

Marine reserves: patterns of adult movement of the coral trout (*Plectropomus leopardus* (Serranidae))

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Abstract: Movements of *Plectropomus leopardus* (Serranidae), a major fisheries species, across marine reserve boundaries were investigated on the Great Barrier Reef, Australia. Mark–release–recapture and ultrasonic telemetry were used to assess movements. Mark–release–recapture used hook and line as the method of capture and underwater visual census (UVC) as the “recapture” tool. Catch rates were significantly higher in zones closed to fishing, despite UVC indicating no significant differences in density between closed and open zones. Of 183 fish marked with numerical freeze brands, 93 estimates of movements of branded fish were obtained. No branded fish was recorded to cross the reserve boundaries during the 2-month study, probably due to the initial decision to allocate capture effort evenly across the study area, rather than concentrating it on reserve boundaries. Fish carrying ultrasonic transmitters, and having home ranges straddling reserve boundaries, crossed boundaries on average 15.3 times·month⁻¹. The mean distance moved by freeze branded specimens between capture and recapture was significantly larger in areas closed to fishing than in those open to fishing. However, mean distance moved per day determined by ultrasonic telemetry did not differ between areas closed and open to fishing. This study suggests low flux rates of adult *P. leopardus* across marine reserve boundaries.

Résumé : Les déplacements de *Plectropomus leopardus* (Serranidae), une espèce faisant l’objet d’une importante exploitation commerciale, de part et d’autre des frontières d’une réserve marine ont été étudiés dans la région de la Grande Barrière, en Australie. Pour évaluer les déplacements, on a utilisé une méthode de marquage–recapture et la télémétrie ultrasonique. Pour le marquage–recapture, on a capturé les poissons à l’hameçon, et la « recapture » a consisté en un relevé visuel sous-marin. Les taux de capture étaient significativement plus élevés dans les zones où la pêche était interdite, alors que, selon les relevés visuels sous-marins, il n’y avait pas de différences significatives de densité entre les zones où la pêche était interdite et les zones où la pêche était permise. Sur 183 poissons marqués avec des cryomarques numériques, on a obtenu 93 estimations de déplacements de poissons marqués. Aucun poisson marqué observé n’a traversé les frontières de la réserve durant les 2 mois de l’étude, probablement à cause de notre décision initiale de distribuer l’effort de capture uniformément dans l’aire d’étude plutôt que de le concentrer aux frontières de la réserve. Les poissons portant des émetteurs ultrasoniques et dont le domaine vital chevauche les frontières de la réserve ont traversé les frontières 15,3 fois·mois⁻¹ en moyenne. La distance moyenne parcourue par les spécimens cryomarqués entre la capture et la recapture était significativement plus grande dans les zones où la pêche était interdite que dans les zones où la pêche était permise. Toutefois, les distances moyennes parcourues par jour, déterminées par la télémétrie ultrasonique, étaient similaires dans ces deux types de zone. Cette étude laisse penser que le flux de *P. leopardus* adultes aux frontières de la réserve marine est faible.

[Traduit par la Rédaction]

Introduction

Information about movement patterns of fish is central to the current debate about the use of marine reserves as a fisheries management tool for coral reef environments (e.g., Roberts and Polunin 1991; Russ and Alcala 1996a, 1996b). In a fisheries context, the two major objectives of marine reserves are to ensure continued recruitment supply via maintenance of a critical minimum spawning stock biomass and net export of larvae from reserves (the “recruitment” effect) and potentially to increase or maintain local fishing yields through export of

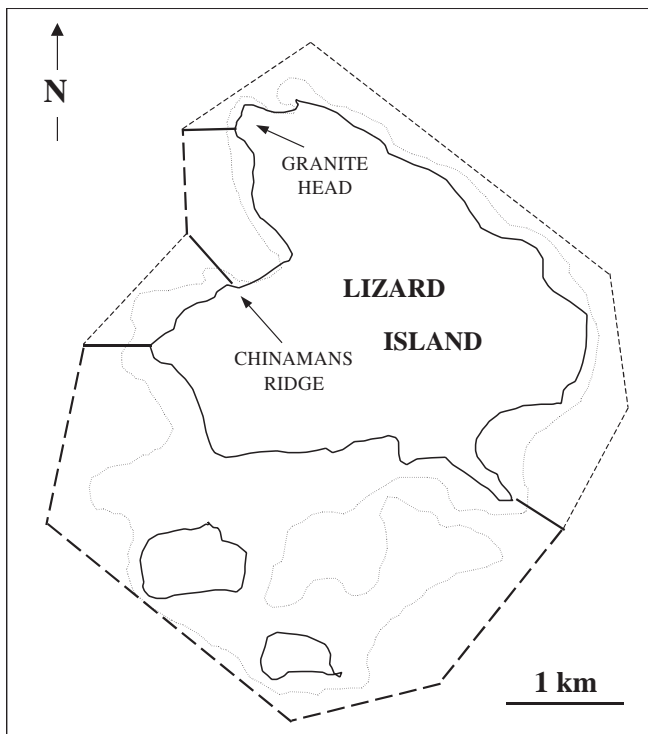
adult biomass of target species from the protected areas to adjacent areas (the “spillover” effect) (e.g., Polacheck 1990; DeMartini 1993; Russ and Alcala 1996a). Marine reserves may form a more cost-effective management option for stock maintenance (e.g., Alcala and Russ 1990; Rowley 1994), particularly for coral reef fisheries, in which more conventional fisheries management strategies are especially difficult to administer (e.g., Russ 1991). The effectiveness of marine reserves, especially in the developing world, appears strongly linked to local fishing community support (e.g., White et al. 1994). Under these circumstances, suggestions of large spatial scale benefits (i.e., stock-wide recruitment) appear often less convincing to communities than promises of local benefits (i.e., spillover) (Russ and Alcala 1996a). Thus, demonstration of movements from protected areas, potentially leading to improved yields in areas adjacent to reserves, may be critical to the acceptance by local fishing communities of marine reserves as a fisheries management option. Therefore, empirical data on rates of movement and crossings of reserve boundaries are required.

