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Patterns of movement of *Plectropomus leopardus* (Serranidae) in relation to spawning aggregations and marine protected areas, as determined by ultrasonic telemetry

> Thesis submitted by Dirk Christoph ZELLER BSc (Hons I) JCU

> > in December 1996

for the degree of Doctor of Philosophy in the Department of Marine Biology James Cook University of North Queensland "Fisbing, if I, a fisber, may protest Of Pleasures is the sweet'st, Of Sports the best, Of Exercises the most excellent, Of Recreations the most innocent. But now the sport is marred, and wot ye why? Fisbes decrease, and fisbers multiply."

Rev. Thos. Bastard, 1498

#### DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

(Dirk Zeller)

12/12/96 (Date)

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(Dirk Zeller)

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#### ABSTRACT

The importance of patterns of movement and space use by fishes to the understanding of population dynamics, community structure and spatial population models, is being increasingly recognised. Despite this realisation, information regarding patterns of movement is rare for fishes. Two important aspects in coral reef fisheries which are affected greatly by the lack of knowledge about movements, are the uncertainties associated with high fishing pressures on spawning aggregations, and the potential use of marine protected areas as a fisheries management strategy.

The main aim of this research was to determine patterns of movement and space use of a species of major fishing importance (*Plectropomus leopardus*, Serranidae), in relation to annual spawning aggregation events, and with respect to existing marine protected area zoning. Given the known limitations of the conventional technique for assessments of movements, i.e. external mark-release-recapture techniques, an alternative methodology, ultrasonic telemetry, was adopted to address these aspects.

The first objective consisted of methodological evaluations of ultrasonic telemetry for use on *P. leopardus* and in coral reef fish and fisheries research in general. The second objective was to estimate home ranges and basic temporal patterns of space use by the study species. The third objective was to locate previously unknown spawning aggregation sites, estimate their minimal catchment areas, and determine patterns of participation and residence of individual fish at aggregation sites. The fourth objective was a comparison of data obtained through telemetry with comparable data collected independently using a mark-release-resignting study, and to evaluate the data obtained through both methods in relation to the existing marine protected area zoning at the study location, with considerations to the use of marine protected areas as a fisheries management tool.

Preliminary assessments of ultrasonic telemetry for use on *P. leopardus* included the evaluation of three ultrasonic transmitter placement methods (force feeding, external attachment, and surgical body cavity insertion) in conjunction with

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three different fish anaesthetics (Metomidate, Phenoxyethanol, and MS-222). The most suitable method of transmitter placement for long-term application in *P. leopardus* was surgical implantation into the body cavity. Attaching transmitters externally led to severe aggravation of the attachment wounds due to repeated attempts by the fish to dislodge the transmitter. Force feeding transmitters was unsuitable due to the short gastric retention times observed (18 to 216 hours). Tricaine methanesulfonate (MS-222) was the anaesthetic chosen due to the ease of induction and maintenance of deep anaesthesia. Post-surgery recovery periods in aquaria avoided field losses due to injury-induced predation, and permitted examination of each specimen prior to release for proper closure and healing of incisions.

The pilot evaluation of telemetry in the coral reef environment, and initial tracking trials indicated that manual ultrasonic tracking using visual triangulation should be conducted by taking bearings at approximately right angles (90°) to each other, with approximate distances of 50-75 m between tracking vessel and estimated location of transmitter. Bearings taken at angles considerably less than 90°, or taken at sharp angles to the prevailing wind, should be avoided. These considerations will result in minimal directional bias of bearings due to wind effects, while ensuring maximum accuracy and precision of position estimates. Observer training prior to tracking, and regular reevaluation of bearing accuracy and precision during tracking sessions is recommended.

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Thirty-nine individual *P. leopardus* (fork length: mean = 49.04 cm, range = 37.6 to 67.5 cm) were tracked successfully between 1993 and 1995. Eight of these were tracked during two subsequent field trips, resulting in 47 separate tracking sessions, comprising a total of 2,024 fish-tracking days. Average minimum area polygon home ranges of *P. leopardus* differed between fish from fringing reefs (10,458.4 m<sup>2</sup> ± 962.3 (SE)) and patch reefs (18,796.9 m<sup>2</sup> ± 3,188.8 (SE)). This difference was caused by differences in width of home ranges, with fringing reef home ranges being narrower than patch reef ones. Length of home ranges did not differ between reef types. Home ranges did not differ between male and female fish, and were stable within and between each tracking session (maximum 202 days between sessions). *Plectropomus leopardus* were day-active, predominantly using a small number of physical locations (3-4

positions) within their home ranges. Mean daily distance moved within home ranges was 192.2 m  $\pm$  5.09 (SE), with the maximum being 1121.8 m. Patterns of space use were relatively consistent throughout the day. Position fidelity was very high at night, with very limited movements.

A distinct pattern of home range use existed in relation to the prevalent current direction, with *P. leopardus* showing a strong preference for utilising positions located in the upcurrent portions of their home ranges. This study demonstrated, for the first time, distinct movements of *P. leopardus* in relation to changes in tidal currents. Thus, the observation commonly made by fishers of better catches on "run on" sides of reefs may be explained by the observed preference of upcurrent positions utilised by coral trout.

Using ultrasonic telemetry, four major spawning aggregation sites of P. leopardus were detected at Lizard Island. Spawning aggregation activities displayed a lunar pattern, with peak activities during new moon periods in the southern-hemisphere spring-early summer period. Of 35 fish tracked during the spawning periods, only 31% participated in spawning aggregations. Thus, this study demonstrated, at least for the periods studied, that a limited number of individuals in the population aggregated in large groups to spawn, despite all specimens being sexually mature. All specimens that aggregated displayed site fidelity with respect to their chosen aggregation site. Highest density estimates of fish at aggregations were 60 fish/1,000 m<sup>2</sup> (1994) and 35 fish/1,000  $m^2$  (1995), based on visual census. The mean distance between home ranges and spawning aggregation sites was 911.95 m  $\pm$  223 (SE) (range: 223 to 5,213 m). Total spawning movement distances back and forth in the spawning season for individual fish ranged from 604 m to over 17 kilometres. One-way inter-reefal movements were recorded for three fish, moving 3, 7.5, and 11 kilometres between release and recapture locations. Total residence time at aggregations differed between males and females. with males spending on average 8 times more time at aggregations than females (males: 316:33 h:min  $\pm$  65:04 (SE), females: 36:42 h:min  $\pm$  17:42 (SE)). Females undertook day or overnight trips only, while males regularly did multi-day trips also.

The reliance on several aggregation sites per reef makes P. leopardus potentially less vulnerable to overexploitation of spawning aggregations, compared to species which utilise fewer sites but in larger numbers per site. However, the strong site fidelity observed for all individuals makes individual aggregations vulnerable to depletion. The low participation rate at major aggregation events, combined with the observation that all recovered tracking specimens showed histological patterns of reproductive activity for the current season, suggested that not all spawning activity took place at the known aggregation sites. This, together with the discovery of several smaller courtship sites, should be regarded as evidence for the possibility of additional, localised spawning events. The movement data obtained indicated within-reef catchment areas covering linear distances of over five kilometres, with some evidence of inter-reefal movements in relation to spawning. The observed differences between male and female fish in residence duration at aggregation sites indicated definite sex dependent variations in turnover rates at these aggregations, making males potentially more vulnerable to fishing pressures on aggregations. The observed sex dependent turnover rates, as well as the problem of visual identification of gender, need to be considered in the use of aggregation events for stock assessment purposes.

A mark-release-resighting study using hook and line as capture, and underwater visual census as resighting tool of fish marked with numerical freeze brands, indicated that catch per unit effort by hook and line was significantly higher in management zones closed to fishing than in zones open to fishing. However, the average density of fish  $(5.31 \text{ fish}/1,000 \text{ m}^2)$  did not differ significantly between management zones. Thus, differences existed in catchability of fish between management zones, providing further evidence that concerns regarding reduced catches by fishers on the Great Barrier Reef may partly reflect behavioural changes in targeted species.

No freeze branded fish were recorded as having crossed the management zone boundaries. However, fish carrying ultrasonic transmitters, and having home ranges straddling management zone boundaries, spent, on average, 27.49% of their time in the 31.23% of their home ranges located in zones open to fishing. These fish crossed zone boundaries at an average rate of 15.27 times/month (range: 3.62 - 29.09 times/month),

indicating that these individuals moved regularly across the zone boundaries. Any of the monitored fish had the chance of being caught outside the closed zone in proportion to the area of home range located in the open zone.

This study successfully demonstrated the viability and suitability of ultrasonic telemetry to the study of fishes on coral reefs. Application of ultrasonic telemetry provided unique information about movement and space use patterns of *P. leopardus* that could not be obtained in any other manner. The information obtained provided not only the basis for future ecological and behavioural investigations of *P. leopardus* and other coral reef fishes, but may serve as the foundation for the development of improved management strategies for long-term sustainable fisheries and marine protected area management on coral reefs.

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## Chapter 1:

## **INTRODUCTION**

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### 1. Introduction

Coral reefs are exploited by a large number of commercial, recreational and especially subsistence fishers, and provide employment and sustenance to millions of people in tropical coastal regions (Salvat 1992). Reef fish stocks around the world are being exposed to rapidly increasing pressures due to fast human population growth and accelerating economic development, leading to drastically rising fishing effort and overexploitation. This is of particular concern with regards to fishing pressures on spawning aggregations, which are often specifically targeted and fished heavily once the location is known to the fishing community (e.g. Johannes et al. 1994, 1995, Anon. 1996). However, only rudimentary understanding exists of the extent or patterns of movements of fishes in relation to spawning aggregations. Strategies such as fishing of spawning aggregations, or the recent drastic increases in the live food fish industry, driven by almost unrealistic prices offered in certain parts of Asia (e.g. Johannes & Riepen 1995), may have dramatic consequences for future yields of fish stocks. As is the case in many temperate fisheries, conventional strategies of resource management appear to fail or cannot be enforced to ensure sustainable resource use (Ludwig et al. 1993). Marine protected areas have been proposed as one alternative, and potentially the only, management option available to maintain reef fish stocks in developing nations, by protecting a minimum spawning stock biomass. An important underlying criterion to ensure local fishing community support for successful implementation of this management strategy is the potential for sustained or even enhanced yields in areas adjacent to protected areas. Implicit in this assumption is the notion of movement of adult fish from protected to adjacent areas ("spillover"). However, there is virtually no empirical data available on such movements for tropical reef fishes of fishing interest. The objective of this research was to determine patterns of movement and space use of a species of major fishing importance (Plectropomus leopardus, Serranidae), in relation to two highly significant aspects affecting reef fisheries worldwide, that is high fishing effort associated with spawning aggregations, and the potential for spillover from marine protected areas.

#### 1.1. Patterns of movement of and use of space by reef fishes

The patterns of movement and space use by an individual can be considered one of the more fundamental demographic parameters influencing ecological patterns of populations (Cameron & Spencer 1985, Gregory et al. 1987, Andrew & Mapstone 1987). Most studies investigating movements and patterns of space use have been conducted primarily in the terrestrial environment. Examples include studies of birds (e.g. Draulan & Vessem 1985, Badyaev et al. 1996), reptiles (e.g. Hailey & Coulson 1996), mammals (e.g. Bertram 1980, Lindstedt et al. 1986, Krebs et al. 1995), and primates (e.g. Harvey & Clutton-Brock 1981). The relevance of patterns of movement and patterns of space use by fishes to the understanding of population dynamics and community structure, is being increasingly recognised (e.g. Robertson 1988, Hestbeck et al. 1991, Hilborn & Walters 1992, Turchin 1996). Yet, despite the acknowledged importance of spatial and activity patterns in population and community ecology (e.g. Cameron & Spencer 1985), such information is rare for fishes. Until recently, most studies investigating movements and use of space in fishes have been undertaken largely in lakes and rivers (e.g. Mesing & Wicker 1986, Cook & Bergersen 1988, Keeley & Grant 1995, Minns 1995). Investigations addressing the question of space use that have been undertaken in the tropical marine environment have largely concentrated on small, easy to observe reef fishes such as pomacentrids and labrids (reviewed in Sale 1991), and acanthurids (e.g. Robertson & Gaines 1986, Robertson 1988). Ouantitative assessment of detailed movement patterns of larger and more mobile species of reef fishes has progressed little since the early studies (e.g. Bardach 1958, Randall 1962, Springer & McErlean 1962), with the possible exception of studies of sharks (Nelson 1990, Holland et al. 1992, 1993b, Morrissey & Gruber 1993a&b). Only more recently have investigations been undertaken into movements and space use of larger species, for example Mullidae (Holland et al. 1993a), Haemulidae (Tulevech & Recksiek 1994) and Carangidae (Holland et al. 1996).

The abundance and diversity of large, predatory fishes on coral reefs is high (Hixon 1991 in Sale 1991), with reports of such fish accounting for up to 54% of total fish biomass at One Tree Island on the Great Barrier Reef (Goldman & Talbot 1976).

One of the most abundant families of large predatory fishes in warm water regions is the Serranidae (eg. Randall & Brock 1960, Randall 1965, Moe 1969, Harmelin-Vivien & Bouchon 1976, Nagelkerken 1979). Our understanding of the biology and ecology of these species is still limited (reviewed by Polovina & Ralston 1987, Brown et al. 1994, Williams & Russ 1994), with research generally concentrating on feeding habits (e.g. Shpigel & Fishelson 1989a, Kingsford 1992, St. John 1995), reproduction (e.g. Thresher 1984, Ferreira 1993a&b, 1995, reviews by Sadovy 1995, 1996, Coleman et al. 1996), or basic abundance and diversity (e.g. Ayling & Ayling 1986, 1992, Alcala 1988, Shpigel & Fishelson 1989b, 1991a, Russ & Alcala 1996b, Watson et al. 1996). The limited understanding of patterns of movement and space use by the larger reef fishes (Moe 1969, Hobson 1974, Munro 1974, Thompson & Munro 1978, Beinssen 1989a, Holland et al. 1993a, 1996, Tulevech & Recksiek 1994, Davies 1995) is of particular concern given the importance of many members of this group to commercial and recreational fisheries throughout the tropical world (Craik 1981, Polovina & Ralston 1987, Bohnsack 1990, Gwynne 1990, Trainor 1991, Gilmore & Jones 1992, Brown et al. 1994, Sadovy 1994, Williams & Russ 1994).

One species of particular relevance on the Great Barrier Reef (GBR), Australia, is *Plectropomus leopardus* (Serranidae), generally known as the common coral trout or coral grouper. This species, together with its congenerics *P. laevis, P. maculatus* and *P. areolatus*, form the major component of the commercial and recreational hook and line catch on the Great Barrier Reef (reviews by Brown *et al.* 1994, Williams & Russ 1994). Scientific investigations of coral trout have examined aspects of abundance (Ayling & Ayling 1986, 1992, Beinssen 1989b), feeding (Choat 1968, Goeden 1978, Kingsford 1992, St. John 1995), reproduction (Ferreira 1993a&b, 1995, Samoilys & Squire 1994), and fundamental parameters of population structure, such as age, growth, and mortality (Goeden 1978, Ferreira & Russ 1992, 1994, 1995, Ferreira 1993a, Brown *et al.* 1994, Russ *et al.* 1995, 1996). Only limited information, however, is available on patterns of movement and space use (Goeden 1978, Samoilys 1987, Beinssen 1989a, Davies 1995). Goeden (1978), using short visual observation periods on SCUBA of unmarked individuals suggested a maximum area of use for the observed individuals of 1,200m<sup>2</sup>, and estimated distances moved (extrapolated to 12 hours) as 0.8 to 2.8 km. Using a

visual mark-release-resighting technique within a limited area, Samoilys (1987) concluded that the range of movements of coral trout may be limited over approximate distances of 2 km along the reef slope, and suggested that the likely home ranges of coral trout might be larger than 4,000m<sup>2</sup>. However, the close physical presence of an observer during these behavioural investigations might have made diver disturbance of P. leopardus a major concern. Furthermore, the time periods of actual observations were very small (7-120 minutes, Goeden 1978), or estimations were based on ratios of resighting and non-resighting of marked fish within a spatially limited study area (Samoilys 1987). Movements of coral trout within a 4 km section of reef at Heron Island on the GBR were reported by Beinssen (1989a), who found that 29% of resignted fish had moved out of the initial 500 m long reef slope release sector within three weeks. In a mark-release-recapture study using fish traps in the Lizard Island lagoon (northern Great Barrier Reef), Davies (1995) recorded the largest movement as being 415 m. Davies also documented overlap in movements of individuals, and concluded that P. leopardus ranged over distances of 200-300 m. In a related, large scale tagging study on a cluster of five neighbouring coral reefs in the central section of the Great Barrier Reef, Davies (1995) reported the majority of recaptures (74%) were recovered within their 2.0 - 2.5 km long reef section of release. The greatest distance travelled by a tagged trout recaptured on hook and line was 4 km. In all of these studies, although occasional larger scale movements were observed (Samoilys 1987: 7 km, Davies 1995: 4 km), the vast majority of movements seemed to be restricted to less than 200-400 meters.

Clearly, patterns of movement and space use influence the dynamics of reef fish populations in manners which are important to improving our understanding of the ecology of these populations. Incorporating estimates of movements into models of population dynamics of reef fishes may substantially increase our understanding of the mechanisms which regulate their abundance and distribution (Robertson 1988, Hilborn & Walters 1992). Such increased understanding forms the foundation for improved management of exploited reef fish resources.

#### **1.2.** Importance of spawning aggregations to coral reef fisheries

Fisheries scientists and managers are beginning to place increasing importance on the understanding of patterns of movement (e.g. Hilborn 1990, Hilborn et al. 1990, Schwarz & Arnason 1990, Hilborn & Walters 1992). The increasing emphasis being placed on spatial population models in fisheries science calls for improved understanding of patterns of movement and space use by individuals and populations (Hilborn & Walters 1992). Of considerable fisheries interest with respect to patterns of movement of large reef fishes is the formation of spawning aggregations, which are a common feature in the reproductive ecology of many tropical serranids (Johannes 1978, Thresher 1984, Sadovy 1994, 1996). The large concentrations of individuals of significant commercial, recreational or subsistence importance for a generally short time period at one location, generally persistent from year to year, has resulted in many fisheries targeting aggregations repeatedly for many years (Thresher 1984, Shapiro 1987, Johannes 1988, Johannes & Squire 1988, Colin 1992, Johannes et al. 1994, 1995, Sadovy 1994, Samoilys & Squire 1994). Intensive fishing at aggregation sites can potentially result in the removal of a large component of the reproductively active fish in a stock over short time periods with relatively small fishing effort. This may have drastic effects on the population as well as on future yields (Shapiro 1987, Ralston 1987, Sadovy 1994, Colin 1992, Johannes et al. 1994). Once the timing and location of aggregation sites are known to fishing communities, the potential for depletion of the stocks associated with these aggregations is very high (Sadovy 1993), and can be very rapid (Johannes 1988, Colin 1992, Johannes et al. 1994). Unsustainably high levels of catches taken from annual spawning aggregations since the early 1960's have undoubtedly contributed significantly to the recent collapse of one of the richest fisheries in the world, the northern cod fisheries (Gadus morhua) off Canada (e.g. Hutchings & Myers 1994, Morgan & Trippel 1996, Myers et al. 1996). Similarly, the gemfish fishery, Rexea solandri, in southern Australia collapsed in 1994 due to intensive targeting of fish on spawning migrations, and Australia's most valuable finfishery for orange roughy, Hoplostethus atlanticus, is in danger of the same fate as spawning aggregations are targeted intensively (Russ 1996). Levels of fishing of spawning aggregations that are considered unsustainable have been reported also for several coral reef fisheries (e.g. Caribbean: reviewed by Sadovy 1994, Palau: Johannes *et al.* 1994, 1995), resulting in drastic reductions in catches, or even the disappearance of aggregations all together (e.g. Bohnsack 1990, Sadovy *et al.* 1994a). Fishers involved in the commercial line fisheries on the Great Barrier Reef have expressed concerns about fishing on aggregations of coral trout, also (Anon. 1996, C. Hagen, pers. com.).

The potential impact of aggregation fishing is cause for concern, given the lack of understanding of the importance of spawning aggregations to the reproductive output, and hence sustainability of recruitment levels, of target species. In general, evidence suggests that smaller serranids (e.g. *Cephalopholis* spp.), while having extended spawning periods, do not appear to aggregate to spawn (Mackie 1993). By contrast, larger species (e.g. *Epinephelus striatus, E. guttatus, Plectropomus* spp.) aggregate to spawn and exhibit shorter reproductive seasons (review by Sadovy 1996). Most studies on spawning aggregations of serranids were undertaken in the Caribbean (review by Sadovy 1994). While early reports of aggregations of serranids in the Pacific exist (e.g. Randall & Brock 1960, Johannes 1978), it is only recently that emphasis is being placed on detailed investigations of such aggregations (Johannes 1988, Johannes & Squire 1988, Johannes *et al.* 1994, 1995). Samoilys & Squire (1994) undertook the first published scientific investigation of a spawning aggregation of *P. leopardus* on the Great Barrier Reef, although anecdotal information was reported earlier (Johannes 1988, Johannes 488).

The potential impact of intensive fishing pressure on spawning aggregations of a given stock will be influenced strongly by several factors. These include the number of distinct spawning aggregation sites for a species per reef, and presumably closely related to this, the density of target species at aggregations, the catchment areas (i.e. from how far individuals move to specific aggregation sites), the participation rates (what proportion of the population participates in any one aggregation event), the residence times of individual fish at aggregation sites, and any potential sex-dependent differences in the participation rates and residence times.

Evidence of the occurrence and location of aggregations exists for several serranid species in the Caribbean (review by Sadovy 1994) and the Pacific (Johannes 1988, Johannes & Squire 1988, Johannes et al. 1994, 1995, Samoilys & Squire 1994). However, in most cases this information is derived directly from the fishing community, with few fisheries independent records (but see Samoilys & Squire 1994). Data on the catchment areas of spawning aggregations and distances moved by individual fish are extremely limited and sketchy. Most data on distances moved are based either on chance recaptures of tagged individuals (Burnett-Herkes 1975 in Shapiro 1987, Colin 1992, Sadovy et al. 1994a, Johannes et al. 1995), or are based on inferences from qualitative observations (Colin et al. 1987, Colin 1992). There is no quantitative information available for large predatory reef fish, that the author is aware of, regarding participation rates or residence duration of individuals at aggregation sites. The impact that intensive fishing may have on spawning aggregations, as well as on any stockrelated interpretation of abundance estimates based on monitoring of spawning aggregations, will depend strongly on whether there is a significant turnover rate of fish in aggregations (Johannes et al. 1994). Clearly, a better understanding of the mechanisms driving the formation, location and catchment areas of spawning aggregations, and patterns of residence at such aggregations, are required urgently to permit the development of appropriate management strategies to ensure continued, sustainable use of these valuable biological resources.

## 1.3. Marine protected areas as a fisheries management tool: the importance of movements

In the context of the present study, understanding of movement and spatial patterns is of central importance to the current debate about the use of marine protected areas as a fisheries management tool for marine systems (e.g. Davis 1981, 1989, Russ 1985, Alcala 1988, Alcala & Russ 1990, Bohnsack 1990, Roberts & Polunin 1991, Carr & Reed 1993, DeMartini 1993, Dugan & Davis 1993, Holland *et al.* 1993a, 1996, Polunin & Roberts 1993, Russ *et al.* 1993, Rowley 1994, Russ & Alcala 1994,

1996a&b, Dayton et al. 1995, Man et al. 1995). Around the world, reef fisheries are under increasing pressure, especially from human population growth, and urban and economic development. These pressures result in intensifying fishing pressures (Ruddle 1996) and the development and expansion of new and potentially destructive fisheries, such as the recent developments in the live food fish trade in South-East Asia (e.g. Johannes & Riepen 1995, Erdmann & Pet-Soede 1996). The consequences to marine resources are being documented in increasing numbers (Russ 1985, 1991, 1996, Russ & Alcala 1989, 1996a&b, Rutherford et al. 1989, Hughes 1994, Dayton et al. 1995, Polunin & Roberts 1996, Reaka-Kudla 1996). Undoubtedly, the major reason for these developments is that conventional fisheries management strategies (such as quota systems, gear and effort restrictions) are difficult or even impossible to administer and enforce in most coral reef fisheries (e.g. Bohnsack 1990, 1996, Polunin 1990, Roberts & Polunin 1991, Russ 1991, Rowley 1994, Dayton et al. 1995, Man et al. 1995, Munro 1996). This realisation of the failure of the historic fisheries management strategies has led to increased attention being directed towards exploring and developing new and innovative management options (Ludwig et al. 1993). The use of marine protected areas as one such alternative, more readily enforceable and cost-effective fisheries management strategy, is increasingly being examined (e.g. Alcala & Russ 1990, Bohnsack 1990, 1996, Roberts & Polunin 1991, Carr & Reed 1993, Dugan & Davis 1993, Dayton et al. 1995, Russ 1996). Coral reef fisheries are generally multi-specific and employ a multitude of fishing gears. These fisheries are defined by a predominance of artisanal and subsistence fishers, generally landing their catches over large areas (Dalzell 1996, Russ & Alcala 1996a&b). Also, the importance of coral reef fisheries may lie in employment and subsistence opportunities for low-income fishers with few alternative employment opportunities (Russ 1991), rather than in the actual yields obtained (~  $5 \times 10^8$  kg yr<sup>-1</sup>, Longhurst & Pauly 1987). Given these complexities and the often limited resources available to developing countries for research and management, marine protected areas may offer a simplified, alternative management option.

The two major, although not exclusive, objectives of marine protected areas in relation to fisheries, are to ensure continued supply of recruits via maintenance of a critical minimum spawning stock biomass, and potentially to increase or maintain local fishing yields through export of adult biomass of target species from the protected areas to fished areas (the "spillover" effect) (e.g. Gitschlag 1986, Beinssen 1989a, Bryant et al. 1989, Russ & Alcala 1989, Alcala & Russ 1990, Bohnsack 1990, Polacheck 1990, Yamasaki & Kuwahara 1990, Roberts & Polunin 1991, DeMartini 1993, Dugan & Davis 1993, Holland et al. 1993a, 1996, Russ et al. 1993, Davies 1995, Rakitin & Kramer 1996, Russ & Alcala 1996a&b). As recent studies have illustrated, marine protected areas clearly enhance the abundance, size and hence biomass of numerous reef fish species (e.g. Buxton & Smale 1989, Russ & Alcala 1989, 1996b, Bennett & Attwood 1991, Polunin & Roberts 1993, Russ et al. 1993). Such studies imply that effects of reduced fishing mortality are larger than any dilution of biomass in the protected area caused by "spillover". On the other hand, some level of net adult export ("spillover") is potentially beneficial to local fisheries. However, only limited empirical data is available regarding movements of fish across protected area boundaries, potentially resulting in yield maintenance or increase in adjacent areas ("spillover"). While some studies have made use of indirect measures of potential emigration and biomass export (e.g. Alcala & Russ 1990, Rakitin & Kramer 1996, Russ & Alcala 1996a), other studies evaluated movements of target species from protected to fished areas using mark-release-recapture techniques (e.g. Gitschlag 1986, Beinssen 1989a, Bryant et al. 1989, Buxton & Allen 1989 in Polunin & Roberts 1991, Yamasaki & Kuwahara 1990, Die & Watson 1992, Davies 1995), or modelled the potential effect of such movements on expected yields (Polacheck 1990, Die & Watson 1992, DeMartini 1993, Russ et al. 1993, Attwood & Bennett 1995). However, as far as was possible to ascertain, only one study measured emigration rates from a protected area directly (Attwood & Bennett 1994). However, all tagging effort in their study was limited to the inside of the protected area, with no tagging undertaken in adjacent waters, preventing any estimate of net flux in any direction, and thus any estimate of net export ("spillover").

The effectiveness of marine protected areas, especially in the developing world, is heavily dependent on support from local fishing communities (Cabanban & White 1981, White 1988, Alcala & Russ 1990, Bohnsack 1990, White *et al.* 1994). Under these circumstances, promises of local benefits (i.e. "spillover") appear often more

convincing or encouraging to communities than suggestions of large scale benefits (i.e. stock wide recruitment) (Russ & Alcala 1996a). Thus, demonstration of movements from protected areas, potentially leading to improved yields in areas adjacent to reserves, may be critical to the public acceptability of the concept of marine protected areas as a fisheries management option. Therefore, empirical data on rates of movements and crossings of protected area boundaries (net fluxes) by target species are urgently required.

## 1.4. Mark-release-recapture: the conventional technique for assessment of movement

Traditionally, external tagging or marking and the use of a mark-releaserecapture study constitutes the most commonly used method to examine and quantify movement in fishes (e.g. Shepherd 1988, Hilborn & Walters 1992). Historically, questions regarding population size, capture probabilities and mortality rates of target species were the primary objectives of tagging studies (e.g. Ricker 1975, Nichols & Pollock 1983, Lebreton *et al.* 1992, Nichols 1992). Only more recently has the importance of tagging to document movement patterns of relevance to fisheries research and management been realised and emphasised (e.g. Hilborn 1990, Hilborn *et al.* 1990, Schwarz & Arnason 1990, Hilborn & Walters 1992, Schweigert & Schwarz 1993).

External tags of the anchor or dart tag type, which are anchored between dorsal pterygiophores, are the most commonly used form of tagging in fish studies (e.g. Davies 1995). These tags have the advantage of being economical, relatively small and easy to apply to the study animal, and thus allow large samples to be tagged. These external tagging techniques are nevertheless known to have several limitations (reviewed by Kearney 1989) which often cannot be addressed adequately. Of primary concern are generally unknown tag-induced mortality rates and apparent high loss rates of external tags in coral reef fishes (e.g. Whitelaw & Sainsbury 1986, Davies 1995). Furthermore, recapture rates are generally low, and tag returns rely on chance recaptures of tagged specimens either by the researchers, or more commonly by commercial and recreational

fishers using fisheries dependent recapture methods (e.g. hook & line or fish traps, Davies 1995).

Of particular relevance to the present investigation is the fact that data obtained through conventional mark-release-recapture studies are usually limited to knowledge of a single point of capture, point of recapture and the distance and time interval between these two events. Such recapture information from single recaptures, after what is often a long term liberty, can be misleading, since the exact distance moved and the patterns of movement are unknown. Therefore, techniques such as simple mark-releaserecapture studies generally provide only incomplete descriptions of patterns of movements and use of space by free-ranging fishes. Thus, a technique such as external tagging, combined with a mark-release-recapture study, appears not very suited to address those aspects of patterns of movement and space use of importance to research and management of tropical reef fisheries as outlined above, namely patterns of movements and residence associated with annual spawning aggregations, and the determination of patterns of movement of individuals in relation to marine protected area boundaries.

## 1.5. Ultrasonic telemetry: an alternative technique for assessments of movement patterns

Clearly there is a great and urgent need for specific information on patterns of movement and space use, especially for the larger reef fishes of fishing significance. However, such information is generally difficult or impossible to obtain by conventional external mark-release-recapture techniques alone. In contrast, ultrasonic telemetry, i.e. remote monitoring of fish carrying transmitters emitting pulses of ultrasound detectable by the observer from a distance, may represent the ideal tool to address those questions of particular concern in the present context for larger reef fishes. Ultrasonic telemetry is a technique which can be used effectively under circumstances which limit the use of more traditional methods (review by Nelson 1990), and may thus permit determination of patterns of regular movements and space use by *P. leopardus*, as well as assess

movements in relation to spawning aggregation events and marine protected area boundaries.

The value of remote tracking of animals which are either difficult to observe visually due to size or habitat considerations, or are extremely shy and easily disturbed in their natural behaviour by the presence of an observer, has been recognised by terrestrial ecologists for some time. This recognition has lead to the development and regular use of radiotelemetry techniques for terrestrial use (e.g. Amlaner & MacDonald 1980, Mech 1983, Kenward 1987, White & Garrott 1990), which are considered powerful tools for their potential to provide unbiased data on an animal's use of space over time (Aebischer *et al.* 1993).

Comprehensive reviews of telemetry and its use in the aquatic environment are provided by Stasko & Pincock (1977), Ireland & Kanwisher (1978), Mitson (1978), Harden-Jones & Arnold (1982), Hawkins & Urquhart (1983) and Nelson (1990). Radio tags have been used successfully to track fish in shallow fresh water (e.g. Stasko & Pincock 1977, Diana *et al.* 1990), but have proven to be unreliable in larger, deeper waterbodies due to rapid fading of radio signals at depths over 10 m (e.g. Diana *et al.* 1990). Traditional radio telemetry is not suitable for the marine environment, as electromagnetic waves are highly attenuated by salt water, in contrast to sound waves which have much more favourable propagation characteristics (Hawkins *et al.* 1980). Furthermore, due to the resonant characteristics of the relatively small sized output transceivers used in fish tracking transmitters, only ultrasonic frequencies are applicable (Nelson 1990).

Ultrasonic telemetry is considered to be the most effective means of obtaining information about movements in free-living marine fishes (Kaseloo *et al.* 1992), and can make significant contributions to studies of movement directions, distances, speed and rates of movements, as well as home ranges and activity levels (Hart & Summerfelt 1975). The suitability of ultrasonic telemetry as a tool for fisheries research is only slowly being realised (see review by Nelson 1990). Earliest records of the development and use of ultrasonic telemetry date back to the 1950's (e.g. Trefethen 1956, Trefethen

et al. 1957, both in Bass & Rascovich 1965). Historically, this technique has been and still is used primarily with pelagic animals (e.g. Bass & Rascovich 1965, Carey & Robison 1981, Klimley et al. 1988, Holland et al. 1990a&b, Pepperell 1990, Bruce & Strong 1991, Carey & Scharold 1992, Pepperell & Holland 1992, Klimley 1993, O'Dor et al. 1993) or in temperate environments (e.g. Hawkins 1980, Clark & Green 1990, Matthews et al. 1990, O'Dor et al. 1994, 1995, Bradbury et al. 1995, Seino et al. 1995). Most ultrasonic telemetry studies of fishes associated with coral reefs have concentrated on sharks (e.g. review by Nelson 1990, and studies by Holland et al. 1992, 1993b, Morrissey & Gruber 1993a&b). Early attempts (1970-1980) to use ultrasonic tags for teleost fish studies at Lizard Island appear to have been less successful, primarily due to the then technical limitations of the ultrasonic equipment, resulting in low power output and variable signal reception (F. Talbot pers. com.). Not until more recently have successful attempts been made of the use of ultrasonic telemetry with coral reef fishes, with studies investigating patterns of movement, distribution and dispersal of the goatfish Mulloides flavolineatus (Holland et al. 1993a) and the carangid Caranx melampygus (Holland et al. 1996) in Hawaii, and examination of dusk and dawn movements by the haemulid Haemulon plumieri in the Caribbean (Tulevech & Recksiek 1994). The only published record of ultrasonic tracking of a serranid involved three Nassau groupers (Epinephelus striatus) being monitored for 24 hour periods (Carter et al. 1994). They were recorded as being most active around sunrise and sunset, and randomly moving over a coral encrusted area of approximately 80 x 160 meters. No published account exists of the use of ultrasonic telemetry in the study of reef fishes on the Great Barrier Reef.

This paucity of studies using telemetry on coral reefs is surprising, given the obvious advantages and benefits that can be derived from the use of telemetry. Telemetry systems can make a remote tracking approach to the study of patterns of movement and space use possible. Such an approach may overcome the inherent shortcomings of the traditional mark-release-recapture studies using external markings, and may also eliminate some of the major restrictions placed on visual observations, such as observer disturbance and SCUBA limitations, which currently limits much of the investigations of coral reef fishes to studies of smaller species. Ultrasonic telemetry

will allow the extensive, regular monitoring of movements and space use patterns over extended periods without disturbance to the animal. The main concern regarding ultrasonic telemetry (as is the case for terrestrial radio-telemetry) relates to the potential influence the presence and placement of the transmitter might have on the behaviour of the animal. Clearly, proper assessment and choice of appropriate placement method is critical to the successful application of this technique. Ultrasonic telemetry provides the opportunity to address the issues so urgently required and relevant for a better understanding of fisheries resources.

#### 1.6. Objectives and outline of this study

The major aim of this research was the determination of patterns of movement and space use of *P. leopardus* in relation to two important aspects presently affecting reef fisheries worldwide, that is high fishing effort associated with annual spawning aggregations, and the potential effects of marine protected areas. Given the apparent limitations of the conventional external marking and mark-release-recapture techniques, an alternative methodology, ultrasonic telemetry, was adopted to address these aspects.

The general approach in this study consisted of a methodological assessment of ultrasonic telemetry, a technique little used on coral reef fishes, and an extensive application of the technique to the evaluation of patterns of movement of *P. leopardus*.

The first objective comprised methodological developments for the use of ultrasonic telemetry (such as transmitter placement techniques and choice of fish anaesthetic) and an evaluation of the suitability of ultrasonic telemetry for use in coral reef fish and fisheries research (Chapter 3). The results from this evaluation lead to the subsequent adoption of the most suitable methodology for successful application of telemetry to *P. leopardus* as described in Chapter 2. The second objective was to use ultrasonic telemetry to document basic home ranges and spatial and temporal patterns of activity of *P. leopardus* (Chapter 4). Location of previously unknown spawning aggregation sites for coral trout around the chosen study location, and estimation of
minimal catchment areas for, and patterns of participation and residence at, aggregations through ultrasonic tracking comprised the third objective (Chapter 5). A further objective was a comparison of data obtained through telemetry with comparable data collected independently using a mark-release-resighting study. The mark-release-resighting method employed freeze branding as an external marking technique for individual identification of specimens and standard underwater visual census techniques as the resighting tool. The data on movement patterns and population parameters obtained through the mark-release-resighting and ultrasonic tracking studies were evaluated in relation to the existing marine protected area zoning at the study location, with considerations to the use of marine protected areas as a fisheries management tool (Chapter 6).

The relevance of the data and results obtained using ultrasonic telemetry with respect to the suitability of this technique to the coral reef environment, the importance of the major findings to the management of coral reef fisheries, and the implications these findings have for the concept of marine protected areas as a management strategy for reef fisheries are drawn together, and priorities for future research are identified in Chapter 7 (fisheries and management implications).

Chapter 2:

# **GENERAL METHODS**

# 2.1. Introduction

Ultrasonic telemetry has been used infrequently on coral reef fishes (e.g. Holland *et al.* 1993a, 1996). As such, detailed methodological evaluation, development and modification for effective use in the structurally and biologically complex coral reef environment was required. This chapter and the following chapter will deal with these considerations. The present chapter introduces the study location, and details the general methods and procedures eventually adopted for the ultrasonic tracking component of this project. Chapter 3 discusses the preliminary evaluation and comparison of various anaesthetic, transmitter placement and telemetry tracking techniques conducted during the pilot phase of this study. The methods used for Chapter 6 will be described therein.

# 2.2. Study location:

This study was conducted at Lizard Island, northern Great Barrier Reef, Australia (Lat. 14° 40' S; Long. 145° 28' E) between January 1993 and December 1995 (Table 2.1). Lizard Island is a high, continental island, situated in the Great Barrier Reef lagoon approximately 15 km from the outer barrier reefs and 30 km from the east coast of northern Australia. Lizard Island is surrounded by fringing reefs, and encloses a local reef lagoon, together with three nearby, small islands (Palfrey, South and Bird Islands) (Fig. 2.1). Waters around the island are relatively shallow (20-30m). The majority of this study was conducted on the north, north-east and west sides of the island, these areas being more sheltered from the prevailing south-east winds.

# 2.3. Ultrasonic telemetry

### 2.3.1. Fish capture

All fish used for ultrasonic telemetry were caught on hook and line, using 8/0 hook size and frozen West Australian pilchards (*Sardinops neopilchardus*) as bait. This

technique is well suited for catching *Plectropomus leopardus*, and is the standard catch technique used by the Great Barrier Reef (GBR) commercial and recreational line fisheries, in which *P. leopardus* is the major target species. Capture effort was spread evenly around the northern end of Lizard Island in 1993 and 1994, but extended to include most of the western side of the island during the last year of the study (1995). For transport to the research station, fish were placed in plastic transport containers (~50 litre capacity) with a regular supply of fresh seawater. Aquarium facilities used at the Lizard Island Research Station included several 500 litre and 1000 litre tanks, as well as one 2000 litre tank. The station has continuous flow through seawater supply and air outlets for water circulation.

### 2.3.2. Ultrasonic equipment

**Ultrasonic transmitters**: Four types of transmitters from two manufacturers were used in this project (see Table 2.2 for product summary). Frequencies available were: 50.0; 60.0; 65.5; 69.0 and 76.8 kHz. Multiple transmitters operating on the same frequency could be distinguished by their unique pulse rate characteristics (pulses min<sup>-1</sup>), by counting pulses manually over a 15 or 30 second period. While the V8 transmitter was the smallest and lightest, hence potentially least disturbing item for the fish, its major drawback was the relatively short life span of individual batteries (21 days, Table 2.2). While increased life span can be obtained by using more batteries combined into one multiple battery pack, this quickly negates the advantage of small size and low weight. For the purpose of this study, the smallest transmitter/battery combination used was a V8 in conjunction with battery packs consisting of up to three batteries, providing approximately 60 days life span. The recent development of V8 and V16 units with built in delayed start circuitry (F. Voegeli, Vemco, pers. com.) does provide for increases in the field life span once the animal is released after recovery periods in aquaria.

**Transmitter assembly and activation details**: All Vemco units consisted of transmitter and separate battery units permanently encased in epoxy resin. For activation, battery wires were soldered to the appropriate terminals on the transmitter

unit. The gap between transmitter and battery was filled with silicone to provide protection against water penetration, and allowed to dry for 24 hours. With the exception of the acoustic transducer in the first 1 cm of the transmitter unit, the completed unit was encased in heatshrink plastic for additional water protection. Sonotronics units were pre-assembled and delivered fully encased in a plastic shell, and were equipped with a magnetic reed switch for activation prior to use.

**Tracking equipment**: The tracking equipment consisted of a multi-channel, frequency synthesised VR-60 receiver (Vemco) without pulse rate decoder option, in conjunction with a directional 50-80 kHz hydrophone (V-10, Vemco). A parallel switched omnidirectional 50-80 kHz hydrophone (VH-65, Vemco) was used occasionally for broad area searches for signals. The tracking equipment was powered by a dedicated heavy-duty 12v battery, or for shorter periods by the VR-60 internal back-up battery. Use of a dedicated battery resulted in recharge intervals of 3-6 weeks of continuous day-time operation.

#### 2.3.3. Placement of ultrasonic transmitters

For evaluation and comparisons of various anaesthetic, transmitter placement, and suture methods see Chapter 3. The procedures adopted for this study are described here:

Freshly caught specimens were retained in aquaria for a short acclamation period (1-3 days), and were not fed during the 24 hours prior to the transmitter placement procedure (Nemetz & MacMillan 1988). Fish were placed in an anaesthetic bath containing MS-222 (Tricaine methanesulfonate) at a concentration of 80 mg  $L^{-1}$  seawater (Thomas & Robertson 1991). Deep anaesthesia was judged to have been achieved once loss of reflex reactivity, as defined by McFarland & Klontz (1969), had set in. Symptoms included loss of locomotion, very shallow opercular movements, and total loss of reactivity, muscle tone and equilibrium. Once anaesthetised, each fish was measured (fork length, FL) and externally tagged with two standard T-bar anchor tags (Hallprint Pty Ltd, Australia).

The transmitter placement technique chosen for this study (surgical body cavity insertion) required the anaesthetised fish to be placed inverted into an operating cradle (V-shaped, inclined trough) lined with wet, synthetic chamois cloth. The skin of the fish was kept moist throughout the operation, and gills were continuously oxygenated by flooding with alternating volumes of anaesthetic solution and fresh seawater. All surgical implements were disinfected in 70% ethanol and soaked in Tamodine<sup>™</sup>, a povidone-iodine solution specifically designed as a fish-antiseptic (VETARK Professional, United Kingdom). The incision area was located parallel to the midventral line on the left hand side of the fish, approximately 1-2 cm anterior to the anus and 1-2 cm lateral of mid-ventral line (Plate 2.1). Three to four rows of scales were removed from the area of planned incision using forceps. After removal of scales, the area of incision was cleaned thoroughly with Tamodine<sup>™</sup> solution. A 2-3 cm longitudinal (anterior-posterior) incision was made through the musculature into the body cavity, taking care not to damage any internal organs (Plate 2.1). Transmitters (V8, V16 or Xtal depending on the size of the fish) were disinfected in ethanol (sensu Burger et al. 1994), dried and coated in antiseptic cream (Savlon<sup>®</sup>) prior to careful insertion into the body cavity (Plate 2.2). Transmitters were oriented parallel to the longitudinal axis of the body. The incision was then closed using 6-8 surgical staples (Ethicon Proximate III<sup>TM</sup> skin staplers) as suggested by Mulford (1984), Filipek (1988) and Mortensen (1990) (Plate 2.3). Once the staples were in place, the incision area was again cleaned with Tamodine<sup>™</sup>, and the fish given an intraperitoneal injection of the antibiotic tetracycline (50 mg kg<sup>-1</sup> of fish, Hart & Summerfelt 1975, McFarlane & Beamish 1987), before being returned to the aquarium tanks for recovery. The duration of the operational procedure was between 10-15 minutes per fish.

# 2.3.4. Post-operative recovery

Recovery from anaesthesia took 5-15 minutes, and in most cases individual fish remained passive and hidden under shelter for at least 1-6 hours after surgery. Most fish were swimming actively and displaying their usual inquisitive behaviour within 12-24 hours after surgery (Plate 2.4). Many individuals fed within 2-3 days after surgery, but

often did not retain food (i.e. regurgitated). Feeding involving retention of food usually started within 4-6 days post-surgery. This varied, however, with individual fish. Fish were fed daily with West Australian pilchards (*Sardinops neopilchardus*), each pilchard containing 50 mg of the antibiotic tetracycline. Weighted doses of powdered tetracycline were prepared in "000" sized gelatine capsules. The capsules were filled with seawater, closed and embedded in the body cavities of the food items (pilchards).

Every 2-3 days the free-swimming fish in the aquaria were examined visually, without handling, to assess the status of the wound. Fish were judged ready for release after 10-14 days if no sign of infection or opening of the wound was observed. Only fish that appeared to behave normally and which fed regularly were considered for release.

Fish were removed from the aquarium by lowering the water level from maximum aquarium capacity (depth ~80 cm) to 20-25 cm and gently picking up the fish by supporting individuals underneath the gill and anal fin area. If fish appeared stressed the eyes were covered using a wet chamois cloth. Most fish could be picked up without the need to restrain them with a firm grip. Fish were released only if the incision was closed and the wound area appeared "clean", without signs of infection or tissue necrosis. In cases of minor infection or inflammation fish were returned to the aquarium for a further recovery period (a maximum of three weeks). Any fish with a reopened incision was removed from the aquarium and anaesthetised. The transmitter was removed, the incision closed, and the individual released after 1-2 days of recovery.

