UNIVERSITY OF HAWAII LIBRARY

4304

AN EMPIRICAL EVALUATION OF THE DESIGN AND FUNCTION OF A SMALL MARINE RESERVE (WAIKĪKĪ MARINE LIFE CONSERVATION DISTRICT)

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAI'I IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

ZOOLOGY

MAY 2003

By
Carl G. Meyer

Dissertation Committee:

Kim Holland, Chairperson
David Greenfield
James Parrish
John Stimson
John Sibert

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Kim Holland, for his advice, financial support and encouragement, and my committee members for their advice and reviews of my manuscripts. I would also like to thank tracking volunteers who assisted during this study, especially Aaron Bush, Steve Kajiura, Kanesa Duncan, Tim Fitzgerald, Sabrina Clark, Brett Schumacher, Karen Gavey, Nick Whitney, Ling Ong and Eric Conklin. I am grateful to Richard Pyle and Alan Friedlander for their help with Microsoft Access. I would also like to thank the Waikiki Aquarium who provided important logistical support for the tracking study. This work was conducted in accordance with the animal use protocols of the University of Hawaii. Funding for this work was provided by the Division of Aquatic Resources (State of Hawaii Department of Land and Natural Resources), the University of Hawaii Sea Grant College Program, and by the Hawaii Coral Reef Initiative.

ABSTRACT

The effectiveness of a small (0.34km^2) "no fishing" marine reserve (Waikīkī Marine Life Conservation District) was empirically evaluated by quantifying three components of reserve design and function: (1) spatial adequacy for containing daily movements of target species; (2) abundance and size of reef fishes in the reserve and adjacent fished areas; and (3) distribution and impact of fishing activities at the reserve site. Reef fish movements were quantified using a combination of sonic tracking and conventional identification tags. Tracked fishes were typically site-attached to well-defined home ranges and had predictable patterns of behavior including a crepuscular 'commute' between separate day and night habitats. Surgeonfishes (*Naso unicornis*) had relatively small home ranges that were strongly associated with high rugosity habitat contained within reserve boundaries. Goatfishes (*Mulloidichthys flavolineatus*) and jacks (*Caranx melampygus* and *C. sexfasciatus*) had home ranges that were relatively large, and extended from the reserve into adjacent fished areas. Mobile species (goatfish and jacks) used a combined area of 1.013 km^2, indicating that the existing reserve is too small to fully protect these species.

Abundance & size of both target and non-target species was greater in reserve than in adjacent fished areas, suggesting that fishing is not the only factor determining patterns of fish abundance and size at Waikīkī. Habitat complexity is generally greater in the reserve than in adjacent fished areas and appears to be an important factor determining patterns of fish abundance and size at Waikīkī. Spear and shoreline pole &

line fishing were the dominant fishing activities at Waikīkī. Spear fishing had a higher catch per unit effort (kg/man h) and caught larger fish than pole & line fishing. Fishing activities were patchily distributed and clustered around public shoreline access points close to free parking. Some fishing did occur inside the reserve but at significantly lower levels than in adjacent fished areas. Little fishing occurred in the areas immediately adjacent to the northern and seaward reserve boundaries, suggesting that a fishing impact buffer zone exists around the reserve. This phenomenon may partly explain why mobile target species remain abundant inside the reserve despite daily excursions into adjacent, unprotected areas.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS iii

ABSTRACT iv

LIST OF TABLES vii

LIST OF FIGURES ix

CHAPTER 1 GENERAL INTRODUCTION 1

ARE SMALL MARINE RESERVES EFFECTIVE? 1
DESCRIPTION OF STUDY SITE 4

CHAPTER 2 FISH MOVEMENTS, HABITAT USE AND DISPERSAL PATTERNS 7

INTRODUCTION 7
METHODS 8
RESULTS 12
DISCUSSION 28

CHAPTER 3 FISH ABUNDANCE, SIZE AND DISTRIBUTION 56

INTRODUCTION 56
METHODS 57
RESULTS 61
DISCUSSION 63

CHAPTER 4 THE IMPACT OF FISHING ON RESERVE FUNCTION 77

INTRODUCTION 77
METHODS 81
RESULTS 84
DISCUSSION 89

CHAPTER 5 GENERAL DISCUSSION 107

LITERATURE CITED 113

LIST OF TABLES

Table **Page**

2.1. Summary of tracking data from five *N. unicornis* 42

2.2. Summary of tracking data from four *M. flavolineatus* 42

2.3. Summary of tracking data from two *C. melampygus* 43

2.4. Summary of fishes tagged and released in the Waikīkī reserve and pulse fished area. 44

2.5. Summary of Waikīkī tag recapture data. 45

2.6. Summary of tag recapture and dispersal data for fishes captured inside Waikīkī reserve. 46

2.7. Summary of tag resighting data for fishes tagged at Waikīkī 46

3.1. List of fishes counted at Waikīkī 69

3.2. Mean overall biomass (g $15min^{-1}$) of target and non-target species in reserve and fished areas. 70

3.3. Percent difference between mean overall biomass of reserve and fished areas 71

3.4. Mean overall size of target and non-target species in reserve and fished areas 72

3.5. Percent difference between mean overall fish size at reserve and fished areas. 73

4.1. Summary of gear type frequencies observed during shoreline patrols at Waikīkī ... 95

4.2. Results of multifactorial analysis of variance for densities of all fishing activities observed at Waikīkī 96

4.3. Results of analysis of variance for densities of pole & line, spear and other fishing activities observed at Waikīkī 97

4.4. Results of analysis of variance for densities of fishing activities observed in the permanently fished (FA), pulse fished (PF) and reserve (R) areas at Waikīkī 97

4.5. Results of analysis of variance for densities of fishing activities observed during day and night at Waikīkī 97

4.6. Results of analysis of variance for densities of fishing activities observed on weekdays and weekends at Waikīkī 98

4.7. Results of analysis of variance for densities of fishing activities observed during summer and winter at Waikīkī 98

4.8. Summary of catches observed at Waikīkī during shoreline patrols and opening day surveys 99

4.9. Catch Per Unit Effort calculated from shoreline patrol data..... 102

4.10. Estimated annual catch (t) of reef fishes by area and gear type at Waikīkī..... 102

4.11. Summary of catch rates (CPUE, catch per unit effort) and catch composition from spear and pole & line fishing on reefs in Hawai'i and the South Pacific. 102

4.12. Estimated annual yields (t km^{-2} $year^{-1}$) from fisheries operating in relatively small (<10 km^2) areas of fringing reef habitat around the Pacific..... 104

LIST OF FIGURES

Figure **Page**

1.1. Location of study site on the south coast of O'ahu. 6

2.1. Kernel and MCP home ranges of three *Naso unicornis* 47

2.2. Diel variation in activity of unicornfish #5 48

2.3. MCP home range size of five *N. unicornis* 49

2.4. MCP home range of *Mulloidichthys flavolineatus* #1 50

2.5. Kernel home range of *M. flavolineatus* #4 51

2.6. MCP home range size of four *M. flavolineatus* 52

2.7. Kernel home ranges of two *Caranx melampygus* 53

2.8. Composite MCP including movement data from all 13 tracked fishes 54

2.9. Frequency of recaptures versus distance from release location 55

3.1. Distribution of mean acanthurid biomass among reef habitat zones in reserve and fished areas 74

3.2. Distribution of mean balistid biomass among reef habitat zones in reserve and fished areas. 74

3.3. Distribution of mean carangid biomass among reef habitat zones in reserve and fished areas 75

3.4. Distribution of mean mullid biomass among reef habitat zones in reserve and fished areas 75

3.5. Distribution of mean scarid biomass among reef habitat zones in reserve and fished areas. 76

4.1. Mean density of fishing activities at Waikīkī 105

4.2. Diel variation in mean density of fishing activities at Waikīkī 105

4.3. Frequency of reef fish families (and octopus) in catches at Waikīkī 106

4.4. Size frequency distribution of catches of reef fishes taken at Waikīkī 106

CHAPTER 1

GENERAL INTRODUCTION

Are small marine reserves effective?

Concern is growing that coral reef ecosystems are seriously overexploited in many areas of the world (McManus 1988, McClanahan & Muthiga 1988, Sadovy 1989, 1997, Roberts & Polunin 1993, Johannes & Riepen 1996, Jennings and Kaiser 1998). The problem is particularly severe in developing countries where overfishing is often compounded by habitat destruction (Alcala 1988, Alvarez 1995, Johannes & Riepen 1996, Pet 1997, Jennings & Kaiser 1998, Russ & Alcala 1989, 1998a). Conventional fisheries management methods, developed for temperate, single species fisheries, have failed to prevent overexploitation because such methods are poorly suited to the complexity of coral reef fisheries (Roberts 1991, 1993, Roberts & Polunin 1991, 1993, Jennings & Polunin 1996). Marine reserves (areas closed to fishing) are increasingly suggested as a simple solution to this complex problem (Roberts 1991, Roberts & Polunin 1991, 1993, Roberts et al. 1995 Bohnsack 1996). The growing popularity of marine reserves as alternative management tools stems from the many anticipated benefits of these areas, such as increased target organism abundance and size within reserves, and enhanced fishery yields in adjacent fishing grounds (Roberts 1991, 1993, Bohnsack 1996). Yet, despite widespread establishment of marine reserves, many of the anticipated benefits remain unsupported by empirical data (Edgar & Barret 1997, Bohnsack 1998).

To date most studies have focused on the abundance and size of targeted species in marine reserves, and have frequently demonstrated greater abundance and size of targeted species within these areas (Dugan & Davis 1993, Polunin & Roberts 1993, Roberts 1993, 1995, Jennings et al. 1995, McClanahan & Kaunda-Arara 1996, Rakitin & Kramer 1996, Edgar & Barrett 1997, Wantiez et al. 1997, Russ & Alcala 1998b). However, many of the same studies also yielded counter-intuitive results, such as equal or greater abundance and size of some targeted species outside protected areas (Polunin & Roberts 1993, Roberts 1993, Jennings et al. 1995, McClanahan & Kaunda-Arara 1996, Rakitin & Kramer 1996, Wantiez et al. 1997, Russ & Alcala 1998b). These mixed results suggest that in some cases reserves have a neutral or negative effect on abundance of some species, or that other environmental factors have a greater impact on fish abundance and size than the presence of the reserve.

A common, untested assumption of these studies is that greater abundance and size of fishes occurs within these areas because of a 'reserve effect' (i.e., fishes are protected from fishing mortality within reserves). A true reserve effect requires two major assumptions to be met: (1) fishes are site attached to home ranges contained inside reserve boundaries, and (2) fishing mortality is excluded from reserve areas. The probability of a reserve effect occurring decreases with decreasing reserve size for two main reasons: (1) the ratio of fish home range size to reserve area increases with decreasing reserve size and eventually reaches a threshold where home range size exceeds reserve size, and (2) habitat diversity inside reserves decreases with decreasing reserve size and ultimately results in critical habitats lying outside reserve boundaries.

Thus, for each location and target species, there is a minimum reserve size below which a significant reserve effect no longer occurs because most individuals frequently cross boundaries in the course of their daily movements.

It may be difficult to assess the true effectiveness of small reserves simply by censusing fish populations because other factors may result in relatively high fish abundance in these areas. For example, a tendency to select areas of prime fish habitat for reserve sites may bias census results because these are areas of naturally high fish abundance even when impacted by fishing. Fishing activity in the area surrounding small reserves could also determine the abundance and size of fishes within reserve boundaries. For example, fish abundance may remain relatively high inside small reserves when fishing mortality is low in the area outside the reserve because individuals that cross boundaries are rarely captured. Conversely, if fishing mortality is high outside the reserve, then fish abundance may be low inside because individuals that cross the reserve boundaries are frequently captured. Thus a small reserve containing prime fish habitat may appear effective (i.e., have relatively high fish abundance and size), particularly when fishing mortality is low in the surrounding area, even though it does not actually effectively protect fishes.

There are a variety of negative consequences associated with inadequate reserve size: (1) fishing activity outside reserve boundaries can directly reduce fish abundance and size inside the reserve and compromise the ability of these small reserves to produce other anticipated benefits. (2) Perceived effectiveness of these small reserves could result

in the establishment of additional small, and equally ineffective reserves in other areas. (3) Failure of small reserves to produce anticipated benefits may discredit the use of reserves as management and conservation tools even though the general concept is scientifically valid.

These concerns are pertinent because marine reserves are frequently viewed as encroaching on human activities, especially fishing, and consequently social and political pressures typically favor the establishment of relatively small (<1 km^2) reserves. The boundaries of these small reserves are typically set according to purely anthropocentric criteria, and thus the ability of these small reserves to effectively protect resident fishes and thereby produce other anticipated benefits is unclear. The goal of the present study is to empirically evaluate the effectiveness of an established small marine reserve using several different methods. Three major questions were addressed;

1. Are reserve size and habitat content adequate to contain fish movements?
2. Are fish abundance and size greater inside the reserve than in adjacent fished areas?
3. How does fishing activity influence reserve function?

Study site

The study site consisted of a 7 km stretch of high-energy fringing reef situated on the south shore of O'ahu, Hawaiian Islands, divided into three management zones: (1) a 'no take' marine reserve (Waikīkī Marine Life Conservation District); (2) a 'pulse fished'

zone (Waikīkī –Diamond Head Fisheries Management Area) and (3) an area continually open to fishing (Figure 1.1). Removal of marine life from Waikīkī Marine Life Conservation District (MLCD) has been prohibited since 1988, and the adjacent Waikīkī Fisheries Management Area (FMA) has undergone alternate years of fishing and closure (i.e., 'pulse fishing') since 1988. Nighttime spear fishing, trapping, and netting (except throw or hand netting) are prohibited in the pulse fished area even during open seasons. Signs posted at intervals along the shoreline of the reserve and pulse fished area show the reserve boundaries, regulations and a telephone number for reporting violations. The reserve and pulse fished areas have seaward boundaries that run parallel to the shore at a distance of 455 m (500 yds) offshore from the high-water mark. They respectively cover 750 m and 1900 m of shoreline and enclose areas of approximately 0.34 km^2 and 0.86 km^2. Marine habitat inside the reserve consists of high-energy fringing reef which is subdivided into four well-defined habitat types: (1) A sheltered back reef area consisting of shallow (<1 m) reef interspersed with deeper (2-3 m) sandy areas and backed by sandy beaches; (2) An extensive flat, shallow (<1 m) reef table located seaward of the back reef area; (3) A narrow band of high rugosity reef crest forming the seaward margin of the reef table; (4) A deeper (>4 m) fore reef area of large sand patches and flat, hard reef substrate located seaward of the reef crest. Back reef, reef table and reef crest habitats on adjacent fished reefs and inside the pulse fished area are similar to those inside the reserve. Fore reef habitat in the pulse fished and permanently fished areas is generally deeper (4-10 m), and more rugose than inside the reserve.

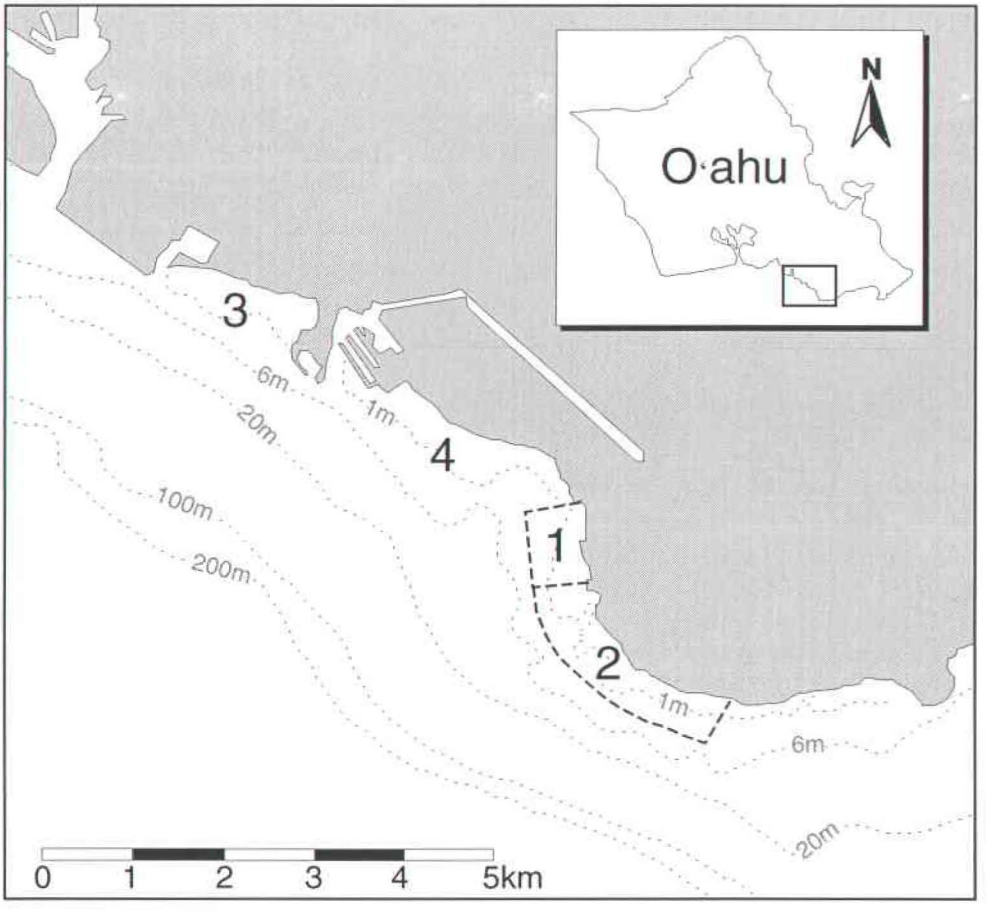

Figure 1.1. Location of study sites on the south coast of O'ahu. 1. Waikīkī Marine Life Conservation District (MLCD). 2. Waikīkī Fisheries Management Area (FMA). 3. & 4. Areas continually open to fishing. Shaded area = land, bold dashed line = MLCD and FMA boundaries.

CHAPTER 2

FISH MOVEMENTS, HABITAT USE AND DISPERSAL PATTERNS

Introduction

Anticipated biological benefits of marine reserves are contingent on the ability of these areas to effectively protect resident fishes from fishing mortality (Bohnsack 1993, DeMartini 1993, Rakitin & Kramer 1996, Nowlis & Roberts 1999). In order to achieve this goal, the size and habitat content of reserves must be adequate to contain fish movements inside reserve boundaries (Bohnsack 1993, Dugan & Davis 1993, Kramer & Chapman, 1999, Nowlis & Roberts 1999), and effective protection of entire assemblages of reef fishes requires reserves that are large enough to contain the home ranges of even the most wide-ranging species. In theory this could be achieved simply by making marine reserves relatively large, thereby maximizing the probability of containing fish movements (Nowlis & Roberts 1999); however, in practice strong resistance from fishers has often restricted reserves to relatively small (<1 km^2-15 km^2) areas (Dugan & Davis 1993, Bohnsack 1998). An important question is whether these existing reserves are large enough to effectively protect fishes.

This question has remained largely unanswered because little is known about the movement patterns and home range size of even commonly targeted coral reef fishes (Polunin & Roberts 1993, Holland et al 1996, Chapman & Kramer 1999), and consequently reserve designers have been unable to empirically determine minimum effective reserve sizes (Dugan & Davis 1993, Bohnsack 1998). The solution is to

quantify the movement patterns, home range size and habitat use of a variety of reef fish taxa in order to understand how much these behavioral characteristics vary, and to determine how much space would be required to protect the most wide-ranging species (*Nowlis & Roberts* 1999).

The goal of the present study is to empirically determine whether an existing small reserve (Waikīkī MLCD) provides effective protection for a wide range of reef fish taxa by quantifying the movements, habitat use and dispersal of fishes captured inside the reserve. Several criteria were used to select species for investigation: (1) species should be representative of a broad range of feeding guilds; (2) species should be commonly targeted by subsistence, commercial and recreational fishers; (3) species should be relatively abundant in the study site; and (4) most species should have wide geographic distributions (i.e., should occur throughout the Indo-Pacific region). These criteria were used to select four reef fish families (Acanthuridae, Carangidae, Mullidae and Scaridae), representing three major feeding guilds (herbivores, benthic carnivores and piscivores) for tag and release studies. One representative species from each of the three feeding guilds was chosen for acoustic tracking studies.

Methods

Active tracking

Short-term movement patterns, habitat use and home range size of the selected target species were determined using acoustic telemetry (active tracking). The fishes used in the telemetry studies were captured inside the Waikīkī reserve using surround and

barrier nets, or by hand from nighttime refuge holes (unicornfish), and anaesthetized with MS-222 (0.1 g/l). Sonic transmitters (V8-2L, 0.8 cm diameter, 3.0 cm long, Vemco, Halifax, Nova Scotia) with individualized frequencies (ranging between 65.4 kHz and 76.8 kHz) and a 21-day nominal battery life were attached to the dorsal surface of each unicornfish and jack with stainless steel wire (Holland et al. 1996, Meyer & Holland 2001), and surgically implanted into the body cavities of the goatfishes (Holland et al. 1993, Meyer et al. 2000). Each fish was also tagged with a serially numbered, 8.0 cm plastic dart identification tag (Hallprint, South Australia). Fishes were released at point of capture immediately after resuscitation. No tracking data were collected from unicornfishes during the first five days after release because initial observations indicated that newly released unicornfishes remained in refuge holes for several days.

Tracking was conducted from a 4 m kayak and a 5.5 m skiff equipped with directional hydrophones, acoustic receivers, and navigational and communications equipment (Holland et al. 1992, 1993, 1996, Meyer et al. 2000, Meyer & Holland 2001). During tracking, fish location was recorded at 15-minute intervals as X, Y coordinates on a chart of the study site created from high resolution aerial photos of the Waikīkī coastline. Positional data were also collected from a handheld Global Positioning System unit (Garmin 12XL). The tracking vessel was maneuvered to within 5-10 m of the fish whenever positional fixes were taken. The veracity of this distance estimate was periodically corroborated by comparing signal strength with the position of a snorkeler in visual contact with a transmitter-equipped fish. Each transmitter-equipped fish was typically tracked on several occasions throughout the ~21 day transmitter battery life. On

each of these occasions fishes were followed continuously for up to 96 h, during which tracking vessel operators were switched every two hours either from the shore, or by using a second kayak as a shuttle.

Tracking Data Analysis

Tracking data were analyzed using the Animal Movement extension (Hooge and Eichenlaub 1997) for ArcView® (Environmental Systems Research Institute, Inc., Redlands, California). The site fidelity of each fish was first tested by comparing observed movements with 100 random walks incorporating the actual sequence of distances traveled by fish during each 15 minute interval (Okubo 1980, Spencer et al. 1990, Hooge et al. 2000). Minimum convex polygons were used to describe the maximum area covered by each fish (MacDonald et al. 1980, Klimley & Nelson 1984, Spencer et al. 1990, Meyer et al. 2000, Hooge et al. 2000). To increase spatial resolution, probabilistic kernel home ranges were calculated for each fish (Worton 1989, Seaman and Powell 1996, Hooge et al. 2000). Kernel home ranges highlight areas used most frequently by animals and thus provide higher resolution information on use of habitat and space than convex polygon techniques.