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Fig. 1. Map of Lizard Island showing the general study area. Indicated are the Great Barrier Reef Marine Park management zone patterns and associated reserve boundaries. The study was limited to the north, northeastern, and western sides of the island, which were more sheltered from the prevailing southeast winds. The short-dashed lines outline the zones open to fishing for commercial and recreational fishers, the long-dashed lines outline the zones closed to fishing (reserves), the solid lines indicate the locations of marine reserve boundaries, and the dotted line is the reef contour outline.



The most common method to quantify movements of post-settlement fish is a mark–release–recapture study (e.g., Hilborn and Walters 1992) using external tags of the anchor or dart tag type (e.g., Recksiek et al. 1991). External tags are economical, small, and fast to apply to the animal and permit large samples to be tagged. However, tag loss rates are high in coral reef fishes (e.g., Whitelaw and Sainsbury 1986). An alternative tagging method uses thermal marking techniques. With fishes, both hot (e.g., Hargreaves 1992) and cold branding (e.g., Knight 1990) have been used. Retention times of marks are highly variable and species specific, with 2 years the maximum period recorded (Hargreaves 1992).

Tagged fish can be recaptured by the same fishing gear used for initial capture or be resighted by underwater visual census (UVC). The established suitability of UVC for assessing coral trout (*Plectropomus leopardus*) (Serranidae) populations and the satisfactory levels of readability of cold brands reported for coral trout (Samoilys 1987) provide an unique opportunity to utilise standardised underwater census techniques of individually identifiable fish to assess movement patterns of coral trout.

Ultrasonic telemetry is probably the most effective means of obtaining information on fish movements (e.g., Zeller 1997a, 1997b, 1998). The suitability of ultrasonic telemetry as a tool for fisheries research is only slowly being realised

(Nelson 1990). Telemetry can make remote tracking of movement possible. Such an approach may overcome the shortcomings of traditional mark–release–recapture studies using external markings (Nelson 1990). Furthermore, it circumvents restrictions of visual observations on SCUBA, which limit most investigations of coral reef fishes to studies of smaller species in shallow water.

The primary objective of this study was to determine patterns of adult movement and space use by coral trout with respect to marine reserve boundaries. The initial predictive hypothesis was that flux rates are affected by potential density gradients in relation to marine reserve boundaries. The secondary objective was to compare two different techniques for assessment of movements: mark–release–recapture and ultrasonic telemetry. It was hypothesised that the two techniques should reveal similar patterns of movement. This is the first study to compare conventional mark–release–recapture (external marking combined with UVC) with ultrasonic telemetry on the same species in the same location.

Materials and methods

Study site and sampling protocol

The study was conducted on the sheltered western and northern sides of Lizard Island, northern Great Barrier Reef, Australia (14°40'S, 145°28'E). The study area contained within-reef marine park management zone boundaries between areas where fishing was and was not allowed (closure duration 12 years, Fig. 1). The external mark–release–recapture study was undertaken during August–October 1995, while ultrasonic tracking was conducted throughout 1993–1995.

Initial capture of specimens for marking was by hook and line, undertaken by two contracted commercial fishers in August 1995, each working independently from 4.1-m aluminium dinghies and each using standard commercial reef line fishery techniques. To distribute effort evenly, the study area was divided into four sections, each ~3 km long. Each fisher fished two “sessions” per day (morning and afternoon), with average duration per session of 4 h. Each location where a dinghy anchored and fished will be referred to as a “hang.” To spread fishing effort evenly within the four sections, minimum (15 min) and maximum (60 min) hang times were allocated. Maximum fishing depth was set at 10 m to facilitate recaptures by visual census (see below). Coral trout caught at each hang were kept in bins supplied with fresh seawater. For each hang, fishers recorded location (using aerial photographs), start and finish time of fishing (hook-line hours), number of coral trout caught, and the storage bin corresponding to each hang. Hook-line hours were defined as the actual time period a baited hook was in the water and available to the fish. All incidental, nontarget bycatches were released. At the end of fishing a hang, the location was marked with a small, numbered marker buoy attached to a lead weight. This permitted cross-validation of location of individual hangs at the end of each session and allowed fishers to release marked fish at their exact capture location. Collected fish were brought to a centrally anchored boat after each hang for freeze branding.

Freeze branding technique

Prior to freeze branding, each fish was measured (fork length, FL) and tagged with two standard T-bar anchor tags (Hallprint Ltd., Holden Hill, Australia). Individual numerals were freeze branded onto the caudal peduncle on each side of the specimen using branding irons. Branding irons consisted of copper block bases with individual numerals (25 × 25 × 2 mm) on each iron. The branding duration for each numeral was 10 s, and fish were returned to holding tanks between

each numeral brand to reduce stress. To ensure proper recooling of branding irons between applications, each numeral was returned to the coolant (liquid nitrogen, -196°C) for at least 1 min before reuse. After branding, individuals were released at the exact location of capture. In February 1995, a freeze branding trial showed that numerals remained readable underwater for a maximum of 3 months.