# 2.3.5. Aquarium maintenance

A continuous supply of fresh seawater was available, and each aquarium was treated twice daily with 2.5ml 100L<sup>-1</sup> of Myxazin<sup>TM</sup> (Waterlife Research Industries, UK), a commercially available broad-spectrum bactericide and protozoastatic agent for aquarium use. Substrata in aquaria were suction-cleaned daily after feeding to remove leftover food and waste material. Fish quickly became accustomed to the cleaning procedure and showed little sign of stress. In fact, most individuals showed

considerable interest and curiosity. After initial (January-February 1993) occurrences of "gas bubble" disease due to supersaturation of dissolved atmospheric gas in the water supply, caused by the aquarium pumping facilities (Weitkamp & Katz 1980), all water was gravel filtered prior to use (Plate 2.5). No further incidents of gas bubble disease occurred.

## 2.3.6. The tracking and navigational technique

Seven field trips were made over the course of this study (January 1993 - December 1995, Table 2.1). For methods and details of preliminary ultrasonic telemetry and field tracking trials conducted during the pilot study (January - February 1993) see Chapter 3.

Fish to be released from aquaria were transported in 50 litre containers and released at their location of capture, based on reef feature identification using aerial photos during initial capture. Tracking commenced immediately upon release. Individual fish could be identified by the transmitter frequency and the different pulse rates on each frequency (pulses min<sup>-1</sup>).

The basic tracking technique followed the small vessel techniques described by Holland *et al.* (1985, 1992). Two different vessels were used for tracking. For the early tracking trials during the pilot study, a 4.1 m, open aluminium dingy powered by a 10 hp outboard engine was used (Plate 2.6). However, this boat provided little protection from rain, wind and saltspray, which reduced the endurance of the tracking personnel. Furthermore, this type of environment had the potential for damaging the electronic equipment, despite the equipment being protected in a custom built housing (Plate 2.6). Therefore, for the majority of the tracking project (July 1993 - December 1995) a 7.4 m aluminium, half-cabin workboat with shallow draft and powered by 36 hp diesel engine was used (Plate 2.7). This setup permitted continuous operation by a single operator during the tracking periods.

Navigation was visual, using landmarks and reef features identifiable on colour aerial photos (5,000 feet altitude, Australian Surveying & Land Information Group, Canberra). During searches of reefs in areas adjacent to Lizard Island (see Chapter 5) Global Positioning System and standard coastal navigation techniques were used. During the second field trip (July-October 1993) a 24-hour tracking program was conducted to assess possible night-time movements by *P. leopardus*. For night-time position fixing and navigation, labelled marker buoys with reflective tape were located at regular intervals along the fringing reef edge throughout the study area. Except on moonless nights, it was possible to identify landfeatures and buoys without an additional light source. If required, a hand-held spotlight was used for locating and identifying marker buoys.

Exact position fixing of fish equipped with ultrasonic transmitters was by visual triangulation (White & Garrot 1990) using reef- and land-features identifiable on aerial photos. Crossbearings at approximately  $90^{\circ}$  to first bearing permitted location of the signal to be determined to within approximately 10-20 m. Pilot investigations indicated that the least biased bearings could be obtained at angles of  $0^{\circ}$  and  $90^{\circ}$  to the prevailing wind direction (see Chapter 3). Emphasis was placed on avoiding adverse wind directions (e.g.  $45^{\circ}$  to the wind), or taking bearings at angles less than  $90^{\circ}$  (see Chapter 3). If signals or bearings were not distinct, or could be received from one direction only (i.e. the fish was inside a cave or under an overhang) a technique of "drive-over" (also known as "ground-zero tracking", Nelson 1990) was employed to determine the exact location. The vessel was manoeuvred carefully in the direction of the highest signal intensity until the signal became omnidirectional, followed by a 180° reversal of direction of the signal, indicating the exact position of the specimen (see also Clark & Green 1990, Matthews *et al.* 1990).

Two signal reception problems did occur occasionally:

 Having two or more transmitters on the same frequency in one area at the same time. This resulted in a multiple overlay of pulse rates, making individual identification and especially exact position fixing difficult, as the VR-60 receiver used was not equipped with a pulse rate decoder. However, considerable planning effort was put into spatial allocation of transmitters to fish from across the whole study area to minimise or avoid this situation. Therefore, this reception problem occurred rarely, and was observed mainly in relation to movements associated with spawning aggregations (Chapter 5). Furthermore, with practice it was possible to optimise the directional sensitivity of the directional hydrophone in relation to each transmitter, through strategic spatial positioning of the tracking boat, and establish fish identification and position by concentrating on the slight differences in signal intensity. Clearly, this was only possible if fish were not exactly in the same location. In this manner separate positions were distinguished as close to each other as approximately 20-50 meters.

2. A reception problem arose when several fish on different frequencies were in close proximity, as transmitters on different frequencies sometimes interfered with each other. Hence the signal from one frequency often "bled" (*sensu* Matthews *et al.* 1990) onto the frequency channel of the transmitter currently tracked. With experience it was easy to recognise and ignore these signal "bleeds".

In order to confirm locations, cross-validate observer bearing accuracy, as well as to examine specimens visually during the tracking periods, occasional underwater relocations of fish were undertaken on SCUBA (Plate 2.8). Two methods were used:

- 1. Surface-tethered and -guided relocation. The tracking boat was anchored in close proximity to the signal source. A dive team, carrying the V-10 directional hydrophone with an extension cable, descended to the bottom. One person remaining in the boat used the surface receiver (VR-60) to determine signal intensity while communicating with the dive team via a surface-to-diver voice communication system (Divelink 3.0, Divelink Pty., Western Australia). Through the information on the signal intensity provided by the tracking person at the surface, divers were able to determine the direction of the strongest signal, and hence the direction in which to search for the specimen. This procedure was extremely time consuming, cumbersome and required good coordination between divers and the surface person.
- 2. Relocation using an independent underwater receiver. During 1994 it was possible to aquire a diver-held ultrasonic receiver (VUR-455, Vemco). This made

relocation of fishes by divers independent of surface connections, and provided an easy and fast means of locating specimens being tracked. Method (1) was abandoned after the successful trial of this receiver.

### 2.3.7. Termination of tracking: Collection and determination of sex of fish

Towards the end of the projected battery life-span of transmitters, fish were located using the technique described above and collected using a speargun. Collected specimens were dissected to remove the transmitter and examine the success of placement of the unit. Gonads were removed and preserved in gonad fixative FAACC (formaldehyde-acetic acid-calcium chloride; L. Winsor, pers. com.). Recovered transmitters were cleaned, old batteries discarded, and the transmitter unit disinfected in ethanol for reuse.

**Gonad histology**: To determine the sex of each fish, and gauge its reproductive status, histological analysis was conducted. Middle portions of gonads were embedded in paraffin and sectioned transversely at 5  $\mu$ m thickness, and stained using Mayer's haematoxylin-eosin (Ferreira 1993a&b). The classification of individuals into different gonadal developmental stages followed Moe (1969) and Ferreira (1993a&b).

**Table 2.1:**Dates of field trips made during this study, indicating the primary taskundertaken during each trip.Chapter references indicate the chapterscovering the relevant section of the project.

Dates	Task	Chapter		
Jan Feb. 1993	Pilot study	2; 3		
July - Oct. 1993	• Initiation of tracking during the spawning	4; 5		
	season			
Feb Mar. 1994	Initiation of tracking	4		
	during the non-spawning			
	season			
Aug Nov. 1994	• Tracking during the	4; 5		
	spawning season	:		
Feb Mar. 1995	• Tracking during the non-	4		
	spawning season			
	• Mark-release-resighting	6		
	pilot study			
May 1995	• Mark-release-resighting	6		
	pilot study (recapture)			
Aug Dec. 1995	• Tracking during the	4; 5		
	spawning season			
	• Mark-release-resighting	6		
	study			

Table 2.2: Specifications of ultrasonic transmitters used during this project. Several transmitters working on the same frequencies were used simultaneously through judicious planning of spatial distribution of tracking specimens. The column labelled "Application" refers to the type of placement this unit was used for in this study: F: force feeding; E: external attachment; I: internal placement.

Company	Туре	Frequency (kHz)	Dimension in millimetres (diameter x length)	Nominal life-span (days)	Weight (g) in water	Application
Vemco (Canada)	V8-2L	65.5; 69.0; 76.8	8 x 38	21	3.5	<b>F; E;</b> I
	V16-4L	50.0; 60.0; 65.5; 69.0; 76.8	16 x 65	268	10	I
	V16-6L	50.0; 60.0; 65.5; 69.0; 76.8	16 x 90	476	14	I
Sonotronics (USA)	Xtal-87	60.0; 65.5; 76.8	17 x 95	84-208*	~9	I

\* Life-span is frequency dependent



Plate 2.1: Location of incision area on *P. leopardus* used for insertion of ultrasonic transmitters into the body cavity. The incision was located parallel to the mid-ventral line, approximately 1-2 cm anterior to the anus and 1-2 cm lateral of mid-ventral line. Fish was fully anaesthetised in MS-222 prior to commencement of surgical prodecure.



**Plate 2.2:** Insertion of disinfected ultrasonic transmitter into the body cavity of *P. leopardus*. Transmitters were positioned carefully parallel to the longitudinal axis of the body. The skin of specimens was kept moist, and gills were continuously oxygenated by flooding with anaesthetic solution and fresh seawater.



Plate 2.3: Incision area after closure using six surgical staples. After placement of staples, the incision area was cleaned using a specifically designed fish-antiseptic, and each fish given an intraperitoneal injection of the antibiotic tetracycline. Specimens were returned to the aquarium for recovery from anaesthesia



Plate 2.4: Plectropomus leopardus became accustomed to aquarium conditions quickly, displaying their ususal inquisitive behaviour within a few days.
Regular cleaning and maintenance work on the aquaria did not disturb or stress coral trout, but rather caused considerable interest.



Plate 2.5: The installation of simple gravel filters in the water inlet to each aquarium was sufficient to reduce the supersaturation of dissolved atmospheric gas caused by the aquarium pumping facilities. This eliminated the occurrence of "gas-bubble" disease in *P. leopardus*. Gravel filters consisted of dead coral rubble placed inside plastic buckets fitted with numerous holes for drainage, and suspended below each water inlet pipe.



Plate 2.6: The small, open aluminium dinghy used for ultrasonic tracking during the early part of this study. The ultrasonic receiver was located inside the custom-built wooden housing near the stern, and the directional hydrophone was located at the bottom of the stainless-steel pole on the starboard side of the dinghy. The hydrophone pole could be rotated horizontally by 360°, and was vertically adjustable to a depth of approximately 1 m below the level of the keel. The general design was based on Holland *et al.* (1992).



Plate 2.7: The larger vessel (7.4 m) used for ultrasonic tracking for the majority of the study, providing weather protection for the operator and electronic equipment. The pole with the directional hydrophone was positioned close to the steering and engine controls, permitting continuous operation by a single operator for extended periods. The very shallow draft of this vessel allowed working in waters as shallow as 1 m. General principle based on Holland *et al.* (1985).



Plate 2.8: *Plectropomus leopardus* equipped with an ultrasonic transmitter implanted into the body cavity observed during regular visual examinations of tracking specimens. The remaining scar tissue from the successful surgical implantation of the transmitter is visible on the ventral portion of the body cavity, slightly anterior to the anus (arrow). Clearly visible near the anterior end of the dorsal fin is also one of the two standard T-bar anchor tags used for ease of visual recognition of tracking specimens.



Figure 2.1: Map of Lizard Island showing the general study area used for ultrasonic tracking of *P. leopardus* during 1993-1995. Tracking was generally restricted to the north, north-east and western side of the island, as these areas were more sheltered from the prevailing south-east winds. Major reef area and land-features are indicated.

Chapter 3:

# PRELIMINARY METHODOLOGICAL DEVELOPMENTS

# 3.1. Introduction

Several preliminary assessments were undertaken in an effort to determine the most suitable techniques for successful application of ultrasonic telemetry to reef fish and the coral reef environment. These assessments, conducted during the pilot phase of the project, included:

- Comparison of fish anaesthetics and determination of most appropriate transmitter placement technique.
- Preliminary assessment of ultrasonic telemetry in the coral reef environment.
- Initial tracking trials of fish equipped with transmitters.

The present chapter presents the various comparisons and trials of methods undertaken, and illustrates the findings leading to the adoption of the techniques ultimately used and outlined in the preceding chapter.

# 3.2. Evaluation of anaesthetics and transmitter placement methods

Anaesthetic solutions are used regularly to sedate fishes during various husbandry and handling activities (see Lemm 1993). The effects for each drug vary and selection depends on the criteria to be met. Criteria include speed of anaesthetic induction and recovery, depth and safety margin of anaesthesia achieved, and level of physiological stress caused by exposure to the specific agent. Gilderhus & Marking (1987) point out that definitions of efficiency and handleability can be subjective and vary depending on the individual user. Thus each anaesthetic agent has advantages and disadvantages depending on the species of fish, environment and purpose of use, and the subjective preferences of the user. Hence it is recommended to examine various drugs for each specific occasion.

Successful and easy maintenance of deep anaesthesia combined with gentle recovery were the criteria of major concern in this study, rather than induction and recovery times. Three anaesthetic drugs readily available were trialed during the initial phase of the project: Hypnodil<sup>™</sup> (active ingredient: Metomidate), Phenoxyethanol and MS-222 (active ingredient: Tricaine methanesulfonate).

**Hypnodil<sup>TM</sup>** (Metomidate) is a water-soluble non-barbiturate hypnotic compound, and induces sleep rather than general anaesthesia (Mattson & Riple 1989). Effective concentrations reported in the literature range from 0.5-7 mg L<sup>-1</sup>, with short induction times of 1-9 minutes and slower recovery periods ranging from 6-19 minutes (Gilderhus & Marking 1987, Mattson & Riple 1989, Thomas & Robertson 1991, Ross *et al.* 1993). The safety margins are considered to be very high, as concentrations up to 300% higher than the effective dosages did not cause any mortalities (Mattson & Riple 1989). In the present study Hypnodil<sup>TM</sup> was evaluated at a concentration of 7 mg L<sup>-1</sup>. Specimens were found to be fast in response (1-3 minutes), but relatively slow to recover (10-20 minutes) compared to the other agents examined.

**Phenoxyethanol** has been tested previously with concentrations ranging from  $0.1 \text{ ml } \text{L}^{-1}$  to 0.6 ml L<sup>-1</sup> (McFarland & Klontz 1969, Mattson & Riple 1989), resulting in induction periods of 3-30 minutes (McFarland & Klontz 1969, Gilderhus & Marking 1987). Recovery periods ranged from as short as 2.5 minutes (Mattson & Riple 1989) to as long as 30 minutes (McFarland & Klontz 1969). However, most studies recorded rapid recovery within 4-7 minutes (e.g. Gilderhus & Marking 1987). Mattson & Riple (1989) found respiratory movements ceased at higher concentrations (0.5-0.6 ml L<sup>-1</sup>), and concluded that Phenoxyethanol has a lower safety margin with regards to depth and intensity of anaesthesia, compared to Metomidate and MS-222. During the pilot project Phenoxyethanol was used at a concentration of 0.5 ml L<sup>-1</sup>, with induction and recovery periods of 3-5 minutes and 5-10 minutes, respectively.

**MS-222** (**Tricaine methanesulfonate**) is a widely used fish anaesthetic and registered for use on food fish in the U.S.A. (Gilderhus & Marking 1987). Effective concentrations range from 25-100 mg  $L^{-1}$ , with rapid induction (1-6 minutes) and fast recovery in 3-15 minutes (McFarland & Klontz 1969, Gilderhus & Marking 1987, Mattson & Riple 1989, Thomas & Robertson 1991). Maintenance of anaesthesia is

considered excellent (McFarland & Klontz 1969). However, margins between effective and lethal concentrations appear to be narrow (Gilderhus & Marking 1987). During these trials MS-222 was used at a concentration of 80 mg  $L^{-1}$ , resulting in induction periods of 1-3 minutes and recovery times of 5-15 minutes. Maintenance of anaesthesia was good and recovery behaviour was calm and without reactive side effects. MS-222 is known to create a toxic condition if used in seawater or in direct sunlight. All use of the agent was conducted in the shade and protective clothing was worn while handling the solution.

Techniques that have been developed for attaching telemetry units to study animals utilise one of three general methods. All three methods were trialed for placement of ultrasonic transmitters in *Plectropomus leopardus*:

- Stomach placement (force feeding): Oral insertion of transmitter unit into the stomach of the animal (e.g. Hawkins *et al.* 1980, Clark & Green 1990, Matthews *et al.* 1990, Armstrong *et al.* 1992, Holland *et al.* 1992, 1993b). This is the least intrusive method, neither resulting in any external protrusion of the unit, nor requiring any surgical procedure.
- External attachment: Unit is attached externally to the animal, either using harnesses (e.g. birds: Badyaev et al. 1996; mammals: Douglas 1992), or directly attached to the musculature (e.g. fish: Arnold & Holford 1979, Matthews et al. 1990, Bradbury et al. 1995, Holland et al. 1990b, 1996).
- Internal surgical placement: Transmitters are surgically implanted into the animal, most commonly under the skin (e.g. Korschgen *et al.* 1996) or into the body cavity (e.g. Mellas & Haynes 1985, Diana *et al.* 1990, Holland *et al.* 1993a).

The procedure for stomach placement (force feeding) consisted of inserting a soft plastic tube (12 mm diameter) through the oesophagus into the stomach of the anaesthetised fish (*sensu* Moser *et al.* 1990, Holland *et al.* 1992). The transmitter (Vemco V8: 8 x 38 mm) was then pushed through the plastic tubing into the stomach using a small wooden rod.

**External attachment** consisted of attaching transmitters directly to the dorsal musculature using the technique described by Holland *et al.* (1990b, 1996). Two plastic cable ties were inserted through the dorsal musculature between pterygiophores in mid-dorsal position below the dorsal fin. Dummy transmitters (equal in weight and size to V8 units) were attached to cable ties and positioned to lie parallel to the body of the fish, thus minimising drag (Plate 3.1).

The technique of body cavity insertion involved intrusive surgery (e.g. Hart & Summerfelt 1975, Holland *et al.* 1993a) and is described in detail in Chapter 2.

Due to limited aquarium space it was not possible to evaluate all combinations of anaesthetics and placement methods simultaneously. Hence two separate experiments were conducted. The first, **experiment A**, consisted of examining the least intrusive transmitter placement technique (force feeding) with all three anaesthetics. In **experiment B** the two intrusive placement techniques (external attachment and body cavity insertion) were trialed in conjunction with the two most suitable anaesthetics as determined after experiment A.

#### 3.2.1. Experiment A: Force feeding

In an attempt to minimise the stress and physical trauma potential tracking specimens were to be exposed to, a non-invasive technique (i.e. force feeding) for transmitter placement was considered to be advantageous. All three anaesthetics were trialed in conjunction with force feeding of transmitters to determine if there was a detectable difference in retention times of transmitters due to the anaesthetic agent used. It was hypothesised that use of the hypnotic, relaxing agent Hypnodil<sup>®</sup> (Metomidate) would result in the longest retention times due to the reported low stress levels caused by this compound (Thomas & Robertson 1991, Ross *et al.* 1993). Coral trout, and serranids in general, are known to regurgitate their stomach contents easily, particularly when exposed to stressful conditions (pers. obs.).

### 3.2.1.1. <u>Methods:</u>

Twenty-one specimens of *P. leopardus* were available for this trial. Fish were assigned randomly to each of the three anaesthetic treatments (n= 7): Metomidate (7 mg  $L^{-1}$ ), Phenoxyethanol (0.5 ml  $L^{-1}$ ) and MS-222 (80 mg  $L^{-1}$ ). Individual fish were anaesthetised, tagged with two T-bar anchor tags for individual identification, fork length measured, and an individually numbered dummy transmitter inserted into the stomach as described above. Dimensions and weight of the dummy transmitters were identical to Vemco V8 units. For recovery, fish were returned to the aquaria. All specimens were fed daily using West Australian pilchards (*Sardinops neopilchardus*). Aquaria were examined every two hours during daytime and once during nighttime (between  $10^{00}$  and  $12^{00}$  PM). The start of each visual inspection period was taken as the maximum transmitter retention period for any recovered units. The experiment was terminated upon recovery of all dummy transmitters.

Data were analysed for differences in retention times between anaesthetic agents using a single factor analysis of covariance (ANCOVA). Size of fish (FL) was incorporated as a covariate, to account for potential effect of size of fish on the retention time of transmitters. Prior to analysis the assumptions underlying the ANCOVA were evaluated. Homoscedasticity was examined using Cochran's test (Underwood 1981), data were examined for normality, and the assumption of similar correlations of covariate with the dependent measure in all cells of the design was examined by testing within cell regressions. Student-Newman-Keuls test (SNK) was carried out as a multiple comparison of means after the analysis (Underwood 1981).

#### **3.2.1.2.** <u>Results:</u>

Observed retention times ranged from 18 to 216 hours, with some indications of longer retention periods for larger fish (Fig. 3.1, r = 0.6205, N=21). The ANCOVA indicated a significant difference in mean retention times between anaesthetic agents used at the  $\alpha$  level of 0.05 (Table 3.1). Further examination of this effect using SNK test illustrated that the use of MS-222 as anaesthetic resulted in a shorter retention

period of force fed transmitters compared with the use of either Phenoxyethanol (p = 0.00419) or Metomidate (p = 0.00082). Mean gastric retention times did not differ with the use of either Phenoxyethanol or Metomidate (p = 0.21591). On average, fish anaesthetised with MS-222 retained the dummy transmitters for only 42.0 hours ( $\pm 9.71$  SE), in contrast to 118.0 hours ( $\pm 17.22$  SE) and 147.42 hours ( $\pm 23.77$  SE) for Phenoxyethanol and Metomidate, respectively (Fig. 3.2).

# **3.2.1.3.** <u>Discussion</u>

While the use of Metomidate (Hypnodil<sup>TM</sup>) did result in the highest mean retention time (Fig. 3.2), the difference was only statistically significant in comparison with MS-222. The considerably shorter retention period makes the use of MS-222 the least suitable anaesthetic agent for force fed placement of ultrasonic transmitters in *P*. *leopardus*.

However, even the longest mean retention time recorded for transmitters placed in the stomachs of *P. leopardus* (147.42 hours or 6.15 days, Metomidate), was considered unsatisfactory for the purpose of longer term tracking during spawning periods. While being the least intrusive and hence physically least traumatic transmitter placement method, force feeding is clearly not suited for use with *P. leopardus* for any duration exceeding 1-6 days.

### **3.2.2.** Experiment B: External attachment versus body cavity insertion

Given the exclusion of force feeding as a suitable transmitter placement method due to the demonstrated short retention periods, the use of the other two placement options (external attachment and body cavity insertion) were evaluated in a subsequent experiment. Due to the aquaria space restrictions it was not possible to evaluate all three anaesthetics simultaneously in conjunction with the two alternative transmitter placement methods. It has been suggested that the suppression of a stress response due to the use of Metomidate makes this a very valuable drug for the routine handling of fishes (Ross *et al.* 1993). However, slightly elevated levels of the stress hormone corticosteroid are considered to be beneficial for resistance to stress trauma, thus making Metomidate potentially less suitable in situations involving severe stress, such as surgical procedures (Thomas & Robertson 1991). Given the nature of the intended, intrusive manipulations to be undertaken in the second experiment (external attachment; surgical body cavity insertion), it was decided to discontinue the use of Metomidate due to concerns that the lack of raised corticosteroid hormone might adversely affect wound healing.

#### 3.2.2.1. <u>Methods:</u>

The experiment investigated the effect of two anaesthetic compounds (Phenoxyethanol and MS-222) and two transmitter placement methods (external attachment and body cavity insertion) in a fully factorial design. All specimens were allocated randomly to treatment factors and treatment level combinations. The transmitter placement treatment consisted of five treatment levels (Fig. 3.3): external and internal placement treatments, external and internal placement controls (full surgical or attachment procedure but without transmitter placement), and handling control (anaesthesia with basic handling only). All fish received the same preliminary handling: prior to treatment, each fish was removed from the aquarium, anaesthetised in one of the two anaesthetic solutions, weighed (to the nearest 50 g), fork length measured, and each fish double tagged using standard T-bar anchor tags. Handling control fish were returned to the aquaria for recovery. External attachment treatment consisted of inserting two disinfected nylon cable-ties through the dorsal musculature between pterygiophores using a sharp, hollow stainless steel needle. A dummy transmitter was attached to the cable-ties, which were cinched down and trimmed, holding the transmitter in place (Plate 3.1). The fish received an intraperitoneal injection of the antibiotic tetracycline (50 mg kg<sup>-1</sup> of fish, Hart & Summerfelt 1975, McFarlane & Beamish 1987), before being returned to the aquarium for recovery. The procedure took approximately 5-8 minutes. External attachment control fish underwent the same procedure, except neither cable-ties were inserted nor transmitter attached after puncturing the dorsal musculature, and the fish were returned to the aquaria after 8 minutes. Internal placement treatment consisted of full surgical insertion of a dummy

transmitter into the body cavity as described in Chapter 2. Duration of the procedure was 10-15 minutes. Internal placement control fish were treated identically, except no transmitter was placed in the body cavity prior to closure of the incision. These control fish were returned to the aquaria after a 15 minute manipulation period.

A total of 20 *P. leopardus* distributed in five aquaria were available for this experiment, resulting in two replicates per treatment combination (Fig. 3.3). Fish from each aquarium were assigned to treatments randomly. Wet weight (to the nearest 50 g) of each individual was recorded prior to and at the termination of the experiment. Daily, fish were provided with food in the form of West Australian pilchards (*Sardinops neopilchardus*), and each individual was examined visually without handling, to record general condition, behaviour, feeding and apparent wound status (if visible).

The experiment was terminated after 24 days, due to increasing occurrence of gas-bubble-trauma (see Chapter 2), which caused early mortalities and influenced the behaviour of fish (i.e. lethargy and cessation of feeding) from all experimental groups. Upon termination, wounds were examined and classified as non-healed (open wound, exposed flesh), partially healed (at least 40-50% wound closure), aggravated (ripped, or inflamed/secondary infection), or healed (wound essentially closed, possibly minor inflammation). Subsequently, dummy transmitters were removed and fish were weighed.

The majority of assessment was based on the observations made during the aquarium recovery period, the inspection of wounds, and transmitter placement and condition after termination of the experiment. The change in weight during the experiment (weight<sub>after</sub> - weight<sub>before</sub>) was analysed using a univariate two-factor analysis of covariance (ANCOVA). Occurrence of gas-bubble-trauma (yes/no) was incorporated as a covariate, to account for the potential influence of the disease on the final weight of the experimental animals The statistical assumptions underlying the ANCOVA were examined prior to analysis. Homoscedasticity was evaluated using Cochran's test (Underwood 1981), data were examined for normality, and the assumption of similar correlations of covariate with the dependent measure in all cells of the design was

examined by testing within cell regressions. Student-Newman-Keuls test (SNK) was carried out as a multiple comparison of means after the analysis (Underwood 1981).

# 3.2.2.2. <u>Results:</u>

The change in weight of the experimental fish over the duration of the experiment differed significantly between transmitter placement treatments applied (p = 0.0178, Table 3.2). Fish in the external treatment group (carrying external transmitters) displayed a significant reduction in weight compared to all control groups, which gained weight, while the internal treatment group showed no change in mean weight during the experiment (Table 3.3, Fig. 3.4). The decrease in weight observed in external treatment fish (-200 g, Fig. 3.4) can be considered a substantial weight loss, given the time period (24 days) and pre-experiment weight of animals (mean = 1075 g, range = 800-1500 g).

Fish with external transmitters were observed to spend much of their time attempting to rub the site of transmitter attachment against the substratum, and generally appeared agitated. Furthermore, most fish initiated feeding within two days of treatment, except for fish in the external treatment group (Table 3.4). Clearly, the externally placed transmitters disturbed the experimental fish and caused abnormal behaviour.

The analysis suggested also that the use of Phenoxyethanol possibly may lead to a reduction in weight through time (Fig. 3.5). However, this trend was not statistically significant (p = 0.0641, Table 3.2).

Observational records summarised in Table 3.4 illustrated some differences in the effects of the different transmitter placement methods and anaesthetics. All fish anaesthetised in MS-222 attained deep and easily maintained anaesthesia, whereas 40% of fish exposed to Phenoxyethanol did not reach deep anaesthesia (Table 3.4). This resulted in observable tail movements and/or uncontrolled twitching of the animal during handling or treatment. Occasional powerful tail twitching and cramp-like convulsions were observed also in some of these specimens during the early recovery period.

Some of the specimens which showed signs of gas-bubble-trauma early, never started feeding (Table 3.4). This gas-supersaturation phenomenon was observed on fish from all treatments, in some cases as early as four days after initiation of the experiment. All fish inflicted with gas-bubble-trauma ceased feeding soon after the first signs became apparent, and became very lethargic and unresponsive to visual or food stimuli.

Examination of transmitter placement wounds after the termination of the experiment revealed some consistent patterns (Table 3.4). After 24 days the incisions made into the body cavities of internal control and internal treatment fish were essentially healed (although some minor inflammations did exist). The puncture wounds through the dorsal musculature of fish with externally attached transmitters were all aggravated and in some cases enlarged due to repeated attempts at dislodgments. Wounds on external control fish were either healed or partially healed, but showed no signs of further aggravation.

#### 3.2.2.3. Discussion

Based on the observations and results of the analysis it became obvious that external attachment of ultrasonic transmitters was not a viable option for *P. leopardus*. Coral trout clearly were disturbed by the existence of the external package, with repeated dislodgment attempts influencing their normal behavioural patterns. Similar behaviour was noted during external attachment trials with other species (e.g. Mellas & Haynes 1985). Furthermore, the delayed onset of feeding observed in the external treatment specimens (Table 3.4) supports this conclusion.

While body cavity insertion is the technically most difficult method, it was considered to provide the least side-effects if applied successfully, and was selected as the method of choice for this study (see also Moore *et al.* 1990). Wound closure was observed within 10-14 days in most cases, and infections were reduced and/or

eliminated with the regular use of the antibacterial treatment of the water (Myxazin<sup>®</sup>), and regular doses of oral antibiotic (tertracycline). Both these treatments were introduced subsequent to the transmitter placement experiment described here.

Several authors have reported that fish anaesthetised with Phenoxyethanol do not attain deep anaesthesia, i.e. do not lose reactivity and sensitivity to touch and pressure (Gilderhus & Marking 1987, Mattson & Riple 1989). This was noted in the present experiment in some specimens during the surgical procedure, with twitching and flapping of the caudal fin. Of major concern also were occasional cramp-like convulsions and powerful tail twitching observed during recovery of the experimental animals (also noted by Mattson & Riple 1989), with the potential to damage the fresh wound closures and danger of injury to the fish due to contact with walls or shelters in the aquaria.

Recently, additional concern has been expressed regarding the potential for damage to the olfactory system of fishes due to Phenoxyethanol. Losey & Hugie (1994) suspected that the chemical senses of fishes anaesthetised with Phenoxyethanol may be impaired.

An increase in plasma stress hormone levels has been noted in fish anaesthetised in MS-222 (Puceat *et al.* 1989, Thomas & Robertson 1991), resulting in increased stress levels for 24-72 hours (Harrell 1992). This increase in stress levels appears to be due to the way this agent acts. MS-222 causes reduced gill ventilation due to depression of medullary respiratory centers, resulting in hypoxia (Tytler & Hawkins 1981 in Mattson & Riple 1989). This may also explain the narrow safety margin noted by Gilderhus & Marking (1987), as high concentrations (> 100 mg L<sup>-1</sup>) quickly lead to anoxia and death. However, temporarily raised levels of the corticosteroid stress hormone may be beneficial for resistance to severe physical trauma, such as experienced during intrusive surgery (Thomas & Robertson 1991). As such, the use of MS-222 may even be advantageous and have the potential to assist in wound healing and recovery after surgical procedures. Furthermore, Losey & Hugie (1994) did not observe any negative effects of MS-222 with regards to potential damage to olfactory sense observed with Phenoxyethanol.

In light of concerns regarding the lack of deep anaesthesia and poor recovery behaviour observed with Phenoxyethanol on the one hand, and the ease of induction and maintenance of deep anaesthesia, as well as the potential positive effect of raised stress hormone level on resistance to physical trauma during the use of MS-222 on the other hand, it was decided to continue using MS-222 for the rest of this study.

# **3.2.3.** Further evaluation of the selected placement technique

In order to reduce occurrence of secondary tissue infections with associated possible reopening of the incision and loss of transmitters, a trial was run to examine the efficacy of surgical cyanoacrylate adhesive (Histoacryl<sup>®</sup> blue, Braun, Germany) as a sealing compound in conjunction with surgical staples. However, the tissue adhesive dissolved, pealed off, or was rejected within 1-2 days of surgery (see also Nemetz & MacMillan 1988 p. 192). The severe tissue necrosis observed by Kaseloo *et al.* (1992) when cyanoacrylate adhesive was used in conjunction with sutures was not clearly evident in the present case. However, individual fish were not removed from aquaria for detailed examination during the 8-14 day healing period.

Cyanoacrylate adhesives (e.g. Histoacryl<sup>®</sup>) in some cases appear to cause adverse tissue reaction in fishe's. Furthermore, the requirement of basically dry tissue for successful adhesion of the glue (Cochrane 1985, Nemetz & MacMillan 1988, Kamer & Joseph 1989, pers. obs.) makes the use of cyanoacrylate adhesive rather difficult in fishes. Using tissue adhesives without sutures was considered inappropriate due to postoperative tension placed on the incision by the inserted transmitter (Alhopuro *et al.* 1976), reported to result in reopening of incisions in as little as 24 hours (Kaseloo *et al.* 1992).

After further consultation with a surgeon (Dr Oscar Horky, Sydney, Australia) a small trial (n = 4) was conducted in 1995 to use standard suture material instead of

surgical staples for the closure of surgical incisions. Braided silk sutures (Ethicon<sup>TM</sup>, Johnson & Johnson) were trialed in preference to monofilament nylon (Ethilon<sup>TM</sup>) or monofilament polypropylene (Prolene<sup>TM</sup>), as it was found to be faster and easier to make and place reliable suture knots using braided material. Individual sutures were placed approximately 5-8 mm apart. Knots were tied using horizontal pressure to maximise apposition of skin edges, while avoiding tissue creasing and overlap (*sensu* Irvin 1981 in Kaseloo *et al.* 1992). With practise, time required for closure of incisions with sutures was found to be equal to staples (but see Mulford 1984, Mortensen 1990), and considerably more control over suture placement, and especially skin-to-skin apposition, was possible. Visual examination of experimental fish indicated externally fully closed wounds after 6-8 days. Two of these experimental fish were subsequently released and tracked. Visual inspections of both fish during the tracking interval indicated good closure and non-infected, well healed incisions. One individual was recovered after 35 days at large. The wound was fully healed with no signs of infections.

In light of these experiences, future studies should consider the use of standard sutures instead of surgical staples, at least for coral trout. The suggested reduction in operating time through the use of staples (Mulford 1984, Mortensen 1990) was not observed. The use of a stapler often resulted in badly placed or poorly closed staples, which had to be replaced (see also Mortensen 1990). Such time consuming misplacement did not occur with sutures. Sutures permitted considerably more control over placement, closure and tissue apposition. While the use of braided silk sutures compared to monofilament material might not be ideal, due to increased possibility of tissue infection caused by capillary action along the individual strands of the braided suture material (Crane 1983, Nemetz & MacMillan 1988), it was observed that the ease of making reliable knots with braided silk sutures was an advantage over the use of the monofilament alternatives (e.g. Ethilon<sup>™</sup>, Prolene<sup>™</sup>). However, with more practise, secure knots can easily be achieved with monofilament material. This appears to provide the cleanest and safest technique for closing body wall incisions in coral trout, providing for reduced chances of secondary infections (e.g. Mortensen 1990), and hence reduced recovery periods.
### 3.2.4. Summary of anaesthetic and transmitter placement trials

For use as anaesthetic in *P. leopardus*, Tricaine methanesulfonate (MS-222), was the most suitable anaesthetic compound for intrusive manipulations, such as internal transmitter placement. A deep anaesthesia could be achieved and maintained easily, and the reported, associated raise in corticosteroid hormone level might aid in wound healing and the resistance to secondary infections. Metomidate (Hypnodil<sup>®</sup>), while resulting in the least stress, appeared more suited for limited handling and possibly force feeding (longest retention time) based on the present observations and experimentation. Phenoxyethanol, on the other hand, is a more stressful and less suitable anaesthetic agent, due to lack of deep anaesthesia. As such, clearly it is not suited for intrusive manipulations. Nevertheless, use of Phenoxyethanol resulted in longer force-fed transmitter retention times then did MS-222.

With respect to the three transmitter placement techniques trialed, external attachment clearly is not suited for use with *P. leopardus*. It was observed that externally attached transmitters resulted in drastic changes in behaviour of the animal (continuos dislodgment attempts), considerable weight loss, and resulted in aggravated attachment wounds. Clearly, one has to consider that *P. leopardus* is a demersal fish living in the structurally complex coral reef environment, which enhances the opportunity of the fish to attempt dislodgement.

Force feeding, while being non-intrusive and, as far as could be determined in this experiment, not influencing the behaviour of the experimental animal in any noticeable manner, is of limited use in *P. leopardus* due to the rapid rejection rate, resulting in potential tracking periods of only a few hours to several days.

Surgical implantation of ultrasonic transmitters into the body cavity was demonstrated to be the most suitable technique for the long-term tracking of coral trout. The fast return to regular feeding observed in internal treatment and control fish (2-7 days, Table 3.3), and the apparent normal behaviour of these fish supported the decision

to use body cavity insertion as the transmitter placement technique chosen for the remainder of this study.

# 3.3. Assessment of ultrasonic telemetry in the coral reef environment

The increased use of radio telemetry in terrestrial ecology has resulted in the development of substantial methodological procedures to assess the accuracy (bias and precision), and the optimal techniques of telemetry receiver location (e.g. White & Garrott 1990). However, no such field procedures or evaluations appear to be published or developed for ultrasonic telemetry. Given the paucity of detailed studies using ultrasonic telemetry, particularly in the coral reef environment (but see Gruber *et al.* 1988, Holland *et al.* 1993a, 1996, Morrissey & Gruber 1993a&b), as well as the presence of substantial levels of biological background noise on coral reefs (Cato & Bell 1992, McCauley 1995), a preliminary, standardised field test using stationary transmitters was undertaken. Given that wind and sea-state are known to influence the detectability of sound transmission in water (Mackay 1968, Pincock & Voegeli 1990, Jellyman *et al.* 1996), and since the study location (Lizard Island) regularly experiences tradewind conditions of between 15-25 knots, any effect of direction of prevailing wind on detectability or directional bias of observed sound signals needed to be addressed. Thus, the primary objectives of this field evaluation were:

- Establish the accuracy of directional bearings in relation to prevailing wind direction.
- Evaluate observer differences in bias and precision of bearings in relation to prevailing wind direction.
- Determine the optimal angle between bearings and the distance between the tracking boat and the sound source, in order to obtain position estimates which minimise error polygons.

### 3.3.1. <u>Methods</u>

The experiment was conducted using the VEMCO V16 ultrasonic transmitter type (see Table 2.2 for specifications). The test transmitter was attached to a marker buoy 15 cm above the substratum in approximately 6-8 m water depth, and the location of the transmitter was marked with a surface buoy. Three 200 m transects were run from the moored transmitter in relation to the prevailing wind direction at the time of the experiment (Fig. 3.6):

- 0 degree: Transmitter located directly upwind from any position on transect.
- 45 degree: Transmitter located at an angle of 45° downwind from the prevailing wind direction.
- 90 degree: Transmitter located at right angles to the prevailing wind direction, as seen from any position on the transect.

Small marker buoys were positioned at intervals of 25 m along each transect, starting at 50 m from the transmitter location (i.e. 50, 75, 100, 125, 150, 175 and 200 m), resulting in 21 individual positions for the three angular transects (Fig. 3.6). Replicated bearings to the transmitter for each distance and angle combination were obtained using the following data collection protocol:

One person was assigned as the observer, and was wearing a blind fold during the complete session, providing sight of the ultrasonic receiver only. The second person operated the tracking boat. The boat handler anchored the tracking boat at the marker buoys in random order, and recorded the true compass bearing from the directional hydrophone to the transmitter mooring buoy. Subsequently, the blind-folded observer determined the perceived maximum directional signal strength using the directional hydrophone. The corresponding compass bearing of the directional hydrophone (observed bearing) was recorded by the boat handler. The direction of the hydrophone was changed haphazardly by the boat handler, and the procedure repeated by the observer. Six replicate observed bearings were taken at each of the seven distances on the three angular transects. Subsequently, observer and boat handler exchanged positions, and the same procedure was repeated for the second observer, resulting in a total of 252 observed bearings. Average wind strength during the trial ranged from 5-15 knots.

Data was assessed for accuracy, bias and precision using the method described by Lee *et al.* (1985) and White & Garrott (1990). Accuracy is the discrepancy between true and observed measurement (Sokal & Rohlf 1981), and was defined as error ( $\varepsilon$  = true bearing - observed bearing). Error of a consistent nature (positive or negative) is called bias, and has a mean error ( $\overline{E}$ ) distinctly different from zero. Precision, being a measure of the repeatability of observed bearings, was defined by the standard deviation (SD).

Each set of two bearings taken from two of the three angular transects permitted estimation of error polygon parameters (polygon area and maximum diagonal dimension). For the purpose of this study only bearing pairs from equal distance locations (e.g. 50 m x 50 m) were utilised for error polygon determination. Error polygons were determined using the largest and smallest directional bearing observed at each distance marker buoy for each of the three angular transect combinations ( $0^{\circ}$  to  $45^{\circ}$ ,  $45^{\circ}$  to  $90^{\circ}$ , and  $0^{\circ}$  to  $90^{\circ}$ ). Thus, the error polygon parameters obtained in this analysis represented the largest possible error polygon estimates obtainable from the observed data.

Spatial position data for transmitter and distance marker buoys were converted to X and Y coordinates using SIGMASCAN<sup>®</sup>. All compass bearings were converted to X and Y coordinates using the WILDTRACK<sup>®</sup> Apple MacIntosh computer program (Todd 1993, University of Oxford). Data were analysed using EXCEL<sup>®</sup> and STATISTICA<sup>®</sup>. Statistical analyses included Shapiro-Wilk test for normality of frequency distributions, Kruskal-Wallis non-parametric ANOVA and paired t-test. All data were examined for violations of underlying statistical assumptions prior to analysis (Sokal & Rohlf 1981, Zar 1984) and data log<sub>10</sub> transformed where applicable. Given that the angular scale of measurements comprised only a portion of a full circle, and absolute direction of angles were of no direct interest, it was possible to treat data as measured on a linear scale (Zar 1984, Cain 1989).

## 3.3.2. <u>Results</u>

Overall, bearing errors ( $\epsilon$ ) were distributed normally (Shapiro-Wilk W <sub>[252]</sub> = 0.9828, p = 0.4636), and the overall bias (mean error) appeared minimal ( $\overline{E} = -1.61^{\circ} \pm$ 0.5805 SE, Fig. 3.7). However, evaluation of bearing errors by angular transect ( $0^{\circ}$ , 45° vs. 90°) indicated that only the bearing distribution for the 90° transect displayed a normal distribution (Table 3.5, Fig. 3.8c), with the 0° transect distribution appearing strongly platycurtic (Kurtosis K = -0.802, Fig. 3.8a), and the  $45^{\circ}$  distribution negatively skewed (Skewness g = -0.698, Fig. 3.8b). Subsequent comparison by non-parametric ANOVA indicated a significant difference in mean bearing error between transects (Kruskal-Wallis H  $_{[2, n = 252]} = 22.1018$ , p = 0.0000). The 90° transect displayed the least bias ( $\overline{E} = -1.50^{\circ} \pm 0.7163$  SE, Fig. 3.9), the 0° transect had slightly larger, positive bias with increased variation ( $\overline{E} = 2.09^{\circ} \pm 1.077$  SE, Fig. 3.9), and the 45° transect showed strong, negative bias with considerable spread ( $\overline{E} = -5.43^{\circ} \pm 1.0210$  SE, Fig. 3.9). Thus, the amount, as well as directionality of the recorded bias in observed bearings was influenced by the angle between prevailing wind and transect from tracking boat to sound source. Bearings taken directly into the wind  $(0^{\circ} \text{ transect})$ , while showing only small bias, displayed broad spread in observed bearings, resulting in reduced accuracy. Bearings taken at 45° to the wind were consistently negatively biased, suggesting that the sound source was located further upwind than the true bearing to the transmitter indicated. Most satisfactory performance was recorded for bearings taken at right angles to the wind  $(90^{\circ} \text{ transect})$ , with small negative bias and limited spread.

In light of the observed overall differences in bias and accuracy between angular transects, it was decided to examine possible observer differences in bias for each transect separately. Results indicated that bias differed between observers only for the  $0^{\circ}$  transect (Kruskal-Wallis H [1, n = 84] = 6.2384, p = 0.0125), with observer two showing a distinct positive bias ( $\overline{E} = 4.62^{\circ} \pm 1.3730$ ) compared to observer one ( $\overline{E} = -0.43^{\circ} \pm$ 

1.5820, Fig. 3.10). Both observers displayed an equally strong, negative bias on the 45° transect (Kruskal-Wallis H  $_{[1, n = 84]} = 0.2089$ , p = 0.6476,  $\overline{E}_{observer 1} = -5.24^{\circ} \pm 1.5523$ ,  $\overline{E}_{observer 2} = -5.62^{\circ} \pm 1.3452$ , Fig. 3.10). For the 90° transect, observers did not differ significantly in bias (Kruskal-Wallis H  $_{[1, n = 84]} = 2.6034$ , p = 0.1066), although the first observer displayed more negative bias ( $\overline{E} = -2.71^{\circ} \pm 0.9920$ ) than the second observer ( $\overline{E} = -0.29^{\circ} \pm 1.0106$ ) (Fig. 3.10). Thus, a significant difference in bias between observers was only recorded for bearings taken directly into the prevailing wind (0° transect), the overall observed, strong negative bias at 45° to the wind was consistent for both observers, and the 90° transect showed the least bias and smallest variation for both observers.

Evaluation of differences in precision between observers was examined also for each angular transect separately. Although replicate bearings taken by two observers can be identical and independent, they are related simply by the physical location of the ultrasonic transmitter with respect to the tracking boat (Lee *et al.* 1985). Thus, to test for differences in precision between observers, paired t-tests were used to compare precision estimates (SD). While observer one consistently obtained a better mean precision on all three transects (i.e. lower SD, Fig. 3.11), the difference between observers was not significant for either transect (Table 3.6).

Evaluation of the maximum error polygon parameters obtained during the trial evaluation indicated some clear patterns, both with respect to distance between sound source and tracking boat, and angular combination of position bearings taken. The 0°- $45^{\circ}$  transect bearing combination clearly produced the largest error polygon area and, with few exceptions, length estimates, regardless of distance between sound source and tracking boat (Fig. 3.12). The  $45^{\circ}$ -90° transect bearings combinations generally produced similar results (Fig. 3.12). A distinct exception was observed at a distance of 50 m, where this combination resulted in the smallest polygon area and length. Overall, however, the 0°-90° transect bearings combination consistently resulted in the smallest polygon parameter estimates, irrespective of distance from which bearings were taken (Fig. 3.12). The best results for this angle combination were obtained at distances of 50 to 75 m from the sound source, providing maximum error polygon diameters of 58.5 m

and 34.5 m, respectively. These error polygon diameter estimates appear large, as they were obtained from the combination of the largest and smallest bearings recorded. As such they represented the "worst case scenario". Subsequent evaluation of observer bearing precision during full-scale fish tracking sessions was undertaken through cross-validation of observed bearings through visual examination of locations of fish equipped with transmitters. These cross-validation checks were undertaken regularly throughout the tracking program, and illustrated drastically improved bearing accuracy and precision compared to those observed during this trial.

