

Population structure of aggregations, and response to spear fishing, of a large temperate reef fish *Cheilodactylus fuscus*

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ABSTRACT: Strip transect surveys of the large temperate rocky reef fish *Cheilodactylus fuscus* revealed size- and sex-structured populations across seasons and 3 conditions of wave exposure, from an estuary to the open coast. Large, mostly male, fish (>30 cm fork length) predominated on the open coast and in deeper water (>10 m), while smaller fish predominated in the more protected estuarine areas and in the subtidal regions (<5 m), particularly during the winter to spring recruitment period. Aggregations of *C. fuscus* were geographically persistent, varying in their size and sex composition over 2 yr, which suggested an ontogenetic migration from shallow and protected areas to more exposed coastal locations. Reasons defining the location of aggregations were unclear, as multivariate analysis of 29 habitat characteristics of 13 aggregation sites versus 6 similar control sites revealed no significant difference. Fish re-colonised the same location 2 to 4 mo after a summer and a winter experiment removed >70% of the adults by intense spear fishing. Experimental sites were recolonised by >20 cm males and females, and rarely by juveniles. There was no significant difference between the pre- and post-removal estimates of home range of tagged fish at removal sites or in controls.

KEY WORDS: Cheilodactylidae · Habitat use · Population structure · Disturbance · Spear fishing · Environmental impact

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INTRODUCTION

Cheilodactylid fishes, commonly known as morwongs, are an important component of the fish communities inhabiting temperate reefs in Australia, New Zealand, Japan, South America and South Africa (Leum & Choat 1980, Branden et al. 1986, Lincoln Smith & Mann 1989, McCormick 1989a,b). The red morwong *Cheilodactylus fuscus* is a large conspicuous fish, and primarily a benthic carnivore (Bell 1979, Lockett & Suthers 1998). It does not form part of a significant commercial fishery, but as one of the largest resident species (maximum length 65 cm), it is a primary target species for spear fishers in southeast Australian waters (Johnson 1985, Lincoln Smith et al. 1989).

Cheilodactylus fuscus is a gregarious species and individuals remain affiliated with the one aggregation at a fixed location for years (Lowry & Suthers 1998). A study of movement patterns (Lowry & Suthers 1998) indicated significant differences between night-time and daytime home ranges. During the day fish remain associated with aggregations located exclusively on boulder habitat. During the night these site-specific aggregations disperse as fish move over a wide variety of substrate types to feed, occupying an area double the size of the daytime (1900 m²) home range. Red morwong also exhibit a marked fidelity for the home aggregation, with displaced fish traversing 200 to 900 m over 1 to 3 d, crossing ostensibly identical habitat and other aggregations to return to the point of capture (Lowry & Suthers 1998).

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Temperate reef habitats are heterogeneous, with environmental gradients influencing patterns of distribution and abundance of resident species (Jones 1984a,b, Gillanders & Kingsford 1998). Factors such as relative exposure to wind and waves, changes in depth, and associated changes in habitat complexity, act to influence patterns of abundance and community structure (Choat & Ayling 1987, Macpherson & Duarte 1991, Angel & Ojeda 2001). Local factors such as the nature and complexity of the substrate and the associated algal assemblages will also have a major influence on resident fish populations (Choat & Ayling 1987, Holbrook et al. 1990, 1994). The site-associated substrate-specific nature of red morwong populations makes it an ideal species to examine possible environmental factors influencing the position of aggregations.

Spear fishing may affect the structure of aggregations composed of long-lived resident species such as *Cheilodactylus fuscus*. Spear fishers constitute only a small percentage of recreational effort, but their catch is highly selective for the larger target species (Lincoln Smith et al. 1989), resulting in a reduction in the abundance and modal size-distribution of popular target species (Harmelin et al. 1995, Jouvenel & Pollard 2001). While it has been established that spear fishing will have local impacts on population dynamics and structure, particularly in the more accessible shallow inshore waters, previous research has been limited to the larger 'trophy' species. The dynamics of the recovery of these impacted populations are poorly understood (Pollard et al. 1996).

Our first aim was to describe the seasonal size and sex composition of red morwong at sheltered and exposed locations from estuarine to coastal habitats. We often found the fish to occur in aggregations, so the second objective was to determine whether the population structure (fish density, size, sex composition) of specific aggregations varied amongst seasons, locations or depths over time. The third objective was to determine what environmental and habitat characteristics defined the geographically persistent aggregation sites, by comparing them to apparently similar, unoccupied sites. Finally we wished to investigate the effect of 2 intense spear fishing efforts on the re-aggregation and subsequent behaviour and home range of the remaining, individually tagged fish by asking the questions: If adult morwong were so site specific, then would re-colonisation only occur by the small or sub-adult fish? If there were no particular habitat characteristics of aggregation sites, then would new aggregations re-establish at the same site? We also expected the remaining fish to expand their home range if fish density within the aggregation was a limiting factor.

MATERIALS AND METHODS

Population surveys. Population surveys were carried out at 2 locations within Sydney Harbour and a third located on the open coast, with the 3 locations providing a gradient in wave exposure (Table 1). The estuary location (at Manly, Fig. 1) was the most sheltered, with a broad sub- and inter-tidal region, dominated by large

Table 1. Summary of the aim, the site code and location (see Fig. 1), the general methods used at each of the study locations and *Cheilodactylus fuscus* aggregations, and dates

Aim	Site code	Location	Method	Objective	Dates
Population surveys	Estuary Middle Coast	Manly Middle Head Shark Point	5 × 20 m transects at 3 depths	Comparison of size and sex between site and depth	Mar 1993 to May 1994
Aggregation structure	M1 M2 M3 SP	Middle Head Middle Head Middle Head Shark Point	Aggregation counts	Comparison of size and sex between aggregations	Sep 1993 to May 1995
Habitat characteristics	6 control sites and 13 populated sites including M1, M2, M3, C1, R1, R2,	Sydney Harbour	29 habitat variables	Measurements of proximity of all aggregations to suite of physical variables	Jun 1993 to Nov 1993
Spear fishing removal experiment	R1 R2 C1 C2	Quarantine Middle Head Middle Head Hat Head	Weekly aggregation counts, spear fishing and location of tagged fish	Monitor abundance, before and after spear fishing, of ag- gregation and home range of tagged fish	(1) Dec 1992 to Jan 1993 (2) Apr to Jun 1995