Resighting method and recapture effort distribution

"Recaptures" were resightings of freeze branded specimens during UVC. Two separate resighting surveys were made during September (D.C. Zeller) and October (D.C. Zeller and G.R. Russ) 1995, being 1 and 2 months after the freeze branding, respectively. Resighting effort, while spread over the complete study area, was concentrated in those areas with highest densities of freeze branded fish. General emphasis was placed on reef slope habitats, where coral trout are most abundant (Kingsford 1992).

The sampling unit was a 100×5 m transect. The transect length of 100 m was chosen to minimise the occurrence of zero counts of target species. Choice of transect width (5 m) was based on the minimum underwater visibility encountered around Lizard Island. Transect tapes were laid while conducting the surveys to avoid attraction of or disturbance to the fish by previously laid tapes (Fowler 1987). Start and end points of each transect were marked with surface buoys for recording the spatial position of transects from the surface after each census. All censuses were between datum (lowest astronomical tide) and the 10-m depth contour (or sand-reef interface), with an average census depth of 6–8 m. A total of 167 and 141 transects were sampled in September and October 1995, respectively, covering a total area of 154 000 m^2 . During each census, all coral trout sighted within the transect width and up to 5 m in front of the projected transect line were counted and their location along the transect recorded to the nearest metre. Sightings of tagged fish were recorded and visible freeze brands identified. Any tagged coral trout observed outside the transect were investigated similarly and recorded, but clearly marked as a nontransect recapture on the data sheets.

Ultrasonic telemetry

Of 39 individual coral trout tracked using ultrasonic telemetry between 1993 and 1995 by Zeller (1997a, 1997b, 1998), eight fish had home ranges straddling existing management zone boundaries in the study area. The methods used for ultrasonic telemetry are described in Zeller (1997a, 1997b). The average tracking period per specimen for the eight fish straddling reserve boundaries was 52.3 days.

Data analysis

The spatial position data for hook and line capture locations, visual census transects, fish sighting locations, and ultrasonic tracking positions were digitised from calibrated aerial photographs. Distances moved between capture and resighting and during ultrasonic tracking were calculated using CALHOME[®] (Kie et al. 1996). Patterns of movement were evaluated with respect to reef habitat type (fringing versus patch reefs), management zones (open versus closed to fishing), reserve boundaries, and time period between recaptures: 1 month between initial capture on hook and line (August 1995) to first UVC (September 1995, UVC 1), 2 months between initial capture to second UVC (October 1995, UVC 2), and 1 month between first and second UVCs (UVC 1–2).

Statistical analyses included *t*-test, analysis of variance (ANOVA), χ^2 homogeneity tests, and linear regression. Statistical assumptions underlying the parametric analyses were examined prior to analysis and data were \log_{10} transformed where appropriate (Sokal and Rohlf 1981). All means are reported as means \pm SE.

Results

Initial capture of coral trout on hook and line for freeze branding resulted in a fishing effort of 174 individual hangs

consisting of 72 h and 5 min of hook and line fishing. Thus, on average, each hang was fished actively for 24 min. A total of 216 coral trout were caught, resulting in an overall catch-per-unit-effort (CPUE) of 2.9 coral trout-hook-line hour^{-1} . The CPUE differed significantly between management zones closed and open to fishing (*t*-test: $t_{[172]} = 3.07$, $p = 0.003$), with a CPUE of 3.2 ± 0.50 and 1.2 ± 0.26 coral trout-hook-line hour^{-1} inside reserves ($n = 100$ hangs) and in open zones ($n = 74$ hangs), respectively. Of the 216 captured fish, 21 were judged to be injured and sacrificed, and 12 were kept for ultrasonic transmitter implantation (additional tracking was undertaken between 1993 and 1995, Zeller 1997a, 1997b). Hence, 183 of the initial 216 coral trout were released at their capture site after tagging and freeze branding.

The total available reef area, as defined for the visual census survey (datum to 10 m) comprised 750 966 m^2 in the study area (44% open, 56% closed to fishing). Given that the September (167 transects) and October (141 transects) surveys covered an area of 154 000 m^2 , the two surveys sampled 11.1 and 9.4%, respectively, of the available, census-defined reef in the study area.

During the two UVC surveys, 817 coral trout were sighted, consisting of 440 and 377 fish for the first and second census, respectively. Of the total sightings, 44 (UVC 1) and 26 (UVC 2) were recaptures (resighting) of freeze branded individuals. Thus, recapture (resighting) rates were 24.0% (44 of 183) and 14.2% (26 of 183) for UVC 1 and UVC 2, respectively. Based on the total fish counts and area covered by the transects, an overall density estimate of 5.3 ± 0.26 coral trout-1000 m^2 reef area $^{-1}$ was derived. A breakdown of total census data by reef habitat (i.e., fringing versus patch reef) indicated counts of 362 and 455 coral trout in the 128 and 180 transects conducted in fringing and patch reef habitats, respectively. These counts resulted in density estimates of 5.7 ± 0.40 coral trout-1000 m^2 for fringing reef and 5.1 ± 0.34 coral trout-1000 m^2 for patch reef habitats. Evaluation of UVC data by reef management zones (i.e., open versus closed to fishing) showed that 164 and 653 coral trout were counted in the 72 and 236 transects sampled in the open and closed zones, respectively. Thus, density estimates of 4.6 ± 0.39 and 5.5 ± 0.32 coral trout-1000 m^2 were obtained for open and closed zones, respectively. Density estimates for open and closed zones did not differ significantly (*t*-test: $t_{[306]} = 0.49$, $p = 0.624$).

