M. B. Lowry · I. M. Suthers

Home range, activity and distribution patterns of a temperate rocky-reef fish, *Cheilodactylus fuscus*

Abstract Red morwong (*Cheilodactylus fuscus*; Cheilo-dactylidae: Perciformes), are large temperate rocky reef fish that are patchily distributed in local aggregations of 3 to >100 fish. The home ranges and aggregating behaviour of red morwong were investigated using external tags ($n = 114$, over 35 mo) and ultrasonic transmitters ($n = 9$ over 20 d) at coastal and estuarine sites in southeast Australia. Adult red morwong had a mean home range during the day of 1865 m^2 (SE = 268). Night movement, determined by ultrasonic telemetry, indicated a significantly greater mean home range of 3639 m^2 (SE = 416). Home range did not differ significantly with size or sex. Fish movements were greatest and aggregation sizes varied most during the non-reproductive mid-summer period. Tagged fish ($N = 20$) displaced 200 to 900 m returned in 1 to 3 d to the point of capture, often traversing open sand habitat and other aggregations. During the day, fish were commonly found on bouldered habitat. During the night, these site-specific aggregations fragmented as fish dispersed over a variety of substrata, with crepuscular peaks in activity. Therefore, estimates of habitat-specificity and feeding patterns collected only by day may give misleading results.

Introduction

Cheilodactylid fish, commonly known as morwongs, are an important component of the fish communities inhabiting temperate reefs in Australia, New Zealand,

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Japan, South America and South Africa (Leum and Choat 1980; Branden et al. 1986; Lincoln Smith and Mann 1989; McCormick 1989a, b). Red morwong (*Cheilodactylus fuscus*) are benthic carnivores (Bell 1979; Lockett 1993), and do not form part of any significant commercial fishery. As one of the largest of the resident species (maximum standard length of 65 cm), it is often targeted by spearfishers (Lincoln Smith et al. 1989). There is little or no information detailing habitat use and patterns of movement for cheilodactylids, except for the banded morwong, *C. spectabilis*, of New Zealand (Leum and Choat 1980; Sano and Moyer 1985; McCormick and Choat 1987; McCormick 1989a, b).

The New Zealand studies did not fully address the possible importance of diurnal-activity patterns and the significance of nocturnal foraging behaviour. Accurate interpretation of habitat use relies on observations carried out over diurnal and seasonal time frames. Monitoring the behaviour of known individuals, identified by external dart tags and ultrasonic transmitters can detect changes in behaviour and habitat use which have been beyond the methodology of other similar studies.

This study aimed to develop an estimate of the home range area and to interpret the effects of size, sex, season, and day/night on home range. We show how diurnal and seasonal variation and behaviour such as homing, aggregating and substratum preference influence home range and habitat use.

Materials and methods

Study area

Observations were carried out at three sites: Middle Head in Sydney Harbour, Shark Point 12 km south of the southern headland of Sydney Harbour and Jervis Bay, ≃230 km south of Sydney (35°04′S; 150°45′E: Fig. 1). The majority of observations were carried out at the Middle Head site. A strip of reef 290 m × 180 m was mapped in detail to determine subtidal topography and the distribution of each substratum type (Fig. 2). The shallows were characterised by a strip of macroalgae dominated by *Ecklonia*
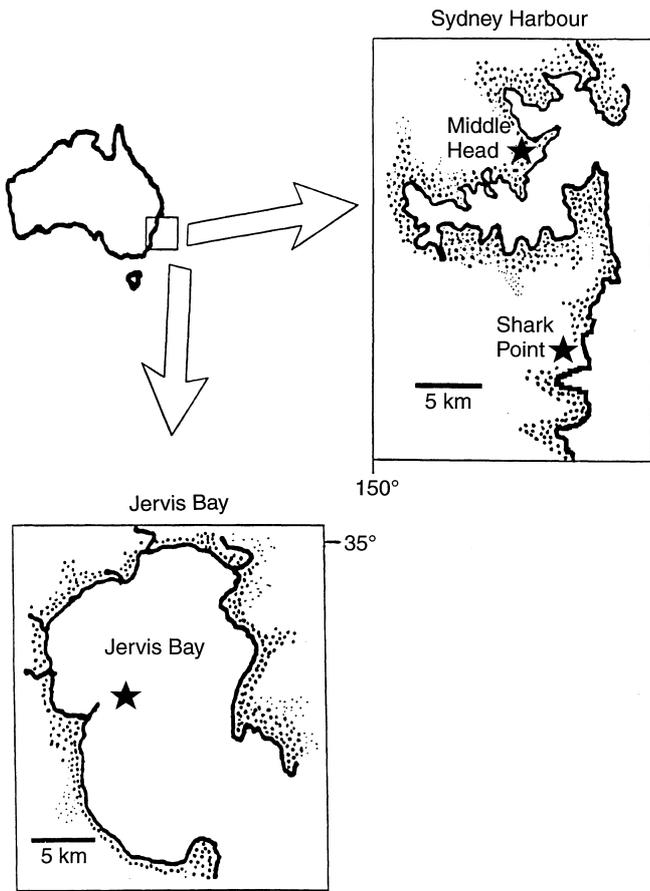
Fig. 1 Location of tagging sites Middle Head, Shark Point and Jervis Bay, south-east Australia
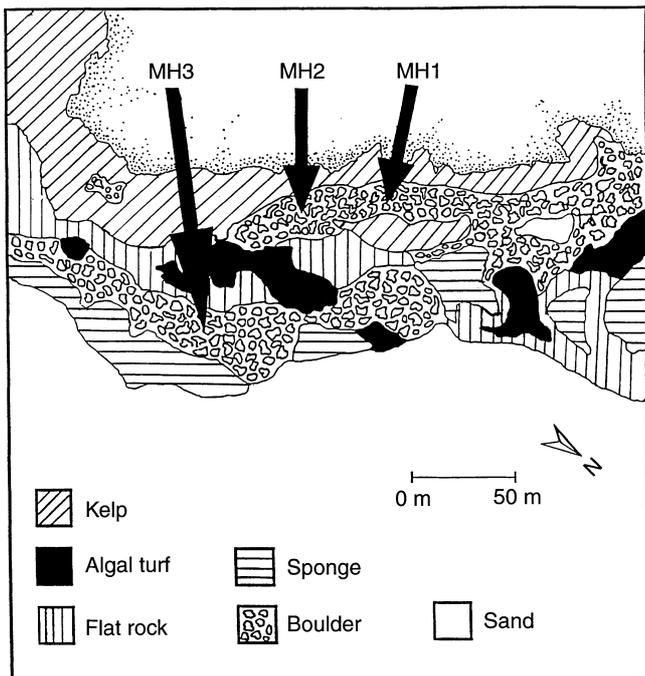