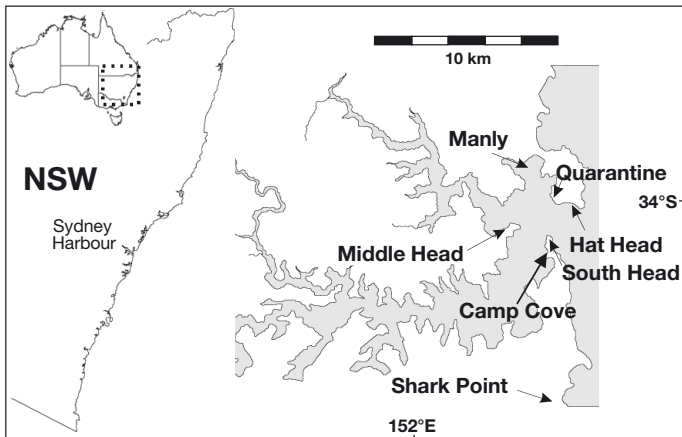


Fig. 1. Study locations: the estuary (E, Manly), middle (M, Middle Head) and open ocean coastal (C, Shark Point). The 4 aggregation sites (M1, M2, M3 at Middle Head, and SP at Shark Point), the 2 removal sites (R1, R2) and control sites (Middle Head, Camp Cove) are listed in Table 1

flat rock covered in turfing furoid algae. Large rocks and overhangs, interspersed with areas of small boulders and *Eklonia*, were found between depths of 2 and 7 m. The bottom was covered with approximately equal amounts of sand and shell fragments, changing to fine sand towards the maximum depth of 14 m. The area of reef extended 25 to 35 m from land.

The middle location (at Middle Head, Fig. 1) was more exposed to the wind and oceanic swell, with some protection from the northern and southern headlands of the harbour. *Eklonia* dominated the shallower areas. Mid depths and the deeper areas had large boulder fields interspersed with areas of flat bare rock, sponges and algal turf. The rocky reef extended further from the land than in the estuary location (approximately 180 m) before it reached the sandy bottom at a depth of 15 m.

The coastal location (at Shark Point, Fig. 1) was the deepest and highest energy environment of the 3 sites, with similar subtidal topography to that of the middle location. The deeper areas were composed exclusively of large boulder fields interspersed with sand and *Eklonia* to a maximum depth of 26 m.

Strip transects (20 × 5 m) were carried out at each site over 15 mo at each depth category: shallow (0 to 5 m), medium (5 to 10 m), and deep (>10 m). Fish were classified by estimated size (fork length)—small (10 to 20 cm), medium (20 to 30 cm) or large (>30 cm)—and by sex (males, females and unknown). Sex determination relied on the ability to distinguish sexual dimorphic features (Schroeder et al. 1994), where males had a distinctive optic tubercle, which was reduced in females. Fish that could not be accurately identified as males or females were classed as unknown.

Aggregation structure. Total counts of aggregations were carried out to detect differences in the number, size and sex composition of resident fish among 4 aggregations. Counts were carried out using SCUBA at 3 aggregations at Middle Head (M1, M2, and M3) and at an aggregation on the open coast (SP, Shark Point) on a weekly basis over a 20 mo period. Counts were carried out by first identifying the abundance, size and sex of all clearly visible fish, before an additional count was carried out to detect any fish inhabiting the crevices and overhangs.

Habitat characteristics of aggregations. *Cheilodactylus fuscus* exhibited a preference for bouldered habitat, although there were many areas of apparently similar habitat that remained unpopulated. In an attempt to explain why one area was preferred to another, sites were characterised according to a set of 29 habitat criteria (Table 2) and compared to apparently similar locations without fish, to determine what factors influence site choice. The 29 variables were classified into 5 broad types: fish, depth, percentage cover, holes, and structures (Table 2). The third variable, *Parma* density, refers to *P. microlepis*, a territorial damselfish (Pomacentridae) which has been frequently observed to dart, challenge or chase the much larger red morwong. Shelter places were categorised as holes, crevices, cliffs and artificial structures. Artificial structures and structures of terrestrial origin such as tree trunks and logs were also recorded. Thirteen aggregations and 6 control sites without fish, located at 7 different locations in the Sydney Harbour region, were investigated.

The immediate vicinity of each site was surveyed using an 8 m length of weighted rope. With the rope anchored to the centre of the aggregation, relevant features were recorded as the rope was moved in a circle until the entire area (200 m²) had been surveyed. Measurements of width, depth, length and the distances to kelp, sponges, low tide zone and other aggregations were carried out with a 1 m rule, a 30 m measuring tape and a 100 m weighted rope. An index of topographic complexity (Leum & Choat 1980) was determined by summing the estimated 2D 'cover' of hard substrata within the area.

Removal experiments (spear fishing). To determine the effect of population density on behaviour and the dynamics of re-aggregation, 2 removal experiments were carried out at 2 aggregations: R1 (Quarantine Bay) during the summer, and R2 (Middle Head) during the winter, both within Sydney Harbour. Control sites, where abundance and home range were monitored, were located at C1 (Middle Head) and C2 (Hat Head; Table 1, Fig. 1).

Total counts of the target aggregations were carried out to provide baseline data on the size, sex and distrib-

Table 2. *Cheilodactylus fuscus*. Explanation of variables used to determine the physical characteristics of aggregations. Aggregations are defined by at least 3 fish in an area of 200 m²