Distances moved

A total of 93 measures of distances moved by freeze branded specimens between time periods were recorded during the two visual census surveys (Table 1). The distance measures obtained represent linear distances between points of capture and (or) visual recapture. Multiple resightings (two or more sightings of the same individual) and resightings recorded outside the predetermined transect limits while censusing were included also. There was no clear relationship between distances moved and size of individual fish ($r^2 = 0.032$, $p = 0.086$, $n = 93$). The movement distance estimates obtained through resightings ranged from 4 to 387 m (overall mean = 94.9 ± 9.48 m) between individual points of capture and (or) resighting.

Mean distance moved between recapture occasions differed between the two reef habitats (fringing and patch reefs) examined (*t*-test: $t_{[91]} = 2.92$, $p = 0.004$). Fish on patch reefs moved,

Table 1. Sample sizes of distances moved for coral trout between the three time periods and two-factor ANOVA comparing distances moved of freeze branded fish between the three time periods and between management zones.

Time period	No. of distances obtained		No. of fish with multiple sightings
	Open	Closed	
UVC 1 ^a	9	43	5
UVC 2	7	24	1
UVC 1–2	3	7	1
Total	19	74	7
Grand total	93		

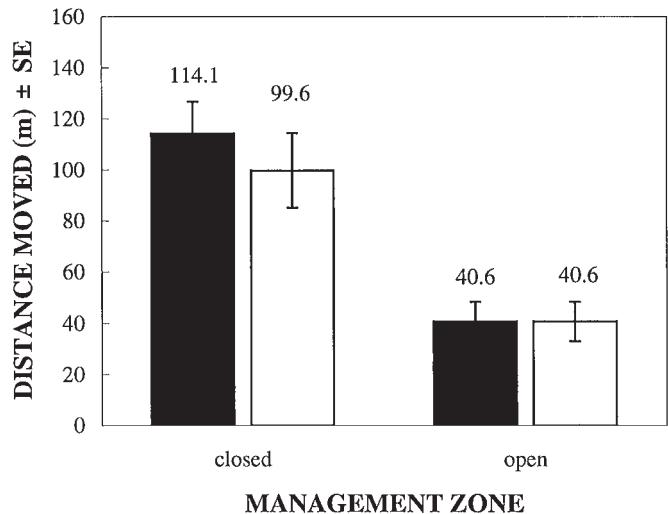
Source of variation	Mean square	df	F	p
Fringing and patch reef fish (n = 93)				
Time period	0.4019	2	2.308	0.1055
Zone	1.3266	1	7.617	0.0071
Time period × zone	0.1235	2	0.709	0.4949
Residual	0.1742	87		
Fringing reef fish only (n = 56)				
Time period	0.1735	2	0.824	0.4447
Zone	0.8995	1	4.269	0.0440
Time period × zone	0.1634	2	0.775	0.4659
Residual	0.2107	50		

^aExample for UVC 1: 44 individual marked fish were resighted (see Results section), of which five fish were resighted two or more times (i.e., 39 single sightings, two double sightings, and three triple sightings), resulting in a total number of distances obtained of 52 (i.e., nine in open plus 43 in closed zone).

on average, 48.3 m more between recapture occasions than fish on fringing reefs (patch reefs: mean = 129.0 ± 20.50 m, fringing reefs: mean = 80.7 ± 10.83 m). A two-way comparison of mean distances moved between the factors management zones (closed and open to fishing) and time periods indicated that fish from closed zones moved further between recapture occasions than did fish from open zones ($p = 0.007$, Table 1; Fig. 2). Given that fish moved further on patch reefs than on fringing reefs, but no branded fish were resighted on patch reefs in the open zone, the analysis was repeated on a subset of data consisting only of fringing reef fish ($n = 56$, Table 1). The data subset (excluding patch reef data) resulted in reduced distances moved for fish from closed reefs (from 114.1 ± 12.57 to 99.6 ± 14.63 m, Fig. 2). Nevertheless, fish from fringing reefs closed to fishing did move further between recaptures than fish from fringing reefs open to fishing ($p = 0.044$, Table 1; Fig. 2).

Mean distances moved per day, as determined using ultrasonic telemetry, did not differ between habitats (t -test: $t_{129} = 0.91$, $p = 0.370$; patch reefs: mean = 200.6 ± 19.79 m, fringing reefs: mean = 178.0 ± 15.41 m) or between management zones (t -test: $t_{129} = 0.94$, $p = 0.356$; closed zone: 201.6 ± 17.49 m, open zone: 163.5 ± 13.19 m). However, the habitat and management zone patterns observed in the telemetry data appear similar to those in the mark–resighting data. A direct comparison of distances moved between the two methods indicated that the daily distances moved recorded through telemetry were larger than those obtained from the visual census surveys (t -test: $t_{1127} = 5.46$, $p < 0.0001$). Fish carrying ultrasonic

Fig. 2. Effect of management zones on the distances moved by coral trout (time periods between resightings pooled). Comparison between management zones closed and open to fishing for complete data set (solid bars, $n = 93$) and fringing reef data subset (open bars, $n = 56$). Depicted are means ± SE. Means are indicated numerically.



transmitters moved, on average, 186.6 ± 11.96 m·day⁻¹, while freeze branded fish moved 94.9 ± 9.48 m between recapture occasions.

