

CRYPISIS IN *PARAXANTHUS BARBIGER* (DECAPODA: BRACHYURA): MECHANISMS AGAINST VISUAL PREDATORS

Karen C. Manríquez, Luís M. Pardo, R. J. David Wells, and Alvaro T. Palma

(KCM) Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile (kmanriquez@udec.cl);

(LMP) Universidad Austral de Chile, Instituto de Biología Marina, Laboratorio Costero Calfuco, Casilla 567, Valdivia, Chile (luisparado@uach.cl);

(RJDW) Texas A&M University, Department of Marine Biology, 5007 Avenue U, Galveston, Texas 77551, U.S.A. (rwells4@lsu.edu);

(ATP) Departamento de Ecología, Pontificia Universidad Católica de Chile and Center for Advanced Studies in Ecology and Biodiversity (CASEB), Alameda 340 Casilla 114-D, Santiago, Chile (apalma@bio.puc.cl)

A B S T R A C T

Marine organisms have evolved a suite of responses to minimize the exposure to predators. Visual crypsis is one such strategy to avoid predation. *Paraxanthus barbiger* (Poeppig, 1836) is a species that exhibits different color morphotypes over heterogeneous substrates as a means of protection against visual predators. Our main objectives were to quantify the occurrence of color morphotypes over a three-year period and to investigate, via an experimental approach, on the possible mechanisms involved that would provide crypsis to this species. Field surveys occurred over a three-year period at two nearby sites on the central Chilean coast. Initial observations indicated that small juvenile *P. barbiger* exhibited higher degrees of color polymorphism than larger (> 20 mm carapace width) conspecifics. Furthermore, survival rates of small (< 10 mm carapace width) *P. barbiger* exposed to predators increased on heterogeneous substrata under both natural and laboratory conditions. Laboratory experiments further demonstrated that newly settled *P. barbiger* actively select heterogeneous substrata. Hence, cryptic responses of this species might reduce predation-mediated mortality through color pattern disruption of individuals with respect to their environment.

KEY WORDS: brachyurans, Chilean coast, crypsis, predation

INTRODUCTION

The ecological and evolutionary success of many organisms depends, among other factors, on their ability to cope with predation. Predation can reduce, increase or disrupt the relative abundance of organisms in a given environment (Taylor, 1984). However, predation can differentially affect individuals, particularly species that undergo important ontogenetic size changes and are therefore more susceptible to predation (Palma & Steneck, 2001). Predation in marine systems represents an important agent regulating population size, particularly in species with complex life cycles where the impact of predation is particularly high on recently settled individuals. Many organisms (terrestrial as well as marine) exhibit multiple strategies for avoiding predation such as behavioral changes, morphology, and color and chemical composition, among others (Main, 1987; Stachowicz and Hay, 1996; Fiorito and Gherardi, 1999; Boal et al., 2000; Palma and Steneck, 2001; García and Sih, 2002; Palma et al., 2003).

In the marine realm, brachyuran decapod crustaceans undergo a transition involving different pelagic larval stages that, after a variable period in the plankton (hours to months), settle into a benthic environment and recruit into the adult population (Butman, 1987; Palma et al., 2003). Newly settled decapods, are particularly vulnerable to visual predators (Wahle and Steneck, 1992; Beck, 1995; Stachowicz and Hay, 1996; Palma et al., 1998), and have been shown to experience high

losses due to predation (Palma et al., 1998). Thus, it is important to identify the mechanisms responsible for mediating predation during the early life stages of marine decapods.

Several studies exist describing mechanisms associated with the reduction of losses due to predation in decapods, such as the use of heterogeneous structures of the environment as shelter (Wahle and Steneck, 1992; Beck, 1995; Stachowicz and Hay, 1996; Mima et al., 2003), decorating behavior (Wicksten, 1979; Cruz-Rivera, 2001), detection of predators through chemical signals (Weissburg, 1994; Welch et al., 1997; Finelli et al., 2000) and visual crypsis with the surrounding environment (Palma and Steneck, 2001; Palma et al., 2003). Aside the obvious differences, an important article that revises the diverse mechanisms utilized by mobile preys (exemplified by sea hares) highlights the relevance of several passive and active anti-predatory behaviors triggered by predators (Johnson and Willows, 1999). The very detailed description and discussion about the different defense mechanisms in sea hares can serve as reference for the type of mechanisms utilized by brachyuran decapods.