Variable	Characteristic
RM	Number of red morwong in the aggregation
RM ob	Mean number of red morwong in aggregation over observation period
Pa	Mean number of Parma (<i>Parma microlepsis</i>) observed within 200 m ² area
Depth	Depth of the aggregation
Kelpd	Distance to the nearest kelp bed
Spongcl	Distance to the nearest cluster of sponges
Lowtd	Distance to shore
D2	Percentage of total area covered with hard substrate
Fr	Percentage of D2-area covered with flat rock
Sb	Percentage of D2-area covered with small boulders (diameter < 1 m)
Lb	Percentage of D2-area covered with large boulders (diameter > 1 m)
Os	Percentage of total-area covered by soft substrate
Sand	Percentage of Os-area covered by sand
Spong	Percentage of Os-area covered by sponges
Shell	Percentage of Os-area covered by shells
Weed	Percentage of Os-area covered by weed
Kelp	Percentage of weed-area covered by kelp
Other weed	Percentage of weed-area covered by other algae
H/S&S	Number of holes that have a small (<50 cm) entrance and are shallow (depth < 50 cm)
H/S&D	Number of holes that have a small (<50 cm) entrance and are deep (depth > 50 cm)
H/M&S	Number of holes that have a medium (50–100 cm) entrance and are shallow (depth < 50 cm)
H/M&D	Number of holes that have a medium (50–100 cm) entrance and are deep (depth > 50 cm)
H/L&S	Number of holes that have a large (>100 cm) entrance and are shallow (depth < 50 cm)
H/L&D	Number of holes that have a large (>100 cm) entrance and are deep (depth > 50 cm)
C/S	Number of crevices (gaps between rocks) that are <50 cm deep and 50 cm wide
C/D	Number of crevices (gaps between rocks, etc.) that are >50 cm deep and 50 cm wide
PbB	Number of places between boulders which are <50 cm wide, and boulders are not bigger than 2 m in diameter
Cliffs	Number of cliffs that are at least 5 m long and 2 m high
Art St	Number of artificial structures (pallet, log, metal-doors, etc.)

ution. Approximately 1/3 of the fish were dart tagged at each site and their position monitored to determine home range over 4 wk prior to removal (Lowry & Suthers 1998). The numbered dart tags were colour coded to permit identification from a distance. All non-tagged fish were then removed by spearing. Locations of the tagged fish were recorded on weekly dives for the following 4 mo. Changes in home range after removal of the rest were calculated using the method outlined in Lowry & Suthers (1998). Total counts of tagged and untagged fish by size and sex were also recorded.

Analyses. The total density, percentage size (small, medium, large), and percentage sex composition (unknown, male, female) of transect data from the estuarine, middle and coastal locations were analysed by 6 separate 3-factor ANOVAs. To partition the orthogonal and fixed effects of season (4), location (3) and depth (3, n = 6), transects were conducted over the 3 mo of each season. All percentage data were arc-sin transformed to homogenise the variance (thus satisfying Cochran's test). The 15 mo survey included 2 winters, which were initially compared in a separate analysis, found not to be significantly different, and thus averaged to produce balanced data. Principal component analysis (PCA) was used to ordinate the 6 variables composed of the aver-

age percentage sex and percentage size composition (columns) at each location and season combination (12 rows). We used PCA to ordinate collinear data, such as percentage composition, and provide a quantitative measure of what each component actually meant.

For the aggregation percentage composition, similar 2-factor ANOVAs were used, to partition the effects of season (4) and aggregation (4, n = 6 aggregation counts conducted over the 3 mo of each season; some counts were discarded at random to produce balanced data). To determine the effects of season and aggregation on size/sex composition, a similar PCA as before was conducted.

Multidimensional scaling (MDS) analysis was used to determine which of the 29 habitat variables (using standardised data) were associated with the formation of aggregations. The stress value indicates the degree to which the data are distorted in order to fit the required dimensions. A stress value above 0.2 is unacceptable, and a value below 0.15 indicates minimal distortion (Clarke 1993). ANOVA was used to determine the significance of changes in the home range of before and after removal experiments. The post-hoc Student Newman Keuls (SNK) test was used to discriminate among means.

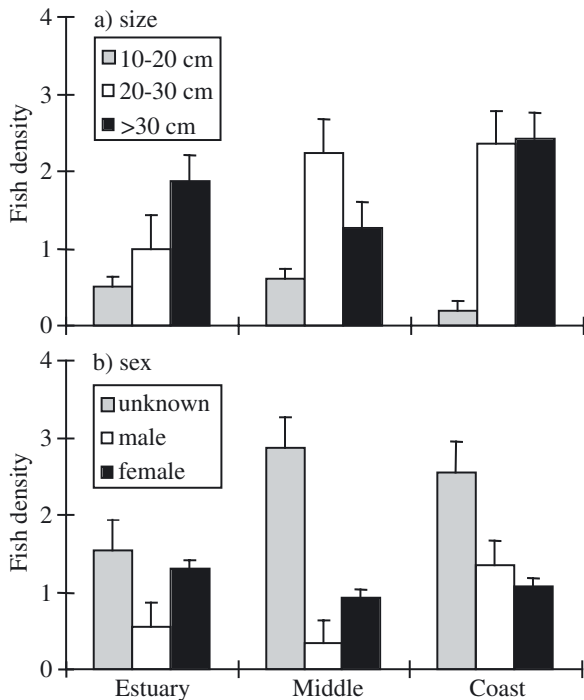


Fig. 2. *Cheilodactylus fuscus*. Average density (per 100 m²) of (a) each size class (small, 10 to 20 cm; medium, 20 to 30 cm; large, >30 cm fork length), and (b) each sex class (unknown, male, female) at the 3 locations, averaged over seasons and depths. Error bars are SE

RESULTS

Population survey

Densities increased from a low of 3.4 ± 0.24 fish (all values from here given as fish per 100 m² \pm SE) at the estuarine location, to 4.1 ± 0.34 fish at the middle location, reaching a maximum of 5.0 ± 0.43 fish at the coastal location. The 3 locations supported different densities of the 3 size and sex classes (Fig. 2). Transects at the estuary location revealed a distribution of increasing numbers of fish from small to large. The middle location was dominated by the medium size classes and the coastal location had few small fish but a large proportion of medium and large fish. Of the fish able to be identified by sex, females outnumbered males at both the estuary and middle locations, while at the coastal location there were proportionally more males than females. At all locations, a high proportion of the population could not be sexed.