## 3.3.3. <u>Conclusions</u>

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The following points are considered to improve the accuracy and precision of position estimation for ultrasonic tracking studies in coral reef environments. It should be noted that signal strength and detectability will vary greatly depending on behaviour patterns of the fish species tracked (e.g. Matthews *et al.* 1990), and the specific characteristics of the local environment (e.g. rugosity and/or variable levels of background noise):

- The most appropriate angular combination for bearings was  $0^{\circ}$  to  $90^{\circ}$ :
  - in relation to the prevailing wind direction, resulting in highest accuracy and least bias, and
  - ii) with respect to minimising the size and dimension of error polygons.
- Bearings taken at sharp angles to the prevailing wind (e.g. 45°) should be avoided, in order to reduce possible bias.
- Observer training and familiarisation with local conditions and species specific patterns prior to full-scale tracking, combined with regular cross-validation during tracking sessions is strongly recommended.
- Distances of approximately 50-75 m from the sound source (transmitter) provided location estimates with the smallest error polygon parameters. If uncertainty about signal or directionality of signal exists, it is suggested to utilise a "drive-over" technique to verify exact location of tracking specimen.

## **3.4.** Field tracking trials

In order to verify the experimental findings from the aquaria study, and eliminate the possibility that these findings were influenced or caused by any unknown confounding effects due to the captive conditions, the two most suitable long-term transmitter placement techniques (external and body cavity placement) were trialed under field conditions.

In January 1993, two specimens of *P. leopardus* (FL 43.1 cm & 58.9 cm) were equipped with external transmitters (V8) as described above (Section 3.2.2.). After a 15 minute recovery period in fresh seawater aboard the tracking vessel, they were released at their respective capture sites. Both fish inhabited part of a patch reef (approximately 240 m long x 52 m wide) in the Lizard Island lagoon backreef area (Trial Site I; Fig. 3.13). Release and initial behaviour was observed on snorkel, and a continuous 24 hour tracking program initiated. Positions were recorded approximately every 1/2 hour or whenever a change in position occurred, by means of triangulation utilising visual reef markers for orientation. Visual verification of recorded positions and general condition and behaviour of specimens were undertaken regularly on snorkel.

Both fish were monitored continuously for four days. The range of their movements was very limited, the larger specimen not moving more than 25 m, while the smaller fish had a maximum distance between recorded locations of 55-60 m, with most movements, however, limited to approximately 10 m. As far as could be determined, both coral trout spent considerable time inside shelter, resulting in low signal strength reception accompanied by limited reception angles. This was confirmed during visual observations, with both specimens relatively shy and usually out of sight inside the reef matrix. For this location unusually high reef shark activity (mainly reef blacktip, *Carcharhinus melanopterus*, and reef whitetip sharks, *Triaenodon obesus*) was recorded repeatedly during visual observation periods. The tracking trial was terminated after four days, and both fish collected using speargun.

Both specimens showed similar patterns of aggravation of the external placement wounds, and the skin underneath the transmitter was rubbed sore. Repeated dislodgment attempts (or snagging of the external transmitter on the reef substratum) had caused the cable ties to cut deep into the dorsal musculature, resulting in considerably increased external wounds and loosened transmitters. It can be speculated that the aggravated wounds (representing an injured fish) may have contributed to the increased reef shark activity observed during the tracking trial. The observed aggravated wound status exceeded those observed in the aquarium specimens (experiment B, section 3.2.2.), and these results clearly supported the decision to not consider further the use of external transmitter placement for *P. leopardus*.

The second field trial utilised internal transmitter placement (body cavity insertion). Two specimens of *P. leopardus* (FL 59.0 cm & 42.9 cm) were captured at Trial Site II (Fig. 3.13), V8 transmitters implanted into the body cavity as described in Chapter 2, and fish released at the capture site immediately after having recovered from anaesthesia (~ 15 minutes). Both fish displayed an identical pattern, taking shelter immediately after release (observed on snorkel) and were never resighted. The signal received from the ultrasonic transmitters turned weak once the specimens had taken shelter, and remained weak throughout the following 24-48 hours. No physical locations could be recorded. By the third day both signals were received strong and clear, and were recorded in the same location. The signals displayed unexpected movement patterns, continuously roaming the entire patch reef (approximately 400 m x 400 m). Visual confirmation of signal source indicated that both transmitters were inside a whitetip reef shark (*Triaenodon obesus*). The immediate, post-surgery release of *P. leopardus* had resulted in mortality due to predation within 28-72 hours after release.

Obviously, releasing a coral trout immediately after surgery meant releasing an injured fish, which became a prime target for reef fish predators. Therefore, it was decided to retain any future tracking specimens for a recovery period in aquaria until the implant incision was healed. In light of the wound status observations made during aquaria experiment B (section 3.2.2.), such a recovery period would be in the order of

eight days to three weeks. This procedure proved to be successful during all subsequent field trips.

## 3.5. Recommendations for use of ultrasonic telemetry with coral reef fishes

The observations and experimental results obtained from the preliminary methodological evaluation presented in this chapter led to the adoption of the following general ultrasonic telemetry methods and procedures, which are discussed in detail in Chapter 2.

The most suitable ultrasonic transmitter placement method for long-term application in *P. leopardus* was surgical implantation into the body cavity. Attaching a transmitter externally led to severe aggravation of the attachment wounds due to repeated dislodgment attempts or snagging of the transmitters. Force feeding transmitters was discontinued due to the short gastric retention times observed. MS-222 (Tricaine methanesulfonate) was the anaesthetic chosen due to the ease of induction and maintenance of deep anaesthesia, with the potential additional benefit of improved recovery from physical trauma due to elevated levels of the corticosteroid hormone. The post-surgery aquarium recovery period (up to three weeks) avoided losses due to injury-induced predation, and permitted examination of each specimen prior to release for proper incision closure and healing.

Ultrasonic tracking using visual triangulation should be conducted by taking bearings at approximately right angles  $(90^{\circ})$  to each other, with approximate distances of 50-75 m between tracking vessel and ultrasonic transmitter. Bearings taken at angles less than 90°, or taken at sharp angles to the prevailing wind, should be avoided. These considerations will result in minimal directional bias of bearings, while ensuring maximum accuracy and precision of estimates. If uncertainty about signal or directionality of signal exists, it is suggested to utilise a "drive-over" technique to verify exact location of tracking specimen. Observer training prior to tracking, and regular reevaluation of bearing accuracy and precision during tracking sessions is recommended.

**Table 3.1:** Results of the analysis of covariance (ANCOVA) of three different<br/>anaesthetic agents on the retention time of force-fed ultrasonic transmitters<br/>in *P. leopardus*. Fork length of the experimental fish was included as<br/>covariate. Indicated are: degrees of freedom (df), mean squares, *F*-values<br/>and probability values; n = 21.

Source	df	Mean Square	F	р
Anaesthetic	2	8731.63	4.7619	0.0228
Covariate (FL)	1	6473.98	3.5307	0.0775
Residual	17	1833.63		

Table 3.2: Results of the analysis of covariance (ANCOVA) of change in weight of the experimental *P. leopardus* due to anaesthetic agent (2 levels) or transmitter placement method (5 levels) used. Occurrence of gas-bubble-trauma was incorporated as covariate. Indicated are: degrees of freedom (df), mean squares, *F*-values and probability values; n = 20.

Source	df	Mean Square	F	р
Anaesthetic	1	66,125.00	4.4495	0.0641
Placement Treatment	4	78,892.30	5.3086	0.0178
Anaesth. x Placement	4	5,646.48	0.3799	0.8176
Covariate (Trauma)	1	5,000.00	0.3364	0.5761
Residual	9	14,861.11		

Table 3.3: Multiple comparison of means test (SNK) comparing the change in weight of *P. leopardus* during experiment B for the five different transmitter placement treatment levels examined. <u>Treatments</u>: C: handling control; EC: external attachment control; ET: external attachment treatment; IC: internal placement control; IT: internal placement treatment.

Treatment	С	EC	ET	IC	IT
С	-		•		
EC	0.57628	-			
ET	0.01493	0.02363	-		-
IC	0.35794	0.40706	0.05309		_
IT	0.29893	0.42750	0.04563	0.67394	-

Table 3.4:Observational records for aquarium experiment B. Treatments:C:handling control;EC: external attachment control;ET: externalattachment treatment;IC: internal placement control;IT: internalplacement treatment.Anaesthetic:MS: MS-222;P: Phenoxyethanol.

Fish	Treatment	Anaesthetic	Response	Day of	Gas-	Wound status
			during	first	bubble-	
			anaesthesia	feeding	trauma	
1	С	MS	deep	2	YES	-
. 2	С	MS	deep	2	NO	-
3	С	P	twitching	2	NO	-
4	С	P	deep	2	NO	-
5	EC	MS	deep	-	YES	partially healed
6	EC	MS	deep	2	NO	healed
7	EC	P	deep	-	YES	partially healed
8	EC	Р	twitching	2	YES	healed
9	ET	MS	deep	10	YES	aggravated
10	ET	MS	deep	-	YES	aggravated
11	ET	Р	deep	10	NO	aggravated
12	ET	P	twitching	7	NO	aggravated
13	IC	MS	deep	2	NO	healed
14	IC	MS	deep	2	NO	healed
15	IC	Р	deep	7	YES	healed
16	IC	Р	deep	7	NO	healed
17	T	MS	deep	2	NO	healed
18	T	MS	deep	2	NO	healed
19	T	Р	deep	2	NO	healed
20	T	P .	twitching	-	YES	healed

Table 3.5:Results of Shapiro-Wilk test for normality of frequency<br/>distributions of bearing errors ( $\epsilon$ ) for each of the three angular<br/>transects (0°, 45°, and 90°). Presented are Shapiro-Wilk W<br/>statistic, sample size (n) and probability values. Data from both<br/>observers were pooled.

Angular transect	W	n	р
0°	0.9580	84	0.0299
45°	0.9423	84	0.0017
90°	0.9847	84	0.8008

Table 3.6:Results of paired t-tests comparing mean precision between<br/>observers for each angular transect. Indicated are t value, degrees<br/>of freedom (df) and probability value.

Angular transect	t	df	р
0°	1.2599	6	0.2545
45°	1.5819	6	0.1648
90°	0.6859	6	0.5184



Plate 3.1: Plectropomus leopardus carrying a dummy ultrasonic telemetry transmitter attached externally to dorsal musculature during the transmitter placement trials (sensu Holland et al. 1990a, 1996). Dummy units were of same dimensions and weight as fully functional Vemco V8 transmitters.



Figure 3.1: Correlation of gastric retention time of force fed ultrasonic transmitters versus fork length of *P. leopardus*, as determined in experiment A. N = 21, r = 0.62. The three different anaesthetic agents are indicated.



Figure 3.2: Mean gastric retention times (+/-SE) of force fed ultrasonic transmitters in *P. leopardus* anaesthetised with three different anaesthetic agents. Mean retention time for MS-222 was significantly lower than for the other two agents. N = 21.



Figure 3.3: Schematic representation of experimental design for experiment B. <u>Anaesthetics</u>: MS-222: tricaine methanesulfonate, Phenoxy: phenoxyethanol. <u>Placement Treatments</u>: C: handling control; EC: external attachment control; ET: external attachment treatment; IC: internal placement control; IT: internal placement treatment.



Figure 3.4: Change in mean weight (before - after) of *P. leopardus* as determined in experiment B. Negative weight values indicate a loss in weight. Presented are means (g +/- SE). <u>Placement treatments</u>: C: handling control; EC: external attachment control; ET: external attachment treatment; IC: internal placement control; IT: internal placement treatment. n = 20.



Figure 3.5: Mean weights of *P. leopardus* before and after experiment B, separated by the two anaesthetics used. Error bars were not presented for clarity. n = 20.



- Figure 3.6: Schematic representation of the experimental setup utilised for evaluation of bearing accuracy, bias and precision using ultrasonic telemetry. The location of the tethered transmitter is indicated, and the three transects of 200m length each were oriented in relation to the prevailing wind direction during the experiment:
  - 0°: Transect directly down wind from transmitter

45°: Transect at 45 degree to the wind direction

90°: Transect at right angle to the wind



Figure 3.7: Frequency distribution of bearing errors ( $\varepsilon$  = true bearing - observed bearing) during the ultrasonic telemetry evaluation trial. Data pooled for observers and the three angular transects. N = 252.



Figure 3.8: Frequency distributions of bearing errors ( $\varepsilon$  = true bearing - observed bearing) during the ultrasonic telemetry evaluation trials, separated into the three angular transects in relation to the prevailing wind direction. Data pooled for observers. A: 0° transect. B: 45° transect. C: 90° transect. N = 84 for each transect.



Figure 3.9: Mean bearing errors (\*/. SE), indicating potential bias, recorded during the ultrasonic telemetry evaluation trials, separated by the three angular transects in relation to the prevailing wind direction. Data pooled for observers. Mean values are indicated. N = 252.



## Angular transect

Figure 3.10: Mean bearing errors (\*/ SE, n = 42) for each observer on each angular transect, illustrating the difference in observed bias between the two observers for the transect facing directly into the prevailing wind (ie 0°). Mean values are indicated.



Figure 3.11: Mean precision (\*/. SE, n = 7) of observed bearings for each observer on each angular transect, recorded during the ultrasonic telemetry evaluation trials.



Figure 3.12: Maximum error polygon parameters for each identical distance pair for each of the three possible angular transect combinations. Error polygons were calculated using the largest and smallest angular bearings recorded from equi-distant positions for each of the three possible angle combinations during the ultrasonic telemetry evaluation trials. Data pooled for observers. A: Maximum error polygon area (m<sup>2</sup>). B: Maximum diameter of error polygon (m).



Figure 3.13: Location map of the backreef area of Lizard Island used for the ultrasonic tracking field trial of *P. leopardus*. The enlargement (lower map) indicates the two trial sites utilised.
Trial Site I: Location of external attachment trial (water depth 4-5 m). Trial Site II: Location of internal placement trial (water depth 6-10 m).

## Chapter 4:

## HOME RANGES AND ACTIVITY PATTERNS OF

## PLECTROPOMUS LEOPARDUS

## 4.1. Introduction

A home range is defined in ecology as an area traversed by an individual within it's normal activities (Burt 1943 in White & Garrott 1990). Therefore, home ranges can be considered to be a function of time as well as space (Bekoff & Mech 1984, White & Garrott 1990). A more functional, operational definition of home ranges implies that an individual exhibiting site fidelity is judged to occupy a home range (Spencer *et al.* 1990). Reviews on techniques of numeric estimation of home ranges are provided by Macdonald *et al.* (1980), Worton (1987) and White & Garrott (1990).

The temporal usage pattern of space by an individual can be considered one of the more basic demographic parameters influencing ecological patterns of populations and species (Cameron & Spencer 1985, Gregory *et al.* 1987, Andrew & Mapstone 1987). Studies investigating home ranges have been conducted mainly in the terrestrial environment. Examples include studies of birds (Draulan & Vessem 1985, Badyaev *et al.* 1996), reptiles (Hailey & Coulson 1996), mammals (Bertram 1980, Lindstedt *et al.* 1986, Krebs *et al.* 1995), and primates (Harvey & Clutton-Brock 1981).

Despite the acknowledged importance of spatial and activity patterns in population and community ecology (e.g. Cameron & Spencer 1985), such information is rare for tropical marine fishes. Knowledge of these usage patterns is considered to be of great importance in the determination of size and correct placement of marine protected areas (Bohnsack 1990). Until recently, most studies related to home range and activity patterns in fishes have been undertaken in lakes and rivers (e.g. Mesing & Wicker 1986, Cook & Bergersen 1988, Keeley & Grant 1995, Minns 1995). Investigations addressing the question of space use that have been undertaken in the tropical marine environment, have largely concentrated on small, easily observed reef fishes such as pomacentrids and labrids (reviewed in Sale 1991) and acanthurids (e.g. Robertson & Gaines 1986). More recently, investigations of home ranges included studies of larger species, for example Mullidae (Holland *et al.* 1993a), Haemulidae (Tulevech & Recksiek 1994), Carangidae (Holland *et al.* 1996), and sharks (Nelson 1990, Holland *et al.* 1993b, Morrissey & Gruber 1993).

Members of the family Serranidae are considered to be among the most abundant predatory fish in many warm water regions (e.g.. Randall 1963, Nagelkerken 1979), and in several of these areas they form a major component of fisheries catches (Craik 1981, Bohnsack 1990, Gwynne 1990, Trainor 1991, Sadovy 1994, Williams & Russ 1994). Despite their economic significance, relatively little is known about the habitat and space usage patterns of these fishes (Moe 1969, Hobson 1974, Munro 1974, Thompson & Munro 1978). While some behavioural work has been done on serranids, most studies have concentrated on the smaller epinephelids (e.g. Shpigel & Fishelson 1989a&b, 1991a&b, Mackie 1993) and *Anthias* (Shapiro 1986).

Basic home range estimates for larger serranids are rare, and are often based on limited observations (Bardach, 1958, Springer & McErlean 1962, Carter 1988). Some attempts at home range estimation using ultrasonic telemetry have been made for the Nassau grouper, *Epinephelus striatus* (Carter *et al.* 1990). Furthermore, Colin (1995) indicated that adult Nassau groupers in the Bahamas had overlapping home ranges, with adult males and females sharing space. However, actual sizes of home ranges, or the time period of the estimates was not presented.

The coral trout *Plectropomus leopardus* forms the major component of the commercial and recreational line fishery on the Great Barrier Reef in Australia (Williams & Russ 1994). Despite the importance of this species, investigations into space use patterns have received very limited attention. To date, the two principle studies attempting to investigate home ranges in coral trout were based on visual observations on SCUBA of marked (Samoilys 1987) or even unmarked individuals (Goeden 1978). Some methodological concerns arise from these studies. Firstly, the close physical presence of an observer during these investigations might have made diver disturbance of *P. leopardus* a major concern. Furthermore, the time periods of actual observations were very small (7-120 minutes, Goeden 1978), or estimations were based on ratios of resighting and non-resighting of tagged fish within a limited study area (Samoilys 1987). Movements of coral trout within a 4 km section of reef at Heron Island (Great Barrier Reef) were reported by Beinssen (1989a). This study found that

29% of resighted coral trout had moved out of the initial 500 m long reef slope release site within three weeks. Davies (1995), as part of a mark-release-recapture study using fish traps, obtained 17 returns for P. leopardus out of 65 tagged, with the largest recorded movements being 415 m. Davies also documented overlap in movements of individuals, and concluded that P. leopardus ranges over distances of 200-300 m. In a related study, Davies (1995), using commercial fishers, tagged 4,627 P. leopardus on a cluster of five neighbouring reefs in the central section of the Great Barrier Reef. During five sampling trips spread over a two year period, the majority (74%, n = 143recaptures) were recovered within their 2.0 - 2.5 km long reef section of release. The greatest distance travelled by a tagged trout recaptured on hook and line was 4 km. In a currently ongoing trapping study, Hilomen tagged and released 22 P. leopardus in the Lizard Island lagoon between 1994 and 1996 (pers. com.). Of the 16 recaptures obtained, 12 had moved less than 100 m from the initial capture site (time at large: mean = 75 days  $\pm$  23.1 (SE), range: 1-218 days), three had moved less than 200 m (mean = 77 days  $\pm$  73.67 (SE), range: 3-225 days), while only one animal had moved 1,500 m during 367 days. In all these studies, although occasional larger scale movements were observed (Samoilys 1987: 7 km, Davies 1995: 4 km, Hilomen 1996: 1.5 km), the vast majority of movements seemed to be restricted to less than 200-400 meters.

Technological developments since the early studies by Goeden (1978) and Samoilys (1987), have resulted in the commercial availability of reliable ultrasonic telemetry systems. Maintaining a non-intrusive (i.e. non-disturbing) observer distance is possible with smaller, more stationary or slow swimming species, such as pomacentrids and labrids, but is clearly less feasible with the larger and more mobile commercially exploited reef fishes. Telemetry systems make a remote tracking approach to the study of basic home ranges and activity patterns possible. Such an approach overcomes the inherent shortcomings of visual observations (observer disturbance and SCUBA limitations), and provides a more reliable and accurate estimate of home ranges. Few attempts have been made to use ultrasonic telemetry on coral reef fish (but see Holland *et al.* 1993a, 1996), with most studies concentrating on sharks (e.g. Nelson 1990, Holland *et al.* 1992, 1993b, Morrissey & Gruber 1993). The aims of the present study were to utilise ultrasonic telemetry as a nonintrusive, remote monitoring technique to:

- provide the first unequivocal documentation of the size of home ranges of *Plectropomus leopardus*,
- investigate the basic activity patterns of coral trout,
- · examine movements in relation to observed water currents,
- and address the temporal stability of home ranges of *P. leopardus* over a maximum period of one year.

## 4.2. Methods

### 4.2.1. Study site

Ultrasonic tracking of *P. leopardus* was conducted primarily on the western, northern and north-eastern sides of Lizard Island, Northern Great Barrier Reef (Lat.  $14^{0}$  40' S; Long.  $145^{0}$  28' E, as these areas are more sheltered from the prevailing south-east winds (Fig. 4.1). The capture and release locations of tracked specimens were distributed over a large area around Lizard Island, in order to:

- 1. utilise specimens from both patch and fringing reef habitats,
- avoid ultrasonic signal overlay from transmitters on the same frequency, making correct identification of individuals and correct determination of physical location more difficult (see Chapter 2), and
- 3. incorporate the spawning aggregation study described in Chapter 5.

## 4.2.2. Ultrasonic tracking method

A detailed description of capture and handling procedures, methods for placement of transmitters and the general tracking techniques are presented in Chapter 2. Specimens of *P. leopardus* used for ultrasonic tracking were captured on hook and line, and released at the capture sites after successful recovery from implantation of transmitters. Position monitoring of specimens commenced immediately after release,

but data collected during the first 24 hours were not included in any subsequent analyses. Continuous monitoring of all specimens was attempted throughout the study. Considerable effort was allocated to locating each fish at least three to four times per day for the duration of the tracking period. However, data collection was restricted on numerous occasions due to inclement weather or logistic failures (e.g. equipment breakdowns).

At the end of the expected battery life of the transmitter or at the termination of each tracking period, specimens were collected by speargun for recovery of transmitters and for sex-determination of specimens. Histological techniques used for gender determination followed those described by Ferreira (1995).

### 4.2.3. Home range estimates and use patterns

The minimum convex polygon (Jennrich & Turner 1969), representing a nonstatistical measure of dispersion over the total area used by an individual, was chosen as the measure of home range area (Winter & Ross 1982, Danielson & Swihart 1987). Home ranges were measured from a minimum area convex polygon drawn around all position records, excluding:

1. positions recorded during the first day after release (i.e. acclimation period),

2. positions recorded only once during the tracking period, and

3. movements clearly associated with spawning aggregations.

In addition to the area measure of the polygon, two linear dimensions were calculated: 1) The largest diagonal of the home range area (termed: maximum linear dimension), which is indicative of the length of each home range area, and 2) the minimum linear dimension, defined as the largest width of the polygon, measured perpendicular to the maximum linear dimension.

In order to evaluate what factors were likely to influence the home range estimates, measures of available reef area were made, and average densities of coral trout in the areas occupied by each tracking specimen were determined. For patch reef habitats, the reef parameter chosen was available reef area  $(m^2)$  to the 20 m depth contour or to the reef-sand interface. Given the contiguous nature of fringing reef habitats, the most appropriate measure of reef area was the average width of the fringing reef in the area of occupancy of an individual fish. This mean value was calculated from three width measurements per home range, one made at either end of the range plus one made in the centre of the range. Width of the fringing reef was measured from the Lowest Astronomical Tide Datum (0 meter Datum) to the 20 m depth contour or to the reef-sand interface, whichever came first. All estimates of reef parameters were digitised from calibrated aerial photos and aerial photo mosaic maps with overlayed depth contours (Sunmap, 1:7500, Queensland Government).

The density estimates of coral trout used as a variable in the home range parameter evaluation, were obtained from underwater visual census data collected in 1995 during a separate part of this project. The visual census data provided trout density estimates which form part of an estimate of movements and potential flux rates across Marine protected area boundaries (Chapter 6).

Visual examination of usage patterns of home ranges were undertaken using 50% and 75% utilisation distributions. These utilisation distributions were calculated using the adaptive kernel method (Cameron & Spencer 1985, Worton 1989). Adaptive kernel estimates were not used for statistical purposes. The 50% and 75% contours were taken as representing the core area of activity, i.e. the geographic locations within the home range of greatest use. For comparisons between different times of day, days were divided into three approximately even four hour periods: AM (nautical twilight - 1000 h), Mid-day (1000 h - 1400 h) and PM (1400 h - nautical twilight).

Information on tidal currents was obtained through personal observations during dives, and from field records of observed water movements made from the boat during tracking periods. Timing of tides was based on Queensland Tide Tables (Queensland Dept. of Transport 1993, 1994 & 1995).
Attempts were made to observe on SCUBA some of the more readily used positions recorded for tracked specimens. Wherever possible these positions were assigned to one of three habitat types: "shelter sites", "current pressure points/potential feeding sites" or "cleaning stations of Labroides spp.". "Shelter sites" were defined as clearly identifiable caves, overhangs or crevices being used by the tracked specimen during the observation period, while "pressure/feeding sites" related to observation of currents encountering reef structures, often associated with concentrations of small planktivorous fishes (primarily Pomacentridae and Caesionidae). "Cleaning station" was assigned only if actual cleaning behaviour by Labroides spp. was observed, and neither of the other two habitat types could be assigned.

In order to gauge if there was any shift in the home ranges of individuals through time, linearity ratios were calculated for each tracked specimen (Bell & Kramer 1979 in Danielson & Swihart 1987). This is the ratio of distance between an individuals first and last recorded position and the total distance moved during the complete tracking period of each individual. It thus represents a measure of directedness of movements, with values being small if movements are back and forth, and unity if movements are unidirectional. In order to evaluate the persistence of home ranges over longer time periods, several fish were tracked over two separate time periods.

#### 4.2.4. Data analyses

The spatial position data obtained through ultrasonic tracking were digitised from calibrated aerial photos using SIGMASCAN<sup>®</sup>. All home range parameters were calculated using SAS<sup>®</sup> executable program routines written by White & Garrott (1990), CALHOME<sup>®</sup> (Kie *et al.* 1994, U.S. Forest Service) on IBM compatible computers, and WILDTRACK<sup>®</sup> (Todd 1993, University of Oxford) on Apple MacIntosh.

Incremental area analysis was undertaken on the ultrasonic telemetry data to determine those tracked specimens which provided robust estimates of home range areas (Kenward 1990). The temporal order of fixes for each specimen was randomised before construction of the incremental area curves for each home range. Home range estimates were only included if the range estimates stabilised with increasing sample sizes, i.e.. if their incremental area curves reached an asymptote.

Statistical analyses used were t-tests, Analysis of Variance (ANOVA), Analysis of Covariance (ANCOVA), and linear and multiple regression techniques. All data were examined for violations of underlying statistical assumptions prior to analysis (Sokal & Rohlf 1981, Underwood 1981) and data log<sub>10</sub> transformed where applicable. Ratio data were analysed using natural log transformations (Underwood 1981). All analyses were conducted using STATISTICA<sup>®</sup>.

## 4.3. Results

A total of 39 individual *P. leopardus* (fork length: mean = 49.04 cm, range = 37.6 cm to 67.5 cm) were tracked successfully between 1993 and 1995, providing sufficient data for asymptotic home range stabilisation (Kenward 1990). The incremental area analysis indicated that robust home range estimates were achieved with between 48 and 140 fixes. Of the 39 specimens, eight were tracked during two subsequent field trips. This resulted in 47 separate tracking sessions, comprising a total of 2,024 fish-tracking days and 8,002 individual position fixes. Most tracking occurred on the sheltered, western side of the island. However, several fish were located on the more exposed north-eastern and eastern side of Lizard Island (Fig. 4.1).

# **4.3.1.** Basic home range parameters

The mean size of the minimum area polygon home ranges of *P. leopardus* was 13,651.9 m<sup>2</sup>  $\pm$  1464.4 (SE; range: 3,455.0 m<sup>2</sup> - 47,160.0 m<sup>2</sup>). Two different reef types are represented at Lizard Island: patch reef and contiguous fringing reef. Initial examination of home ranges revealed obvious differences in the general shape of home ranges for fish from the two reef types (e.g. patch reef: Fig. 4.2a, PL30; fringing reef: Fig. 4.2b, PL10). Taking into account differences in size of individual fish (fork length) and sample sizes per home range estimate (number of fixes per estimate), a significant

difference was detected in the mean home range area between the two dominant reef types (ANCOVA, F  $_{[1, 43]} = 9.37$ , p = 0.0038). Home range areas of *P. leopardus* were on average 44.36% larger on patch reefs (18,796.9 m<sup>2</sup>) than on fringing reefs (10,458.4 m<sup>2</sup>, Fig. 4.3a).

Comparison of the maximum linear, diagonal dimension of home ranges (i.e., maximum length) between the two reef types indicated that the length of home ranges did not differ between fringing and patch reef fish (ANCOVA, F [1, 43] = 0.66, p = 0.4188). On average, the maximum linear dimension of home ranges as calculated by minimum area polygons was 223.0 m  $\pm$  10.5 SE (range: 118.9 m - 376.9 m). However, as would be expected from Fig. 4.2, the minimum linear dimension (i.e. home range width) did differ between reef types (ANCOVA, F [1, 43] = 24.97, p = 0.00001). On average, home ranges of *P. leopardus* were 1.78 times wider on patch reefs than on fringing reefs (Fig. 4.3b).

Assessment of differences in home ranges between male and female specimens were restricted to 32 tracking periods, based on the 26 fish (13 male & 13 female) that could be recovered for gender determination by histology. Analyses of covariance, using fork length and tracking sample size as covariates, indicated that there were no significant differences in either area, maximum or minimum linear dimension of home ranges between male and female *P. leopardus* (F<sub>[1, 28]</sub> = 3.26, p = 0.0817; F<sub>[1, 28]</sub> = 1.78, p = 0.1939; F<sub>[1, 28]</sub> = 0.88, p = 0.3551, respectively). However, graphical examination of home range parameters indicated a tendency towards larger home ranges for male coral trout, particularly for the area measurement of home range (Fig. 4.4).

Evaluation of the relationships between home range parameters (home range area, maximum and minimum dimensions) and size of individual fish, local trout densities, tracking sample size and the measure of available reef dimension (patch reef area or fringing reef width) for both habitat types revealed some clear patterns for the patch reef habitat. For *P. leopardus* on patch reefs, home range area (adjusted  $r^2 =$ 0.8423, F<sub>[4, 13]</sub> = 23.0, p < 0.0001), maximum dimension (adjusted  $r^2 = 0.6666$ , F<sub>[4, 13]</sub> = 9.49, p < 0.0008), as well as minimum dimension (adjusted  $r^2 = 0.6299$ , F<sub>[4, 13]</sub> = 8.24, p < 0.0015) displayed strong relationships with the variables examined. Specifically, 73.72%, 58.60%, and 49.25% of variability in home range area, maximum, and minimum dimension were explained by total available reef area, respectively (Table Neither local trout density nor sample size contributed significantly to the 4.1). relationships. The size of fish (FL) did make a significant contribution to the relationship with minimum dimension, explaining 31.05% of variability (p= 0.0309, Table 4.1). Thus, the present data suggests strongly that, for patch reef environments, coral trout home ranges (measured as area, maximum, or minimum dimension) are strongly positively correlated with total available patch reef area. The minimum dimension (i.e. width) of home ranges of coral trout living on patch reefs is furthermore influenced by the size of the fish. Hence, the larger the patch reef on which coral trout live, the larger the observed area, length and width of home ranges. However, larger coral trout manage to establish wider home ranges on patch reefs than smaller fish.

For fringing reef habitats the situation was not as clear. The relationship between home range area and the independent variables reef dimension (fringing reef width), local trout density, fish size and home range sample size was significant (adjusted  $r^2 = 0.7150$ , F [4, 24] = 18.56, p < 0.0000), with only local trout density not contributing significantly to the relationship (p = 0.2153, Table 4.2). Reef width alone accounted for most of the observed variability in home range area (65.52%, Table 4.2). No detectable relationship existed between maximum linear dimension of home ranges and the variables examined (adjusted  $r^2 = 0.0700$ , F<sub>[4, 24]</sub> = 1.53, p = 0.2259). However, reef width, as well as local trout densities accounted for significant variation in minimum home range dimension (adjusted  $r^2 = 0.4595$ , F [4, 24] = 6.95, p < 0.0007). Reef width explained 37.57%, and local trout densities 18.99% of observed variability in home range width (Table 4.2). Thus, while the length of home ranges of coral trout inhabiting fringing reefs appeared not to be influenced by any of the factors examined, the observed area and width of home ranges were primarily, but not exclusively, influenced by available fringing reef width.

Thus it appears that the size of home ranges (area, maximum and minimum dimension) of *P. leopardus* living on patch reefs is influenced predominantly by the

available reef area, whereas the width of fringing reefs, while explaining a large proportion of variation in area and width of home ranges, does not account, to any large extent, for the variation in maximum dimension of fringing reef home ranges.

## **4.3.2.** Home range usage patterns

### 4.3.2.1. Day/night activity patterns

During the first tracking period in August-October 1993, six individuals were monitored for day/night activity patterns. Position records for 60 fish-nights were obtained, with 128 night-time position records out of a total of 689 records for August-October 1993. On average, *P. leopardus* utilised fewer positions at night than during the daytime (F  $_{[1, 10]} = 11.65$ , p = 0.006, Fig. 4.5). It was observed that the most commonly used night-time positions (e.g. PL1 Fig. 4.6a) were also some of the most regularly frequented locations during the daytime (Fig. 4.6b). Therefore, no specific positions, used exclusively at night were recorded. Visual examination of recorded positions on SCUBA revealed that seven of the 13 most commonly used night-time positions for all six fish had clearly identifiable crevices, overhangs or caves.

Position fidelity at night was very high, with no nocturnal change in positions occurring on 88.3% of all monitored nights. On only 11.7% of monitored nights did a fish change its position once during the night. The mean distance moved during nocturnal relocations was 58.3m (median = 42.4m, range: 39.3m - 114.6m). Based on these observations, it was concluded that nocturnal activity by *P. leopardus* was minimal. Therefore, all subsequent tracking periods were restricted to daylight hours only.

#### 4.3.2.2. General activity patterns

Combining all 47 separate tracking periods (n = 31 fish with single tracking period, plus n = 8 fish with two separate tracking periods), coral trout were observed to

utilise a mean of  $12.1 \pm 0.55$  (SE) positions per individual fish (range: 5-19 positions/fish). Accepting the definition of "most commonly used" positions as being those which contribute  $\geq 10\%$  of records per fish per tracking period each, the mean number of most commonly used positions recorded for *P. leopardus* was  $3.5 \pm 0.18$  (SE) per individual fish. This can be illustrated by the adaptive kernel utilisation distributions. Two typical representatives are illustrated here (PL25, Fig. 4.7a & PL31, Fig. 4.7b). In both cases two positions accounted for 50% of all observations made during the tracking period (red contour, Fig. 4.7), while 75% of all tracking records for each fish were obtained from 3-4 positions within their respective home ranges (green contour, Fig. 4.7). Thus, coral trout appear to be utilising preferentially a small number of actual physical locations (i.e. positions) within their home ranges, at which they were recorded for the majority of time.

Comparisons of the utilisation distributions with the polygon home range areas indicated in the graphs, also illustrate that the core areas of activity (i.e. most commonly recorded positions) were not necessarily located in the centers of the home range areas as was the case for specimen PL31 (e.g. Fig. 4.7b). More common was the observation that positions associated with the reef slopes were the preferred locations and usually represented positions associated with the outside edge of the polygon home range areas (e.g. Fig. 4.7a).

In order to evaluate potential differences in home range usage patterns throughout the day, the number of positions used during separate parts of the day were examined. Days were divided into three approximately even four hour periods: AM, Mid-day and PM. Analysis of variance detected no difference in the mean number of positions used during the three different time periods (F  $_{[2, 138]} = 1.88$ , p = 0.1566). On average, a fish used 9.1 ± 0.28 (SE) different positions during each time period (Fig. 4.8). Evaluation of the point percentage utilisation distributions indicated a relatively consistent pattern of use of positions throughout the day (e.g. PL40, Fig. 4.9).

#### 4.3.2.3. Effect of tide on use of home ranges

In 12 of 47 tracking sessions (n = 11 individuals, one individual tracked on two separate occasions), a distinct pattern of home range use could be distinguished in relation to observable current direction. Specimens showed a strong preference for utilising positions located in the upcurrent portions of their respective home range areas. This preference is illustrated through the graphical presentation of the 50% and 75% utilisation distribution contours of the adaptive kernel. Overall, the average distance between center points of the 50% utilisation distributions (i.e. core areas of use) favoured during each tidal stage was 106.8m  $\pm$  9.84 (SE, range: 66.6m - 176.9m).

The most obvious tidal pattern was shown by fish inhabiting North Point. Being the northernmost projection of Lizard Island (Fig. 4.1), this location is characterised by strong, directional tidal currents. Fish number PL1 (August - October 1993, Fig. 4.10a) displayed a very strong current related pattern of home range use. During incoming tides (rising tides), 75.5% of all position records were recorded from five positions located on the upcurrent side of its home range, with three positions accounting for 57.1% of records (Fig. 4.10b). An even stronger pattern was observed during outgoing (ebbing) tide, with one single position accounting for 72.5% of records (Fig. 4.10c).

A similar pattern was observed at North Point during the September - November 1994 and February - March 1995 tracking periods. Individual PL 7 was released and tracked for 79 days during the 1994 period (PL7a, Fig. 4.11a). This individual was left at large for a further 82 days, and tracked again in February 1995 for an additional 33 days (PL7b, Fig. 4.12a). During the 1994 tracking period, position number 3 alone accounted for 14.9% of all records during incoming tide, with only position number 1 (44.9%) being used more frequently (Fig. 4.11b). Similarly, during February - March 1995 the same individual spent 47.8% of all incoming tide records at four major upcurrent positions (including position number 3, Fig. 4.12b). Again, position number 1 accounted for the majority of records (30.4%). During ebbing tide the pattern was even more consistent, with three upcurrent positions (positions 1, 5 & 6) accounting for

79.4% and 75.0% of records for the 1994 and 1995 tracking periods, respectively (Figs. 4.11c & 4.12c). The preponderance of position 1 during both tidal stages can be explained by the fact that this position represented a major shelter site, with large caves and crevices. It was used extensively by numerous large reef fishes (pers. obs.). Removal of data from position 1 resulted in an even more obvious pattern of preference for upcurrent positions in relation to the tidal status (Figs. 4.11d, e & 4.12d, e).

A similar pattern of orientation with regards to the prevailing current was recorded during August - October 1993 at Osprey Island reef, on the sheltered, western side of Lizard Island (Fig. 4.1). Specimen PL2 displayed a clear pattern of preference for positions on the upcurrent side of the local reef, which was particularly evident during the rising tides (Fig. 4.13a). A shift in core area of use could be discerned during outgoing tides (Fig. 4.13b), during which current flow was observed to be less evident (per. obs.).

A strong tidal pattern of home range use was observed also during the August -December 1995 tracking period. Specimen PL39 inhabited an isolated patch reef near the northern end of Lizard Island (Fig. 4.14a). Again, a very distinct pattern of position use was observed in relation to tidal status, with positions 1, 3 & 8 accounting for 65.4% of records during incoming tides (Fig. 4.14b). In contrast, positions 2, 4 & 6 represented 78.2% of all records during ebbing tides (Fig. 4.14c). The above positions could be clearly identified as being on that side of the patch reef which represented the upcurrent, "pressure" side during the respective tidal stage.

Tidal variation in the use of its home range was also displayed by individual PL9, tracked during September - November 1994 near Granite Point at the northern end of Lizard Island (Fig. 4.15a). with respective upcurrent positions used preferentially during each tidal stage (Fig. 4.15b,c). A more subtle shift in home range use in relation to tidal current was observed for three other specimens tracked at this location. Individuals PL3, PL4 (both 1993) and PL11 (1994) displayed a preference for positions in the upcurrent portion of their respective home ranges during each tidal stage (Figs. 4.16a,b; 4.17a,b & 4.18a,b). One observation common to three of the four fish at this

location (PL4, PL9, PL11) was of particular interest. Each fish had one position which was heavily utilised during both tidal stages. These positions accounted for, on average,  $33.6\% \pm 4.04$  (SE) of records. These positions (PL9 pos. 0, PL4 pos. 4, PL11 pos. 4; Figs. 4.15, 4.17, 4.18) actually represented the same physical location on the fringing reef. Examination of this location on SCUBA revealed a strong near-vertical ridge projecting seaward from the surrounding reef slope. This phenomenon may result in the creation of a localised "pressure" point, with either side of the ridge being a suitable upcurrent location during either tidal stage.

The common use of one position during both tidal stages was noted previously (PL7 pos. 1, Fig. 4.11 & 4.12), and also occurred in three other fish displaying tidal orientation. Individual PL5 (1993), while showing a shift in core area (50% utilisation distribution) in relation to tidal water flow, did use position 3 during both tidal stages (Fig. 4.19a,b). Similarly, *P. leopardus* inhabiting the patch reef areas on the western side of the island exhibited similar patterns, with PL32 displaying a strong preference for one position (pos. 0, Fig. 4.20a,b).

Another patch reef fish (PL27) displayed strong orientation with regards to outgoing tides (Fig. 4.21b), with a less clear pattern during incoming tide periods (Fig. 4.21a). Observable currents around this patch reef were dominated by ebbing flow, which coincided with the prevalent wind direction (SE) and the predominant outflow patterns of the Lizard Island reef lagoon (Fig. 4.1).

#### 4.3.2.4. Effect of habitat type on home range

A total of 568 different positions were recorded during this study. Based on visual examination by SCUBA of some of the most regularly used positions, 209 (36.8%) could be assigned to one of the three habitat types "shelter site", "pressure/feeding site" or "cleaner station". Of the three types, 129 positions were described as potential "shelter site", 73 positions as "pressure/feeding site" and only 7 could be distinctly allocated to the "cleaning station" type. Overall, the percentage of records per individual fish which could be attributed to the known positions was 35.4%

 $\pm$  3.26 (SE) for "shelter sites", 24.6%  $\pm$  3.25 (SE) for "pressure/feeding sites", and 9.2%  $\pm$  2.44 (SE) for "cleaning stations". There was no difference in the mean percentage use of recorded positions per individual fish for either of the three allocated habitat types between the three different day-time periods examined (AM, Mid-day and PM; Table 4.3).

### 4.3.2.5. Distances moved

The ultrasonic tracking data indicated that the average minimum recorded mean distance moved by individual *P. leopardus* per day within their home ranges was 192.2 m  $\pm$  5.09 (SE). These distance estimates obtained represent the minimum distance moved by individuals per day, and was based on position records obtained repeatedly during the day. The largest recorded distance moved per day by an individual fish within its home range was 1121.8 m. There was no difference in the mean distance moved per day between fish from patch or fringing reefs (t [1179] = 1.44, p = 0.149), despite the observed difference in home range area noted above.

In order to relate the distances moved per day to the size and shape of home ranges, a movement pattern ratio was calculated based on mean daily distances moved divided by the home range parameter (maximum, minimum linear dimensions, and  $\sqrt{home}$  range area). In relation to both home range maximum linear dimension and home range area, no difference was detected in the movement pattern ratios between fringing and patch reef fish (t [40] = 1.749, p = 0.087; t [40] = 0.647, p = 0.521), with mean ratios ( $\pm$  SE) of 0.90  $\pm$  0.06 and 1.71  $\pm$  0.26, respectively. Thus, on a daily basis, coral trout appear to move linear distances nearly equivalent to the maximum linear dimension (i.e. 0.90  $\pm$  0.06) of their home range areas. However, in relation to the minimum linear dimension of the home ranges (i.e. width), a significant difference was found in the movement pattern ratios between reef types (t [40] = 2.606, p = 0.013). Fish on fringing reefs moved, on average, distances equivalent to 2.61 times the width of their home ranges, while patch reef fish moved the equivalent of 1.67 times the width of their home ranges (Fig. 4.22a).

Evaluation of the effect of sample size (i.e. number of position fixes per day) on the calculated daily distances moved within their home ranges, indicated the potential for an asymptotic relationship (R = 0.7325), with a potential asymptotic daily distance moved of 560.6 m (Fig. 4.22b). Clearly this does not represent the maximum mean daily distance moved, which was recorded as 835.5 m ± 175.5 (SE) (Fig. 4.22b). Note that distance estimates based on >15 fixes per day were based on sample sizes of <= 2. However, based on this relationship, one could assume that, on average, an estimate of 50% and 75% of daily movement distances could be obtained with 8 and 14 position fixes per day (Fig. 4.22b).

#### 4.3.2.6. Persistence of home ranges through time

In order to evaluate the spatial persistence of home ranges throughout the time period of each tracking session, the linearity ratio for each individual was calculated. Overall, the linearity ratio was very low, indicating that most of the regular movements recorded were back and forth rather than uni-directional. The overall mean linearity ratio was  $0.036 \pm 0.011$  (SE) with a range of 0.00 - 0.480 (n = 47). There was no difference between fish from fringing and patch reefs (t [45] = 1.725, p = 0.091). Clearly, there was no shift in home ranges by individual fish during each tracking session.

Comparisons of the calculated home ranges for each of the eight fish tracked on two separate occasions indicated almost complete overlap of ranges between tracking sessions (Fig. 4.23). Thus home ranges displayed temporal stability over the time periods examined. This observation is also supported by the low linearity ratios of combined observations from both tracking periods for each fish, with a mean ( $\pm$  SE) of 0.020  $\pm$  0.015 and range 0.00 - 0.118. Linearity values did not differ between multiple tracked and single tracked fish (t [37] = 0.523, p = 0.904).

Thus, home ranges were stable within and between each tracking session. Hence, the home range concept can be considered a correct representation of the use of space by individual coral trout, at least over the time frames examined in this study.

## 4.3.3. Summary of results

Using ultrasonic telemetry, the following basic parameters of space use and activity patterns of *P. leopardus* were determined:

- Average minimum area polygon home ranges of *P. leopardus* differed between fish from fringing and patch reefs, being 10,458.4 m<sup>2</sup> ± 962.3 (SE) and 18,796.9 m<sup>2</sup> ± 3,188.8 (SE), respectively.
- The observed differences in home range areas between reef types was caused by differences in width of home ranges, with fringing reef ranges being narrower than patch reef ranges. Length of home ranges did not differ between reef types.
- Home ranges for female and male *P. leopardus* did not differ in either area or linear dimensions.
- Available reef area was the major factor explaining the variation in home ranges for fish living on patch reefs. Size of fish was of secondary importance in relation to width of home ranges only.
- While length of home ranges of coral trout living on fringing reefs was not influenced by either of the variables examined, the observed home range area and width were primarily, but not exclusively, influenced by available fringing reef width.
- *Plectropomus leopardus* was confirmed to be day-active, with very limited movements during night-time periods. Position fidelity was very high at night.
- Predominantly, coral trout utilised only a small number of physical locations (i.e. 3-4 positions) within their home ranges.
- No differences were recorded in position use in relation to time of day, indicating a relatively consistent pattern of position use throughout the day.
- A distinct pattern of home range use could be distinguished in relation to the prevalent current direction. *Plectropomus leopardus* showed a strong preference for utilising positions located in the upcurrent portions of their respective home range areas.