Fig. 2 *Cheilodactylus fuscus*. Location of the three aggregations at Middle Head site and subtidal substratum types

radiata (13%). The deeper areas were comprised of extensive boulder fields (20%), interspersed with exposed flat rock (7%), or areas encrusted with a variety of turfing algae and sponges (19%). The margin was sharply delineated by sand beds (40%) at the maximum depth of 11 m. Shark Point was an area of exposed coastline 320 × 110 m, deeper than the other sites, with the boulder field extending to 28 m. The Jervis Bay site consisted of a patch reef of ≃340 × 200 m surrounded by sand at a maximum depth of 12 m. Both the Shark Point and Jervis Bay sites offered similar proportions of the same habitat types as at Middle Head.

Sampling and external tags

Cheilodactylus fuscus were captured using a submerged 15 m × 4 m, 2 cm stretched-mesh monofilament barrier-net, floated on the top and weighted at the bottom. The net was manoeuvred into position around the aggregation by divers using SCUBA. Fork length and weight were recorded on capture and sex was visually determined from the relative length of the ocular tubercle (Schroeder et al. 1994). Fish were injected with a 30 mg/kg dose of tetracycline (McFarlane and Beamish 1987) to reduce the risk of infection and to provide a means to validate age by determining the periodicity of annuli formation in the sagittal otoliths (Lowry unpublished data).

A tag applicator (Matthews and Bell 1979) was used to lock the barb of the tag behind an inter-neural spine. Hallprint™ dart tags, individually colour-coded with electrical insulation ("heat shrink") were used to identify individual fish. All fish were double-tagged, and a proportion of the tagged fish were observed immediately after release to determine the effect of tagging. Submerged reference-markers positioned at regular intervals ensured accurate positioning of marked fish over subsequent dives. Fish were tagged on ten occasions over 21 mo at the three sites (Table 1). The majority were captured from aggregations MH1, MH2, and MH3 at Middle Head (Fig. 2). Additional fish were tagged at Shark Point and the more remote site at Jervis Bay to determine any spatial variability.

A total of 114 fish were fitted with dart tags, and a further three fish could be identified by marks or scars. Tag-loss over the initial 24 to 48 h period and subsequent difficulty in identifying fouled tags (Lowry unpublished data) resulted in only 68 tagged/scarred fish with the required observations (minimum of three resightings)

Table 1 *Cheilodactylus fuscus*. Number of fish and location of capture for all dart ($N = 117$)- and ultrasonic ($* N = 6$)- tagged fish

Site, Location	Date		(N)
Middle Head			
MH1	6 Apr	1992	(15)
	20 May	1992	(8)
	9 July	1992	(9)
	2 Sep	1992	(7)
	12 May	1993	(12)
	30 June	1993	(2*)
MH2	7 Mar	1994	(2*)
	12 May	1993	(9)
	30 June	1993	(1*)
MH3	7 Mar	1994	(3*)
	13 Jan	1994	(31)
	7 Mar	1994	(1*)
Shark Point			
SP1	21 Sep	1993	(8)
Jervis Bay			
JB1	17 July	1992	(15)
(Total)			(123)

for a home-range estimate. The locations of tagged fish were observed at the Middle Head and Shark Point sites on an approximately weekly basis over 2.5 yr. Total counts of all *Cheilodactylus fuscus* occupying the aggregations at the Middle Head and Shark Point sites were also recorded. The Jervis Bay site was monitored every 3 to 4 mo, and data collection there was limited to recording the presence or absence of tagged fish.

Homing

Observations of fish released immediately after tagging suggested that the fish returned to the point of capture. To investigate the ability of this species to return to a specific location, 20 fish were captured from two aggregations at Middle Head (MH1 and MH2) on 12 May 1993, tagged, and released at three locations 200 to 900 m from the point of capture (Fig. 3). Four were released at the point of capture as a control group. The return of these displaced, tagged fish to the point of capture was observed on six dives over the following two weeks.

Ultrasonic tags

Preliminary night dives indicated a marked change in behaviour, as site-specific aggregations evident during the day dispersed at night. Ultrasonic transmitters provided a means of determining the extent and nature of these nocturnal movements.

Prior to the insertion of the tag, fish were anaesthetised in a solution of benzocaine, and a small incision ≃2 cm long was made along the ventral midline. After inserting the tag, the incision was closed with silk sutures.

Observations of fish immediately after the application of both dart and ultrasonic tags indicated that after a short period of re-adjustment (< 10 min) there was no observable tag-induced change in behaviour. After 10 to 12 d, the incisions had healed and the fish appeared healthy.