Among the factors mentioned above, visual crypsis is one of the least known anti-predatory mechanisms employed by brachyuran decapods and is defined as the possession of color or shape that resembles that of the surrounding environment (Hacker and Madin, 1991). Cryptic color has been shown to reduce vulnerability against visual predators

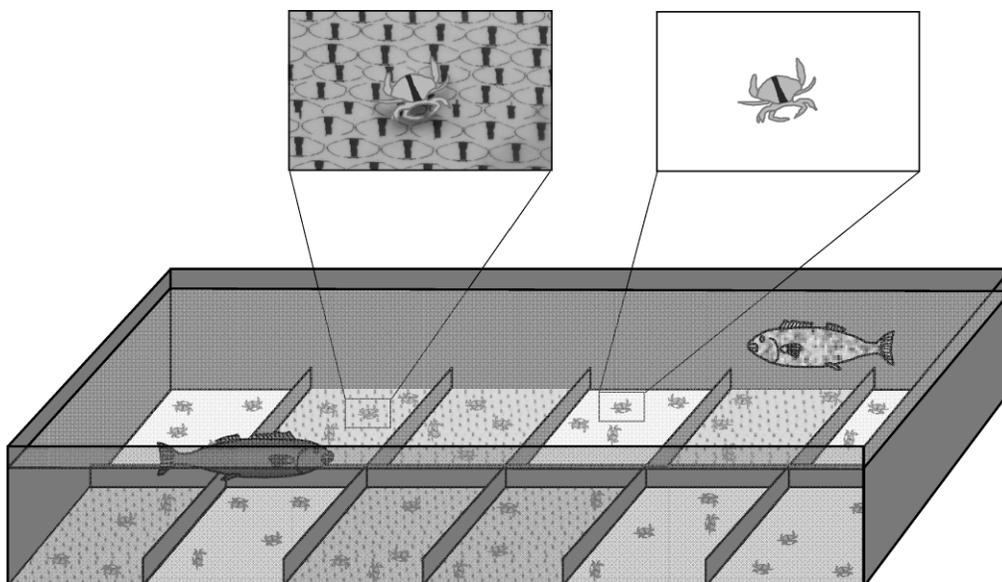


Fig. 1. Diagram representing the layout of the experiment designed to quantify the predation rate upon small (3-5 mm CW) *P. barbiger* exposed to two species of predatory fish (*Sebastes capensis* and *Pinguipes chilensis*).

(Main, 1987), and has been suggested as an important selective process for differential habitat use by prey species (Mercurio et al., 1985, Johnson and Willows, 1999). Studies by Hogarth (1978) and Palma et al., (2001, 2003) have suggested color polymorphism that disappears as individuals reach larger sizes as a common pattern among newly settled brachyuran decapod species.

Merilaita et al. (1999) proposed a model that considers the optimization of cryptic color in heterogeneous environments. This model takes into account factors that affect the survivorship of individuals over a given habitat, such as possession of cryptic color, the probability of encountering a visual predator on a specific habitat that could increase or decrease survivorship, prey detection ability of predators, and the prey's probability of escaping based on color patterns. Merilaita (1998) also suggests that visual crypsis of isopods represents an antipredatory trait through a mechanism of contour and shape disruption by blending individuals against the shape and geometry of the background.

Along the central coast of Chile several species of crabs display cryptic colors (Palma et al., 2003), an attribute particularly conspicuous in the species *Paraxanthus barbiger* (Poepfig, 1836). Juvenile *P. barbiger* exhibit different morphotypes, which may provide protection against visual predators (mainly fishes), turning them cryptic, particularly on the heterogeneous cobbles and shell-hash matrix where they naturally occur. The diverse color patterns exhibited by juvenile *P. barbiger* range from white (including a combination of brown and black stripes and spots), brown (with a combination of white spots and stripes), and tan (with a combination of diverse colored stripes and spots), among others. As individuals grow the color patterns disappear and the adult light purple color becomes dominant (Palma et al., 2003).