The PCA plot of the transect data of the average 3 size and 3 sex percentage contributions defines 3 groups primarily based on location (Fig. 3), with the first 2 principal components explaining 95% of the among-location variation. The one exception is the estuary-

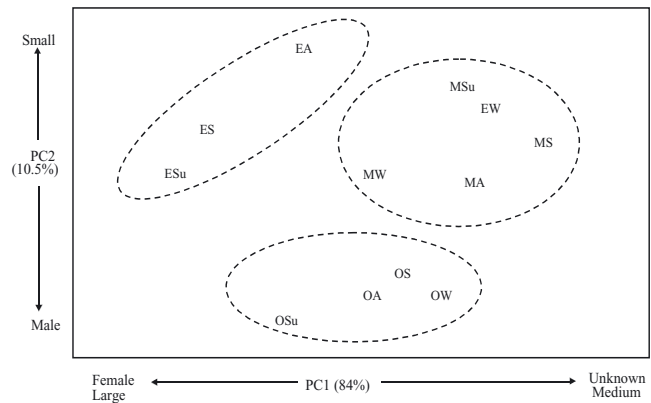


Fig. 3. *Cheilodactylus fuscus*. Plot of principal component analysis of the distribution of size (small, 10 to 20 cm; medium, 20 to 30 cm; large, >30 cm fork length) and sex (unknown, male, female) with season (S: spring; Su: summer; A: autumn; W: winter). Distribution determined by transects at 3 locations: estuary (E), middle (M) and open ocean coast (O). Included are the variances explained by each component and the variables that have the highest correlation with each component

winter distribution, which had a greater portion of the smaller, juvenile fish. Factors responsible for the groupings identified by PCA analysis are more clearly defined by examining the interaction of size and sex with season and depth at each location.

There was a significant interaction in the percentage small-size composition among season, location, and depth, with depth accounting for the majority of explained variance (Table 3a, ANOVA, $p < 0.05$). At the estuary location, the percentage of small fish was significantly less in spring and summer compared to winter (SNK test, $p < 0.05$), while at the middle location the percentage of small fish was significantly greater in spring than in winter (SNK test, $p < 0.05$). Thus, as the percentage of small fish increased at the estuary location from a minimum in spring to a maximum in winter, there was a complementary reduction in the proportion of small fish at the middle location (Fig. 4a). The coastal location was occupied by a relatively stable population structure, with a consistently low proportion of small fish throughout the year and high percentage of the large and medium fish in each season (Fig. 4a).

Size of fish varied at different depths at both the estuary and middle locations (Fig. 4b), with significantly more smaller fish in the shallow depth category (<5 m depth) (Table 3a). At the coastal location there was a high percentage of large fish found at all depth classes.

The proportion of male fish varied only among locations, with a significantly greater proportion across all depths and seasons at the coastal location compared to the other 2 locations (Table 3, SNK test $p < 0.05$). Depth

Table 3. *Cheilodactylus fuscus*. ANOVA table of (a) transect data at 3 locations across an estuarine to ocean gradient, and (b) aggregation data for 4 aggregations (Fig. 1). S: season (n = 4); L: location (n = 3); A: aggregation (n = 4). *p < 0.05; **p < 0.01

df	Small fish (<20 cm)			Medium fish (20–30 cm)			Large fish (>30 cm)			Male fish			Female fish			Indeterminate sex					
	SS	MS	F	SS	MS	F	SS	MS	F	SS	MS	F	SS	MS	F	SS	MS	F			
(a) Source																					
S	0.43	0.14	1.38	0.56	0.19	0.90	3.23	1.08	4.33	**	0.72	0.24	2.00	0.64	0.21	1.15	0.83	3.26	*		
L	0.62	0.31	3.01	2.46	1.23	5.92	3.38	1.69	6.78	**	0.86	0.43	3.56	1.22	0.61	3.31	1.22	0.61	2.40	ns	
D	4.84	2.42	23.47	1.26	0.63	3.03	2.01	1.00	4.03	*	0.54	0.27	2.24	0.65	0.32	1.76	4.13	2.06	8.10	**	
SxL	1.29	0.22	2.09	0.89	0.15	0.72	4.80	0.80	3.22	**	1.07	0.18	1.49	2.66	0.44	2.41	6.14	1.02	4.02	**	
SxD	0.66	0.11	1.06	0.87	0.15	0.70	1.34	0.22	0.90	ns	0.24	0.04	0.33	0.80	0.13	0.72	2.53	0.42	1.66	ns	
LxD	0.51	0.13	1.25	3.19	0.80	3.84	2.36	0.59	2.37	*	0.61	0.15	1.28	2.14	0.53	2.90	4.39	1.10	4.31	**	
SxLxD	2.32	0.19	1.87	2.94	0.24	1.18	1.57	0.13	0.52	ns	1.27	0.11	0.88	1.05	0.09	0.48	4.29	0.36	1.40	ns	
Residual	180	18.55	0.10	37.33	0.21		44.82	0.25			21.67	0.12		33.09	0.18		45.83	0.25			
Total	215	29.21		49.49			63.52				26.98			42.23			71.02				
(b) Source																					
S	0.832	0.277	10.35	2.312	0.771	6.9	0.578	0.193	1.18	ns	0.426	0.142	4.37	0.733	0.244	2.35	2.094	0.698	13.3	**	
A	0.12	0.04	1.49	2.899	0.966	8.65	4.331	1.444	8.82	**	7.849	2.616	80.54	4.543	1.514	14.55	0.835	0.278	5.3	**	
SxA	0.538	0.06	2.23	1.673	0.186	1.66	0.458	0.051	0.31	ns	0.655	0.073	2.24	0.903	0.1	0.96	2.075	0.231	4.39	**	
Residual	80	2.144	0.027	8.936	0.112		13.1	0.164			2.599	0.033		8.324	0.104		4.198	0.053			
Total	95	3.634		15.82			18.47				11.53			14.5			9.201				

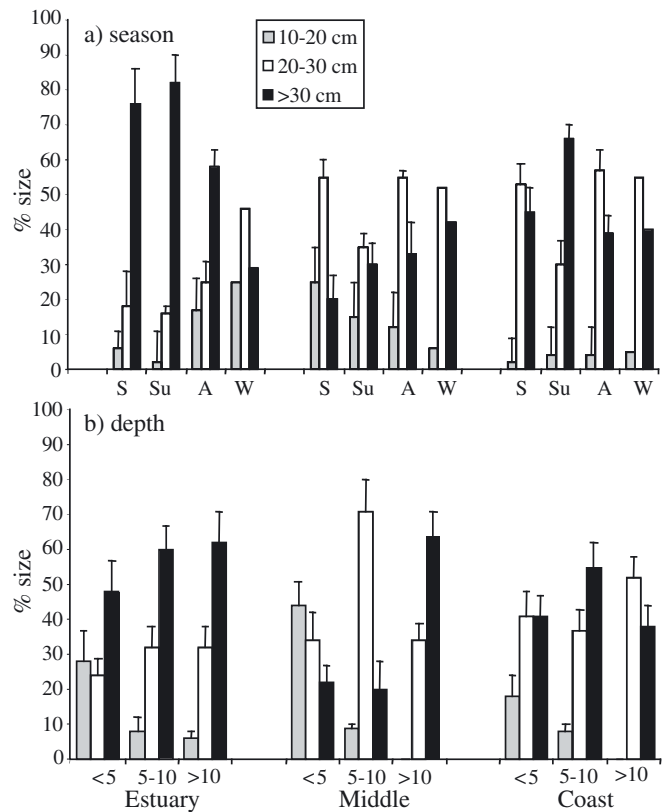


Fig. 4. *Cheilodactylus fuscus*. Proportions of each size class at each location (a) in each season—spring (S), summer (Su), autumn (A) winter (W)—and (b) at each depth—shallow (<5 m), medium (5 to 10 m), deep (>10 m). Error bars are SE

