Social spacing in the temperate marine goby *Coryphopterus nicholsi*

K. S. Cole*

Department of Zoology, University of Alberta; Edmonton, Alberta, Canada

Abstract

Coryphopterus nicholsi is a temperate marine goby that occupies rock rubble in protected subtidal areas along the Pacific coast of North America. In field populations, fish of all sizes and both sexes are found in the same habitat. All observed fish over 25 mm standard length defended space during both the reproductive and the non-reproductive seasons, with territory size being directly correlated with fish size. There was peripheral overlap of territories, particularly between adjacent adult conspecifics of different size classes, but also with smaller fish that had territories centered in the interstices of larger territories. However, zones of overlap were used at different times by space-sharing fish so that defended areas remained temporally discrete. Access to areas of overlap appeared to be determined by dominance rank. More dominant (usually larger) fish used areas of overlap at will; the defense and use of shared areas by less dominant fish was contingent upon the absence of larger fish. Social organization in *C. nicholsi* appears to be defined by a combination of territorial behavior and dominance relationships among adjacent individuals, permitting the coexistence of all members of the population under circumstances of limited habitat availability.

Introduction

Patterns of space use among solitary, territorial fishes have received much attention in recent years. However, the majority of studies has been on tropical and subtropical marine fishes typically associated with coral reefs (Keenleyside, 1972; Myrberg and Thresher, 1974; Sale, 1974; Thresher, 1976; Reese, 1978; Robertson *et al.*, 1979; Nursall, 1981). Considerably less information is available on

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* Present address: Department of Biology, University of Saskatchewan; Saskatoon, Saskatchewan S7N OWO, Canada

territoriality among temperate marine fish. Often, space defense is short-term and seasonal (Carlisle, 1961; Brown and Green, 1976; Hixon, 1981). However, studies of some permanently territorial, temperate marine species show a diversity of social organizations related to site defense (Clarke, 1970; Moran and Sale, 1977; Larson, 1980 a).

Coryphopterus nicholsi, the blackeye goby, is a protogynous hermaphroditic, temperate marine fish (Cole, 1983). The range of this species extends from Baja California to the Queen Charlotte Islands of British Columbia (Hart, 1973). Individuals occupy the shallow subtidal region along protected rocky shores, and are reputedly territorial year-round (Wiley, 1973), but no details are available. The present study was undertaken to examine spatial and behavioral aspects of space defense in a field population of *C. nicholsi*. Four questions were addressed: (1) Is territoriality of *C. nicholsi* seasonal or permanent? (2) What members of the population defend space? (3) How is space partitioned among individuals? and (4) What behavioral mechanisms maintain social spacing?

Material and methods

Study area

The study area was an undisturbed, subtidal, rock-rubble patch approximately 8 × 60 m, at the entrance of Bamfield Inlet, off Barkley Sound (Lat. 49°N., Long. 125°W) on the west coast of Vancouver Island, British Columbia. The rubble, consisting of rocks 5 to 45 cm in diameter, rested on a bed of sand-shell (a mixture of fine and coarse sand and small shell fragments) and was bounded above by a *Nereocystis luetkeana* bed (0- to 4-m depth) and below by a sloping silt plain (12$^+$-m depth). Four quadrats measuring 2 × 2 m, and divided into four equal sectors, were set one meter apart along a depth contour 7 m below mean low tide. Subsequent observations were carried out on the fish found within each quadrat.

Study fish

Coryphopterus nicholsi is a monomorphic species; both males and females bear similar cryptic, pale-tan coloring that can change rapidly to pale orange or a dark-mottled brown. Differentiation of the sexes by external morphology can only be done by examining the genital papilla (Wiley, 1973). Individuals can grow to a maximum of 100-mm standard length (Cole, 1983), and may live for five years (Wiley, 1973). In my study area, *C. nicholsi* inhabits rock rubble patches at depths of 3 to 20 m, and use crevices or holes excavated under rocks for retreat when startled. During daylight hours they take up positions near their retreats, and make rapid forays to capture both benthic and planktonic food items (Cole, 1982 a).

Most fish within the quadrats did not bear scars or other permanent distinguishing morphological marks that could be used as natural tags. Artificial tagging attempts at other sites resulted in high rates of disappearance (Cole, 1982 a), so this method of identification could not be used to study undisturbed populations. Hence, most fish in this study could not be reliably identified over the entire eight-month period. However, short-term marks, such as lost scales or frayed fins, helped considerably in identifying several individuals over shorter periods of time.