Paraxanthus barbiger recruits year round, but more intensively during the spring and summer months over shell-hash and cobble bottoms (Palma et al., 2006; Pardo et al., 2007), and numerically represents the dominant crab

species of the shallow subtidal north-central Chilean coast (Palma et al., 2006). This species is also a predominant component in the diet of several different species of benthic and demersal fish, such as *Pinguipes chilensis* (Valenciennes, 1833), *Sebastes capensis* (Valenciennes 1833), *Protatilus jugularis* (Valenciennes, 1833), *Eleginus maclovinus* (Cuvier & Valenciennes, 1830), and *Cheilodactylus variegatus* (Valenciennes, 1833) (Bahamonde, 1950; Meléndez, 1989; Retamal, 1995; Palma and Ojeda, 2002; González and Oyarzún, 2003). However, recent experiments using exclusion cages suggest predators have little impact on the local abundance of juvenile *P. barbiger* (Pardo et al., 2007). Thus, crypsis displayed by juvenile *P. barbiger* may serve a function of reducing exposure to predators.

Our research involved three main objectives: 1) to quantify the color morphs present in *P. barbiger* among different ontogenetic stages, 2) to experimentally assess the effectiveness of possessing a cryptic color during the juvenile stage, and 3) to identify plausible mechanisms through which the cryptic color displayed by juveniles of *P. barbiger* confers them an effective protection, particularly against visual predators.

MATERIALS AND METHODS

Collection of Specimens and Study Sites

Selected individuals to quantify the color patterns in *P. barbiger* were obtained from two sites near the Hualpén Peninsula, spaced several hundred meters apart, south of the San Vicente Bay nearby Concepción, Chile. One of the sites (Lenga) is located on the bay side of the peninsula (36°44'43.6"S, 73°11'14.6"W) and the other site (Ensenada) is located on the west side of the peninsula (36°45'19.2"S, 73°11'46.2"W). Samples of organisms were obtained by suction sampling cobble and shell-hash bottoms (Holm, 1990; Palma et al., 2003), from average depths of 10 m utilizing an airlift device with a 1 mm mesh size bag attached to its end (methodology utilized by Wahle and Steneck, 1991; Palma and Steneck, 2001; Palma et al., 2006). Two divers haphazardly placed 50 × 50 cm frames on the bottom and loose material was removed through the suctioning device. Ten frames were surveyed monthly at each site from June 2002 to July 2004 and a total of 3369 individuals of this species were collected. Samples were transported to