Continuous remote monitoring of *N. unicornis* foraging habitat

To determine medium-term (up to 1 month) fidelity of *N. unicornis* to a daytime foraging habitat and to document use patterns of this habitat, an omni-directional hydrophone was placed in the middle of a 2-3 m deep channel where unicornfishes were frequently seen browsing on algae and refuging in holes in the channel walls. The

hydrophone was connected via a cable to an acoustic receiver and laptop computer on shore. The system was programmed to listen for the presence of a frequency-coded transmitter at two-minute intervals. Range testing indicated that the system was able to detect transmitters inside the channel but not beyond it's margins. A single unicornfish that used the channel for foraging but occupied a refuge hole outside the detection range of the system was selected for monitoring.

Long-term site fidelity and dispersal

Between April 1995 and February 2001, all target species caught in the Waikīkī reserve and adjacent areas were tagged with externally visible dart tags and released. Each fish was measured on a foam-padded tagging board and a serially numbered, 8.0 cm long plastic dart tag (Hallprint, South Australia) was inserted into the dorsal musculature and anchored between the dorsal fin pterygiophores. Fishes captured inside the Waikīkī reserve were tagged on the left side of the dorsal fin and fishes captured in adjacent areas were tagged on the right. Each tag carried a reward notice and a telephone number. Tagged fishes recaptured by scientific personnel were remeasured and released. Fishers who called the fish tagging 'hot-line' to report catching a tagged fish were sent a reward together with a chart or aerial photograph on which they were asked to mark the specific recapture location. A data sheet with sections for reporting species captured, fish size (total length), tag number, date & time of capture and gear type was also included together with a return-address, postage-paid envelope in which to return the completed chart and data sheet. Conventional tag recapture data were supplemented with resightings of tagged fishes during underwater visual census (UVC) surveys of fish

populations (Chapter 3). UVC data were collected from throughout the study area (a 6 km stretch of coastline), and the species, size and tag placement (left or right side of dorsal fin) of any tagged fish sighted was recorded.

Results

Acoustic Tracking

Naso unicornis - Movement patterns and habitat use

Five *N. unicornis* (33.8 to 46.6 cm FL) were each tracked on up to four occasions over periods spanning between 5 and 22 days (Table 2.1). Total track duration ranged from 24 to 118 hours. All unicornfishes tracked were strongly associated with high rugosity reef habitat and showed high fidelity to refuge holes. Unicornfishes were typically most active during the day and quiescent in refuge holes at night. None of the tracked unicornfishes used the deeper (>4 m) flat reef and sand habitat seaward of the reef crest. Two broad patterns of movement and habitat use ('commuting' and 'foraying') were observed during tracking. Two unicornfishes tracked in reef crest habitat 'commuted' between a nighttime refuge hole and daytime habitat situated several hundred meters further along the reef crest. Highly directional movements between day and night habitats occurred within 15-30 minutes of sunset and sunrise each day. Unicornfishes exhibiting this commuting behavior did not return to nighttime refuge holes during daylight hours and snorkel observations revealed that these fishes were typically associated with schools of conspecifics during the day. The movements of two unicornfishes tracked in back reef habitat were centered around refuge holes from which they would periodically emerge to make short (5-15 min), solitary 'forays' into adjacent

areas of high algal cover situated within 10 - 40 m of their holes. Both of these unicornfishes showed high fidelity to their respective refuge holes during both day and night, and overall spent more than 90% of their time inside these holes. A third unicornfish tracked in back reef habitat was largely quiescent in a refuge hole between dawn and midnight but left this location in the early morning hours, and moved slowly to a location 170 m further north where it spent 2-3 h before returning to it's primary refuge hole at dawn. A synopsis of the movement patterns of the five unicornfishes tracked is given below to illustrate the general behavioral patterns described above.

Unicornfish #1 (FL = 43.9 cm) was captured by surround netting a hole in the wall of a small sandy channel in the NE corner of the reserve (Figure 2.1) and was tracked on two occasions spanning 5 days, for a total of 79 h. Unicornfish #1 remained in it's refuge hole for most (92%) of the track and made only three brief (15 minute) excursions; at 16:00 and 03:45 fish #1 moved 65 m to an area of high algal cover on the opposite (seaward) side of the channel, and at 06:45 it moved up and down along 10 m of the channel wall immediately adjacent to it's refuge hole. One week later the transmitter signal was relocated in the refuge hole but was found to be coming from a shed transmitter. Unicornfish #1 was recaptured 67 days later in a net set in the area of the channel that the fish had visited during it's brief excursions from it's refuge hole.

Unicornfish #2 (FL = 38.5 cm) was captured by surround netting in the same sandy channel used by Fish #1 and was tracked on 3 occasions, spanning 22 days, for a total of 51 h. Unicornfish #2 showed high fidelity to a refuge hole in the channel wall and

remained in this hole for the majority (84%) of the track. Daylight hours were almost entirely spent in or within a few meters of this hole. Unicornfish #2 was only observed to make one brief (8 minute) daytime foray along a 50 m section of the shoreward channel wall before returning to its refuge hole; however, fish #2 left it's refuge hole after midnight each night and swam slowly north 170 m along the seaward channel wall, to an area of holes and ledges at the northern end of the channel where it became quiescent. Unicornfish #2 left this area at around 05:30 each morning and moved slowly back to its daytime hole, taking 45 minutes to complete the journey and arriving at around sunrise.

Unicornfish #3 (FL = 33.8 cm) was captured by surround netting an area of reef crest habitat (Figure 2.1) and was tracked on 3 occasions, spanning 20 days, for a total of 118 hours. Throughout the tracks fish #3 remained in high relief reef crest habitat and showed high fidelity to both day and nighttime habitats. Daylight hours were primarily spent moving up and down a 10 m stretch of reef crest toward the center of the reserve, and snorkel observations revealed that fish #3 was associated with foraging schools of surgeonfishes during these periods. Schools consisted of 5 - 100 *N. unicornis* ranging in size from 30 - 60 cm TL and sometimes included several similar size *Acanthurus xanthopterus*. Unicornfish #3 became more active in the hour preceding sunset and swam back and forth along up to 140 m of reef crest habitat north of its primary daytime habitat. Shortly after sunset fish # 3 swam steadily and directly north along the reef crest to a nighttime refuge hole situated 370 m away from it's daytime habitat. Unicornfish # 3 remained quiescent in this hole during the hours of darkness and left the hole shortly before sunrise each morning and swam south along the reef crest toward it's daytime

habitat, stopping en route for up to four hours at a location midway between it's night and day habitat.

Unicornfish #4 (FL = 46.6 cm) was captured by surround netting a ledge in the back reef habitat and was tracked on three occasions, spanning 13 days, for a total of 24 h. Fish #4 was relocated in different areas on the three occasions that it was tracked and was the only unicornfish that was observed using both back reef and reef crest habitats. Four days after release fish #4 was relocated under the same back reef ledge where it was captured and remained there without moving for the following 24 h. Five days later (10 days after release) fish #4 was relocated at 14:30 in reef crest habitat 210 m from it's original point of capture, in the same area that fish #3 occupied during daytime. Unicornfish #4 remained in this area, making localized movements until dusk when the track had to be suspended due to technical difficulties. Two days later, fish #4 was relocated at 14:15 in reef crest habitat 250 m south of its previous location. Unicornfish #4 remained in this area making localized movements until 18:00 when it became more active, moving back and forth along 75 m of reef crest to the north of it's daytime habitat. At sunset (18:30) fish #4 moved steadily 300 m north along the reef crest to an area close to where it had first been observed in the reef crest. Unicornfish #4 remained quiescent in this area throughout the night, during which time the transmitter signal gradually faded and failed shortly before dawn the following morning.

Unicornfish #5 (FL = 40.3 cm) was captured by hand from a hole in shallow (<2 m) habitat on the shoreward side of a back reef sandy channel (Figure 2.1) and tracked on

5 occasions, spanning 13 days, for a total of 63 h. Unicornfish #5 showed high site fidelity to this refuge hole and spent the majority (94%) of the tracks inside the hole. Unicornfish #5 remained quiescent inside its refuge hole at night and made brief forays into areas of high algal cover during the day. Most such forays were 2 – 11 minutes in duration, during which time fish #5 would typically swim 20 m from its hole to the nearby channel where it would move slowly back and forth along up to 20 m of the algal covered channel wall. Unicornfish #5 also made occasional forays into the shallow algal covered habitat immediately adjacent to its refuge hole. The interval between forays varied from 15 min to 3 h but was typically about 1 h. On two occasions fish #5 made longer daytime forays (up to 1 h 30 min) from its hole but still used the same 20 m stretch of the channel. During one of these longer forays fish #5 was observed foraging on macroalgae that had collected on the channel floor. Subsequent remote monitoring using the hardwired omni-directional hydrophone revealed that fish #5 made daily, multiple short (2-15 minute) forays into this foraging habitat over a 7-week period (the lifespan of the transmitter battery). Longer forays (up to 2 h) were also occasionally recorded. Unicornfish #5 was most active during daylight hours but also made nighttime forays into its foraging habitat. The frequency of forays increased steadily from the early hours of the morning, reached a peak at around 09:00 and then fluctuated throughout the day with secondary peaks at noon, mid-afternoon and around dusk (Figure 2.2). Activity decreased sharply in the hours immediately after sunset but then peaked again around midnight. The number of daily forays and occurrence of nocturnal forays varied throughout the monitoring period.

To determine whether the tidal cycles were influencing the activity patterns of fish #5, the frequency of forays was compared with the frequency of water depths (height above chart datum) that occurred during the tidal cycle. Frequency of forays at different tidal levels was significantly different from the natural frequency of water depths occurring during the tidal cycle ($p<0.01$). Unicornfish #5 was significantly more active during mid stages of the tide than during high and low stages of the tide. To determine if the frequency of nocturnal forays by fish #5 was related to nocturnal light levels, the activity patterns of fish #5 were compared with lunar phase. Although a significant association existed between lunar phase and nocturnal activity of fish #5 ($p<0.001$), the frequency of nighttime forays into foraging habitat was lowest during the full and new moon, and highest during the first and last quarters of the lunar cycle. Unicornfish #5 was subsequently recaptured from its refuge hole 14 weeks after initial release, the dead transmitter was removed and the fish was released.

Naso unicornis - Site fidelity and home range size

The site fidelity of each unicornfish tracked was tested by comparing the actual tracking data against 100 Monte Carlo random walks. The movements of four of the five fishes tracked were found to be significantly ($p<0.001$) more constrained than random movement paths indicating that these fishes were site attached. The movements of the remaining fish (fish #4) were not significantly ($p>0.1$) more constrained than random movement paths. The overall size and shape of the home ranges of each tracked fish was determined using minimum convex polygons (MCP) incorporating all positional fixes (Figure 2.3). MCP home range size of the four site attached unicornfishes varied from

325 to 7650 m^2 (mean = 3717 m^2) and was smaller in back reef habitat than on the reef crest (Table 2.1, Figure 2.3). Differences in behavior patterns accounted for much of the differences in unicornfish home range size. Unicornfishes that showed only 'foray' type behavior had smaller MCP home ranges than unicornfishes that commuted between separate day and night habitats. Mean distance traveled per 24 h was 2-10 times higher for commuting than for foray type behavior (Table 2.1). Unicornfish #4, which did not show significant site fidelity, used 57400 m^2 of reef habitat and traveled a minimum of 1653 m during only 24 h of tracking (Figure 2.3, Table 2.1). Thus the MCP generated from the movements of fish #4 was 7.5 - 176 times larger than the home ranges of the site attached fishes, and fish #4 traveled 3 - 40 times further per 24 h than these other fishes. Although unicornfish MCP home ranges varied in size by an order of magnitude, closer examination of habitat use through probabilistic kernelling indicated that only a small proportion of the larger home ranges was used intensively and core activity spaces were similar for all unicornfishes tracked (Table 2.1, Figure 2.1).

The movements of all five unicornfishes tracked were contained within the boundaries of the Waikīkī reserve (Figure 2.3). The MCP home ranges of the four site attached fishes each occupied from 0.1 – 2.25% (mean = 1.09%) of the total reserve area, and the movements of unicornfish #4 occupied an MCP equivalent to 16.88% of the total reserve area (Table 2.1). Although most unicornfish MCP home ranges occupied only a small proportion of the total reserve area, the daily 'commutes' carried out by several fishes took them back and forth across 24-52% of the total reserve width.

Mulloidichthys flavolineatus - Movement patterns and habitat use

Four *M. flavolineatus* (26.0 to 32.3 cm FL) were each tracked on up to three occasions over periods spanning between 2 and 14 days (Table 2.2). Total track duration ranged from 8 to 49 hours. Typically, tracked goatfishes were quiescent in resting schools associated with high rugosity reef habitat during the day and active in areas of soft substrate during the night. Tracked goatfishes used back reef, reef crest and fore reef habitats inside, and sandy substrates outside, Waikīkī reserve. Highly directional movements between day and night habitats occurred within 15-30 minutes of sunset and sunrise each day. These crepuscular movements were in a northerly direction at dusk and a southerly direction at dawn. A synopsis of the movement patterns of the four goatfishes tracked is given below to illustrate the general behavioral patterns described above.

Goatfish #1 (32.3 cm FL) was captured at dusk in a gill net set perpendicular to the reef crest in the central area of the reserve and tracked continually for a total of 46 h (two diel cycles). Goatfish # 1 was quiescent in a school of conspecifics among high rugosity reef crest habitat during the day and became active at sunset moving from reef crest habitat to areas of soft substrate (Figure 2.4). At night fish #1 moved periodically between distant patches of soft substrate, spending several hours moving slowly around each patch. Areas visited by fish #1 varied on the two nights that it was tracked. At dusk on the first night fish #1 moved 400 m inshore to a sandy channel situated in reserve back reef habitat just 20 m from shore where it remained until 02:38 when contact with the fish was lost when it made a rapid move along the shoreline toward the northern reserve boundary. On the second night fish #1 initially moved 250 m north from its daytime

habitat to an area just outside the reserve northern boundary and 250 m from shore. After moving slowly around in this location for 2 h, fish #1 moved rapidly 450 m south to a location 220 m beyond the seaward reserve boundary and 700 m from shore. One hour later fish #1 moved rapidly 1000 m south to a location 450 m beyond the southern reserve boundary and 550 m from shore. Goatfish #1 moved steadily around in this general area until 05:00 when it left and moved steadily north along the reef crest, arriving back at its daytime habitat by 05:30.

Goatfish #2 (27.3 cm FL) was captured at dusk in a gill net set perpendicular to the reef crest in the center of the reserve and was tracked on 2 occasions spanning 14 days, for a total of 8 h. One week after release fish #2 was relocated during the day in a location close to shore, 800 m north of its original site of release and 500 m beyond the northern reserve boundary. Contact was lost with the fish shortly thereafter but it was found again one week later at a site 1200 m from the previous position, 600 m from point of release, 300 m south of the reserve seaward boundary and 800 m from shore.

Goatfish #3 (28.3 cm FL) was captured at dusk in a gill net set perpendicular to the reef crest in central area of the reserve and was tracked continually for 41 h (two diel cycles). Following release, fish #3 moved steadily north along the reef crest to a location just outside the northern reserve boundary. Goatfish #3 spent both nights that it was tracked moving steadily around in this area until just before sunrise when it moved 100 m south to a daytime habitat just inside the reserve where it remained quiescent until sunset.

Goatfish #4 (26.0 cm FL) was captured by surround netting a school of *M. flavolineatus* that occupied a sandy channel in back reef habitat in the NE corner of the Waikīkī reserve (Figure 2.5) and was tracked on 2 occasions spanning 10 days, for a total of 49 h (two diel cycles). During daytime fish #4 remained quiescent resting on the sandy bottom close to the channel wall. At dusk fish #4 became active and moved 250 m north to a shallow sand patch, close to shore, where it moved slowly around throughout the night, returning to its daytime habitat shortly before sunrise. Goatfish #4 returned consistently to the same nighttime habitat on each night that it was tracked and was subsequently recaptured in this location at night, 55 days after termination of the track.

Mulloidichthys flavolineatus - Site fidelity and home range size

The site fidelity of each goatfish tracked was tested by comparing the raw tracking data against 100 Monte Carlo random walks. The movements of three of the four goatfishes tracked were found to be significantly ($p<0.001$) more constrained than random movement paths indicating that these fishes were site attached. The movements of the remaining goatfish (fish #2) were not significantly ($p>0.1$) more constrained than random movement paths. The overall size and shape of the home ranges of each tracked goatfish were determined using minimum convex polygons (MCP) incorporating all positional fixes (Figure 2.6). MCP home range size of the three site attached goatfishes varied from 33,214 to 515,710 m^2 (mean = 220,189 m^2)(Table 2.2, Figure 2.6). Mean distance traveled per 24 h varied from 2103 to 3209 m (mean = 2622 m)(Table 2.2). Goatfish #2, which did not show significant site fidelity, used 269,428 m^2 of reef habitat, which was within the MCP home range size of the other goatfishes tracked (Table 2.2,

Figure 2.6). Kernel home range analyses indicated a patchy use of space by goatfishes. Ninety-five percent of goatfish movements occurred in an area equivalent to 25-60% of their respective MCP home ranges, and goatfish kernel home range size varied between fishes by an order of magnitude (Table 2.2, Figure 2.6). The total space (MCP home range) used by each goatfish was equivalent to between 10 and 152% (mean = 68.5%) of the total reserve area (Table 2.2), and three of the four goatfishes tracked ranged beyond reserve boundaries (Figure 2.4 & 2.6).

Caranx melampygus - Movement patterns, habitat use, site fidelity and home range size

Two *C. melampygus* (32.5 and 42.7 cm FL) were tracked continuously for 2 and 4 days (46.5 and 96 h) respectively (Table 2.3). Both *C. melampygus* were relatively quiescent for most of the day and night, and very active during crepuscular periods. Highly directional movements between separate day and night habitats occurred within 30 minutes of sunset and sunrise each day. Both fishes used reef crest and fore reef habitats inside and outside the reserve, and shared a common nighttime habitat. The movements of both *C. melampygus* tracked were significantly ($p<0.05$) more constrained than random movement paths, indicating that these fishes were site attached. The two jacks had similar size MCP home ranges (Table 2.3) that were equivalent to approximately two thirds of the total reserve area, but overlapped reserve boundaries because of their elongated shapes (Figure 2.7). Both jacks had highly polarized patterns of habitat use, with intensively used day and night habitats situated at opposite ends of a narrow, elongated home range.

Jack #1 (32.5 cm FL) was captured at dusk in a gill net set perpendicular to the reef crest in the central area of the reserve and tracked continuously for a total of 46.5 h (two diel cycles). Following release at 21:30, jack #1 moved directly 400 m north to a nighttime habitat just outside the northern reserve boundary (Figure 2.7). Fish #1 remained in this location making only localized movements until sunrise when it moved rapidly 500 m further north to a daytime habitat along the edge of a reef 500 m from shore. Fish #1 remained in this location, moving slowly around a 15,000 m^2 area, until dusk, when it became very active, first moving rapidly around its daytime habitat before returning directly to its nighttime habitat. Fish #1 repeated this pattern of movements over the following diel cycle.

Jack #2 (42.7 cm FL) was captured at dusk in a gill net set perpendicular to the reef crest in the central area of the reserve and tracked continuously for a total of 96 h (four diel cycles). Following release at 09:45, jack #2 initially moved onto the reef crest in the central area of the reserve where it remained until dusk. At dusk jack #2 became very active, initially moving rapidly back and forth along 250 m stretch of the reef crest, before moving directly north to the nighttime habitat used by jack #1. Jack #2 remained in this location making only localized movements until sunrise when it moved rapidly 800 m south along the reef crest to a daytime habitat straddling the southern reserve boundary. Snorkel observations revealed a large (100-200 individuals) school of conspecifics in high rugosity habitat at this location. Jack #2 remained fairly quiescent at this location until dusk when it became very active, first moving rapidly back and forth along an area of high rugosity habitat for 30 minutes, and then moving directly north

along the reef crest to its nighttime habitat just outside the northern reserve boundary. Jack #2 repeated this pattern of behavior over the following three diel cycles.

Caranx sexfasciatus

Two *Caranx sexfasciatus* (36.6 & 39.7 cm FL) were tracked simultaneously for 13 h. Both fishes were captured by surround netting a resting school of *C. sexfasciatus* that occupied a sandy channel in back reef habitat in the NE corner of the Waikīkī reserve. Following release at 08:30, both fishes remained quiescent in the resting school of conspecifics until sunset when they left the sandy channel and moved steadily north together along the reserve shoreline, crossing the northern reserve boundary within 30 minutes and heading 300 m further north (1000 m north of their daytime habitat), at which time the fishes separated. Contact was then maintained with a single individual. This individual remained highly active in the general area several hundred meters north of the reserve, alternately moving along the reef edge and seawall close to shore, and then moving up to 300 m offshore until contact was lost at 21:30. Neither fish returned to daytime habitat the following day, and snorkel observations revealed that the entire resting school had dispersed from this location.

Spatial adequacy of the Waikīkī reserve

In order to quantify the minimum area required to contain the home ranges of all fishes tracked at Waikīkī, a composite convex polygon was created from all the tracking data (Figure 2.8). The composite polygon was approximately 3 times the size of the existing reserve, covering a total area of 1 km^2. Frequently used habitat that lay outside

the existing reserve included the area immediately north of the reserve (used by 7 of the 8 goatfishes and jacks tracked) and soft substrates situated south of the seaward reserve boundary (used by 3 of the 4 goatfishes tracked).

Tag and release

From December 1995 to March 2001, 1459 fishes from 34 species in 5 families were captured, tagged and released in the Waikīkī reserve and adjacent pulse fished area (Table 2.4). The number of individuals tagged varied among species because of differences in their relative abundance and vulnerability to capture, and one to three species typically accounted for the majority of tag releases in each family. The total number of goatfishes and surgeonfishes (relatively abundant and vulnerable to capture) tagged exceeded the total numbers of parrotfishes and jacks (less abundant and harder to capture) by up to an order of magnitude. Tagged fishes were recaptured inside the reserve and pulse-fished areas by research personnel using handnets and barrier nets. These recaptures were made during the course of fish tagging activities carried out at specific locations within each site. Tagged fishes were also captured up to 25 km away from the Waikīkī reserve by recreational and commercial fishers using spear, hook & line, traps and nets.

One hundred and eleven fishes from 14 species in 5 families were recaptured after times at liberty ranging from 1 to 665 days (mean = 85 days)(Table 2.5). Seventy percent of all recaptures occurred within 250 m of the point of release, and only 10% occurred at distances greater than 500 m from the point of release (Figure 2.9). The raw recapture

data were heavily skewed and were log transformed to meet normality assumptions prior to parametric analyses. Overall there was no significant correlation between dispersal distance (distance between points of release and recapture) and time at liberty ($r=0.175$, $df=100$, $p>0.05$), but fish size was significantly positively correlated with dispersal distance ($r=0.352$, $df=100$, $p<0.01$). An analysis of variance indicated that mean dispersal distance varied significantly between families ($F=18.3$, $df=4,95$, $p<0.0001$). Post hoc Bonferroni pairwise comparisons of means revealed that this difference was due primarily to the large dispersal distance evident for 4 jacks, which dispersed significantly farther than all other families except scarids. The only other significant difference in mean dispersal distance was between acanthurids (N=35) and scarids (N=13) (the latter dispersing farther). Jacks dispersed 20-80 times further on average than the other families; however, these results were based on the recapture of only four jacks, of which 3 were *Caranx sexfasciatus* from a large daytime school that was resident in the reserve for several months but dispersed a few weeks after fishes from this school were tagged and released. A single *C. melampygus* was also recaptured 2410 m from its point of release in the reserve.

