Distribution patterns of *Tetrapygus niger* (Echinodermata: Echinoidea) off the central Chilean coast

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**ABSTRACT:** We investigated spatial distribution and temporal occurrence patterns of *Tetrapygus niger* in the subtidal zone off the central Chilean coast from March to November 1990. The shallowest portion of the subtidal zone and the shallowest edge of the kelp forest of *Lessonia trabeculata* appeared to be important recruitment zones for this species. We found a significant number of recruits along the bed border, and a marked decrease of urchin abundance toward the center of the kelp. Data obtained in September and November outside the kelp bed showed juvenile urchins (i.e. <24 mm test diameter (TD)) strongly associated with crevices. Size-frequency distributions at 2 m depth for those months also showed a large trough of intermediate-sized individuals (i.e. 15 to 30 mm TD). Temporal analysis of size-frequency distributions of individuals collected outside the kelp showed a relatively slow shift of modes between March and September and a major modal shift from September to November. Density values of urchins found in November were relatively low; however, the individuals appeared aggregated.

**INTRODUCTION**

Sea urchins are one of the most common components of near-shore marine ecosystems worldwide, often playing an important ecological role in shallow subtidal environments (Lawrence 1975, Harrold & Pearse 1987). *Tetrapygus niger* (Molina, 1782) is a conspicuous arboacoid occurring along the temperate Pacific coast from northern Peru to the Strait of Magallanes (southern Chile), extending from the intertidal zone to 40 m depth (Larrain 1975). Despite this species being the most abundant species of sea urchin on the central Chilean coast, little quantitative information has been gathered on key aspects of its biology and ecology. In this paper we document basic information about spatial distribution and temporal occurrence patterns of a population from the central Chilean coast.

**MATERIALS AND METHODS**

Sea urchins were collected at Punta de Tralca (33° 35′ S, 71° 42′ W) off the central Chilean coast. The substrate of the subtidal zone at this site consists of sloping bedrock with large rocks and boulders in the shallowest portion (0 to 6 m depth) and an increasing proportion of sand at greater depth (6 to 18 m). An extensive kelp bed of the brown macroalga *Lessonia trabeculata* occurs in this deeper area.

Sea urchins were sampled inside and outside the kelp forest using SCUBA from March 1990 to November 1990. Outside the kelp, samples were taken during March, June, September and November. In each of these samples, 3 transects were carried out perpendicular to the shore. Three 0.25 m² quadrat samples (Pringle 1984) were taken from each of 3 different depth ranges (1 to 2.5, 3 to 4, and 5 to 6 m; hereafter designated 2, 4 and 6 m respectively) according to a stratified sampling design (Elliott 1977). All sea urchins...
found within each quadrat were collected, placed in labelled plastic bags and fixed in a 5 to 10% solution of buffered formalin-seawater mixture. In the laboratory, the sea urchins were counted and their test diameters (TD) measured with a caliper to the nearest 0.1 mm. The gonads of individuals collected in June and September were removed, blotted on a paper towel, and weighed to the nearest 0.1 g (wet wt). Gonad indices (GI) were computed as wet gonad mass/wet body mass \times 100 for individuals of 2 different size classes (i.e. 30 to 40 mm TD and 40 to 50 mm TD). Statistical analyses were done on angular transformed data. Mean values of TD and GI were compared using 1-way ANOVAS followed by Student-Newman-Keuls (SNK) multiple comparisons tests (Sokal & Rohlf 1981).

During September and November all small sea urchins found in crevices outside the kelp forest were collected along a bathymetric transect. Individuals were taken with forceps and deposited in sampling bags of 1 to 2 mm mesh size, counted and measured as described above. Likewise during November, 18 quadrats per depth were haphazardly taken from 2, 4 and 6 m respectively. Abundance and spatial distributional patterns of sea urchins were computed. In order to establish the spatial distributional patterns of *Tetrapygus niger* during this month, Morisita’s index of dispersion (I_p) was used. This is a good comparative index when each sample contains the same number of sampling units (Elliot 1977).