- Mean daily distance moved by coral trout within their home range was 192.2 m ± 5.09 (SE), with the maximum recorded daily distance moved being 1121.8 m. No differences existed in movement distances between reef types.
- Based on the relationship between sampling effort and daily distances moved, it was determined that, on average, an estimate of 50% and 75% of total daily movement distances can be obtained for *P. leopardus* with approximately 8 and 14 position fixes per day, respectively.
- Home ranges were stable within and between each tracking session. The home range concept can be considered a correct representation of the use of space by individual coral trout, at least over the time frames examined in this study.

# 4.4. Discussion

The data presented in this study represent the first comprehensive documentation of home ranges and basic activity patterns of *Plectropomus leopardus*. These estimates were obtained by means of ultrasonic telemetry, resulting in observations free from disturbance of the specimens by the presence of observers.

### 4.4.1. Home ranges

The measure of home range area chosen, i.e. minimum area convex polygon, represents a non-statistical measure of the total area used by an individual (Danielson & Swihart 1987). As such, it has the advantage of not being very sensitive to the assumption of independence of successive telemetry observations (autocorrelation) (Cameron & Spencer 1985), as well as becoming increasingly accurate with increasing sample size, even when autocorrelation increases (Swihart & Slade 1985). White & Garrott (1990) pointed out that, in general, two consecutive position fixes can be considered statistically independent if sufficient time has elapsed for the animal to move from one end of the home range to the other. Given the relatively long sampling interval between fixes in the present study in relation to home range areas, and the size and swimming ability of the species concerned, any autocorrelation was considered

minimal. Thus, the polygon home range areas calculated in the present study can be considered, conservatively, as the *minimum* area of the home range of *P. leopardus*. Clearly, polygon range outlines provide the most intuitive area outline of spatial activity, i.e. the outer boundary of the area used by an individual.

In contrast to the area outline calculated by the polygon method, the utilisation distribution based on the adaptive kernel method (Worton 1989) attempts to visually illustrate the usage patterns of observed positions within the home range (Anderson 1982, Krebs *et al.* 1995). The 50% and 75% contour utilisation distributions (Kie *et al.* 1994) were used for visual evaluation of patterns of use of home ranges only, and no statistical analyses were performed using kernel estimates.

Most detailed investigations of space use patterns of reef fish have generally concentrated on smaller, more site-attached species (e.g. Fitch & Shapiro 1990, Williams 1991 and references therein). Detailed, quantitative assessment of home ranges of larger and more mobile species has progressed little since the early, pioneering studies (e.g. Bardach 1958, Randall 1962, Springer & McErlean 1962), with the possible exception of shark studies (Nelson 1990, Holland *et al.* 1992, 1993b, Morrissey & Gruber 1993).

The data obtained in the present study demonstrates clearly, for the first time, the actual sizes of home ranges of *P. leopardus* (range:  $3,455 \text{ m}^2$  to  $47,160 \text{ m}^2$ ), as well as indicating that different reef types (i.e. patch or fringing reef) have distinct influences on the size and shape of home ranges of coral trout. Limited home range information is available for only a few of the larger serranids which are of fisheries significance. Based on visual observations of 22 tagged individuals within a 100 x 100 m grid over a 152 day period, Shapiro *et al.* (1994) estimated the home ranges of *Epinephelus guttatus* on inshore reefs in Puerto Rico to range from 112 to  $5,636 \text{ m}^2$ . Their estimates were based on fish measuring 12.4 - 29.8 cm SL, with individual sample sizes of only 13-57 position records per fish. Given the sensitivity of the polygon home range method in relation to small sample size (White & Garrott 1990), one has to consider these area estimates with caution, as they might represent underestimates of the true home range.

areas. Carter (1988) and Carter *et al.* (1994) reported that three ultrasonically tagged Nassau groupers (*Epinephelus striatus*) randomly moved over a coral encrusted area approximately 80 x 160 meters, and appeared most active around sunrise and sunset. Adult Nassau groupers studied by Colin (1995) were reported to have overlapping home ranges of unspecified size. Goeden (1978) reported the largest estimates of area of use for *Plectropomus leopardus* as approximately 1,200m<sup>2</sup>, based on short term visual observations (7-120 minutes). Samoilys (1987), based on a visual resighting study within a limited area, suggested that the range of movements of coral trout were limited over approximate distances of 2 km along the reef slope, and proposed that the likely home ranges of coral trout might be larger than 4,000m<sup>2</sup>.

Data on space use of larger reef fishes could only be obtained through nonintrusive observation methods, gathering spatial information over longer time periods. The data obtained here through ultrasonic telemetry suggests also, that the previous investigations into serranid home ranges most likely represent underestimates.

No difference in home ranges between male and female *P. leopardus* was recorded. Different sized home ranges for males and females have been described for smaller, often territorial serranids, with females having smaller home ranges than males, e.g. *Cephalopholis miniata* (Shpigel & Fishelson 1991b) and *C. cyanostigma* (Mackie 1993). However, no such relationship has been determined for larger serranids. The home range investigation reported by Shapiro *et al.* (1994) studied only female fish, while Carter *et al.* (1994) did not report whether any differences existed between the two females and one male specimen tracked.

Of particular interest is the observation that body size of coral trout did not contribute significantly to the variation in home ranges, at least within the size range investigated in this study (37.6 - 67.5 cm fork length). A similar result was obtained for smaller *Epinephelus guttatus* (Shapiro *et al.* 1994), while Samoilys (1987) recorded larger individuals of *Plectropomus leopardus* to have larger areas of short-term movements, based on 15 minute visual observation periods. The relationship between home range and body size has been examined in relatively few studies of fish, with most

work done in freshwater systems (e.g. Mesing & Wicker 1986, Grant & Kramer 1990, Minns 1995) or on sharks (Morrissey & Gruber 1993). Grant & Kramer (1990) demonstrated that body size explained 87% of variation in home range of salmonids, and home range length was positively correlated with age, length and weight of freshwater Largemouth Bass (Mesing & Wicker 1986). Minns (1995), using published data sets, proposed that there was an allometric relationship between home range size and body size for temperate freshwater fish. The extensively studied small coral reef labrid Thalassoma bifasciatum showed a clear, positive correlation between home range size and body size (Fitch & Shapiro 1990). Such positive correlations were demonstrated also for juvenile lemon sharks (Morrissey & Gruber 1993). Thus, while correlations between body size and home range exist for many fishes, current data does not support this notion for large serranids. Furthermore, given the broad size range of sex change in P. leopardus (Ferreira 1995), it is not surprising that a lack of correlation between home range and body size is reflected in the absence of a sexual pattern in home range size, as noted above.

#### 4.4.2. Patterns of use of home ranges

The most distinct pattern of use of space by *P. leopardus* was observed in relation to tidal currents. Clear preferences for positions in the upcurrent portions of their home ranges were observed in those specimens for which reliable current information was available. A distinct shift in center of activity was recorded with change in current direction on the turn of tides.

*P. leopardus* has been observed to orientate itself into local currents, and was recorded in larger numbers near reef channels which had stronger currents (Kingsford 1992). Furthermore, feeding activity is said to be highest during flood and high tide (Goeden 1978). Orientation in the watercolumn in relation to tidal waterflow has been examined in some marine studies, but has generally concentrated on selective tidal stream transport in estuarine and intertidal areas (Greer Walker *et al.* 1978, Arnold & Cook 1984, Quinn *et al.* 1989, Levy & Cadenhead 1995; Moore *et al.* 1995). Bray (1981), in a study on a temperate kelp forest damselfish, documented this planktivore

undergoing daily foraging movements in relation to water currents. Adult fish invariably aggregated at the upcurrent end of the patch reef studied, and responded quickly to changes in current direction. Large *Paralabrax clathratus*, a piscivorous predator, also tended to aggregate towards the upcurrent end of the study site (Bray 1981). On coral reefs, movements by fish in relation to prevailing water currents have generally concentrated on planktivorous species (Hobson 1974, Thresher 1983). Fitch & Shapiro (1990), summarising previous studies, found that in areas with distinct current flow, *Thalassoma bifasciatum* was located in groups upcurrent and spent the day feeding on plankton.

The home ranges recorded for Plectropomus leopardus were observed to be stable within as well as between consecutive sampling trips. This suggests that, at least for the time periods examined in this study (maximum 202 days between sampling trips), coral trout maintained stable areas of activity, and did not show any dispersion or turnover. Over the three year time span of this study, contact was lost with 11 coral trout equipped with transmitters. Of these 11 "losses", three specimens were subsequently returned by fishers (see Chapter 5), three transmitters were recovered from the animals home range area after being physically rejected by the fish, one fish was recovered from its established home range with transmitter missing, and two specimens were recovered carrying inactive transmitters. Thus, only two "lost" specimens remained unaccounted for, whereas the clear majority of "losses" could be accounted for through physical rejections of units (n = 4) or battery and/or electronic failure (n = 2). It has been suggested that other serranids may shift their home ranges over time (Bardach 1958, Shapiro et al. 1994). The very low linearity ratios recorded for P. leopardus, both within and between trips, also supports the notion that most of the recorded movements were back and forth within a limited area, rather than directional. Linearity values calculated for juvenile lemon sharks inhabiting a shallow lagoon (mean linearity = 0.044) also indicated high rates of revisitation of a preferred area (Morrissey & Gruber (1993).

All *P. leopardus* tracked in the present study showed regular preferences for a small number of positions within their home ranges, which they frequented repeatedly

throughout the day. While P. leopardus is considered to be relatively site-attached (e.g. Cappo & Brown 1996), detailed information regarding use of locations within home ranges was lacking. Some investigations have attempted to address basic movements of coral trout, but were either limited to visual observations over short time periods (with associated diver disturbance of the specimens, Goeden 1978, Samoilys 1987), or relied on chance recaptures of tagged individuals (Beinssen 1989b, Davies 1995). The relatively sedentary behaviour recorded in the present study for P. leopardus corresponds to observations that large coral trout do frequently remain at single locations for extended periods (e.g. Samoilys 1987). In the Caribbean, Epinephelus guttatus, was observed also to remain in one position for extended times (Shapiro et al. 1994). Studies of temperate marine and freshwater fishes using ultrasonic telemetry have found also that individuals regularly spend the majority of their time in a small fraction, or core area, of their home ranges (Mesing & Wicker 1986, Bradbury et al. 1995). Other vertebrates have also been reported as using home range areas with variable intensity (e.g. Nursall 1981, Springer 1982).

Evolutionary advantages of preference for site attachment, or preferred location use, by *P. leopardus* may involve reduced risk of predation due to superior knowledge of local shelter sites (Fricke 1980 in Sale 1991, Bray 1981, Mace *et al.* 1983 in Swingland & Greenwood 1983, Bradbury *et al.* 1995). Availability of shelter has been suggested as a major factor underlying the distribution of many fishes (e.g. Smith 1961 in Parrish 1987, Talbot 1965, Goldman & Talbot 1976). An alternative, or additional, advantage for repeated use of known locations has been suggested in the improved fitness due to ready access to food resources whose location is known and can therefore be exploited economically (Covich 1976 in Bray 1981, Mace *et al.* 1983 in Swingland & Greenwood 1983, Bradbury *et al.* 1995).

Most *P. leopardus* examined in the present study showed a distinct preference for reef slope locations. This finding reflects earlier observations that highest densities of coral trout were recorded on the reef slopes (Choat 1968, Kingsford 1992). Thus, while the total size of the observed home ranges indicated that *P. leopardus* regularly utilises substantial areas of their local reef habitat, the preference displayed for a small number of predominantly slope positions supports the notion of considerable local siteattachment.

While it was not possible to identify and assign a habitat type to each recorded position, the results obtained clearly indicate that over 50% of the records were obtained from shelter and pressure/feeding sites, the majority of which (35.4%) were considered predominantly shelter locations. Serranids have been shown to make regular use of shelter, and are generally dependent on hard substrata (Williams 1991, Shapiro *et al.* 1994). Significantly, Parrish (1987) suggested that, based on the relative breadth of diet shown by many serranids, habitat reliance is based more on shelter than on prey distribution.

The high level of inactivity during nocturnal periods demonstrated in the present study, supports earlier visual observation on *Plectropomus* spp. (e.g. Johannes 1988, 1989). Carter *et al.* (1994) indicated that Nassau grouper equipped with ultrasonic transmitters were most active immediately following sunrise and just prior to sunset, and remained inactive at night.

### 4.4.3. Management implications

The information obtained in the present study provides not only the fundamentals for future ecological and behavioural investigations, but may serve as the foundation for the development of improved management strategies for long-term sustainable fisheries and marine protected area (MPA) management. The documentation of distinct preference by *P. leopardus* for upcurrent reef locations illustrated in the present study, for the first time provides unequivocal support to the observation made by commercial and recreational fishers that coral trout catches are higher on the "run on" side of a reef (Davies 1993, C. Hagen pers. com.). The "run on" side of a reef is the side where tidal currents push onto the reef, and usually varies with change of tide. Thus, the differences in catch per unit effort between "run on" and "run off" sides of reefs reported by fishers may, to a large extent, be the result of local

movements of fish to upcurrent locations, rather than purely changes in catchability or vulnerability to the fishing gear with the change of tide.

Recently, increasing interest is being expressed worldwide in the possible use of marine protected areas as the potentially most viable tool for sustainable coral reef fisheries management (Alcala 1988, Alcala & Russ 1990, Bohnsack 1990, 1993, Polacheck 1990, Roberts & Polunin 1991, DeMartini 1993, Polunin & Roberts 1993, Rowley 1994, Man et al. 1995, Holland et al. 1993a, 1996, Russ & Alcala 1996). Public acceptability of the concept of MPAs rely to a large extent on the documentation and estimation of potential flux rates of target species across MPA boundaries and the impact of such fluxes on local fisheries yield (Alcala & Russ 1990, Bohnsack 1990, Russ et al. 1993, Russ & Alcala 1996). Transfer rates of animals between protected and unprotected areas are influenced to a large extent by the boundary permeability (Buechner 1987) and the size of the protected area relative to the normal movement patterns and home ranges of the target species (Holland et al. 1993a, 1996). Thus, the concept of flux rates has, as one of it's most basic parameters, the principle of home range size, as well as basic activity and movement patterns (Minns 1995). Hence, the home range estimates and daily movements of P. leopardus reported here, provide the first step in gaining insights into the estimation of potential flux rates of this species in relation to marine protected areas.

# 4.5. Conclusions

- While individual *Plectropomus leopardus* regularly utilise home range areas of several thousand square meters, the majority of time is spent at a small number of locations. Furthermore, home ranges of individual coral trout are persistent through time, for the time period examined. Thus, previous observations regarding the assumed site-attached nature of *P. leopardus* are validated. However, movements within established home ranges regularly span 200-300 m.
- The shape and sizes of home ranges are influenced strongly by the type of reef inhabited, and no sex-specific differences exist. Available reef area appears to be the major determining factor of home ranges for *P. leopardus*.
- This study unequivocally demonstrates, for the first time, the distinct movements of *P. leopardus* in relation to changes in tidal currents. Thus, the observation commonly made by fishers of better catches on "run on" sides of reefs may be explained by the observed preference of upcurrent positions utilised by coral trout.
- It is demonstrated clearly that ultrasonic telemetry is the most suitable tool for evaluation of home ranges and movements of large reef fishes. This has clear implications for the acquisition of data urgently required for the evaluation of the use of marine protected areas as fisheries management tools for reef fishes of commercial and recreational fishing significance.

**Table 4.1:** Multiple regressions of the three home range parameters (area, maximum and minimum linear dimensions) against the variables "available reef area", "fish size (FL)", "tracking sample size" and "local trout densities", for *P. leopardus* living on patch reefs. Shown are overall regression p-values and adjusted  $r^2$ , as well as p-values for the individual variables (italics for significance at the  $\alpha = 0.05$  level) and the percentage of variability in home range parameters explained by each variable, based on partial correlation coefficients.

	Home Range Parameters						
	p-values			adjusted r <sup>2</sup>			
	Area	Length	Width	Area	Length	Width	
Overall	< 0.0001	< 0.0008	< 0.0015	0.8423	0.6666	0.6299	
regression			·				
	p-values			% variability explained			
Individual	Area	Length	Width	Area	Length	Width	
variables							
Reef Area	0.0000	0.0009	0.0035	73.72	58.60	49.25	
FL	0.8198	0.2429	0.0309	0.41	10.32	31.05	
Sample Size	0.6358	0.2655	0.3099	1.78	9.43	7.91	
Trout Density	0.8055	0.3943	0.2162	0.48	5.64	11.51	

**Table 4.2:** Multiple regressions of the three home range parameters (area, maximum and minimum linear dimensions) against the variables "available reef width", "fish size (FL)", "tracking sample size" and "local trout densities", for *P. leopardus* living on fringing reefs. Shown are overall regression p-values and adjusted  $r^2$ , as well as p-values for the individual variables (italics for significance at the  $\alpha = 0.05$  level) and the percentage of variability in range parameters explained by each variable, based on partial correlation coefficients.

	Home Range Parameters						
	p-values			adjusted r <sup>2</sup>			
	Area	Length	Width	Area	Length	Width	
Overall	< 0.0000	0.2259	0.0007	0.7150	0.0700	0.4595	
regression							
	p-values			% variability explained			
Individual	Area	Length	Width	Area	Length	Width	
variables							
Reef Width	0.0000	0.0600	0.0009	65.52	13.97	37.57	
FL	0.0426	0.7971	0.0814	16.04	0.28	12.12	
Sample Size	0.0034	0.3248	0.3757	30.56	4.04	3.28	
Trout Density	0.2153	0.9128	0.0260	6.32	0.05	18.99	

Table 4.3:Analyses of variance for position records of known habitat type between<br/>different times of the day (AM, Mid-day, PM). Data for all individual P.<br/>leopardus were pooled.

Variable	Source of variation	df	MS	F	P
Shelter	Time of day	2	0.00286	0.4447	0.6422
	Residual	105	0.06425		
					>
Pressure/feeding	Time of day	2	0.00549	0.0782	0.9248
	Residual	90	0.07024		
Cleaning	Time of day	2	0.02997	1.4069	0.2754
	Residual	15	0.02130		



Figure 4.1: Locations of individual *P. leopardus* tracked with ultrasonic telemetry between 1993-1995 around Lizard Island (northern Great Barrier Reef, Australia). Locations of tracking specimens around the island are indicated (n = 39). Numbers associated with locations indicate the number of specimens tracked at that location. Prevailing wind direction is from the south-east.



Figure 4.2: Maps of representative home ranges of *P. leopardus*, illustrating the differences in general shape of home ranges in the two reef habitat types. Black circles: Position records for each fish. Polygon outline: Polygon home range outline. A) Patch reef fish PL30 inhabiting the backreef area on the western side of Lizard Island (tracking period = 120 days). B) Fringing reef fish PL10 inhabiting the northern end of the island. Note the more elongated home range (tracking period = 46 days).



Figure 4.3: Differences in home range parameters between fringing and patch reefs for *P. leopardus* tracked by ultrasonic telemetry. Plotted are means +/- SE (fringing reefs: n = 29 tracking sessions; patch reefs: n = 18 tracking sessions), and mean values are presented numerically.
A) Mean area of convex polygon home range. B) Mean minimum linear home range dimension (home range width).



Figure 4.4: Comparison between female (n = 13) and male (n = 13) P. leopardus tracked by ultrasonic telemetry for the three home range parameters examined. Plotted are mean +/- SE, and mean values are presented numerically. A) Mean area of the polygon home range. B) Mean minimum linear home range dimension (width). C) Mean maximum linear home range dimension (length).



Figure 4.5: Observed mean number (+/-SE) of positions used by *P. leopardus* during day-time and night-time tracking periods. Comparison was based on the 1993 tracking period (n = 6 fish), as night-time tracking was discontinued thereafter.



Figure 4.6: Maps illustrating the utilisation distribution contours of the adaptive kernel of a representative specimen of *P. leopardus* tracked in 1993.
+: Position records obtained through ultrasonic tracking. All recorded positions are displayed in both graphs. Blue: 90% utilisation distribution contour. Green: 75% utilisation distribution contour.
A) Utilisation distributions at night. B) Utilisation distributions during the day.



Figure 4.7: Utilisation distributions of two representative *P. leopardus* inhabiting the same reef area, illustrating the preference for a small number of locations. +: Position records. Blue: 90% utilisation distribution contour. Green: 75% utilisation distribution contour. Red: 50% utilisation distribution contour. A) Specimen PL25, depicting a typical preference for positions (red) associated with the local reef slope. B) Specimen PL31, illustrating a less common situation of a centrally located core area of activity (red).



Figure 4.8: Comparison of number of positions used during different parts of the day. Shown are mean number of positions (+/- SE). On average, *P. leopardus* utilised 9.1 (+/- 0.28) positions during each day-time period.



Figure 4.9: Utilisation distribution of core area of activity for a typical P. leopardus (PL 40), separated by time of day. +: Position records.
Green: 75% utilisation distribution contour. Red: 50% utilisation distribution contour. A) Morning (nautical twilight - 1000 h). B) Mid-day (1000 h - 1400 h). C) Afternoon (1400 h - nautical twilight).



Figure 4.10: Maps illustrating the different patterns of home range use by *P. leopardus* PL1 in relation to tidal currents. Arrows indicate direction of tidal currents. +: Position records. Black line: Polygon home range. Green: 75% utilisation distribution contour. Red: 50% utilisation distribution distribution contour. A) Total polygon home range outline. B) Utilisation distribution during incoming (flooding) tide.
C) Utilisation distribution during outgoing (ebbing) tide.





Figure 4.11: Maps illustrating the different patterns of home range use by *P. leopardus* PL7 in relation to tidal currents during the Sept.-Nov. 1994 tracking period. Arrows indicate direction of tidal currents. Numbers of key positions are indicated. +: Position records. Black line: Polygon home range. Green: 75% utilisation distribution contour. Red: 50% utilisation distribution distribution contour. A) Polygon home range outline. B) Utilisation distribution during incoming (flooding) tide. C) Utilisation distribution during incoming tide. D) Utilisation No. 1 was removed. E) Utilisation distribution during outgoing tide.





Figure 4.12: Maps illustrating the different patterns of home range use by *P. leopardus* PL7 in relation to tidal currents during the Feb.-Mar. 1995 tracking period. Arrows indicate direction of tidal currents. Numbers of key positions are indicated. +: Position records.
Black line: Polygon home range. Green: 75% utilisation distribution contour. Red: 50% utilisation distribution contour. A) Polygon home range outline. B) Utilisation distribution during incoming (flooding) tide. C) Utilisation distribution during incoming tide. Data for the major shelter position No. 1 was removed.


Figure 4.13: Maps illustrating the different patterns of home range use by *P. leopardus* PL2 in relation to tidal currents. Arrows indicate direction of tidal currents. Numbers of key positions are indicated.
+: Position records. Black line: Total polygon home range.
Green: 75% utilisation distribution contour. Red: 50% utilisation distribution contour. A) Utilisation distribution during incoming (flooding) tide. B) Utilisation distribution during outgoing (ebbing) tide.



Figure 4.14: Maps illustrating the different patterns of home range use by *P. leopardus* PL39 in relation to tidal currents. Arrows indicate direction of tidal currents. Numbers of key positions are indicated.
+: Position records. Black line: Total polygon home range.
Green: 75% utilisation distribution contour. Red: 50% utilisation distribution contour. A) Total poygon home range area outline. B) Utilisation distribution during incoming (flooding) tide. C) Utilisation distribution during outgoing (ebbing) tide.



Figure 4.15: Maps illustrating the different patterns of home range use by *P. leopardus* PL9 in relation to tidal currents. Arrows indicate direction of tidal currents. Numbers of key positions are indicated.
+: Position records. Black line: Total polygon home range.
Green: 75% utilisation distribution contour. Red: 50% utilisation distribution contour. A) Total poygon home range area outline. B) Utilisation distribution during incoming (flooding) tide. C) Utilisation distribution during outgoing (ebbing) tide.





Figure 4.16: Maps illustrating the different patterns of home range use by *P. leopardus* PL3 in relation to tidal currents. Arrows indicate direction of tidal currents. +: Position records. Black line: Total polygon home range. Green: 75% utilisation distribution contour. Red: 50% utilisation distribution contour. A) Utilisation distribution during incoming (flooding) tide. B) Utilisation distribution during outgoing (ebbing) tide.



Figure 4.17: Maps illustrating the different patterns of home range use by *P. leopardus* PL4 in relation to tidal currents. Arrows indicate direction of tidal currents. Number of key position is indicated.
+: Position records. Black line: Total polygon home range.
Green: 75% utilisation distribution contour. Red: 50% utilisation distribution contour. A) Utilisation distribution during incoming (flooding) tide. B) Utilisation distribution during outgoing (ebbing) tide.



Metric Grid East (m)

Figure 4.18: Maps illustrating the different patterns of home range use by *P. leopardus* PL11 in relation to tidal currents. Arrows indicate direction of tidal currents. Number of key position is indicated.
+: Position records. Black line: Total polygon home range. Green: 75% utilisation distribution contour. Red: 50% utilisation distribution during incoming (flooding) tide. B) Utilisation distribution during outgoing (ebbing) tide.



Metric Grid East (m)

Figure 4.19: Maps illustrating the different patterns of home range use by *P*. *leopardus* PL5 in relation to tidal currents. Arrows indicate direction of tidal currents. Number of key position is indicated.
+: Position records. Black line: Total polygon home range.
Green: 75% utilisation distribution contour. Red: 50% utilisation distribution contour. A) Utilisation distribution during incoming (flooding) tide. B) Utilisation distribution during outgoing (ebbing) tide.



Figure 4.20: Maps illustrating the different patterns of home range use by *P. leopardus* PL32 in relation to tidal currents. Arrows indicate direction of tidal currents. Number of key position is indicated.
+: Position records. Black line: Total polygon home range. Green: 75% utilisation distribution contour. Red: 50% utilisation distribution during incoming (flooding) tide. B) Utilisation distribution during outgoing (ebbing) tide.



Figure 4.21: Maps illustrating the different patterns of home range use by *P. leopardus* PL27 in relation to tidal currents. Arrows indicate direction of tidal currents. ?: Indicates uncertainty about current flow . +: Position records. Black line: Total polygon home range.
Green: 75% utilisation distribution contour. Red: 50% utilisation distribution contour. A) Utilisation distribution during incoming (flooding) tide. B) Utilisation distribution during outgoing (ebbing) tide.



Figure 4.22: Evaluation of the distances moved by *P. leopardus* on a daily basis within their home ranges, as determined by ultrasonic telemetry.
A) Mean movement pattern ratios (+/- SE) for fringing reef and patch reef fish. Ratio was based on the mean daily distance moved divided by the minimum linear home range dimension (home range width). Mean values are presented numerically also. B) Effect of increasing sample size (number of position fixes per day) on the mean daily distance moved estimates (+/- SE) obtained from ultrasonic tracking records. Data suggested a potential asymptotic relationship, with a potential asymptotic mean daily distance moved by *P. leopardus* of 560.6 m (dashed line). Sampling efforts to obtain 75% and 50% of estimated asymptotic mean daily distance moved are indicated also.



Figure 4.23: Maps illustrating the stability of home ranges through time for representative *P. leopardus* tracked by ultrasonic telemetry over two separate sampling periods. A) Polygon home range outlines for specimen PL7, tracked during 1994 (red) and 1995 (green). Time period between successive tracking periods: 91 days. B) Polygon home range outlines for specimen PL22, tracked in early 1995 (red) and late 1995 (green). Time periods: 202 days. C) Polygon home range outlines for specimen PL30, tracked in early 1995 (red) and late 1995 (green). Time period between successive tracking periods: 202 days.

Chapter 5:

# MOVEMENTS OF PLECTROPOMUS LEOPARDUS IN RELATION

# TO SPAWNING AGGREGATIONS

# 5.1. Introduction

Reproductive strategies and the resulting consequences drive the life history of species and populations (Johannes 1978, Thresher 1984). These reproductive decisions and strategies have been found to be exceptionally difficult to examine in marine fishes (Thresher 1984). However, more recently substantial advances have been made in the description of the basic reproductive biology of some commercial families of tropical fishes, such as lethrinids (e.g. Ebisawa 1990), lutjanids (Grimes 1987, Davis & West 1993) and serranids (Ferreira 1993, 1995, Shapiro *et al.* 1993, Brown *et al.* 1994, Carter *et al.* 1994, Sadovy *et al.* 1994, Tucker 1994, Sadovy 1995, Sadovy & Colin 1995, Coleman *et al.* 1996).

One of the major aspects of the reproductive behaviour of coral reef fishes is the common occurrence of spawning aggregations (Thresher 1984). These aggregations have been reported to form either on a daily basis with associated movements over short distances (Johannes 1978, Thresher 1984, Colin & Clavijo 1988, Myrberg *et al.* 1988, Mazeroll & Montgomery 1995), or occur on a seasonal basis as a result of large-scale migrations (e.g. Shapiro 1987, Colin 1992, Shapiro *et al.* 1993).

Hypotheses put forward to explain the phenomenon of spawning aggregations at specific locations fall into two main categories: hypotheses regarding larval biology and hypotheses regarding adult biology (Robertson 1991 in Sale 1991). Proponents of the former suggest that the release of eggs at specific locations, resulting in eggs being swept offshore by currents, may improve dispersal and survival of pelagic eggs (e.g. Doherty *et al.* 1985), or the release of large numbers of eggs in one location over a short time period may result in increased egg survival due to swamping (satiation) of egg predators (Johannes 1978). Alternatively, adult activity may include the enhancement of mate choice opportunity in otherwise widely dispersed, low density populations (Shapiro *et al.* 1993). In addition, social interactions may become enhanced, influencing future decisions regarding the reproductive value of changing sex in hermaphroditic fishes, based on social control of, or influence on, sex change (Thresher

1984, Shapiro 1987). However, as Samoilys & Squire (1994) point out, both hypotheses are not mutually exclusive.

Spawning aggregations have been documented for many species through direct observations, e.g. acanthurids (Robertson 1983, Mazeroll & Montgomery 1995), labrids (Warner 1995), Caribbean serranids (Shapiro 1987, Colin 1992, Shapiro *et al.* 1993, Sadovy *et al.* 1994), or indirectly inferred from catch and reproductive information (Ebisawa 1990). In contrast, the reproductive ecology of the tropical, Indo-Pacific serranid *Plectropomus* spp. has received considerably less attention. However, spawning aggregations of *P. areolatus* have been reported in Palau (Johannes 1981) and the Solomon Islands (Johannes 1988). On the Great Barrier Reef, the first scientific investigation of spawning aggregations of *P. leopardus* was reported in 1994 (Samoilys & Squire 1994), although anectodal information was reported earlier (e.g. Johannes 1988, Johannes & Squire 1988).

The importance of spawning aggregations in the commercially important reef fish species of the Indo-Pacific has received increasing attention in recent years (Brown *et al.* 1994, Samoilys & Squire 1994, Johannes *et al.* 1995). The large concentrations of individuals of high commercial, recreational or subsistence importance for a generally short time period in one location, usually consistent from year to year, has resulted in many fisheries utilising existing aggregations repeatedly over many years (Thresher 1984, Shapiro 1987, Colin 1992, Sadovy 1994, Samoilys & Squire 1994). Efficient fishing at aggregation sites can result in the removal of a large proportion of the reproductively active fish in a stock, which may have devastating effects on the population as well as on future fishery yields (Shapiro 1987, Ralston 1987, Sadovy 1994, Colin 1992, Johannes *et al.* 1994). The recent collapse of the north Atlantic cod fishery can to a large extent be attributed to overfishing of spawning stock biomass (e.g. Hutchings & Myers 1994, Morgan & Trippel 1996, Myers *et al.* 1996).

The effects of intensive fishing pressure on spawning aggregations of the stock, as well as the potential usefulness of aggregations for stock assessments (Brown *et al.* 1994, Johannes *et al.* 1994), is strongly influenced by several, previously undetermined

factors. These include the number of distinct spawning aggregation sites per reef, and presumably closely related to this, the catchment areas (i.e. how far do individuals move to specific aggregation sites?), the participation rates (what proportion of the population participates in any one aggregation event?), the residence times of individual fish at aggregation sites, and any potential sexual differences in the participation rates and residence times.

Information regarding the catchment areas of spawning aggregations and distances moved by individual fish are extremely limited and incomplete. Most data on distances moved are based either on chance recaptures of tagged specimens (Burnett-Herkes 1975 in Shapiro 1987, Colin 1992, Sadovy *et al.* 1994, Johannes *et al.* 1995), or are based on inferences from qualitative observations (Colin *et al.* 1987, Colin 1992). There is no quantitative information available for large predatory reef fish (that the author is aware of), regarding participation rates or residence duration of individuals at aggregation sites. Any stock-related interpretation of abundance estimates at spawning aggregations and observed sex ratios will depend strongly on whether there is a significant turnover rate of fish during the existence of an aggregations, and the participation rates and residence times at these aggregations for a given species are urgently required for relevant stock assessment and fisheries management in relation to spawning aggregation events.

The major objectives of this chapter can be divided broadly into two sections:

#### **Catchment area evaluation**

The evaluation of catchment areas of spawning aggregations of *Plectropomus leopardus* requires the location of aggregation sites around Lizard Island to be determined through tracking of specimens equipped with ultrasonic transmitters. Once individual aggregation sites have been idenitified, actual catchment areas of aggregations can be estimated by measuring the distances moved between established home ranges (Chapter 4) and aggregation sites through ultrasonic tracking.

#### Use patterns of spawning aggregations

The patterns of use of spawning aggregations by *P. leopardus* will be examined by comparing the lunar pattern of build-up of aggregations as determined by underwater visual census of spawning aggregations with the behaviour of individually tracked specimens. Ultrasonic tracking will permit the quantification of participation rates of *P. leopardus* at aggregation events, and the description of timing of movements to and from spawning aggregation sites. Finally, the aggregation site residence patterns of individuals will be determined, with regards to residence time and number of spawning trips undertaken, and any sex-specific differences in the patterns of use of aggregation sites will be evaluated.

## 5.2. Methods

#### 5.2.1. Timing and spatial distribution of ultrasonic tracking

Ultrasonic tracking effort was restricted to the western, northern and northeastern sides of Lizard Island, Northern Great Barrier Reef (Lat.  $14^0 40^{\circ}$  S; Long.  $145^0$ 28' E, Fig. 5.1), as these areas are more sheltered from the prevailing south-easterly winds. Emphasis was placed on spreading the capture and release locations of tracked specimens across the whole study area, in order to increase the likelihood of detecting the largest number of potential spawning aggregation sites, and to determine the likely catchment areas of each spawning aggregation site.

Three of the five tracking periods in this project took place during the springearly summer period in the southern hemisphere, between August and December in 1993, 1994 and 1995 (Table 2.1). This is the annual spawning period reported for P. *leopardus* on the Northern Great Barrier Reef (Samoilys & Squire 1994). A total of 35 fish were tracked during the three tracking periods in the spawning season, with tracking periods ranging up to 97 days per fish.

#### 5.2.2. Method of ultrasonic tracking

For a detailed description of the general capture, handling, transmitter placement methods and general tracking techniques, see Chapter 2. Tracked specimens of *P. leopardus* were captured on hook and line, with capture effort spread evenly across the study area. Fish were released at the capture sites after successful implantation and recovery of specimens, and tracking of specimens commenced immediately after release. Positional data collected during the first 24 hours after release were not included in any subsequent analysis. Throughout each tracking period, emphasis was placed on continuous monitoring of all specimens. It was attempted to locate each fish at least three to four times per day for the duration of the tracking period. However, logistic restraints (e.g. equipment breakdowns) or bad weather sometimes restricted data collection to one or two fixes per day. Tracking had to be suspended for short periods on some occasions due to unusually strong northerly winds (September 1993 & October 1994).

At the end of each tracking period, specimens were collected by speargun in order to recover transmitters and determine the sex of specimens. Histological techniques used for gender determination followed those described by Ferreira (1995) for *P. leopardus*.

#### 5.2.3. Underwater visual census

In order to confirm the existence of spawning aggregation sites as determined by movements of tracked specimens, underwater visual censuses were conducted during 1994 and 1995. Censuses were spread across the complete lunar periods in order to gauge general abundances of *P. leopardus* at spawning sites. After initial, widespread searches of each newly detected spawning site, a core area of  $50 \times 20$  meters was censused. During each 20 minute census, these core areas were searched intensively and all sighted coral trout counted, sizes estimated, male courtship colour and behaviour noted, and tracked specimens identified where possible. Identification of tracked

specimens was achieved by specimen-specific tagging patterns using standard T-bar anchor tags (1993), or by use of a diver held ultrasonic receiver (1994-95).

## 5.2.4. Data analysis

Data was examined graphically and analysed for diel and lunar patterns of spawning movements, with particular emphasis on residence times and distances moved with regards to spawning activities. All activities within the established home ranges of the tracked specimens were excluded from analysis of spawning activities, and are covered in the previous chapter (Chapter 4).

The spatial location data obtained from the ultrasonic tracking was digitised from aerial photos using SIGMASCAN<sup>®</sup>. Distances moved and speed of movements from home ranges to spawning aggregation sites were analysed using the home range analysis program WILDTRACK<sup>®</sup> on an Apple MacIntosh computer. For the calculations of residence times at the spawning aggregation sites and the timing of movements to and from the sites, only those movement occasions were considered which included position monitoring of twilight evening and early next morning positions. This was done to avoid overestimates of residence times and to ensure that the correct departure times were recorded.

Graphical data presentation was emphasised, and statistical analyses (t-test, ANOVA, ANCOVA, linear regression,  $\chi^2$ -test) were performed using STATISTICA<sup>®</sup>. Statistical assumptions underlying the various analyses were examined prior to analysis (e.g. Homogeneity of variances: Cochrans test; Normality: Residual plots), and data log<sub>10</sub> transformed where appropriate. Proportion variables were transformed to arcsine  $\sqrt{p}$  (Sokal & Rohlf 1981).

# 5.3. Results

Of the 39 coral trout tracked in the overall study (see Fig. 4.1), 35 were tracked during the spawning periods. Of these 35 specimens 13 (31.1%) were recorded as moving to spawning aggregation sites during these periods. Eight individuals were male, four were female and one specimen could not be recovered for gender determination (Table 5.1). A total of 1,698 tracking days and 6,647 time-location data points were obtained during the spawning periods.

## 5.3.1. Location and description of spawning aggregation sites

During the period of this study four major aggregation sites of *P. leopardus* were detected around Lizard Island through movements of fish equipped with ultrasonic transmitters. Two of the sites were tentatively identified in 1993, and confirmed in 1994 (Granite Head [GR] & North Point [NP], Fig. 5.1), while the two backreef sites (BR1 & BR2, Fig. 5.1) were located during 1995.

In all cases, aggregations were situated on the lower reef slope at a depth of 15-20 m, which represented the deepest part of the reef slope at Granite Head and North Point. Both backreef aggregations (BR1 & BR2) appeared to continue to a depth of at least 25 m, but visual observations and censuses were restricted to 20 m due to legal scientific dive depth restrictions. All four locations were located at the down-current position of the local reef structures, with medium to strong tidal currents being experienced regularly, running either off the reef or parallel to the reef edge (Fig. 5.1).

Courtship activities were observed also during SCUBA surveys at three additional locations during 1995 (A, B & C, Fig. 5.1). Small groups of *P. leopardus*, consisting of at least two males being observed to display courtship colours (e.g. Plate 5.1) and behaviour towards groups of 2-6 other coral trout (presumably females).

#### 5.3.2. Catchment areas: Distances moved to spawning sites

Due to the emphasis placed on spatial spreading of tracking specimens throughout the study location (see Fig. 4.1), the one-way geographic distances between established home ranges and spawning aggregation sites for *P. leopardus* equipped with transmitters varied widely, with an average one-way distance of 911.95 m  $\pm$  232.64 (SE) (range: 223.0 - 5,212.99 m, Table 5.2, Fig. 5.2). Treating the individual geographic home range\spawning site distances as a covariate for each specimen in the statistical analysis, the total distance moved to spawning aggregation sites (return trips and multiple trips) did not differ between male and female *P. leopardus* (ANCOVA F <sub>[1,9]</sub> = 0.7869, p = 0.3981). Taking into account return trips and multiple movements to aggregation sites, the average total distance moved ( $\pm$  SE) by coral trout in relation to spawning during the tracking periods was 5,223.46 m ( $\pm$  1,315.15), ranging from 604.24 m to the maximum recorded total distance moved of 17,274.20 m.

Of particular interest was fish PL 21 (male), which undertook regular movements between its home range and the spawning aggregation site at Granite Head, a distance of 863.71 m (Fig. 5.2), over a 19 day period during 1994. This individual made 10 trips to the spawning aggregation site, with two trips being multi-day (two and three days duration) and on two occasions this fish made two trips back and forth on the same day. Thus PL 21 covered 17,274.2 m over this 19 day period in spawning aggregation movements alone.

The average minimum speed of movement to and from the aggregation site for PL 21 was 10.94 m/min  $\pm$  1.53 (SE) (Table 5.2). For all fish and all occasions with home range and spawning site fixes on the same day, the overall average minimum speed of movements in relation to spawning aggregation sites was 9.58 m/min  $\pm$  1.17 (SE), with a range of 2.90 - 20.40 m/min (Table 5.2).

Two non-tracked fish marked using freeze-branding on the 21-August-1995 and the 22-September-1995 as part of a related experiment (see Chapter 6) were sighted on the 24-October-1995 at the North Point spawning aggregation site during SCUBA surveys. The distances between sites of first capture and location of resighting were 3,000 m and 650m, respectively (Fig. 5.3).

Additional data of particular interest relate to the recapture of three coral trout carrying ultrasonic transmitters. One specimen (fork length = 48.0 cm) was captured initially on the 22-August-1993 (4 days post-new moon) at the Granite Head spawning aggregation site. It was released at the capture site on the 8-September-1993 after recovery from transmitter implantation. Ultrasonic tracking contact in the Granite Head area was lost seven days after release. The fish was recaptured by commercial fishers in early June 1996, in a deeper water (~40 m) offreef area, known amongst commercial fishers as "The Gutter", approximately 11 kilometers north-north-west of Lizard Island (Fig. 5.4).

Specimen two (fork length = 55.4 cm) was caught for transmitter implantation on the 19-October-1994 (full-moon) at the Granite Head spawning aggregation site. Within three days of release, ultrasonic tracking contact was lost with this fish. It was recaptured by recreational fishers on the 25-October-1995, and the ultrasonic transmitter returned. A subsequent interview with the fisher could position the recapture site only as "Petricola shoals", an extensive area of widely dispersed shallow to medium deep reef areas to the north of Lizard Island. The direct, linear distance between initial capture site (Granite Head) and the southernmost part of the shoal area recorded on nautical charts is approximately 3 kilometres (Fig. 5.4).

The third coral trout (fork length = 44.1 cm) was initially caught at the Granite Head spawning aggregation site also, on the 4-October-1994 (one day before new moon). Tracking contact was lost eight days after release. This fish was recaptured on the 6-October-1995 at Eyrie reef by commercial fishers assisting in the "Effects of Line and Spearfishing Experiment" conducted by the "Cooperative Research Center for Reef Research" (J.C.U. Townsville, C. Davies, pers. com.). The direct linear distance between site of initial capture and location of recapture is approximately 7.5 kilometres (Fig. 5.4). All three recaptures can be classified as inter-reefal movements, and also represent long distance movements away from a known spawning aggregation site.

## 5.3.3. Use patterns of spawning aggregation sites

## 5.3.3.1. Lunar pattern and participation rates

Spawning aggregation activities by the tracked specimens showed distinct patterns of lunar activity. The number of tracking specimens present at the four spawning sites was highest during new moon periods (Fig. 5.5a), with the highest participation observed during the early November new moon in 1994 (Fig. 5.5b) and the late October new moon in 1995 (Fig. 5.5c). No movements to aggregation sites or movements significantly outside of established home ranges were ever recorded during tracking periods outside the reported spring spawning season. The only specimen recorded as reproductively active during the 1993 spawning period tracking session (individual PL4) was tracked during August-September only. It moved to the spawning site at Granite Head (GR) prior to the full moon in early September, and remained at this spawning site for a complete lunar cycle (full moon to full moon, Fig. 5.6). Regular visual assessments on SCUBA of the spawning aggregation sites at North Point and Granite Head were undertaken during the time periods considered not to be spawning season, i.e. February-March 1994 and 1995, and May 1995. No courtship or aggregating behaviour were observed during these periods.

Underwater visual censuses conducted at the Granite Head and North Point aggregation sites during October-November 1994 showed the highest trout counts over the new moon periods in October and November, with the highest count of 60 fish/1000  $m^2$  observed two and three days before the October new moon at the Granite Head site (Fig. 5.7a). Similar censuses conducted at all four spawning aggregation sites between September and December 1995 resulted in a peak count of 35 fish/1000  $m^2$  observed at Granite Head one day prior to the October new moon (Fig. 5.7c). All four locations displayed the same pattern, with highest densities of aggregating coral trout during this October new moon period, with a secondary peak prior to the November new moon (Fig. 5.7b). Smaller aggreggations were observed at these sites over each new moon period examined (Fig. 5.7).

On numerous occasions tagged fish carrying ultrasonic transmitters were identified and observed during visual censuses of the spawning aggregations (Table 5.3). Six of the nine observed specimens were identified visually as male by the readily recognisable male courtship colours and behaviour (Plate 5.1). The behavioural sex determination was confirmed through gonad histology upon recovery of the tracking specimens at the end of the tracking periods (Table 5.3). It was not possible on all occasions to identify males by their behaviour patterns during the visual census, e.g.. on the 3-October-1994 fish PL 9 was present but "*inactive*" and was not identified visually as male until the next census on the 5-October (Table 5.3). Similarly in 1995, PL 35 was not identified as male until the census on the 22-November, with the prior census (18-November) recording this fish as "*inactive*" (Table 5.3). Thus, while male tracking specimens were present 11 times during the visual censuses, on only seven occasions were they identified correctly as males by their behaviour patterns, within the time-frame of regular aggregation site censuses. Hence, 36.4% of the time a known male fish was observed during the visual census it was not identified correctly as a male.

#### 5.3.3.2. Timing of movements

Movements of tracked specimens to, as well as from, spawning aggregation sites occurred throughout the day (Fig. 5.8). A distinct preference for late afternoon movements to the aggregation sites was detected, with 41.2% of all movements to the aggregation sites being recorded between 1630 h and 1930 h (Fig. 5.8a). Time of departure from the spawning aggregation sites was more widely spread throughout the day, with a gradual drop in departure rate discernible throughout the day (Fig. 5.8b). However, 31.1% of all departures occurred between 0730 h and 1030 h, with 60% of departures occurring during the mornings (Fig. 5.8b). The mean time of arrival differed from the mean time of departure (ANOVA, p < 0.001, Table 5.4), and this pattern was the same for both sexes (p = 0.225, Table 5.4).