Although the sample size of jack recaptures was extremely small and there were no significant differences between the mean dispersal distances of most of the families tagged, the frequency and distance at which fishes tagged inside the reserve were recaptured beyond its boundaries suggest that dispersal patterns may vary among the families investigated (Table 2.6). For example, although none of the 35 recaptures from the 356 acanthurids tagged inside the reserve occurred outside its boundaries, 12 of 57

(21%) goatfish recaptures, 7 of 13 (54%) parrotfish recaptures, and all 4 jack recaptures occurred outside the reserve boundaries. Maximum dispersal distance also varied considerably between families, with parrotfishes, goatfishes and jacks respectively dispersing up to 1.4 km, 7.6 km and 25.2 km from their point of release inside the Waikīkī reserve.

Underwater Visual Census sightings of tagged fishes

Between 1998 and 2001, 162 tagged fishes from four families were sighted during 513 visual census counts carried out in the reserve (204 counts) and adjacent areas up to 2 km south and 4 km north of the reserve (309 counts)(Table 2.7). One hundred and seventeen of these sightings occurred inside the reserve, of which 115 (98.3 %) were of fishes originally tagged inside the reserve boundary (i.e., tagged on the left side of the dorsal fin). Only 2 of 338 fishes tagged outside the reserve were sighted inside the boundary (1 mullid, 1 acanthurid). Only 8 tagged fishes (7 mullids, 1 acanthurid) sighted outside the reserve were originally tagged and released inside the reserve, and all such sightings were within 100 m of the reserve boundary. No tagged fishes were sighted during 262 visual census counts undertaken outside the area of tag and release operations (the Waikīkī reserve and northern end of the pulse fished area). The resighting rate (tag sightings per 100 fish tagged) for acanthurids pooled (N=74 resightings) was 1.7 times that for mullids pooled (N=81 resightings) and 4.2 times that for scarids pooled (N=6 resightings) (Table 2.7). No tagged carangids were resighted.

Discussion

Daily movements, home range size and habitat use

Several behavioral trends were common to all the species tracked at Waikīkī. Fishes were generally site attached to well-defined home ranges and had predictable patterns of behavior and habitat use, including crepuscular migrations between separate day and night habitats. All species tracked were strongly associated with rugose habitat for at least part of the diel cycle and demonstrated a patchy use of space within their home ranges; however, characteristic interspecific differences in habitat use, activity patterns and home range size also occurred.

Bluespine unicornfishes (*N. unicornis*) were site attached to relatively small home ranges in rugose habitat, and were primarily active during daylight hours, quiescent in refuge holes at night, and typically refuged in the same holes on successive nights for at least several weeks or months. Two different daily movement patterns ('commuting' and 'foraying') were observed in unicornfishes. Commuters made daily, crepuscular migrations of several hundred meters along predictable paths between daytime foraging habitat and nighttime refuge holes, whereas foraying unicornfishes made multiple, brief excursions from refuge holes to nearby foraging areas. Foraying unicornfishes used the same area during both day and night, spent more than 90% of their time in their refuge holes, and did not undertake daily migrations. The timing of forays was less predictable than the daily migrations undertaken by commuters and may be influenced by the tidal cycle.

White goatfishes (*M. flavolineatus*) were quiescent in resting schools associated with rugose habitat during day, dispersed rapidly from these locations at dusk, moved extensively over areas of soft substrate at night, and returned to daytime habitat at dawn. Goatfish home range sizes varied by an order of magnitude at Waikīkī and were typically large relative to the total reserve area. Goatfish home range size was 1-2 orders of magnitude larger than unicornfish home range size. White goatfish behavior, habitat use and home range size observed in Waikīkī fringing reef habitat was consistent with that previously described in patch reef habitat (Holland et al. 1993).

Blue jacks (*C. melampygus*) were site attached to narrow, elongated home ranges situated along high rugosity reef crest habitat. Blue jacks were quiescent at night, minimally active during day, and very active during crepuscular periods when they commuted along the reef between day and night habitats situated at opposite ends of their home ranges. Two blue jacks tracked at Waikīkī used a common nighttime habitat. Blue jack home range size at Waikīkī was large relative to the total reserve area and similar to that of *M. flavolineatus*. *Caranx melampygus* behavior and home range size in fringing reef habitat at Waikīkī was generally consistent with that observed in patch reef habitat at Coconut Island (O'ahu)(Holland et al. 1996). For example, *C. melampygus* at Coconut Island also made crepuscular migrations between separate day and night habitats situated at opposite ends of home ranges oriented along the patch reef wall, and shared a common nighttime habitat; however, *C. melampygus* were typically more active during daytime at Coconut Island than at Waikīkī. Bigeye jacks (*C. sexfasciatus*) were quiescent in resting

schools associated with rugose habitat during day, active along reef edge and over sand at night, and used similar size areas to *C. melampygus*.

Site attachment to well-defined home ranges or territories is a strategy shared by a wide variety of reef fishes, including acanthurids (Robertson 1983, Choat & Bellwood 1985, Montgomery et al. 1989, Craig 1996), carangids (Holland et al. 1996), chaetodontids (Fricke 1986, Reese 1989, Tricas 1989, Yabuta & Kawashima 1997, Righton et al. 1998), cheilodactylids (Lowry & Suthers 1998), haemulids (Burke 1995), labrids (Thresher 1979, Barrett 1995), pomacanthids (Sakai & Kohda 1995), mullids (Holland et al. 1993, Meyer et al. 2000), scarids (Overholtzer & Motta 1999) and serranids (Shapiro 1987, Zeller 1997). This strategy may be widespread because it allows reef fishes to find shelter and food in predictable locations, and this ability may be crucial for survival in the reef environment. There is abundant evidence to suggest that shelter is highly important to reef fishes. For example, a wide variety of reef fishes are known to use refuge holes (Helfman 1978, Atkins 1981, Dubin & Baker 1982, Walsh 1984, Shulman 1985, Randall 1996, Meyer 2000, Nagelkerken et al. 2000) and some species show fidelity to (Meyer 2000), or actively defend these holes (Walsh 1984, Shulman 1985). There is also a strong, general association between reef fish abundance (numbers and biomass) and structural or topographical complexity of reef substratum (McClanahan 1994, Grigg 1994, Friedlander & Parrish 1998a), and the abundance and size of holes in the reef is the single most important predictor of fish biomass (Friedlander & Parrish 1998a).

All species tracked in the present study were associated with high rugosity habitat during the quiescent phases of their diel cycles, and displayed predator avoidance behaviors (schooling and refuging in holes) during these periods. These observations suggest that rugose habitat functions as a refuge from predation for a wide range of reef fish taxa. The juxtaposition of structurally complex reef and flat, soft substrates allows nocturnally active species such as goatfishes to exploit prey resident in these open areas and retreat to the relative safety of the reef during the day. Two families (acanthurids and carangids) also used rugose habitat during periods of activity, suggesting that this is also an important foraging habitat for some species. For example, rugose habitat has a higher surface area for algal growth than flat substrate, and this may enable herbivores to combine access to abundant food with easy access to shelter. High fish abundance and group spawning by prey species in areas of rugose habitat may make these areas attractive to predatory jacks and also provide them with locations from which to stage ambushes (Sancho 2000, Sancho et al. 2000). Although site attachment to high rugosity areas appears to have been an evolutionarily advantageous strategy for many reef fishes, the predictable occurrence of aggregations of reef fishes in such areas increases their susceptibility to capture by humans and makes them vulnerable to overexploitation (Grigg 1994, Meyer 2000). However, strong site attachment and predictable patterns of habitat use also make reef fishes good candidates for protection within marine reserves and the results of this and other studies (Grigg 1994, McClanahan 1994, Randall 1996, Friedlander & Parrish 1998a, Meyer 2000, Nagelkerken et al. 2000, Friedlander 2001) clearly demonstrate that reserves intended to protect coral reef fishes should ideally *include high rugosity reef habitat.*

Daily crepuscular migrations between separate refuging and foraging areas have been described for a wide variety of reef fishes, including acanthurids (Walsh 1984, Mazeroll & Montgomery 1995, Mazeroll & Montgomery 1998), carangids (Holland et al. 1996), embiotocids (Sakurai & Nakazono 1995), haemulids (Ogden & Ehrlich 1977, Helfman et al. 1982, Quinn & Ogden 1984, Burke 1995, Nagelkerken et al. 2000), lutjanids (Nagelkerken et al. 2000), mullids (Holland et al. 1993, Meyer et al. 2000) and scarids (Ogden & Buckman 1973, Dubin & Baker 1982). Some authors suggest that the very precise timing of these migrations (Quinn & Ogden 1984, Holland et al. 1993, Sakurai & Nakazono 1995, Holland et al. 1996, Meyer 2000) may be an adaptation to avoid predation (Helfman 1978, Dubin & Baker 1982, Quinn & Ogden 1984). However, increases in *C. melampygus* activity at dawn and dusk suggest that some predatory species may time hunting activities to coincide with crepuscular migrations in order to take advantage of the increased vulnerability of reef fishes moving between day and night habitats (Helfman 1986). Reef fish migrations between day and night habitats are typically 100-600 m (Ogden & Ehrlich 1977, Dubin & Baker 1982, Walsh 1984, Holland et al. 1993, Sakurai & Nakazono 1995, Holland et al. 1996, Meyer et al. 2000) and occasionally up to 1.5 km (Mazeroll & Montgomery 1998). Crepuscular migrations observed in this study were comparable to those described in previous studies, ranging from 100 to 1000 m. The foraying behavior exhibited by two unicornfishes in the present study may represent an alternative strategy available when refuge holes occur close to foraging areas, and may enable unicornfishes to reduce predation risk by spending the majority of time in these holes. A similar phenomenon occurs in the striped parrotfish (*Scarus iserti*) in which terminal phase males, that are permanently territorial during the

day, either sleep on their territories or migrate up to 375 m along fixed routes to sleeping spots (Dubin & Baker 1982). In order to fully protect reef fishes from fishing mortality, marine reserves must be large enough to contain daily movements, including crepuscular migrations, and the present study demonstrates the value of acoustic telemetry as a tool for elucidating such behavior and determining minimum effective reserve size.

Fishes tracked in the present study showed a preference for a small number of locations within a larger home range area. This is a pattern common to a variety of other reef fishes (Bradbury et al. 1995, Holland et al. 1996, Zeller 1997, Meyer et al. 2000), and probably results from the spatially patchy distribution of food and shelter in the reef environment (Sale 1989). Thus reef topography determines resource distribution and therefore ultimately determines home range morphology and patterns of behavior. For example, in the present study, the long, narrow band of high rugosity reef crest habitat resulted in long, narrow home ranges for commuter unicornfishes in this area of the reef, whereas foraying unicornfishes had smaller, more compact home ranges in back reef areas where refuge holes occurred adjacent to areas of high algal cover. Goatfish movements were oriented to sand patches, and thus goatfish home range size and shape reflected the distribution of these sand patches. Results of other reef fish tracking studies also suggest that home range size and shape reflects local reef topography and distribution of key habitats. For example, *Plectropomus leopardus* have smaller, narrower home ranges in continuous fringing reef habitat than on isolated patch reefs (Zeller 1997), and the home ranges of goatfishes (Holland et al. 1993, Meyer et al. 2000)

and jacks (Holland et al. 1996) conformed to the insular topography of patch reefs inside a sheltered bay.

Site attachment and dispersal

The pattern of recaptures and resightings of conventionally tagged reef fishes at Waikīkī was generally consistent with tracking results and strongly suggests that most individuals are highly site attached to permanent home ranges, whereas a few disperse to distant locations. For example, 70% of recaptures occurred within 250 m of release sites, which is well within the home range dimensions of most fishes tracked at Waikīkī, and only 10% of recaptures occurred at distances greater than 500 m from release sites. Only 8 fishes tagged inside the Waikīkī reserve were resighted outside the reserve, and all such sightings were within 100 m of the reserve boundary. No tagged fishes were sighted beyond the locations where tag and release operations were carried out (the Waikīkī reserve and the northern end of the pulse fished area). Recapture and resighting results may indicate that dispersal patterns reflect differences in home range size between families. Species with relatively large home ranges (e.g., mullids and carangids) apparently dispersed further and more frequently than species with relatively small home ranges (e.g., acanthurids); however, these recapture data must be interpreted with caution because of the extremely small sample sizes involved (e.g., N= 4 jack recaptures). Some of these apparent differences in dispersal may be artifactual because the probability of being captured outside reserve boundaries, or not being resighted, increases with increasing home range size even for fishes that are highly site attached. For example, goatfishes and jacks tracked in the present study had home ranges that spanned up to 1

km of reef, suggesting that recaptures of these species within 1 km of a release site probably do not constitute genuine dispersal (i.e., emigration from an established home range). However, some recaptures clearly occurred at distances that greatly exceeded maximum home range dimensions of tracked species, and these distant recaptures were restricted to families with relatively large home ranges (goatfishes and jacks).

Several previous tagging studies indicated that a wide variety of coral reef fish species were highly site attached in both fringing reef (Chapman and Kramer 2000) and patch reef habitats (Holland et al. 1993, 1996, Meyer et al. 2000). Chapman and Kramer (2000) tagged 1443 reef fishes from 35 species in the Barbados Marine Reserve (BMR) and an adjacent fished area. Tagged fishes from 23 species were all recaptured or resighted within 100 m of their release sites and only two fishes from two species moved more than 500 m between sites of release and recapture or resighting. The maximum distance between release and recapture or resighting sites was 616 m, and no fishes tagged inside the BMR were recaptured in the adjacent fished area. The scale of daily movements of fishes tracked in the present study suggests that the limited distances between release and recapture or resighting locations in the BMR study were consistent with site attached fishes being recaptured or resighted at different locations within stable home ranges. In a tag and release study of goatfishes (*M. flavolineatus* and *Parupeneus porphyreus*) and a jack (*C. melampygus*) carried out on a small patch reef reserve (Coconut Island, O'ahu), 67-100% of recaptures occurred within the reserve boundaries (Holland et al. 1993, 1996, Meyer et al. 2000). A small number of *C. melampygus* dispersed up to 72.4 km from Coconut Island, but unlike the Waikīkī study, there were no

confirmed distant recaptures of the two goatfish species (Holland et al. 1993, 1996, Meyer et al. 2000).

A general pattern of high site fidelity of most individuals and dispersal of a few nomadic individuals (dispersal polymorphism) occurs widely among terrestrial animals (Parker 1984, Swingland 1984), and has also been described in bottom-dwelling fish species (Roberts & Polunin 1991, Attwood & Bennett 1994). For example, genetic polymorphism with respect to dispersal behavior is thought to explain differential dispersal patterns of the surf-zone teleost *Coracinus capensis* from a South African marine reserve (Attwood & Bennett 1994). Genetically mediated differential dispersal behavior is unconditional and therefore occurs regardless of environmental conditions (Swingland 1984). Such unconditional dispersal is quite distinct from the conditional, density-dependent dispersal (Chitty 1967) that is widely anticipated as a mechanism for the export of fish biomass ('spillover') from mature marine reserves (Roberts & Polunin 1993, Guénette et al. 1998, Chapman & Kramer 1999, Jennings 2000). The existence of genetically 'resident' and 'nomadic' fishes in reef fish populations appears to be a more likely explanation for the limited dispersal of fishes from the Waikīkī reserve and Coconut Island (e.g. Holland et al. 1993, 1996, Meyer et al. 2000) than density-dependent emigration. Nomadic fishes were apparently much less common than resident individuals at Waikīkī, suggesting that export of biomass from Waikīkī reserve is low or negligible for most species.

Previous studies in a wide range of geographical locations have found low or negligible export of coral reef fishes from marine reserves (Holland et al. 1993, Corless et al. 1997, Zeller & Russ 1998, Chapman & Kramer 2000, Meyer et al. 2000). Corless et al. (1997) suggested that limited emigration of fishes from the Soufriere Marine Management Area might be attributable to the recent (1 year) establishment of the reserve, and noted that current theory suggests that the probability of fishes relocating their home sites will increase markedly at the higher fish densities that characterize mature protected areas (e.g., Chapman & Kramer 1999). However, both the present study (Tables 2.5, 2.6 & 2.7, Figure 2.9) and several other recent studies (Holland et al. 1993, Zeller & Russ 1998, Chapman & Kramer 2000, Chiappone & Sullivan-Sealey 2000, Cole et al. 2000, Meyer et al. 2000) have found little or no emigration from reserves that have been in existence for up to several decades. A few studies claim to have demonstrated spillover using underwater visual surveys and analysis of catch data from around marine reserves (e.g., Rakitin & Kramer 1996, Russ & Alcala 1996b, Chapman & Kramer 1999), but the spatial scale of these studies was very limited, with survey areas extending only a few hundred meters beyond reserve boundaries. Results of these studies are consistent with the sighting and capture of fishes resident within home ranges that straddle reserve boundaries. The number of resident 'boundary-straddling' individuals will increase as a function of general increases in fish abundance inside reserves following reserve protection. Whereas some may regard this phenomenon as spillover it may be completely unrelated to density-dependent dispersal. Capture of these 'boundary-straddling' fishes will directly impact fish abundance inside reserves and may

be unsustainable at high levels of fishing mortality, particularly if reserves are relatively small.

Conditional dispersal from reserves may be naturally limited by the high site fidelity and home ranging behaviors of resident reef fishes. Mechanisms other than the widely invoked density-dependent spillover (e.g., Roberts & Polunin 1993, Guénette et al. 1998, Chapman & Kramer 1999, Jennings 2000), such as limited recruitment (Roberts & Polunin, 1991) or increased predation of juvenile recruits within reserves (Tupper & Juanes 1999), may be primarily responsible for regulating fish population densities inside reserves. Although emigration of juvenile or adult fishes from reserves to adjacent fished areas may be negligible for many coral reef species, retention of fishes within reserve boundaries can still benefit fisheries through the export of reproductive products (e.g., Roberts & Polunin 1993, Guénette et al. 1998, Chapman & Kramer 1999, Nowlis & Roberts 1999, Nowlis 2000), and this benefit will be maximized by the anticipated larger size and greater reproductive output of fishes inside reserve boundaries (Roberts & Polunin 1993, Guénette et al. 1998, Chapman & Kramer 1999).

Design and function of marine reserves

Acoustic tracking clearly demonstrated that most jacks and goatfishes captured inside the Waikīkī reserve routinely crossed boundaries into adjacent fished areas in the course of daily movements. Two main factors were responsible for fish home ranges overlapping reserve boundaries: (1) Home range size was large relative to the total reserve area, and (2) Critical habitat was situated outside the existing reserve boundaries.

These results suggest that the present design of the Waikīkī reserve does not guarantee protection for these heavily targeted families because a high proportion of resident fishes are regularly exposed to fishing activity. High fishing mortality in the area adjacent to the existing reserve could directly decrease fish abundance inside the reserve, reducing anticipated biological benefits that are contingent on greater fish abundance and size inside these areas. However, the general pattern of site attachment to well defined home ranges shown by fishes at Waikīkī suggests that a larger reserve area could be highly effective in protecting even species with relatively large home ranges. Analysis of the total space and habitat used by all tracked fishes suggests that the existing reserve should be at least tripled in size to protect species such as goatfishes and jacks, and that the expansion should be both seaward and along the shoreline.

It will not be feasible to collect empirical fish movement data from most intended reserve areas, but the consistent home ranging behavior seen in the present and previous studies (Holland et al. 1993, 1996, Meyer et al. 2000) suggest that there are several general design principles that could be used to maximize reserve effectiveness. For example, minimum reserve dimensions should be based on habitat and space requirements of species with relatively large home ranges, because species with smaller home ranges are likely to be protected within the same areas. The distance traveled during crepuscular migrations appears to determine maximum daily home range dimensions. These daily migrations are generally less than 1 km, but may range up to 1.5 km, and are frequently oriented parallel to the reef edge, suggesting that reserves should be large enough to accommodate fish movements of this magnitude. Gross reef

topography could be used as a simple guide for determining where reserve boundaries should be placed. In order to reduce the probability of fish home ranges extending into unprotected areas, reserve boundaries should be placed along natural borders between discrete areas of habitat rather than dividing regions of contiguous habitat. This approach has also been suggested by Roberts & Polunin (1991), Barrett (1995) and Chapman & Kramer (2000), who suggested that sandy areas adjacent to reefs function as natural barriers to strongly reef associated species. However, it is also important to note that the sandy habitats adjacent to reefs are important foraging habitats for some species that refuge in the reef (Holland et al. 1993, Meyer et al. 2000, present study) and that reserves that exclusively protect hard reef habitats may fall short of their multispecies conservation goals. A practical solution would be to protect both reef and sand substrates within reserves but still use natural borders between habitats as a guide for positioning reserve boundaries.

Results of the present study indicate that coral reef fishes are generally site attached to well-defined home ranges, but that home range size and habitat requirements vary between species. Although site attachment to well defined home ranges makes coral reef fishes well suited to conservation in marine reserves, reserve design (size, habitat content and boundary placement) must address interspecific variation in home range size and habitat requirements in order to provide effective protection for a wide range of species. Effective reserves should be able to maintain high fish abundance and size inside reserve boundaries even when fishing mortality in surrounding areas is high. Reserves that are too small, or lack critical habitats, are unlikely to meet this goal because

of the high probability that resident fishes will cross into fished areas and be captured. Both the present and previous studies found that some fishes disperse (emigrate) from reserves, but that dispersal is limited to relatively few individuals even when reserves are well established. This limited emigration may result from polymorphic dispersal behavior rather than from density-dependent dispersal, suggesting that 'spillover' from reserves may be inherently limited and may not increase as reserves mature. Although the spillover concept is a popular selling point for marine reserves, retention of fishes inside reserves can still benefit adjacent areas through the export of reproductive products (Carr & Reed, 1993).

Table 2.1. Summary of tracking data from five *N. unicornis* captured and released within the Waikīkī reserve.

	Fish Number				
	1	2	3	4	5
Fork Length (cm)	43.9	38.5	33.8	46.6	40.3
Duration of track (h)	79	51	118	24	63
Behavior type	Foray	Commute	Commute	Mixed	Foray
MCP home range size (m^2)	325	6026	7650	57400*	865
Kernel home range – 50% (m^2)	839	818	824	1181*	845
Kernel home range – 95% (m^2)	1847	2268	5484	6619*	2344
Mean distance traveled (m/24 h)	41	489	464	1653	246
% of total reserve area used	0.1	1.77	2.25	16.88	0.25

* Not significantly site attached

Table 2.2. Summary of tracking data from four *M. flavolineatus* captured and released within the Waikīkī reserve.