Method of observation

Underwater observations on activities of fish were carried out between December 1979 and July 1980, using SCUBA. Dives were carried out at slack low or slack high tide, whichever occurred during the morning daylight hours. Each quadrat was observed for two 40-min periods on consecutive days, approximately every two weeks (weather permitting), resulting in a total of 54 observation hours on all four quadrats over an eight-month period.

Activity levels of fish were usually low enough to permit observing all fish within a single quadrat for 40 min, and recording their movements and the frequency and location of various behavioral events on a substrate map outlining rocks and sandshell patches on each quadrat. The locations of cover(s) formed by excavations under rocks were also recorded for each fish, when known. On each dive, the size of each fish observed was also noted; small: 25- to 55-mm standard length (SL); medium: 55- to 70-mm SL; large: 70+-mm SL. Assignment to one of these size categories was initially done with the use of handheld models of known size. Later, residents of a known size category were used to assess the size of adjacent fish.

One nocturnal observation was made at the study site; strong night lights were used to locate gobies and record their activities and locations.

At the end of the eight months (July 1980), as many fish as possible were collected from the four observation quadrats, using an anaesthetic, 2-phenoxy-ethanol, and a slurp gun. The collected individuals were measured, and the papilla and gonads examined to determine their sex.

Behaviors recorded and data analyses

The initial selection of behaviors used to record activities of fish was based on behaviors observed in laboratory populations. The location and frequency of occurrence of several aggressive, reproductive, and maintenance behaviors, including approach, avoid, attack, display, chase, feed, sit in open, perch on rock, and sit under cover, were recorded during field observations (detailed descriptions in Cole, 1982 a). Complete areas of activity could not be determined on single dives, since activity levels were low. Therefore, the locations of all the activities observed for each fish were summed over 6 to 8 dives, and an area of activity was constructed. Fish bearing natural marks were easily identified over this inverval. Unmarked fish occupying the same site on consecutive dives, showing similar size and appearance, and showing behavioral constancy (i.e. the use of the same cover, resting sites, preferred perching sites, or consistent paths of movement within an active area) were treated as the same individual, and a single area of activity was constructed.

The eight-month diving period was divided into four time intervals, each representing approximately 200 observation minutes per quadrat, and a single area of activity was determined for each fish observed in each time interval. The first two intervals (December, January–February) constituted the end of the non-reproductive season for *Coryphopterus nicholsi*, and the third and fourth (April–May, and June–July) comprised most of the reproductive season (Cole, 1982 b).

Entire areas of activity on the substrate maps were measured with the use of a planimeter. When areas of activity of adjacent fish overlapped, the exclusive (i.e. unshared by conspecifics) portion of each individual area was also measured. In addition, the frequency of initiated aggression was calculated for each fish that possessed an area of activity. Then the total area of activity, the exclusive area of activity, and the frequency of initiated aggression were compared with the size of fish and season. As each quadrat had different numbers of fish, the data from each quadrat were analyzed separately (unbalanced two-way ANOVA, Steel and Torrie, 1960).

In addition, from each area of activity, the location of aggressive (chase, bite, display), feeding, and station maintenance behaviors (sit on substrate, sit under cover, perch on rock) were categorized as occurring on the periphery, or within the central portion of the area of activity, and the relative frequency of occurrence of these three groups of behaviors was compared (Student's t-test, Sokal and Rohlf, 1969), depending upon their location.

Where conditions for parametric tests were not met (test for normality, test for homogeneity of variance; Sokal and Rohlf, 1969), non-parametric tests were used (Siegel, 1956).

Small fish were more difficult to see, and more secretive in their behavior, than medium and large-sized fish, and activity rates were correspondingly lower. Therefore, the areas of activity for individuals of this size group were not included in the data analyses.

Results

Fish distribution

Within the four quadrats, all but the very small individuals (less than 25-mm SL) defended space throughout the year, indicating a permanent territorial social system. Seven large, four medium-sized, and two small fish bearing permanent natural markings and followed over the eight-month period maintained and defended space in the same locations. Areas of activity were characterized primarily by aggressive, feeding, and station maintenance (i.e. sitting on the substrate, under cover, or perching on a rock) events. Aggressive events occurred mainly on the periphery of areas of activity, while feeding occurred both peripherally and centrally, and station maintenance was predominantly central to areas of activity (Table 1). Typically, individuals perched on a rock or rested on the substrate in a central location, often near cover, and made short, rapid forays out towards the perimeter, either to feed, or attack an intruder.