Vemco V2 transmitters, each 38 mm × 8 mm and weighing 5.3 g (Vemco 1994) were inserted into nine fish in two experiments carried out at the Middle Head site. In the first study (30 June 1993), three fish were fitted with transmitters; the second investigation (7 March 1994) deployed a further six tags. The length, sex and capture point of all the fish tagged in the biotelemetry trials are detailed in Table 2. One of the transmitters used in the second biotelemetry trial failed after only 2 d. Estimates of night range for the second biotelemetry trial are based primarily on five fish.

Tracking

Tags transmitted within the 65 to 77 kHz frequency range. Each transmitter was identified by a specific combination of frequency and pulse rate. By moving the directional hydrophone through an arc, the direction of the signal was resolved. Signal strength was used to determine the proximity of the tagged fish. Observations were carried out in shifts of 6 to 8 h; each fish was located at hourly intervals. Time and estimated position were recorded on a map. The track of each of the fish was then developed over successive readings. To partition day movement from night movement, home-range calculations were based on the observed movements of each fish per shift.

To determine the accuracy of transmitter fixes, a diver fitted with a transmitter was located and a weighted buoy was used to mark the position. Distance between the estimated and actual position of the tag was determined. Trials were carried out over a variety of depths and substrata. The mean distance between actual and estimated position determined from nine attempts was 3.4 m (SE = 1.38). Detection range of the transmitter varied from 10 m to a maximum of ≃80 m, depending on sea state and obstructions impeding the path of the signal.

The battery life for the V2 tags was ≃12 d (Vemco 1994). Each run was halted after 10 d so that the remaining transmission time could be use to locate and recapture the fish.

Analysis

Observed positions of the fish were translated into co-ordinate files, and home range was calculated using the Anderson (1982) Fourier-transformation model. Anderson analysis expresses home range as a minimum area versus probability function or "MAP" value. This defines home range as the minimum area encompassed by an arbitrary percentage of the total observations. The two most commonly used values are the MAP50 (or core area) and MAP95, representing the minimum area bounded by 50 or 95% of the total observations for each fish, respectively. A comparison of the cal-
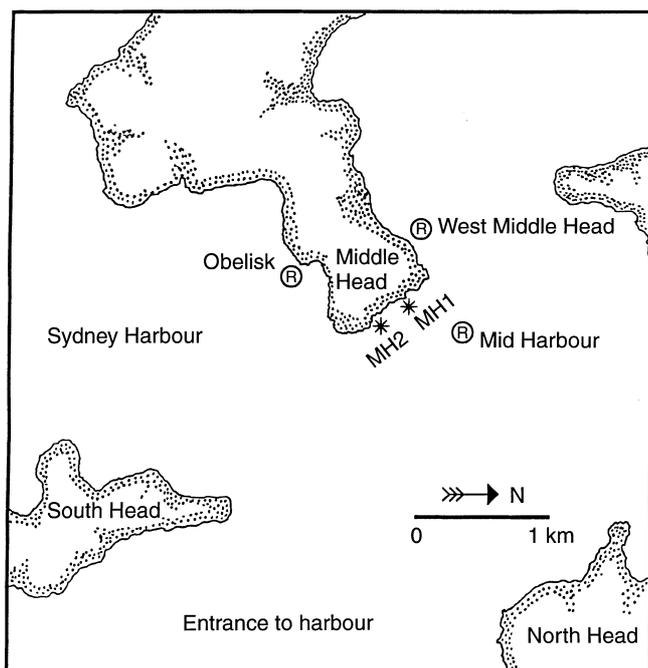
Fig. 3 *Cheilodactylus fuscus*. Capture and release points (®) used in homing experiment. Fish were captured from Aggregations MH1 and MH2

Table 2 *Cheilodactylus fuscus*. Fork length, weight, sex, number of nights observed and point of capture for both biotelemetry tagging experiments (*F* females; *M* males). Sites as in Fig. 2

Length (cm)	Weight (g)	Sex	No. of nights observed	Aggregation
Tagged 30 June 1993				
29	500	F	11	MH1
30	525	M	9	MH1
30	480	F	8	MH2
Tagged 7 March 1994				
35.5	950	M	12	MH1
30.5	560	F	10	MH1
29.5	450	M	14	MH2
29.5	460	F	12	MH2
29.5	490	F	8	MH3
(Total)			(84)	

culated core and extended home ranges provides a means of evaluating the temporal variation in the area used by the species being studied. A significant difference between the core and extended ranges would indicate that there is variation in the area being used over time resulting from possible seasonal or ontogenetic effects on habitat use. The Anderson utilisation-distribution model is the preferred method of analysis as it also allows comparisons between the long-term time-series data developed from the visual tagging and the shorter time scale of the biotelemetry.

Statistical analyses were carried out using SPSS Version 6.0 (Nie et al. 1970). Homogeneity of variance was tested using Levene's method, and all data were transformed using the $\ln(x + 1)$ transformation, as necessary, to ensure normality.

Results

Fish size

Cheilodactylus fuscus from the four locations MH1, MH2, MH3 and SP1 ranged in size from 16 to 44 cm fork length ($N = 117$, mean $= 28.4$ cm $\pm$ 0.4 SE; Fig. 4). Of the 67 fish sexed (Schroeder et al. 1994), 70.6% were female, 23.5% male and the remaining 5.9% exhibited no obvious sexual dimorphism and were classified as sub-adults. Males were significantly larger (34.1 cm $\pm$ 1.2) than females (27.6 cm $\pm$ 0.54) and sub-adults (21.2 cm $\pm$ 1.7) (ANOVA $df = 2$, 64, $p < 0.001$). Fish tagged from MH3 were significantly larger than those from the other two aggregations (MH1 and MH2) at Middle Head (29.3 cm $\pm$ 0.8, 26.9 cm $\pm$ 0.6 and 26.6 cm $\pm$ 0.7), respectively. Fish tagged from the deeper Shark Point site were significantly larger than those captured from Middle Head, with a mean length of 35.6 cm $\pm$ 1.7 (ANOVA $df = 3$, 98, $p < 0.001$).