	Fish Number			
	1	2	3	4
Fork Length (cm)	32.3	27.3	28.3	26.0
Duration of track (h)	46	8	41	49
MCP home range size (m^2)	515710	269428*	111644	33214
Kernel home range – 50% (m^2)	13766	-	4369	2028
Kernel home range – 95% (m^2)	153498	-	29990	19666
Mean distance traveled (m/24 h)	3209	-	2103	2554
% of total reserve area used	152	79	33	10

* Not significantly site attached

Table 2.3. Summary of tracking data from two *C. melampygus* captured and released within the Waikīkī reserve.

	Fish Number	
	1	2
Fork Length (cm)	32.5	42.7
Duration of track (h)	46.5	96
Behavior type	Commute	Commute
MCP home range size (m^2)	229234	208264
Kernel home range – 50% (m^2)	17104	23296
Kernel home range – 95% (m^2)	83040	148632
Mean distance traveled (m/24 h)	3285	4408
% of total reserve area used	67	61

Table 2.4. Summary of fishes tagged and released and recaptured in the Waikīkī reserve and pulse fished area.

Species	Number Tagged	Recaptures		Fork Length (cm)		
		N	%	Minimum	Maximum	Mean
Acanthurus blochii	6	0	0	19.6	28.8	23.6
Acanthurus dussumeiri	26	0	0	16.3	34.3	23.7
Acanthurus leucopareius	7	0	0	18.4	23.0	20.7
Acanthurus nigrofuscus	26	1	3.8	15.3	22.3	18.1
Acanthurus nigroris	35	0	0	18.8	24.1	21.8
Acanthurus triostegus	144	26	18.1	14.5	21.5	17.4
Acanthurus xanthopterus	1	0	0	20.5	-	-
Ctenochaetus strigosus	5	1	2 0	15.4	16.5	16.2
Naso lituratus	35	0	0	16.0	27.8	22.7
Naso unicornis	134	7	5.2	13.9	46.6	27.1
Acanthuridae Total	**419**	**35**	**8.4**	**13.9**	**46.6**	**21.9**
Alectis indicus	1	0	0	23.2	-	-
Carangoides ferdau	1	0	0	24.6	-	-
Carangoides orthogrammus	1	0	0	24.1	-	-
Caranx ignobilis	2	0	0	27.7	28.5	28.1
Caranx melampygus	49	1	2.0	15.2	44.0	29.1
Caranx sexfasciatus	25	3	12.0	28.1	40.8	35.6
Gnathanodon speciosus	1	0	0	16.5	-	-
Scomberoides lysan	15	0	0	20.6	41.0	28.5
Carangidae Total	**95**	**4**	**4.2**	**15.2**	**44.0**	**30.4**
Lutjanus fulvus	2	1	5 0	14.2	26.5	20.4
Lutjanus kasimira	18	1	5.6	14.2	28.1	19.3
Lutjanidae Total	**20**	**2**	**1 0**	**14.2**	**28.1**	**19.4**
Mulloidichthys flavolineatus	129	2	1.6	14.0	34.0	23.8
Mulloidichthys vanicolensis	221	7	3.2	12.8	30.5	2
Parupeneus bifasciatus	2	0	0	18.1	21.9	2
Parupeneus cyclostomus	5	0	0	19.3	28.5	23.3
Parupeneus multifasciatus	371	43	11.6	13.1	28.5	19.1
Parupeneus pleurostigma	9	0	0	16.7	31.4	21.7
Parupeneus porphyreus	29	5	17.2	14.5	38.5	21.2
Upeneus arge	17	0	0	2	31.0	23.9
Mullidae Total	**783**	**57**	**7.3**	**12.8**	**38.5**	**20.4**
Calotomus carolinus	62	12	19.4	18.7	44.0	34.0
Chlorurus perspicillatus	1	0	0	42.0	-	-
Chlorurus sordidus	1	0	0	21.3	-	-
Scarus rubroviolaceus	6	0	0	25.9	48.6	40.2
Scarus dubius	1	0	0	24.1	-	-
Scarus psittacus	71	1	1.4	16.5	34.2	22.5
Scaridae Total	**142**	**13**	**9.2**	**16.5**	**48.6**	**28.5**
Grand Total	**1459**	**111**	**7.6**	**12.8**	**48.6**	**22.2**

Table 2.5. Summary of Waikīkī tag recapture data.

Species	N (%)	Days At Liberty				Distance Traveled (m)			
	Recaptured	Min	Max	Mean	(SE)	Min	Max	Mean	(SE)
A. nigrofuscus	1 (3.8)	41	-	-		<250	-	-	
A. triostegus	26 (18.1)	1	66	19	(4)	0	250	135	(26)
C. strigosus	1 (20.0)	7	-	-		0	-	-	
N. unicornis	7 (5.2)	1	314	89	(75)	0	250	174	(39)
Acanthuridae	**35 (8.4)**	**1**	**314**	**29**	**(11)**	**0**	**250**	**140**	**(22)**
C. melampygus	1 (2.0)	233	-	-		2410	-	-	
C. sexfasciatus	3 (12.0)	26	82	55	(16)	475	25207	14100	(7250)
Carangidae	**4 (5.4)**	**26**	**233**	**99**	**(46)**	**475**	**25207**	**11177**	(5901)
L. fulvus	1 (50.0)	20	-	-		50	-	-	
L. kasimira	1 (5.6)	107	-	-		0	-	-	
Lutjanidae	**2 (10.0)**	**20**	**107**	**64**	**(44)**	**0**	**50**	**25**	**(25)**
M. flavolineatus	2 (1.6)	52	275	164	(112)	175	254	215	(40)
M. vanicolensis	7 (3.2)	4	275	108	(36)	175	6739	1427	(917)
P. multifasciatus	43 (11.6)	1	406	75	(16)	0	7613	397	(197)
P. porphyreus	5 (17.2)	15	642	228	(114)	0	2628	1022	(548)
Mullidae	**57 (7.3)**	**1**	**642**	**97**	**(18)**	**0**	**7613**	**589**	**(197)**
C. carolinus	12 (19.4)	7	665	173	(58)	85	1400	378	(113)
S. psittacus	1 (1.4)	12	-	-		0	-	-	
Scaridae	**13 (9.8)**	**7**	**665**	**161**	**(55)**	**0**	**1400**	**349**	**(108)**
Grand Total	**111 (7.6)**	**1**	**665**	**85**	**(13)**	**0**	**25207**	**839**	**(313)**

Table 2.6. Summary of tag recapture and dispersal data for fishes captured inside the Waikīkī reserve.

Family	Number Tagged	Number Recaptured	% Of Recaptures From Outside Reserve	Maximum Dispersal Distance (m)
Acanthuridae	356	29	0	-
Carangidae	83	4	100	25207
Lutjanidae	6	2	0	-
Mullidae	555	34	21	7613
Scaridae	121	7	57	1400

Table 2.7. Summary of tag resighting data for fishes tagged at Waikīkī.

Species	N Tagged	N Resightings	Resighting rate (Resightings per 100 fish tagged)	N Emigrants Observed	
				From reserve	From pulse fished area
A. nigrofuscus	26	3	11.5	0	0
A. nigroris	35	1	2.9	0	0
A. triostegus	144	24	16.7	0	0
A. xanthopterus	1	6	600.0	0	0
C. strigosus	5	4	80.0	0	0
N. lituratus	35	3	8.6	0	0
N. unicornis	134	33	24.6	1	0
Acanthuridae Total	**419***	**74**	**17.7**	1	**0**
L. fulvus	2	1	50.0	0	0
M. flavolineatus	129	11	8.5	0	0
M. vanicolensis	221	2	0.9	0	0
P. multifasciatus	371	65	17.5	7	1
P. porphyreus	29	3	10.3	0	0
Mullidae Total	**783***	**81**	**10.3**	7	**1**
C. carolinus	62	5	8.1	0	0
C. sordidus	1	1	100.0	0	0
Scaridae Total	**142***	**6**	**4.2**	**0**	**0**
Grand Total	**1459**	**162**	**11.1**	**8**	**1**

*Including tagged individuals never resighted

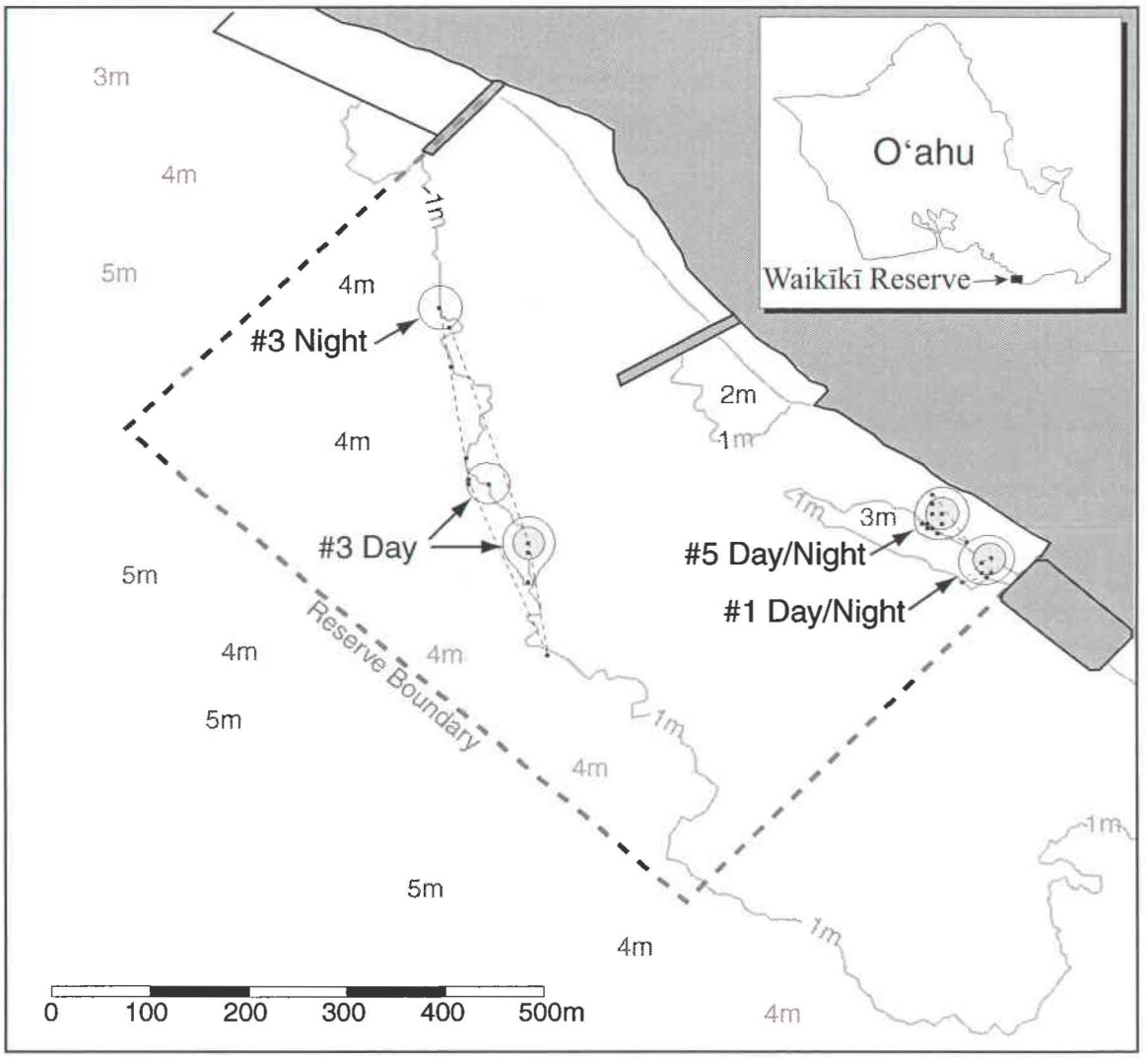

Figure 2.1. Kernel and MCP home ranges of three *Naso unicornis* tracked in the Waikīkī reserve. Dark shaded area = land, solid gray line = 1 m depth contour, dashed gray line = reserve boundary. Fine bold dashed line = MCPs (all positional fixes). Bold, unshaded contours = 95% kernel home range. Bold, light gray shaded contour = 50% kernel home range.

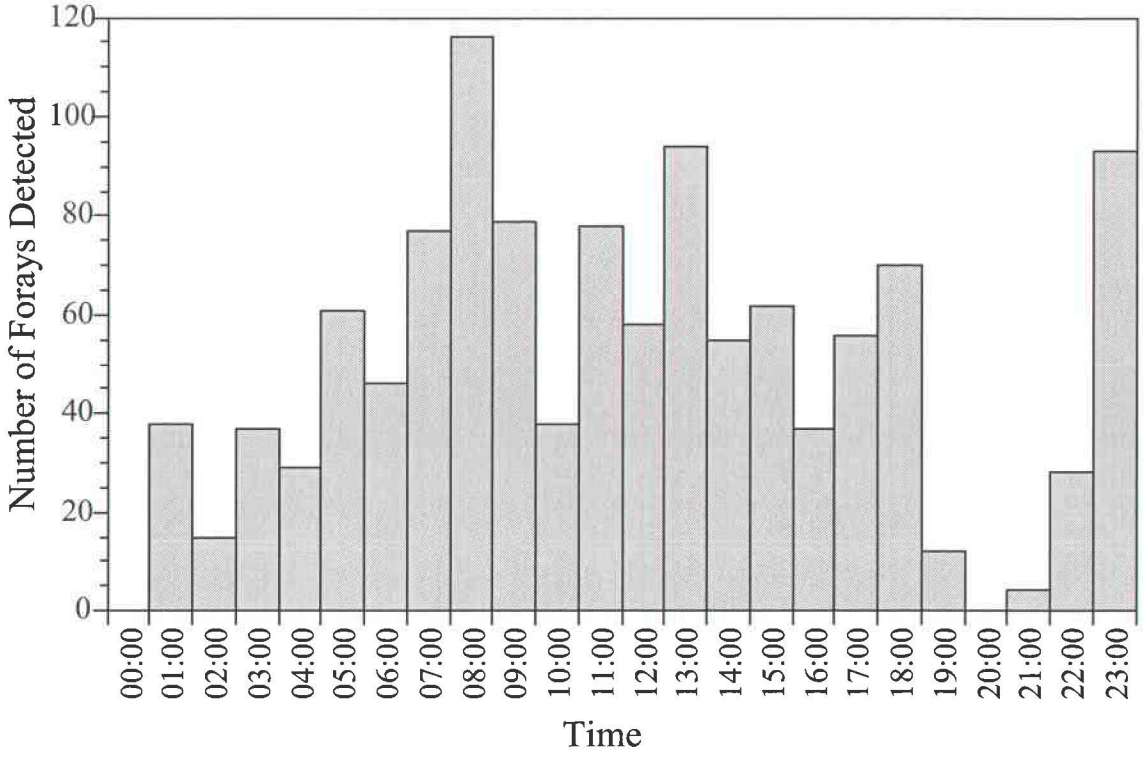

Figure 2.2. Diel variation in the frequency of forays into foraging habitat by unicornfish #5.

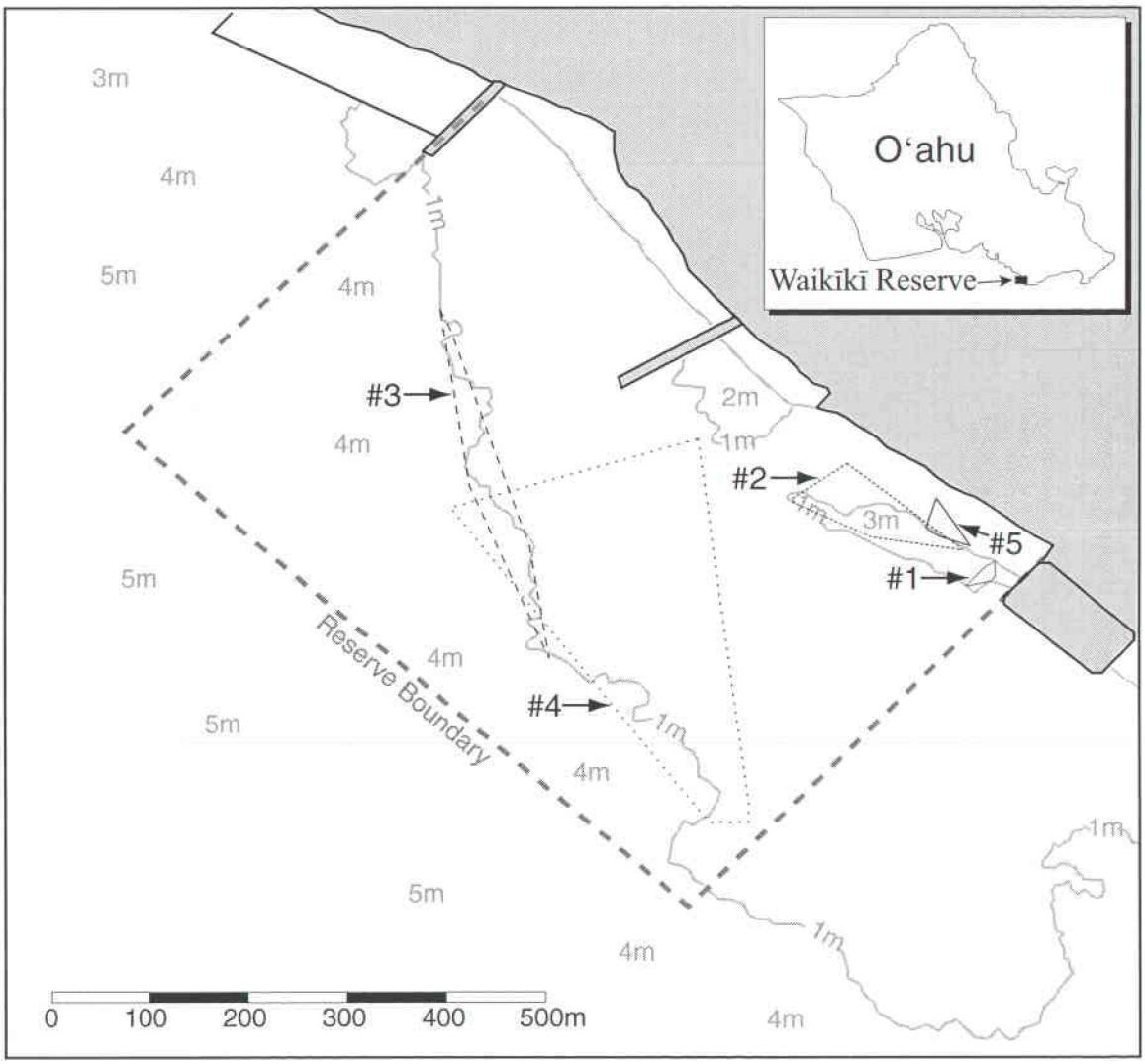

Figure 2.3. MCP home range size of five *N. unicornis* tracked in the Waikīkī reserve. Shaded area = land, solid gray line = 1m depth contour, dashed gray line = reserve boundary, bold lines (dotted, dashed and solid) = minimum convex polygons (MCP) denoting home range borders of each fish. MCP's include all positional fixes.

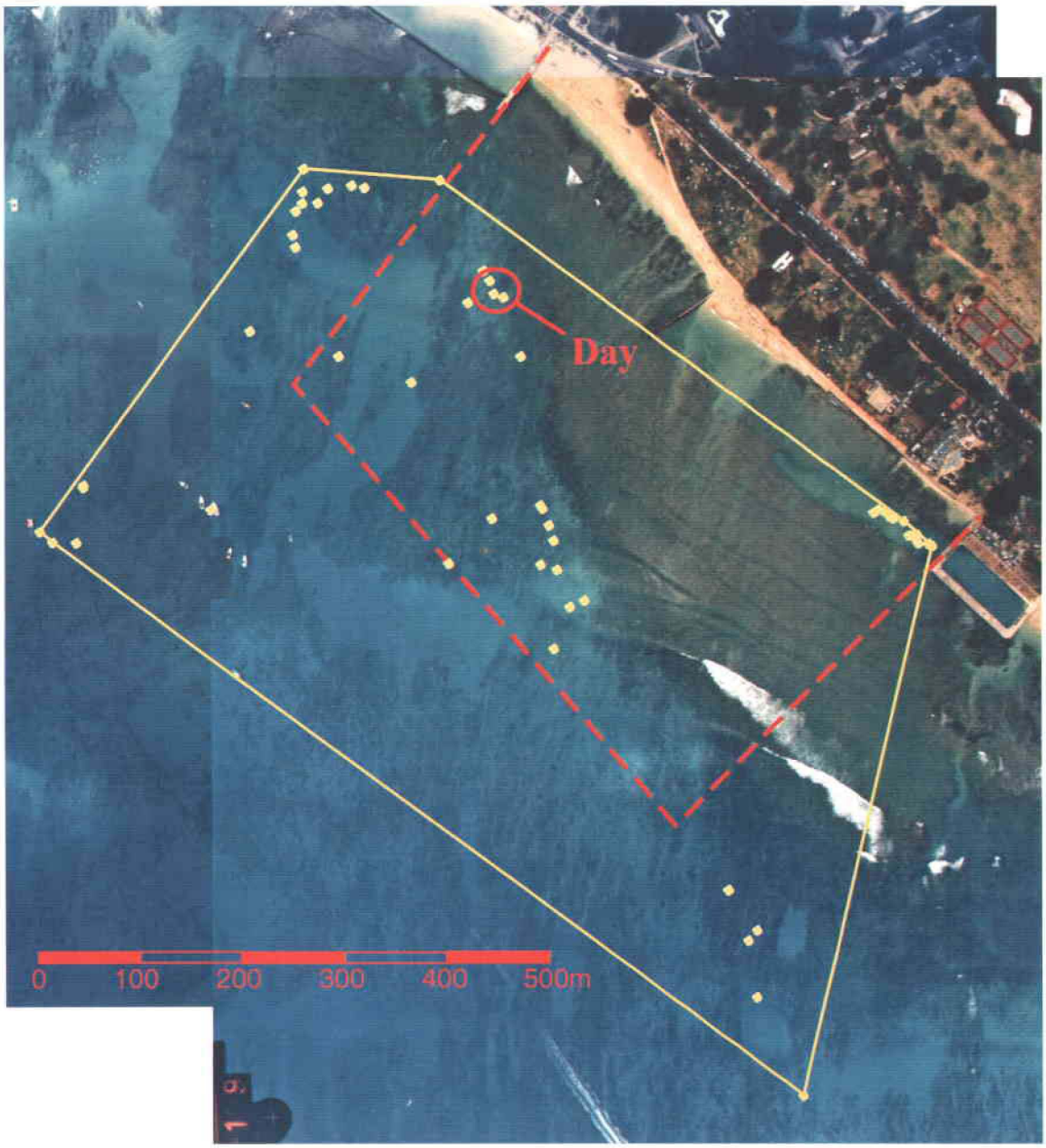

Figure 2.4. MCP home range of *Mulloidichthys flavolineatus* #1 tracked in the Waikīkī reserve. Dashed red line = reserve boundary, solid yellow line = MCP home range boundary, yellow points = positional fixes for *M. flavolineatus* #1.