Reserve boundary movements

No cross-boundary movements between zones closed and open to fishing were recorded from freeze branded specimens. Of the 183 freeze branded fish released, only 10 individuals had their capture–release location within ~500 m either side of a reserve boundary (Fig. 1). Of these 10 branded specimens, four resightings were recorded during the two visual census surveys. The average distance moved between capture and resighting locations was 35.6 ± 1.64 m, with a range of 33.2–37.0 m.

During the 1993–1995 ultrasonic tracking study, eight coral trout equipped with transmitters had home ranges that straddled the reserve zone boundaries at Granite Head and at Chinamans Ridge (Fig. 3). On average, 31.5 and 68.8% of the home ranges of these fish were located in the open and closed zones, respectively (Table 2). Based on the number of times a fish was recorded on either side of the boundary, these fish spent, on average, 27.5 ± 10.81% of their time in the zone open to fishing (Table 2). The total number of boundary crossings recorded for the specimens being tracked ranged from 2 to 64 (mean = 27.5 ± 8.6) for tracking periods of 8 and 66 days, respectively (Table 2). The data were standardised to crossings per day and crossings per month (based on a 30-day month). The observed specimens averaged 0.5 crossing·day⁻¹ or 15.3 crossings·month⁻¹ (range from 3.6 to 29.1·month⁻¹, Table 2). Thus, coral trout tracked using ultrasonic telemetry would cross reserve boundaries bisecting their home ranges from once every 10 days to daily (Table 2).

Discussion

The present study attempted to quantify movement patterns of

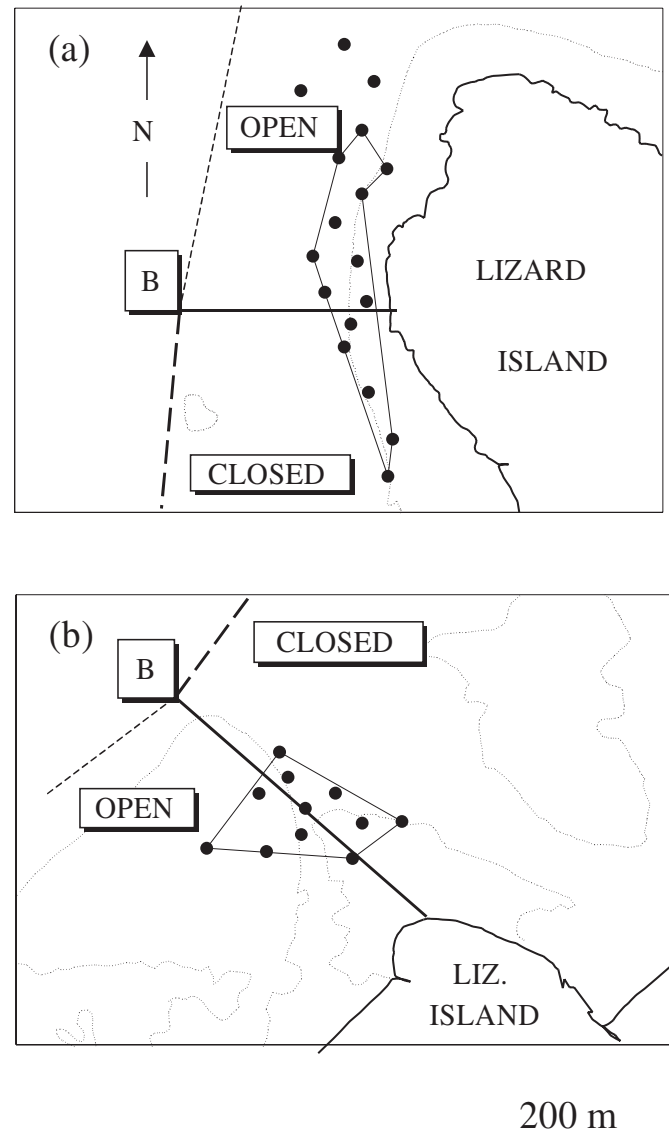
coral trout in relation to marine reserves, using UVC of individually marked animals and ultrasonic telemetry. The objectives were to assess the implications of adult movements for marine reserves and to compare movement information gained by the two methods.

This study presents the first data on bidirectional rates of movement across marine reserve boundaries of a coral reef fish of major fisheries significance. The data obtained for rates of boundary crossings by coral trout equipped with ultrasonic transmitters and with home ranges straddling marine reserve boundaries indicated that, on average, each coral trout crossed the boundary in either direction once every 2 days. Thus, these fish moved regularly across zone boundaries. Furthermore, the percentage of home range located in the open zones (mean = 31.2%) and the amount of time spent in the open zone (mean = 27.5%) corresponded relatively closely, suggesting approximately even use of unfished and potentially fished areas. The very low rates of exchange of fish across management boundaries, except for those fish with home ranges straddling the boundaries, argue that properly managed reserves may be very effective in protecting spawning stock biomass of coral trout populations on the Great Barrier Reef.