Effects of size and sex on day home-range (external tags)

Home-range estimates and movements were established from 560 h of observations on 117 tagged and/or scarred
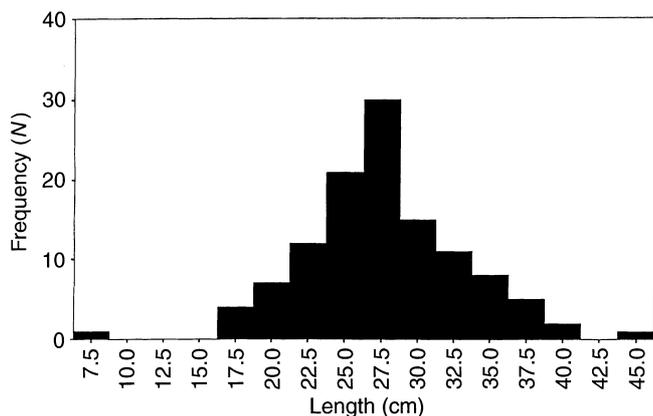

Fig. 4 *Cheilodactylus fuscus*. Frequency histograms of tagged and scarred fish as a function of fork length ($N = 117$)

Table 3 *Cheilodactylus fuscus*. Mean home-range estimates (m², at MAP50 and MAP95 levels) and SE for day-based dart tags and night-based ultrasonic tags. N for dart tags includes those individuals with three recorded locations; N for ultrasonic tags equals number of tagged fish multiplied by number of observation periods [*Day/night* comparison of day and night home-range estimates; *Aggregation* home-range estimates for the three aggregations at Middle Head (*MH1, MH2, MH3*) and aggregation at Shark Point (*SP1*); *Night* comparison of home-range estimates determined for each night trial]

Variable	MAP50 (SE)[a]	MAP95 (SE)[a]	(N)
Day/night			
Day, dart tags	705.5 (108.0)	1864.5 (267.9)	(68)
Night, ultrasonic tags	1418.3 (170.4)	3638.8 (416.4)	(84)
Aggregation			
MH1 (day)	544.4 (98.1)	1544.0 (267.5)	(30)
MH2 (day)	650.7 (183.3)	1840.3 (514.3)	(9)
MH3 (day)	1061.6 (270.9)	2616.8 (658.1)	(23)
SP1 (day)	228.5 (74.2)	619.5 (205.0)	(6)
Night			
June 1993 (night)	465.6 (86.3)	1296.4 (248.0)	(27)
March 1994 (night)	1869.6 (224.6)	4748.3 (544.8)	(57)

[a] MAP expresses home range as minimum area vs probability function (see "Materials and methods – Analysis" for details)

fish over a 35 mo period (April 1992 to February 1995). Of these 117 fish, 68 had the required minimum of three observations. Home-range estimates were calculated using a mean number of 10.4 ± 0.8 SE observations. Diel observations resulted in a mean home-range estimate (MAP95) of 1865 m² $\pm$ 268 SE (Table 3). Fish identified by scars and not tags were observed more often for longer periods than any of the dart-tagged fish, suggesting that the difference in the frequency of observations between tagged individuals was not a result of behavioural differences but due to the loss and fouling of tags (Lowry unpublished data).

There was no significant difference in home-range area between males and females (ANOVA, $df = 1$, 47, $p > 0.7$), nor was there any significant correlation between fork length and home range at the MAP50 or MAP95 levels, $r = 0.04$, 0.02, respectively.

Effects of aggregation and season on diel home-range

Both MAP50 and MAP95 home-range estimates for MH3 were significantly larger than for any of the other aggregations (ANOVA, $df = 3$, 64 $p < 0.05$, Table 3. Total counts of aggregations (Fig. 5) indicated seasonal fluctuations in aggregation size. Aggregation MH3 varied in size from a mean of 5 (± 5 SE) fish in June to 84.5 (± 4.5 SE) in December. The increase in numbers was associated with a decrease in the number of fish in the other aggregations (Fig. 5).

Difficulties in relocating the aggregation at the Jervis Bay site restricted the analysis there to a record of the number of tagged fish observed as a measure of the
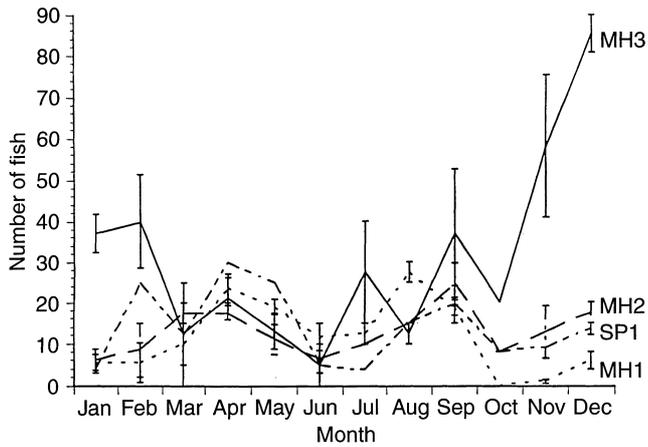
Fig. 5 *Cheilodactylus fuscus*. Mean (±SE) pooled monthly total counts at MH1, MH2 and MH3 (Middle Head) and SP1 (Shark Point). (Aggregations monitored from October 1993 to May 1995)

persistence of fish in this area, and no MAP area could be calculated. After an initial reduction in the sightings of tagged fish, 20% of the tagged population was still present after 19 mo, indicating a similar site-fidelity to that of fish tagged in Sydney Harbour.