During September, 3 additional transects were carried out perpendicular to the shore inside the kelp bed. Three quadrat samples (0.25 m²) were taken between holdfasts from each of 3 depth ranges (6 to 7, 8 to 9, and 10 to 11 m; hereafter 7, 9 and 11 m respectively). Addi-
tional samples of sea urchins inhabiting holdfasts and stipes of *Lessonia trabeculata* (between 6 and 7 m depth) were taken. These individuals were counted and measured as described above.

**RESULTS**

Size-frequency distributions of sea urchins found outside the kelp showed major recruitment events of <30 mm TD individuals at 2 and 4 m in June and September respectively (Fig. 1).

Small individuals (<24 mm TD) were rare (5.6% of all sea urchins sampled). Individuals of <24 mm TD were considered as juveniles since they did not have gonads. A large number of juveniles (70% of the total) were found in the crevices during September and November. All sea urchins in crevices were found at depths <2.5 m. Along the bathymetric gradient including all microhabitats outside the kelp bed, juveniles were mainly found at 2 m rather than at 4 and at 6 m (79% versus 10.5 and 10.5% respectively). Of the 356 individuals sampled in September, 98 (27.5%) were juveniles. Of these juveniles, 57 (58.2%) were found inside the kelp bed (16 on holdfasts of *Lessonia trabeculata* and 41 between plants), whereas 41 (41.8%) were found outside the kelp. Twenty-four (58.5%) juveniles sampled outside the kelp bed in September were found in crevices. In November, all juveniles were found in crevices. On the other hand, 36 of the 41 juveniles (88%) sampled between plants inside the kelp in September were found at the shallowest edge of the kelp (7 m).

The analysis of size-frequency distributions of all sea urchins sampled at 2 m depth in September and November outside the kelp bed, including juveniles in crevices, showed a new mode between 7 and 12 mm TD in September, and between 12 and 15 mm TD in November (Fig. 2). A large gap separated these small sea urchins from the large ones (15 and 25 mm TD in September, and 17 and 30 mm TD in November).

Inside the kelp bed, 92 individuals were sampled between holdfasts in September along the bathymetric gradient. Of these, 65 (69.2%) were found at the shallowest edge of the kelp (7 m depth), of which 55.4% were juveniles (Fig. 3). The number of individuals as
well as the percentage of juveniles clearly decreased together with depth (Fig. 3).

A temporal analysis of size-frequency distributions of all sea urchins at all depths outside the kelp bed showed the presence of 3 modes in March: between 22 and 25, between 32 and 35, and between 40 and 45 mm TD (Fig. 4a). These modes shifted slightly in June. The first mode was particularly conspicuous as a result of recruitment during this month (Fig. 4b). Between June and September a major shift occurred in the 25 mm TD mode, appearing very close to the second mode (Fig. 4c). During this period, both the second and third modes remained almost stationary (Fig. 4c). In November, however, the size distribution was highly skewed towards small sizes (Fig. 4d).

No significant differences were detected between sea urchins collected in June and September outside the kelp bed, with the exception of males from 30 to 40 mm TD, which had significantly lower mean values (± SE) in September than in June (GI = 2.28 ± 0.28 and 3.79 ± 0.26 respectively; 1-way ANOVA, p < 0.001, and a posteriori SNK test). Females from 40 to 50 mm TD collected inside the kelp bed in September had significantly higher mean gonad indices than those sampled outside the bed (GI = 5.96 ± 0.91 and 4.22 ± 0.39 respectively; 1-way ANOVA, p = 0.05, and a posteriori SNK test).

Density estimates based on 54 quadrats haphazardly sampled outside the kelp bed in November showed values of 10.9, 16.2 and 15.3 ind. m⁻² at 2, 4 and 6 m depth respectively, and an aggregated spatial distribution pattern (I₀ = 1.65, 3.06 and 2.16 at 2, 4 and 6 m depth respectively; p < 0.001).

**DISCUSSION**

The occurrence of a large number of small-sized individuals of *Tetrapygus niger* at 2 m depth in June and the presence of the most juveniles in crevices and cracks at depths less than 2.5 m in September and November indicate that the shallower portions of the subtidal zone, and probably the lower intertidal zone as well, are important nursery areas for this species on the central Chilean coast. Cancino & Santelices (1984) documented a larval settlement pattern of a large suite of species, including *Tetrapygus niger*, in holdfasts of the kelp *Lessonia nigrescens*, which form a dense belt delimiting the lower intertidal zone of the central coast (Ojeda & Santelices 1984). Recruitment of *T. niger* in holdfasts of *L. nigrescens* occurs mainly during summer (Vásquez & Santelices 1984).