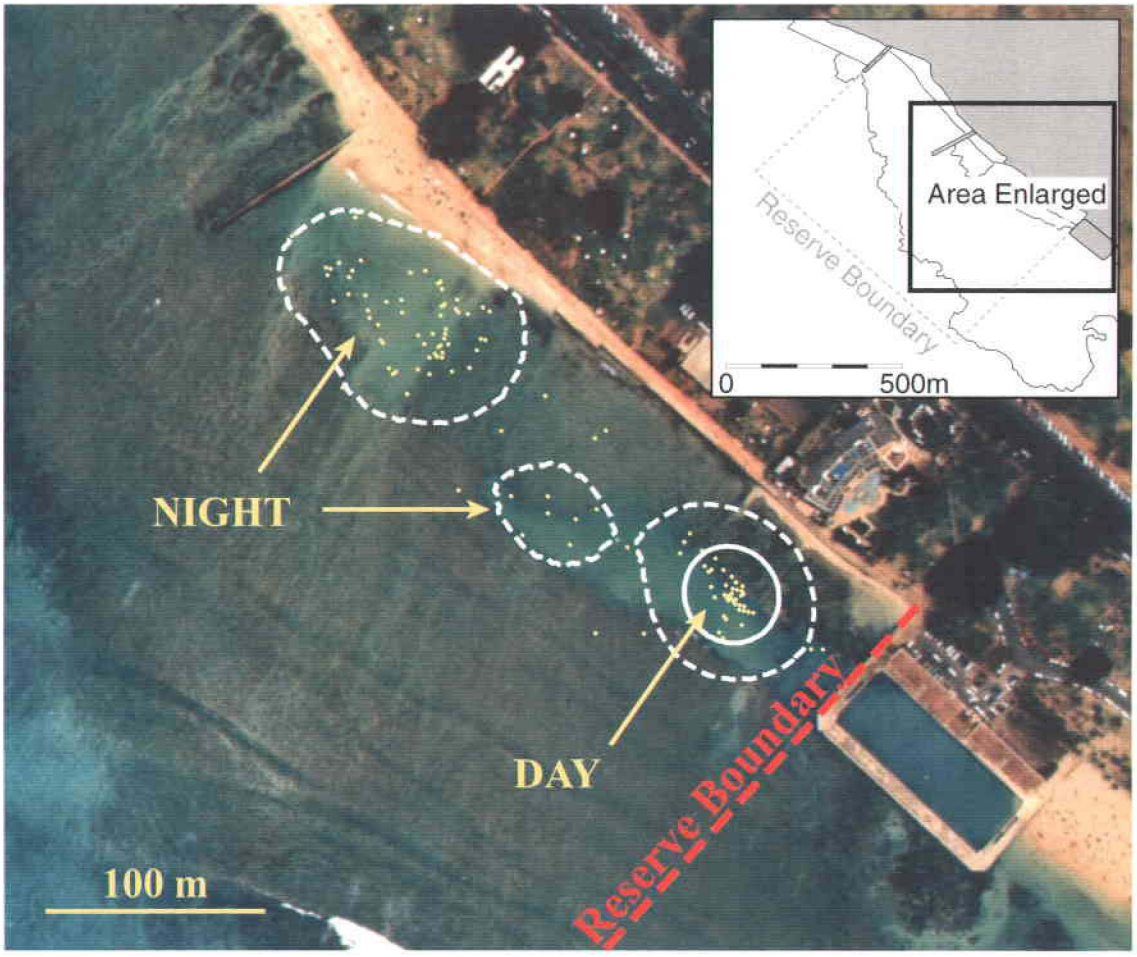

Figure 2.5. Kernel home range of *M. flavolineatus* #4. Dashed white contour = 95% kernel, solid white contour = 50% kernel, yellow points = positional fixes for *M. flavolineatus* #4.

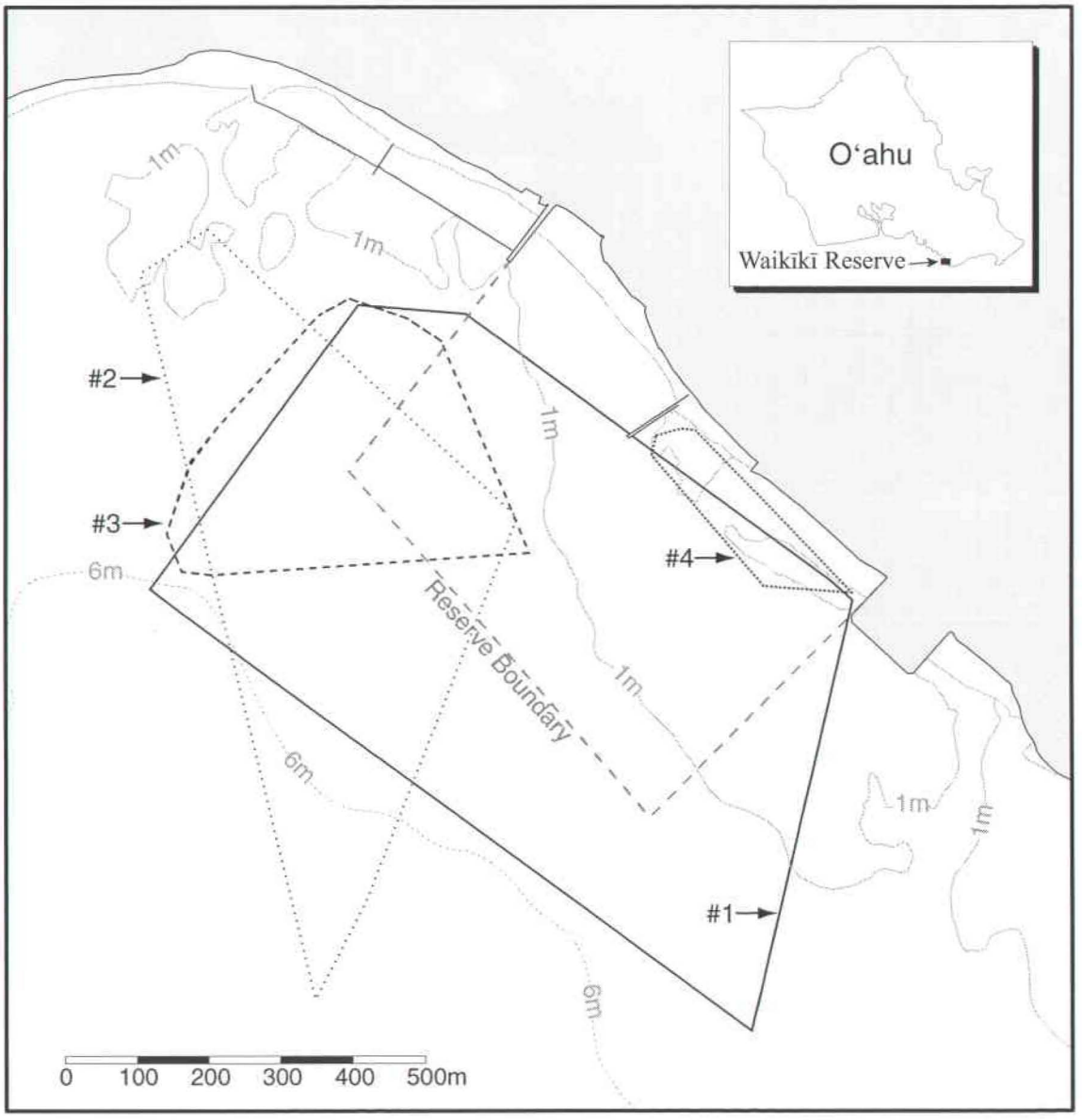

Figure 2.6. MCP home range size of four *M. flavolineatus* tracked in the Waikīkī reserve. Shaded area = land, solid gray line = 1m depth contour, dashed gray line = reserve boundary, bold lines = minimum convex polygons (MCP) denoting home range borders of each fish. MCP's include all positional fixes.

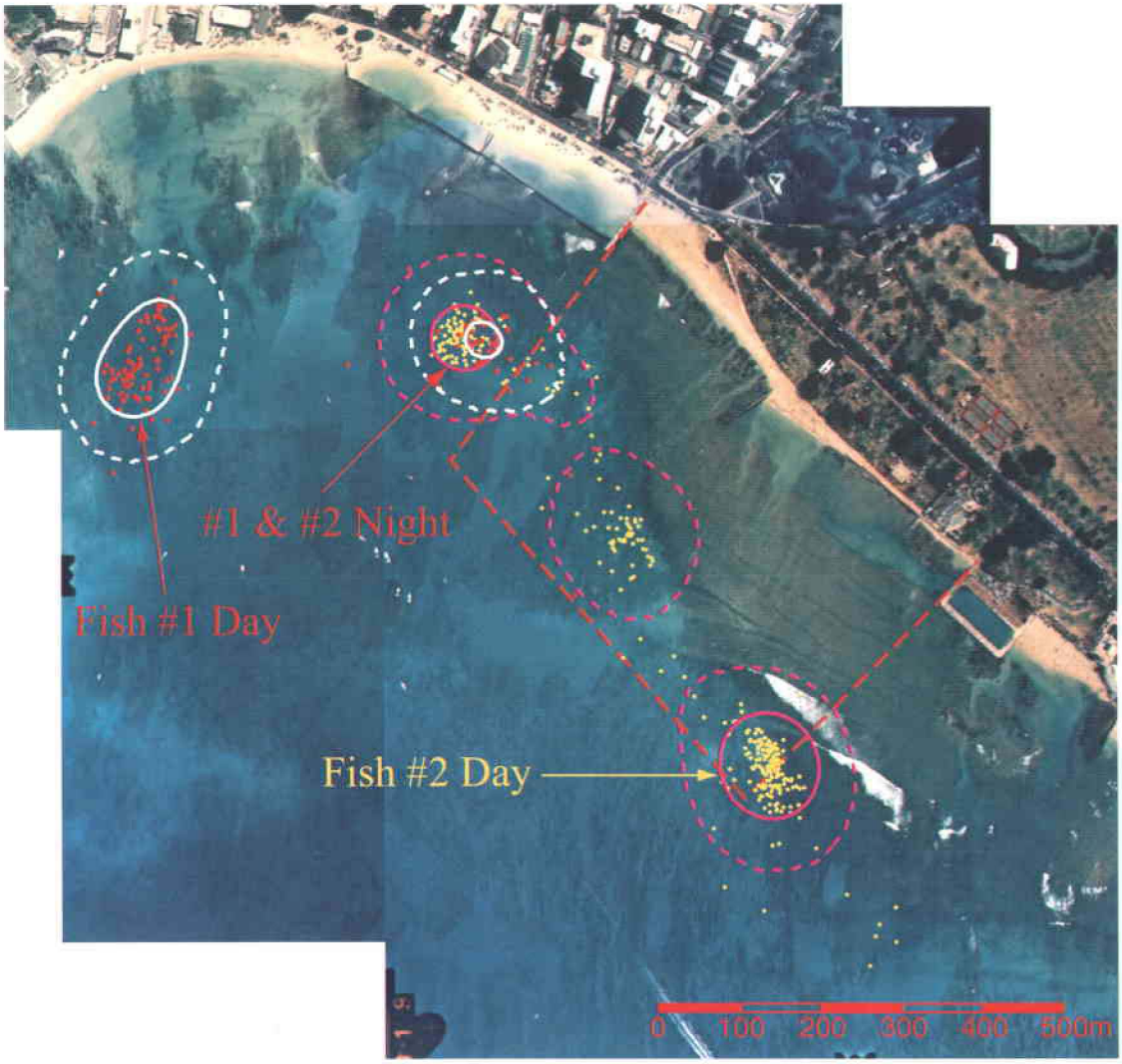

Figure 2.7. Kernel home ranges (KHR) of two *C. melampygus* captured inside Waikīkī reserve. Dashed red line = reserve boundary, dashed white contour = *C. melampygus* #1 95% KHR, solid white contour = *C. melampygus* #1 50% KHR, red points = all positional fixes for *C. melampygus* #1, dashed pink contour = *C. melampygus* #2 95% KHR, solid pink contour = *C. melampygus* #2 50% KHR, yellow points = all positional fixes for *C. melampygus* #2.

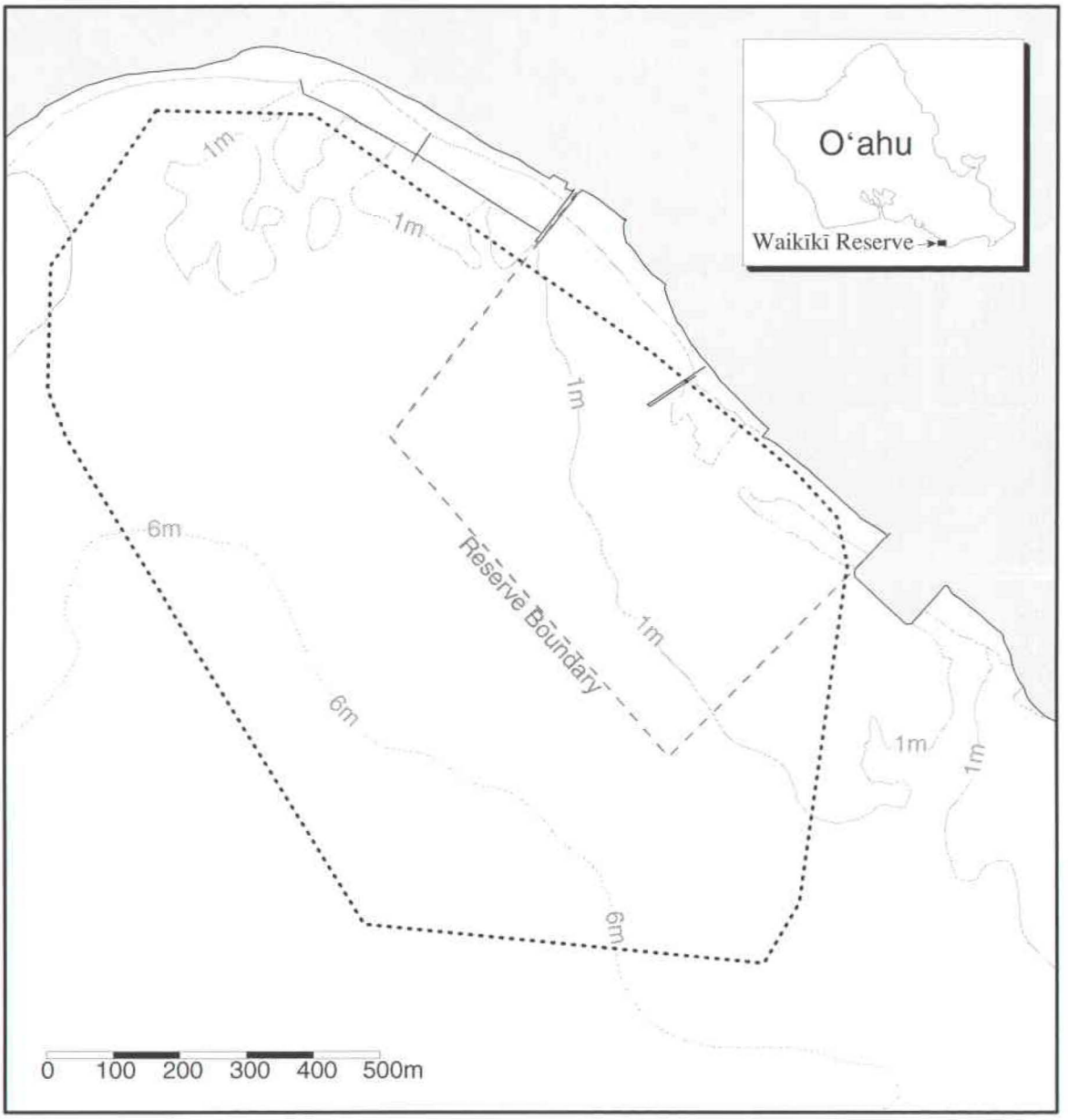

Figure 2.8. Composite MCP including movement data from all 13 tracked fishes (bold dashed line).

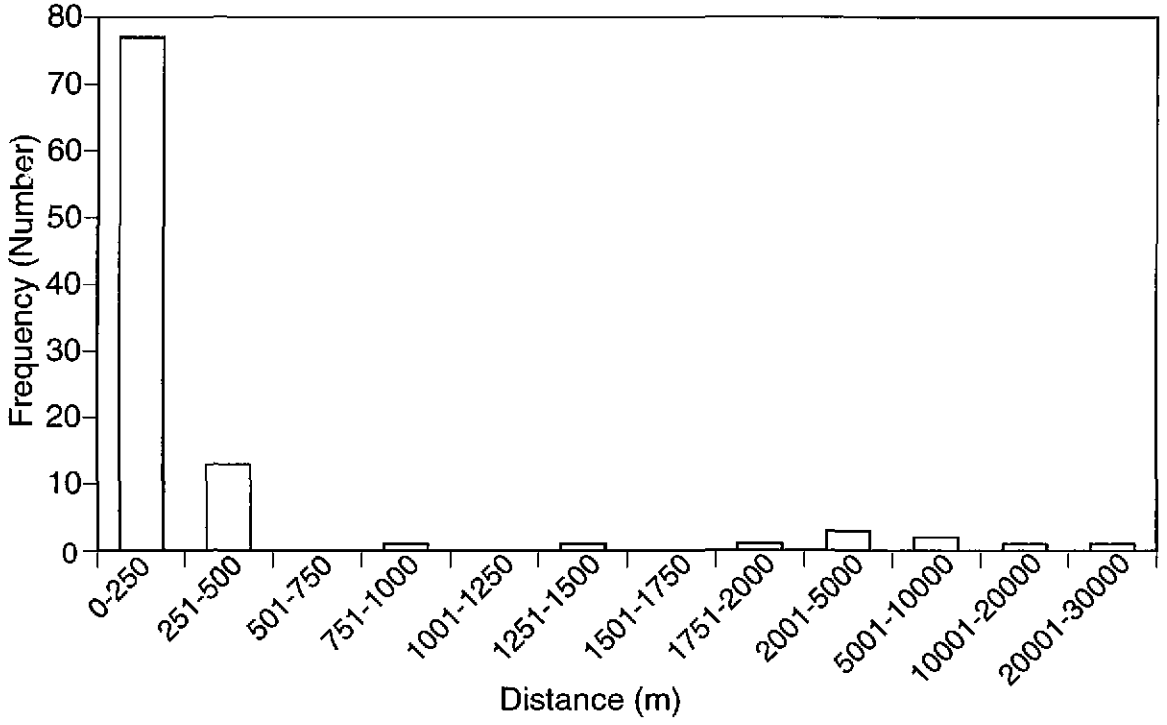

Figure 2.9. Frequency of tagged fishes recaptured at various distances from the point of original release at Waikīkī.

CHAPTER 3

FISH ABUNDANCE, SIZE AND DISTRIBUTION

Introduction

The most obvious and widely anticipated effects of 'no-take' reserve protection are greater abundance and size of fishes inside reserve boundaries than in comparable fished habitats (Roberts & Polunin 1991, 1993, Bohnsack 1996, Russ 2002). Many theoretical benefits of reserves to other, fished areas are contingent on these effects (Roberts & Polunin 1991, 1993, Bohnsack 1996, Russ 2002). For example, greater fish abundance inside reserves may result in 'spillover' (emigration to adjacent fished areas), and larger size of fishes in reserves may greatly enhance reproductive output from these areas (Roberts & Polunin 1991, 1993, Bohnsack 1996, Russ 2002). Consequently, fish abundance and size are frequently chosen variables in studies of marine reserve effectiveness (Halpern in press). Although the presence of a reserve is only one of the factors that may potentially influence fish abundance and size in that area (Rakitin & Kramer 1996, Chiappone & Sullivan Sealey 2000, Halpern in press), quantification of these variables is important for assessing reserve effectiveness.

The present study compares fish abundance and size in a small, 'no-take' marine reserve with those in two adjacent fished sites (a continually fished site and a 'pulse-fished' site).

Two specific hypotheses, based on anticipated reserve effects, are tested;

Fish Abundance

H_0 = No difference in abundance between fished sites and reserves

H_1 = Fish abundance greater inside reserve boundaries

H_2 = Fish abundance greater outside reserve boundaries

Fish Size

H_0 = No difference in size between fished sites and reserves

H_1 = Fish size greater inside reserve boundaries

H_2 = Fish size greater outside reserve boundaries

Methods

The impact of fishing on reef fishes at Waikīkī was estimated by comparing fish abundance and size at two "impact" sites (continually fished and pulse fished), with a geographically adjacent "control" reserve site (the 'no-take' Waikīkī Marine Life Conservation District) (Rakitin & Kramer 1996, Tissot & Hallacher, 1999). Differences in fish abundance and size between the reserve and fished sites were assumed to result from fishing and not other factors, such as habitat differences. In order to minimize the influence of habitat differences on census results, a 6-km stretch of fringing reef adjacent to the reserve (Figure 1.1) was examined to locate fished habitats that most closely resembled the reserve habitats (Grigg 1994, McClanahan & Kaunda-Arara 1996). The fringing reef was subdivided into four well-defined habitat zones (back reef, reef flat, reef crest and fore reef). The reef crest habitat zones of both reserve and fished areas were the

most structurally complex of the four habitat zones surveyed, but reef crest structural complexity in the reserve was different from that in the fished areas. The reserve reef crest was a single, continuous stretch of high rugosity habitat, whereas the reef crest in the fished areas consisted of smaller patches of high rugosity habitat interspersed with low rugosity reef and sand channels. The three other habitat zones (back reef, reef flat and fore reef) had much lower structural complexity than the reef crest, but reserve back reef habitat contained more holes and ledges than back reef habitats in the fished areas. Conversely, the fore reef habitat in the fished areas had a steeper gradient and was more rugose than the equivalent reserve habitat zone. Potential habitat matches were initially identified using low-altitude, natural-color aerial photography (e.g., Sluka et al., 1994) and then groundtruthed by divers. Fished habitats that most closely resembled habitat inside the reserve were selected as locations for "impact" fish counts.

Abundance and size of fishes at Waikīkī were initially quantified using standard 5 x 50 m underwater visual belt transect methodology (Brock 1954, Sale and Douglas, 1981, Brock 1982), but avoidance behavior by resource species resulted in unrepresentatively low counts inside the transect sampling corridor. For this reason, a modified 'timed swim' version of the transect method was used to obtain more representative samples. Each timed swim consisted of a 15-minute snorkel through one of the four distinct reef habitat zones (e.g., reef crest)(Polunin & Roberts 1993, Rakitin & Kramer 1996), during which the observer swam slowly in a straight line and recorded the number and size (total length (TL) to the nearest 5cm) of all target species encountered in that habitat. The use of a 15-minute survey time limit, instead of a narrow (i.e., 5 x 50m)

belt transect, effectively broadened the area surveyed and thus minimized flight distance effects (avoidance errors), and helped to integrate small scale patchiness (schools) and include species that occur at low densities (Grigg 1994, McClanahan & Kaunda-Arara 1996). In order to ensure accuracy of fish length estimates, observers were trained to estimate total lengths of captive fishes and fish diagrams until they were able to assign fishes to the correct 5 cm size bins. Accuracy during visual censuses was further enhanced by using preformatted data sheets that included a scale bar divided into 5 cm increments.