explained the greatest proportion of variance of the unknown or indeterminate sex (Table 3a). The proportion of female fish significantly varied among season × location and location × depth (Table 3a). The proportion of female fish significantly decreased from spring to winter at estuary and increased at middle, reciprocated by the unknown percentage (Fig. 5a). Coastal had relatively high percentage of juveniles and similar proportions of the male and female fish in each season. The numbers of male and female fish significantly increased with depth at both the estuary and middle locations (Fig. 5b, SNK test p < 0.05), and males dominated at the deepest coastal zone.

Aggregation structure

All aggregations comprised between 15 and 25 fish, except for M3 where numbers increased during October and November to a maximum of 75 in December, and declined back to 15 to 25 in late summer. Aggregation data on percentage size and sex composition using PCA determined that 90% of the variation could

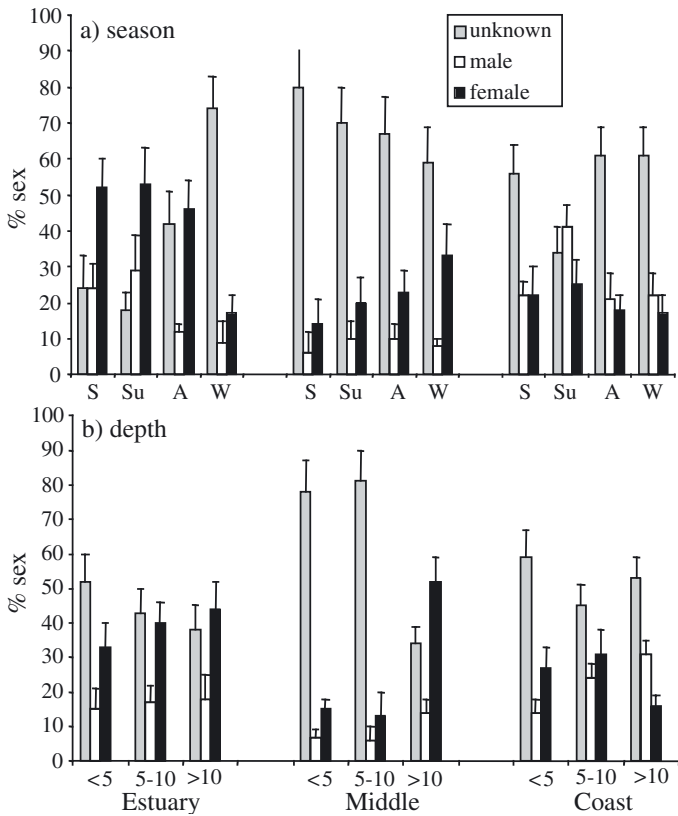


Fig. 5. *Cheilodactylus fuscus*. Proportions of each sex class at each location (a) in each season—spring (S), summer (Su), autumn (A), winter (W)—and (b) at each depth—shallow (<5 m), medium (5 to 10 m), deep (>10 m). Error bars are SE

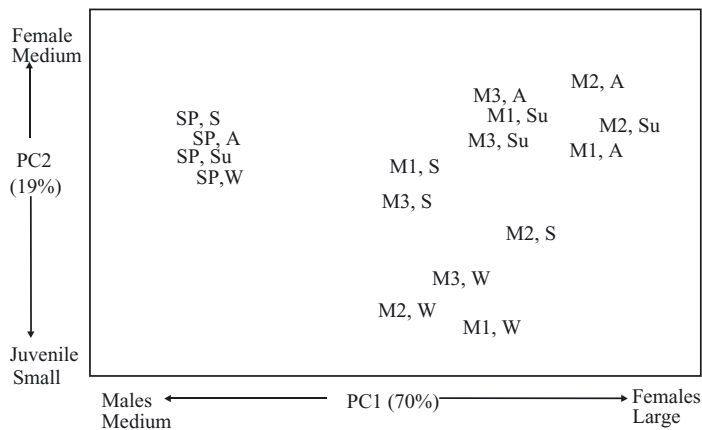


Fig. 6. *Cheilodactylus fuscus*. Plot of principal component analysis for total counts for the size (small, 10 to 20 cm; medium, 20 to 30 cm; large, >30 cm) and sex (unknown; male; female) of aggregations with season (S: spring; Su: summer; A: autumn; W: winter). Aggregations were located at Middle Head (M1, M2 and M3) and Shark Point on the open coast (SP.). Included is the percentage variance explained by each component and the variables that have the highest correlation with each component

be explained by the first 2 components. The plot indicated 2 main groupings separated by PC1 (medium/males versus large/females; Fig. 6), where the Shark Point aggregation is clearly separate as a stable population with limited variation in size and sex between seasons. Females predominated at the Middle Head aggregations (Fig. 6). M1, M2 and M3 aggregations were separated by PC2, with all 3 aggregations dominated in winter by small fish of unknown sex (Fig. 6). The spring aggregations were intermediate between winter and summer/autumn.

SP had a greater proportion of large-sized fish and less small fish than any of the other aggregations (Fig. 7a). M1, M2 and M3 were dominated by females with the proportion of female fish in each aggregation between 58 and 73%. SP indicated an opposite trend, with males making up 73% of all observations (Fig. 7b).