Nocturnal home ranges (ultrasonic tags)

To ensure that night home-range estimates were not biased by day movement, the home range for each fish was calculated using the positions determined on each night. Table 2 lists the number of nights each fish was observed.

The mean nocturnal MAP95 home range of 3639 m^2 (±416 SE) was significantly greater than that observed during the day (1865 m^2 ± 268 SE). Home range values also differed significantly at the MAP50 level (ANOVA,

Fig. 6 *Cheilodactylus fuscus*. Comparison of distribution (distance, m) of fish at night; determined by biotelemetry of Aggregation MH1 on 30 June 1993 ($N = 2$, **a**) and 7 March 1994 ($N = 2$, **b**)
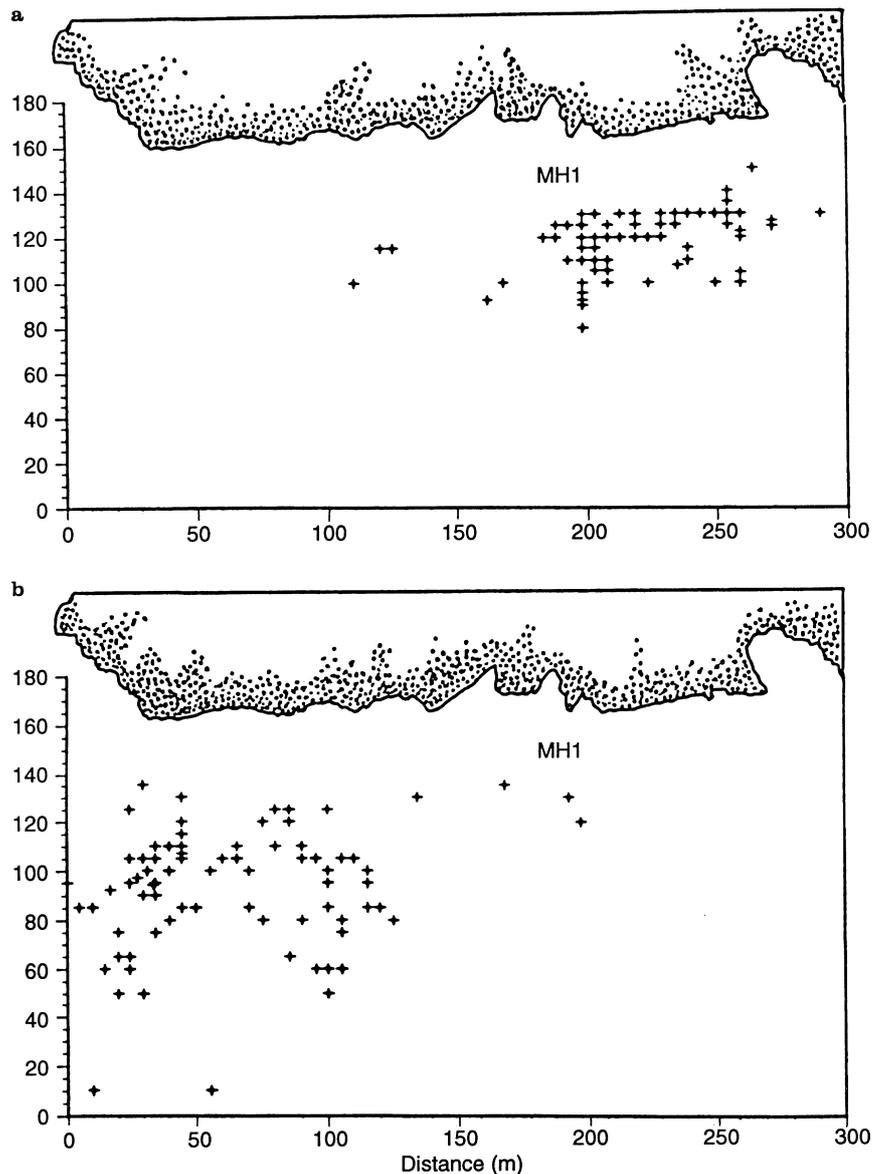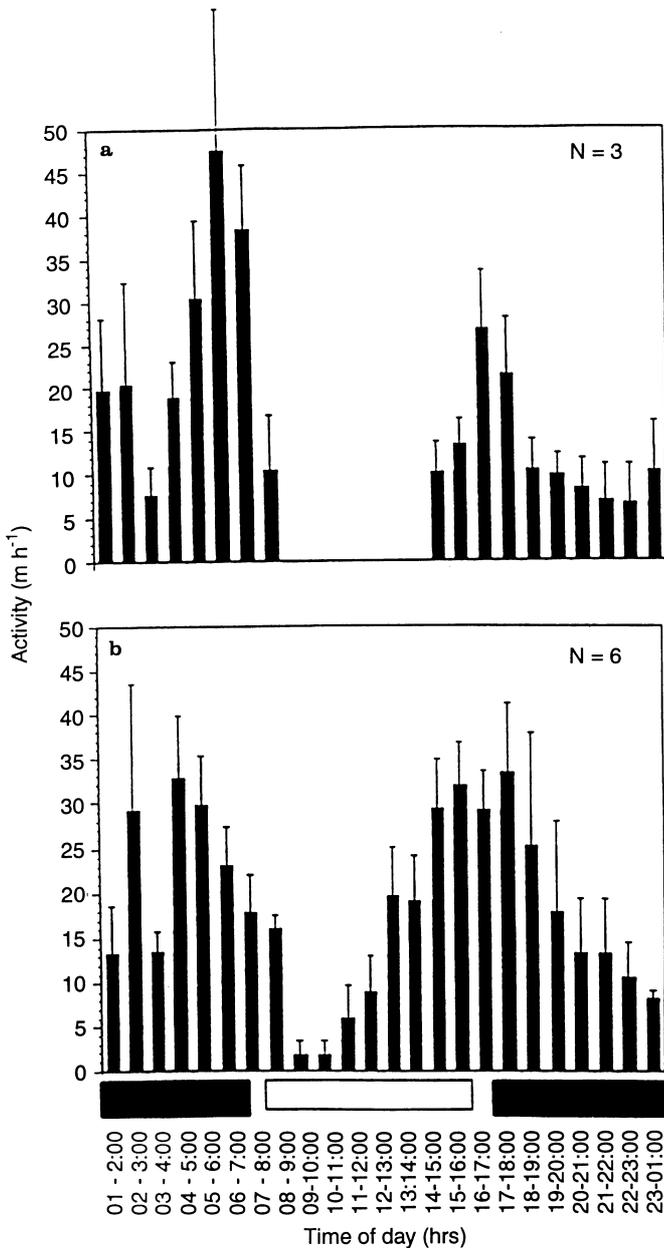
Fig. 7 *Cheilodactylus fuscus*. Night activity (mean ± SE distance moved h⁻¹) during both biotelemetry trials. **a** Trial 1, tagging date 30 June 1993; **b** Trial 2, tagging date 7 March 1994