Based on visual counts of fish within quadrats over the eight-month period, the mean population density was $6.0 + 0.6$ fish per m^2. With the use of anaesthetic, 83 fish were collected on the four quadrats, covering a wide range of sizes. Fourteen large males (the smallest was 70.6-mm SL; the largest was 83.2-mm SL), and two large females (75.0 and 83.8-mm SL) were collected. Fourteen medium-sized males (61.2- to 69.8-mm SL) and twenty-one medium-sized females (56.8- to 68.9-mm SL) were also collected. Lastly, three small males (49.3- to 52.8-mm SL)

and twenty-nine small females (41.0- to 53.8-mm SL) were caught. Thus, small and medium-sized fish outnumbered large fish, and were predominantly female; larger-sized fish were predominantly male.

During a single night dive in June of 1980, approximately 400 m^2, including the four observation quadrats, were scanned for the presence of *Coryphopterus nicholsi*. In an area that contained an estimated 2 000 to 3 000 gobies (based on daylight counts of small areas), only one goby was seen; it was partially under cover. On the four study quadrats, known retreat spaces were examined, and most contained a single goby, located at the rear of the excavated chamber. There was no evidence of nocturnal sharing of refuge.

Territory distribution

Territories were neither similar in size, nor distributed uniformly throughout the habitat. Small fish occupied an excavated refuge and defended a small area around it. The excavated shelter was often interstitial to the defended areas of larger fish, or on a common border between two larger territories, with the surrounding defended area extending into adjacent territories of larger fish.

Territories of adjacent medium and larger-sized fish also overlapped frequently (Fig. 1). However, overlap was mainly on the periphery of defended areas, and cover was rarely included in the overlapped area. In 116 territories mapped, the locations of 129 covers used for shelter by defending fish were known; in only seven instances was

Table 1. The mean number of behavioral events occurring on the periphery (P) and centrally (C) in all areas of activity of large and medium-sized fish in each quadrat ($Q_1 - Q_4$). Variances are in parentheses; n indicates the number of areas of activity used to calculate mean values. Asterisks indicate levels of significance (*, 0.05; **, 0.01; ***, 0.001; Student's t-test) for differences between peripheral and central occurrence of activities

		Large-sized fish				Medium-sized fish			
		Q_1	Q_2	Q_3	Q_4	Q_1	Q_2	Q_3	Q_4
Aggression	P	0.88 (1.63)	1.59 (2.79) **	1.20 (2.96)	1.97 (3.36) ***	0.50 (0.69) *	0.53 (0.85) *	0.48 (0.65) *	0.62 (1.13) *
	C	0.71 (0.91)	0.59 (0.52)	0.60 (0.54)	0.72 (1.54)	0.17 (0.25)	0.13 (0.18)	0.13 (0.11)	0.17 (0.21)
Feeding	P	1.94 (3.70)	1.28 (1.85)	2.05 (5.55)	1.85 (3.93)	1.39 (1.57)	1.07 (1.00) ***	2.65 (4.93)	1.59 (3.76) **
	C	1.65 (5.40)	0.83 (1.87)	1.80 (3.26)	1.62 (5.67)	1.69 (6.10)	0.06 (0.84)	1.95 (5.55)	0.52 (0.46)
Sit, Perch or Under Cover	P	3.53 (3.54) **	4.52 (4.59) ***	5.45 (5.75) ***	4.44 (13.94) ***	5.19 (4.10)	4.37 (5.23)	3.95 (4.50) ***	3.72 (6.54)
	C	9.06 (38.88)	10.27 (65.03)	11.60 (53.24)	15.74 (131.27)	7.42 (50.47)	4.17 (12.54)	9.68 (50.37)	5.55 (28.45)
	n	17	29	20	39	36	30	40	29
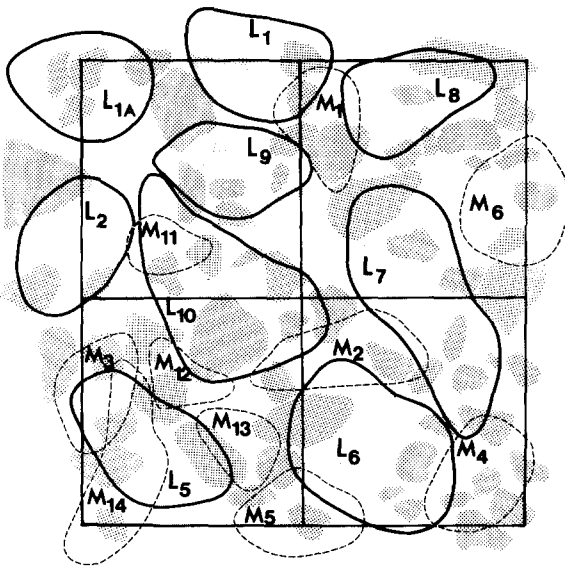
Fig. 1. Areas of activity of large (solid line) and medium-sized (dashed line) fish in Quadrat 4, compiled over the April–May time interval. Shaded areas outline rocks. Numbers and letters designate individual fish. 2×2 m quadrat is partitioned into four 1-m^2 sectors

