed between fish and bare substrata, revealing the importance of biological substratum for the abundance of this species (see Fig. S1b).

The abundance of benthic kelp *Lessonia trabeculata* also varied significantly between sites (GLM;

df = 6, $F = 13.62$, $p < 0.00001$). The highest abundances were observed at Zapallar followed by Los Molles, both of which contained more than 2 individuals per m^2 . El Frances, Quintay, and Algarrobo had similar abundances of kelp, whereas Montemar lacked a kelp bed (see Fig. 2b). Moreover, neither depth nor the interaction of depth and site influenced the abundance of this habitat-forming species (GLM; df = 6, $F = 1.16$, $p = 0.3$).

We detected a significant positive association between the abundance of kelp and sea sponges and bryozoans at both transect and site levels. On the contrary, a significant negative association was observed between kelp abundance and foliose algae at both small and large spatial scales. A negative trend in abundance between kelp and bare substratum was observed at the transect level but not at the site level (see Fig. S2 in the Supplement).

Laboratory choice experiment

The behavioral preference of 75 individuals of *H. cunninghami* evaluated in the choice chamber resulted in 22 preferring crustose algae, 21 preferring lithic substrata, 16 preferring corticated foliose algae, 12 individuals showing no choice, and only 4 individuals choosing the kelp treatment. This distribution was significantly different from the expected distribution of H_0 (15:15:15:15:15; BCD test, df = 74, n = 5, $p = 0.01$). Crustose algae and lithic (small boulder, cobbles) substrata were chosen significantly more often than the expected frequency and foliose algae were selected just above the expected frequency. The treatments identified as no choice and kelp were chosen significantly less often than the expected frequency (Fig. 4a).

Field-predation experiment

The mortality rate of tethered fish varied significantly between kelp and non-kelp habitats (t -test, df = 6, $t = 2.58$, $p = 0.04$). A 61% proportional mortality rate was detected in kelp habitats while a 27% mortality rate was detected in non-kelp habitats (Fig. 4b). The predatory fishes that preyed upon tethered *H. cunninghami* included *Auchenionchus microcirrhis*, *Calliclinus genicuttatus*, *Cheilodactylus variegatus*, and *Pinguipes chilensis* in the kelp-dominated habitat; juvenile and adult *P. chilensis* were the only predatory fishes observed in non-kelp-dominated habitats.

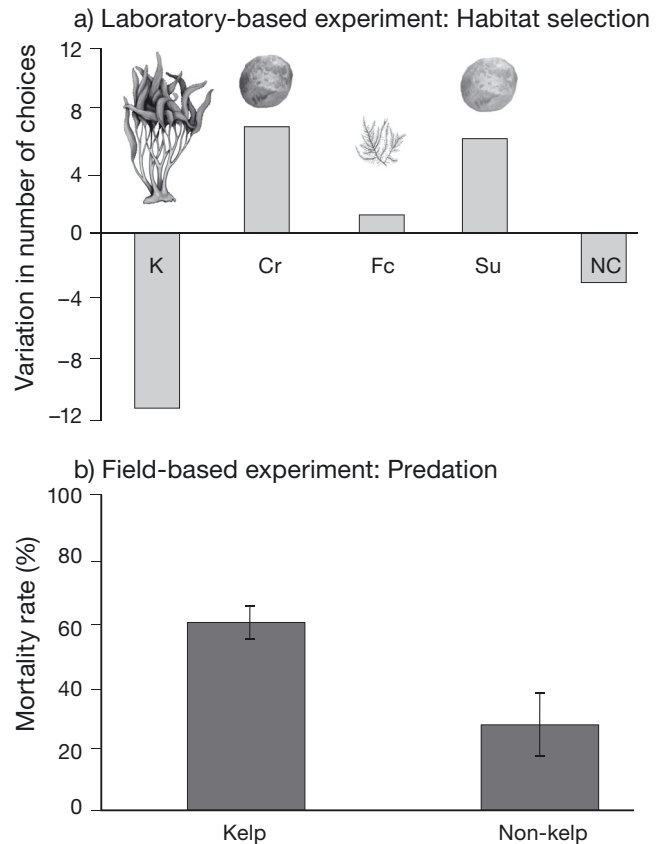


Fig. 4. (a) Laboratory-based experiment on *Helcogrammoides cunninghami* behavioral preference for microhabitats, illustrated as deviation of habitat selection frequency from the expected null distribution (see 'Materials and methods: Laboratory choice experiment' for expected distributions in each of the experiments). K: Kelp; Cr: crustose algae; Fc: foliose algae; Su: substrate made of boulders; NC: no choice. (b) Field-based predation experiment, mean (\pm SE) mortality rate of tethered *H. cunninghami* in 2 contrasting habitats