Length estimates of fishes from visual censuses were converted to weight using the allometric length-weight conversion: $W = aSL^b$, where parameters a and b are constants, SL is standard length in mm, and W is weight in grams (Polunin & Roberts 1993, McClanahan & Kaunda-Arara 1996, Friedlander and Parrish 1997). Total length (from the midpoint of each 5cm size class) was converted to SL by using published and web-based conversion factors (www.fishbase.org). Species-specific length-weight fitting parameters were obtained from Hawai'i Cooperative Fishery Research Unit unpublished data and web-based sources (www.fishbase.org). In the cases where length-weight information did not exist for a given species, the parameters from similar bodied congeners were used (McClanahan & Kaunda-Arara 1996, Friedlander and Parrish 1997).

From 1998 to 2001 a total of 513 timed swims were carried out in the reserve (204 counts) and adjacent fished sites (pulse fished site 166 counts, continually fished site 143 counts). Sampling was restricted to the winter months because of high surf and

resultant low underwater visibility during summer months. Twenty-three target species (commonly harvested by fishers) and 3 relatively large non-target species were surveyed (Table 3.1). Non-target species were surveyed to evaluate the assumption that fishing is primarily responsible for differences in fish abundance and size between reserve and fished sites (e.g., Tissot & Hallacher, 1999). The major predictions of this assumption are that abundance and size of non-target species should not differ between reserve and fished sites.

Numerical abundance was transformed to biomass for statistical analyses in order to minimize the impact of new year class recruits (that are not directly affected by fishing) on results (Grigg 1994, Russ & Alcala 1998a). Fish biomass data were log transformed and analyzed using a two-way analysis of variance without replication (Sokal & Rohlf 1995). Factors included management regime ("site") and reef habitat zone ("habitat"). A similar protocol was used to analyze fish size data. In cases where a species was present in all habitat zones of all sites (N=8), two way ANOVAs were carried out on fish size data. In cases where species were not observed in all habitat zones in all three sites (N=18), size data were analyzed using successive one-way ANOVAs with site and habitat zone as the independent factors.

The overall relative magnitude and direction of differences in abundance and size between reserve and fished sites were calculated using a simple percentage difference formula (Rakitin & Kramer 1996, Tissot & Hallacher 1999).

1. Percent difference = $((B_{impact}-B_{control})/B_{control})*100$
2. Percent difference = $((S_{impact}-S_{control})/S_{control})*100$

Where B = biomass expressed as grams per 15 minute count, and S = overall mean size (total length in mm). Thus, a negative percent difference would indicate lower biomass (or size) at the fished site relative to the reserve, whereas a positive value would indicate the opposite pattern.

Results

Twenty-three fishery species and 3 non-fishery species from 7 reef fish families were censused during the study (Table 3.1). The species monitored included representatives from a wide range of feeding guilds, but overall fish biomass was dominated by herbivores (67%) and carnivores (31%)(Table 3.2). Several clear trends in fish abundance were common to each of the sites surveyed. The total biomass of each trophic level and family surveyed was dominated by a few (1-3) species. For example, *N. unicornis* accounted for 52-71% of overall mean acanthurid biomass and 40-52% of overall mean herbivore biomass in each of the three zones, and *M. vanicolensis* accounted for 42-81% of overall mean goatfish biomass (Table 3.2).

The overall mean biomass of most (22 out of 26) species surveyed was lower in the fished sites than in the reserve (Table 3.3), and lower in the permanently fished site than in the pulse-fished site (16 out of 26 species); however, only 11 species (42%) showed a significant (ANOVA, $P<0.05$) effect of site on mean biomass, and this included

1 of the non-fishery species (Table 3.3). Mean biomass of these 11 species was significantly lower in the fished sites than in the reserve. Most (24 out of 26) species showed a significant effect of habitat zone on mean biomass, and 14 out of 26 species showed a significant site x habitat zone interaction (Table 3.3).

The spatial distribution of fish biomass at Waikīkī was closely associated with spatial variation in habitat complexity. Biomass of all families surveyed was consistently higher in the high rugosity reef crest habitat zones of both reserve and fished areas than in three other, lower rugosity habitat zones (back reef, reef flat and fore reef) (Figures 3.1-3.5). Mean biomass of target families (Acanthuridae, Carangidae, Mullidae, Scaridae) was higher in the reserve reef crest than in fished reef crest, but mean biomass of non-target balistids was similar in the reef crest habitats of reserve and fished areas. The distribution of fish biomass among the back reef, reef flat and fore reef habitat zones varied both between families and between reserve and fished areas. For example, acanthurid and scarid biomass was higher in reserve back reef and reef flat habitat zones, than in the corresponding fished habitat zones, but this pattern was not observed in the balistids, carangids and mullids. Target family biomass was higher in the fore reef habitat of the fished area than in the reserve fore reef, but non-target balistid biomass was similar in the fore reef habitats of reserve and fished areas.

Overall mean size of most (21 out of 26) species surveyed was smaller in the pulse-fished site than in the reserve, but only half (13 out of 25) of the species surveyed had smaller mean sizes in the permanently fished site than in the reserve (Table 3.4 &

3.5). All 3 non-fishery species surveyed were smaller in the pulse fished site than the reserve, but only 1 non-fishery species was smaller in the permanently fished site than the reserve (Table 3.4 & 3.5). Most species surveyed (20 out of 26) showed a significant (ANOVA, $P<0.05$) effect of site on mean size, and this included all 3 non-fishery species (Table 3.5). Most (21 out of 26) species also showed a significant effect of habitat zone on mean size, and in all 8 cases where a two-way ANOVA was possible, a significant site x habitat zone interaction was detected (Table 3.5).

Discussion

There was a general trend of greater fish abundance (biomass) and size inside the Waikīkī reserve than in adjacent fished areas, and 40% of the fish species surveyed at Waikīkī were significantly larger and more abundant in the reserve than in the adjacent fished sites. However, an assumption that these differences are entirely due to fishing is invalid because size and abundance of 2 of the 4 non-fishery species was also significantly higher in the reserve than in adjacent fished sites (Tables 3.2 & 3.3). A strong association between habitat complexity and fish biomass (and size) appears to be the dominant factor determining fish distribution patterns at Waikīkī. This does not rule out a 'reserve effect' on fish abundance and size, but rather suggests that the demonstration of any such effect is confounded by the presence of 'better' habitat inside the Waikīkī reserve than in adjacent fished areas. Thus, although the data support a general hypothesis of greater fish abundance and size inside the Waikīkī reserve, it is not possible to unequivocally attribute this to a reserve effect.

Other comparable studies of reserve effectiveness in coral reef habitats have also found higher fish abundance, biomass and size in protected than fished areas (McClanahan & Shafir 1990, Polunin & Roberts 1993, McClanahan & Kaunda-Arara 1996, Rakitin & Kramer 1996, Russ 2002), and a recent broad review of 89 studies of marine reserve effectiveness, from a wide geographic range, found that the majority (>80%) concluded that creation of marine reserves resulted in greater fish abundance and/or size inside reserves (Halpern in press). Both the present study and most of these previous studies lacked baseline data from before reserve establishment, and simply compared established reserves with separate fished areas (Roberts & Polunin 1991, Roberts 1993, Russ & Alcala 1996a, Russ 2002, Halpern in press). The major problem with this sampling design is that differences in fish abundance and size between reserve and fished areas may have existed before reserve establishment because of intrinsic differences between sites (Roberts & Polunin 1991, Roberts 1993, Roberts 1995, Jennings et al. 1995, Rakitin & Kramer 1996, Russ & Alcala 1996a, Edgar & Barret 1997, Chiappone & Sullivan Sealey 2000, Russ 2002).

Differences in habitat complexity between reserve and fished areas are of particular concern because of the strong positive correlation between habitat complexity and reef fish abundance (Roberts & Ormond 1987, Grigg 1994, McClanahan 1994, Roberts 1995, Rakitin & Kramer 1996, Friedlander & Parrish 1998a, Sarramegna 2000). Several recent studies involving purely spatial comparisons of reserve effectiveness have attempted to control for habitat differences among sites. Methods employed typically involve comparison of control and impact sites based on qualitative or quantitative

evaluations of habitat characteristics. These include simple habitat descriptions (Russ & Alcala 1989, 1996b), visual classification of habitat complexity using arbitrary point scales (Sluka et al. 1994, 1996, 1997, Polunin & Roberts 1993) and empirical measurements of rugosity and benthic community composition (McClanahan & Shafir 1990, Rakitin 1994). However, no two natural areas are truly identical, and a combination of sample size and the resolution with which habitat characteristics are measured will ultimately determine the outcome of any statistical analyses performed (Edgar & Barret 1997). A finding of 'no significant difference' in habitat characteristics between control and impact sites (e.g., Polunin & Roberts 1993, Rakitin 1994) could be viewed as a 'type II' error in which measurement resolution was too coarse, or sample size too small, to detect differences (Edgar & Barret 1997).

Despite the problem of intrinsic variation between control and impact sites, some authors argue that the sheer number of 'positive' results from geographically varied locations indicates that marine reserves are effective in increasing fish abundance and size within their boundaries (Roberts and Polunin 1991, Halpern in press). The main problem with this argument is that many existing reserves may have been sited in locations of aesthetic appeal containing exceptional areas of habitat and naturally high fish abundance (Roberts 1993, 2000, Woodley 1985, Kenchington 1988). Consequently, the high proportion of positive results may reflect human preferences for aesthetically appealing reserve sites rather than widespread reserve effectiveness.

Inherent natural variability in reef topography probably makes it impossible to unequivocally demonstrate reserve effectiveness using purely spatial comparisons. A better approach would be to use a more robust 'BACI' study design (Before/After Control/Impact; Stewart-Oaten et al. 1986, Underwood 1993, Edgar & Barret 1997, Tissot & Hallacher 1999, Russ 2002, Halpern in press) that incorporates reserve and fished sites that are sampled both before and after reserve establishment. The important test with this design is not whether a variable (e.g., mean biomass) is greater inside or outside marine reserves, but how the variable changes with time within the reserve relative to outside (Edgar & Barret 1997). To date studies of reserve effectiveness that incorporate a BACI design are relatively rare (Roberts 1995, Russ & Alcala 1996a, Russ 2002, Halpern in press) and have produced mixed results. BACI studies have variously found that target species abundance: (1) increased only inside reserves (Russ & Alcala 1989, 1996a, Bohnsack 1990, Wantiez et al. 1997), (2) increased in both reserve and fished areas (Roberts et al. 2001), (3) increased only in fished areas (Russ & Alcala 1989), and (4) did not change significantly (Russ & Alcala 1989, Wantiez et al. 1997). Wantiez et al. (1997) also showed that abundance of some non-target species increased significantly in reserves. Variability in BACI study results probably reflects the complex interactions between the variables of reserve design (location, size, habitat content), target species ecology (habitat preferences, movement patterns, growth, recruitment) and fishing activities (method, intensity, location) around reserves.

In reserves that are too small to contain daily movements of resident individuals, target species abundance inside the reserve may be directly influenced by the fishing

activities occurring outside the reserve. When fishing effort is relatively low outside the reserve boundaries, reserve residents have a low probability of capture even when regularly crossing into fished areas. Conversely, if fishing effort is high outside the reserve, reserve residents crossing into fished areas have a high probability of capture, and differences in abundance of target species between reserve and fished areas may be diminished or absent. It is hard to assess how vulnerable existing small and apparently 'effective' reserves may be to increasing fishing effort in surrounding areas, because there have been relatively few empirical studies of the daily movements of target species, and empirical data on fishing activities around reserves are also scarce (Halpern in press). Both the present study and the widely cited studies of Apo Island (Philippines; Russ & Alcala 1989 et seq.) feature reserves that are small (0.34 and 0.11 km^2 respectively) and contain habitat that is more structurally complex than adjacent fished areas. Fish movement data from Waikīkī clearly demonstrate that some 'resident' target species cross from the reserve into fished areas on a daily basis (Chapter 2). If daily fish movements of the same magnitude occur at Apo Island, then fish from the Apo reserve must also move into fished areas on a daily basis. Yet at both Waikīkī and Apo Island, fish biomass is generally higher inside reserves than in adjacent fished areas, despite daily boundary crossing by reserve residents. Greater habitat complexity inside reserves cannot entirely explain how these small reserves maintain a higher biomass of vagile species that roam frequently and extensively into fished areas. One simple explanation might be that this is a result of relatively low fishing mortality in the areas adjacent to the reserves. This seems unlikely at Apo Island where the non-reserve area is fished by up to 200 municipal fishers using traditional fishing gear (bamboo traps, hooks and lines, gill

nets and spears), and fishing is estimated to remove 25% of total fish biomass annually (Russ & Alcala 1996b, 1998). Alternatively, there may be more complex explanations, such as that protecting core areas of complex habitat within a larger home range buffers fish against high fishing effort. The influence of fishing activities on the patterns of fish abundance at Waikīkī will be addressed in the following chapter.

Table 3.1. List of fishes counted at Waikīkī. Information on diet and trophic level is derived from Randall (1985, 1996).

FAMILY & SPECIES	TROPHIC LEVEL	DIET
Acanthuridae		
Acanthurus achilles	Herbivore	Filamentous algae
Acanthurus blochii	Herbivore	Diatoms, detritus
Acanthurus dussumieri	Herbivore	Diatoms, algae, detritus
Acanthurus leucopareius	Herbivore	Filamentous algae
Acanthurus triostegus	Herbivore	Filamentous algae
Acanthurus xanthopterus	Herbivore	Diatoms, detritus
Ctenochaetus strigosus	Detritivore	Detritus
Naso lituratus	Herbivore	Coarse leafy macroalgae
Naso unicornis	Herbivore	Coarse leafy macroalgae
Carangidae		
Caranx melampygus	Carnivore	Fishes and mobile invertebrates
Mullidae		
Mulloidichthys flavolineatus	Carnivore	Mobile invertebrates and fishes
Mulloidichthys vanicolensis	Carnivore	Mobile invertebrates and fishes
Parupeneus bifasciatus	Carnivore	Mobile invertebrates and fishes
Parupeneus cyclostomus	Carnivore	Fishes and mobile invertebrates
Parupeneus multifasciatus	Carnivore	Mobile invertebrates and fishes
Parupeneus pleurostigma	Carnivore	Mobile invertebrates and fishes
Parupeneus porphyreus	Carnivore	Mobile invertebrates and fishes
Scaridae		
Calotomus carolinus	Herbivore	Benthic algae
Chlorurus perspicillatus	Herbivore	Benthic algae and live coral
Chlorurus sordidus	Herbivore	Benthic algae
Scarus psittacus	Herbivore	Benthic algae
Scarus rubroviolaceus	Herbivore	Benthic algae
Kyphosidae		
Kyphosus bigibbus	Herbivore	Benthic algae
Balistidae		
*Melichthys niger**	Herbivore	Algae and zooplankton
*Rhinecanthus rectangulus**	Omnivore	Algae, detritus and invertebrates
Zanclidae		
*Zanclus cornutus**	Omnivore	Sponges and algae

*Non-fishery species

Table 3.2. Mean overall biomass (g per 15-min count) of target and non-target species in reserve and fished areas. Biomass values are averaged across reef zones.

Family & Species	Mean (SE) Biomass (g 15-min count)					
	Reserve		Pulse Fished		Fished	
Acanthuridae						
Acanthurus achilles	106	(26)	286	(67)	180	(82)
Acanthurus blochii	640	(159)	372	(153)	268	(155)
Acanthurus dussumieri	140	(59)	241	(89)	6	(5)
Acanthurus leucopareius	995	(432)	733	(293)	22	(14)
Acanthurus triostegus	3772	(605)	1723	(403)	846	(173)
Acanthurus xanthopterus	509	(321)	364	(281)	0	(0)
Ctenochaetus strigosus	174	(36)	146	(45)	14	(8)
Naso lituratus	2913	(345)	871	(176)	666	(137)
Naso unicornis	22749	(2751)	5140	(1466)	3574	(877)
Carangidae						
Caranx melampygus	4405	(2356)	81	(22)	141	(57)
Mullidae						
Mulloidichthys flavolineatus	1899	(344)	1463	(234)	2221	(696)
Mulloidichthys vanicolensis	12578	(3091)	3997	(999)	2247	(796)
Parupeneus bifasciatus	31	(18)	9	(3)	0	(0)
Parupeneus cyclostomus	53	(38)	9	(5)	10	(9)
Parupeneus multifasciatus	797	(60)	618	(62)	720	(116)
Parupeneus pleurostigma	7	(4)	10	(7)	3	(3)
Parupeneus porphyreus	128	(27)	24	(10)	138	(44)
Scaridae						
Calotomus carolinus	1534	(268)	208	(48)	665	(198)
Chlorurus perspicillatus	535	(190)	346	(140)	169	(61)
Chlorurus sordidus	819	(197)	275	(74)	152	(60)
Scarus psittacus	2314	(491)	398	(75)	319	(68)
Scarus rubroviolaceus	3047	(518)	1150	(335)	276	(66)
Kyphosidae						
Kyphosus bigibbus	3066	(1454)	503	(223)	555	(268)
Balistidae						
Melichthys niger	1226	(239)	1230	(289)	953	(241)
Rhinecanthus rectangulus	1073	(95)	843	(83)	947	(142)
Zanclidae						
Zanclus cornutus	266	(30)	221	(23)	511	(75)

Table 3.3. Percent difference between mean overall biomass of reserve and fished areas. A negative percent difference indicates lower biomass at fished sites relative to the reserve area. P-values are reported for a two-way ANOVA analysis of biomass data.

Family & Species	Percent Difference from Reserve Mean		ANOVA P-Values		
	Pulse Fished	Fished	Site	Habitat	S * H
Acanthuridae					
Acanthurus achilles	171	70	0.15	<0.01*	<0.01*
Acanthurus blochii	-42	-58	0.16	<0.01*	0.21
Acanthurus dussumieri	72	-96	0.26	<0.01*	0.56
Acanthurus leucopareius	-26	-98	<0.01*	0.01*	0.19
Acanthurus triostegus	-54	-78	<0.01*	<0.01*	<0.01*
Acanthurus xanthopterus	-29	-100	0.07	0.03*	0.02
Ctenochaetus strigosus	-16	-92	0.28	0.03*	<0.01*
Naso lituratus	-70	-77	<0.01*	<0.01*	<0.01*
Naso unicornis	-77	-84	<0.01*	<0.01*	<0.01*
Carangidae					
Caranx melampygus	-98	-97	0.28	<0.01*	0.60
Mullidae					
Mulloidichthys flavolineatus	-23	17	0.02*	<0.01*	0.15
Mulloidichthys vanicolensis	-68	-82	0.36	<0.01*	0.03*
Parupeneus bifasciatus	-70	-100	0.08	<0.01*	0.22
Parupeneus cyclostomus	-83	-81	0.95	0.56	0.63
Parupeneus multifasciatus	-22	-10	0.03*	<0.01*	<0.01*
Parupeneus pleurostigma	43	-52	<0.01*	<0.01*	<0.01*
Parupeneus porphyreus	-81	8	0.12	0.56	0.37
Scaridae					
Calotomus carolinus	-86	-57	<0.01*	<0.01*	<0.01*
Chlorurus perspicillatus	-35	-68	0.58	<0.01*	0.21
Chlorurus sordidus	-66	-81	0.07	<0.01*	<0.01*
Scarus psittacus	-83	-86	<0.01*	<0.01*	0.06
Scarus rubroviolaceus	-62	-91	0.16	<0.01*	<0.01*
Kyphosidae					
Kyphosus bigibbus	-84	-82	<0.01*	<0.01*	<0.01*
Balistidae					
Melichthys niger	0	-22	0.320	<0.01*	0.18
Rhinecanthus rectangulus	-21	-12	<0.01*	<0.01*	<0.01*
Zanclidae					
Zanclus cornutus	-17	92	0.420	<0.01*	<0.01*

*P<0.05

Table 3.4. Mean overall size (total length in mm) of target and non-target species in reserve and fished areas. Values in parentheses are 1 standard error of the mean.

Family & Species	Mean Size (mm)		
	Reserve	Pulse Fished	Fished
Acanthuridae			
Acanthurus achilles	138 (4)	138 (2)	170 (5)
Acanthurus blochii	216 (4)	243 (7)	262 (5)
Acanthurus dussumieri	203 (11)	189 (6)	218 (13)
Acanthurus leucopareius	190 (3)	167 (2)	155 (15)
Acanthurus triostegus	122 (0)	129 (1)	115 (1)
Acanthurus xanthopterus	218 (6)	197 (3)	- -
Ctenochaetus strigosus	136 (3)	134 (2)	135 (8)
Naso lituratus	191 (2)	164 (4)	196 (4)
Naso unicornis	223 (1)	204 (3)	194 (2)
Carangidae			
Caranx melampygus	354 (7)	148 (7)	185 (6)
Mullidae			
Mulloidichthys flavolineatus	199 (1)	193 (2)	225 (3)
Mulloidichthys vanicolensis	205 (1)	178 (1)	166 (2)
Parupeneus bifasciatus	143 (16)	115 (10)	80 -
Parupeneus cyclostomus	242 (20)	122 (19)	255 (75)
Parupeneus multifasciatus	153 (2)	115 (2)	158 (3)
Parupeneus pleurostigma	144 (11)	87 (2)	205 (25)
Parupeneus porphyreus	187 (6)	168 (10)	191 (12)
Scaridae			
Calotomus carolinus	212 (6)	209 (11)	128 (9)
Chlorurus perspicillatus	252 (17)	301 (23)	70 (2)
Chlorurus sordidus	189 (11)	144 (7)	171 (7)
Scarus psittacus	116 (3)	77 (2)	63 (2)
Scarus rubroviolaceus	295 (9)	220 (13)	105 (5)
Kyphosidae			
Kyphosus bigibbus	201 (3)	205 (6)	220 (5)
Balistidae			
Melichthys niger	244 (4)	228 (4)	197 (4)
Rhinecanthus rectangulus	192 (2)	182 (3)	202 (3)
Zanclidae			
Zanclus cornutus	117 (2)	109 (2)	157 (3)

Table 3.5. Percent difference between mean overall fish size at reserve and fished areas. A negative percent difference indicates smaller size at fished sites relative to the control area. P-values are reported for a two-way ANOVA analysis of size data.