There are only limited empirical data on movements of postsettlement fish across management zone boundaries, potentially resulting in yield increases in areas outside the protected area (i.e., spillover). While some studies have attempted to use indirect measures of potential emigration and biomass export (e.g., Alcalá and Russ 1990; Russ and Alcalá 1996a), other studies have utilised mark–release–recapture techniques to evaluate movements of target species from protected to fished areas (e.g., Gitschlag 1986; Beinssen 1989) or modelled the potential effect of such movements on expected yields (e.g., Polacheck 1990; Russ et al. 1992; DeMartini 1993). However, only one study, to the authors' knowledge, measured emigration rates from a protected area directly. Attwood and Bennett (1994) tagged 11 022 fish over a 5.5-year period in a South African temperate water surf-zone marine reserve. Of the 9.1% total recaptures (research and fisheries), 17.8% had moved outside the 50-km-long protected area. However, all tagging effort was restricted to the inside of the reserve, with no tagging undertaken in adjacent waters.

Recent studies modelling the effect of marine reserves on the potential yield per recruit to areas adjacent to reserves suggested that moderate increases were possible outside of reserve areas (Polacheck 1990; Russ et al. 1992; DeMartini 1993). However, these studies indicated that yield per recruit would only increase if very high fishing mortalities existed outside the protected areas and rates of transfer of fish were high. Furthermore, DeMartini (1993) concluded that any enhancement in yield per recruit would be restricted to areas close to the reserve. This was supported empirically by Russ and Alcalá (1996a), who showed that the increases in density and species richness of large predators associated with a protected area in the Philippines were most pronounced near (within a few hundred metres of) the reserve. In the present study, density was 20% higher in the closed areas, but this difference was not statistically significant, and the fishing pressure around Lizard Island is moderate (by Australian standards) to light (by developing country standards). Therefore, one would not expect net movements (displacements or relocations) of coral trout to areas outside the closed zones in response to density

Fig. 3. Representative examples of home ranges of two coral trout straddling marine reserve boundaries during 1993–1995. Circles represent position records of coral trout obtained using ultrasonic telemetry. Polygon outlines indicate minimum area polygon home ranges of specimens, short-dashed lines outline the zone open to fishing for commercial and recreational fishers, long-dashed lines outline the marine reserve (closed to fishing), and solid lines marked "B" indicate the locations of marine reserve boundaries. (a) Specimen PL 9 living at a location called Granite Head (see Fig. 1); (b) specimen PL 31 living at a location called Chinamans Ridge (see Fig. 1).



gradients. This ignores the potential for bait attraction during fishing, and as such represents a minimum rate of availability.

The lack of observed movements across reserve boundaries during the UVC surveys of freeze branded fish indicated strongly the necessity of concentrating considerable tagging effort near boundaries, followed by repeated, multiple recapture surveys. Due to the even distribution of initial capture as well as UVC effort in the present study, relatively little catch and recapture effort was allocated directly to boundaries.

Table 2. Home range usage information determined with ultrasonic telemetry for coral trout whose home ranges straddled reef management zone boundaries at Lizard Island.

Fish	% home range		% time spent in open zone	No. of boundary crossings	Tracking duration (days)	Boundary crossings per day	Boundary crossings per month
	Open zone	Closed zone					
1	91.2	8.8	89.9	2	8	0.25	7.5
2	15.9	84.1	17.5	53	62	0.86	25.7
3	42.3	57.7	57.8	7	58	0.12	3.6
4	11.5	88.5	14.2	64	66	0.97	29.1
5	0.5	99.5	4.5	8	23	0.35	10.4
6	2.0	98.0	4.4	14	97	0.14	4.3
7	37.4	62.6	23.1	50	52	0.96	28.9
8	49.1	50.9	8.5	22	52	0.42	12.7
Mean	31.5	68.8	27.5	27.5	52.25	0.51	15.3

Note: Included are the percentage distribution of home ranges between zones, percentage time spent in the zone open to fishing, and rates of crossing of zone boundaries.

Beinssen (1989) obtained a similar result in a study of reef fish movement in relation to an existing reserve boundary at Heron Island (southern Great Barrier Reef). Of 273 coral trout tagged, 13.9% were subsequently resighted during underwater visual surveys 3–4 weeks after tagging. Of these resightings, 17% had moved less than 500 m, 8% had moved 500–1000 m, and 4% had moved 1000–1500 m from the tagging location. However, only one fish was recorded to have crossed the reserve boundary, moving at least 500 m from the closed to the open zone. In contrast, Davies (1995) reported that 35% of coral trout recaptures had moved out of the 1.5- to 2.5-km reef block in which they were released and attributed these movements to spawning behaviour (see also Zeller 1997a, 1998). Future investigations require concentration of capture and recapture effort close to boundaries, with gradual reduction in effort with distance from boundaries.

When attempting to interpret the observed difference in distance moved between the two different data collection methods (ultrasonic telemetry versus UVC of marked animals), it should be recognised that both represent different measures. Ultrasonic telemetry provided data on the average distance moved by each fish per day, based on several position records per day sampled over substantial time periods (mean 52.3 days, Table 2). Daily movements generally consisted of several movements back and forth throughout each specimen's home range (Zeller 1997a, 1997b). Thus, it is a measure of average total distance moved during a day. In contrast, the distance measure obtained through UVC of marked coral trout represented a once-off linear measure of displacement between two points in time at least 1 month apart, and thus should be lower than the average total distance moved per day. The findings supported this expectation. This result has important implications for design of studies to measure the spillover effect of marine reserves.