DISCUSSION

Our study combined field and laboratory experimental and observational evidence to produce key insights into microhabitat selection by a common temperate reef fish, showing that small-scale selectivity and biotic interactions such as predation can help explain broader patterns of abundance in this species according to site-specific habitat conditions across central Chile. The distribution of *Helcogrammoides cunninghami* derives from an attempt of individuals to discriminate between both the quality of the habitat and how habitat itself is distributed (availability). Specifically, the underuse of kelp habitats in the laboratory and the field appears to be due to increased predation in kelp stands. Biotic interactions are known to heavily influence animal distribution and

habitat use in Chilean rocky intertidal environments (Aguilera & Navarrete 2011, Manzur & Navarrete 2011), but ours is the first test of this assertion on Chilean subtidal reefs. These mechanisms influence both the population density and demographics of reef fishes with bipartite life histories (Shima 2001, McDermott & Shima 2006), and in the case of *H. cunninghami*, appear to drive regional patterns of abundance. Selective preferences for habitats that provide shelter and/or food are most likely an evolutionary response to increased population fitness in a heterogeneous environment such as that found on temperate reefs.

We found that kelp, which is generally considered to be the major habitat-structuring species in the region, is negatively correlated with this species' preferred habitat type (understory macroalgae) at both transect and site levels. Kelps reduce the abundance of understory algae by shading, scouring and/or through allelochemical exudates (Kennelly 1987, 1989). Reduction of understory algae by kelp may limit the amount of habitat available for cryptic species such as *H. cunninghami* by decreasing the availability of their prey and refuges from predators. Secondly, there are more benthic predators in kelp beds (Angel & Ojeda 2001, Graham 2004, Pérez-Matus et al. 2012), and more species tend to forage in these systems, which may yield greater inter-specific competition for food. Habitat availability (mainly microhabitat) and predation risk within kelp beds are small-scale phenomena and both (not analyzed together in the present study) probably affected the abundance of juvenile and adult triplefins at broad spatial scales in our field surveys.

The aversion to kelp habitats in both field and laboratory observations is strong evidence that triplefin abundances may be related to the availability of suitable habitat at mesoscales, a common pattern of habitat/species distributions (Munday 2002, Wellenreuther et al. 2008). Individuals tend to discriminate between habitat types in order to get rewards from their selection and this can be observed by differences in abundance between habitat types (Cote et al. 2013, Fulton et al. 2016). Our field experiment revealed that this reef fish exhibits strong preference toward particular biogenic habitats (i.e. foliose algae, encrusting algae) and avoids bare substrate. This is probably due to a lack of both appropriate refuge and food availability (Brooker et al. 2013). Algae provide habitat for prey species of the triplefin, while foliose algae and bryozoans may provide shelter from predators. However, the preference for biological substrata was not apparent at the non-kelp site (Montemar). This could be an indication that in the

absence of the greater predation risk associated with kelp beds, triplefins show less aversion to relatively higher risk microhabitats with less protective cover. Combined with our field-predation results, it appears that predation risk is the primary mechanism driving this behavior.