Analysis of aggregations by size class indicated a significant interaction in the size and sex of fish between site and season (Table 3b, $p < 0.05$). The seasonal distribution of size classes was most apparent at M1, M2 and M3 aggregations (Fig. 7a). Small fish were found in the highest proportions at all of the 4 aggregations during winter, the medium size-class increased

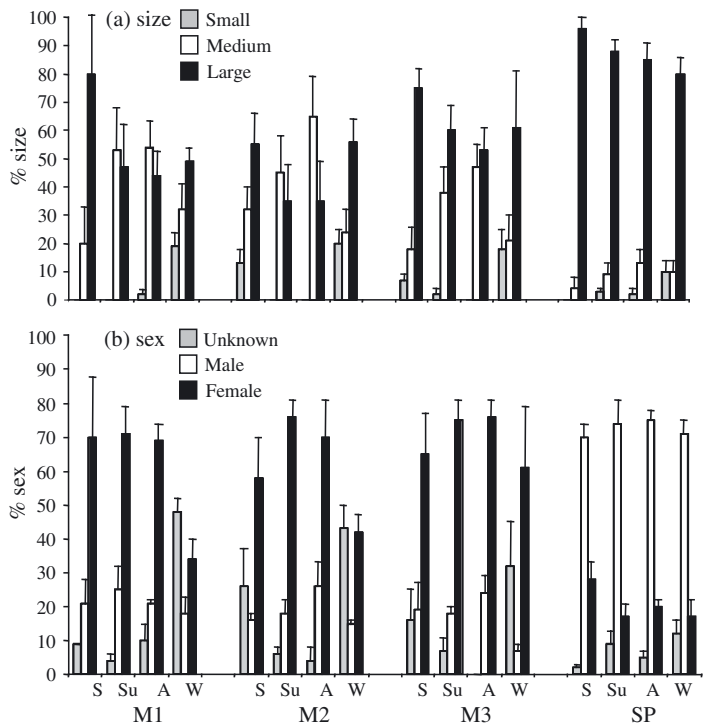


Fig. 7. *Cheilodactylus fuscus*. Proportions of (a) each size class and (b) each sex class occupying aggregations (Middle Head: M1, M2, M3; Shark Point: SP) in each season: spring (S); summer (Su); autumn (A); and winter (W). Error bars are SE

to a maximum over the spring to autumn period, decreasing in winter. Large fish were evident at all sites throughout all of the seasons, and clearly dominated the population throughout the year at SP.

Females dominated the M1, M2 and M3 aggregations (Fig. 7b), while there was a greater abundance of male fish at SP. Analysis of aggregation data by sex indicated a significant interaction between season and aggregation (Table 3b, ANOVA). The percentage of unknown fish occupying M1, M2 and M3 reached a maximum in the winter after a gradual decline in fish of unknown sex over the summer to spring period. SP again proved to be the exception, with male fish making up the largest proportion of all fish in all seasons.

Aggregations and habitat characteristics

The Bray-Curtis cluster dendrogram, and the corresponding MDS plots, of the 29 standardised habitat characteristics (Table 2) did not indicate any signifi-

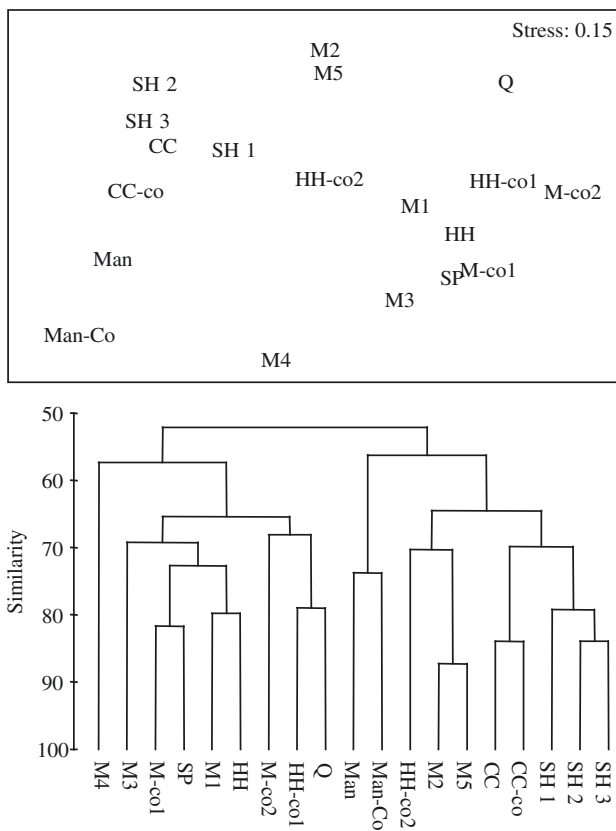


Fig. 8. *Cheilodactylus fuscus*. Multi dimensional scaling (MDS) plot and cluster analysis of the physical variables measured to characterise aggregations. Locations: South Head (SH1, 2, 3). Middle Head (M1, 2, 3, 4); Manly (Man); Camp Cove (CC); Quarantine (Q); Hat Head (HH). Control locations are indicated by suffix 'co'. Stress value indicated in top right corner

cant difference between the geographically and temporally persistent aggregation sites and similar sites with no aggregation (Fig. 8). The 60% similarity split the 19 sites approximately into half, with no particular or logical groupings of sites. Analysis of similarity (ANOSIM) found no significant difference between aggregation and control sites ($R = 0.83$, $p = 0.16$).

Spear fishing experiments

The first (summer) removal experiment of all non-tagged fish at Site R1 was carried out over a 4 wk period with 19 fish removed over 5 dives. The first fish to return to the aggregation site were the larger females, which had previously dominated the population (Fig. 9). The total numbers and sex composition of the aggregation reached pre-impact levels (15 to 20 fish) over the following 4 mo. Importantly, there were few small fish of unknown sex in the emergent population.