The comparison between UVC of marked animals and ultrasonic telemetry clearly illustrated that ultrasonic tracking provides more accurate information on patterns of movement by providing more data points per individual fish (Zeller 1997a, 1997b, 1998). However, given the cost and complexity of ultrasonic telemetry, a combination of detailed investigations of transmitter-equipped fish with a large marking study utilising repeated UVCs of marked animals to obtain densities and movement rates is recommended.

The densities of coral trout recorded in zones closed to fishing (5.5 ± 0.32 fish·1000 m⁻²), while 20% higher than in open zones (4.6 ± 0.39 fish·1000 m⁻²), were not significantly higher. Recent studies have provided evidence that marine reserves enhance the abundance, size, and hence biomass of numerous reef fish species (e.g., Russ and Alcala 1989, 1996b). In the present study, the overall density, as well as densities in the open and closed zones, compared well with other density estimates for coral trout from the Great Barrier Reef (review by Williams and Russ 1994). Williams and Russ (1994) indicated that, while the evidence was reasonably good that closing areas to fishing increased density, it was not unequivocal. Several studies detected no significant difference in density of coral trout between open and closed zones up to 8 years after closure (Williams and Russ 1994). It is possible that the general fishing pressure on reefs open to fishing on the Great Barrier Reef may not be high enough to significantly affect densities (Williams and Russ 1994). Furthermore, it has been suggested that infringements of zoning rules may be common enough in the line fisheries on the Great Barrier Reef to result in significant fishing pressure in supposedly closed areas (Williams and Russ 1994). Alternatively, the lower catches regularly reported by fishers in open zones may be the result of lower catchability, rather than lower densities in open zones (Beinssen 1989). This implies a behavioural difference of coral trout towards bait in open and closed areas. Fishing pressures around Lizard Island could be considered moderate, consisting predominantly of recreational fishing effort (D.C. Zeller, personal observation). Infringements of existing zoning rules were not observed to occur regularly during this study, possibly due to the close proximity and high activity levels of the local research station and resort. Nevertheless, the experimental line capture data obtained in this study strongly support the notion of reduced levels of catchability of coral trout in the zones open to fishing, with CPUE 2.58 times lower in open zones than in closed zones, despite densities not being significantly different. The CPUE data recorded in the present study were slightly lower than those recorded by Davies (1995). Davies (1995), using commercial fishers for a large-scale tagging study in the central section of the Great Barrier Reef, reported CPUE of 2.26–7.44 coral trout·line⁻¹·h⁻¹. Thus, the results obtained in the present study clearly support the previously reported observations and may explain the common

concern of reduced catches on heavily fished reefs expressed by line fishers.

Coral trout in closed zones moved greater distances between capture and resighting than those in zones open to fishing. The observed differences cannot be explained simply by population structure differences, as densities, although slightly lower in open zones, did not differ significantly between zones. Also, the size distribution of coral trout in the general study area did not differ significantly between management zones (Zeller 1997a). Furthermore, as ultrasonic tracking indicated, home ranges did not vary significantly in area, length, or width between management zones (Zeller 1997a). Given the very small sample size of visual resightings in open zones ($n = 19$) and the fact that the UVC results for distances moved were based on two points in time (capture and resighting), one would have to treat this result with caution. Fish tracked with ultrasonic telemetry did not differ significantly in the distance moved per day in either zone. However, ultrasonic telemetry suggested that fish moved nearly 20% greater distances in closed areas. It is difficult to hypothesise an ecological or biological reason for these results, particularly given that the population structure and density appeared similar between zones.

The lack of a clear relationship between distances moved and size of fish recorded during the UVC surveys indicated that size alone was not a good indicator of movement range for coral trout. Patch reef fish moving further than fringing reef fish is possibly due to differences in the shape of home ranges of coral trout. Home ranges of fish living on patch reefs are wider but not longer than home ranges on fringing reefs (Zeller 1997b). Thus, it is possible to resight fish on patch reefs at greater distances from the initial capture location than is possible for fringing reef fish. Ultrasonic telemetry data support this, with mean distances moved per day not differing between the two habitats. Thus, on average, fish in either habitat moved similar distances per day, but there was more chance of resighting freeze branded fish on patch reefs further from the location of capture than was the case for fish on fringing reefs.

Conclusions and recommendations

This study recorded very low rates of flux of postsettlement coral trout across marine reserve boundaries at Lizard Island. However, ultrasonic telemetry did indicate that individuals with home ranges incorporating boundaries moved regularly between zones. While there were no significant differences in densities of coral trout between open and closed zones, the CPUE was considerably higher in closed zones than in open zones. Thus, clear differences existed in catchability of coral trout between management zones, providing further evidence that reported concerns regarding reduced catches by fishers on the Great Barrier Reef may partly reflect behavioural changes in targeted species. It is strongly recommended that estimation of flux rates with respect to marine reserves be based on controlled manipulations of fishing effort and incorporate a dual approach, combining ultrasonic telemetry to provide detailed information on movements with large-scale marking and visual resighting or recapture studies, with strong emphasis on intensive, multiple resighting opportunities near boundaries.