#### 5.3.3.3. Residency at aggregation sites

All 13 reproductively active tracked specimens displayed aggregation site fidelity throughout the tracking periods. Each fish utilised only one of the four sites monitored throughout the tracking periods (Fig. 5.2). While most fish appeared to utilise that site closest to their observed home ranges (e.g. PL 42, PL 29, Fig. 5.9), the male fish PL 34 utilised a spawning aggregation site on a neighbouring patch reef (742 m from its home range, Fig. 5.10a), despite the existence of a well established aggregation site nearer to its home range (325 m distance), which was used by two other fish from the same patch reef (PL 35 & PL 36, Fig. 5.10b & c). Movements to the preferred site were recorded repeatedly for PL 34 throughout the tracking period (Fig. 5.11). Furthermore, this fish was not recorded at the spawning site closest to its home range (Fig. 5.10a).

Aggregation residence time, defined as the time period between first and last position record obtained during continuous monitoring at the aggregation sites, was calculated for each separate trip made by an individual to an aggregation site. Total residence times at the spawning aggregation sites differed between males and females  $(t_{[10]} = 2.9508, p = 0.0145)$ , with males spending, on average, 8.76 times more time at the spawning aggregation sites than did females (Fig. 5.12). A relatively weak, non-significant relationship between total residence time and size of fish (fork length) for male *P. leopardus* was observed ( $r^2 = 0.2596, p = 0.197$ , Fig. 5.13). No relationship was detected for the small sample of females obtained ( $r^2 < 0.0001, p = 0.998$ ).

A breakdown of spawning trips into day-trips, overnight-trips and trips lasting several days (multi-day), revealed that, for all fish combined, overnight trips contributed 43% of all occurrences, while multi-day trips accounted for 25.9% (Fig. 5.14a). The proportion of each trip type did differ between males and females ( $\chi^2_{[2]} = 7.7303$ , 0.025 > p > 0.01). Females undertook proportionally more day trips than male fish, and, in contrast to males, were never observed to make multi-day spawning excursions (Fig. 5.14b). The mean number of trips made to the spawning aggregation sites by each fish did not differ between the sexes ( $t_{[10]} = 0.800$ , p = 0.442, Fig. 5.15a). However, further examination of the data set indicated that three out of the four females undertook only a single excursion (median = 1, range = 1-15, Fig. 5.15c), while seven out of eight males moved to the spawning aggregation sites on more than one occasion (median = 7, range = 1-18, Fig. 5.15c). Existing evidence suggests that larger fish undertake more trips to spawning aggregation sites than do smaller fish ( $r^2 = 0.3887$ , p = 0.0303, Fig. 5.15c), a pattern that is more distinct for male *P. leopardus* ( $r^2 = 0.5978$ , p = 0.0244, Fig. 5.15c).

## 5.3.4. Summary of results

- Using ultrasonic telemetry, four major spawning aggregation sites of *Plectropomus leopardus* were detected at Lizard Island.
- Of all trout tracked during the 1993-95 spawning periods, only 31% participated in spawning aggregations.
- Distances moved from home range to aggregation sites ranged from 223m to 5,213 m (mean = 911.95 m ± 223 SE).
- Total spawning movement distances back and forth in the spawning season ranged from 604 m to over 17 kilometres.
- The average minimum speed of movements to spawning aggregations was 9.58 m/min, with a maximum speed recorded of 20.4 m/min.
- One-way inter-reefal movements were recorded for three fish, moving 3, 7.5, and 11 kilometres between release and recapture locations.
- Spawning aggregation activities displayed a lunar pattern, with peak activities during new moon periods.
- Underwater observations revealed that approximately 36% of the time a known male *P. leopardus* was recorded during visual censuses at the aggregations sites, it could not be sexed based on courtship colours or behaviour.
- Mean time of arrival at and departure from aggregation sites differed, with arrivals occurring predominantly in the afternoon and departures peaking in the morning.

- All specimens displayed site fidelity with respect to their chosen spawning aggregation site.
- Total residence time at aggregations differed between males and females, with males spending on average 8 times longer at the aggregations than females.
- Females seemed to undertake day or overnight trips only, while males regularly did multi-day trips also.
- Larger fish appeared to undertake more spawning trips than smaller fish.

# 5.4. Discussion

The formation of spawning aggregations forms a central feature in the reproductive ecology of many tropical serranids (Thresher 1984, Sadovy 1994). Such aggregations often provide a major opportunity for fishers to harvest large yields over short time periods with relatively small fishing effort (Colin 1992). Once such aggregation sites and times are known to the fishing community, the potential for depletion of the stocks associated with these aggregations is very high (Sadovy 1993), and can be very rapid (Johannes 1988, Colin 1992, Johannes *et al.* 1994). The consequences of severe depletions of aggregations are unknown (Sadovy 1994), but might be dependent on species specific usage patterns of aggregation sites. A clear understanding of the mechanisms driving the formation, location and catchment areas of, and patterns of residence at such aggregations are required urgently to permit the development of appropriate management strategies to ensure continued, sustainable use of these valuable biological resources.

The majority of previously published studies on spawning aggregations of serranids were conducted in the Caribbean, with evidence of the location and formation of aggregations existing for a number of species (review by Sadovy 1994). While initial reports of aggregations of serranids in the Pacific were reported decades ago (Randall & Brock 1960, Johannes 1978), it is only recently that the focus is beginning to intensify on detailed investigations of such aggregations (Johannes 1988, Johannes & Squire 1988, Johannes *et al.* 1994, 1995). Only one scientific investigation of a spawning

aggregation of *P. leopardus* on the Great Barrier Reef has been published (Samoilys & Squire 1994). All the currently available investigations have in common the fact that the initial location of aggregations was derived from information from fisheries. The present study represents the first attempt at locating spawning aggregations of a recreationally and commercially significant coral reef fish through a fisheries independent, remote tracking technique (ultrasonic telemetry) on a reef which had no previously published reports of aggregation sites for *P. leopardus*.

## 5.4.1. Locations and catchment areas of aggregation sites

Sadovy (1994) emphasised the need to determine the geographic locations and duration of spawning aggregations. Such information is very limited at the present, even for the more extensively studied Caribbean serranids (Shapiro 1987), and based entirely on reports from the fishing community. As early as 1972 Smith reported two aggregation sites of the Nassau grouper, *Epinephelus striatus*, about 30 nautical miles (approximately 55 km) apart in the Bahamas. Colin (1992) reported on two spawning aggregations of the Nassau grouper in the Bahamas being 20 nautical miles (approximately 36 km) apart. At the Cayman Islands, only one aggregation site per island is reported for *E. striatus* and *E. guttatus* (Colin et al. 1987).

The four spawning aggregation sites of *P. leopardus* recorded in the present study were based on the monitoring of ~12km of island coastline, which represents approximately  $^{2}/_{3}$  of the total coastline of the island (not including the lagoon area). The existence and regular use of several aggregation sites indicates that multiple spawning aggregation sites per reef might occur for *P. leopardus* on the Great Barrier Reef. Samoilys & Squire (1994), using visual searches on SCUBA, reported finding two aggregation sites approximately one kilometre apart on a mid-shelf study reef approximately 6 x 6 km in size. Clearly, the present study might not have detected all the possible spawning aggregation sites around Lizard Island. Based on the characteristics of the aggregation sites recorded here (i.e. depth, current profiles , projection of local reef structures), additional potential spawning sites might be located at South Island point and Lizard Head/lagoon entrance (see Fig. 5.1). Spawning

aggregation activities by herbivorous fishes has been observed at the Lizard Head location (M. McCormick, pers. com.). Further monitoring would need to be undertaken to determine the suitability of these two locations. Clearly, the observations regarding location of aggregation sites at Lizard Island recorded in this study, may assist in determining possible aggregation sites of coral trout on other reefs on the Great Barrier Reef.

All four sites displayed distinct currents moving away from a local reef projection, indicating that current direction may play an important role, as suggested by Johannes (1978). Plectropomus leopardus is considered to be primarily a pair-spawner (Samoilys & Squire 1994), and, as reported for other serranids (Colin 1992), actual spawning rushes appear to be a relatively rare event, having been observed only during a very narrow time window around sunset (Samoilys & Squire 1994). These observations lend support to the larval biology hypothesis, based on predominant currents and lastlight spawning (Barlow 1981, Lobel 1989). This suggests that the release of eggs at specific locations, resulting in them being swept offshore by currents, may improve dispersal and survival of pelagic eggs (e.g. Doherty et al. 1985), or the release of large numbers of eggs in one location over a short time period may result in increased egg survival due to swamping (satiation) of egg predators (Johannes 1978). However, whether such characteristics are the determining factor for the choice of spawning locations remains to be determined. Drift buoy studies conducted by Colin (1992), for example, suggested no apparent advantage of the chosen aggregation site of the Nassau grouper Epinephelus striatus due to current patterns. This might indicate that water currents might be of secondary importance. Hence, social interactions (the adult biology hypothesis) cannot be ruled out (e.g. Thresher 1984, Shapiro 1987, Shapiro et al. 1993). However, all water currents observed in the present study during late afternoon observations (both during tracking and SCUBA observations) indicated medium to strong movements of currents away from the surrounding reef structures. Clearly they are not exclusive and require further experimental investigations.

Thus, all available evidence suggests that *P. leopardus* populations have multiple aggregation sites on each reef. This appears to contrast with the pattern

observed for *P. areolatus* in Palau, where approximately 10 aggregation sites are located at roughly 20 nautical mile intervals (~36 km) over the the entire sheltered length of the Palau archipelago (Johannes *et al.* 1994, L. Squire, pers. com.). These aggregation sites are well known to local fishers, and are fished regularly (L. Squire, pers. com.). This pattern appears to be similar to that reported for a congeneric species, *P. laevis*, which is thought to form large aggregations on a few sites on the Great Barrier Reef (Johannes & Squire 1988, C. Hagen pers. com.).

The spawning movements observed in the present study represent the first records of two-way movements from home locations to spawning sites followed by a Considerable one-way distances moved in relation to subsequent return home. spawning aggregations have been recorded from tagged individuals or inferred in the investigations of Caribbean serranids. Burnett-Herkes (1975 in Shapiro 1987) recorded movements of 10 Epinephelus guttatus ranging from 0-13 km, based on commercial returns of tags applied at a known spawning site in Bermuda. These findings suggest that E. guttatus may disperse over areas of several kilometres after spawning activities. Colin et al. (1987) based an inference of catchment areas of spawning aggregations on the assumption that, since only one spawning site of E. striatus was known on each of the three Cayman Islands, fish would migrate 15-50 km to spawn. Movements of tagged red grouper (E. morio) over distances of 18-45 miles were reported by Moe (1969). Individual E. striatus have been reported to move 110 km to a spawning aggregation site in the Bahamas (Colin 1992), and even 240 km between spawning areas in Belize (Carter et al. in Sadovy 1994). In relation to spawning of serranids in the Pacific, information on movements are at present limited. The recaptures of three Epinephelus polyphekadion tagged at an aggregation site in Palau were 3, 4 and 6 nautical miles from the tagging location, after a maximum time at large of 2 weeks (Johannes et al. 1995). The authors also report that these recaptures were from patch reefs isolated from the original tagging reef, implying movements between reefcomplexes to join spawning aggregations (Johannes et al. 1995). Additional recaptures in this study appear to have been obtained since then, with a maximum reported movement of 10 nautical miles (L. Squire pers. com.). Johannes (1988) estimated the maximum distance Plectropomus areolatus would have to move to reach a spawning aggregation site at a location in the Solomon Islands as about 10 km, based on locations of known aggregation sites and distribution of "suitable habitats, i.e. coral communities".

After participation at aggregation events, all tracked fish did return to their original home ranges from which they had moved. The fortuitous recapture of three specimens initially caught at the spawning aggregation site Granite Head in 1993/94, and recaptured in reefal habitats 3 to 11 km from this Lizard Island spawning aggregation site, suggests strongly:

#### a) interreefal movements of P. leopardus do occur, and

b) spawning aggregations may attract fish from areas other than the local reef at which the aggregation site is located.

However, it is possible that these fish were displaced from their original home range area at Granite Head through social interactions with other coral trout, due to their absence during transmitter implant and recovery. Nevertheless, given that the other specimens tracked all remained at their capture location to re-establish home ranges lends strong support to the potential for intereefal movements as part of spawning. Movements of P. leopardus between reefs has been recorded reliably only once (Davies 1995), and was associated with reefs in very close proximity (0.2 km) and with evidence of a corridor of suitable intereefal habitat (hard substratum). Given this short distance and the presence of interreefal habitat, this movement reported by Davies falls clearly within the normal home range movements of P. leopardus (see Chapter 4). In the present study, the nature of interreefal habitat around Lizard Island is not well known. The waters between Lizard Island, Petricola shoals and Eyrie reef are between 22 & 28 meters deep, and the bottom topography is not charted adequately. However, several hard-bottom habitats, in addition to substantial sand and seagrass areas, are known to exist in these intereefal areas, mainly due to recreational fishing interests (L. Pearce, C. Davies & L. Vale pers. com.). Future tracking studies should consider the possibility of P. leopardus moving offshore into interreefal habitats.

## 5.4.2. Usage patterns of aggregation sites

The movements to spawning sites recorded through ultrasonic tracking in this study, corresponded with the build up of aggregations recorded in the underwater visual censuses. Principally, the data supports the previously reported build up of aggregations of *Plectropomus* spp. in relation to the lunar cycle, with peak abundances over the new moon periods, and minor aggregations over the full moon. Highest abundances of *P. leopardus* just prior to new moon, based on underwater visual census, were reported by Samoilys & Squire (1994) on the Great Barrier Reef, and also for *P. areolatus* in the Solomon Islands (Johannes 1988), and for *P. areolatus*, *Epinephelus polyphekadion* and *E. fuscoguttatus* in Palau (Johannes *et al.* 1994, 1995). On the other hand, studies on some of the Caribbean serranids, e.g. *Epinephelus striatus* and *E. guttatus* report highest aggregations over the full moon periods (e.g. Colin 1992, Shapiro *et al.* 1993).

Of particular interest in the present study is the fact that, while attendance at the spawning aggregation site was highest over the new moon periods, many tracked fish remained at, or returned to the aggregation sites during the full moon period. This was especially evident for male P. leopardus, with a median number of seven trips to the aggregation sites per tracked specimen. In Palau, several individual P. areolatus, tagged at the monitored spawning aggregation sites in previous months, were resighted during subsequent months (Johannes et al. 1995). It is particularly interesting to note that all individuals resignted were reported to be male (based on size and colouration). Repeated presence at aggregation sites of P. leopardus was also implied by Brown et al. (1994), who recorded tagged coral trout being present during two subsequent new moon periods, while not being recorded at the intervening full moon. However, monitoring was not continuous in their study, particularly outside of the new moon time period. Therefore, short term visits by tagged fish over the full moon period (or at other times) might easily have been missed. Such short term visits (i.e. day- or overnight trips) accounted for 74% of all recorded movements to the monitored aggregation sites in the present study.

The observed timing of movements to the spawning aggregation sites, with 41% of movements between 1630 h and 1930 h, lends support to the observed build up of numbers at aggregation sites during the day (Brown *et al.* 1994). Johannes *et al.* (1994) also reported counts of *Epinephelus fuscoguttatus* and *E. polyphekadion* to nearly double in the late afternoon of the day before the new moon.

The pattern of predominantly late arrival at and early departure from aggregation sites (over 60% of departures occurred in the morning), irrespective of sex of fish, indicates that *P. leopardus* uses the daytime for movements from home ranges to spawning sites. This is supported by the fact that none of the observed movements of tracked specimens took more than one daytime period. Colin (1992) stressed that the timing of movements to and from aggregations is not well known. However, he does report having observed several groups of *Epinephelus striatus* moving during the afternoon in one direction past the aggregation he was monitoring, and a few days later, a smaller group moving in the morning the other way. Of particular interest are the observations of *P. areolatus* in the Solomon Islands being seen to leave the aggregation sites in small groups around 0700 h on the day after the new moon, with virtually the complete aggregation (300+ fish) having departed by 0720 h (Johannes 1988).

The pattern of arrival and departure recorded in the present study illustrates clearly that the narrow time window of actual spawning rushes observed during the dusk period is of primary importance and appears to represent the major spawning time (Samoilys & Squire 1994, Colin 1992). However, based on these observations alone, the possibility of dawn spawning cannot be ruled out. Johannes (1988) noted the observation of artisanal fishers in the Solomon Islands of spawning rushes of *P. areolatus* in the early morning as well as at dusk. It remains to be verified if this observation truly represents regular early morning spawning activities of *Plectropomus* spp.. Early morning assessments of spawning aggregation activities are required to address this question.

The low rate of participation at spawning aggregation sites by tracked specimens observed, i.e. 31% of all tracked individuals took part at one or more aggregation events, could be due to:

- Potential trauma or stress associated with capture, handling or transmitter attachment. This may lead a fish to delay its reproductive effort for some time, or even inhibit reproduction for the season (Pankhurst & Van Der Kraak in press). However, histological examination of the gonads of tracked specimens subsequently recovered which were not recorded to move to one of the aggregation sites monitored, indicated that all were reproductively active. Males had ripe gonads, with sperm ducts filled with spermatozoa, and females had mature, heavily vascularised and scarred ovaries, indicating spawning activities during the current reproductive season (S. Adams pers. com.).
- It is possible that not all reproductive activity occurs at major aggregation sites. Localised spawning activities may account for the lack of movements by some of the tracked specimens to the major aggregation sites detected. This is supported by the detection, in 1995, of three smaller courtship locations around Lizard Island (A, B & C, Fig. 5.1). Significantly, similar reports of non-participation in large spawning movements were reported by Colin (1992), with an unspecified proportion of adults being reported as remaining resident at home areas. Whether or not most reproductive effort occurs exclusively at large spawning aggregation sites, is of critical importance in devising suitable management strategies (Sadovy 1994), and requires detailed quantification.
- Individual variation in the seasonal timing of reproductive effort. Some of the tracked specimens captured for transmitter implantation might have either participated in spawning aggregation events very early in the season (i.e. prior to initial capture), or were preparing to spawn late in the year, i.e. after the tracking period terminated. As mentioned above, all recovered, non-aggregating specimens showed signs of reproductive activity in the year of tracking.

The present study presents the first detailed record of pattern of residence at spawning aggregation sites by individual fish. Some very clear differences in the

residence patterns at aggregations were observed between male and female P. *leopardus*. Males spend considerably longer at spawning sites than females, with stays of several days (multi-day) accounting for over 30% of all spawning movements of males. This evidence of longer stays for males is in accordance with histological information suggesting continuous spawning activity by males (Ferreira 1995), possibly over several days. Furthermore, build-up of aggregations of P. areolatus in the Solomon and Palau Islands have been reported to initially consist of males arriving several days before females (Johannes 1988, Johannes et al. 1994, 1995). The notion of longer stays may also be supported by the observation of large male P. leopardus setting up small territories on aggregation grounds on the Great Barrier Reef (Samoilys & Squire 1994). Sex dependent spatial and temporal patterns of presence on spawning grounds have also been reported for other fishes, such as the temperate water atlantic cod, Gadus morhua (Morgan & Trippel 1996). Male fish were recorded to arrive at spawning grounds first, while females moved into the area when ready to spawn and left once spawning was completed. Males of this species are known to set up temporary spawning territories, which females enter to spawn (Brawn 1961 in Morgan & Trippel 1996). However, no data on patterns or duration of residence were presented.

Male *P. leopardus* also possibly undertake more trips to spawning aggregation sites than females (median number of trips: 7 vs. 1), although this difference was not statistically significant. However, as larger fish seem to undertake more trips than smaller fish ( $r^2 = 0.389$ ), one might argue that, given the existence of protogynous hermaphroditism in *P. leopardus*, there will be a tendency for males (being on average larger than females) to undertake more trips. This observation is supported by the stronger relationship between number of trips and fish size for males ( $r^2 = 0.598$ ).

In contrast to males, females did day and overnight trips only, and were never recorded to stay for multiple days at the aggregation sites. The absence of any observed multi-day stays at aggregation sites by female coral trout might indicate that females do not undergo repetitive daily spawning events. This is supported by the observations that hormone induced ovulation of female *Plectropomus* spp. produced viable eggs only in the first of up to three consecutive nights (Tucker 1994, Tucker & Fitzgerald 1994).

Furthermore, hormone induced spawning in *Epinephelus striatus* resulted in spawning intervals of 28-75 days (Head et al. 1996). This does not contradict with observations made by Samoilys & Squire (1994) of repeated spawning rushes by the same female on any single day. Shapiro et al. (1993) reported repeated sightings of identically sized clusters, as well as an identified individual of Epinephelus guttatus at recognisable locations, over two to four days during the peak aggregation period in Puerto Rico, and suggested that the same individuals remained at the site for the duration of the aggregation. However, they did not identify members of the clusters, or indicate the sex of the individual. It is possible that females of this species may stay at the spawning aggregation sites for longer, if they have to travel distances of tens or even hundreds of kilometers to get there. Unfortunately, the limited number of female P. leopardus tracked to spawning aggregation events in the present study makes any generalised conclusions regarding repeated, multiple spawning by females difficult. Future studies clearly need to address this shortfall by targeting individuals selectively, either through developing non-destructive sexing techniques for specimen selection, or by preferentially targeting smaller individuals for tracking.

## 5.4.3. Use of aggregations for stock assessment

Spawning aggregations of serranids provide not only the possibility to monitor reproductive events closely, but may represent an unique opportunity for stock assessments and monitoring of relative changes in abundance of otherwise widely distributed and sparsely scattered populations (Johannes 1980, Shapiro *et al.* 1993, Johannes *et al.* 1994). However, as identified in the present study, in order to utilise aggregations of *P. leopardus* for stock assessment purposes, the following points need to be considered:

1. Based on the results obtained in the present study, only 31% of the monitored population of coral trout equipped with transmitters participated in spawning aggregation events. Such a low rate of participation may suggest that not all reproductive activity of *P. leopardus* occurs at major aggregation sites, or that considerable individual variation in seasonal timing of reproductive effort exists.

Either possibility may greatly influence any stock assessment undertaken at aggregation sites only. These results suggest strongly that any assessments clearly should attempt to evaluate the participation rate at aggregation events by the species to be monitored, and assess the potential for substantial year to year variation in this participation rate.

- 2. The observed significant difference in use patterns of aggregation events between male and female *P. leopardus*, especially in relation to residence time and probably even number of trips. This clearly results in sex specific turnover rates at aggregations. If, as the data suggests, most female coral trout only undertake one trip over the approximate two month tracking periods (corresponding to the peak, but not exclusive reproductive season), during which they might stay on average only 36 hours, this would clearly result in significantly higher turnover rates over the lunar cycle lifespan of any aggregation. Therefore, two repeated aggregation censuses on two separate days have a high likelihood of counting different females, but the same male individuals. In contrast, a single census would greatly underestimate the female stock component.
- 3. The problem of identification of sex during censuses at aggregations. Given the observed differences in usage patterns by the sexes, it is important to be able to estimate the sex ratio of fishes recorded at aggregation sites. Based on the visual recording of tracked specimens, it became apparent that 36% of the times a known male P. leopardus was seen at an aggregation site, it was not identified as a male based on observable courtship colours and behaviour. Samoilys & Squire (1994) state that during the major spawning aggregation that they monitored, 20% of observed P. leopardus were >50 cm, and presumed to be predominantly male (based on Goeden 1978). Of these large fish, 85% were confirmed to be male by courtship Hence, 15% of fish >50cm could not be sexed visually during their colours. observations. The discrepancy between their estimate and observations in this study could be based on the fact that they excluded fish <50 cm (some of which can be male). The fact that a proportion of the male population present at the aggregation site cannot be sexed during visual censuses, will have to be taken into account in relation to turnover rates and stock estimates. Furthermore, the observations undertaken by Samoilys & Squire consisted of behavioural observations, resulting in
longer time periods being allocated to the observation of individuals. For stock assessment purposes, one needs to consider that it would be a visual census situation, not a behavioural observation period, and hence involve relatively short observation periods per individual. Thus, larger proportions of males might not be identified accurately during each census. Therefore, the 36% of unsexed males found during the present underwater visual census component might be more applicable to the visual census monitoring situation.

The concentration of individuals at spawning aggregation sites provides a potentially unique opportunity to assess relative changes in stock structure, and hence allow more reliable determination of un-sustainable fishing pressures than can be obtained with censuses of a dispersed population. However, the participation rate of individuals at aggregation events (i.e. proportion of the population), and in particular the sex specific differences reported here will have to be accounted for in any attempt to use monitoring of aggregations for stock assessment purposes of *Plectropomus* spp..

### 5.5. Conclusions

- The clear documentation, using ultrasonic telemetry, of multiple, major spawning aggregation sites for *P. leopardus* on the chosen study reef, has some distinct implications for fisheries management strategies. The reliance of populations of *P. leopardus* on several aggregation sites per reef makes this species potentially less vulnerable to overfishing on aggregations, compared to species which utilise fewer sites in larger numbers, such as *P. laevis* and *P. areolatus* (Johannes 1988, Johannes & Squire 1988). However, the strong site fidelity observed for all individuals makes individual aggregations vulnerable to depletion.
- Based on the present tracking information, only 31% of monitored individuals participated in spawning events at one of the major aggregation sites. However, all recovered specimens showed clear signs of reproductive activity for the current reproductive season. This clearly indicates that not all spawning activities took place

at the known large aggregation sites, and should be regarded as strong evidence for the possibility of additional numerous, localised spawning events. This was further supported by the discovery of several smaller courtship sites. These results lend further support to the notion that *P. leopardus* stocks might be more resilient to fishing pressures on aggregations than reported for some of the other serranid species.

- The movement data obtained indicates within-reef catchment areas covering linear distances of over five kilometres. Some evidence suggests the possibility of interreefal movements in relation to spawning. However, this evidence is still circumstantial and such movements might be limited. Interrefal movements are most likely dependent on the interreefal habitats. Hence, the available evidence suggests that stocks of *P. leopardus* on each reef are dependent primarily on aggregation sites on their home reef for reproductive activities. Thus, sustainable management of at least some of the major aggregation sites on each reef might be appropriate for the long term maintenance of localised stocks of *P. leopardus*.
- The observed differences between male and female *P. leopardus* in residence duration at aggregation sites indicates definite sex dependent variations in turnover rates at these aggregations. Assuming similar vulnerability to the fishing gear for each sex, the longer residence times of males makes these fish considerably more vulnerable to aggregation fishing pressures.
- The observed sex dependent turnover rates, as well as the problem of visual gender identification, complicates the use of aggregation events for stock assessment purposes. However, further quantification of these factors may permit their incorporation into the assessments.

Table 5.1:Tracking periods, size and gender of the 13 P. leopardus recorded to<br/>move to spawning aggregation sites during 1993-95, out of the total of 35<br/>fish tracked during the three spawning periods monitored. Telemetry<br/>contact with fish PL 11 was lost before the specimen could be recovered<br/>for sex determination.

Fish	Tracking period	Tracking period	Fork length	Sex
ID	start	end	( <b>cm</b> )	
PL 4	15-August-1993	2-October-1993	52.5	male
PL 9	9-September-1994	10-November-1994	58.5	male
PL 11	19-September-1994	23-November-1994	47.4	?
PL 12	21-September-1994	20-November-1994	49.4	female
PL 13	19-September-1994	22-November-1994	48.5	male
PL 14	19-September-1994	21-March-1995	54.3	male
PL 20	31-October-1994	10-November-1994	43.9	female
PL 21	26-October-1994	24-November-1994	54.0	male
PL 29	13-March-1995	27-November-1995	49.1	female
PL 34	12-October-1995	27-November-1995	51.3	male
PL 35	10-October-1995	1-December-1995	46.3	male
PL 36	10-October-1995	1-December-1995	48.6	male
PL 42	24-October-1995	1-December-1995	51.8	female

Table 5.2:Minimum speed of movements to and from the spawning aggregation<br/>sites, for individual PL 21 and all *P. leopardus* combined. Basic one-way<br/>home range-spawning aggregation site distances are listed also. Data is<br/>based on observations with consecutive home range and spawning<br/>aggregation site fixes only (n = 20).

		All specimens		
Statistic	PL 21 speed (m min <sup>-1</sup> )	Overall speed (m min <sup>-1</sup> )	One way distance (home range-spawning site) (m)	
Mean	10.94	9.58	911.95	
SE	1.53	1.17	232.64	
Min.	3.64	2.90	223.00	
Max.	20.45	20.45	5,212.99	

Table 5.3:Records of tracked P. leopardus observed and identified during<br/>underwater visual censuses of spawning aggregations. The activity by<br/>the fish during the census was recorded as either "courtship" (displaying<br/>male courtship colours and behaviour) or "inactive" (i.e. no courtship<br/>behaviour). The histologically determined sex of the individuals is also<br/>indicated. Locations of spawning aggregation site censuses: GR:<br/>Granite Head; BR2: Backreef site 2; BR1: Backreef site 1; NP: North<br/>Point.

Year	Fish ID	Census	Location	Activity	Behavioural	Histology
		date			sex	
					determination	
1994	PL 9	3-Oct.	GR	inactive	?	
	PL 9	5-Oct.		courtship	male	male
	PL 12	3-Oct.		inactive	?	
	PL 12	9-Nov.		inactive	?	female
	PL 14	5-Nov.		courtship	male	male
	PL 14	10-Nov.		courtship	male	
	PL 21	13-Nov.		courtship	male	male
1995	PL 29	22-Oct.	BR2	inactive	?	female
	PL 34	22-Oct.		courtship	male	male
	PL 34	7-Nov.		inactive	?	
	PL 34	18-Nov.		inactive	?	
	PL 35	18-Nov.	BR1	inactive	?	
	PL 35	22-Nov.		courtship	male	male
	PL 36	22-Nov.		courtship	male	male
	PL 42	22-Nov.	NP	inactive	?	female

Table 5.4:Analysis of variance comparing the time of day of movements between<br/>male and female *P. leopardus* and the time of day of arrival and departure<br/>from the spawning aggregation sites. Data were arcsine square-root<br/>transformed due to the circular nature of time data.

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Treatment	Mean Square	d.f.	F	P
Sex	0.0357	1	1.4856	0.2252
Arrival-Departure	0.3258	1	13.5430	0.0003
Sex x Arrival-Departure	0.0278	1	1.1555	0.2845
Residual	0.0241	124		



Plate 5.1: Ultrasonically tracked *P. leopardus* specimen number PL 14 (fork length = 54.3 cm) displaying male courtship colours (*sensu* Samoilys & Squire 1994) during SCUBA observations at spawning aggregation site Granite Head in November 1994 (depth 20 m). Note yellow T-bar anchor tag near dorsal fin used for visual recognition of tracking specimens. A second coral trout is faintly recognisable further in the background, below and to the left of PL 14.



Figure 5.1: Locations of major spawning aggregations and minor courtship sites of *P. leopardus* at Lizard Island (northern Great Barrier Reef, Australia), as identified through ultrasonic telemetry and underwater visual surveys on SCUBA between 1993-1995. Two possible additional locations suitable as aggregation sites are indicated (Lizard Head, South Island Point). Prevalent tidal currents are indicated (arrows). Prevailing winds from south-east. *Major aggregation sites (black):* NP: North Point, GR: Granite Head, BR1: Backreef Site 1, BR2: Backreef Site 2. *Minor courtship sites (grey):* A: Osprey Island, B: Corner Beach Reef, C: Palfrey Island.



Figure 5.2: Locations of home ranges of the 13 *P. leopardus* tracked using ultrasonic telemetry between 1993-1995 which participated at aggregation events, and schematic movement paths to their respective spawning aggregation sites (thin arrows). Numerals indicate the number of tracked fish resident at each location. Grey circles: Locations of home ranges. Black circles: Spawning aggregation sites.



Figure 5.3: Location of initial capture & release (August 1995) of *P. leopardus* marked externally with freeze-brands, and movements to visual resighting during underwater visual surveys of the spawning aggregation site at North Point in October 1995. Grey circles: Location of capture, mark & release. Black circle: Resighting location at spawning aggregation site North Point.



Figure 5.4: Initial capture and release location at Granite Head (GR) spawning aggregation site during new moon periods in 1993/1994 of three *P*. *leopardus* equipped with ultrasonic transmitters. Contact with specimens was lost shortly after release. Locations of recapture of fish by scientific, commercial and recreational fishers on neighbouring reefs one and three years after initial capture indicates inter-reefal movements by coral trout. Direct linear distance paths are indicated (3, 7.5, 11 km). Black circle: Location of initial capture and release at Granite Head. Grey circle, ?: Best estimate of recapture locations that was obtainable from fishers.



Figure 5.5: Number of P. leopardus equipped with ultrasonic transmitters present at spawning aggregation sites per day, pooled for all four major spawning aggregation sites. A) Data for all tracking periods (1993-1995) pooled, and standardised to one lunar cycle (full moon to full moon). B) Data for 1994 tracking period, standardised to two consecutive lunar cycles.
C) Data for the 1995 tracking period, standardised to two consecutive lunar cycles. Black circles: Full moon. White circles: New moon.



Figure 5.6: Representative time plot of presence of *P. leopardus* PL4 (a male) at the spawning aggregation site Granite Head during 1993. Black horizontal lines indicate time periods of presence at the aggregation site. Vertical spacing of the lines serves to illustrate separate spawning site trips only. The time period indicated as a grey vertical band represents interruption of the tracking program due to bad weather (no data). Black circles: Full moon. White circles: New moon.



Figure 5.7: Underwater visual census counts of P. leopardus observed during the late afternoons at the spawning aggregation sites. Counts were conducted over 50 x 20 m areas in each census during a single pass on SCUBA. Dates of censuses with zero counts are indicated by \*. Black circles: Full moon. White circles: New moon. A) Total 1994 census counts at the two spawning aggregation sites known at that time (Granite Head & North Point). B) Total 1995 census counts at all four aggregation sites combined. C) Total counts of 1995 censuses from the largest aggregation site only (Granite Head).



Figure 5.8: Percentage distribution of arrival (A, n = 55 observations) and departure (B, n = 45 observations) from spawning aggregation sites for ultrasonically tracked *P. leopardus* during 1993-1995, grouped into three hour intervals. Graphs contain spawning movement occasions only if fixes included late afternoon and early morning twilight sampling.



Figure 5.9: Maps illustrating home ranges and spawning aggregation sites utilised by two representative specimens of *P. leopardus*. +: Home range positions.
Black circles: Positions of fish recorded during movements associated with spawning events, including those corresponding to locations of recorded spawning aggregations. A) Fringing reef fish PL 42 inhabiting the north-eastern side of Lizard Island, showing the home range area in a location locally known as Bommie Bay, and the spawning aggregation site at North Point used by this specimen (distance = 2,043 m). B) Patch reef fish PL 29 inhabiting the backreef area on the western side of the island. The spawning aggregation site used by PL 29 (Backreef Site BR2) was located at the western side of the outermost patch reef in 20-25 m water depth (distance = 952 m).



Figure 5.10: Maps showing the unusual choice of a spawning aggregation site on a neighbouring patch reef by one of the male *P. leopardus* inhabiting the same patch reef on the backreef area on the western side of Lizard Island. Black circles: Spawning aggregation sites. +: Home range positions. A) Fish PL 34 utilised a spawning aggregation site located 742 m away on the neighbouring patch reef, despite the existence of a well established spawning site on the home patch reef. B & C) Both PL 35 (B) and PL 36 (C) used the local spawning aggregation site (distance 284-326 m, respectively).

B)

Metric Grid North (m)

A)

C)



Figure 5.11: Time plot illustrating the presence of *P. leopardus* PL 34 at the spawning aggregation site BR 2 during 1995. Black horizontal lines indicate the time periods of stay at the aggregation site. This specimen did four separate trips to the aggregation site. The grey horizontal line (14-October to 20-October) indicates the time during which tracking contact was lost with PL 34 in the home range area (vertical spacing for illustrative purposes only). Spawning aggregation site BR 2 was detected through re-acquisition of ultrasonic signal from PL 34 at this site on the 20-October. Black circles: Full moon. White circles: New moon.



Figure 5.12: Total residence time (h:min +/- SE) for female and male *P. leopardus*, averaged over all tracking specimens participating in spawning aggregation events during 1993-1995 (n = 12). Mean values are presented numerically also.



Figure 5.13: Relationship between total residence time at spawning aggregation sites and body size (fork length) for male *P. leopardus* tracked during 1993-1995.



Figure 5.14: Percentage distribution of day-, overnight- and multi-day trips to spawning aggregation sites undertaken by *P. leopardus* tracked during 1993-1995. A) Overall distribution, indicating predominance of overnight trips. Percentage values indicated numerically. B) Breakdown of trip type by gender. Note the absence of females undertaking multi-day trips, and the predominance of females in the day-trip category.



Figure 5.15: Comparison of number of spawning trips undertaken by female and male *P. leopardus* tracked during 1993-1995, and the relationship between number of trips and size of fish (fork length). A) Mean number (+/- SE) of trips of female and male coral trout observed by ultrasonic telemetry during 1993-1995. B) Relationship between number of trips and body size for all coral trout, suggesting an increase in number of trips with increasing size of fish. C) Relationship between number of trips an increase in number of trips and body size for male coral trout, suggesting an increase in number of trips with increasing body size. Female fish are superimposed for illustration purposes, but not included in regression.

A)

B)

C)

# Chapter 6:

# MOVEMENTS, SPATIAL PATTERNS AND POPULATION ESTIMATES OF *PLECTROPOMUS LEOPARDUS*: IMPLICATIONS FOR MARINE PROTECTED AREAS

# 6.1. Introduction

In recent years the importance of movements of fishes to the understanding of population dynamics and patterns of community structure, has been increasingly recognised (e.g. Robertson 1988, Hestbeck et al. 1991, Turchin 1996). Of particular interest is the increasing importance allocated to movement information by fisheries scientists and managers (e.g. Hilborn 1990, Hilborn et al. 1990, Schwarz & Arnason 1990, Hilborn & Walters 1992). In the context of the present study, information about movement and spatial patterns are of central importance to the current debate about the use of marine protected areas as a fisheries management tool for coral reef environments (e.g. Davis 1981, 1989, Russ 1985, Alcala 1988, Alcala & Russ 1990, Bohnsack 1990, Roberts & Polunin 1991, Carr & Reed 1993, DeMartini 1993, Dugan & Davis 1993, Holland et al. 1993a, 1996, Polunin & Roberts 1993, Russ et al. 1993, Rowley 1994, Russ & Alcala 1994, 1996a&b, Dayton et al. 1995, Man et al. 1995). In a fisheries context, the two major, although not exclusive, objectives of marine protected areas are to ensure continued recruitment supply via maintenance of a critical minimum spawning stock biomass, 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. Gitschlag 1986, Beinssen 1989a, Bryant et al. 1989, Russ & Alcala 1989, Alcala & Russ 1990, Bohnsack 1990, Polacheck 1990, Yamasaki & Kuwahara 1990, DeMartini 1993, Holland et al. 1993a, 1996, Russ et al. 1993, Davies 1995, Rakitin & Kramer 1996, Russ & Alcala 1996a&b).

It has been suggested that marine protected areas may form a more cost-effective management option for stock maintenance (e.g. Alcala 1988, Davis 1989, Alcala & Russ 1990, Roberts & Polunin 1991, Rowley 1994, Dayton *et al.* 1995, Man *et al.* 1995). This may be the case particularly for coral reef fisheries, in which more conventional fisheries management strategies are especially difficult to administer (Bohnsack 1990, Polunin 1990, Roberts & Polunin 1991, Russ 1991). Coral reef fisheries are generally multi-specific and multi-gear, with a predominance of artisanal and subsistence fishers spread over large areas. Furthermore, the importance of coral reef fisheries may not lie so much in the actual yields (~ 5 x  $10^8$  kg yr<sup>-1</sup>, Longhurst &

Pauly 1987), but rather in employment and subsistence opportunities for low-income fishers with few alternative employment opportunities (Russ 1991). Given these complexities and the often limited resources available to developing countries for research and management, marine protected areas may offer a simplified, alternative management option.

The effectiveness of marine protected areas, especially in the developing world, appears strongly linked to local fishing community support (Cabanban & White 1981, White 1988, Alcala & Russ 1990, Bohnsack 1990, White *et al.* 1994). Under these circumstances, suggestions of large scale benefits (i.e. stock wide recruitment) appear often less convincing or encouraging to communities than promises of local benefits (i.e. "spillover") (Russ & 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 of marine protected areas as a fisheries management option. Therefore, empirical data on rates of movements and crossings of protected area boundaries by target species are urgently required.

The most commonly used method to address and quantify movements generally involves external tagging or marking and the use of a mark-release-recapture study (e.g. Shepherd 1988, Hilborn & Walters 1992, Diffendorfer *et al.* 1995). Historically, tagging methods have been used primarily to address population size, capture probabilities and mortality rates of target species (e.g. Ricker 1975, Nichols & Pollock 1983, Lebreton *et al.* 1992, Nichols 1992). However, more recently, the importance of marking or tagging to document movement patterns of relevance to fisheries research and management has been stressed (e.g. Hilborn 1990, Hilborn *et al.* 1990, Schwarz & Arnason 1990, Hilborn & Walters 1992, Schweigert & Schwarz 1993). Hilborn *et al.* (1990) estimated that the increased value to North American fisheries that could be obtained through information gained from fish marking exceeds US\$ 1 x  $10^9$  yr<sup>-1</sup>.

The most widely used form of tagging in fish studies utilises external tags of the anchor or dart tag type, which are anchored between dorsal pterygiophores (e.g. Davies 1995). These tags have the advantage of being economical, relatively small and fast to

apply to the animal, permitting large samples to be tagged. However, they are known to have several limitations (reviewed by Kearney 1989), including high tag loss rates in coral reef fishes (e.g. Whitelaw & Sainsbury 1986, Davies 1995). Furthermore, most recaptures generally rely on returns from the fisheries or research surveys using fisheries dependent recapture methods (e.g. hook & line or fish traps, Davies 1995).

An alternative tagging method employs thermal marking techniques, generally known for their agricultural use as cattle brands. With fishes, both hot (e.g. Coombs et al. 1990, Hargreaves 1992) and cold branding (e.g. Raleigh et al. 1973, Bryant et al. 1990, Knight 1990, Moser et al. 1990) has been used. Retention times of marks is highly variable, with the maximum period recorded being 2 years (Hershberger et al. 1982 in Hargreaves 1992). Species specific differences in mark retention times between hot and cold branding methods have been reported also (e.g. Coombs et al. 1990). Hot brands have been reported to injure fish more than cold brands, but were faster to apply and considered more convenient, as long as access to an appropriate heating or power source is guaranteed (Hargreaves 1992). Cold brands on the other hand, while resulting in less injury, are thought to be slower to develop and may be difficult to read initially (Cane 1981), as well as requiring supplies of appropriate cooling agents (e.g. liquid nitrogen). Thermal marking appears to have been used with a coral reef fish only once before (Samoilys 1987). Samoilys, using 25mm x 35mm branding irons with a mixture of dry ice and acetone as cooling agent, found that 75% of individual numeric brands on Plectropomus leopardus were positively identified up to 150 days after tagging during SCUBA observations. Significantly, Samoilys reported that, on average, brand retention was good for the first two months, with brands starting to fade thereafter. However, maximum brand recovery (i.e. positive identification) was 289 days. Unlike the standard tags mentioned above, large sized thermal brands permit visual identification of individually marked fish underwater from a distance on SCUBA for periods up to 150 days (Samoilys 1987).

Underwater visual census surveys conducted along standardised transects have been used extensively for obtaining abundance and density estimates of fishes in the freshwater (e.g., Ensign *et al.* 1995) and marine environments (Brock 1954, Brock 1982, Bellwood & Alcala 1988, Ayling & Ayling 1986, 1992, 1994, Ayling *et al.* 1992). The use of visual census surveys as a sampling technique for coral reef fish was reviewed by Cappo & Brown (1996), and has received detailed analysis of precision, accuracy, bias and efficiency, particularly in relation to coral reef fishes (e.g., Sale & Sharp 1983, Bell *et al.* 1985, Thresher & Gunn 1986, St. John *et al.* 1990, Mapstone & Ayling 1993).

The established suitability of underwater visual census surveys for assessing coral trout populations, and the satisfactory levels of readability of cold brands reported for *P. leopardus* (Samoilys 1987), provided an unique opportunity to utilise standardised underwater census techniques of individually identifiable fish to assess and estimate movement patterns of *P. leopardus*. Furthermore, this is the only study so far that has permitted the direct comparison between a conventional mark-release-recapture method (external marking combined with underwater visual census) and a detailed ultrasonic telemetry study undertaken concurrently on the same species and in the same location. In addition, the existence of established marine park zoning boundaries at the study location (Lizard Island, Great Barrier Reef) provided the opportunity to experimentally address the question of movements in relation to marine protected areas. The primary objectives of this study were:

- Evaluate movement patterns, spatial distribution and population size of *P. leopardus* using a standardised mark-release-resignting technique, combining a fisheries based initial capture technique (hook & line) with a fisheries independent resignting method (underwater visual census).
- Compare results obtained from the mark-release-resighting study with comparable data collected independently using ultrasonic telemetry.
- Assess the implications of these data to the existing marine protected area zoning at Lizard Island.

# 6.2. Methods

#### 6.2.1. Study site and sampling protocol

This study was conducted along the sheltered western, northern and northeastern sides of Lizard Island, Northern Great Barrier Reef (Lat. 14<sup>0</sup> 40' S; Long. 145<sup>0</sup> 28' E), during August - October 1995 (Fig. 6.1). Initial capture of target species by hook and line was undertaken by two contracted commercial fishers (Mr C. Hagen & Ms J. Byron) over a nine day period (18-26 August 1995). Fish were caught using 80 lb (36 kg) breaking-strain handlines rigged with a running sinker and a single 8/0 or 9/0 hook baited with West Australian pilchard (*Sardinops neopilchardus*). Each fisher worked independently from a 4.1 m aluminium dinghy.

To distribute effort evenly, the study area was divided into 4 sections, each approximately 3 km long. Each fisher fished two "sessions" per day, with average duration of four hours per session. Each location where a dinghy anchored and fished will be referred to as a "hang" (sensu Davies 1995). In order to distribute fishing effort evenly within the allocated sections, hang times were allocated (minimum: 15 mins; maximum: 60 mins). A maximum fishing depth was set at 10 m, in order to avoid fishing effort being allocated to deep reefs. Reefs deeper than 10 m could not be sampled easily for recaptures, because of dive limitations (see section 6.2.3. below). Target species (Plectropomus leopardus) caught at each hang were kept in numbered 50 litre bins and regularly supplied with fresh seawater. For each hang, fishers recorded exact location (using aerial photos), start and finish time of fishing (hook-line-hour), number of trout caught and the storage bin number corresponding to each hang. Hookline-hours were defined as the actual time period a baited hook was in the water and available to the fish. All incidental, non-target by-catch was released. Furthermore, 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 spatial location of individual hangs by the author at the end of each session. These marker buoys also aided the fishers to the correct location for the return and release of tagged fish at their

exact capture location. Collected fish were brought to a centrally anchored boat after each hang, for freeze branding by the author.