The shallowest edge of the bed of *Lessonia trabeculata* (i.e. 7 m depth) constitutes another important recruitment zone of *Tetrapygus niger*. Both juvenile and adult sea urchins greatly decreased in number with increasing depths. This differential pattern in abundance between habitats dominated by kelp and those devoid of macroalgae has been described for numerous sea urchin species from different geographic regions, such as in *Strongylocentrotus purpuratus* and *S. franciscanus* (Pears et al. 1970), *S. droebachiensis* (Lang & Mann 1976), and *Evechinus chloroticus* (Andrew & Choat 1985). Several hypotheses have been suggested to explain such a recurrent distributional pattern, among them predation upon...
labeled by filter-feeders inhabiting kelp fronds (Pearse et al. 1970), predation by planktivorous fishes, tendency for larvae to settle soon after they receive appropriate cues upon entering the kelp (Tegner & Dayton 1981), and post-settlement processes (e.g. differential mortality) (Rowley 1989).

Outside the kelp bed, juvenile *Tetrapygus niger* used crevices as microhabitat. Recruits of this species also occur under the spine canopy of adult *Loxechinus albus*, a sympatric but less common sea urchin species along this coast (unpubl. obs.). A similar phenomenon has been reported for juvenile *Strongylocentrotus droebachiensis* and *S. purpuratus*, which obtain protection under adult *S. franciscanus* (Duggins 1981). The presence of juveniles associated with topographic irregularities such as crevices, depressions and interstices of rocks and cobble, and their association with adult spine canopies (sensu Tegner & Dayton 1977), have been largely related with a behavioral defense mechanism against predation (Andrew & Chat 1982, Tegner & Levin 1983, Breen et al. 1985, Ojeda & Dearborn 1991, Scheibling & Hamm 1991). Three alternative but non-exclusive hypotheses have been advanced to account for the above peculiar but widely observed pattern of juvenile distribution of sea urchins: (1) substrate selection by larvae, (2) differential mortality of metamorphosed larvae or juveniles on distinct microhabitats, and (3) secondary migration by juveniles (see Cameron & Schroeter 1980, Rowley 1989).

It is possible that an ontogenetic shift in behavior of juvenile *Tetrapygus niger* from being cryptic (hiding in crevices) to being more exposed may contribute to the large trough in the size-frequency distribution observed in September and November. This ontogenetic shift may occur in sea urchins of about 15 mm TD, being the juveniles most exposed to fish predators (e.g. *Graus nigra*, which is the most important predator of this species; see Moreno 1972, Fuentes 1982). Similar explanations have been suggested for other sea urchin species which exhibit analogous distributional patterns (Andrew & MacDiarmid 1981, Scheibling & Hamm 1991). High predation rates on intermediate-sized sea urchins and the formation of stationary modes composed of several year classes explaining bimodal size distributions have been proposed as alternative but non-exclusive hypotheses for a number of species (see Tegner & Dayton 1981, Andrew & Chat 1982, Himelman et al. 1983, Tegner & Levin 1983, Himelman 1986, Ojeda & Dearborn 1991).

Temporal analysis of size-frequency distribution of individuals collected outside the kelp forest showed a relatively slow shift of modes between March and September, especially between June and September, with the exception of the 25 mm TD mode. The slow shift observed for individuals larger than 30 mm TD during this period could be due, in part, to energy allocation to reproduction since *Tetrapygus niger* reaches its maximum gonad maturity by the end of the winter, with main spawning events in spring (Zamora 1989). The major modal shifts observed from September to November could be due to a somatic growth following the spawning season. Benthic algae, which represent an important food resource for *T. niger* (Contreras & Castilla 1987), have their greatest growth during spring (Ojeda & Santelices 1984).

Our study provides novel data related to basic biology and ecology aspects of this common sea urchin off the central Chilean coast. Further studies are necessary to understand the processes determining the recruitment and distribution patterns described in this work.

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**LITERATURE CITED**


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