Home range values based on the movements of 4 tagged fish before and after removal were not significantly different (ANOVA, $df 1,4$, $p > 0.05$). Home

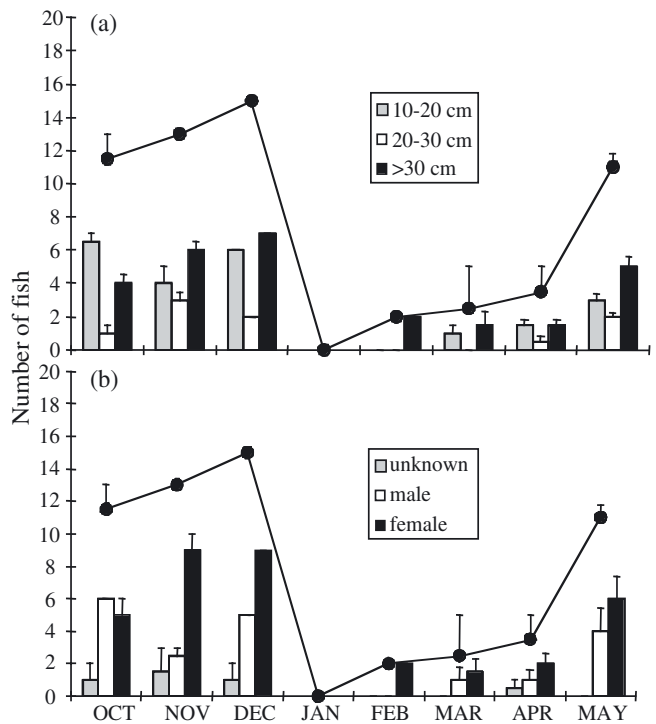


Fig. 9. *Cheilodactylus fuscus*. Summer removal (Expt 1) at site R1. showing total abundance of (a) each size class of all non-tagged *C. fuscus* before and after removal, and (b) each sex class of all non-tagged fish before and after removal, and the total number occupying the aggregation over this period (solid line). Error bars are SE

Table 4. *Cheilodactylus fuscus*. Home range (m²) and SE before and after removal experiment 1 (R1) and 2 (R2), and control aggregations (C1 and C2)

Removal	Aggregation		Control	
	Before	After	Before	After
R1	1356 ± 454	1286 ± 326	1235 ± 298	969 ± 189
R2	885 ± 123	824 ± 104	1017 ± 321	1151 ± 200

range values (MAP 95) did not vary significantly between pre and post removal at either the R1 site or in the control aggregation C1 (Table 4). Tagged fish at R1 remained in close proximity to the point of capture, and did not exhibit any identifiable change in behaviour. Immigrants moving into the site aggregated in the same areas as before.

The second (winter) removal experiment of all non-tagged fish was carried out over 2 mo at the R2 site, with a total of 49 fish removed. Total counts of individuals occupying the aggregation in the 3 mo prior to removal indicated a stable population of 60 to 80 fish dominated by large females (Fig. 10a). Total numbers quickly recovered to pre-spearfishing levels within 1 mo of

the cessation of spearing; however, there was a reduction in the number of small fish in the censuses taken over the 3 mo post spearing (Fig. 10). Home range values based on the observed movements of 12 tagged fish before and after removal were not significantly different at either the impacted site (R2) or the control (C2) (ANOVA, df 1,12, $p > 0.05$).

DISCUSSION

Population structure of red morwong

The transect data at the estuary, middle and coastal locations revealed strong structure in the size and sex composition of red morwong among locations and seasons. In general, populations may be strongly structured by gradients in physical changes (Rakocinski et al. 1992). Differences in size and sex may be due to variations in the substrate type or depth, which represent ontogenetic niches. Previous studies have demonstrated the link between substrate type and depth and the size and sex of fish which structure temperate reef communities (Leum & Choat 1980, Jones 1984a,b, Matthews 1990, McGhee 1994, Gillanders & Kingsford 1998), and red morwong appears to be no exception.

We found that, in general, smaller fish were predominant in the shallows and larger fish predominate in the deeper areas. Smaller fish may select shallow habitat, as consistently observed among locations, and with other members of the genus (Leum & Choat 1980, McCormick 1989a). The occurrence of larger individuals in deeper water has been observed in a variety of species (Clarke 1977, Choat & Ayling 1987, Macpherson & Duarte 1991). Smaller *Cheilodactylus fuscus* (<20 cm) have a significantly different diet than the adults (Lockert & Suthers 1998). Juvenile red morwong feed on invertebrates in the foliose algal turf, which is most abundant in the shallows where it is warm and presumably most productive, while adults move over a wide variety of deeper habitat, feeding mainly at night. The transition in diet and the associated ontogenetic shift in substrate preference indicate that the distribution of juvenile *C. fuscus* is primarily linked to food (primarily amphipods, Lockett & Suthers 1998), while the distribution of the adult population may be linked to shelter.

The autumn-winter increase in the small/unknown sex fraction of the population reflects the recruitment of juveniles to the more protected estuary location. The peak spawning period for *Cheilodactylus fuscus* occurs during autumn and early winter (Lowry 1997). The early life-history of this genus is characterised by an extended larval pelagic phase of approximately 8 to 12 mo before settlement occurs (Vooren 1972). Therefore, after autumn spawning, *C. fuscus* may also settle

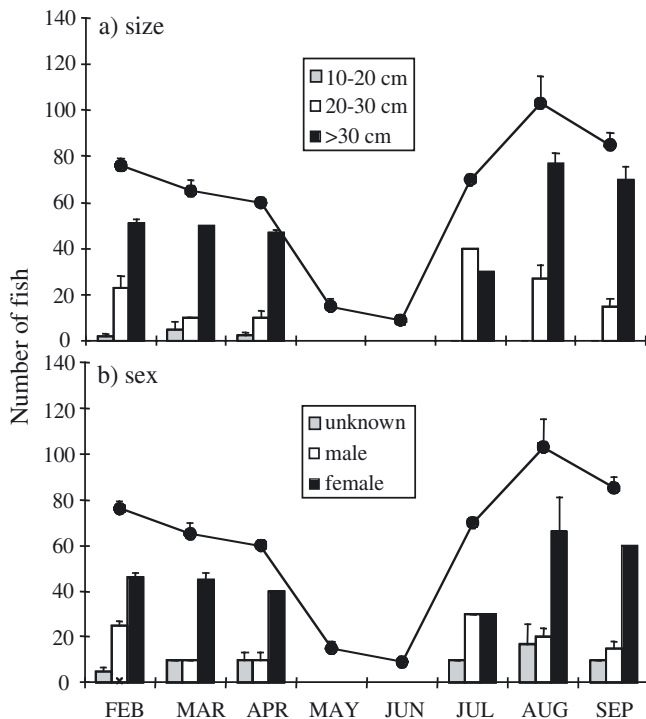


Fig. 10. *Cheilodactylus fuscus*. Winter removal (Expt 2) at site R2, showing total abundance of (a) each size class of all non-tagged fish before and after removal, and (b) each sex class of all non-tagged fish before and after removal, and the total number occupying the aggregation over this period (solid line). Error bars are SE

in shallow marginal habitats during late summer, which is consistent with the subsequent peak in small 10 to 20 cm fish abundance we observed over winter at the estuary location (Fig. 3). Subsequent growth is associated with a progressive movement from the protected estuary location to the adult coastal aggregations. Large males remain associated with the most exposed coastal locations with possible movement of females to these locations during spawning. This interpretation of the life history is consistent with the transect counts of the estuary and middle locations, showing seasonal fluctuations in the large size fraction. These changes appear to be representative of a size-associated ontogenetic habitat shift driven by growth and the associated changes in diet and habitat requirements. Similarly, seasonal patterns in size distribution of *Sebastes* species are mediated by variation in habitat quality, reflecting the changes in abundance of macroalgal cover (Matthews 1990) or an ontogenetic habitat shift associated with size-associated changes in diet and the distribution of food types (Schmitt & Holbrook 1984). Further examination of the life history and movements of the small size class of *C. fuscus* is required, possibly using natural otolith microchemistry signatures (e.g. Gillanders & Kingsford 1996).