Family & Species	Percent Difference from Reserve Mean		ANOVA P-Values		
	Pulse Fished	Fished	Site	Habitat	S * H
Acanthuridae					
Acanthurus achilles	0	23	<0.01*	<0.01*	N/A
Acanthurus blochii	13	22	<0.01*	<0.01*	N/A
Acanthurus dussumieri	-7	7	0.396	0.105	N/A
Acanthurus leucopareius	-12	-18	<0.01*	<0.01*	N/A
Acanthurus triostegus	5	-6	<0.01*	<0.01*	<0.01*
Acanthurus xanthopterus	-9	NA	<0.01*	<0.01*	<0.01*
Ctenochaetus strigosus	-2	-1	0.834	0.059	N/A
Naso lituratus	-14	3	<0.01*	<0.01*	<0.01*
Naso unicornis	-9	-13	<0.01*	<0.01*	<0.01*
Carangidae					
Caranx melampygus	-58	-48	<0.01*	<0.01*	N/A
Mullidae					
Mulloidichthys flavolineatus	-3	13	0.037	<0.01*	<0.01*
Mulloidichthys vanicolensis	-13	-19	<0.01*	<0.01*	N/A
Parupeneus bifasciatus	-19	-44	0.313	0.20	N/A
Parupeneus cyclostomus	-49	5	<0.01*	0.128	N/A
Parupeneus multifasciatus	-25	4	<0.01*	<0.01*	<0.01*
Parupeneus pleurostigma	-40	42	<0.01*	<0.01*	N/A
Parupeneus porphyreus	-10	2	0.402	0.616	N/A
Scaridae					
Calotomus carolinus	-2	-39	<0.01*	<0.01*	N/A
Chlorurus perspicillatus	19	-72	<0.01*	<0.01*	N/A
Chlorurus sordidus	-24	-10	<0.01*	<0.01*	N/A
Scarus psittacus	-34	-46	<0.01*	<0.01*	<0.01*
Scarus rubroviolaceus	-26	-64	<0.01*	<0.01*	N/A
Kyphosidae					
Kyphosus bigibbus	2	9	0.039	<0.01*	N/A
Balistidae					
Melichthys niger	-7	-19	<0.01*	<0.01*	N/A
Rhinecanthus rectangulus	-5	6	<0.01*	<0.01*	<0.01*
Zanclidae					
Zanclus cornutus	-6	34	<0.01*	<0.01*	N/A

*P<0.05

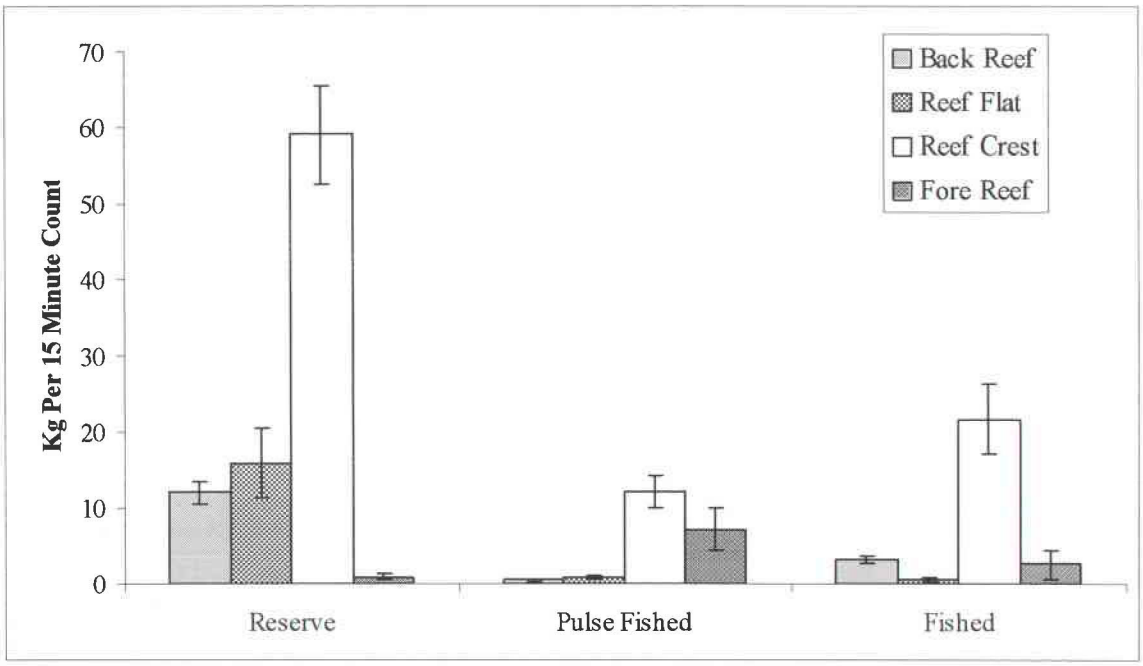

Figure 3.1. Distribution of mean acanthurid biomass (kg per 15-min count) among reef habitat zones in reserve and fished areas. Error bars are +/- 1 standard error of the mean.

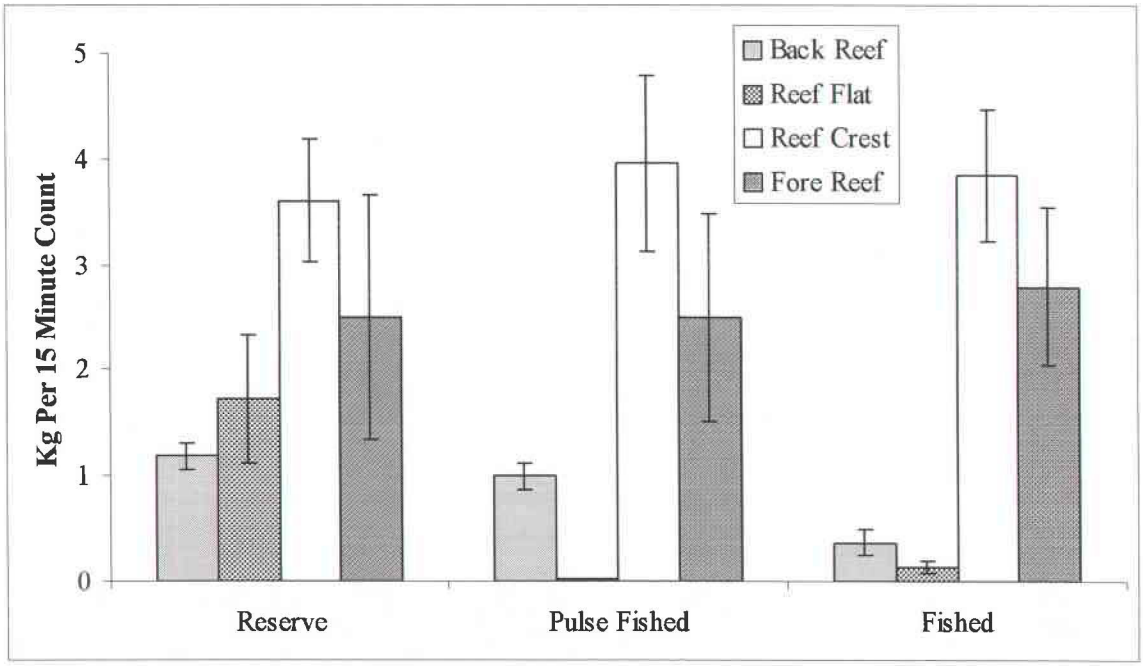

Figure 3.2. Distribution of mean balistid biomass (kg per 15-min count) among reef habitat zones in reserve and fished areas. Error bars are +/- 1 standard error of the mean.

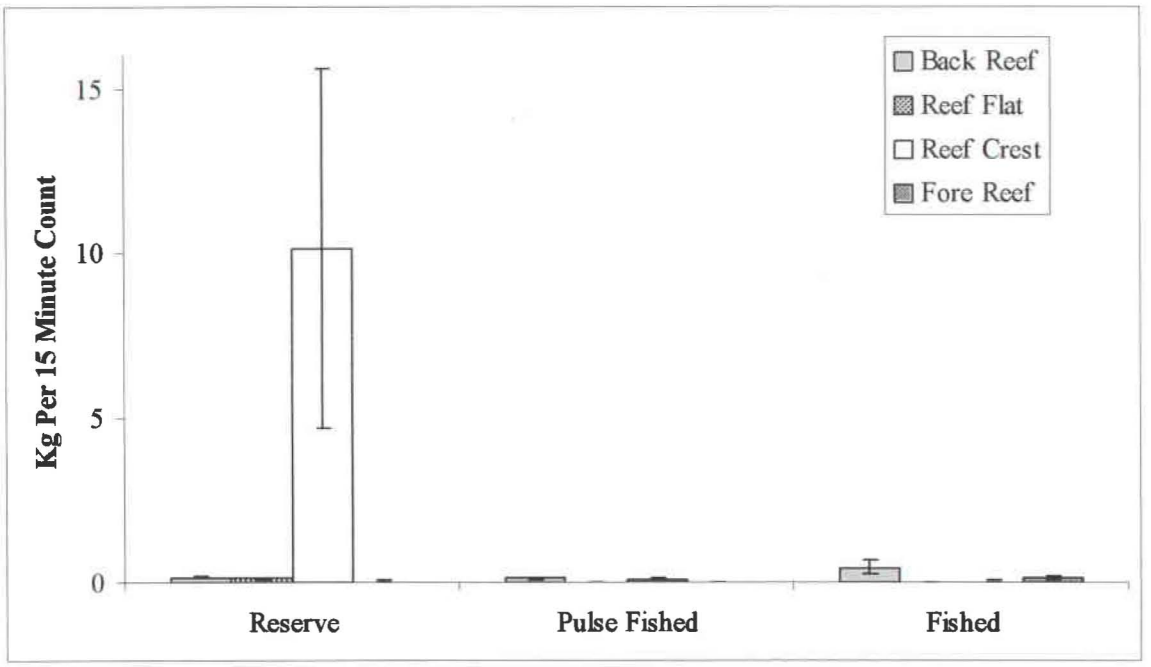

Figure 3.3. Distribution of mean carangid biomass (kg per 15-min count) among reef habitat zones in reserve and fished areas. Error bars are +/- 1 standard error of the mean.

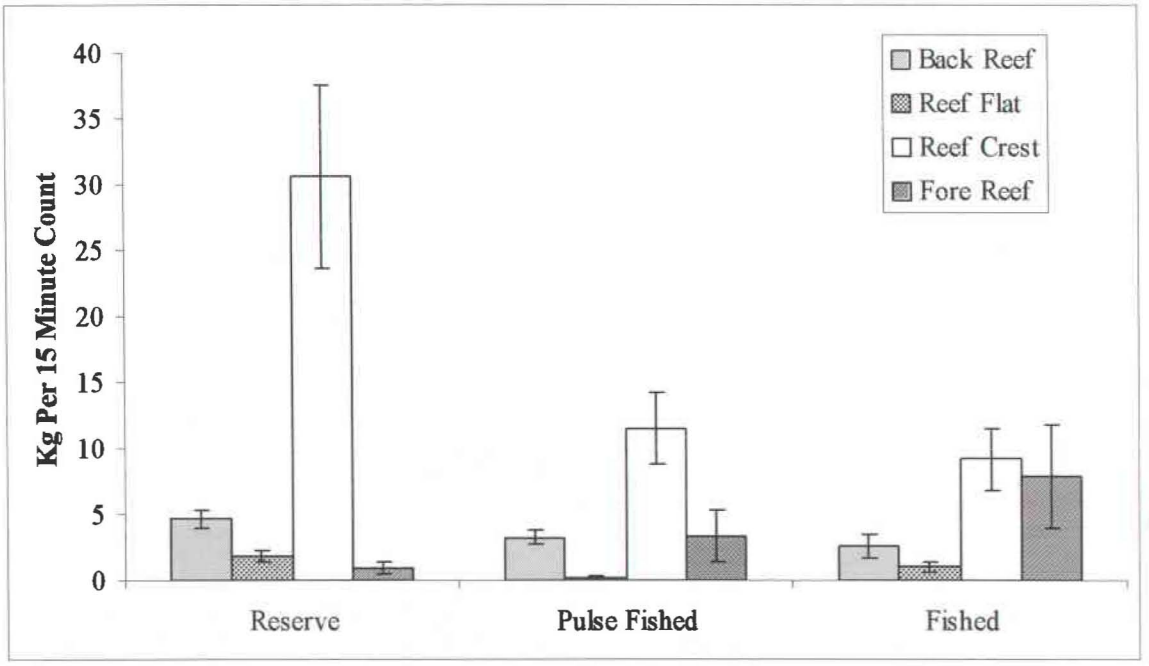

Figure 3.4. Distribution of mean mullid biomass (kg per 15-min count) among reef habitat zones in reserve and fished areas. Error bars are +/- 1 standard error of the mean.

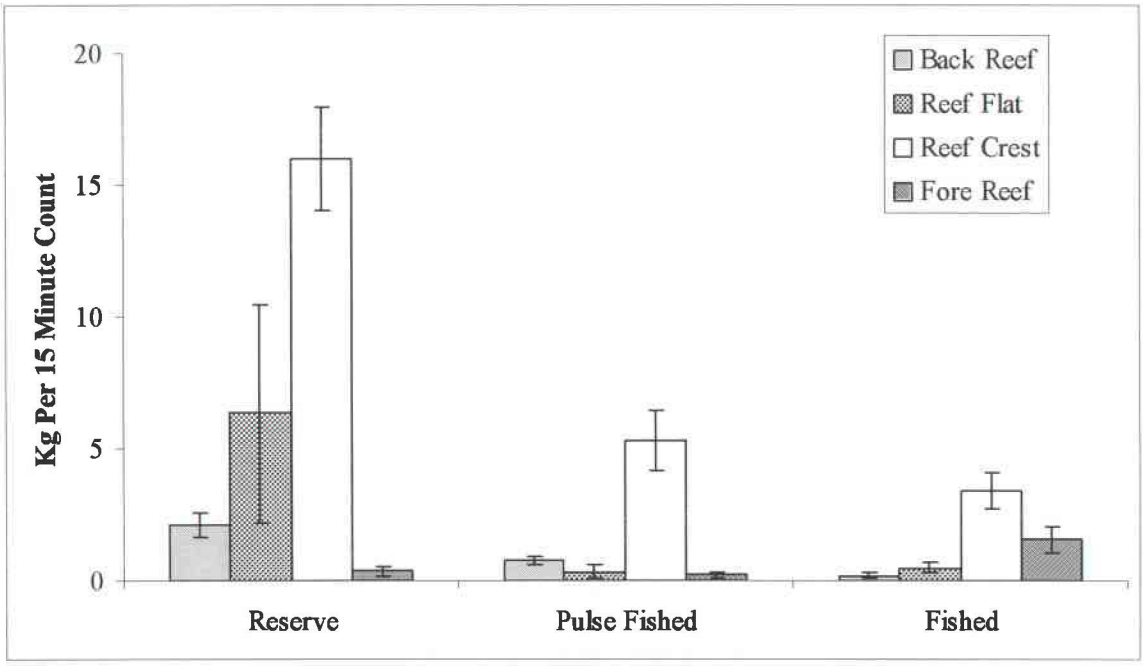

Figure 3.5. Distribution of mean scarid biomass (kg per 15-min count) among reef habitat zones in reserve and fished areas. Error bars are +/- 1 standard error of the mean.

CHAPTER 4

THE IMPACT OF FISHING ON RESERVE FUNCTION

Introduction

The anticipated benefits of marine reserves are contingent on providing marine organisms with an effective refuge from fishing. An effective refuge from fishing requires compliance with reserve 'no-fishing' regulations, yet fishing activities are rarely quantified in studies of reserve effectiveness (Russ 2002). Most authors implicitly assume that greater target species abundance or size within reserve boundaries indicates that no significant fishing is occurring inside that reserve (Russ 2002). This assumption is invalid because greater target species abundance or size could still occur in illegally fished reserves if they contain more complex habitat than legally fished areas (Roberts & Ormond 1987, Grigg 1994, McClanahan 1994, Roberts 1995, Rakitin & Kramer 1996, Friedlander & Parrish 1998a, Sarramegna 2000).

Fishing activity outside the boundaries of unfished reserves could also influence target species abundance and size in a variety of ways (Rakitin & Kramer 1996). High fishing mortality outside reserve boundaries should cause large, easily detectable differences in abundance and size between these outside fished areas and well protected areas inside (Chiappone & Sullivan Sealey 2000). Low fishing mortality outside reserve boundaries might not cause any detectable differences between reserve and fished areas, but could allow existing, intrinsic differences to persist. In situations where reserves are too small to contain daily movements of target species, fishing outside reserve boundaries

could directly impact target species size and abundance inside the reserve. Under these circumstances, high fishing mortality outside reserve boundaries might reduce target species abundance in both reserve and fished areas because reserve residents are frequently captured during their daily excursions into fished areas. Low fishing mortality outside small reserves might allow existing patterns of abundance and size to persist despite daily movements of reserve residents across boundaries into fished areas. It is the interactions between intrinsic natural patterns of fish abundance and size, recruitment, reserve design (size & habitat content), and fishing activities that produce patterns of abundance and size observed in and around marine reserves. Greater target species abundance or size in reserves is not in itself unequivocal proof of a 'reserve effect' (Russ 2002). Empirical data on fishing activities in and around marine reserves may be important for interpreting spatial patterns of target species abundance observed during reserve studies.

Target species abundance and size were generally greater inside the Waikīkī reserve than in adjacent fished areas (Chapter 3), despite daily excursions by reserve residents across boundaries into fished areas (Chapter 2). A similar spatial distribution of abundance and size was also evident in non-target species, suggesting that better habitat inside the reserve was at least partly responsible for the patterns observed (Chapter 3). The presence of more complex habitat inside the reserve than in adjacent fished areas confounds demonstration of any 'reserve effect' using only spatial comparisons of fish abundance and size. Quantifying the type, location and impact of fishing activities at

Waikīkī may help to determine whether a reserve effect is contributing to the observed spatial distribution of fish abundance and size.

The small size of the existing Waikīkī reserve may preclude effective protection for some more mobile species because they frequently cross from the reserve into fished areas (Chapter 2); however, a *de facto* reserve effect (Bohnsack 1996) may occur if compliance with existing reserve regulations is combined with low fishing mortality in fished areas used by mobile reserve residents during their daily migrations. Alternatively, fishing mortality may be generally low at Waikīkī and the observed distribution of fishes may simply reflect intrinsic variation in habitat complexity. Actual fishing mortality (F) is difficult to quantify because natural and fishing mortality are effectively inseparable without knowledge of population structure (Jennings & Lock 1996, Russ 2002). Other parameters, such as fishing effort (E), are easier to quantify, and may serve as an indirect measure of fishing mortality under the assumption that F increases with increasing E (Russ 2002). The present study addressed three major questions about fishing activities at Waikīkī; 1. Does 'significant' illegal fishing occur inside Waikīkī reserve? 2. Do current patterns of fishing activity at Waikīkī create a *de facto* extension of the official reserve? 3. Are yield and exploitation rates at Waikīkī high or low? The first question assumes that a reserve effect requires fishing mortality inside the reserve to be at least significantly lower than in adjacent fished areas, if not zero (Russ 2002). The substitution of fishing effort for fishing mortality allows the following hypotheses to be tested;

H_0 = No difference in fishing effort between reserve and fished area

H_1 = More fishing effort occurs in fished areas than reserve

H_2 = More fishing effort occurs in reserve than fished areas

The second question assumes that low fishing mortality in the fished areas immediately adjacent to the official reserve effectively increases reserve size. This allows the following reserve size hypotheses to be tested;

H_0 = No difference between effective and official reserve areas

H_1 = Effective reserve area > official reserve area

H_2 = Effective reserve area < official reserve area

The third question assumes that the annual yield (t km^{-2}) and exploitation rate (annual % of standing stock captured) of reef fishes at Waikīkī provide an indirect measure of fishing mortality that can be compared with published yield data from other coral reef fisheries to determine whether F at Waikīkī is relatively high or low. The following yield hypotheses are tested;

H_0 = No difference between annual yield at Waikīkī and annual yield in other comparable fisheries

H_1 = Annual Waikīkī catch < average annual reef fish catch in other comparable fisheries

H_2 = Annual Waikīkī catch > average annual reef fish catch in other comparable fisheries

Methods

Fishing Activity Patterns

Fishing activities at Waikīkī were quantified using a roving creel survey methodology (Malvestuto et al. 1978, Everson, 1994). The study site shoreline was patrolled at 2 h intervals and the number, location and type of fishing activities observed within 455m (500yds) of the high water mark were recorded. The seaward boundary applied to shoreline surveys was equivalent to the official seaward boundaries of both reserve and pulse fished areas. Habitat for several hundred meters beyond this seaward boundary was primarily sand and flat reef, and supplementary observations indicated that very few fishing activities occurred in this area. A total of 460 shoreline patrols were carried out between June 1998 and August 2001. Sampling was stratified to include data from summer, winter, all days of the week, and throughout the diel cycle.

Catch

Two methods were used to quantify catch and effort at Waikīkī: (1) Catches observed during shoreline patrols were recorded, and (2) In situ interviews were conducted with fishers to obtain specific details of catch and fishing effort. Catches were inspected whenever possible and captured organisms were identified to the lowest possible taxa. The total lengths of any fish captured were estimated to the nearest 5 cm. Interviewed fishers were asked how long they had been fishing, what they had caught, and the type and amount of fishing gear that they were using. Interviews were carried out opportunistically during regular shoreline patrols. Additional catch and effort data were collected on the first day of open season for the pulse-fished area. Opening day attracted

relatively large numbers of fishers and provided an opportunity to collect a large amount of synoptic catch and effort data. Observers were placed at all major points of entry and exit to pulse fished area from dawn onward on opening days. All spear fishers were intercepted and interviewed as they exited the water, and pole fishers were interviewed when they ceased fishing.

Data analyses

Fishing activity counts were transformed to densities (number km^{-2}) in order to allow direct comparison between fished and reserve areas of different sizes. Fishing activity data were log transformed and analyzed using a multifactorial General Linear Model (Sokal & Rohlf 1995). Factors included gear type (pole & line, spear and other gears), area (permanently fished, pulse fished and reserve), time of day (day or night), type of day (weekend or weekday), season (summer or winter) and the status of the pulse-fished area (open or closed). Interactions between area, gear type and the other factors were also included in the model. The effects of individual factors on mean densities of fishing activities were evaluated using partial ANOVAs with post hoc Bonferroni pairwise comparison of means. χ^2 analyses were used to evaluate associations between the frequency of gear type use and area, and between the frequency of illegal fishing in the reserve and the status of the pulse-fished area.

χ^2 analyses were used to test the significance of associations between the frequency of reef fish families in catches and the gear type used. The size frequencies of

spear and pole & line catches were compared using a Kolmogorov Smirnov two sample test. The effect of gear type on mean size of fishes captured was tested using an ANOVA with post hoc Bonferroni comparison of means. Length estimates of fishes from creel censuses were converted to weight using methods described in Chapter 3.

Two different methods were used to calculate Catch Per Unit Effort (CPUE) of pole & line and spear fishing. The first ($CPUE_1$) was a conventional method where the total catch from each individual fishing 'trip' was divided by the total time spent fishing, to give units of either 'number h^{-1}' or 'kg h^{-1}'. A pole & line fishing trip was defined as the total time elapsed between first deployment and last retrieval of the fishing line, with effort adjusted for the number of lines deployed simultaneously by each fisher. A spear fishing trip was defined as the total time elapsed between entry and exit from the water. The second ($CPUE_2$) was an alternative method where the catch in each sampling stratum (i.e., survey time + area + gear type) was divided by the total number of activities observed in that stratum, to give 'number caught $activity^{-1}$'. This second method assumed that total fishing effort expended is directly proportional to the number of activities observed.