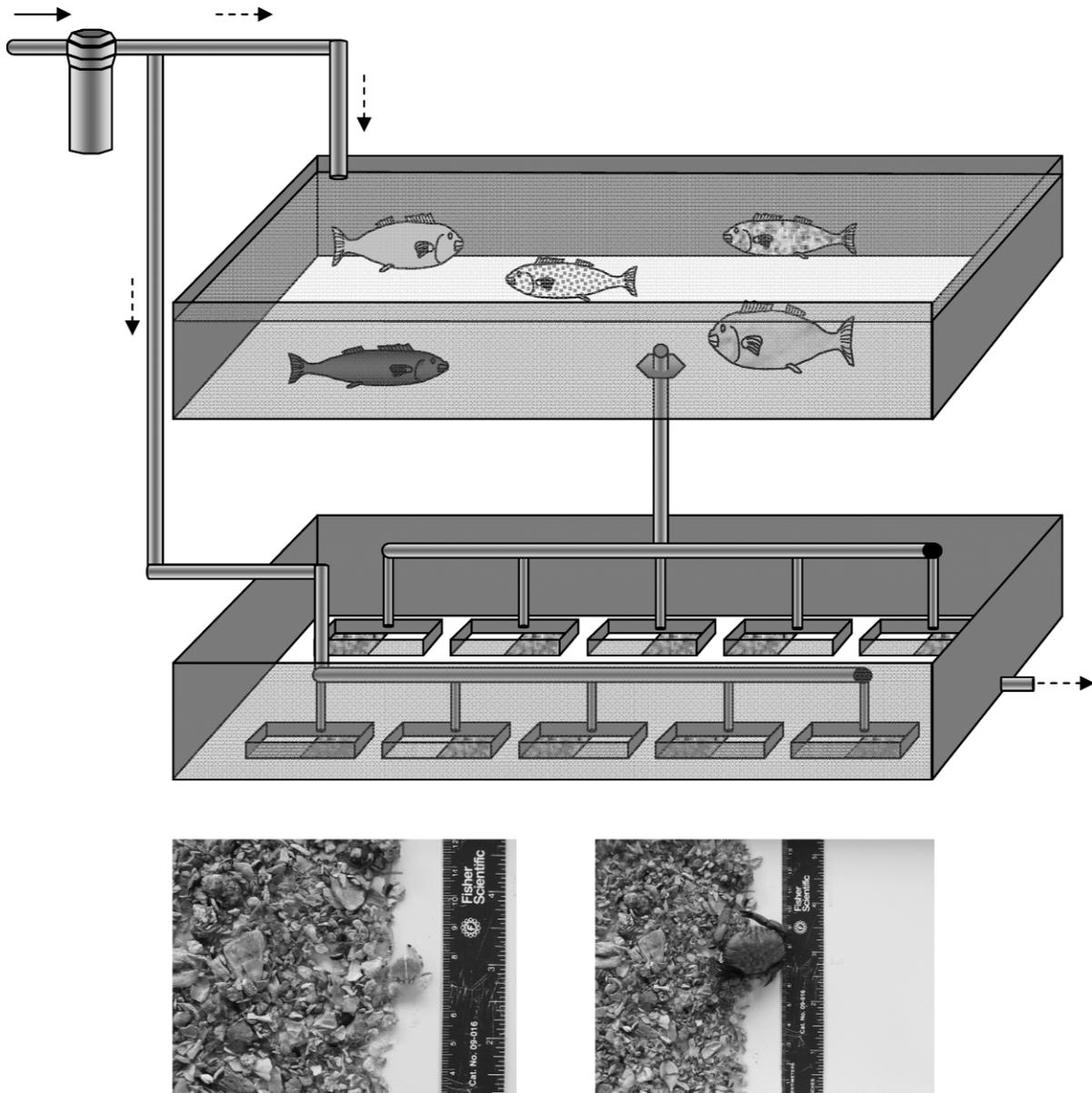


Fig. 2. Diagram representing the layout of the experiment designed to quantify the differential use of substrate types (shell-hash vs. bare) by two different size classes of *P. barbiger* (< 10 and 25-30 mm CW) under the presence of fish odor and of filtered water without the presence of fish (arrows indicate direction of water flow).

the nearby lab where individuals were sorted, measured to the nearest mm carapace width (CW), individual color patterns were recorded and placed individually in small containers inside a large tank with a continuous flow-through sea water system. Individuals were fed daily with clam tissue and kept in containers until used in experimental trials.

Quantification of Color Patterns in *Paraxanthus barbiger*

The identification and quantification of color patterns associated with the different size ranges was done following the methods of Palma et al. (2003). We quantified the color polymorphism in all the individuals surveyed by employing a standardized color classification scheme in which crabs colored differently than the drab purple adults were considered polychromatic. A total of 59 color patterns (all variations on a theme) were identified; however, we summarized them into 5 broad morphs (categories) for our analyses. For example, individuals with white background carapace can have different colored spots, however, we grouped them all in the single category of white with spots. As with other decapods (Palma and Steneck, 2001) the color of individual crabs only changed between molts. Fifteen

size classes were determined (in mm carapace width, CW), ranging from 3 to > 60. We use a two way ANOVA to test for changes in diversity of color morphs among sampling years and sizes. Data were log-transformed to meet the assumption of homogeneity of variance which was achieved using the Levine test. In addition, we determined the size at which individuals of *P. barbiger* attained the adult monochromatic morph using a logistic regression equation between size classes and color condition (cryptic or monochromatic). We used the inverse prediction function of this equation to estimate the size (with 95% confidence intervals) at which 50% of crabs had attained the monochromatic color. We used the likelihood ratio test to detect differences in the size of change among years, null differences were found. Since the factor year did not improve the logistic model we therefore pooled years to perform a reduced model, where only size was an independent factor (Hosmer and Lemeshow, 2000).