#### 6.2.2. Freeze branding technique

Capture data collected by the commercial fishers were cross-checked for correct location and hang details before fish were freeze branded. Prior to freeze branding, each fish was measured (fork length, FL) and tagged with two standard T-bar anchor tags (Hallprint Pty Ltd, Australia). Individual numerals were freeze branded onto the caudal peduncle on each side of the specimen using branding irons (Plate 6.1). Branding irons were those used by Samoilys (1987), and consisted of copper block bases with individual numerals ( $25 \times 25 \times 2 \text{ mm}$  in size) on each iron. The branding duration for each numeral was 10 seconds (see section **6.2.2.1**. below), 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:  $-196^{\circ}$  C) for at least one minute before reuse. After successful branding (Plate 6.2), marked individuals were returned by fishers for release at the exact location of capture.

#### 6.2.2.1. Freeze branding trial

In February 1995 a freeze branding trial was conducted to determine the most suitable duration of brand application. Eight coral trout were kept under aquarium conditions. Branding was randomly assigned to one of four brand durations (5, 10, 15 or 20 seconds). Fish were retained in the aquaria for three weeks and inspected periodically. After three weeks, the five-second brands were barely readable, 10-second brands were considerably clearer and distinct, while some 15-second and many 20-second brands had burned into muscle tissue underlying the skin, producing infected, open wounds. Therefore, in order to reduce chances of secondary infections, the 10-second brand duration was chosen (see also Samoilys 1987).

A field trial was conducted subsequently to examine what proportion of brands (10 seconds) could still be read after three months. Samoilys (1987) found that freeze brands using dry ice (frozen CO<sub>2</sub>) as coolant remained dark and visible for 1-2 months before starting to fade. The field trial consisted of 25 coral trout, which were double tagged with T-bar anchor tags, branded (10 sec.; cooling agent: liquid nitrogen) and released at the capture sites during late February and early March 1995. After three months an underwater visual census survey was undertaken, covering a 13,750 m<sup>2</sup> area. The survey consisted of searching five meter wide transects of 100-400 meters distance. The distances varied depending on depth and dive-bottom time available. Transects were allocated only to areas of capture and release of branded specimens. A total of 35 Plectropomus leopardus were sighted, 12 (34.28%) of which were marked with at least one freeze brand or T-bar anchor tag. Five of the 12 marked coral trout (41.66%) had freeze brand numbers on at least one side of their bodies which were still readable. Thus, 14.28% of all trout sighted during this survey were identifiable by their brand number. However, brands were often faint or washed out, requiring close approach by the observer for correct identification (Plate 6.3). Based on these estimates three months was considered the maximum limit for use of this freeze brand technique for underwater visual census of coral trout.

#### 6.2.3. Resighting method and effort distribution

A visual "recapture" technique was employed using standardised underwater visual census (UVC) surveys. "Recaptures" consisted of resightings of the freeze branded specimens during visual census. Two separate recapture occasions were conducted during September (D. Zeller) and October (D. Zeller & G.R. Russ) 1995, being one and two months after the freeze branding, respectively. Resighting effort was distributed evenly across reefs within the entire study area. In fringing reef environments survey transects followed the reef contour. Patch reefs were surveyed with transects along the reef edge, as well as transects across the patch reef, using compass bearings for orientation and direction. General emphasis was placed on the reef slope habitat, where *P. leopardus* are most abundant (Choat 1968, Kingsford 1992).

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The basic sampling unit consisted of 100 m x 5 m belt transects. The transect length of 100 m was chosen to minimise the occurrence of zero abundance counts of target species (A.M. Ayling pers. com.). Choice of transect width (5 m) was based on the average underwater visibility in some areas around Lizard Island. Transect tapes were laid while conducting the surveys, in order to avoid causing attraction of or disturbance to the fish community by previously laid tapes. Start and end points of each transect were marked with surface buoys for recording the exact spatial position of transects from the surface after each census. All census transects were restricted to the depth strata between datum (lowest astronomical tide) and the 10 m depth contour (or sand-reef interface). Transect depth was limited to a maximum of 10 meters, with average census depth maintained at 6-8 meters to allow maximum dive bottom-times for sampling efficiency.

During each census, all coral trout sighted within the transect width and up to 10 meters in front of the projected transect line were counted, sizes (TL) were estimated in 5 cm size classes, and their location along the transect line recorded to the nearest meter. Sightings of tagged fish were recorded and visible freeze brands identified where possible (Plate 6.4). Any tagged trout observed outside the transect were investigated similarly and recorded, but clearly marked as a non-transect recapture on the data sheets. Size estimation was trained prior to conducting the survey using the "stick" method (Bell *et al.* 1985). Furthermore, any size estimates of resighted freeze branded fish were used as ongoing verification of the accuracy of visual estimation using lengths measured during the freeze branding process. Any potential growth increments since tagging would clearly not exceed the 5 cm size groups used for allocation.

#### 6.2.4. Data analysis

The spatial position data for line capture locations ("hangs"), visual census transects, fish sighting locations, and the available reef area measures were digitised from calibrated aerial photos using SIGMASCAN<sup>®</sup>. Distances moved between capture and resighting were calculated using CALHOME<sup>®</sup> (Kie *et al.* 1994, U.S. Forest service) on IBM<sup>®</sup> compatible computers, and all data were analysed using STATISTICA<sup>®</sup>.

Population size estimates were calculated using mark-release-recapture formulae in Ricker (1975), mark-release-resighting estimates using NOREMARK<sup>®</sup> (White 1996), and estimates of density derived from visual census coupled with area estimates of available reef substratum.

The patterns of spatial distribution and movements of *P. leopardus* were examined using the data obtained from the mark-release-resighting study, and were compared to data obtained through ultrasonic tracking of individual specimens (see Chapters 2 and 4 for details of ultrasonic telemetry methodology and home range estimations). Of particular interest were the distances individual fish had moved between initial capture and resighting, and the patterns of dispersion of *P. leopardus* at the spatial scale of transects, i.e. 500 m<sup>2</sup>. Both these aspects were evaluated with respect to reef habitats (fringing vs. patch reefs), management zones and associated boundaries (closed and open to fishing), and time period between recaptures. The three time periods considered during analysis were:

- 1. Initial capture on hook & line (August 1995) to first underwater visual census (September 1995, UVC 1). Total time: approximately one month.
- 2. Initial capture on hook & line to second underwater visual census (October 1995, UVC 2). Total time: approximately two months.
- 3. First census to second census (UVC 1-2). Total time: approximately one month.

The data collected during the visual census study permitted the calculation of estimates of population sizes of *P. leopardus*. Two separate estimation techniques were applied, one based on the mark-release-resighting information and the second based on the density estimates obtained during the visual census surveys. The mark-release-resighting estimates calculated were: the Joint Hypergeometric Maximum Likelihood Estimator (JHE, Neal *et al.* 1993), the Minta-Mangel Bootstrap Estimator (MM, Minta & Mangel 1989), the Bowden Model Estimator (BM, Bowden 1993), as well as the traditional mark-recapture estimators of Petersen (Ricker 1975), Bailey (1952 in Ricker 1975).

Statistical analyses involved t-test, analysis of variance and covariance (ANOVA & ANCOVA), Mann-Whitney U-test, and  $\chi^2$  homogeneity and goodness-of-fit tests. Statistical assumptions underlying the various parametric analyses were examined prior to analysis (e.g. homogeneity of variances: Cochrans test; normality: residual plots), and data was log<sub>10</sub> transformed where appropriate (Sokal & Rohlf 1981, Underwood 1981). Non-parametric statistics were applied if transformation failed to satisfy the assumptions underlying parametric analyses.

# 6.3. Results

Initial capture of *P. leopardus* on hook & line conducted by the two contracted commercial fishers over a nine day period, resulted in 174 individual "hangs", with 72 hours & 5 minutes of total hook-line-hours. Thus, on average, each "hang" was fished actively for 24 minutes. A total of 216 *P. leopardus* were caught, resulting in an overall catch-per-unit-effort (CPUE) of 2.99 coral trout per hook-line-hour. The catch per unit effort differed between management zones closed and open to fishing (t [172] = 3.0652, p = 0.0026), with a CPUE of 3.17 and 1.23 coral trout per hook-line-hour in closed (n = 100 "hangs") and open (n = 74 "hangs") zones, respectively. Of the 216 captured fish, 33 were either kept for ultrasonic transmitter implantation (n = 20), or were judged to be hooked badly (throat- or severely gill-hooked) and sacrificed (n = 13). Hence, 183 of the initial 216 coral trout were released at their capture site after tagging and freeze-branding.

The visual census effort distribution resulted in 308 separate transects being sampled, covering an area of 154,000 m<sup>2</sup> (Table 6.1). Sampling effort was allocated as 167 transects and 141 transects for first and second survey, respectively (Table 6.1). The total available reef area, as defined for the visual census survey (i.e. datum - 10 m) comprised 750,966 m<sup>2</sup> in the general study area (Table 6.1, Fig. 6.1). Thus, the two census surveys sampled respectively, 11.12% and 9.39% of the available, census-defined reef area in the general study area (Table 6.1).

During the two UVC surveys a total of 817 coral trout were sighted, consisting of 440 and 377 fish for first and second census, respectively (Table 6.2a). Of the total sightings, 44 (UVC 1) and 26 (UVC 2) were recaptures (resighting) of freeze branded individuals. Thus, recapture (resighting) rates were 24.04% and 14.21% for UVC 1 and UVC 2, respectively (Table 6.2a). Based on the total fish counts and area covered by the transects, an overall density estimate of  $5.31 \pm 0.2585$  (SE) coral trout per 1,000 m<sup>2</sup> of reef area was derived (Table 6.2a). A breakdown of total census data by reef habitat (i.e. fringing vs. patch reef), indicated sightings of 362 and 455 coral trout in the 128 and 180 transects conducted in fringing and patch reef habitats, respectively (Table 6.2b). These abundance counts resulted in density estimates of  $5.66 \pm 0.4018$  (SE) coral trout per 1,000 m<sup>2</sup> for fringing reef, and  $5.06 \pm 0.3374$  (SE) coral trout per 1,000 m<sup>2</sup> for patch reef habitats (Table 6.2b). Evaluation of UVC data by reef management zones (i.e. open vs. 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 (Table 6.2c). Thus, density estimates of  $4.56 \pm 0.3880$  (SE) and  $5.53 \pm 0.3148$  (SE) coral trout per 1,000 m<sup>2</sup> were obtained for open and closed zones, respectively (Table 6.2c). Density estimates for open and closed zones did not differ significantly (t  $_{[306]} = 0.4904$ , p = 0.6242).

#### 6.3.1. Size distributions

The size frequency distributions of fish encountered during the mark-releaseresighting study did not differ between reef management zones open and closed to fishing ( $\chi^2_{[11]} = 11.91$ , 0.5 > p > 0.25, Fig. 6.2a & b). The average size of fish recorded in open zones did not differ significantly from those observed in closed zones (t<sub>[1040]</sub> = 1.6015, p = 0.1096, Fig. 6.2c). Similarly, the size distribution of fish did not differ between fringing and patch reef habitats ( $\chi^2_{[11]} = 14.61$ , 0.25 > p > 0.1, Fig. 6.3a & b), with the average size of fish not differing significantly between either habitat (t<sub>[1040]</sub> = 1.4071, p = 0.1597, Fig. 6.3c). However, the size distribution for fish collected by hook & line did differ significantly from the size distribution obtained by visual census ( $\chi^2_{[11]}$ = 43.62, p < 0.001, Fig. 6.4a & b). The average size of fish collected by hook & line was 5.17 cm larger than the average size recorded by visual census (Mann-Whitney U  $_{[216,826]} = 6.1129$ , p < 0.001, Fig. 6.4c).

#### 6.3.2. Distances moved

A total of 93 measures of distances moved by branded specimens between time periods were recorded during the two visual census surveys (Table 6.3). Overall, there was no clear relationship between distances moved and size of individual fish ( $r^2 =$ 0.0324, p = 0.0859, n = 93, Fig. 6.5). The distance estimates obtained through visual census resightings ranged from 4.12 m to 387.20 m (overall mean = 94.89 m ± 9.48 (SE)) between individual points of capture and/or resighting (Fig. 6.5). The distance measures obtained represent straight linear distances between points of capture and/or visual recapture. Multiple resightings and resightings recorded outside of the predetermined transect limits while censusing were included also (Table 6.3).

Mean distance moved between recapture occasions differed between the two reef habitats (fringing and patch reefs) examined (t  $_{[91]} = 2.9207$ , p = 0.0044). Fish on patch reefs moved, on average, 48.3 m more between recapture occasions than fish on fringing A two-way comparison of mean distances moved between reefs (Fig. 6.6a). management zones (closed and open to fishing) and between time periods indicated that fish from closed zones moved further between recapture occasions than did fish from open zones (p = 0.0071, Table 6.3b, Fig. 6.6b). Given that patch reef fish were recorded as moving further than fringing reef fish (see previous analysis), but were not represented in the open zone data component, the two-way analysis between management zones and time periods was re-analysed using a subset of data consisting only of fringing reef fish (n = 56, Table 6.3c). While the data subset (excluding patch reef data) resulted in reduced distances moved for fish from closed reefs (from 114.11 m  $\pm$  12.57 (SE) to 99.64 m  $\pm$  14.63 (SE), Fig. 6.6b), fish from fringing reefs closed to fishing nevertheless did move further between recaptures than did fish from fringing reefs open to fishing (p = 0.0440, Table 6.3c, Fig. 6.6b). A direct three-way comparison of distances moved between the factors reef habitat (fringing vs. patch reefs), management zone (closed vs. open to fishing) and time periods between recaptures (UVC 1 vs. UVC 2 vs. UVC 1-2) was not possible due to the lack of resightings of branded individuals on patch reefs open to fishing during either of the two visual census surveys. This resulted in missing treatment levels (habitat: patch, zone: open, time period: UVC 1, UVC 2, UVC 1-2), thus compromising direct statistical comparison. In order to evaluate the effects of the three factors, habitat type was analysed separately.

Mean distances moved per day, as determined using ultrasonic telemetry (Chapter 4), did not differ between habitats (t  $_{[34]} = 0.9078$ , p = 0.3704) or between management zones (t  $_{[34]} = 0.9367$ , p = 0.3555). However, it is worth noting that the habitat and zone patterns observed in the telemetry data appear similar in trend to those recorded for the mark-resighting study (Fig. 6.7). Despite the difference in the two data types obtained by each of the two collection methods, i.e. one representing average daily distances moved (ultrasonic telemetry), the other single linear distance between capture and resighting at least one month later (visual census), a direct comparison of distances moved between the two methods was undertaken. This comparison indicated clearly that the daily distances moved recorded through telemetry were larger than those obtained from the visual census surveys (t  $_{[127]} = 5.4597$ , p < 0.0001). Telemetry fish moved, on average, 186.61 m  $\pm$  11.96 (SE) per day, while freeze branded fish moved 94.89 m  $\pm$  9.48 (SE) between recapture occasions (Fig. 6.8).

Basic home range parameters (home range area, length and width) derived from data determined through ultrasonic telemetry (Chapter 4) were examined for differences between management zones open and closed to fishing. Only coral trout whose home range did not cross zone boundaries were used for the analysis (n = 38). Taking into account differences in size of individual fish (FL) and sample sizes per home range estimate (number of telemetry fixes per estimate), no significant differences were detected for either home range area, length or width between zones open or closed to fishing (Table 6.4).
#### 6.3.3. Management zone boundary movements

Of the 183 freeze branded fish released, 10 individuals had their capture/release location within ~500 m either side of a management zone boundary (Fig. 6.1). 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  $35.62 \text{ m} \pm 1.64$  (SE), with a range of 33.24 - 37.01 m. No cross-boundary movements between zones closed and open to fishing were recorded.

During the 1993-1995 ultrasonic tracking study, eight P. leopardus equipped with transmitters had home ranges which straddled the management zone boundaries at Granite Head and at Chinaman's Ridge (Lizard Island, Fig. 6.9). On average, 31.23 % and 68.76 % of the home ranges of these fish were located in the open and closed zones, respectively (Table 6.5). Based on the number of times a fish was recorded on either side of the boundary, these fish spent, on average, 27.49  $\% \pm 10.81$  (SE) of their time in the zone open to fishing (Table 6.5). The total number of boundary crossings recorded for the specimens being tracked ranged from 2 to 64 (mean =  $27.5 \pm 8.6$  SE) for tracking periods of 8 and 66 days, respectively (Table 6.5). In order to derive estimates of rates of crossings, the data were standardised to crossings per day and crossings per month (based on a "30 day month"). On average, the observed specimens undertook crossings at the rate of 0.51 per day or 15.27 per month, with the lowest rate being 3.62 crossings per month, and the highest being 29.09 per month (Table 6.5). Thus, P. leopardus tracked using ultrasonic telemetry, would cross management zone boundaries bisecting their home ranges between approximately once daily to at least once every 10 days (Table 6.5).

### 6.3.4. Dispersion pattern

The frequency distribution of number of coral trout per transect did not conform to a Poisson distribution for the combined surveys ( $\chi^2_{[6]} = 107.60$ , p << 0.001, Table 6.6). The variance-mean ratio of 1.94 clearly indicated that the observed distribution of *P. leopardus* was clumped at the scale of 500 m<sup>2</sup> (Table 6.6). Examining the pattern of

dispersion of coral trout by reef habitat indicated that fish were not distributed randomly, both on fringing reefs ( $\chi^2_{[5]} = 25.52$ , p << 0.001, Table 6.6) and on patch reefs ( $\chi^2_{[5]} = 75.40$ , p << 0.001, Table 6.6). In both habitat types, trout were clumped, with variance-mean ratios of 1.83 and 2.03, for fringing and patch reefs respectively (Table 6.6). The assessment of dispersion patterns of coral trout in relation to management zones indicated that the observed distribution of number of trout per transect in zones closed to fishing did not conform to a Poisson distribution ( $\chi^2_{[6]} = 115.31$ , p << 0.001, Table 6.6). With a variance-mean ratio of 2.11, fish in zones closed to fishing were clearly clumped (Table 6.6). In contrast, trout dispersion in zones open to fishing was random, with a variance-mean ratio of 0.98 ( $\chi^2_{[4]} = 8.53$ , 0.1 > p > 0.05, Table 6.6).

## 6.3.5. Population size estimates

All population estimators using mark-resighting data returned very similar results, with population estimates ranging from 1,890 (BM) to 2,134 (MM) for the census-defined depth strata in the section around Lizard Island used for the study (Table 6.7a, Fig. 6.10). The area of reef with census-defined depth strata used for this study was 750,966 m<sup>2</sup> (Table 6.7b). Estimation of population size based on the density estimates obtained during the visual census surveys (5.31 fish/1000m<sup>2</sup>) for the same census-defined area, resulted in an estimate of 3,988 fish (Table 6.7a, Fig. 6.10).

Assuming that the coral trout distribution and density observed in the study area is representative for census-defined depth strata for the whole of Lizard Island reef, one can scale up the obtained population estimates to the available reef area of 2,503,809 m<sup>2</sup> (Table 6.7b). This resulted in extrapolated population size estimates ranging from 6,301 (BM) to 7,115 fish (MM) for mark-resighting estimates, and 13,295 fish based on the visual census density estimate (Table 6.7a, Fig. 6.10).

To what extent these estimates were underestimates of total population size of P. *leopardus* for Lizard Island was uncertain, as considerable reef area lies between 10 and 20 meter depth, as well as above datum (Table 6.7b). However, most of the very

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shallow waters representative of the extensive reef flats primarily associated with the lagoon environment were excluded from the population estimations, as they are thought to be very poor trout habitats. Dive restrictions made it unfeasible to efficiently sample depths > 10 m, hence no markings and resightings were undertaken for this depth stratum. If one assumes that density and distribution of coral trout are similar for areas between 10-20 m as they were recorded for datum to 10 m, the population estimates for mark-resighting data and density based estimates ranged from 11,461 (BM) to 24,182 (density) fish over a reef area of 4,553,331 m<sup>2</sup> (i.e. datum to 20 m depth, Table 6.7, Fig. 6.10).

#### 6.3.6. Summary of results

- A total of 216 *P. leopardus* were caught using hook & line with a fishing effort (hook-line-hour) of 72 hours & 5 minutes. This resulted in a CPUE of 2.99 trout per hook-line-hour.
- CPUE was significantly higher in zones closed to fishing than in zones open to fishing.
- Visual recapture (resignting) rates of 24.04% and 14.21% were obtained for *P. leopardus* during surveys one and two months after initial freeze branding, respectively.
- The average density of coral trout in the study area was 5.31 trout/1000m<sup>2</sup>. Density estimates did not differ significantly between reef habitat types or between management zones.
- The mean size of fish captured by hook & line was 5.17 cm larger than the mean size recorded in visual census surveys.
- No clear relationship existed between distance moved from initial capture to resighting and size of fish ( $r^2 = 0.0324$ ).
- *P. leopardus* inhabiting patch reefs were recorded to have moved further between capture and resighting than had fish on fringing reefs.
- Coral trout in management zones closed to fishing were recorded to have moved further between capture and resighting than had fish in zones open to fishing.

- In contrast to the results obtained during the mark-release-resighting study, coral trout tracked using ultrasonic telemetry did not move greater mean distances per day in either habitat type or management zone.
- The mean distance moved per day as recorded by ultrasonic telemetry was larger than the mean distance freeze branded fish had moved between capture and resighting at least one month later.
- Home range parameters (area, length & width) of coral trout equipped with ultrasonic transmitters did not differ between management zones.
- No freeze branded fish located near management zone boundaries were recorded as having crossed the boundaries.
- Coral trout carrying ultrasonic transmitters, and having home ranges straddling management zone boundaries, spent, on average, 27.49% of their time in the 31.23% of their home ranges located in zones open to fishing.
- Using ultrasonic telemetry data, *P. leopardus* with home ranges that straddled management zone boundaries were recorded to cross zone boundaries at an average rate of 15.27 times/month (range: 3.62 29.09 times/month).
- *P. leopardus* were strongly clumped in their patterns of spatial dispersion on the scale of 500 m<sup>2</sup>. Only in zones open to fishing were coral trout recorded to be distributed randomly.
- Mark-release-resighting population estimators suggested population sizes of between 6,301 and 7,115 coral trout for the defined depth strata (datum 10 m) for the Lizard Island reef area.
- Population estimates based on the visual census derived density estimate, indicated a population size of 13,295 fish for the census defined depth strata.
- Extrapolation to the whole reef substratum area around Lizard Island (datum 20 m) resulted in suggested population sizes of between 11,481 (lowest resighting estimate) and 24,182 (density estimate) coral trout.

## 6.4. Discussion

This study attempted to quantify movement patterns and population size of P. *leopardus* using underwater visual census (UVC) of individually marked animals. The primary objectives were to compare movement information gained through this method with data obtained by ultrasonic telemetry (see Chapter 4), and assess the implications of adult movement patterns for marine protected areas.

The mark-release-resighting study recorded recapture rates of 14 and 24% for the two separate UVC surveys, covering a two month period. These recapture rates are high and relate to the relatively short time period of the recapture study. A similar high recapture rate over a short time period was observed by Beinssen (1989b), who recorded a 13.9% visual resighting rate three to four weeks after tagging 273 coral trout at Heron Island, Great Barrier Reef. Other studies conducted over longer time periods, using more traditional tagging and recapture techniques, resulted in considerably lower rates of recapture for P. leopardus. Brown et al. (1994), in a study conducted on the Great Barrier Reef reported 14 recaptures (by recreational fishers) from a total of 699 tagged coral trout, resulting in an overall recapture rate of 2.0% over the 2.15 year period of the study. Davies (1995), in a fish trapping study at Lizard Island, tagged 80 fish, with a recapture rate of 6.25% after at least one year at large. In a related study, Davies (1995), using commercial fishers, tagged 4,627 trout on 5 neighbouring reefs, and recorded overall recapture rates (research and general public returns) of 9.57% over the two year period of the study. In a study currently in progress in the lagoon at Lizard Island, Hilomen (pers. com.) obtained recapture rates of 41.2% for P. leopardus. However, this was based on a small sample size of n = 17 coral trout tagged, with repeated sampling, using baited traps, in the same locations over time (average time to recapture = 94 days). Tagging studies on other species of reef fish elsewhere reported recapture rates slightly higher than those generally recorded for P. leopardus above. Holland et al. (1993a), in a study investigating movement patterns of the mullid Mulloides flavolineatus in Kaneohe Bay, Hawaii, reported a recapture rate of dart tagged specimens of 15.4% with the maximum time period at liberty being 531 days. In a corresponding study of the carangid Caranx melampygus at the same location, a recapture rate of 20.7% with a

mean time at large of 135.7 days  $\pm$  120.7 (SD) was recorded (Holland *et al.* 1996). In a study on two species of snappers in deeper waters off Texas, Fable (1980) observed recapture rates of 5.6% (*Lutjanus campechanus*) and 4.9% (*Rhomboplites aurorubens*), over time periods of 30-847 days. Previous studies on the same species, reviewed by Fable, indicated higher recapture rates for one species (*L. campechanus*: 12.5-33%), but lower rates for the second (*R. aurorubens*: 0-4.1%).

A significant difference in size frequency distribution of P. leopardus was recorded between the methods of capture and recapture utilised in this study, with the mean size of trout captured by hook and line being larger than the mean size obtained during the underwater visual census surveys. As the results indicated, coral trout smaller than 20 cm were not represented in hook and line catches, despite being sighted during UVC. Large specimens, on the other hand, appeared to be sampled equally by both methods. Thus, sampling of coral trout using the commercial hook and line method resulted in a skewed size frequency distribution with under-representation of small size classes. Ralston (1982, 1990) suggested the potential for hook selectivity influencing the observed size distribution of line catches, with small fish not being able to physically accommodate large hooks, while large fish may pull free, or break lines. Recently suggestions have been put forward that the common practise of using minimum legal size limits as a management option in fisheries (e.g. Hancock 1992), as well as intensive fishing pressure per se, may result in evolutionary selection processes favouring slower growing fish (Bergh & Getz 1989, Parma & Deriso 1990, Policansky 1993 in Dayton et al. 1995). Such selective mortality caused by fishing may influence the reproductive potential and genetic variability of populations, with associated potential fisheries recruitment problems resulting in potentially reduced future productivity of the stock (Policansky 1993 in Dayton et al. 1995, Goodyear 1996, Zhao et al. in press). Thus, assessment methods for population structure (size and age based, see Ferreira & Russ 1995, Newman et al. 1996) which are fisheries independent and not size selective are required to monitor any changes in size distribution of populations (see also Hilborn & Walters 1992 for review of effects of selectivity on fisheries samples). Clearly, underwater visual census provides the ideal tool for evaluation of size selectivity of hook & line techniques for coral reef fisheries. The biased sampling distribution observed in the present study will need to be accounted for when utilising fisheries based catch data.

# 6.4.1. Comparison of results obtained with UVC and ultrasonic telemetry

The evaluation of spatial patterns obtained through UVC indicated that coral trout were dispersed in a clumped pattern. A notable exception to this pattern was the trout dispersion in zones open to fishing, which was random (see section 6.4.2. below). Initially it would appear surprising that coral trout should display a clumped pattern of distribution at the scale examined, given that P. leopardus maintained well established home ranges over substantial time periods (for at least 200+ days, see Chapter 4). The observed distribution pattern was particularly interesting, given that the measured home ranges were considerably larger (mean =  $13,651.9 \text{ m}^2 \pm 1464.4 \text{ SE}$ , Chapter 4) than the spatial scale evaluated here for dispersion patterns (i.e. transect area of  $500m^2$ ). However, Williams (1991) suggested that distribution patterns observed in coral reef fishes were a reflection of the distribution of habitat patches, which are not uniform. Furthermore, fish within these patches were often not distributed uniformly (e.g. Sale 1972a in Williams 1991). The clumped distribution observed here lends support to previous observations that distributions of larger, more mobile species appear linked to availability of food, and are influenced by the distribution of shelter locations (e.g. Talbot 1965, Goldman & Talbot 1976, Williams 1991). This is supported strongly by the data obtained using ultrasonic telemetry, with coral trout spending the majority of their time at shelter or feeding sites, or cleaning stations (Chapter 4).

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 *P. leopardus*, at least when using tagging techniques combined with small numbers of recaptures (resighting) of individuals. Of particular interest was the difference in recorded distances moved within reef habitats, with patch reef fish moving further than fringing reef fish between capture and resighting. This is possibly a consequence of the differences in the physical dimensions of home ranges of coral trout, with home ranges of fish living on patch reefs being wider but not longer than home

ranges on fringing reefs (see Chapter 4). The observed difference may therefore simply be a matter of geometry of home ranges, with potentially the same likelihood of similar distance moved being recorded in relation to length of home ranges for a patch reef fish as for a fringing reef fish, while recording larger distances moved for patch reef fish than for fringing reef fish in relation to width of home ranges. Hence, it may be possible to record overall larger distances moved between capture and single resighting for patch reef fish, simply because, on average, their home ranges are wider. This is supported by the data recorded through ultrasonic telemetry, that mean distances moved per day did not differ for trout from the two habitats (see Fig. 6.7a). Thus, fish in either habitat, on average, moved the same 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.

When attempting to interpret the observed difference in recorded distance moved between the two different data collection methods (i.e. ultrasonic telemetry vs. UVC of marked animals), it should be recognised that both represent slightly different measures. Ultrasonic telemetry provided data which permitted the calculation of the average distance moved by each fish per day, based on numerous position records per day sampled over substantial time periods. Daily movements generally consisted of several movements back and forth throughout each specimens home range, thus resulting in larger estimates. It therefore represented 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 one month apart, and therefore was expected to be lower than the average total distance moved per day as derived from ultrasonic telemetry data.

# 6.4.2. Implications of adult movement patterns for marine protected areas

The use of marine protected areas as an additional or alternative fisheries management tool has received increasing attention over the last few years (e.g. Alcala & Russ 1990, Bohnsack 1990, 1996, Roberts & Polunin 1991, Carr & Reed 1993, Dugan & Davis 1993, Dayton *et al.* 1995). It has been considered, in comparison to traditional

management measures, a cost-effective and potentially more readily enforceable strategy to sustain fish stocks, particularly on coral reefs (e.g. Alcala 1988, Davis 1989, Alcala & Russ 1990, Bohnsack 1990, 1993, 1996, Polacheck 1990, Roberts & Polunin 1991, Carr & Reed 1993, DeMartini 1993, Dugan & Davis 1993, Polunin & Roberts 1993, Russ et al. 1993, Rowley 1994, Russ & Alcala 1994, 1996b, Man et al. 1995). The two major objectives of the use of marine protected areas in fisheries management are protection of a critical spawning stock biomass to ensure recruitment supply to fished areas by larval dispersal and possible enhancement or maintenance of yields to areas adjacent to reserves by adult movements (Alcala & Russ 1990, Bohnsack 1990, Roberts & Polunin 1991, Dugan & Davis 1993, Russ et al. 1993, Russ & Alcala 1996a&b). Recent studies have provided strong evidence that marine protected areas enhance the abundance, size and hence biomass of numerous reef fish species (e.g. Buxton & Smale 1989, Russ & Alcala 1989, 1996b, Bennett & Attwood 1991, Polunin & Roberts 1993, Russ et al. 1993). However, there is only limited empirical data regarding movements of fish across management zone boundaries, potentially resulting in yield increases in areas outside the protected area. While some studies attempted to use indirect measures of potential emigration and biomass export (e.g. Alcala & Russ 1990, Rakitin & Kramer 1996, Russ & Alcala 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 1989a, Bryant et al. 1989, Buxton & Allen 1989 in Roberts & Polunin 1991, Yamasaki & Kuwahara 1990, Davies 1995), or modelled the potential effect of such movements on expected yields (Polacheck 1990, Die & Watson 1992, DeMartini 1993, Russ et al. 1993, Attwood & Bennett 1995). However, only one study, to the authors knowledge, measured emigration rates from a protected area directly. Attwood & 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 of 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. They concluded that the stock may be polymorphic with respect to dispersal behaviour, and the rate of emigration of tagged fish was time dependent. The nomadic component of the stock was estimated to leave the protected area at an estimated exponential rate of 0.011 d<sup>-1</sup>, with approximately 10% of the tagged population being nomadic. Thus, a total emigration rate of 0.4  $yr^{-1}$  was extrapolated, assuming that the proportion of nomads did not change. The study presented here represents the first data on rates of cross-boundary movements of a coral reef fish of major fisheries significance in relation to marine protected areas and their boundaries.

The data obtained for rate of boundary crossings by P. leopardus equipped with ultrasonic transmitters, and with home ranges straddling management zone boundaries, indicated that, on average, each coral trout crossed the boundary in either direction once every two days. This clearly indicated that these fish moved regularly across zone boundaries. Furthermore, the percentage of home range located in the open zones (mean = 31.23 %) and the amount of time spent in the open zone (mean = 27.49 %) corresponded relatively closely, suggesting approximately even use of unfished and potentially fished areas. Recent studies modelling the effect of marine protected areas on the potential yield per recruit to areas adjacent to reserves suggested that moderate increases were possible outside of protected areas (Polacheck 1990, DeMartini 1993, Russ et al. 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 & Alcala (1996a), who showed that the increases in density and species richness of large predators associated with a protected area in the Philippines was most pronounced nearest (within a few 100 meters) to the reserve. Given that the fishing pressure around Lizard Island is moderate (for Australian standards) to light (by developing country standards), one would not expect to have observed net movements (displacements or relocations) of coral trout to areas outside the closed zones related to potential density gradients. Density was 20% higher in the closed areas, but this difference was not statistically significant. However, any of the monitored fish had the chance of being caught outside the closed zone 27.49 % of the time. This is ignoring the potential bait attraction during fishing, and as such represents a minimum rate of availability. It should be noted also that the very low rates of exchange of fish across management boundaries, except for those fish with home ranges straddling the boundaries, argues that properly managed marine protected areas may be

very effective at protecting spawning stock biomass of coral trout populations on the Great Barrier Reef.

The lack of observed movements across zone boundaries during the UVC surveys of freeze branded fish indicates strongly the necessity of repeated, multiple surveys in conjunction with large scale marking efforts. A virtually identical result to the one obtained here was recorded by Beinssen (1989a) during a reef fish movement study in relation to an existing reserve boundary at Heron Island (southern Great Barrier Reef). Of 273 coral trout tagged, 38 (13.9%) were subsequently resignted during underwater visual surveys three to four 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 having crossed the reserve boundary, moving at least 500 m from the closed to the open zone. Clearly, any study attempting to investigate flux rates, and potential patterns of dispersion and net exports from marine protected areas, using visual census of marked individuals (or any other standard mark-release-recapture technique) would require very large sample sizes, with repeated sampling with replacement through time to maximise the chances of multiple recaptures of the same individuals (Hilborn et al. 1990). Furthermore, 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. This reduced the chances of maximising branding and resighting effort in areas close to existing boundaries. Future investigations would require more intense concentration of capture and recapture effort in relation to boundaries, for example through utilising a stratified design of capture and sampling effort, with gradual reduction in effort with distance away from boundaries.

The comparison between UVC of marked animals and ultrasonic telemetry clearly illustrated that a technique such as ultrasonic tracking is far more reliable in providing information on patterns of movements, by providing more data points regarding movements of individual fish (e.g. Holland *et al.* 1993a, 1996). However, given the increased cost and complexity of using ultrasonic telemetry, the ideal situation would combine detailed investigations of movement patterns of transmitter equipped

fish with a large marking study utilising repeated underwater visual censuses of marked animals to obtain density as well as net movement rates (see Schwarz & Arnason 1990).

In the present study, the densities of coral trout recorded in zones closed to fishing  $(5.53 \pm 0.3148 \text{ SE})$ , while 20% higher than in open zones  $(4.56 \pm 0.3880 \text{ SE})$ , did not differ significantly between the management zones. The overall density  $(5.31 \pm$ 0.2585 SE), as well as zone densities, compared well with other density estimates for coral trout from the Great Barrier Reef (see Williams & Russ 1994 for review). Their review indicated that, while evidence that closing areas to fishing increased density was reasonably good, the available evidence was equivocal. Several studies detected no significant difference in density of coral trout between open zones and zones closed for up to 8 years (Williams & Russ 1994). It is possible that the general fishing pressure on the surveyed reefs open to fishing on the Great Barrier Reef may not be high enough to significantly affect densities (Williams & Russ 1994). Furthermore, it has been suggested that infringements of zoning rules may be common enough in the commercial and recreational fisheries on the Great Barrier Reef to result in significant fishing pressure to be applied to supposedly closed areas (Williams & Russ 1994, Davies 1995). 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 1989a, Ayling & Ayling 1994, Cappo & Brown 1996). Fishing pressures around Lizard Island could be considered moderate for most of the open areas, with the majority of fishing undertaken by guests and staff members of the local tourist resort, and visiting recreational boat crews (pers. obs.). Lizard Island reefs appear to be fished relatively little by commercial fishers (pers. obs., C. Hagen pers. com.). 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. However, the experimental line capture data obtained in this study strongly supports 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, using commercial fishers for a large scale tagging study in the central section of the Great Barrier Reef, reported CPUE of 2.26 to 7.44 coral trout line<sup>-1</sup> hour<sup>-1</sup>. Thus, the results obtained in the present study clearly support the previously reported observations, and may explain the common concern of reduced catches in heavily fished reefs expressed by fishers.

The present study found no differences in either size frequency distributions or mean sizes of *P. leopardus* between management zones. The evidence of effects of fishing on the size structure of populations of coral reef fishes is relatively strong (review by Russ 1991). Most studies of coral trout detected larger average sizes on reefs closed to fishing (Craik 1981, Ayling & Ayling 1984 in Ferreira & Russ 1995, Beinssen 1989b, Ayling & Mapstone 1991 in Ferreira & Russ 1995). However, Ferreira & Russ (1995) found no significant difference in mean size of *P. leopardus* between reefs open and closed (for up to 7 years) to fishing. They attributed this contrasting result largely to very high variability between replicate reefs, and indicated the importance of increased replication of reefs for improved statistical power in analyses of any potential effect of fishing on coral reef fish populations. Large differences in apparent fishing pressures between replicate reefs open to fishing may have contributed also to the observed results, and effort variation would need to be taken into account in future studies.

The data obtained in this study indicated that coral trout in closed zones had moved greater distances between capture and resighting than fish in zones open to fishing. This, together with the previously mentioned observation of the dispersion pattern of trout in open zones being random, may indicate differences in the behaviour patterns of fish in zones open to fishing. The observed differences cannot be explained simply by population structure differences, as neither densities (although slightly but not significantly lower in open zones) nor size distributions differed significantly between zones. Furthermore, as data collected through ultrasonic tracking indicated, home ranges did not vary significantly in either area, length or width between management zones (see Table 6.4). Given the very small sample size of visual resightings in open zones (n = 18), 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. This is particularly true when one considers that fish tracked using ultrasonic telemetry did not differ in the distance moved per day in either zone (see Fig. 6.7b). Hence it is very difficult to consider an ecological or biological reason for this result, particularly given that the population structure appeared similar between zones. This finding should therefore be considered with caution, and definitive conclusions on distances moved, as derived from UVC of marked animals, have to await further studies.

## 6.4.3. Estimation of population size

The size of the population of *P. leopardus* on the reefs around Lizard Island was estimated to be between 11,461 and 24,182 fish for the complete hard reef substratum area between datum and 20 m depth. Extrapolation of the estimates from the censused depth strata (datum - 10 m) to the 20 m depth contour was based on the assumption that average densities of coral trout were the same for the deeper areas as recorded for the censused depth strata. This assumption seems reasonable, since Mapstone & Ayling (1993) found that coral trout densities were not depth stratified, at least to depths of 20-30 m. There are few examples of abundance or population size estimates for reef fishes using mark-release-recapture (Appeldoorn 1996). Recksiek et al. (1991) used fish traps and an estimation technique for sparse capture-recapture data (Chao 1989) to estimate local abundances of four species of reef fish on a shallow patch reef in Puerto Rico. Only one other study has attempted to estimate population size of coral trout on an individual reef of the Great Barrier Reef. Beinssen (1989b), as part of a tagging study, estimated the population size of coral trout on Boult reef (southern Great Barrier Reef) using the Petersen method. Using 83 tag recaptures out of 375 fish initially tagged in a sample of 2136 fish collected by line fishing over a 14 day experimental period, Beinssen estimated the population size of coral trout on the  $3,420,000 \text{ m}^2$  study reef to be  $8613 \pm 873$  (SE). This estimate compares well with the Petersen estimate of 12,873 fish obtained for the  $4,553,331 \text{ m}^2$  reef area in the present study.

The comparison of population size estimates obtained from density data and mark-release-recapture estimators indicated that the density based estimate was between 1.87 to 2.11 times higher than the estimates based on the resighting of freeze branded specimens. The utilisation of both UVC and mark-release-recapture techniques for estimating coral reef fish abundance and density has been reviewed by Cappo & Brown

(1996). The authors concluded that UVC has been demonstrated to be a precise way of assessing coral trout density. On the other hand, mark-release-recapture techniques, while used effectively for estimation of survival rates (e.g. Burnham *et al.* 1987, Lebreton et al. 1992), age and growth validation (e.g. Ferreira & Russ 1992, 1994, Davies 1995) and movement studies (e.g. Hilborn 1990, Hilborn *et al.* 1990, Schwarz & Arnason 1990, Hilborn & Walters 1992, Schweigert & Schwarz 1993), were considered to be less reliable for estimation of population sizes (Cappo & Brown 1996). Given the limitations in reliability of mark-release-recapture based population estimates, one has to consider the estimates obtained in the present study (i.e. 11,461 to 12,940 fish) as most likely to be underestimates. Furthermore, given that UVC derived density estimates are generally found to underestimate true fish abundances, at least for abundant, shy or cryptic species (Stone *et al.* 1979, Brock 1982, St. John *et al.* 1990), one could consider the density based population estimate derived in this study (e.g. 24,182 coral trout) as the better, albeit potentially conservative, estimate of population size of *P. leopardus* on the reef around Lizard Island.

## 6.5. Conclusions and recommendations

- Underwater visual census provided an ideal tool for evaluation of size selectivity of the hook and line technique used by the commercial and recreational fisheries on the Great Barrier Reef. The size selective bias of hook and line observed in this study will need to be accounted for when utilising fisheries dependent data.
- The rate of boundary crossing between management zones by *P. leopardus* obtained using ultrasonic telemetry clearly indicated that individuals with home ranges close to boundaries moved regularly across the zone boundaries. Any of the monitored fish had the chance of being caught outside the closed zone in proportion to the area of home range located in the open zone.
- While there was no conclusive evidence of differences in densities of *P. leopardus* between open and closed zones, the catch-per-unit-effort 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 recreational and commercial fishers on the Great Barrier Reef may partly reflect behavioural changes in targeted species.

- It is strongly recommended that estimation of movement patterns and flux rates with respect to marine protected areas should incorporate a dual approach, combining the highly successful method of ultrasonic telemetry to provide reliable, detailed information on movements, with large scale, stratified marking and visual resighting or recapture studies, with strong emphasis on intensive, multiple resighting opportunities.
- In order to clearly demonstrate if the "spillover" effect exists, and to quantify flux rates and associated potential changes in yield in areas adjacent to marine protected areas, empirical data is required based on controlled experimental manipulations of fishing effort (particularly medium to high levels of effort) over extended time periods. Such experimental data is required urgently to clarify the current discussion about suitability of marine protected areas for enhancement of local fishing yields, especially in the developing world.
- Given the substantial population size of *P. leopardus* on the reef around Lizard Island, as determined in this study, any experimental removal of coral trout in relation to investigations into the effects of marine protected areas, would most likely not adversely impact on the overall population structure or dynamics of this species at Lizard Island.

Table 6.1:Sampling effort for underwater visual census surveys (UVC) conducted<br/>at Lizard Island during September and October 1995. The available<br/>census reef area was defined as hard substratum between datum (lowest<br/>astronomical tide) and the 10 m depth contour or sand-reef interface in<br/>the general study area (western, northern and north-eastern side of Lizard<br/>Island).

	Nos. of		Available	
	transects	Area sampled	census reef	Percentage
UVC	(100 x 5 m)	( <b>m</b> <sup>2</sup> )	area (m <sup>2</sup> )	area sampled
. 1	167	83,500	750,966	11.12
2	141	70,500	750,966	9.39
Total	308	154,000		

Table 6.2: Resighting data for underwater visual census (UVC) surveys conducted in September and October 1995 at Lizard Island. A) Data presented by survey (UVC 1 vs. UVC 2), B) breakdown by reef habitat type (fringing vs. patch reef), and C) breakdown by reef management zone (open vs. closed to fishing).

A)

UVC	Nos. of brands released (August)	Nos. of brands resighted	Recapture rate	Total trout count	Density per 1,000 m² (± SE)
1	183	44	24.04%	440	5.27 (0.3499)
2		26	14.21%	377	5.35 (0.3848)
			Overall	817	5.31 (0.2585)

B)

Reef habitat	Total fish count	Nos. of transects (100x5 m)	Transect area (m <sup>2</sup> )	Density per 1,000 m <sup>2</sup> (± SE)	
fringing	362	128	64,000	5.66 (0.4018)	
patch	455	180	90,000	5.06 (0.3374)	
Total	817	308			

C)

Management zone	Total fish count	Nos. of transects (100x5 m)	Transect area (m <sup>2</sup> )	Density per 1,000 m <sup>2</sup> (± SE)	
open	164	72	36,000	4.56 (0.3880)	
closed	653	236	118,000	5.53 (0.3148)	
Total	817	308			

Table 6.3: A) Sample sizes of distances moved between time periods for *P. leopardus*. Presented are the three time periods (UVC 1, UVC 2, UVC 1-2), the number of separate distance measures obtained, and the number of multiple resightings. B) Two factor ANOVA comparing distances moved of freeze branded fish between the three time periods and between management zones. Data consisted of fringing and patch reef fish. Indicated are: mean square, degrees of freedom (df), F-values and p-values. n = 93. C) Two factor ANOVA comparing distances moved of freeze branded fish between the three time periods and between management zones. Data consisted of fringing reef fish only. Indicated are: mean square, degrees of freedom (df), F-values and p-values. n = 56.

A)

Time period	Nos. of distances obtained	Nos. of multiple sightings
UVC 1	52	5
UVC 2	31	1
UVC 1-2	10	1
Total	93	7

**B**)

Source of variation	Mean Square	df	F	р
time period	0.4019	2	2.308	0.1055
zone	1.3266	1	7.617	0.0071
time period x zone	0.1235	2	0.709	0.4949
residual	0.1742	87		

C)

Source of variation	Mean Square	df	F	p
time period	0.1735	2	0.824	0.4447
zone	0.8995	1	4.269	0.0440
time period x zone	0.1634	2	0.775	0.4659
residual	0.2107	50		

Table 6.4: Analysis of covariance comparing three home range parameters (home range area, length & width) between management zones open and closed to fishing, for fish tracked using ultrasonic telemetry. Size of individual fish (FL) and sample size (number of ultrasonic telemetry fixes per estimate) were treated as covariates. Mean squares, degrees of freedom (df), F and p values are indicated for each home range parameter analysed.

home range	Source of	Mean	df	F	р
parameter	variation	Square			
area	zone	0.0395	1	0.5948	0.4459
	residual	0.0665	34		
				·	
length	zone	0.01043	1	0.4681	0.4989
	residual	0.0223	34		
width	zone	0.1314	1	3.837	0.0584
	residual	0.0343	34		

Table 6.5:Home range usage information determined with ultrasonic telemetry for<br/>
P. leopardus whose home ranges straddled reef management zone<br/>
boundaries at Lizard Island. Included are the percentage distribution of<br/>
home ranges between zones, time spent in the zone open to fishing, and<br/>
information related to the rate of crossing of zone boundaries.