Aggregation population structure was also influenced by site, season and depth. The size/sex depth relationship with the larger males occupying the deeper areas of the reef has also been demonstrated for a number of different temperate reef species (Sale 1978, McCormick 1989a) and has been found to be a general pattern structuring the fish fauna of New Zealand's reefs (Choat & Ayling 1987). We interpret the aggregations as 2 types. Type 1 aggregations were associated with more protected areas, dominated by larger resident females with seasonal movements of smaller juveniles in spring and winter, while Type 2 were located in more exposed locations, characterised by large resident males with little or no variation in the overall numbers or the size and sex of the population (e.g. Shark Point). Type 1 aggregations exhibit seasonal movements between aggregations (Lowry & Suthers 1998) and seasonal influxes of smaller juvenile fish. Type 2 aggregations are clearly distinct, with little seasonal change in the proportion of size and sex, and may represent a stable endpoint in the geographic ontogeny of this species.

Habitat characteristics that determine local population density

Aggregated populations may provide the required population densities needed to secure local habitat from intra-specific competition and act as a mechanism to stabilise the spatial distribution of the species

(Brown & Orians 1970). The advantages associated with site associated aggregated populations can vary seasonally. For example, *Cheilodactylus spectabilis* occupies a similar niche but uses caves associated with the boulders as spawning sites (McCormick 1989b; while possible, no such behaviour was observed for *C. fuscus*). We selected 29 habitat characteristics based on the morwong's preference for physical structures, grazing habits, and harassment by *Parma*, yet no obvious factor was revealed.

Aggregations of other temperate reef species, such as copper rockfish *Sebastes caurinus*, quillback rockfish *Sebastes maliger*, brown rockfish *Sebastes auriculatu* and surf perch *Embiotoca lateralis* are influenced by the proximity of appropriate shelter sites to feeding areas (Matthews 1990, Holbrook & Schmitt 1992). Previous work, however does not indicate any relationship between the location of aggregations and feeding sites for *Cheilodactylus fuscus* (Lowry & Suthers 1998).

Recent work indicates that learned recognition of conspecifics and even individual fish have important implications in understanding how populations are structured (Brown & Laland 2003, Griffiths 2003). Memory built up over the lifetime of such a long-lived species may be a feasible means of explaining the observed site specificity. Other theories invoke genetic or life history memories to explain fidelity to a certain area (e.g. Breder 1976), or Hallacher (1984) suggests that the site specificity and goal-directed homing ability might be a result of an internal template developed as a result of prior experience or natural selection.

Effects of spear fishing

Red morwong re-aggregated at the same site, suggesting either some unknown site-specific characteristic, or the influence of the surviving fish. Several repopulation studies show that the presence of conspecifics promotes the appearance of both adults and new recruits (Jones 1984b). The new aggregation was generally composed of all size classes, and not just the small fish as was expected, although the recovery varied between sites. The recovery after the summer removal at R1 was relatively slow, taking approximately 4 mo to return to pre-removal numbers, of small, medium and large fish. Recovery of the winter removal at R2 was rapid by comparison, with numbers of medium and large fish occupying the aggregation exceeding the pre-removal numbers within a month after removal. Whilst the general structure of the community in terms of size and sex was maintained at R1, the post spearing population at R2 had few small, 10 to 20 cm, fish. These differences can be explained in terms of the seasonal distribution of recruits and the

variation in local population densities between sites. The aggregation size and local population density at the R1 experiment was lower than at R2, limiting the opportunities of recruits to the area from adjacent populations with overlapping home ranges. Beckley (1985) studied the re-colonisation of cheilodactylids after localised depletion and concluded that the proximity of neighbouring areas with unaffected populations of fish was an important factor favouring rapid repopulation. The absence of the smaller size class from the aggregation at R2 is a result of the seasonal distribution of recruits. Larvae settle and thence migrate as small fish to the estuary location in winter and to the middle location (including R2) in spring and summer. Beckley (1985) observed a similar pattern of re-colonisation in tide pools, with the highest proportion of juvenile cheilodactylids occurring in winter.

The remaining tagged fish did not increase their day-time home range after the >70% reduction in fish density in either experiment. There were no detectable differences in the before or after home range at either of the sites, indicating that local population densities do not have a significant impact on home range, although there could have been an effect on their night-time home range. Nevertheless, the remaining tagged fish quickly occupied the larger, deeper crevasses formerly inhabited by the larger individuals, suggesting the importance of crevice abundance, even though this was not evident in our habitat assessment.

The movement of new fish into the site after the removal of the majority of the existing population suggests that the existing population was in some way obstructing these individuals, yet *Cheilodactylus fuscus* was never observed to display aggression or territoriality to other species or conspecifics. A small non-aggregated proportion of the population represents a transient, surplus group, from which depleted aggregations are repopulated. Terrestrial species limited by nest-site shortage have a similar floating population (Brown & Orians 1970).

Spearfishing may have a significant impact on such a long-lived resident population. There is evidence that spearing is responsible for the localised depletion of cheilodactylid populations in New Zealand (Cole et al. 1990). Spearing selectively removes the larger size class and has the potential of removing a large proportion of the males. The role of other factors such as ontogenetic development and reproductive ecology in mediating the observed changes to structure are not fully understood. Further study is needed to confirm the relationship between habitat, aggregation type and ontogenetic migration, how representative observed aggregation types are of the wider population, and the longer-term effects that spear-fishing events and their timing have on the resultant population.

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