Assessment of Cypsis-Mediated Predation Rates

Cryptic-mediated predation upon juveniles of *P. barbiger* was experimentally evaluated in the field. Juveniles (11.2 ± 3.1 mm CW) with polymorphic

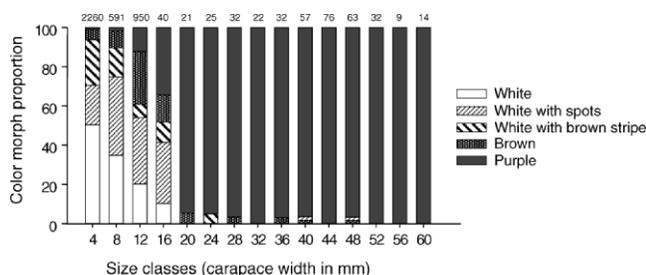


Fig. 3. Proportion of the most common color morph patterns of *P. barbiger* by size class. Numbers above each bar represent the total number of individuals quantified within each size class.

colors were individually tethered on ceramic plates (20 × 20 cm) representing two different types of substrata. One set of 20 individuals were tethered on bare (white) plates and 41 individuals were tethered on plates with natural shell-hash (previously rinsed and dried) that was glued to the surface forming a thin layer. Individuals were tethered using 2.7 kg resistant monofilament by creating a knot and securing with instant glue to the rear end of the carapace. A short (10 cm long) monofilament, attached to the center of the plate was used to secure each individual to the plate, thus allowing them to move freely within this range. To test for the effectiveness of the technique and to minimize interpretation problems, all plates with tethered individuals were left inside a flowing seawater tank for 24 h prior to deployment in the field.

To determine if color and shape contour disruption corresponds to a crypsis-mediated mechanism in *P. barbiger* we designed a laboratory experiment using 3–5 mm CW individuals that were exposed to predatory fish. This size range exhibits the greatest frequency of occurrence of color patterns (Palma et al., 2003). A total of 288 individuals of the most frequent color morph (white with a brown stripe) were placed on bottoms with contrasting color. A large tray (2.2 × 0.9 × 0.24 m) with flowing seawater was subdivided in 12 equal-size sections using rigid 5-cm tall opaque plastic sheets and two types of artificial bottom patterns were randomly used to cover the bottom. The subdivisions allowed the fish to freely swim throughout the tank but prevented crabs from leaving their individual sections (Fig. 1). The lack of crab movement was tested after observing no change in the number of crabs remaining inside individual sections for 48 h prior to the inclusion of fish in the system. Artificial bottoms consisted of white, plastic covered sheets of paper, half of them fully covered (printed) with the shape, size and color pattern of the crabs selected for this experiment (white with brown stripe, see details in Fig. 1). The substrata units were randomly placed in order to fully cover the bottom of the tank (Fig. 1). Two known predators of *P. barbiger* (*S. capensis* and *P. chilensis*) were used in this experiment as they are locally abundant demersal fish that have diets comprised of *P. barbiger* (Bahamonde, 1950; Ojeda and Fariña, 1996; González and Oyarzún, 2003). Fish were acclimated for at least two weeks before inclusion into large flowing seawater tanks. A total of 12 adult fish (6 of each species) were used in the experiment and one individual of each species was included inside the experimental tank during each 12 hour trial. Trials started with the addition of 48 individuals of *P. barbiger* (groups of 4 inside each subdivision) and the fish soon after. At the end of each trial missing crabs were counted and the remaining were retrieved. Experiments were repeated 6 times (trials) and in each opportunity both fish and crabs (surviving ones) were replaced and bottom types randomly reassigned. The percentage of crabs eaten from each substrate type was compared using a paired *t* test where each trial was considered a replicate. An alpha level of 0.05 was considered in the study (Zar, 1996).