$df = 1, 150, p < 0.05$). All day/night home-range values are listed in Table 3.

In addition to nocturnal observations, two fish from MH1 tagged with transmitters (March 1994) were monitored for a 5 h period during the day. The position of each of these fish was recorded six times over the 5 h period, and indicated no movement from the aggregation. Fish tagged from other aggregations proved more difficult to detect, until the evening period of high activity.

Nocturnal home range was calculated from two seasonal trials (June 1993 and March 1994). Home ranges

between the two trials varied significantly at both the MAP50 and MAP95 levels (Table 3; ANOVA, $df = 1, 82, p < 0.05$). The home range of fish captured from the three Middle Head aggregations in March 1994 did not reveal any significant differences in night home-range. A comparison of the night movement of fish tagged from the same aggregation indicates seasonal differences in the location of the area being used. Scatter plots comparing the observed positions of fish captured from the same aggregation (MH1) over the two biotelemetry trials show that during the first trial (June 1993) movement was closely associated with the home aggregation (Fig. 6a). The area used by those fish captured from the same aggregation for the second trial (March 1994) was not closely associated with the aggregation, with activity focused on a different area of the site (Fig. 6b).

Activity (ultrasonic tags)

Activity, measured as mean distance moved per hour, peaked at dawn and dusk with limited movement during the day (Fig. 7). The same pattern was indicated by the direct observations of externally tagged fish (Fig. 8). Diel movement was restricted to the home aggregation, while at night fish moved extensively over a greater proportion of the site. No significant differences were found between the average distance moved in the two seasons, although the period of activity was extended during the summer (Fig. 7b).

There were significant differences between core (MAP50) and extended (MAP95) home ranges for both day (ANOVA, $df = 1, 165, p < 0.001$) and night (ANOVA, $df = 1, 134, p < 0.05$). These differences between the core and extended estimates of home range reflect seasonal and crepuscular variations in behaviour.

Homing

Of the 16 fish displaced from the point of capture by 200 to 900 m, 75% returned to their origin within 12 d. Fish released at the control site remained there. Fish released at Obelisk, the most distant site from the point of capture (900 m), had a lower percentage recovery than fish released at either of the other sites (Table 4).

Habitat preference

Aggregated populations were substratum-specific, preferring the rugose boulder habitat. This habitat preference is clearly evident from field observations (Fig. 9), with the majority of fish during the day sheltering in caves or lying between the crevices which characterise the bouldered substratum. The dispersion of these aggregated populations at night (Fig. 8b) is reflected in the clear diurnal variation in substratum use. The preference