cover in the area of overlap between two territories. In two such cases, a second cover was located in the exclusive portion of the defender's territory.

Spatial overlap occurred on territories of both large and medium-sized fish, but fish overlapped significantly less with conspecifics of the same size class (i.e. large with

large), than with those of a larger or smaller size class (Table 2).

In each quadrat, the total territory size was significantly greater for large fish than medium-sized fish (Table 3), but was unaffected by season, except in Quadrat 3. Larger fish also had significantly larger exclusive areas of territory (that portion not used by any other conspecific) than did medium-sized fish in Quadrats 1, 2, and 4, (Table 4); there was no significant difference in Quadrat 3. In all quadrats, the exclusive area of territory was unaffected by season.

Behaviors associated with space defense

Territory borders were defended by aggressive behavior that generally consisted of simple chase events, often originating from a stationary point central to the defended area. Chasing by one fish generally resulted in avoidance by another. Subsequently, the aggressor would sink to the substrate for 2 to 10 s, then rapidly move to a frequently used perching or resting site. When a chased fish did not flee, aggression always escalated to displays by both fish. Displays consisted of dorsal, anal, caudal, and sometimes pectroral fin erection, branchiostegal membrane extension and mouth gaping, and tailbeating, and was often followed by biting. These displays generally occurred on the border of two adjacent territories of similar-sized fish, while chase-avoidance interactions usually occurred between a larger and smaller fish. Although recognition of individual

Table 2. The proportion of entire territory area overlapped with other large and medium-sized fish for (a) large and (b) medium-sized fish defending territories. Mean values are given for each time period and each quadrat (Q_1 to Q_4). M is grand mean; V is variance; Dmax and P values are based on Kolmogorov-Smirnov 2-sample test

(a) Proportional overlap of large fish territories:

	With large fish				With medium fish			
	Q_1	Q_2	Q_3	Q_4	Q_1	Q_2	Q_3	Q_4
Dec.	0	0	0.01	0.06	0.08	0.01	0.06	0.01
Feb.	0	0.05	0	0.06	0.08	0.08	0.13	0.13
April	0.02	0.09	0.07	0.01	0.21	0.12	0.15	0.20
June	0	0.07	0.13	0.18	0.17	0.05	0.20	0.12
	M=0.05	V=0.003			M=0.12	V=0.003		
			Dmax=0.56	$p<0.05$				

(b) Proportional overlap of medium-sized fish territories:

	With large fish				With medium fish			
	Q_1	Q_2	Q_3	Q_4	Q_1	Q_2	Q_3	Q_4
Dec.	0.18	0.05	0.08	0.68	0	0	0	0
Feb.	0.07	0.13	0.03	0.37	0	0	0.09	0
April	0.09	0.15	0.07	0.41	0.07	0.05	0.11	0.06
June	0.12	0.09	0.13	0.33	0.08	0	0.12	0.06
	M=0.19	V=0.03			M=0.04	V=0.045		
			Dmax=0.56	$p<0.05$				

Table 3. Mean values ($\bar{x}$) for total areas of activity (m^2) of large and medium-sized fish in each of four quadrats (1$-$4) over four time intervals. n indicates the number of areas of activity used to calculate mean values; N is the grand sample size. F values and levels of significance indicated by asterisks (see Table 1) are based on two-way unbalanced analyses of variance