Table 1. Two-way ANOVA for the colormorphs variation exhibited by individuals of different size classes of the species *Paraxanthus barbiger* quantified during three consecutive years.

	df.	MS	F	P
Year	2	0.1964	6.4374	0.0034
Size	14	0.5410	17.7310	< 0.0001
Year * Size	28	0.0237	0.7771	0.7583
Error	45	0.0305		

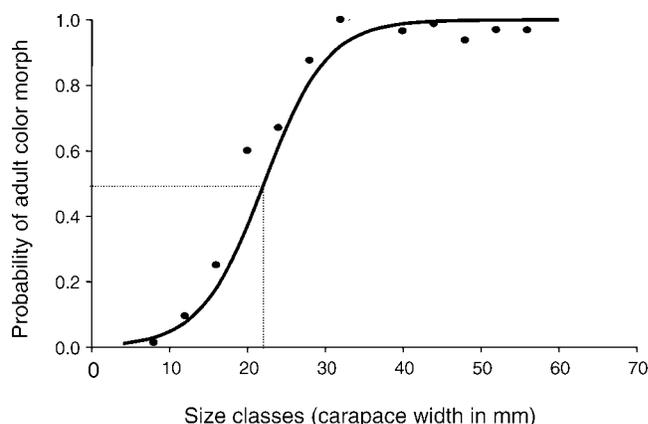


Fig. 4. Logistic regression for the estimation of the 50% probability of individuals attaining the adult monochromatic color morph. Dots correspond to real data.

Substrate Selection Under Predator's Odor Stimulation

Active habitat selection of *P. barbiger* as a response to the presence (odor) of known predators (fish) was experimentally evaluated. Two different size classes of crabs (< 10 and 25–30 mm CW) (factor size) were allowed to choose between two different substrate types (response variable), with and without the odor of predatory fish (factor water type). Selection criteria for the two size classes of crabs were such that small crabs (< 10 mm CW) corresponded to newly settled (young-of-the-year) individuals and the larger crabs (25–30 mm CW) corresponded to individuals that were less susceptible to predation and exhibited fewer color morphs. Ten small plastic trays (20 × 40 × 5 cm) were each divided in two by pasting natural shell hash in one half and leaving the rest bare. Half of the trays received seawater that was previously passed through a standard 25 µm polypropylene filter (control) and the other half received water, which after passing through the same filter, fed the head tank (1.8 × 0.4 × 0.2 m) where one individual of five different predatory fish species (*C. variegatus*, *E. maclovinus*, *P. chilensis*, *P. jugularis*, and *S. capensis*) were kept (Fig. 2). The same experiment was performed twice, by simultaneously placing 9 individuals in the middle of each small tray (experimental unit) and exposed to the stimulus for 3 h. The number of individuals located on the heterogeneous substrate type at the end of each trial was recorded and used as the response variable. Individuals found on the edge of both substrates were discarded from the record. Proportions obtained for each set of trays (10 for small and 10 for large crabs in total) were arcsin transformed to meet both normality and homogeneity of variance assumptions and analyzed by performing a 2-way ANOVA and a 0.05 confidence interval was considered (Zar, 1996).

RESULTS

Quantification of Color Patterns

Wild caught *P. barbiger* exhibited variability in the type of color (color morphs) along its ontogeny, with newly settled individuals (3–5 mm CW) displaying the greatest diversity, in addition to being the most abundant size range (Fig. 3). The most frequent morphs within the smallest size ranges were white and white with darker spots and a brown stripe along the carapace (Fig. 3). The variety of different morphs decreased as individuals attained larger sizes until they adopted the monochromatic adult-type (purple) color. No significant interaction between year and size suggests that the relationship between size and number of different color morphs was consistent for the three years sampled (Table 1). Considering the sum of all field surveys and diversity of color morphs recorded, we grouped them into five color groups (including the adult color) that were predominant (Fig. 3). The size at which individual's change