Fish	% hon	ne range	% time	Number	Tracking	Boundary	Boundary
			spent in	of	duration	crossings	crossings
	open	closed	open	boundary	(days)	per day	per month
	zone	zone	zone	crossings			
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

**Table 6.6:** Patterns of spatial dispersion of *P. leopardus* surveyed using markrelease-resighting. Patterns were examined at the spatial scale of individual transects, i.e. 500 m<sup>2</sup>. Presented are results of the  $\chi^2$ goodness-of-fit tests to Poisson distributions, the variance-mean ratios and the resulting dispersion pattern. Data were examined in total (overall), by habitat type, and by management zone.

	χ <sup>2</sup> [df]	р	variance-mean	dispersion
			ratio	pattern
overall	107.60 [6]	<< 0.001	1.94	clumped
habitat				
fringing reef	25.52 [5]	<< 0.001	1.83	clumped
patch reef	75.40 [5]	<< 0.001	2.03	clumped
zone				
closed	115.31 [6]	<< 0.001	2.11	clumped
open	8.53 [4]	> 0.05	0.98 rando	

Table 6.7: A) Estimates of population size of *P. leopardus* in the study area at Lizard Island, for the depth strata surveyed (datum to 10 m). Estimators used include JHE: Joint Hypergeometric Maximum Likelihood Estimator (Neal et al. 1993), MM: Minta-Mangel Bootstrap Estimator (Minta & Mangel 1989), BM: Bowden Model Estimator (Bowden 1993), PET: Traditional Petersen Method (Ricker 1975), BAIL: Bailey Estimator (Bailey 1952), CHAP: Chapman Estimator (Chapman 1952), population estimate based on coral trout density estimate Density: obtained from visual census surveys. B) Area measurements for hard reef substratum at Lizard Island, using various depth and horizontal location definitions. Area measures were obtained through digitising calibrated aerial photographs.

## **A**)

		JHE	MM	BM	PET	BAIL	СНАР	Density
populat	ion size	2,116	2,134	1,890	2,123	2,096	2,106	3,988
95% CI	lower	1,750	1,969	1,527	1,647	1,633	1,918	-
	upper	2,618	2,242	2,338	2,598	2,558	2,294	-

#### B)

Reef section	Depth strata	area (m <sup>2</sup> )
Study area	datum - 10 m	750,966
Lizard Island	datum - 10 m	2,503,809
Lizard Island	datum - 20 m	4,553,331
Lizard Island	high tide - 20 m	6,036,761



Plate 6.1: External marking of *P. leopardus* with freeze brands, using liquid nitrogen as coolant. Individual numerals (25 x 25 x 2 mm) were branded onto the caudal peduncle on both sides of the fish. Branding duration was 10 seconds. Photo courtesy of R. Grace, Natural History Unit, TV New Zealand.



Plate 6.2: Example of successfully freeze branded numeral on the caudal peduncle of *P. leopardus*. For proper re-cooling of branding irons between application, each numeral was returned to the coolant (liquid nitrogen) for at least one minute. Fish were returned to holding tanks between each numeral brand to reduce stress. Photo courtesy of R. Grace, Natural History Unit, TV New Zealand.



Plate 6.3: *Plectropomus leopardus* carrying freeze brand number 64 on the left caudal peduncle. This specimen was recaptured by recreational fishers three months after freeze branding with ten second brand duration per numeral. After three months numerals started to become faint and wash out, making underwater identification increasingly difficult without close approach by the observer.



Plate 6.4: Plectropomus leopardus freeze brand number 151 recorded during the underwater visual census survey period in September 1995, one month after application of freeze brands. Numerals are distinct, making identification easy. Some brands remained white for extended periods. Most, however, turned dark brown within approximately one month of application. Photo courtesy of R. Grace, Natural History Unit, TV New Zealand.



Figure 6.1: Map of Lizard Island showing the limits of the study area for hook and line capture, and underwater visual census surveys for *P. leopardus* marked with freeze brands during 1995. Indicated also are the Great Barrier Reef Marine Park management zone patterns and boundaries.
Black arrows: Limits of study area. Area was limited to the north, north-eastern and western side of the island, which was more sheltered from the prevailing south-east winds. Blue arrows: Outline the zones open to fishing for commercial and recreational fishers. Green arrows: Outline the zones closed to fishing. Red bars: Indicate the locations of management zone boundaries.



Figure 6.2: Size distribution and mean sizes of *P. leopardus* from the two reef management zones (closed and open to fishing) at Lizard Island. A) Size distribution of fish from closed zones, B) size distribution of fish from open zones, and C) mean size (<sup>+</sup>/. SE) of fish from closed and open zones. Mean sizes are indicated. Note different scales on Y axes of A and B.



Figure 6.3: Size distribution and mean sizes of *P.leopardus* from two reef habitats (fringing and patch reefs) at Lizard Island. A) Size distribution of fish from fringing reefs, B) size distribution of fish from patch reefs, and C) mean size (\*/. SE) of fish from fringing and patch reefs. Mean sizes are indicated. Note different scales on Y axes of A and B.



Figure 6.4: Size distribution and mean sizes of *P.leopardus* obtained through two different collection methods (hook & line and underwater visual census) at Lizard Island. A) Size distribution of fish collected by hook & line, B) size distribution of fish recorded by visual census, and C) mean size (<sup>+</sup>/. SE) of fish obtained with hook & line and visual census. Mean sizes are indicated. Note different scales on Y axes of A and B.



Figure 6.5: Relationship between distance moved between capture (August 1995) and recapture occasions (September & October 1995) and size of individual specimens of *P. leopardus*. Initial capture was by hook & line, with recaptures being by resightings during underwater visual census of freeze branded individuals. Included are  $r^2$  of regression estimate (regression: p = 0.0859, n = 93).



Management zone

Figure 6.6: Effect of reef habitat and management zones on the distances moved by *P. leopardus* (time periods between resightings pooled). Initial capture was by hook & line (August 1995), with subsequent recaptures by resighting of freeze branded specimens during two separate underwater visual census surveys (September & October 1995). Depicted are means (<sup>+</sup> SE). A) Comparison of reef habitats (fringing and patch reefs) n = 93, and B) Comparison between management zones (closed and open to fishing) for complete data set (shaded, n = 93) and fringing reef data subset (clear, n = 56). Means are indicated.



Management zone

Figure 6.7: Effect of reef habitat and management zones on the mean distance moved per day (<sup>+</sup>/. SE) by *P. leopardus* tracked using ultrasonic telemetry during 1993-1995 at Lizard Island (n = 36 tracking occasions). Specimens whose home ranges were straddling zone boundaries were excluded from the analysis. Means are indicated. A) Comparison of reef habitats (fringing and patch reefs). B) Comparison between management zones (closed and open to fishing).



**Collection method** 

Figure 6.8: Comparison of mean distances moved (\*/. SE) by *P. leopardus* between the two different techniques employed. Telemetry (ultrasonic tracking) provided data to measure the mean distances moved per day for each specimen (n = 36 tracking occasions), whereas visual census utilised mark-release-resighting occasions to calculate distances moved by resighted individuals between capture and resighting at least one month later (n = 93). Means are indicated.



Figure 6.9: Representative examples of home ranges of two P. leopardus straddling management zone boundaries during 1993-1995. Black circles: Position records of P. leopardus obtained using ultrasonic telemetry. Polygon outlines indicate minimum area polygon home ranges of specimens. Blue arrows: Outline the zone open to fishing for commercial and recreational fishers. Green arrows: Outline the zone closed to fishing. Red bars: Indicate the locations of management boundaries. A) Specimen PL 9 living at a location called Granite Head. B) Specimen PL 31 living at a location called Chinamans ridge.


# Chapter 7:

# ULTRASONIC TELEMETRY: APPLICATION TO REEF FISHERIES RESEARCH AND MANAGEMENT

The present study represents the first successful use of ultrasonic telemetry, a technique relatively new to coral reef fish ecology (e.g. Holland *et al.* 1993a, 1996), for the investigation of movement patterns of a species of coral reef fish on the Great Barrier Reef, Australia. The major objectives addressed during this project included:

- Evaluation of the suitability of ultrasonic telemetry for use as a remote, non-intrusive monitoring technique for fish ecology and fisheries research on coral reefs.
- Use of ultrasonic telemetry to document home ranges and spatial and temporal patterns of activity of *Plectropomus leopardus*, a species of major commercial and recreational fishing interest in Australia, South-East Asia and the South-Pacific.
- Location of previously unknown spawning aggregation sites of *P. leopardus* around Lizard Island, and estimation of minimal catchment areas for aggregation sites through the tracking of specimens equipped with ultrasonic transmitters. Furthermore, to document use patterns of aggregation sites in relation to participation rates, timing of movements to and from aggregations, and sex-specific patterns of residence duration and frequency of participation at aggregation sites.
- Comparison of data obtained through ultrasonic telemetry with comparable data collected independently using a mark-release-resighting study. The conventional mark-release-resighting method employed freeze-branding as a marking technique for individual identification of specimens and standard underwater visual census techniques as the recapture tool.
- Evaluation of the data on movement patterns and population parameters, obtained through the mark-release-resighting and ultrasonic telemetry studies, in relation to the existing marine park zoning at Lizard Island, with considerations to the use of marine protected areas as a fisheries management tool.

The major findings of this study have been summarised and discussed in their respective chapters. The present chapter will discuss the relevance of the data and results obtained using ultrasonic telemetry with respect to the suitability of this technique to the coral reef environment, the importance of the major findings to the management of coral reef fisheries, and the implications these findings have for the concept of marine protected areas as a management tool in reef fisheries.

# 7.1. Suitability of ultrasonic telemetry for coral reef fish research

The present study has clearly demonstrated the suitability of ultrasonic telemetry for use on reef fish in the highly diverse and structurally complex coral reef environment of the Great Barrier Reef. The information obtained during this project, and particularly during the evaluation study, strongly supports the application of ultrasonic telemetry as reported by Holland *et al.* (1993a, 1996). Concerns regarding the high levels of biological background noise reported from coral reefs (Knowlton & Moulton 1963, Cato & Bell 1992, McCauley 1995), and the high structural complexity of reefs to cause insurmountably high signal loss from the ultrasonic transmitter have not eventuated. While the distance range of reception of ultrasonic signals was drastically reduced in the present reef habitat compared to the advertised range under oceanic conditions (up to 1000-2000 m, Pincock & Voegeli 1990), other studies in complex habitats have recorded reduced transmission distances also (e.g. Matthews *et al.* 1990).

Terrestrial ecologists have recognised for some time the value of remote tracking of target species which are either difficult to observe visually due to size or habitat considerations, or are extremely shy and easily disturbed in their natural behaviour by the presence of an observer. This has lead to the successful development and regular use of radiotelemetry devices and techniques for terrestrial use (e.g. Mech 1983, Kenward 1987, White & Garrott 1990). The terrestrial telemetry literature generally expressed concern about the weight of telemetry transmitters potentially influencing the behaviour of the experimental animals, thus making observations non-representative (e.g. Mech 1983, Kenward 1987, Koehler et al. 1987). Similarly, evaluations have been undertaken for use of telemetry units in the aquatic environment, with studies indicating that transmitter weight should be kept below 2-3% of the weight of the fish (e.g. Winter 1983 in Diana et al. 1990, Summerfelt & Mosier 1984, Mellas & Haynes 1985). These considerations were taken into account in the present study. Knowledge of the established length-weight relationship for P. leopardus (Ferreira & Russ 1994) indicated that even the heaviest transmitter (V16-6L, 14 g, Table 2.2), if used with the smallest fish examined (~ 37 cm FL), still accounted for only 1.98% of body weight of the study specimen. For a larger specimen of 50 cm FL this was reduced to 0.71% of body weight. Clearly the additional weight carried by coral trout equipped with transmitters was negligible. Of more concern in relation to transmitters being implanted into the body cavity of fishes seemed to be the physical size, rather than weight, of the units involved (Knights & Lasee 1996). Concern regarding space limitations in the body cavity of certain species has limited some studies to external attachment of transmitters (e.g. Carangidae: Holland et al. 1996). The additional volume in the body cavity taken up by a transmitter also might influence the feeding behaviour and feeding ecology of individuals (Knights & Lasee 1996). While individual P. leopardus were observed occasionally to regurgitate freshly consumed food items for the first few days after surgery (Chapter 2), regular feeding behaviour was recorded before a fish was released. Tracking specimens were also observed several times on SCUBA during hunting activities. Significantly, both actively courting males, as well as females with visibly distended body cavities (due to hydration of oocytes) were observed at spawning aggregation sites, suggesting little limitations on their behaviour or reproductive activities. Thus, it can be concluded that placement of ultrasonic transmitters in the body cavity of P. leopardus did not influence their behaviour in any noticeable manner. Clearly, other species would need to be evaluated on a species by species basis before internal placement could be extended to these species.

The use of ultrasonic telemetry in this study has resulted in the acquisition of data that is of great relevance to fisheries and marine park management, and generally impossible to obtain accurately in any other fashion. Particularly for larger reef fishes which are difficult to observe visually, ultrasonic telemetry was demonstrated to be unique in being able to provide detailed and accurate information on estimates of home ranges and activity patterns, detection of spawning aggregations and determination of movement and residence patterns at these aggregation sites. The potential of ultrasonic telemetry as a tool for fisheries research is only slowly being realised (see review by Nelson 1990). While dating back to the 1950's (e.g. Trefethen 1956, Trefethen *et al.* 1957, both in Bass & Rascovich 1965), this technique has been and still is used predominantly with pelagic animals (e.g. Bass & Rascovich 1965, Carey & Robison 1981, Holland *et al.* 1990a&b, Pepperell 1990, Pepperell & Holland 1992), sharks (Klimley *et al.* 1988, Nelson 1990, Carey & Scharold 1992, Holland *et al.* 1992,

Klimley 1993, Morrissey & Gruber 1993) and in temperate environments (Hawkins 1980, Clark & Green 1990, Matthews *et al.* 1990, Bradbury *et al.* 1995). Early attempts (1970-1980) to use ultrasonic tags for fish studies on coral reefs have been less successful, primarily due to the technical limitations of the ultrasonic equipment, resulting in low and variable signal reception (F. Talbot pers. com.). Not until more recently have successful attempts been made of the use of ultrasonic telemetry on fishes associated with coral reefs (e.g. Holland *et al.* 1993a, 1996).

In summary, ultrasonic telemetry is a tool highly suited and recommended for use in fisheries biology as well as reef fish ecology. While initial costs may appear high, the kind of data and information that can be obtained with this technique is generally not achievable in any other manner, particularly for larger, more active species, which may also be difficult to observe visually. While the present study restricted itself to address patterns of movements and related behaviour, other avenues for the use of ultrasonic telemetry exist, such as vertical movement patterns (e.g. Holland *et al.* 1990a&b, O'Dor *et al.* 1993) or physiological ecology of species (e.g. Carey *et al.* 1981, Klimley 1993, O'Dor *et al.* 1994). The more recent development of commercially available automatic recording systems for simultaneous, high-resolution 3-D monitoring of several animals equipped with transmitters (O'Dor *et al.* 1995, Seino *et al.* 1995), provides the possibility of new and innovative approaches to investigations of movement and behaviour patterns, as well as eco-physiology of coral reef species.

#### 7.2. Implications for fisheries management

This study recorded, for the first time, movement patterns in relation to annual spawning aggregations in a continuous manner for individuals of a commercially and recreationally important species of reef fish. Using ultrasonic telemetry, four major spawning aggregation sites of *P. leopardus* were discovered at the study reef, and patterns of use and residence of individual fish at the aggregations were recorded. Furthermore, estimates of catchment areas of aggregation sites could be estimated through evaluation of the distances moved by fish equipped with ultrasonic transmitters

between well established home ranges and spawning aggregation sites. Additionally, evidence was obtained of movements of coral trout from aggregation sites at Lizard Island to inter-reefal habitats in deeper water, and between individual reefs, stressing the potential importance of type of inter-reefal habitat, rather than distance or water depth *per se*, as important factors determining potential benthic connectivity between neighbouring reefs.

Over the last few years concerns have been raised over the potential threat to fish stocks due to increasing fishing effort being allocated to the fishing of spawning aggregations (e.g. Sadovy et al. 1994). Such aggregations generally are of central importance to the reproductive ecology of many commercially exploited fishes (e.g. Thresher 1984, Sadovy 1994, 1996). High levels of catches taken from spawning aggregations have undoubtedly contributed significantly to the recent collapse of one of the richest fisheries in the world, the northern cod fisheries off Canada (e.g. Hutchings & Myers 1994, Morgan & Trippel 1996, Myers et al. 1996). Spawning aggregations often provide a major opportunity for fishers to obtain large catches with relatively little fishing effort. This is particularly the case for tropical species (Colin 1992). Once such aggregation sites are known to the fishing community, the potential for depletion of stocks is high (Sadovy 1993, Sadovy et al. 1994), and can be rapid (Johannes 1988, Colin 1992, Johannes et al. 1994). Levels of aggregation fishing that are considered unsustainable have been reported for several coral reef fisheries (e.g. Caribbean: reviewed by Sadovy 1994, Palau: Johannes et al. 1994, 1995), resulting in drastic reductions in catches, or even the disappearance of aggregations all together (e.g. Bohnsack 1990, Sadovy et al. 1994). Fishers involved in the commercial reef line fisheries on the Great Barrier Reef have also expressed increasing concerns about potentially high levels of fishing effort on spawning aggregations of coral trout (Anon. 1996, C. Hagen, pers. com.). The potential impact of fishing on spawning aggregations is of great concern, given the lack of knowledge about the importance of spawning aggregations to reproductive output, and hence sustained recruitment levels of target species.

The results obtained through ultrasonic telemetry in this study have some clear implications for fisheries management, both for fishing of spawning aggregation in general, and for P. leopardus in particular. The existence of several aggregation sites per reef for *P. leopardus* makes this species potentially less vulnerable to overfishing by concentration of fishing effort on aggregation sites (see also Samoilys & Squire 1994), compared to species which use fewer sites in larger numbers, such as the con-generic P. laevis and P. areolatus (Johannes 1988, Johannes & Squire 1988), or some of the larger Caribbean serranids, e.g. Epinephelus striatus (Colin 1992) and E. guttatus (Sadovy et al. 1994). Nevertheless, the strong site fidelity observed for all individual P. leopardus in this study makes individual aggregations vulnerable to depletion once the location is known to fishers. The available evidence suggests that the stock of P. leopardus on a given reef may depend "primarily" on spawning sites on the reef of home range residence for their reproductive output, suggesting that sustainable management of at least some sites on a reef might be beneficial for the long term maintenance of stocks. However, given the observation of some movement between reefs, one cannot dismiss the potential for some exchange between populations on neighbouring reefs. Furthermore, only 31% of coral trout tracked with ultrasonic telemetry participated in aggregation events, despite histological evidence of reproductive activity of fish not attending large aggregation sites during the study period. This indicated that not all reproduction may have taken place at the known sites, and provided strong evidence for the potential existence of localised spawning events away from the major spawning sites.

The observed difference in turnover rates and residence duration at spawning aggregations between male and female fish implied the potential for sex-specific differences in vulnerability to fishing effort at aggregation sites. Male *P. leopardus* were recorded to stay longer and return to aggregation sites more often than females. Similar observations of sex-specific patterns of aggregation have been reported for *P. areolatus* (Johannes 1988, Johannes *et al.* 1994, 1995). Such sex-dependent vulnerability to fishing effort at aggregation sites, together with the tendency for fisheries to selectively target larger size classes, may lead to reduced size at sex change to compensate for the selective removal of the larger, predominantly male component of

protogynous populations (reviewed by Sadovy 1996). Furthermore, such selective fishing pressures may influence evolutionary selection processes favouring slower growing fish (e.g. Parma & Deriso 1990, Policansky 1993 in Dayton et al. 1995), and thus compound the potential effect of the common use of minimum size limits as a management option in fisheries (e.g. Hancock 1992). Such selective mortality may affect reproductive potential and genetic variability of a given stock, potentially leading to reduced productivity of the stock (e.g. Policansky 1993 in Dayton et al. 1995, Goodyear 1996). Furthermore, recent numerical modelling has indicated that protogynous species may be more vulnerable to fishing than gonochoristic species, with all modelled stocks incurring a drastic reduction in reproductive capacity, even at moderate levels of fishing mortality (Huntsman & Schaaf 1994). Bannerot et al. (1987) indicated also that a limited sperm supply, for example through selective removal of the male component of a stock, rendered protogynous populations more susceptible to overfishing due to reproductive failure. Recent proposals for the potential suitability and importance of monitoring of spawning aggregations to assess population trends and relative abundances of otherwise widely distributed populations (e.g. Brown et al. 1994, Johannes et al. 1994, 1995, Sadovy 1996) need to account of the individual and especially sex specific differences in residency and use patterns recorded in this study.

In summary, stocks of *P. leopardus* on the Great Barrier Reef are most likely less vulnerable to exploitation of spawning aggregations than many other serranid species, due to the occurrence of multiple spawning aggregation sites and possible localised spawning events on each reef. Any one specific site may, however, be susceptible to depletion due to strong site fidelity of individuals observed in this study. One potential management approach, currently under consideration on the Great Barrier Reef, is seasonal closure to line fishing during the known spawning times of *P. leopardus* (Anon. 1996). The almost complete lack of knowledge about locations of aggregation sites for many species (e.g. Shapiro 1987, Sadovy 1996) and the paucity of data on sex-specific patterns of participation at spawning events, illustrate that studies such as the present one, using ultrasonic telemetry, can provide this relevant information in a timely and experimentally controlled manner, unlike conventional external tagging studies which rely heavily on chance recaptures. Given the increasing fishing effort being placed on many stocks of coral reef fishes, such as the rapidly and massively expanding live food fish trade (e.g. Johannes & Riepen 1995), reproductive activities and strategies, especially of highly vulnerable aggregating species, need to be taken into account more strongly to ensure sustainable use of this resource for present and future generations of fishers. The recent attempts to protect from fishing some aggregation sites close to population centers in Palau (Johannes *et al.* 1994, 1995) are encouraging.

#### 7.3. Implications for marine protected areas

Almost everywhere reef fisheries are under increasing pressure from urban, economic and human population growth. These pressures lead to more intensive fishing pressures (Ruddle 1996) and the development of new and destructive fisheries (e.g. Johannes & Riepen 1995). The resulting consequences are being documented in increasing numbers (Russ 1985, 1991, 1996, Russ & Alcala 1989, 1996a&b, Rutherford et al. 1989, Hughes 1994, Dayton et al. 1995, Dalzell 1996, Jennings & Lock 1996, Reaka-Kudla 1996). One of the major reasons for these developments is that conventional management strategies (e.g. quota systems, gear and effort restrictions) are difficult or impossible to administer in most coral reef fisheries (e.g. Bohnsack 1990, 1996, Polunin 1990, Roberts & Polunin 1991, Russ 1991, Rowley 1994, Dayton et al. The failure of many historic fisheries 1995, Man et al. 1995, Munro 1996). management strategies has led to calls for increased attention to new or innovative management options (Ludwig et al. 1993). The use of marine protected areas as one alternative, cost-effective and more readily enforceable fisheries management tool is receiving increasing attention (e.g. Alcala & Russ 1990, Bohnsack 1990, 1996, Roberts & Polunin 1991, Carr & Reed 1993, Dugan & Davis 1993, Dayton et al. 1995, Russ 1996). Two of the major objectives of the use of marine protected areas are protection of a minimum spawning stock biomass and possible enhancement or maintenance of local fishing yields in areas adjacent to those being protected (Alcala & Russ 1990, Bohnsack 1990, 1996, Roberts & Polunin 1991, Dugan & Davis 1993, Russ et al. 1993, Russ & Alcala 1996a&b). Implicit to protection of spawning stock biomass is an assumption that excessive "spillover" of biomass (by net adult export) does not completely erode gains in biomass resulting from protection. While recent studies have demonstrated that protecting areas from harvest may lead to increases in abundance, size and hence biomass of numerous fish species (e.g. Buxton & Smale 1989, Russ & Alcala 1989, 1996b, Bennett & Attwood 1991, Polunin & Roberts 1993, Russ et al. 1993), implying that effects of reduced fishing mortality are larger than dilution of biomass in the protected are caused by any "spillover" effect. On the other hand, some level of net adult export ("spillover") is potentially beneficial to local yields. However, very limited empirical data on movements of fish in relation to protected areas, potentially leading to increased yields in adjacent areas (the so called "spillover" effect) exist. Determination of the potential existence and extent of this "spillover" effect may be crucial for public acceptance and community-based support and management of marine protected areas, particularly in the developing world (e.g. Alcala & Russ 1990, Holland et al. 1993a, Russ et al. 1993, Bohnsack 1996, Munro 1996, Russ 1996, Russ & Alcala 1996a&b). While most studies investigating such potential movements have used indirect measures of potential emigration and export of biomass (e.g. Alcala & Russ 1990, Rakitin & Kramer 1996, Russ & Alcala 1996a), others have used conventional external marking or tagging techniques which rely heavily on chance recapture of the marked animals (e.g. Gitschlag 1986, Beinssen 1989a, Bryant et al. 1989, Buxton & Allen 1989 in Roberts & Polunin 1991, Yamasaki & Kuwahara 1990, Die & Watson 1992, Attwood & Bennett 1994, Davies 1995).

The present study has demonstrated clearly the great potential of ultrasonic telemetry to address some of the important yet difficult scientific and management issues relating to marine protected areas. This study was unique in that it presented the first estimation of regular movements of individual fish across management zone boundaries for a species of major commercial and recreational fishing significance on the Great Barrier Reef. Furthermore, this study was the first to comprehensively and concurrently document the basic home ranges and activity patterns of *P. leopardus*. Rates of transfer of animals between protected and unprotected areas are influenced to a large extent by the boundary permeability (Buechner 1987) and the size of the protected area relative to the normal movement patterns and home ranges of the target species (Holland *et al.* 1993a, 1996). Thus, the concept of transfer rates has, as one of it's most

basic parameters, the principle of home range size, as well as basic activity and movement patterns (Minns 1995). Therefore, the comprehensive estimates of home ranges and daily movements of P. leopardus reported here, and obtainable only by ultrasonic telemetry, provided the first step in gaining insights into the estimation of potential transfer rates of this species in relation to marine protected areas. The range of home range sizes determined for *P. leopardus* indicated that marine protected areas need to be large enough to provide adequate space to accommodate home ranges of the larger serranids, if the protection of these species is envisaged. For example, the knowledge gained here suggests that some of the protected coral reef areas that have been studied extensively over the last 10-20 years, such as at Apo and Sumilon Islands in the Philippines (Russ 1985, 1996, Russ & Alcala 1989, 1994, 1996a&b, Alcala & Russ 1990, Russ et al. 1993), may not provide sufficient spatial refuge from fishing pressure for a species such as *P. leopardus*. Nevertheless, other species, potentially with other space requirements, such as lethrinids, lutjanids, carangids and some serranids, which sometimes comprised a large proportion of the catch, clearly have benefited (Alcala & Luchavez 1981, White & Savina 1987, Bellwood 1988, Alcala & Russ 1990, Russ & Alcala 1996a&b).

This study was able to compare data collected using ultrasonic telemetry with comparable data derived from a mark-release-resighting study using standard underwater visual census techniques as the recapture tool. Thus, it was possible to demonstrate the advantages of regular monitoring of individual fish equipped with ultrasonic transmitters compared to chance recaptures of externally marked animals. The results obtained from the comparison of the two methods clearly indicated that position records based on visual sightings may considerably underestimate the distances individual fish move during the course of their activities. It follows that any home range estimates obtained through visual resighting (or physical recapture of tagged fish) would most likely represent underestimates of true home ranges. Thus, any estimates of spatial patterns of area use based on one or even several visual records may lead to underestimation of the real area used by an individual.

Considerations need to be given also to the reproductive strategies employed by many reef fishes, in particular the common occurrence of spawning aggregations (reviewed by Sadovy 1996). Given the heavy fishing pressures exerted on many known spawning aggregations (see 7.1.), incorporation of aggregation sites (potential or known locations) in future marine protected areas should be considered strongly. Yet information on locations of aggregations is very limited for most species. Identifying the locations at which fish spawn, especially aggregating species, is of interest for identifying sources of larvae (Sadovy 1996). It is thus also important in considering the siting of marine protected areas as potential sources of larvae. For example, the proposed concept of networks of marine protected areas as a strategy to protect a minimum spawning stock biomass on a large, country wide basis (e.g. Philippines), requires a knowledge of the major "sources" and "sinks" of larvae (Russ & Alcala 1994, 1996a&b). Furthermore, given that a proportion of coral trout equipped with ultrasonic transmitters were recorded to move substantial distances to participate at aggregation events, any aggregation sites outside of protected areas may result, during spawning periods, in the removal of substantial biomass from what is essentially protected area standing stock. While such movements may fall into the category of "spillover", and hence increase local fishing yields, the potential effect of protection of stock through spatial closure may be negated if substantial proportions of the protected area stock leave for aggregation activities, only to be caught. Hence, such movements, as well as the location of major spawning sites, need to be considered seriously in the evaluation of size and location of future marine protected areas.

In summary, the knowledge gained through the use of ultrasonic telemetry in this project demonstrates that this technique is ideally suited to the evaluation of movement patterns of fishes on coral reefs. Such information is needed urgently to assess the efficacy and potential of marine protected areas as an alternative fisheries management tool, particularly for the developing world. The estimation, using ultrasonic telemetry, of rates of movements across management boundaries (i.e. "spillover"), as well as the incorporation of basic parameters, such as home ranges and activity patterns, and more irregular movements such as those associated with spawning aggregations, will permit

thorough and appropriate assessment of optimal sizes and locations for marine protected areas to ensure long term stock viability.

## 7.4. Future research

The current investigation restricted itself primarily to examination of movements and patterns of space use of *P. leopardus*. However, there are several other aspects of the biology of coral trout that can be addressed by ultrasonic telemetry in future investigations. Significantly, most of the concepts discussed below apply equally to other fish species on coral reefs.

**Behavioural ecology**: Of particular interest would be the examination of social interactions between individuals with overlapping home ranges, and the manifestation of these interactions in the patterns of space use.

**Eco-physiology**: Eco-physiological data can be obtained through the electronic sensing and ultrasonic transmitting of physiological parameters such as heart beat rate or muscle contractions. For example, it should be possible to correlate sudden, abrupt and powerful caudal fin beat sequences of coral trout (e.g. through electromyogram biotelemetry, *sensu* Demers *et al.* 1996), or increased rates of opercular movements before strikes (as recorded regularly during visual observations, pers. obs.) with rates of strikes for prey items during hunting. This, together with an evaluation of the proportion of successful strikes (i.e. food caught), may provide novel insights into energy budgets and rate of predation by species such as *P. leopardus*.

Besides behavioural and eco-physiological investigations, ultrasonic telemetry can be applied effectively to address several important **fisheries management** issues:

Improvements in the knowledge of locations of spawning aggregations and their catchment areas, with considerations of the effects of type of inter-reefal habitats. Of great importance will be further examination of the differences between the sexes in

residence patterns at spawning aggregation sites. In conjunction with such investigations, additional emphasis should be placed on developing methods for reliable, non-sacrificial and non-invasive sex determination of fishes during routine handling or transmitter placement procedures. One such technique showing great promise is ultrasonography, which has been used successfully on fishes (e.g. Mattson 1991, Karlsen & Holm 1994). Availability of such a technique will greatly facilitate the interpretation of data on social interactions and spawning aggregation behaviour and patterns of residence, irrespective of the chances of recovery of the study specimens at termination of tracking.

Evaluation of the "field of capture" (*sensu* Eggers *et al.* 1982, Miller & Hunte 1987, Davies 1989, Arena *et al.* 1994) of the commercially used baited hook and line capture method and other capture techniques (e.g. fish traps) forms an ideal area of investigation. This would allow the investigator to determine the size of the potential catchment area of a "hang". Furthermore, it would be possible to examine the gear susceptibility of a species, i.e. what proportion of target individuals in the field of capture are actually caught. Thus, this approach would permit experimental evaluation of the reported observation of decreasing catchability with increasing fishing duration or fishing pressure. Along similar lines, ultrasonic telemetry could be used to demonstrate any attraction or repulsion of fish caused by the presence of a diver carrying out an underwater visual census in a specific area.

Of major importance would be the detailed evaluation of the potential of "spillover" with respect to marine protected areas. This should be examined both through controlled experimental manipulation via the creation of new protected area boundaries within a previously closed reef section, i.e. using a "virgin" stock, and assessment of movements in/out of existing marine protected areas at locations with high fishing pressure, such as the well studied reserves at Apo and Sumilon Islands in the Philippines. Ideally, such an investigation should consider combining detailed evaluation of movements using ultrasonic telemetry, with a large scale external marking and recapture program, stratified in effort with distance from the zone boundary, both inside and outside of the marine protected areas. This would enhance the chances of

detecting and evaluating "spillover" effects with regards to distance from boundary through potentially increased recaptures through fishers engaged in their normal activities.

In addition to the investigative issues addressed above, several technical improvements and recommendations have emerged during this study:

The major recommendation with respect to surgical placement of ultrasonic transmitters relates to the closure of incisions. Based on the results and observations obtained during surgery in this study, the use of surgical staples as a primary means of incision closure is not recommended, at least for species such as *P. leopardus*. Instead, future investigations should make use of the superior levels of control over tissue apposition and suture tension that can be achieved with regular surgical suture materials such as braided silk or monofilament fibres. The greatly improved wound edge alignment possible with regular sutures will result in faster wound healing and reduced opportunities for secondary infections, thus reducing aquarium recovery periods.

If stomach placement through force feeding of transmitters is the only viable option, insertion of food items following the transmitter insertion may be advantageous in increasing the retention times. This possibility should be evaluated in a replicated, controlled aquarium experiment, followed by an experimental field evaluation.

Utilisation of automatic ultrasonic recording systems set up as grids of receivers for simultaneous, high-resolution monitoring of several animals equipped with transmitters is strongly recommended. Availability of such a system will greatly improve the accuracy and precision of position estimation, and increase the number of animals that can be accurately monitored in any one location, while drastically reducing tracking personnel and tracking vessel requirements and costs.

Any future use of conventional external marking techniques to assist in ultrasonic telemetry investigations, e.g. into "spillover" effects of marine protected areas, should involve a stratified experimental design, with both capture and recapture effort stratified in relation to distance from marine protected area boundaries.

### 7.5. General conclusions

- Ultrasonic telemetry was demonstrated to be a research tool that is well suited for use on coral reefs, providing information that is generally unachievable with more conventional techniques. Concerns regarding the effects of transmitter attachments should be evaluated on a species by species basis. Surgical insertion into the body cavity is the preferred method for long term monitoring. Further use of ultrasonic telemetry in coral reef fish and fisheries research is highly recommended.
- Application of ultrasonic telemetry to the study of *P. leopardus*, provided data on locations, participation rates and sex dependent patterns of use of spawning aggregations that have distinct implications to the understanding of the reproductive behaviour and strategies of *P. leopardus*, and possibly other protogynous species.
- The data on movements across marine park zone boundaries derived from ultrasonic telemetry, as well as the basic movement and space use patterns recorded for the study species, were illustrated to have great potential in the interpretation and assessment of effects of fishing and the use of marine protected areas as a fisheries management tool.
- This study was able to address questions fundamental to the understanding of the behaviour, ecology and reproductive strategies of the serranid *P. leopardus*. The information obtained provides not only the basis for future ecological and behavioural investigations of *P. leopardus* and other coral reef fishes, but may serve as the foundation for the development of improved management strategies for long-term sustainable fisheries and marine protected area management on coral reefs.

# REFERENCES

## **References:**

- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecol.* 74(5):1313-1325.
- Alcala, A. C. 1988. Effects of protective management of marine reserves on fish abundances and fish yields in the Philippines. *Ambio* 17:194-199.
- Alcala, A. C., and T. Luchavez. 1981. Fish yield of the coral reef surrounding Apo Island, central Visayas, Philippines. Proc. Fourth Int. Coral Reef Symp. 1:69-73.
- Alcala, A. C., and G. R. Russ. 1990. A direct test of the effects of protective management on abundance and yield of tropical marine resources. J. Cons. int. Explor. Mer. 46:40-47.
- Alhopuro, S., A. Rintala, H. Salo, and V. Ritsila. 1976. Tissue adhesive vs. sutures in closure of incision wounds. A comparative study in human skin. Annales Chirurgiae et Gynaecologiae 65:308-312.
- Amlaner, C. J., and D. W. MacDonald. 1980. A handbook on biotelemetry and radiotracking, 1st ed. Oxford: Pergamon Press.
- Anderson, D. J. 1982. The home range: a new nonparametric estimation technique. *Ecol.* 63(1):103-112.
- Andrew, N. L., and B. D. Mapstone. 1987. Sampling and the description of spatial pattern in marine ecology. Oceanogr. Mar. Biol. Annu. Rev. 35:39-90.
- Anonymous. 1996. Discussion Paper No. 2: Queensland Tropical Coral Reef Fish Species. Prepared for the Queensland Fisheries Management Authority by the Reef Fish Management Advisory Committee, Australia. 68 pp.
- Appeldoorn, R. S. 1996. Model and method in reef fishery assessment. In *Reef fisheries*, 1st ed., (Ed.) N. V. C. Polunin, and C. M. Roberts. London: Chapman & Hall.
- Arena, G., L. Barea, and O. Defeo. 1994. Theoretical evaluation of trap capture for stock assessment. Fish. Res. 19:349-362.
- Armstrong, J. D., A. D. F. Johnstone, and M. C. Lucas. 1992. Retention of intragastric transmitters after voluntary ingestion by captive cod, Gadus morhua L. J. Fish Biol. 40:135-137.

- Arnold, G. P., and P. H. Cook. 1984. Fish migration by selective tidal stream transport: first results with a computer simulation model for the European continental shelf. In *Mechanisms of fish migration*, 1st ed., (Ed.) J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill. New York: Plenum Press.
- Arnold, G. P., and B. H. Holford. 1979. The physical effects of an acoustic tag on the swimming performance of plaice and cod. J. Cons. int. Explor. Mer. 38:189-200.
- Attwood, C. G., and B. A. Bennett. 1994. Variation in dispersal of Galjoen (Coracinus capensis) (Teleostei: Coracinidae) from a marine reserve. Can. J. Fish Aquat. Sci. 51:1247-1257.
- Attwood, C. G., and B. A. Bennett . 1995. Modelling the effect of marine reserves on the recreational shore-fishery of the south-western Cape, South Africa. S. Afr. J. mar. Sci. 16:227-240.
- Ayling, A. M., and A. L. Ayling. 1986. A biological survey of selected reefs in the Capricornia section of the Great Barrier Reef Marine Park. Unpublished report to the GBRMPA, Australia.
- Ayling, A. M., and A. L. Ayling. 1992. Crown of thorns and coral trout density on three central section reefs: 1983-1989. Great Barrier Reef Marine Park Authority Research Publication No. 15:54pp.
- Ayling, A. M., and A. L. Ayling. 1994. Bramble reef replenishment area- 1993 and 1994 surveys. Unpublished report to Great Barrier Reef Marine Park Authority. 52 pp.
- Badyaev, A. V., W. J. Etges, and T. E. Martin. 1996. Ecological and behavioral correlates of variation in seasonal home ranges of wild turkeys. J. Wildl. Manage. 60(1):154-164.
- Bailey, N. J. J. 1952. Improvements in the interpretation of recapture data. J. Anim. Ecol. 21:120-127.
- Bannerot, S., W. W. Fox, and J. E. Powers. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean. In *Tropical snappers and groupers. Biology and fisheries management*, (Ed.) J. J. Polovina, and S. Ralston. Boulder: Westview Press.
- Bardach, J. E. 1958. On the movements of certain Bermuda reef fishes. Ecol. 39:139-146.
- Barlow, G. W. 1981. Patterns of parental investment, dispersal and size among coral reef fishes. Env. Biol. Fish. 6:65-85.

- Bass, G. A., and M. Rascovich. 1965. A device for the sonic tracking of large fishes. Zoologica: NY Zoological Society 50(8):75-84.
- Beinssen, K. 1989a. *Heron Reef demersal reef fish movement study*. Interim report. Report for the Dept. of Conservation, Parks & Wildlife.
- Beinssen, K. 1989b. Results of the Boult Reef replenishment area study. Final report. Report by the Dept. of Conservation, Parks & Wildlife.
- Bekoff, M., and L. D. Mech. 1984. Simulation analysis of space use: Home range estimates, variability, and sample size. Beh. Res. Meth. Instr. & Comp. 16(1):32-37.
- Bell, J. D., G. J. S. Craik, D. A. Pollard, and B. C. Russell. 1985. Estimating length frequency distributions of large reef fish underwater. *Coral Reefs* 4:41-44.
- Bellwood, D. R. 1988. Seasonal changes in the size and composition of the fish yield from reefs around Apo Island, central Philippines, with notes on methods of yield estimation. J. Fish Biol. 32:881-893.
- Bellwood, D. R., and A. C. Alcala. 1988. The effect of a minimum length specification on visual estimates of density and biomass of coral reef fishes. *Coral Reefs* 7:23-27.
- Bennett, B. A., and C. G. Attwood. 1991. Evidence for recovery of a surf-zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa. *Mar. Ecol. Prog. Ser.* 75:173-181.
- Bergh, M. O., and W. M. Getz. 1989. Stability and harvesting of competing populations with genetic variation in life history strategy. *Theor. Pop. Biol.* 36:77-124.
- Bertram, B. 1980. The Serengeti radio tracking program 1971-73. In A handbook on biotelemetry and radiotracking, 1st ed., (Ed.) C. J. Amlaner, and D. W. MacDonald. Oxford: Pergamon Press.
- Bohnsack, J. A. 1990. The potential of marine fishery reserves for reef fish management in the US Southern Atlantic. NOAA Technical Memorandum NMFS-SEFC-261, 40pp.
- Bohnsack, J. A. 1993. Marine reserves: They enhance fisheries, reduce conflicts, and protect resources. *Oceanus* 36(3):63-71.
- Bohnsack, J. A. 1996. Maintenance and recovery of reef fishery productivity. In *Reef fisheries*, 1st ed., (Ed.) N. V. C. Polunin, and C. M. Roberts. London: Chapman & Hall.

- Bowden, D. C. 1993. A simple technique for estimating population size, Fort Collins, USA: Dept. of Statistics, Colorado State University.
- Bradbury, C., J. M. Green, and M. Bruce-Lockhart. 1995. Home range of female cunner, *Tautogolabrus adspersus* (labridae), as determined by ultrasonic telemetry. *Can. J. Zool.* 73:1268-1279.
- Bray, R. N. 1981. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. *Fish. Bull.* 78(4):829-841.
- Brock, R. E. 1982. A critique of the visual census method for assessing coral reef fish populations. *Bull. Mar. Sci.* 32(1):269-276.
- Brock, V. E. 1954. A preliminary report on a method of estimating reef fish populations. J. Wildl. Manage. 18:297-308.
- Brown, I. W., P. Doherty, B. Ferreira, C. Keenan, G. McPherson, G. Russ, M. Samoilys, and W. Sumpton. 1994. Growth, reproduction and recruitment of Great Barrier Reef food fish stocks. Final Project Report, Fisheries Research and Development Corporation Project No. 90/18, Australia.
- Bruce, B. D., and W. R. Strong. 1991. The white shark: a research update. Aust. Soc. Fish Biol. Newsletter 21(2):28.
- Bryant, H. E., M. R. Dewey, N. A. Funicelli, G. M. Ludwig, D. A. Meineke, and L. J. Mengal. 1989. Movement of five selected sports species in Everglades National Park. Bull. Mar. Sci. 44(1):515.
- Bryant, M. D., C. A. Dolloff, P. E. Porter, and B. E. Wright. 1990. Freeze branding with CO<sub>2</sub>: An effective and easy to use field method to mark fish. Am. Fish. Soc. Sym. 7:30-35.
- Buechner, M. 1987. Conservation in insular parks: simulation models of factors affecting the movement of animals across park boundaries. *Biol. Cons.* 41:57-76.
- Burger, B., D. DeYoung, and D. Hunter. 1994. Sterilization of implantable transmitters. *Tel. Quat.* 7(3):3-4.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on releaserecapture, American Fisheries Society Monograph Vol. 5.

- Buxton, C. D., and M. J. Smale. 1989. Abundance and distribution patterns of three temperate marine reef fish (Teleostei: Sparidae) in exploited and unexploited areas off the southern cape coast. *Journal of Applied Ecology* 26:441-451.
- Cabanban, A. S., and A. T. White. 1981. Marine conservation program using nonformal education at Apo Island, Negros Oriental, Philippines. *Proceedings of the fourth International Coral Reef Symposium* 1: 317-321.
- Cain, M. L. 1989. The analysis of angular data in ecological field studies. *Ecol.* 70(5):1540-1543.
- Cameron, G. N., and S. R. Spencer. 1985. Assessment of space-use patterns in the hipid cotton rat (Sigmodon hipidus). Oecologia 68:133-139.
- Cane, A. 1981. Tests of some batch-marking techniques for rainbow trout (Salmo gairdneri). Fish. Manag. 12:1-8.
- Cappo, M., and I. W. Brown. 1996. Evaluation of sampling methods for reef fish populations of commercial and recreational interest. CRC Reef Research Centre, Technical Report No. 6, Townsville, 72 pp.
- Carey, F. G., and B. H. Robison. 1981. Daily patterns in the activities of swordfish, Xiphias gladius, observed by acoustic telemetry. Fish. Bull. 79(2):277-292.
- Carey, F. G., and J. V. Scharold. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar. Biol.* 106:329-342.
- Carey, F. G., J. M. Teal, and J. W. Kanwisher. 1981. The visceral temperature of mackerel sharks (Lamnidae). *Phys. Zool.* 54:334-344.
- Carr, M. H., and D. C. Reed. 1993. Conceptual issues relevant to marine harvest refuges: Examples from temperate reef fishes. *Can. J. Fish Aquat. Sci.* 50:2019-2028.
- Carter, J. 1988. Grouper mating ritual on a Caribbean reef. Underw. Nat. 17:8-11.
- Carter, J., G. J. Marrow, and V. Pryor. 1994. Aspects of the ecology and reproduction of Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. *Proc. Gulf Carib. Fish. Inst.* 43:65-111.
- Cato, D. H., and M. J. Bell. 1992. Ultrasonic ambient noise in Australian shallow waters at frequencies up to 200 kHz. MRL Technical Report, MRL-TR-91-23, RAN, Australia.
- Chao, A. 1989. Estimating population size for sparse data in capture-recapture experiments. Biometrics 45:427-438.