Time interval		Quadrat 1		Quadrat 2		Quadrat 3		Quadrat 4	
		Large	Medium	Large	Medium	Large	Medium	Large	Medium
Dec.	$\bar{x}$	0.18	0.08	0.19	0.04	0.14	0.09	0.21	0.14
	n	4	8	6	6	9	10	9	2
Jan.$-$Feb.	$\bar{x}$	0.17	0.10	0.32	0.12	0.25	0.18	0.24	0.11
	n	5	15	6	12	4	12	11	8
April$-$May	$\bar{x}$	0.26	0.16	0.18	0.13	0.22	0.18	0.27	0.14
	n	5	16	13	14	4	16	12	10
June$-$July	$\bar{x}$	0.17	0.12	0.13	0.11	0.26	0.11	0.25	0.12
	n	7	15	12	7	4	12	11	10
Grand mean		0.14		0.15		0.16		0.20	
Standard deviation		0.09		0.12		0.08		0.12	
N		75		76		71		73	
F_{size}		14.39***		15.06***		21.04***		12.89***	
F_{season}		ns		ns		6.85*		ns	

Table 4. Mean values ($\bar{x}$) for the exclusive portion of all areas of activity (m^2) of large and medium-sized fish in each of four quadrats (1$-$4) over four time intervals. n indicates the number of areas of activity used to calculate mean values; N is the grand sample size. F values and levels of significance indicated by asterisks (see Table 1) are based on two-way unbalanced analyses of variance

Time interval		Quadrat 1		Quadrat 2		Quadrat 3		Quadrat 4	
		Large	Medium	Large	Medium	Large	Medium	Large	Medium
Dec.	$\bar{x}$	0.15	0.05	0.19	0.05	0.11	0.08	0.20	0.07
	n	4	8	6	3	9	9	8	2
Jan.$-$Feb.	$\bar{x}$	0.14	0.09	0.23	0.10	0.19	0.15	0.20	0.07
	n	5	15	5	11	4	12	11	8
April$-$May	$\bar{x}$	0.15	0.11	0.15	0.09	0.12	0.13	0.27	0.07
	n	5	16	9	13	4	15	9	10
June$-$July	$\bar{x}$	0.11	0.08	0.15	0.10	0.14	0.11	0.18	0.10
	n	7	15	8	5	4	4	11	8
Grand mean		0.10		0.13		0.13		0.15	
Standard deviation		0.07		0.10		0.07		0.12	
N		75		60		61		67	
F_{size}		9.83**		12.32***		ns		26.74***	

fish having no natural tags was often difficult following two-week intervals separating each dive series, the locations of aggressive interactions between adjacent conspecifics were often identical over many months, indicating constancy in the locations of territorial boundaries.

Small fish with interstitial territories only defended their areas against other small conspecifics. They avoided medium or large-sized fish, either by going under cover or by moving to that portion of the small fish's territory that did not overlap with the intruder's territory. Thus, spatial overlap of territories did not include temporal overlap of activities. Very small fish (less than 25-mm SL), that had recently settled out of the plankton, were usually ignored by larger fish. These individuals made short, rapid movements over rock surfaces and darted into crevices when startled; they did not appear to defend space at all.

Table 5. Mean values ($\bar{x}$) for frequency of initiated aggressive interactions for all recorded areas of activity. Large and Medium columns indicate mean values based on areas of activity for large and medium-sized fish, respectively. n indicates the number of areas of activity used to calculate mean values. $\bar{X}$ is grand mean; SD is standard deviation; N is the total sample size. Season indicates the observation interval within the total eight month period. F values for seasonal, size, and interaction effects were calculated (2-way unbalanced ANOVA); only F values with $P \le 0.05$ are shown. Asterisks indicate level of significance (see Table 1)