Selection of a preferred habitat is an essential decision with long-term implications for fitness and ultimately drives species distributions (Crowe & Underwood 1998, Franklin et al. 2000, Fulton et al. 2016). As such, we would expect this choice to be instinctual and consistently accurate if a certain habitat is chosen to increase fitness. However, we saw disparities between preferences in laboratory and field observations, particularly in our non-kelp site. For instance, kelp abundance correlates negatively with high quality habitat such as foliose algae (which is preferred by fish at multiple sites) but it was absent at this site (see Fig. S2 in the Supplement). We can provide non-mutually exclusive explanations for the lack of choice for foliose algae in the laboratory experimental chamber. First, triplefins were collected from a nearby non-kelp site (Montemar), which lacks foliose algae as part of the understory. Therefore, we offered a high-quality habitat type (assumed from the field observations) that may not have been readily identifiable by individuals in the laboratory. Another possible explanation is that, prior to our laboratory essays, we removed all the potential prey (i.e. amphipods, small gastropods) from each experimental habitat, which may have reduced their appeal in the assays. Presumably, algal habitats have more epibionts than the crustose algae and bare rock substrates that were preferred in our experiment (Taylor & Cole 1994). Future studies should include both parameters in order to disentangle the roles of predator avoidance versus prey availability in determining these habitat choices (Luttbeg & Sih 2004, Underwood et al. 2004, Pruitt et al. 2012).

Recent evidence suggests that the different substratum types produced by the combined physical and biological elements of the reefscape are key to explaining the distribution and diversification of fish assemblages in temperate reefs (Wellenreuther et al. 2007, Fulton et al. 2016). In temperate rocky reefs, linkages between habitat composition and fish abundance and diversity have been experimentally tested (Levin & Hay 1996, Pérez-Matus & Shima 2010), suggesting that most fishes respond in abundance to different types of habitat. Recently, Fulton et al. (2016) determined that fine-scale microhabitat availability promotes abundance at the regional scale of juveniles and adults of several reef fishes.

In our study, we have found that the heterogeneous nature of rocky reef habitats supports a conspicuous fish community with numerous predators (see Pérez-Matus et al. 2012). Kelp habitats are known to facilitate higher trophic-level fish predators that tend to consume meso-predators/herbivores (Koenigs et al. 2015), which may set negative consequences for the abundance of our focal fish species in this ecosystem. Moreover, kelp abundance is negatively correlated with several understory microhabitats (i.e. algae), which reduces the availability of suitable quality habitat for this species (Kennelly 1989; see Fig. S2 in the Supplement). Thus we hypothesized that this species is more abundant in non-kelp rocky habitat (such as Montemar) than in kelp beds. Although more sampling is needed in non-kelp-dominated habitat, evidence from this study system has revealed that, outside of kelp beds, this fish is a successful predator of benthic eggs guarded by another reef fish, *Chromis crasma* (Navarrete-Fernández et al. 2014). Although we did not detect a significant negative correlation between kelp and this reef fish, presumably due to the dominance of encrusting algae (a preferred habitat for this species) in kelp beds, we consider that the distribution of other microhabitats that are negatively affected by kelp abundance influences the abundance of this cryptic reef fish at a larger regional scale. This provides a first step towards understanding and setting hypotheses for the coupling of both local and regional effects of habitat on the abundance of a reef fish. Identifying the effects of the density of reef fish and the availability of settlement habitat, as well as their combined influence, is important for further analysis of the mesoscale processes affecting the distribution of reef fishes.

The present study provides examples of how small-scale processes, such as behavioral preference for a habitat type, active selection of that habitat's characteristics, and avoidance of high-predation fringe areas, interact and might influence large-scale processes in the abundance and distribution of triplefins. We show evidence of different predatory effects in 2 contrasting habitat types, whereby the attack rate by piscivorous fishes may influence the distribution of *H. cunninghami*. Although we evaluated the effect of biotic interactions and habitat types separately, we consider this as a first step towards understanding the multiple and possibly synergistic mechanisms affecting population sizes and demographics and spatial distribution among sites. However, the hierarchies of these mechanisms affecting population structures and the distribution and abundance of species in the highly heterogeneous kelp forest ecosystem remain to be understood.

Acknowledgements. We thank Teresa Navarrete-Fernández, Maite Paz Goicoechea, Sergio Carrasco, and the SUBE-LAB team for assistance in the field and in the laboratory experiments. We thank Checho from Caleta Zapallar for helping us with the boat and skipper while underwater. Three anonymous reviewers provided helpful comments on earlier drafts of this manuscript. We thank J. P. Saez for illustrations and drawings in the figures. This project was funded by Fondecyt grants #11110351 and #1151094 to A.P.M.

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*Editorial responsibility: Kenneth Heck,
Dauphin Island, Alabama, USA*

*Submitted: December 29, 2015; Accepted: September 6, 2016
Proofs received from author(s): October 13, 2016*