- Chapman, D. G. 1952. Inverse, multiple and sequential sample census. *Biometrics* 8:286-306.
- Choat, J. H. 1968. Feeding habits and distribution of *Plectropomus maculatus* (Serranidae) at Heron Island. *Proc. R. Soc. Qd.* 80(2):13-18.
- Clark, D. S., and J. M. Green. 1990. Activity and movement patterns of juvenile cod, Gadus morhua, in Conception Bay, Newfoundland, as determined by sonic telemetry. Can. J. Zool. 68:1434-1442.
- Cochrane, C. 1985. A sticky solution. Nurs. Mirr. 160(25):32-33.
- Coleman, F. C., C. C. Koenig, and L. A. Collins. 1996. Reproductive styles of shallowwater groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Env. Biol. Fish.* 47:129-141.
- Colin, P. L. 1992. Reproduction of the Nassau groper, *Epinephelus striatus* (Pisces:Serranidae) and its relationship to environmental conditions. *Env. Biol. Fish.* 34:357-377.
- Colin, P. L. 1995. Some aspects of social behaviour of the Nassau grouper, *Epinephelus* striatus (Pisces: Serranidae). Abstract, XXIV International Ethological Conference, Honolulu, Hawaii, August 10-17.
- Colin, P. L., and I. E. Clavijo. 1988. Spawning activity of fishes producing pelagic eggs on a shelf edge coral reef, southwestern Puerto Rico. Bull. Mar. Sci. 43(2):249-279.
- Colin, P. L., D. Y. Shapiro, and D. Weiler. 1987. Aspects of the reproduction of two groupers, *Epinephelus guttatus* and *E. striatus* in the West Indies. *Bull. Mar. Sci.* 40(2):220-230.
- Cook, M. F., and E. P. Bergersen. 1988. Movements, habitat selection, and activity periods of northern pike in eleven mile reservoir, Colorado. Trans. Amer. Fish. Soc. 117:495-502.
- Coombs, K. A., K. J. Bailey, C. M. Herbinger, and G. W. Friars. 1990. Evaluation of various external marking techniques for atlantic salmon. Am. Fish. Soc. Sym. 7:142-146.
- Craik, W. 1981. Recreational Fishing on the Great Barrier Reef. Proc. Fourth Int. Coral Reef Symp. 1:47-52.

- Crane, S. W. 1983. Suture materials. Current techniques in small animal surgery, Section A(1):3-6.
- Dalzell, P. 1996. Catch rates, selectivity and yields of reef fishing. In *Reef Fisheries*, 1st ed., (Ed.) N. V. C. Polunin, and C. M. Roberts. London: Chapman & Hall.
- Danielson, B. J., and R. K. Swihart. 1987. Home range dynamics and activity patterns of *Microtus ochrogaster* and *Synaptomys cooperi* in Syntopy. J. Mamm. 68(1):160-165.
- Davies, C. R. 1989. The effectiveness of non-destructive sampling of coral reef fish populations with fish traps. Honours Thesis. James Cook University, Townsville.
- Davies, C. R. 1993. Inter-reef movement of large reef fishes. Great Barrier Reef Marine Park Authority, Effects of Fishing Project Annual Report 92/93, 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, 203 pp.
- Davis, G. E. 1981. On the role of underwater parks and sanctuaries in the management of coastal resources in the southeastern United States. *Env. Cons.* 8:67-70.
- Davis, G. E. 1989. Designated harvest refugia: The next stage of marine fishery management in California. Calif. Coop. Oceanic Fish. Invest. Rep. 30:53-58.
- Davis, T. L. O., and G. J. West. 1993. Maturation, reproductive seasonality, fecundity, and spawning frequency in *Lutjanus vitta* (Quoy and Gaimard) from the North West shelf of Australia. *Fish. Bull.* 91(2):224-236.
- Dayton, P. K., S. F. Thrush, M. T. Agary, and R. J. Hofman. 1995. Environmental effects of marine fishing. Aqu. Cons. Mar. Freshw. Ecos. 5:205-232.
- De Martini, E. E. 1993. Modeling the potential of fishery reserves for managing Pacific coral reef fishes. Fish. Bull. 91(3):414-427.
- Diana, J. S., D. F. Clapp, E. M. Hay-Chmielewski, G. Schnicke, D. Siler, W. Ziegler, and R. D. Clark. 1990. Relative success of telemetry studies in Michigan. Am. Fish. Soc. Sym. 7:346-352.
- Die, D. J., and R. A. Watson. 1992. A per-recruit simulation model for evaluating spatial closures in an Australian penaeid fishery. Aqu. Liv. Res. 5(3):145-153.

- Diffendorfer, J. E., M. S. Gaines, and R. D. Holt. 1995. Habitat fragmentation and movements of three small mammals (Sigmodon, Microtus, and Peromyscus). Ecol. 76(3):827-839.
- Doherty, P. J., D. M. Williams, and P. F. Sale. 1985. The adaptive significance of larval dispersal in coral reef fishes. *Env. Biol. Fish.* 12:81-90.
- Douglas, R. J. 1992. Effects of radio-collaring on Deer mouse survival and vulnerability to Ermine predation. Amer. Midland Nat. 127:198-199.
- Draulan, D., and J. V. Vessem. 1985. Age related differences in the use of time and space by radio tagged grey herons (Ardea cinera) in winter. J. Anim. Ecol. 54:771-780.
- Dugan, J. E., and G. E. Davis. 1993. Applications of marine refugia to coastal fisheries management. Can. J. Fish Aquat. Sci. 50:2029-2042.
- Ebisawa, A. 1990. Reproductive biology of *Lethrinus nebulosus* (Pisces:Lethrinidae) around the Okinawa waters. *Nipp. Suis. Gakk.* 56:1941-1954.
- Eggers, D. M., N. A. Rickard, D. G. Chapman, and R. R. Whitman. 1982. A methodology for estimating area fished for baited hooks and traps along a ground line. *Can. J. Fish Aquat. Sci.* 39:448-453.
- Ensign, W. E., P. L. Angermeier, and C. A. Dolloff. 1995. Use of line transect methods to estimate abundance of benthic stream fishes. *Can. J. Fish Aquat. Sci.* 52:213-222.
- Erdmann, M. V., and L. Pet-Soede. 1996. How fresh is too fresh? The live reef food fish trade in Eastern Indonesia. NAGA 19 (January):4-8.
- Fable, W. A. 1980. Tagging studies of red snapper (*Lutjanus campechanus*) and vermilion snapper (*Rhomboplites aurorubens*) off the south Texas coast. Contr. Mar. Sci. 23:115-121.
- Ferreira, B. P. 1993a. Age, growth, reproduction and population biology of Plectropomus spp (Epinephelinae:Serranidae) on the Great Barrier Reef, Australia. Ph.D. Dissertation. James Cook University, Townsville, Australia.
- Ferreira, B. P. 1993b. Reproduction of the inshore coral trout *Plectropomus maculatus* (Perciformes:Serranidae) from the Central Great Barrier Reef, Australia. J. Fish Biol. 42:831-844.

- Ferreira, B. P. 1995. Reproduction of the Common Coral Trout Plectropomus leopardus (Serranidae: Epinephelinae) from the Central and Northern Great Barrier Reef, Australia. Bull. Mar. Sci. 56(2):653-669.
- Ferreira, B. P., and G. R. Russ. 1992. Age, growth and mortality of the inshore coral trout *Plectropomus maculatus* (Pisces:Serranidae) from the central Great Barrier Reef, Australia. Aust. J. Mar. Freshwater Res. 43:1301-1312.
- Ferreira, B. P., and G. R. Russ. 1994. Age validation and estimation of growth-rate of a tropical serranid, the coral trout *Plectropomus leopardus* (Lacepede 1802) from Lizard Island, Northern Great Barrier Reef. *Fish. Bull.* 92:46-57.
- Ferreira, B. P., and G. R. Russ. 1995. Population structure of the leopard coral grouper, *Plectropomus leopardus*, on fished and unfished reefs off Townsville, central Great Barrier Reef, Australia. *Fish. Bull*. 93:629-642.
- Filipek, S. 1988. A rapid field technique for transmitter implantation in paddlefish. In Proc. 10<sup>th</sup> int. Symp. of Biotelemetry, (Ed.) C. J. Amlaner. : Univ. Arkansas Press.
- Fitch, W. T. S., and D. Y. Shapiro. 1990. Spatial dispersion and non-migratory spawning in the Bluehead Wrasse (*Thalassoma bifasciatum*). *Ethology* 85:199-211.
- Gilderhus, P. A., and L. L. Marking. 1987. Comparative efficacy of 16 anesthetic chemicals on rainbow trout. N. Amer. J. Fish. Manag. 7:288-292.
- Gilmore, R. G., and R. S. Jones. 1992. Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. *Bull. Mar. Sci.* 51(1):83-103.
- Gitschlag, G. R. 1986. Movement of pink shrimp in relation to the Tortugas sanctuary. N. Amer. J. Fish. Manag. 6:328-338.
- Goeden, G. 1978. A monograph of the coral trout. Qld. Fisheries Service, Australia, Research Bulletin No 1, 42pp.
- Goldman, B., and F. H. Talbot. 1976. Aspects of the ecology of coral reef fishes. In *Biology* and geology of coral reefs, 1st ed., (Ed.) O. A. Jones, and R. Endean. NY: Academic press.
- Goodyear, C. P. 1996. Minimum sizes for Red Grouper: consequences of considering variable size at age. N. Amer. J. Fish. Manag. 16:505-511.
- Grant, J. W. A., and D. L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Can. J. Fish Aquat. Sci. 47:1724-1737.

- Greer Walker, M., F. R. Harden Jones, and G. P. Arnold. 1978. The movements of plaice (*Pleuronectes platessa* L.) tracked in the open sea. J. Cons. int. Explor. Mer. 38:58-86.
- Gregory, P. T., J. M. Macartney, and K. W. Larsen. 1987. Spatial patterns and movements. In Snakes. Ecology and evolutionary biology, 1st ed., (Ed.) R. A. Siegel, J. T. Collins, and S. S. Novak. New York: Macmillan.
- Grimes, C. B. 1987. Reproductive biology of the Lutjanidae: a review. In *Tropical snappers* and groupers: Biology and fisheries management, 1st ed., (Ed.) J. J. Polovina, and S. Ralstone. Boulder: USA.
- Gruber, S. H., D. R. Nelson, and J. F. Morrissey. 1988. Patterns of activity and space utilization of Lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. *Bull. Mar. Sci.* 43(1):61-76.
- Gwynne, L. 1990. A review of the reef line fishery and proposed management measures. A discussion paper. Queensland Fish Management Authority, 16 pp.
- Hailey, A., and I. M. Coulson. 1996. Differential scaling of home-range area to daily movement distance in two African tortoises. *Can. J. Zool.* 74:97-102.
- Hancock, D. A. 1992. Legal sizes and their use in fisheries management. Australian Society for Fish Biology Workshop, Lorne, 1990. Bureau of Natural Resources Proceedings No 13, 1st ed., Canberra: Australian Government Publishing Service.
- Harden-Jones, F. R., and G. P. Arnold. 1982. Acoustic telemetry and the marine fisheries. In *Telemetric studies of vertebrates*. Symposia 49, Zool. Soc. London, 1st ed., (Ed.) C. L. Cheeseman, and R. B. Mitson. London: Academic Press.
- Hargreaves, N. B. 1992. An electronic hot-branding device for marking fish. Prog. Fish-Cult. 54:99-104.
- Harmelin-Vivien, M. L., and C. Bouchon. 1976. Feeding behaviour of some carnivorous fishes (Serranidae, Scorpaenidae) from Tulear (Madagascar). Mar. Biol. 4:329-340.
- Harrell, R. M. 1992. Stress mitigation by use of salt and anesthetic for wild striped bass captured for brood stock. *Prog. Fish-Cult.* 54:228-233.
- Hart, L. G., and R. C. Summerfelt. 1975. Surgical procedures for implanting ultrasonic transmitters into flathead catfish (*Pylodictis olivaris*). Trans. Amer. Fish. Soc. 104:56-59.

- Harvey, P. H., and T. H. Clutton-Brock. 1981. Primate home range size and metabolic needs. Behav. Ecol. Sociobio. 8:151-155.
- Hawkins, A. D., and G. C. Urquhart. 1983. Tracking fish at sea. In *Experimental biology at* sea, 1st ed., (Ed.) A. G. MacDonald, and I. G. Priede. London: Academic Press.
- Hawkins, A. D., G. G. Urquhart, and G. W. Smith. 1980. Ultrasonic tracking of juvenile cod by means of a large spaced hydrophone array. In A handbook on biotelemetry and radiotracking, 1st ed., (Ed.) C. J. Amlaner, and D. W. MacDonald. Oxford: Pergamon Press.
- Head, W. D., W. O. Watanabe, S. C. Ellis, and E. P. Ellis. 1996. Hormone-induced multiple spawning of captive Nassau grouper broodstock. *Prog. Fish-Cult.* 58:65-69.
- Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecol.* 72(2):523-533.
- Hilborn, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Can. J. Fish Aquat. Sci. 47:635-643.
- Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment. Choice, dynamics and uncertainty, 1st ed., New York: Chapman & Hall.
- Hilborn, R., C. J. Walters, and D. B. Jester. 1990. Value of fish marking in fisheries management. Am. Fish. Soc. Sym. 7:5-7.
- Hobson, E. S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull. 71(4):915-1031.
- Holland, K. N., R. Brill, S. Ferguson, R. Chang, and R. Yost. 1985. A small vessel technique for tracking pelagic fish. *Mar. Fish. Rev.* 47(4):26-32.
- Holland, K. N., R. Brill, and R. K. C. Chang. 1990a. Horizontal and vertical movements of Pacific Blue Marlin captured and released using sportfishing gear. *Fish. Bull.* 88:397-402.
- Holland, K. N., R. W. Brill, and R. K. C. Chang. 1990b. Horizontal and vertical movements of yellowfin and bigeye Tuna associated with fish aggregating devices. *Fish. Bull.* 88:493-507.
- Holland, K. N., C. G. Lowe, J. D. Peterson, and A. Gill. 1992. Tracking coastal sharks with small boats: Hammerhead shark pups as a case study. Aust. J. Mar. Freshwater Res. 43:61-66.

- Holland, K. N., J. D. Peterson, C. G. Lowe, and B. M. Wetherbee. 1993a. Movements, distribution and growth rates of the white goatfish *Mulloides flavolineatus* in a fisheries conservation zone. *Bull. Mar. Sci.* 52(3):982-992.
- Holland, K. N., B. M. Wetherbee, J. D. Peterson, and C. G. Lowe. 1993b. Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia* 1993(2):495-502.
- Holland, K. N., C. G. Lowe, and B. M. Wetherbee. 1996. Movements and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. *Fish. Res.* 25:279-292.
- Hughes, T. 1994. Catastrophes, phase shifts, and large scale degradation of a Caribbean coral reef. *Science* 265:1547-1551.
- Huntsman, G. R., and W. E. Schaaf. 1994. Simulation of the impact of fishing on reproduction of a protogynous grouper, the Graysby. N. Amer. J. Fish. Manag. 14:41-52.
- Hutchings, J. A., and R. S. Myers. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Can. J. Fish Aquat. Sci.* 51:2126-2146.
- Ireland, L. C., and J. W. Kanwisher. 1978. Underwater acoustic biotelemetry: procedures for obtaining information on the behaviour and physiology of free swimming aquatic animals in their natural environments. In *The behaviour of fish and* other aquatic animals, 1st ed., (Ed.) D. I. Mostofsky. London: Academic Press.
- Jellyman, D. J., G. J. Glova, and P. R. Todd. 1996. Movements of short-finned eels, Anguilla australis, in Lake Ellesmere, New Zealand: results from markrecapture studies and sonic tracking. N. Z. J. Mar. Fresw. Res. 30:371-381.
- Jennings, S., and J. M. Lock. 1996. Population and ecosytem effects of reef fishing. In Reef fisheries, 1st ed., (Ed.) N. V. C. Polunin, and C. M. Roberts. London: Chapman & Hall.
- Jennrich, R. I., and F. B. Turner. 1969. Measurement of non-circular home range. J. Theoret. Biol. 22:227-237.
- Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Env. Biol. Fish.* 3:741-760.
- Johannes, R. E. 1981. Words of the Lagoon: Fishing and Marine Lore in the Palau District of Micronesia, 1st ed., Berkely: University of California Press.

- Johannes, R. E. 1988. Spawning aggregation of the grouper, *Plectropomus areolatus* (Ruppel) in the Solomon Islands. Proceedings of the 6th International Coral Reef Symposium, Townsville, Australia, Vol.2: 751-755.
- Johannes, R. E., and L. Squire. 1988. Aggregations of coral trout and maori wrasse in the Great Barrier Reef Marine Park. Report to GBRMPA, 10pp.
- Johannes, R. E., and M. Riepen. 1995. Environmental, economic, and social implications of the live reef fish trade in Asia and the Western Pacific. Report to The Nature Conservancy and the South Pacific Forum Fisheries Agency.
- Johannes, R. E., L. Squire, and T. Graham. 1994. Developing a protocol for monitoring spawning aggregations of Palauan serranids to facilitate the formulation and evaluation of strategies for their management. Progress report; South Pacific Forum Fisheries Agency, 23pp.
- Johannes, R. E., L. Squire, T. Graham, H. Renguul, and A. Bukurrou. 1995. *Palau grouper* spawning aggregation research project. 1995 Progress Report.
- Kamer, F. M., and J. H. Joseph. 1989. Histoacryl: Its use in aesthetic facial plastic surgery. Arch. Otolaryngol. Head Neck Surg. 115:193-197.
- Karlsen, O., and J. C. Holm. 1994. Ultrasonography, a non-invasive method for sex determination in cod (*Gadus morhua*). J. Fish Biol. 44:965-971.
- Kaseloo, P. A., A. H. Weatherly, J. Lotimer, and M. D. Farine. 1992. A biotelemetry system recording fish activity. J. Fish Biol. 40:165-179.
- Kearney, R. E. 1989. Tagging- solution or problem? In Australian Society for Fish Biology Tagging Workshop. Proceedings No. 5, (Ed.) D. A. Hancock. Canberra: Aust. Govt. Publ. Serv.
- Keeley, E. R., and J. W. A. Grant. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (Salmo salar). Can. J. Fish Aquat. Sci. 52:186-196.

Kenward, R. 1987. Wildlife Radio Tagging. Academic press: London.

- Kie, J. G., J. A. Baldwin, and C. J. Evans. 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.

- Klimley, A. P. 1993. Highly directional swimming by scalloped hammerhead sharks, Sphyrna lewini, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. Mar. Biol. 117:1-22.
- Klimley, A. P., S. B. Butler, D. R. Nelson, and A. T. Stull. 1988. Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* Griffith and Smith, to and from a seamount in the Gulf of California. J. Fish Biol. 33:751-761.
- Knight, A. E. 1990. Cold branding techniques for estimating atlantic salmon parr densities. Am. Fish. Soc. Sym. 7:36-37.
- Knights, B. C., and B. A. Lasee. 1996. Effects of implanted transmitters on adult Bluegills at two temperatures. *Trans. Amer. Fish. Soc.* 125:440-449.
- Knowlton, R. E., and J. M. Moulton. 1963. Sound production in the snapping shrimps Alpheus (Crangon) and Synalpheus. Biol. Bull. 125(2):311-331.
- Koehler, D. K., T. D. Reynolds, and S. H. Anderson. 1987. Radio-transmitter implants in four species of small mammals. J. Wildl. Manage. 51(1):105-108.
- Korschgen, C. E., K. P. Kenow, W. L. Green, D. H. Johnson, M. D. Samuel, and L. Sileo. 1996. Survival of radiomarked Canvasback ducklings in northwestern Minnesota. J. Wildl. Manage. 60(1):120-132.
- Krebs, C. J., A. J. Kenney, and G. R. Singleton. 1995. Movements of feral house mice in agricultural landscapes. *Aust. J. Zool.* 43:293-302.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62(1):67-118.
- Lee, J. E., G. C. White, R. A. Garrot, R. M. Bartmann, and A. W. Alldredge. 1985. Accessing accuracy of a radiotelemetry system for estimating animal locations. J. Wildl. Manage. 49(3):658-663.
- Lemm, C. A. 1993. Evaluation of five anesthetics on Striped Bass. U.S. Dept. Int. Res. Publ. 196:10.
- Levy, D. A., and A. D. Cadenhead. 1995. Selective tidal stream transport of adult sockeye salmon (Oncorhynchus nerka) in the Fraser River estuary. Can. J. Fish Aquat. Sci. 52:1-12.
- Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time, and body size in mammals. *Ecol.* 67(2):413-418.

- Lobel, P. S. 1989. Ocean current variability and the spawning season of Hawaiian reef fishes. *Env. Biol. Fish.* 24:161-171.
- Longhurst, A. R., and D. Pauly. 1987. *Ecology of tropical oceans*, 1st ed., Orlando, USA: Academic Press.
- Losey, G. S., and D. M. Hugie. 1994. Prior anesthesia impairs a chemically-mediated fright response in a Gobiid fish. J. Chem. Ecol. 20(8):1877-1883.
- Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260:17-18.
- MacDonald, D. W., F. G. Ball, and N. G. Hough. 1980. The evaluation of home range size and configuration using radio tracking data. In A handbook on biotelemetry and radiotracking, 1st ed., (Ed.) C. J. Amlaner, and D. W. MacDonald. Oxford: Pergamon Press.
- Mackay, R. S. 1968. Bio-medical telemetry, 1st ed., New York: Wiley & Sons.
- Mackie, M. 1993. Reproductive biology and social structure of the blue-spotted rock cod, Cephalopholis cyanostigma (Serranidae), and the effects of fishing. Hns. Thesis. James Cook University, Townsville, Australia.
- Man, A., R. Law, and N. V. C. Polunin. 1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. *Biol. Cons.* 71:197-204.
- Mapstone, B. D., and A. M. Ayling. 1993. An investigation of optimum methods and unit sizes for the visual estimation of abundances of some coral reef organisms. Draft report to the GBRMPA, unpublished data.
- Matthews, K. R., T. P. Quinn, and B. S. Miller. 1990. Use of ultrasonic transmitters to track demersal rockfish movements on shallow rocky reefs. Am. Fish. Soc. Sym. 7:375-379.
- Mattson, N. S. 1991. A new method to determine sex and gonad size in live fishes by using ultrasonography. J. Fish Biol. 39:673-677.
- Mattson, N. S., and T. H. Riple. 1989. Metomidate, a better anesthetic for cod (*Gadus morhua*) in comparison with benzocaine, MS-222, chlorobutanol, and phenoxyethanol. *Aquaculture* 83:89-94.
- Mazeroll, A. I., and W. L. Montgomery. 1995. Structure and organization of local migrations in brown surgeonfish (Acanthurus nigrofuscus). Ethology 99:89-106.

- McCauley, R. D. 1995. Aspects of marine biological sound in northern Australia, III: reef associated fish choruses. Prepared for the Defense Science and Technology Organisation, Pyrmont, Sydney; 39pp.
- McFarland, W. N., and G. W. Klontz. 1969. Anesthesia in fishes. Federation Proceedings 28(4):1535-1540.
- McFarlane, G. A., and R. J. Beamish. 1990. Effect of an external tag on growth of sablefish (*Anoplopoma fimbria*), and consequences to mortality and age at maturity. *Can. J. Fish Aquat. Sci.* 47:1551-1557.
- Mech, L. D. 1983. Handbook of Animal Radio-Tracking. Minneapolis: Univ. of Minnesota Press.
- Mellas, E. J., and J. M. Haynes. 1985. Swimming performance and behaviour of rainbow trout (*Salmo gairdneri*) and white perch (*Morone americana*): effects of attaching telemetry transmitters. *Can. J. Fish Aquat. Sci.* 42:488-493.
- Mesing, C. L., and A. M. Wicker. 1986. Home range, spawning migrations, and homing of radio tagged Florida largemouth bass in two central Florida lakes. *Trans. Amer. Fish. Soc.* 115:286-295.
- Miller, R. J., and W. Hunte. 1987. Effective area fished by Antillean fish traps. Bull. Mar. Sci. 40(3):484-493.
- Minns, C. K. 1995. Allometry of home range size in lake and river fishes. Can. J. Fish Aquat. Sci. 52:1499-1508.
- Minta, S., and M. Mangel. 1989. A simple population estimate based on simulation for capture-recapture and capture-resight data. *Ecol.* 70(6):1738-1751.
- Mitson, R. B. 1978. A review of biotelemtry techniques using acoustic tags. In *Rhythmic* activity of fishes, 1st ed., (Ed.) J. E. Thorpe. London: Academic Press.
- Moe, M. A. 1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. *Prof. Papers Series 10*, Florida Dept. of Natural Resources, Marine Research Laboratory, St. Petersburg, Florida. 95pp.
- Moore, A., E. C. E. Potter, N. J. Milner, and S. Bamber. 1995. The migratory behaviour of wild Atlantic salmon (*Salmo salar*) smolts in the estuary of the river Conwy, North Wales. Can. J. Fish Aquat. Sci. 52:1923-1935.
- Morgan, M. J., and E. A. Trippel. 1996. Skewed sex ratios in spawning shoals of Atlantic cod (Gadus morhua). ICES J. Mar. Sci. 53:820-826.

- Morrissey, J. F., and S. H. Gruber. 1993a. Home range of juvenile lemon sharks, Negaprion brevirostris. Copeia 1993(2):425-434.
- Morrissey, J. F., and S. H. Gruber. 1993b. Habitat selection by juvenile lemon sharks, Negaprion brevirostris. Env. Biol. Fish. 38:311-319.
- Mortensen, D. G. 1990. Use of staple sutures to close surgical incisions for transmitter implants. Am. Fish. Soc. Sym. 7:380-383.
- Moser, M. L., A. F. Olson, and T. P. Quinn. 1990. Effects of dummy ultrasonic transmitters on juvenile Coho Salmon. Am. Fish. Soc. Sym. 7:353-356.
- Mulford, C. J. 1984. Use of a surgical stapler to quickly close incisions in striped bass. N. Amer. J. Fish. Manag. 4:571-573.
- Munro, J. L. 1974. The biology, ecology, exploitation and management of Caribbean reef fishes Vb. Serranidae (hinds and groupers). Res. Rep. zool. Dep. Univ. W. Indies 3:1-82.
- Munro, J. L. 1996. The scope of tropical reef fisheries and their management. In *Reef fisheries*, 1st ed., (Ed.) N. V. C. Polunin, and C. M. Roberts. London: Chapman & Hall.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1996. Hypotheses for the decline of cod in the North Atlantic. *Mar. Ecol. Prog. Ser.* 138:293-308.
- Myrberg, A. A., W. L. Montgomery, and L. Fishelson. 1988. The reproductive behaviour of *Acanthurus nigrofuscus* (Forskal) and other surgeonfishes (Fam. Acanthuridae) off Eilat, Israel (Gulf of Aqaba, Red Sea). *Ethology* 79:31-61.
- Nagelkerken, W. P. 1979. Biology of the Graysby, *Epinephelus cruentatus*, on the coral reef of Curacao. *Stud. Fauna Curacao* 60:1-118.
- Neal, A. K., G. C. White, R. B. Gill, D. F. Reed, and J. H. Olterman. 1993. Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. J. Wildl. Manage. 57:436-450.
- 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,* (Ed.) H. L. Pratt, S. H. Gruber, and T. Taniuchi. : NOAA Tech. Rep.: NOAA-NMFS-SWFSC-90.
- Nemetz, T. G., and J. R. MacMillan. 1988. Wound healing of incisions closed with a cyanoacrylate adhesive. *Trans. Amer. Fish. Soc.* 117:190-195.

- Newman, S. J., D. McB. Williams, and G. R. Russ. 1996. Variability in the population structure of *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) among reefs in the central Great Barrier Reef, Australia. Fish. Bull. 94:313-329
- Newman, S. J., D. McB. Williams, and G. R. Russ. in press. Age validation, growth and mortality rates of the tropical snappers (Pisces:Lutjanidae), *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the central Great Barrier Reef, Australia. J. Mar. Freshw. Res.
- Nichols, J. D. 1992. Capture-recapture models. *BioScience* 42(2):94-102.
- Nichols, J. D., and K. H. Pollock. 1983. Estimation methodology in contemporary small mammal capture-recapture studies. J. Mamm. 64(2):253-260.
- Nursall, J. R. 1981. The activity budget and use of territoriality by a tropical blenniid fish. Zool. J. Linn. Soc 72:69-92.
- O'Dor, R. K., J. Forsythe, D. M. Webber, J. Wells, and M. J. Wells. 1993. Activity levels of *Nautilus* in the wild. *Nature* 362:626-627.
- O'Dor, R. K., J. A. Hoar, D. M. Webber, F. G. Carey, S. Tanaka, H. R. Martins, and F. M. Porteiro. 1994. Squid (*Loligo forbesi*) performance and metabolic rates in nature. *Mar. Fresh. Behav. Physiol.* 25:163-177.
- O'Dor, R. K., D. M. Webber, W. Sauer, M. Roberts, and M. Smale. 1995. High resolution, 3-D tracking of squid on spawning grounds with radio-acoustic positioning. In Proc. 13th Int. Symp. Biotelemetry, 1st ed., (Ed.) C. Cristalli, C. J. Amlaner, and M. R. Neuman. Fayetteville: Arkansas Press. pp: 193-198.
- Pankhurst, N. W., and G. Van Der Kraak. in press. Effects of stress on reproduction and growth of fish. In Fish stress and health in aquaculture, 1st ed., (Ed.) G. Iwama. Cambridge: Cambridge University Press.
- Parma, A. M., and R. B. Deriso. 1990. Dynamics of age and size composition in a population subject to size-selective mortality: effects of phenotypic variability in growth. Can. J. Fish Aquat. Sci. 47:274-289.
- Parrish, J. D. 1987. The trophic biology of snappers and groupers. In Tropical snappers and groupers. Biology and fisheries management, (Ed.) J. J. Polovina, and S. Ralston. Boulder: Westview Press.
- Pepperell, J. G. 1990. Australian cooperative game fish tagging program, 1973-87: Status and evaluation of tags. Am. Fish. Soc. Sym. 7:765-774.
- Pepperell, J., and K. N. Holland. 1992. Ultrasonic tracking of tuna and billfish. Aust. Fish. 51(6):26-28.
- Pincock, D. G., and F. A. Voegeli. 1990. Quick course in underwater telemetry systems. Telemetry manual published by VEMCO Ltd., Canada.
- Polacheck, T. 1990. Year round closed areas as a management tool. Nat. Res. Mod. 4(3):327-354.
- Polovina, J. J., and S. Ralston. 1987. Tropical Snappers and Groupers. Biology and Fisheries Management, 1st ed. Boulder: Westview Press.
- Polunin, N. V. C. 1990. Marine regulated areas: an expanded approach for the tropics. *Res. Manag. Opt.* 7:283-299.
- Polunin, N. V. C., and C. M. Roberts. 1993. Greater biomass and value of target coral reef fishes in two small Caribbean marine reserves. Mar. Ecol. Prog. Ser. 100:167-176.
- Polunin, N. V. C., and C. M. Roberts (Eds.). 1996. Reef Fisheries. London: Chapman & Hall. 477 pp.
- Puceat, M., D. Garin, and A. Freminet. 1989. Inhibitory effect of anaesthesia with 2phenoxytethanol as compared to MS222 on glucose release in isolated hepatocytes from rainbow trout (Salmo gairdneri). Comp. Biochem. Physiol. 94(A)(2):221-224.
- Quinn, T. P., B. A. Terhart, and C. Groot. 1989. Migratory orientation and vertical movements of homing adult sockeye salmon, *Oncorhynchus nerka*, in coastal waters. *Anim. Behav.* 37:587-599.
- Rakitin, A., and D. L. Kramer. 1996. Effect of a marine reserve on the distribution of coral reef fishes in Barbados. *Mar. Ecol. Prog. Ser.* 131:97-113.
- Raleigh, R. F., J. B. McLaren, and D. R. Graff. 1973. Effects of topical location, branding techniques and changes in hue on recognition of cold brands in centrarchid and salmonid fish. *Trans. Amer. Fish. Soc.* 3:637-641.
- Ralston, S. 1982. Influence of hook size in the Hawaiian deep-sea handline fisheries. Can. J. Fish Aquat. Sci. 39:1297-1302.
- Ralston, S. 1987. Mortality rates of snappers and groupers. In Tropical snappers and groupers. Biology and fisheries management, (Ed.) J. J. Polovina, and S. Ralston. Boulder: Westview Press.

- Ralston, S. 1990. Size selection of snappers (Lutjanidae) by hook and line gear. Can. J. Fish Aquat. Sci. 47:696-700.
- Randall, J. E. 1962. Tagging reef fishes in the Virgin Islands. Proc. Gulf Carib. Fish. Inst. 14:201-241.
- Randall, J. E. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Caribb. J. Sci.* 3:31-47.
- Randall, J. E. 1965. Food habits of the Nassau grouper (Epinephelus striatus). Report Assoc. Isl. Mar. Lab. Caribbean, 6th meeting: 13-16.
- Randall, J. E., and V. E. Brock. 1960. Observations on the ecology of epinepheline and lutjanid fishes of Society Islands, with emphasis on food habits. *Trans. Amer. Fish. Soc.* 89:9-16.
- Reaka-Kudla, M. 1996. Treasures lost in reef madness. New Scientist (17 February):9.
- Recksiek, C. W., R. S. Appeldoorn, and R. G. Turingan. 1991. Studies of fish traps as stock assessment devices on a shallow reef in south-western Puerto Rico. *Fish. Res.* 10:177-197.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada, No. 191, 382pp.
- Roberts, C. M., and N. V. C. Polunin. 1991. Are marine reserves effective in management of reef fisheries? *Rev. Fish Biol. Fish.* 1:65-91.
- Robertson, D. R. 1983. On the spawning behavior and spawning cycles of eight surgeonfishes (Acanthuridae) from the Indio-Pacific. *Env. Biol. Fish.* 9:193-223.
- Robertson, D. R. 1988. Abundances of surgeonfishes on patch reefs in Caribbean Panama: due to settlement, or post-settlement events. *Mar. Biol.* 97:459-501.
- Robertson, D. R., and S. D. Gaines. 1986. Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecol.* 67:1372-1383.
- Ross, R. M., W. H. Backman, and R. M. Bennett. 1993. Evaluation of the anesthetic Metomidate for the handling and transport of juvenile American shad. Prog. Fish-Cult. 55:236-243.

Rowley, R. J. 1994. Marine reserves in fisheries management. Aqua. Cons. 4:233-254.

- Ruddle, K. 1996. Traditional management of reef fishing. In *Reef fisheries*, 1st ed., (Ed.) N. V. C. Polunin, and C. M. Roberts. London: Chapman & Hall.
- Russ, G. R. 1984. A review of coral reef fisheries. Productivity and processes in island marine ecosystems. Recommendations and scientific papers of the Unesco/IOC sessions on marine science co-operation in the Pacific, at the XVth Pacific Science Congress 1983, pp 74-92.
- Russ, G. R. 1985. Effects of protective management on coral reef fishes in the central Philippines. Proc. Fifth Inter. Coral Reef Symp. 4:219-224.
- Russ, G. R. 1991. Coral reef fisheries: effects and yields. In *The ecology of fishes on coral reefs*, 1st ed., (Ed.) P. F. Sale. San Diego: Academic Press.
- Russ, G. R. 1996. Fisheries management: What chance on coral reefs? NAGA July 1996:5-9.
- Russ, G. R., and A. C. Alcala. 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. *Mar. Ecol. Prog. Ser.* 56:13-27.
- Russ, G. R., and A. C. Alcala. 1994. Sumilon Island Reserve: 20 years of hopes and frustrations. NAGA 7 (3)(July):8-12.
- Russ, G. R., and A. C. Alcala. 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 A. C. Alcala. 1996b. Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecol. Appl.* 6(3):947-961.
- Russ, G. R., A. C. Alcala, and A. S. Cabanban. 1993. Marine reserves and fisheries management on coral reefs with preliminary modelling of the effects on yield per recruit. *Proc. Seventh Inter. Coral Reef Symp.* 2:988-995.
- Russ, G. R., D. C. Lou, and B. P. Ferreira. 1995. A long-term study on population structure of the coral trout Plectropomus leopardus on reefs open and closed to fishing in the Central Great Barrier Reef, Australia. CRC Reef Research Centre, Technical Report # 3, Townsville, 30 pp.
- Russ, G. R., D. C. Lou, and B. P. Ferreira. 1996. Temporal tracking of a strong cohort in the population of a coral reef fish, the coral trout, *Plectropomus leopardus* (Serranidae: Epinephelinae), in the central Great Barrier Reef. Can. J. Fish Aquat. Sci. 53

- Rutherford, E. S., J. T. Tilmant, E. B. Thue, and T. W. Schmidt. 1989. Fishery harvest and population dynamics of gray snapper, *Lutjanus griseus*, in Florida Bay and adjacent waters. *Bull. Mar. Sci.* 44(1):139-154.
- Sadovy, Y. 1993. The Nassau grouper, endangered or just unlucky? *Reef Encounter* 13:10-12.
- Sadovy, Y. 1994. Grouper stocks of the western central atlantic: the need for management and management needs. *Proc. Gulf Carib. Fish. Inst.* 43:43-64.
- Sadovy, Y. 1995. Patterns of reproduction in larger fishes of tropical reefs. *ILFC & ASFB* Conference Abstracts, p106.
- Sadovy, Y. 1996. Reproduction of reef fisheries species. In *Reef fisheries*, 1st ed., (Ed.) N. V. C. Polunin, and C. M. Roberts. London: Chapman & Hall.
- Sadovy, Y., and P. L. Colin. 1995. Sexual development and sexuality in the Nassau grouper. J. Fish Biol. 46:961-976.
- Sadovy, Y., A. Rosario, and A. Roman. 1994. Reproduction in an aggregating grouper, the Red Hind, *Epinephelus guttatus. Env. Biol. Fish.* 41:269-286.
- Sale, P. F. 1991. The ecology of fishes on coral reefs, 1st ed., San Diego: Academic Press.
- Sale, P. F., and B. J. Sharp. 1983. Correction for bias in visual censuses of coral reef fishes. Coral Reefs 2:37-42.
- Salvat, B. 1992. Coral reefs a challenging ecosystem for human societies. Glob. Env. Change 2:12-18.
- 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. Thesis. University of Queensland.
- Samoilys, M. A., and L. C. Squire. 1994. Preliminary observations on the spawning behavior of coral trout, *Plectropomus leopardus* (Pisces:Serranidae), on the Great Barrier Reef. Bull. Mar. Sci. 54(1):332-342.
- Schwarz, C. J., and A. N. Arnason. 1990. Use of tag recovery information in migration and movement studies. Am. Fish. Soc. Sym. 7:588-603.
- Schweigert, J. F., and C. J. Schwarz. 1993. Estimating migration rates of Pacific Herring (*Clupea pallasi*) using tag-recovery data. *Can. J. Fish Aquat. Sci.* 50:1530-1540.

- Seino, S., R. K. O'Dor, T. Hamada, Y. Tsuchiya, M. Tsuchiya, S. Nishihara, and M. Kawahara. 1995. Horseshoe crab *Tachypleus tridentatus* spawning patterns in Japan from acoustic telemetry. In *Proc. 13th Int. Symp. Biotelemetry*, 1st ed., (Ed.) C. Cristalli, C. J. Amlaner, and M. R. Neuman. Fayetteville: Arkansas Press. pp: 205-208.
- Shapiro, D. Y. 1986. Intragroup home ranges in a female biased group of a sex-changing fish. Anim. Behav. 34:865-870.
- Shapiro, D. Y. 1987. Reproduction in groupers. In Tropical snappers and groupers. Biology and fisheries management, (Ed.) J. J. Polovina, and S. Ralston. Boulder: Westview Press.
- Shapiro, D. Y., Y. Sadovy, and M. A. McGehee. 1993. Size, composition, and spatial structure of the annual spawning aggregations of the Red Hind, *Epinephelus* guttatus (Pisces:Serranidae). Copeia 1993(2):399-406.
- Shapiro, D. Y., G. Garcia-Moliner, and Y. Sadovy. 1994. Social system of an inshore stock of the Red Hind grouper, *Epinephelus guttatus* (Pisces: Serranidae). *Env. Biol. Fish.* 41:415-422.
- Shepherd, J. G. 1988. Fish stock assessments and their data requirements. In Fish population dynamics, 2nd ed., (Ed.) J. A. Gulland. NY: John Wiley & Sons.
- Shpigel, M., and L. Fishelson. 1989a. Food habits and prey selection of three species of groupers from the genus Cephalopholis (Serranidae: Teleostei). Env. Biol. Fish. 24:67-73.
- Shpigel, M., and L. Fishelson. 1989b. Habitat partitioning between species of the genus Cephalopholis (Pisces, Serranidae) across the fringing reef of the Gulf of Aqaba (Red Sea). Mar. Ecol. Prog. Ser. 58:17-22.
- Shpigel, M., and L. Fishelson. 1991a. Experimental removal of piscivorous groupers of the genus Cephalopholis (Serranidae) from coral habitats in the Gulf of Aqaba (Red-Sea). Env. Biol. Fish. 31:131-138.
- Shpigel, M., and L. Fishelson. 1991b. Territoriality and associated behaviour in three species of the genus *Cephalopholis* (Pisces: Serranidae) in the Gulf of Aqaba, Red Sea. J. Fish Biol. 38:887-896.
- Smith, C. L. 1972. A spawning aggregation of Nassau grouper *Epinephelus striatus* (Bloch). *Trans. Amer. Fish. Soc.* 101:257-261.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research, 2nd ed., New York: Freeman & Company.

- Spencer, S. R., G. N. Cameron, and R. K. Swihart. 1990. Operationally defining home range: temporal dependence exhibited by hispid cotton rats. *Ecol.* 71(5):1817-1822.
- Springer, J. T. 1982. Movement patterns of coyotes in south central Washington. J. Wildl. Manage. 46:191-200.
- Springer, V. G., and A. J. McErlean. 1962. A study of the behaviour of some tagged south Florida coral reef fishes. *Amer. Midland Nat.* 67:386-397.
- Stasko, A. B., and D. G. Pincock. 1977. Review of underwater biotelemetry, with emphasis on ultrasonic techniques. *Can. J. Fish Aquat. Sci.* 34:1261-1285.
- StJohn, J. 1995. Feeding ecology of the coral trout, Plectropomus leopardus (Serranidae), on the Great Barrier Reef, Australia. Ph.D. Dissertation. James Cook University, Townsville, Austarlia.
- StJohn, J., G. R. Russ, and W. Gladstone. 1990. Accuracy and bias of visual estimates of numbers, size structure and biomass of a coral reef fish. Mar. Ecol. Prog. Ser. 64:253-262.
- Stone, R. B., H. L. Pratt, R. O. Parker, and G. E. Davis. 1979. A comparison of fish populations on an artificial and natural reef in the Florida Keys. Mar. Fish. Rev. 39(12):11-20.
- Summerfelt, R. C., and D. Mosier. 1984. Transintestinal expulsion of surgically implanted dummy transmitters by channel catfish. *Trans. Amer. Fish. Soc.* 113:760-766.
- Swihart, R. K., and N. A. Slade. 1985. Influence of sampling interval on estimates of home range size. J. Wildl. Manage. 49(4):1019-1024.
- Swingland, I. R., and Greenwood. 1983. The ecology of animal movement. Oxford: Clarendon Press.
- Talbot, F. H. 1965. A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa) and its fish fauna. J. Zool. 145:431-470.
- Thomas, P., and L. Robertson. 1991. Plasma cortisol and glucose stress responses of red drum (*Sciaenops ocellatus*) to handling and shallow water stressors and anestesia with MS-222, quinaldine sulfate and metomidate. *Aquaculture* 96:69-86.
- Thompson, R., and J. L. Munro. 1978. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae. J. Fish Biol. 12:115-146.

Thresher, R. E. 1983. Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef lagoon. *Mar. Ecol. Prog. Ser.* 10:137-145.

Thresher, R. E. 1984. Reproduction in reef fishes, 1st ed., NJ: TFH Publications.

- Thresher, R. E., and J. S. Gunn. 1986. Comparative analysis of visual census techniques for highly mobile, reef-associated piscivores (Carangidae). *Env. Biol. Fish.* 17:93-116.
- Todd, I. A. 1993. WILDTRACK. Non-parametric home range analysis for the MacIntosh. Version 1.11 User's Guide, Dept. of Zoology, University of Oxford, UK.
- Trainor, N. 1991. Commercial line fishing. The Qld. Fisherman March(1991):17-25.
- Tucker, J. W. 1994. Spawning by captive serranid fishes: a review. J. W. Aquac. Soc. 25(3):345-359.
- Tucker, J. W., and W. J. Fitzgerald. 1994. Induced spawning of two western tropical pacific groupers, *Plectropomus areolatus* and *Epinehelus fuscoguttatus*, in Palau. Asi. Fish. Sci. 7(1):57-62.
- Tulevech, S. M., and C. W. Recksiek. 1994. Acoustic tracking of adult white grunt, *Haemulon plumieri*, in Puerto Rico and Florida. *Fish. Res.* 19:301-319.
- Turchin, P. 1996. Fractal analyses of animal movements: a critique. *Ecol.* 77(7):2086-2090.
- Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Annu. Rev. 19:513-605.
- Warner, R. R. 1995. Large mating aggregations and daily long-distance spawning migrations in the bluehead wrasse, *Thalassoma bifasciatum*. Env. Biol. Fish. 44:337-345.
- Watson, M., D. Righton, T. Austin, and R. Ormond. 1996. The effects of fishing on coral reef fish abundance and diversity. J. mar. biol. Ass. U.K. 76:229-233.
- Weitkamp, D. E., and M. Katz. 1980. A review of dissolved gas supersaturation literature. Trans. Amer. Fish. Soc. 109:659-702.
- White, A. T. 1988. Marine parks and reserves. Management for coastal environments in Southeast Asia. *ICLARM Education Series* 2:1-36.
- White, A. T., and G. C. Savina. 1987. Reef fish yield and non-reef catch of Apo Island, Negros, Philippines. Asi. Mar. Bio. 4:67-76.

- White, A. T., L. Z. Hale, Y. Renard, and L. Cortesi. 1994. Collaborative and communitybased management of coral reefs. Lessons from experience, 1st ed., Connecticut: Kumarian Press.
- White, G. C. 1996. NOREMARK: Population estimation from mark-resighting surveys. *Wildl. Soc. Bull.* 24:50-52.
- White, G. C., and R. A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data, 1st ed. San Diego: Academic Press.
- Whitelaw, A. W., and K. J. Sainsbury. 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. 1991. Patterns and processes in the distribution of coral reef fishes. In The ecology of fishes on coral reefs, 1st ed., (Ed.) P. F. Sale. New York: Academic Press.
- Williams, D. McB., and G. R. Russ. 1994. Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef. Great Barrier Reef Marine Park Authority Research Publication No. 33, 103 pp.
- Winter, J. D., and M. J. Ross. 1982. Methods in analyzing fish habitat utilization from telemetry data. In: Armantrout N (Ed.), Proc. of the symposium on acquisition and utilization of aquatic habitat inventory information. Am. Fish. Soc. West. Div., pp. 273-279.
- Worton, B. J. 1987. A review of models of home range for animal movement. *Ecol. Model*. 38:277-298.
- Yamasaki, A., and A. Kuwahara. 1990. Preserved area to effect recovery of overfished Zuwai crab stocks off Kyoto Prefecture. In: Proceedings of the International Symposium on King and Tanner crabs, Alaska Sea Grant College Program, University of Alaska, Fairbanks, pp 575-578.
- Zar, J. H. 1984. Biostatistical Analysis, 2nd ed., NJ: Prentice-Hall.
- Zhao, B., J. C. McGovern, and P. J. Harris. in press. Age, growth, and temporal change in size-at-age of the Vermilion Snapper from the South Atlantic Bight. Trans. Amer. Fish. Soc.