Season		Quadrat 1		Quadrat 2		Quadrat 3		Quadrat 4	
		Large	Medium	Large	Medium	Large	Medium	Large	Medium
Dec.	$\bar{x}$	0.75	0.25	1.33	0.17	1.67	0.50	3.44	0.50
	n	4	8	6	9	9	10	9	2
Jan.–Feb.	$\bar{x}$	1.00	0.13	3.17	0.50	0.25	0.50	1.64	0.50
	n	5	15	6	12	4	12	11	8
April–May	$\bar{x}$	2.00	0.69	1.62	0.71	1.50	0.88	2.42	0.40
	n	5	16	13	14	4	16	12	10
June–July	$\bar{x}$	1.29	0.67	0.92	0.57	2.25	0.33	3.09	1.10
	n	7	15	12	7	4	12	11	10
	$\bar{X}$	0.69		1.05		0.85		1.81	
	SD	1.07		1.52		1.17		2.13	
	N	75		76		71		73	
F_{size}		9.86**		14.47***		8.74**		14.87***	

Medium-sized fish successfully defended space against both small fish and other medium-sized fish, and also usually avoided large fish by leaving the area of overlap when chased. This did not, however, prevent such individuals from returning after a short period of time, and defending the same area against others until chased out again. Large fish defended their area against fish of all sizes, and were successfully displaced only upon intrusion into the territories of other large fish.

Because of the size-dependent nature of aggression, large fish had a greater number of potential targets than did medium-sized fish. When the frequencies of aggressive interactions for all recorded areas of activity were compared, larger fish had a higher frequency of initiated aggression than did medium-sized fish in each quadrat, regardless of the time of year during which they were observed (Table 5).

Discussion

When examining natural populations under conditions that restrict observation time, defense-associated aggression can often be too infrequent to delineate territory boundaries completely. Facing a similar problem in avian studies of territoriality, Weeden (1965) proposed the term "space of activity", which is analogous to area of activity in this study. It is difficult to know if such areas of activity are always accurate representations of territories. However, because the periphery of areas of activity in this study were characterized by aggressive events, and the locations of boundaries of areas of activity appeared to remain constant over time, I have assumed that such areas were probably reasonable estimates of actual territory size.

Territorial behavior is characterized by the defense of space (Noble, 1939) or by socially mediated exclusion of individuals from an area (Brown, 1975). Peripheral defense, and subsequent conspecific exclusion from areas of activity in *Coryphopterus nicholsi* indicate that individuals of this species are territorial. In this study, fish of both sexes in the three size classes defended space throughout the year in the same habitat. Thus, Wiley's (1973) suggestion of a permanent territorial system in *C. nicholsi* is supported.

The pattern of spatial partitioning, however, was not one of contiguous, non-overlapping territories. Instead, considerable territory overlap occurred between adjacent adult conspecifics of various size classes, and also with smaller fish that had territories centered around areas interstitial to larger territories. Thus, the use of space by *Coryphopterus nicholsi* involved a combination of territorial defense and space-sharing.

The phenomenon of peripheral territory overlap has been reported in other territorial fishes, including *Abudefduf zonatus* (Keenleyside, 1972), *Hypoplectrus* spp. (Barlow, 1975), and *Sebastes* spp. (Larson, 1980b). In *Coryphopterus nicholsi*, the overlapping pattern of space use primarily resulted from the defense of the same space by individuals of different size classes. As smaller individuals generally avoided larger conspecifics, the zone of overlap with larger fish was used at different times. Therefore, while portions of territories overlapped spatially with one another, temporally, they did not.

Observations from this study indicate a strong dominance component to territoriality in the field. Large fish had complete dominance over all fish within their territory, including smaller conspecifics whose territories were overlapped. Smaller fish, as a rule, were able to exclude

only same-size or smaller fish from their defended areas, and existed in areas of overlap with larger fish through avoidance behavior. Thus, overlap was greater between size classes than within size classes, where fish were more evenly matched in aggressive abilities. The presence of dominance relations among territorially organized fish has been noted in laboratory populations of juvenile sunfish (Greenberg, 1947) and juvenile salmonids (Newman, 1956; Chapman, 1962), and also in field populations of juvenile salmonids (Newman, 1956), and adult damselfish (Myrberg, 1972; Itzkowitz, 1978), and probably plays an important role in many space-sharing social systems where several different size or age-classes of conspecifics occupy the same habitat. However, under space constraints, not all demographically mixed animal groups develop space-sharing social systems. Floaters, homeless individuals that move from area to area and opportunistically obtain space as it becomes available, have frequently been described (Larson, 1980b; Dubin, 1981). The presence of floaters was not readily evident in Coryphopterus nicholsi, but because of the intermittent nature of observations, transients could easily have remained undetected. Within days of collecting individuals from the four quadrats, new medium and large-sized fish appeared, and established themselves (Cole, unpublished data). Whether these individuals invaded from the periphery of the quadrat, or from other areas of the habitat, is unknown.