Fig. 8 *Cheilodactylus fuscus.* Recorded positions of fish captured from Middle Head Aggregations MH1, MH2 and MH3 (positions indicated). **a** Day plot of 598 observations of 114 dart-tagged and three scarred fish over period of 35 mo (April 1992 to February 1995); **b** night plot of 493 observations of six fish fitted with ultrasonic tags over period of 12 d (7 to 19 March 1994)
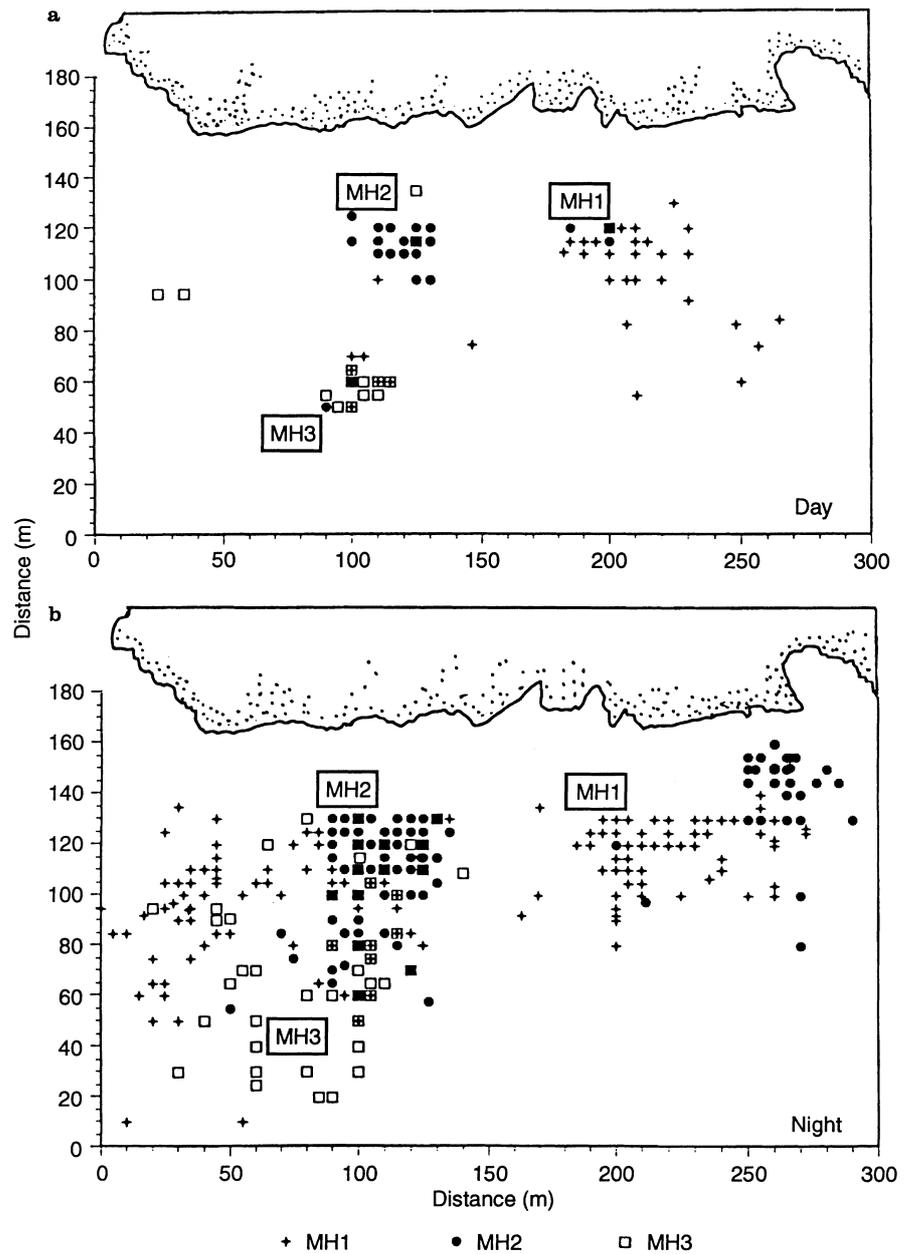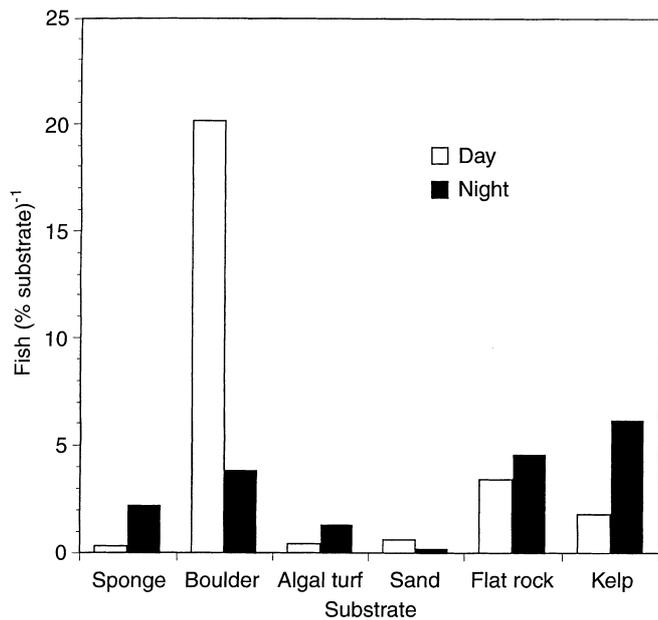

for bouldered habitat is not replaced by any one particular substratum type, with fish adopting a more indiscriminate mode of habitat use (Fig. 9).

Discussion

Our work reveals unsuspected crepuscular and nocturnal activity in the red morwong *Cheilodactylus fuscus*, a finding which could only have been determined with the use of ultrasonic transmitters. Adult red morwong aggregate during the day in the boulder habitat and, except in mid-summer, exhibit a marked fidelity for the home aggregation. Both sexes occupy diel home ranges of $\simeq 2000$ m², which double during their crepuscular feeding forays.

Table 4 *Cheilodactylus fuscus.* Relative times of return of tagged fish removed from home aggregations on 12 May 1993 (*Dist* distance of each release point from capture point; *N*, number of fish released at each site)

Release site	Dist (m)	(N)	First recovery	Median recovery (d)	Last recovery	% recovery
Obelisk	900	(6)	Day 3	3	Day 12	50
Mid Harbour	600	(5)	Day 1	5	Day 32	100
West Middle Head	200	(5)	Day 2	6.5	Day 12	80
Control	0	(4)	Day 1			100

Fig. 9 *Cheilodactylus fuscus*. Substratum use at Middle Head site as a function of time of day. Day substratum-use determined from total observations of all dart-tagged fish (117 fish: April 1992 to February 1995), night substratum-use determined from observations of nine fish over two biotelemetry trials (June 1993, March 1994) (Substratum use calculated as percentage of substratum comprised by each substrate type divided by number of fish observed on respective types)

Seasonal effects and home range

The movement between aggregations was indicated clearly by the fluctuation in the total counts, particularly the large increase in the number of adult fish at MH3 over the summer. A comparison of the location of fish captured from the same aggregation (MH1) also demonstrates this variation in habitat-use. Fish tagged in June remained associated with MH1. However, fish tracked over March used a different region of the site, concentrating on the area around MH3.