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References

- Alcala, A.C., and Russ, G.R. 1990. A direct test of the effects of protective management on abundance and yield of tropical marine resources. *J. Cons. Cons. Int. Explor. Mer.* **46**: 40–47.
- Attwood, C.G., and Bennett, B.A. 1994. Variation in dispersal of Galjoen (*Coracinus capensis*) (Teleostei: Coracinidae) from a marine reserve. *Can. J. Fish. Aquat. Sci.* **51**: 1247–1257.
- Beinssen, K. 1989. Heron Reef demersal reef fish movement study. Report for the Department of Conservation, Parks and Wildlife, Queensland, Australia.
- Davies, C.R. 1995. Patterns of movement of three species of coral reef fish on the Great Barrier Reef. Ph.D. dissertation, James Cook University, Townsville, Australia.
- DeMartini, E.E. 1993. Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fish. Bull. U.S.* **91**: 414–427.
- Fowler, A.J. 1987. The development of sampling strategies for population studies of coral reef fishes. A case study. *Coral Reefs*, **6**: 49–58.
- Gitschlag, G.R. 1986. Movement of pink shrimp in relation to the Tortugas sanctuary. *N. Am. J. Fish. Manage.* **6**: 328–338.
- Hargreaves, N.B. 1992. An electronic hot-branding device for marking fish. *Prog. Fish-Cult.* **54**: 99–104.
- Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. Chapman and Hall, New York.
- Kie, J.G., Baldwin, J.A., and Evans C.J. 1996. CALHOME: a program for estimating animal home ranges. *Wildl. Soc. Bull.* **24**: 342–344.
- Kingsford, M.J. 1992. Spatial and temporal variation in predation on reef fishes by coral trout (*Plectropomus leopardus*, Serranidae). *Coral Reefs*, **11**: 193–198.
- Knight, A.E. 1990. Cold branding techniques for estimating atlantic salmon parr densities. *Am. Fish. Soc. Symp.* **7**: 36–37.
- Nelson, D.R. 1990. Telemetry studies of sharks: a review, with applications in resource management. In *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries*. Edited by H.L. Pratt, S.H. Gruber, and T. Taniuchi. NOAA Tech. Rep. NOAA-NMFS-SWFSC-90.
- Polacheck, T. 1990. Year round closed areas as a management tool. *Nat. Resour. Model.* **4**: 327–354.
- Recksiek, C.W., Appeldoorn, R.S., and Turingan R.G. 1991. Studies of fish traps as stock assessment devices on a shallow reef in south-western Puerto Rico. *Fish. Res. (Amst.)*, **10**: 177–197.
- Roberts, C.M., and Polunin, N.V.C. 1991. Are marine reserves effective in management of reef fisheries? *Rev. Fish Biol. Fish.* **1**: 65–91.
- Rowley, R.J. 1994. Marine reserves in fisheries management. *Aquat. Cons.* **4**: 233–254.
- Russ, G.R. 1991. Coral reef fisheries: effects and yields. In *The ecology of fishes on coral reefs*. Edited by P.F. Sale. Academic Press, San Diego, Calif.
- Russ, G.R., and Alcala, A.C. 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. *Mar. Ecol. Prog. Ser.* **56**: 13–27.

- Russ, G.R., and Alcala, A.C. 1996a. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Mar. Ecol. Prog. Ser.* **132**: 1–9.
- Russ, G.R., and Alcala, A.C. 1996b. Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecol. Appl.* **6**: 947–961.
- Russ, G.R., Alcala, A.C., and Cabanban, A.S. 1992. Marine reserves and fisheries management on coral reefs with preliminary modeling of the effects on yield per recruit. *Proc. Seventh Int. Coral Reef Symp.* **2**: 988–995.
- Samoilys, M.A. 1987. Aspects of the behaviour, movements and population density of *Plectropomus leopardus* (Lacepede) (Pisces: Serranidae) at Heron Island reef, southern Great Barrier Reef, Australia. M.Sc. dissertation, University of Queensland, Brisbane, Australia.
- Sokal, R.R., and Rohlf, F.J. 1981. *Biometry. The principles and practice of statistics in biological research.* Freeman & Company, New York.
- White, A.T., Hale, L.Z., Renard, Y., and Cortesi, L. 1994. Collaborative and community-based management of coral reefs. Lessons from experience. Kumarian Press, West Hartford, Conn.
- Whitelaw, A.W., and Sainsbury, K.J. 1986. Tag loss and mortality rates of a small tropical demersal fish species, *Lutjanus carponotatus* (Pisces: Lutjanidae), tagged with dart and anchor tags. *Aust. J. Mar. Freshwater Res.* **37**: 323–327.
- Williams, D.McB., and Russ, G.R. 1994. Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef. Great Barrier Reef Marine Park Authority Res. Publ. No. 33, Townsville, Australia.
- Zeller, D.C. 1997a. Patterns of movement of *Plectropomus leopardus* (Serranidae) in relation to spawning aggregations and marine protected areas, as determined by ultrasonic telemetry. Ph.D. dissertation, James Cook University of North Queensland, Townsville, Australia.
- Zeller, D.C. 1997b. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). *Mar. Ecol. Prog. Ser.* **154**: 65–77.
- Zeller, D.C. 1998. Spawning aggregations: patterns of movement of the coral trout *Plectropomus leopardus* (Serranidae) as determined by ultrasonic telemetry. *Mar. Ecol. Prog. Ser.* **162**: 253–263.