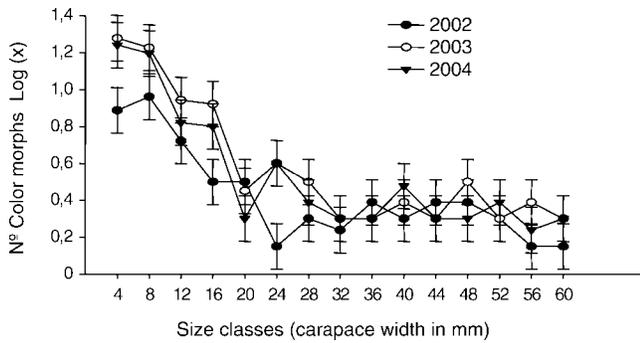


Fig. 5. Variation in the number of color morphs (log transformed) present in *P. barbiger* for 15 size classes quantified during three consecutive years.

to monochromatic color occurred primarily between 23.2 and 26.2 mm CW (logistic regression; Likelihood ratio test to fit model, $G^2 = 1836$, $df = 1$, $P < 0,0001$, logistic $R^2 = 0.74$, Fig. 4). This size-related (ontogenetic) change in color morph was consistent during the three years of surveys (Fig. 5). The probability curve indicates few small individuals do not exhibit cryptic color (1 out of 122) and above 40 mm few individuals were found that displayed cryptic morphs (Fig. 4).

Assessment of Crypsis-Mediated Predation Rates

In the field tethering experiment individual juvenile-size *P. barbiger* that were attached to bare ceramic plates survived less than conspecifics over plates coated with shell-hash. Specifically, 30% survived over bare plates compared to 61% with shell-hash, which is hypothesized to represent a cryptic polychromatic background ($F_{1,59} = 5.452$, $P = 0.023$). In addition, results of the laboratory experiment that contrasted background types further indicated crabs enclosed within subdivisions with the bottom covered with crab-shaped drawings exhibited significantly higher survival rates than those on bare background ($t_{5,0.05} = 4.5$, $P = 0.006$; Fig. 6).

Substrate Selection Under Predator’s Odor Stimulation

Individuals of either size range exposed to the odor of fish were mainly found on the shell-hash substrate (Fig. 7). However, in all cases this behavior was high (around 80%) for small crabs, whereas larger individuals used shell hash in a greater proportion when they were exposed to the odor of fish (Table 2). The significant interaction in the ANOVA between the factors ‘size’ and ‘water type’ suggests that there was an intrinsic tendency to use a more heterogeneous substrate by small individuals regardless of the predator stimulus in comparison with larger ones, which actively seek shelter behavior when exposed to the threat of fish.

DISCUSSION

Paraxanthus barbiger exhibits diverse color morphs that are hypothesized to be cryptic on polychromatic background conditions (i.e., shell-hash). This attribute would confer a certain degree of protection, mainly to small-size individuals, against visual predators. Our results agree with previous findings along the coast of Chile (Palma et al., 2003 and 2006) who identified this species as one of the

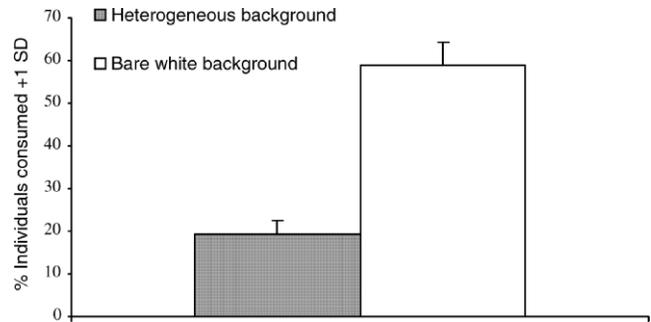


Fig. 6. Percentage of individuals of *P. barbiger* preyed upon by fish inside the experimental arena where individuals were enclosed inside subdivisions with two different types of background (similar crab shape and size vs. bare backgrounds). The total number of individuals utilized in this experiment was 288.

most abundant brachyuran decapods as well as the species displaying the greatest degree of color polymorphism during the early benthic juvenile stage. Camouflage, particularly among marine invertebrates, has been described as a common attribute in species inhabiting environments where visual predators are common (Wicksten, 1979; Hanlon et al., 1999, Merilaita et al., 2001; Palma and Steneck, 2001; Baeza and Stotz, 2003, Sakamoto et al., 2006; Todd et al., 2006; Raimondi et al., 2007). Furthermore, in the shallow subtidal environments of the central Chilean coast several demersal fishes have been identified as important predators upon *P. barbiger* and other brachyuran decapods (González and Oyarzún, 2003).