Factors which determine these fluctuations in aggregation, size and habitat-use are not clear. There is some evidence to suggest that this may be a response to seasonal variation in habitat quality. Variation in the diversity and abundance of prey items can influence home-range area (Choat and Kingett 1982; Kennelly 1983). Seasonal differences are apparent in the diet of the red morwong (Bell 1979), with fish sampled over summer having a much higher proportion of amphipods in their diet than in winter. Similar movement patterns were recorded by Matthews (1990), who found for *Sebastes* spp., that home-range size and the readiness to return to the displaced area depended on seasonal variation in habitat quality. Variation in home-range size between aggregations and the seasonal movement of populations may indicate a flexible strategy for optimal habitat-use (Matthews 1990).

Seasonal movement may also be a function of the reproductive behaviour of this species. McCormick

(1989b) concluded that female choice during the spawning season was a major factor in determining the general distribution pattern of *Cheilodactylus spectabilis*. However, the movement observed in the present study does not appear to be directly associated with reproduction occurring in mid-summer, 6 mo after peak gonadosomatic indices (Lowry unpublished data).

The larger fish occupying MH3 and SP1 aggregations may reflect an ontogenetic stratification of the population, with older, larger, fish occupying the deeper aggregations. A similar trend towards an increase in size with depth was also found by McCormick (1989a) for *Cheilodactylus spectabilis*. The larger home-range values resulting from those fish captured from MH3 may be explained by the fact that the tagging of the sample population on which the home-range estimates were based took place during January, when total counts indicated a high level of immigration to MH3, resulting in a proportion of non-resident fish being tagged and elevated range estimates as these fish returned to the resident aggregation. The results emphasise the importance of adequate sampling through time and space in order not to bias home-range estimates resulting from seasonal phenomena such as migratory events.

Diurnal changes and home range

The home range of *Cheilodactylus fuscus* varies significantly between day and night. Day observations indicate extended periods of limited movement from the home aggregations punctuated by relatively short periods of extensive seasonal movement directed between aggregations. This pattern of behaviour is also evident in terrestrial species, where animals making infrequent trips between non-contiguous home-range areas use corridors between populations (Jaremovic and Croft 1987). Night movement is characterised by non-directional movement over a variety of substrata. Direct observations and gut analysis indicate that this is when feeding occurs (Lockett and Suthers 1998). Other reef species also exhibit a similar strategy, undergoing diel migrations between feeding grounds and sheltered areas (Hobson 1972; Ogden and Buckman 1973; Gladfelter 1979). Observations of *C. spectabilis* carried out by diving revealed no evidence of dawn and dusk peaks in activity (Leum and Choat 1980). This may be a result of the temporal limitations of underwater observations to determine changes in activity patterns during periods of limited visibility.

A comparison of the day/night home-range values should consider the way in which the data were collected. Day (dart-tagged) observations were accumulated over a period of years from ten tagging events, and incorporated seasonal movements. Night observations, limited to the life of the transmitter, are based on mean values of movement over weeks rather than years and are unlikely to incorporate the seasonal movements that

are a significant factor in the estimation of the day home-range. Consequently, our estimates of night home-range are probably underestimates.

Physical characteristics of an animal, such as size, metabolic rate, ontogenetic development, coupled with environmental factors such as the distribution and abundance of food and inter- and intraspecific interactions may determine home range (McNab 1963; Jones and Norman 1986). The metabolic relationship between size and home-range area, with larger terrestrial mammals occupying a larger home range (McNab 1963) is not as applicable to a poikilothermic animal in the marine environment. Fish tagged from the Shark Point aggregation (SP1) were significantly larger but had the smallest home-range area, indicating that the factors that determine the area used are more complex than the resource-budget models used to explain variations amongst terrestrial animals.

Homing

Once established in areas of suitable substrata, aggregations can maintain their occupancy through the ability to return to the same location over time. Homing ability also maintains populations in one area, acting to stabilise spatial distribution; although functionally different, it has a similar purpose to territoriality exhibited in other species (Green 1971; Crossman 1977).

Our homing experiment demonstrated that red morwong can return to the point of capture, with 75% of the displaced fish returning to the home aggregation within 12 d. Fish released at Obelisk had a lower return rate (50%) than fish released from the West Middle Head and Mid Harbour release points (80 and 100%, respectively). The stimuli used to determine direction may include vision through the recognition of landmarks, olfactory stimulation, the use of a sun compass, and the direction of currents (Hasler and Wisby 1958). Fish released in mid-ocean without coastline to provide reference points had the greatest percentage return, while the lowest percentage return was from those fish released at Obelisk, the release point furthermost from the point of capture. Perhaps distance from the point of capture or other aggregations en route may affect the ability to home.

Habitat preference

Aggregations that are not formed as a result of limited or patchy resource distribution, may be a response to exploit a resource not readily captured by the individual (as a group defence against predators or feeding areas: Brown and Orians 1970). It is unlikely that individual morwong occupying the aggregation are defending feeding areas, as aggregations have been shown to dissociate at night, when feeding occurs. Observations clearly indicate that persistent aggregations occur exclusively on bouldered substrata, and individuals move into hiding places between rocks or swim away from the aggregation when harassed. The importance of these high-relief areas has been demonstrated in other studies (Choat and Ayling 1987; Cappo 1995).

Larson (1980) and Hixon (1981) demonstrated that the distribution of species can be influenced by other competitively dominant species. Interspecific defence of territories are common between *Cheilodactylus fuscus* that venture outside the aggregation and *Parma microlepis* (Pomacentridae). An aggregation provides the required local density to ensure the control of an area of suitable substratum. The advantages associated with the occupation of the high-relief areas can vary seasonally. *C. spectabilis* occupies a similar niche, and requires the caves associated with the bouldered substratum as spawning sites (McCormick 1989b).

Variation in the size and structure of aggregations may be related to changes in the quality of habitat or associated with reproductive behaviour. The factors that determine homing behaviour and the effect that limited home range has on the macrobenthic prey abundance are unknown. Further work is necessary to determine the role of inter- and intra specific interactions in determining the population structure and movement patterns of this species.

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