The topography of the rock rubble habitat may also have contributed to the spatial overlap found in this population. Sale et al. (1980) found that juvenile Pomacentrus wardi used "topological deception" in which sites chosen possessed topographical features that allowed juvenile fish to avoid the notice and subsequent aggression of neighbouring adults. On my study site, a defending fish did not always have an unimpeded view of the entire territory, because of the sloping and outcropping nature of the terrain. Since individuals of Coryphopterus nicholsi do not patrol their territory boundaries, but rather make forays from a central perching position or resting spot, some portions of the territory periphery may not always have been visible. In such blind spots, smaller fish could easily take up partial residence. Larson (1980b) described a similar pattern of territory defense and spatial overlap in two Sebastes spp. He suggested that the presence of spatial overlap in Sebastes spp. was due to a lack of patrolling behavior on the part of defenders. In C. nicholsi, the absence of visual access to, and routine patrolling of, territory boundaries likely promoted peripheral overlap between territories of neighbouring conspecifics.

Despite their lower dominance status, smaller fish often managed to maintain an exclusive refuge area by locating it between the territory boundaries of adjacent dominants. Occupation of areas interstitial to adult territories by smaller individuals in a population has been described for several other teleost species (Sale, 1974; Nursall, 1977; Fricke, 1980; Larson, 1980a). Whether or not the interstitial areas defended by smaller Coryphopterus nicholsi are centers of future territories, as suggested

by Nursall (1977) for Ophioblennius atlanticus, is unknown.

In Coryphopterus nicholsi, newly settled and young juveniles were not actively excluded from the habitat occupied by adults; resident C. nicholsi merely seem to ignore very small conspecifics. In this species, there appears to be no alternate habitat available for young fish (Cole, 1982a), but within-habitat refugia, in the form of rock crevices within and between established territories, are abundant. These two factors may be instrumental in promoting the occurrence of a space-sharing social system in this species. With the anemonefish Amphiprion melanopus, the number of anemones is limited and there is no suitable alternative habitat for newly settling fish. In that species, juveniles are also tolerated by, and coexist with, territorial adults (Ross, 1978).

There appears to be a stable year-round social organization characterized by space defense, in Coryphopterus nicholsi. This is based on the constancy of residence by identifiable individuals, and the apparent lack of change in territory size of large and medium-sized fish, over the eight-month observation period encompassing the non-reproductive and reproductive seasons. This pattern is in contrast to some temperate marine fishes that exhibit seasonal territoriality, usually associated with reproduction (Moore, 1970; Stephens et al., 1970) or, less frequently, during a juvenile stage (Brown and Green, 1976). The overall lack of change in territory size in C. nicholsi also differs from that found in Parma microlepis, an Australian temperate pomacentrid that is also territorial all year and shows an expansion of territory area during the reproductive season (Moran and Sale, 1977). The lack of expansion in C. nicholsi under similar conditions may reflect a real permanence of territory boundaries. However, the finding may be an artifact of my method of grouping data according to size class rather than by tracking individuals through the entire eight-month observation period. Thus, any changes in individual territories may have been masked. Under laboratory conditions, both reproductively active males and females do increase their total territory size during the reproductive season; furthermore, the exclusive portions of male territories increase in size within the reproductive season when eggs are present (Cole, 1982a). Long-term field observations on known individuals will be necessary to determine how season affects territory size in situ.

Territory size was also strongly correlated with fish size. This is not an uncommon phenomenon (Schoener, 1968; Simon, 1975; Larson, 1980b), and may reflect the nature of resources for which space defense guarantees access. Shelter appears to be a primary factor in selecting for a territorial social system in Coryphopterus nicholsi (Cole, 1982a), but food requirements (C. nicholsi utilizes both planktonic and benthic prey) may determine the size of the territory.

Until recently, patterns of spatial partitioning reported in fish have often been those of exclusive territories distributed throughout the habitat. In such cases, terri-

toriality is usually associated with only some members of the population, such as adult males (Barlow, 1974; Hixon, 1981). However, in many permanent territory systems, all members of the population require protected space for essential resources. The pattern of spatial partitioning consisting of the temporally segregated use and defense of the same space by different members of the population, as described here, may be more prevalent than is currently appreciated.

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