Results of the field tethering experiment showed that small juveniles effectively suffer important losses due to predation, but individuals present over naturally colored and textured background survive significantly more than those present on bare substratum. Our tethering experiments may not measure natural rates of predation, but rather serve as a proxy for evaluating the relative risk of predation, or the predation potential (Heck and Wilson, 1987; Everett and Ruiz, 1993). Although these results confirm the hypothesized cryptic value of polychromatic juvenile *P. barbiger*, they do not explain the mechanisms involved. In order to approach this, we implemented a laboratory experiment where juvenile crabs were exposed to predatory fish using plain and crab-shape backgrounds. The lower predation rate

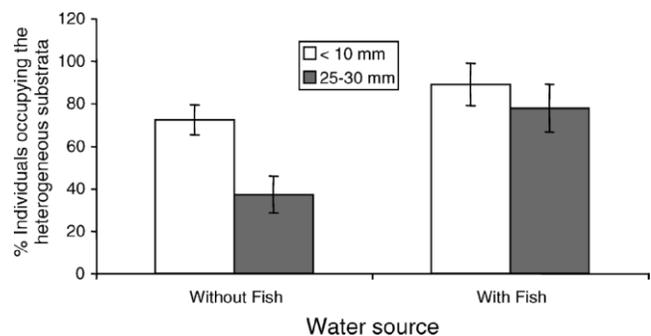


Fig. 7. Percentage of individuals belonging to two different size classes (< 10 and 25-30 mm CW) that occupy the experimental heterogeneous background substrate (shell-hash) under the influence of different water sources (with and without fish odor).

Table 2. Two-way ANOVA for the substrate selection by two size class individuals of *Paraxanthus barbiger* exposed to contrasting water types (with and without the odor of fish).

	df.	MS	F	P
Water type	1	1327,8	13,730	0,0019
Size	1	1854,6	19,177	0,0005
Water type * Size	1	1097,4	11,348	0,0039
Error	16	96,7		

found by individuals that had a crab-shape and color simulated background suggests contour disruption with respect to their surrounding as one possible explanatory mechanism (Merilaita, 1998). The natural environment of *P. barbiger* is composed primarily of shell-hash, and may therefore protect a significant proportion from predators. An additional factor that further enhances the effectiveness of this mechanism is that of reduced mobility of individuals when confronted to predators. Results of the behavioral experiment partially confirmed this hypothesis, whereas all individuals (small as well as medium size juveniles) responded to the odor of predators by preferring the shell-hash over the bare substratum. For small (< 10 mm) individuals the preferential use of heterogeneous substrate was apparently intrinsic and not necessarily linked to the fish stimulus. On the other hand, larger (25-30 mm) individuals effectively reacted to the odor of fish by actively selecting the heterogeneous substrate.

Main (1987) suggests that the sole presence of a physical structure does not provide protection against visual predators, but rather the combination of an active anti-predatory behavior in conjunction with the presence of a structurally complex substrate provides the most effective visual barrier between the predator and its prey. Thus, the effectiveness of the cryptic color patterns exhibited by *P. barbiger* may be enhanced by the ability of individuals to detect chemical signals, a common feature in decapods (Weissburg, 1994; Welch et al., 1997; Johnson and Willows, 1999; Finelli et al., 2000). Our results are therefore consistent with other studies that suggest the existence of color crypsis (Palma and Steneck, 2001; Palma et al., 2003), in combination with their ability of detecting predators and behaving accordingly (Pardo et al., 2007), represents an effective anti-predatory trait that will enhance overall survivorship in a system dominated by visual predators.

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