The annual catch (tonnes) and yield (catch adjusted for area; t km^{-2}) of reef fishes at Waikīkī was estimated using simple extrapolation of survey catch data. The fraction of each year that was sampled during creel surveys was calculated. The total catch that was observed during creel surveys each year was then multiplied by the reciprocal of the fraction of time observed in that year. A correction was applied to catches from the pulse

fished area to account for the pronounced effort (and catch) spike observed on the biennial opening day. This correction factor was derived by averaging the opening day catches across open and closed years, and applying the mean 'January 1' catch to the annual catch derived from shoreline patrol data.

Results

Fishing Activity Patterns

Pole & line and spear were the dominant gear types used at Waikīkī, collectively accounting for 94-98% of all fishing activities observed in each area (Table 4.1, Figure 4.1). Six other gear types were observed during surveys but were an order of magnitude less common, collectively accounting for less than 5% of fishing activities observed (Table 4.1, Figure 4.1). The mean density of fishing activities (number km^{-2}) at Waikīkī varied significantly between gear types (pole & line, spear and other gears), areas (permanently fished, pulse fished and reserve), the time of day (day or night), the type of day (weekend or weekday), and according to the status of the pulse fished area (open or closed) (Table 4.2). There was no significant effect of season (summer or winter) on mean density of combined fishing activities (Table 4.2). Significant interactions between factors (e.g., area x gear type, gear type x time of day; Table 4.2) resulted from differences in fishing activity patterns between areas and gear types at Waikīkī.

The mean density (number km^{-2}) of pole & line fishing activities was significantly higher overall than mean density of spear fishing activities (Table 4.3), but the number of

fishing activities accounted for by each gear type differed significantly among areas (χ^2 = 579.6, d.f. 4, P<0.001). Pole and line fishing dominated activities in the permanently fished area, whereas activities in the reserve and pulse fished area were more evenly divided between pole & line and spear fishing (Table 4.1, Figure 4.1). The mean densities of pole & line fishing and other (non-spear) fishing activities were significantly higher in the permanently fished area than in the pulse fished area (pooled data from open and closed years)(Table 4.4). The mean density of spear fishing activities was significantly higher in the pulse fished (pooled data from open and closed years) than in the permanently fished area (Table 4.4). The biennial opening of the pulse fished area produced a pronounced, short-lived (1 week) spike in the density of fishing activities in both the pulse fished area and adjacent reserve. This spike in activity in both areas was more than seven times the peak densities at other times. For example, 82 spear fishers were observed in the pulse fished area at 08:00 on opening day 2000, whereas a maximum of 11 spear fishers were observed simultaneously in this area at other times of year.

Illegal fishing inside the Waikīkī reserve was observed on 9 % of the shoreline patrols. A total of 54 illegal pole & line fishing events and 35 illegal spearfishing events were recorded. The frequency of illegal fishing in the Waikīkī reserve was significantly associated with the status of the adjacent pulse fished area (χ^2 = 22.0, d.f. 2, P<0.001). Thirty-three (94%) of 35 illegal spear fishing events observed in the reserve occurred when the pulse fished area was open to fishing, and twenty of these occurred on the first

day of open season. Forty-eight (89%) of 54 illegal pole fishing events occurred when the pulse fished area was open, and 29 of these occurred during the first two weeks of open season. Most of these events involved pole & line fishers casting their lines into the reserve from the boundary, or spear fishers venturing just inside the reserve boundary. Nine spear fishers were observed fishing in central areas of the reserve. Although illegal fishing was detected inside the Waikīkī reserve, the mean densities of most fishing activities were significantly lower in the reserve than in the surrounding fished areas (Table 4.4). The only exception to this general pattern was the lack of significant difference between the relatively low mean densities of spear fishing activities in the reserve and permanently fished area (Table 4.4).

There were significant differences between the temporal patterns of pole & line and spear fishing activities. For example, although the mean densities of both spear and pole & line fishing were significantly higher during the day than at night (Table 4.5), each activity had a different, characteristic diel pattern (Figure 4.2). The densities of both activities were close to zero at sunrise and increased sharply during the first hours of daylight. Spear fishing activity reached a mid morning peak and then declined to near zero by sunset, where it remained throughout the night. Pole & line fishing activity peaked in the late afternoon, dropped to around half the peak daytime density at sunset, declined gradually until the early morning hours, and then dropped more rapidly to near zero at sunrise. The mean density of spear fishing activities was significantly higher on weekends than weekdays, and during winter than summer (Tables 4.6 & 4.7). There was

no significant difference between mean weekday and weekend, or between mean seasonal densities of pole fishing activities (Tables 4.6 & 4.7).

Spatial distribution of fishing activities within each area was patchy, with most fishers clustered around points of easy, public access to the shoreline, situated within a short distance of free parking. Pole & line fishers preferred jetties, seawall railings and beaches where they could set up their poles and cast their lines into natural and manmade channels. Spear fishers entered and exited at points of easy access to the water, and were most frequently sighted in areas of high rugosity reef that were within a few hundred meters of preferred access points. A small number of both spear and pole & line fishers used surfboards, kayaks and outrigger canoes to gain access to locations that were relatively far from shoreline access points. The uneven distribution of these 'resources' (free parking, shoreline access, jetties, high rugosity reef) along the Waikīkī coastline resulted in different patterns and densities of fishing activities in the areas adjacent to the north and south boundaries of the Waikīkī reserve. The area immediately adjacent to the southern boundary (Kaimanu Beach Park – pulse fished area) was the most heavily spear fished location in the entire study site and was also a preferred location for pole & line fishers. The area adjacent to the northern boundary had one location favored by pole & line fishers (Kapahulu groin) but was rarely spear fished. There was little fishing activity along the 2.5 km stretch between Kapahulu groin (the northern reserve boundary) and Magic Island (permanently fished area). Magic Island and the entrance channel to Kewalo Basin were the most intensively pole fished areas in the study site, and the reef between these two locations was frequently spearfished.

Catch

A total catch of 657 reef fishes and 110 octopuses was observed during shoreline patrols (167 fish, 31 octopuses) and opening day surveys (490 fish, 79 octopuses). Spear, pole & line and other gear types respectively accounted for 76.9 %, 20.5%, and 2.6% of the total catch of reef fishes. All octopuses were captured by spear. The total (combined) catch included 59 species from 31 reef fish families (Table 4.8). Catch composition varied between gear types; spear catches included 53 species from 23 reef fish families, and pole & line catches included 32 species from 25 families (Table 4.8). Eighteen reef fish families occurred in both spear and pole & line catches, but the frequency with which these families occurred in catches varied significantly among gear types (χ^2 = 183.9, d.f. 6, P<0.0001)(Figure 4.3). For example, acanthurids and scarids collectively accounted for 52% of the total spear catch of reef fishes, but only 2% of pole & line catches. Carangids accounted for 17% of pole & line catches but only 2% of the total spear catch of reef fishes. Mean fish size varied significantly between gear types (ANOVA, df 2, 384, F= 16.9, P< 0.0001). Spear fishing captured significantly larger fishes than pole & line fishing (Bonferroni post hoc test, P<0.001), and the size frequencies of spear and pole & line catches were significantly different (Kolmogorov Smirnov two sample test, D=0.32, P<0.0001)(Figure 4.4).

Spear fishing Catch Per Unit Effort (CPUE) was higher than pole & line CPUE. The mean numerical $CPUE_1$ (number of fish captured per hour) by spear fishing (1.53 ±0.22) was 1.6 times the CPUE by pole & line fishing (0.97 ±0.36), but the difference was non-significant (t = -0.769, df =93, P>0.05). The mean biomass $CPUE_1$ (kg h^{-1}) by

spear fishing was 26 times the biomass $CPUE_1$ by pole & line fishing ($t = -2.295$, $df = 85$, $P < 0.05$)(Table 4.11). A similar trend of higher $CPUE_2$ (number of fish captured per activity observed) for spear fishing than pole & line fishing was also apparent in the shoreline patrol data (Table 4.9). Mean numerical $CPUE_2$ calculated per activity was 2.4-3.2 times as high for spear fishing as for pole & line fishing and varied between areas. $CPUE_2$ for spearfishing was twice as high in the permanently fished area as in the pulse fished area (Table 4.9).

The estimated annual catch (tonnes) of reef fishes varied among gear types and areas at Waikīkī (Table 4.10). Spear fishing produced the largest catch of any gear type in each area, and the largest overall. The estimated annual yield (catch adjusted for area; t km^{-2}) in the reserve was $^1/_6$ to ½ of that in the adjacent fished areas. The estimated annual yield from open years in the pulse-fished area was 3 times the yield in the permanently fished area.

Discussion

Spear and pole & line were the dominant gear types used on the fringing reef at Waikīkī. Several types of net fishing (scoop net, throw net, surround net, gill net) were also occasionally observed, but these were very minor, sporadic components of total fishing activity. Pole & line fishing was the most frequent activity overall, but the relative frequencies of spear and pole & line fishing varied between areas at Waikīkī. Pole & line fishing dominated activities in the permanently fished area, whereas activities in the pulse fished area (and reserve) were more evenly divided between pole & line and

spear fishing. Pole & line and spear fishing activities at Waikīkī had their own characteristic diel patterns. Spear fishing was primarily a daytime activity with peak levels occurring during the morning. Pole & line fishing activity was most frequent during the day but was also common at night. Spear fishing activity was significantly higher on weekends than weekdays, and in winter than in summer. There were no significant weekly or seasonal differences in pole & line fishing activities.

Other comparable shore based surveys have found similar general patterns of fishing activities elsewhere in Hawai'i. Pole & line and spear were the most frequently encountered fishing methods in Kāne'ohe Bay (Everson, 1994), and pole & line fishing was the most common fishing activity in Hanalei Bay (Friedlander, Parrish & Peterson 1995, Friedlander & Parrish 1997). Both Everson (1994) and Friedlander & Parrish (1997) found that pole & line and spear fishing activities were more frequent on weekends and holidays than on weekdays, and concluded that this was a result of the primarily recreational/subsistence nature of the fisheries in Kāne'ohe and Hanalei Bays. Seasonal variation in the frequency of fishing activities was also found in Kāne'ohe (Everson 1994) and Hanalei Bay (Friedlander & Parrish 1997), but the seasonal patterns of high and low fishing activity were the opposite of those observed at Waikīkī (i.e., peak activity was during the summer months). The opposing seasonal trends seen in spear fishing at Waikīkī versus Hanalei and Kāne'ohe, are probably the result of the different conditions seen during summer and winter at these sites. Hanalei Bay and outer regions of Kāne'ohe Bay are both exposed to winter swells generated in the North Pacific, but protected from summer south swells (Friedlander & Parrish 1998b). Waikīkī

is protected from north swells but exposed to summer south swells. Spear fishers favor low surf conditions because spear fishing CPUE is inversely correlated with wave height (Dalzell, 1996). Periods of low surf occur mainly during the summer months in Kāne'ohe and Hanalei Bay, but during the winter at Waikīkī. The lack of significant seasonal differences in pole & line fishing activity at Waikīkī may be because the relatively small summer south swells at Waikīkī (Lee 1982) are less of an impediment to shore based pole & line fishing than the larger winter swells that affect Hanalei.

Spear fishing had a greater overall impact on reef fishes at Waikīkī than shoreline pole & line fishing. Spear fishing had a significantly higher CPUE and caught significantly larger fish than pole & line fishing. Spear fishing accounted for 70% of total reef fish catch at Waikīkī despite accounting for only 25 % of the total number of fishing activities observed. Several families of reef fishes that were major components of the spear fishing catch (e.g., Acanthuridae and Scaridae) rarely occurred in pole & line catches. The active, searching nature of spear fishing meant that this method affected a far larger area of the fringing reef at Waikīkī than the predominantly shoreline based pole & line fishing. Waikīkī pole & line and spear fishing catch rates and catch compositions were similar to those observed elsewhere in Hawai'i, and in other locations in the Pacific (Table 4.11). Carangids and mullids were the primary components of pole & line catches in Hanalei, Kāne'ohe and Waikīkī. Everson (1994) calculated that pole & line CPUE in Kāne'ohe Bay was 0.31 kg per hour, but this included both boat based and shore based pole & line fishing activities. The CPUE estimate of 0.07 kg line-h^{-1} for shore based line fishing at Hanalei Bay (Friedlander & Parrish 1997) was relatively close to that observed

at Waikīkī (0.04 kg line-h^{-1}). Spear fishing catch composition varied between locations in the Pacific, but acanthurids, scarids and mullids were primary components of spear catches in most reef fisheries (Table 4.11). Octopuses were a large component of the spear catch at Waikīkī but not as significant as in Kāne'ohe Bay, where they accounted for 88-92% of the total spear catch (Everson 1994). Mean spear fishing CPUE estimates from coral reef fisheries range from 0.4 to 2.4 kg man-h^{-1} with a mode around 1.2 kg man-h^{-1} (Table 4.11). Waikīkī spear fishing CPUE was in the middle of this range and 30% higher than spear catch rates observed in Kāne'ohe and Hanalei Bay (Table 4.11).

Although illegal fishing was observed in the Waikīkī reserve, the overall density of fishing activities was significantly lower in the reserve than in the surrounding fished areas. Most of the illegal fishing occurred on a few days surrounding the biennial opening of the adjacent pulse fished area. The violations were mainly confined to boundary areas of the reserve and the actual illegal catch observed was minimal (5 fish). These data support the alternate hypothesis that fishing effort is significantly lower in the reserve than adjacent fished areas, and suggest that the Waikīkī reserve provides effective protection for fish that remain inside the reserve boundaries.

The spatial and temporal patterns of fishing activity at Waikīkī resulted in the reserve being sandwiched between an area of high diurnal fishing effort and an area of generally low fishing effort. The area adjacent to the southern reserve boundary (Kaimanu Beach Park) was the most heavily spear fished location in the entire study site, and also a popular location for shoreline pole & line fishing. The area adjacent to the

northern reserve boundary had one jetty popular with pole & line fishers, but little other fishing activity along the next 2.5 km of coastline. Fishing activity was close to zero for at least several hundred meters beyond the seaward reserve boundary. Consequently, species that remain inside the reserve boundaries during the day but cross into fished areas at night (e.g., *Caranx sexfasciatus*, *C. melampygus* and *Mulloidichthys flavolineatus*; Chapter 2) avoided 'high impact' daytime spear fishing effort and only risked capture at night when venturing close (i.e., within casting distance) to the pole & line fishing sites at Kapahulu groin and around Kaimanu Beach Park. Thus current patterns of fishing activity create a spatial and temporal extension of the official reserve area. This may partly explain why vagile target species that frequently cross reserve boundaries at night are still more abundant and larger inside the Waikīkī reserve than in surrounding fished areas (Chapter 3). Although present fishing activity patterns at Waikīkī may create an unofficial extension of the official reserve for some of the more vagile species, a change in fishing activities around the reserve could easily eliminate this effect. For example, legal crepuscular or nighttime gill netting outside the northern or seaward boundaries of the reserve would intercept fishes as they exited the reserve. In order to be resilient to changing patterns of fishing activities outside their boundaries, reserves need to be large enough and include appropriate habitat to contain the entire home ranges of target species.

Estimations of annual yield (kg km^{-2}) at Waikīkī support the contention that the impact of fishing in the reserve is lower than in adjacent fished areas, and that the impact of fishing is higher in the pulse fished area than in the permanently fished area. These

differences are directly related to the densities of fishing activities in each area; the density of spear fishing activities produces the greatest effect on yields. The values derived from shoreline patrols probably underestimate actual annual yields because some catches were either missed, or deliberately concealed. The creel sampling protocol could also have missed occasional high impact fishing techniques (e.g., large gill nets) that have high catching power and could make a large difference to overall annual yield. The estimated annual yields for the fished areas at Waikīkī (0.2-0.58 t km^{-2}) are 1-2 orders of magnitude below those calculated for fisheries operating in similar size areas of fringing reef habitat in other locations in the Pacific (Table 4.12), but close to the annual yield estimate of 0.8 t km^{-2} for Hanalei Bay (Friedlander & Parrish, 1997). These figures suggest that the annual exploitation rates (see footnote Table 4.12) at Waikīkī are relatively low. This contention is further supported by comparing 1979 to1989 estimates of standing stock at Waikīkī before closure of the reserve (1.7-3.6 kg per $100m^{-2}$; Brock and Kam 1993) with annual yield estimates from the present study. This comparison provides a crude annual exploitation rate estimate of 0.6-3.4% (assuming that the estimates before closure are representative of the present standing stock in the fished areas at Waikīkī). Low annual exploitation rates at Waikīkī may make reserve effects (increased abundance or size inside the reserve) harder to detect and leave habitat complexity as the main factor determining the abundance and size patterns of reef fishes at Waikīkī.

Table 4.1. Summary of gear type frequencies (%) observed during shoreline patrols at Waikīkī.

Gear Type	Area			
	Permanently Fished	Pulse Fished	Reserve	All
Pole and Line	88.5	53.7	59.3	71.4
Spear	5.3	43.4	38.5	24.0
Scoop net	4.1	1.7	1.1	2.9
Throw net	1.6	0.7	0.0	1.2
Surround net	0.4	0.0	0.0	0.2
Handline	0.1	0.3	1.1	0.2
Gill net	0.1	0.1	0.0	0.1
Push net	0.0	0.1	0.0	0.0

Table 4.2. Results of multifactorial analysis of variance for densities of fishing activities (number km^{-2}) observed at Waikīkī. Factors included gear type (pole & line, spear and other gears), area (permanently fished, pulse fished and reserve), time of day (day or night), type of day (weekend or weekday), season (summer or winter) and the status of the pulse-fished area (open or closed). Interactions between area, gear type and the other factors were also included in the model. A significant difference ($P < 0.05$) is indicated with an asterisk (*).

Source	df	F	*P*
Location	2, 2274	183.9	<0.001*
Gear Type	2, 2274	341.9	<0.001*
Pulse Status	1, 2274	223.7	<0.001*
Season	1, 2274	<0.1	0.830
Day Type	1, 2274	13.9	<0.001*
Time of Day	1, 2274	44.1	<0.001*
Location x Gear	4, 2274	130.9	<0.001*
Location x Season	2, 2274	6.0	0.003*
Location x Day Type	2, 2274	4.9	0.008*
Location x Time of Day	2, 2274	4.8	0.009*
Gear Type x Pulse Status	2, 2274	63.4	<0.001*
Gear Type x Season	2, 2274	4.2	0.016*
Gear Type x Day Type	2, 2274	1.6	0.211
Gear Type x Time of Day	2, 2274	11.5	<0.001*

Table 4.3. Results of analysis of variance for densities (number km^{-2}) of pole & line (PL), spear (S) and other (O) fishing activities observed at Waikīkī. A significant difference ($P < 0.05$) is indicated with an asterisk (*). Results of post hoc Bonferroni pairwise comparisons of mean densities are indicated as ">" (significantly greater than, $P<0.001$).

Mean Density (S.E.M)			ANOVA			Bonferroni Post Hoc Test
Pole & Line (PL)	Spear (S)	Other (O)	F	df	*P*	
2.56 (0.18)	1.00 (0.19)	0.16 (0.03)	160.2	2, 2298	0.0001*	PL>S>O

Table 4.4. Results of analysis of variance for densities of fishing activities (number km^{-2}) observed in the permanently fished (FA), pulse fished (PF) and reserve (R) areas at Waikīkī. A significant difference ($P < 0.05$) is indicated with an asterisk (*). Results of post hoc Bonferroni pairwise comparisons of mean densities are indicated as ">" (significantly greater than, $P<0.001$) and "=" (no significant difference).

Gear Type	Mean Density (S.E.M)			ANOVA			Bonferroni Post Hoc Test
	Permanently Fished Area (FA)	Pulse Fished Area (PF)	Reserve (R)	F	df	*P*	
Pole & Line	6.91 (0.53)	2.37 (0.27)	0.58 (0.12)	209.6	2, 764	0.0001*	FA>PF>R
Spear	0.43 (0.08)	1.91 (0.43)	0.38 (0.15)	21.8	2, 764	0.0001*	PF>FA=R
Other	0.52 (0.15)	0.13 (0.03)	0.02 (0.01)	33.9	2, 764	0.0001*	FA>PF>R

Table 4.5. Results of analysis of variance for densities of fishing activities (number km^{-2}) observed during day and night at Waikīkī. A significant difference ($P < 0.05$) is indicated with an asterisk (*).

Gear Type	Mean Density (S.E.M)		df	F	*P*
	Day	Night			
Pole & Line	6.88 (0.55)	4.21 (0.38)	1, 765	10.9	0.001*
Spear	3.32 (0.74)	0.41 (0.11)	1, 765	37.0	0.0001*
Other	0.46 (0.13)	0.14 (0.04)	1, 765	9.61	0.002*

Table 4.6. Results of analysis of variance for densities of fishing activities (number km^{-2}) observed on weekdays and weekends at Waikīkī. A significant difference ($P < 0.05$) is indicated with an asterisk (*).

Gear Type	Mean Density (S.E.M)		df	F	*P*
	Weekday	Weekend			
Pole & Line	5.45 (0.39)	6.60 (0.85)	1, 765	0.4	0.519
Spear	1.34 (0.23)	4.13 (1.48)	1, 765	6.5	0.011*
Other	0.30 (0.10)	0.38 (0.09)	1, 765	3.5	0.062

Table 4.7. Results of analysis of variance for densities of fishing activities (number km^{-2}) observed during summer and winter at Waikīkī. A significant difference ($P < 0.05$) is indicated with an asterisk (*).

Gear Type	Mean Density (S.E.M)		df	F	*P*
	Summer	Winter			
Pole & Line	5.86 (0.71)	5.71 (0.42)	1, 765	0.8	0.234
Spear	1.14 (0.22)	2.51 (0.62)	1, 765	11.4	0.001*
Other	0.14 (0.04)	0.40 (0.11)	1, 765	9.3	0.002*

Table 4.8. Summary of catches observed at Waikīkī during shoreline patrols and opening day surveys. Octopuses were not included in the calculation of percentage frequency for spear fishing catches. Underlined values are family totals.

Species Captured	Gear Type					
	Spear		Pole		Other	
	N	%	N	%	N	%
Acanthuridae	171	33.9	2	1.5	10	58.8
Acanthurus achilles	13	2.6	-	-	-	-
Acanthurus blochii	2	0.4	-	-	-	-
Acanthurus dussumieri	2	0.4	-	-	-	-
Acanthurus nigrofuscus	7	1.4	-	-	1	5.9
Acanthurus nigroris	5	1.0	-	-	-	-
Acanthurus triostegus	53	10.5	2	1.5	9	52.9
Ctenochaetus strigosus	65	12.9	-	-	-	-
Naso lituratus	14	2.8	-	-	-	-
Naso unicornis	10	2.0	-	-	-	-
Acanthurus sp.	6	1.2	-	-	-	-
Albulidae (*Albula glossodonta*)	1	0.2	13	9.6	-	-
Apogonidae (*Apogonid sp.*)	-	-	2	1.5	-	-
Aulostomidae (*Aulostomus chinensis*)	2	0.4	1	0.7	-	-
Balistidae	1	0.2	2	1.5	-	-
Rhinecanthus rectangulus	-	-	2	1.5	-	-
Sufflamen fraenatus	1	0.2	-	-	-	-
Balistid sp.	1	0.2	-	-	-	-
Belonidae (*Tylosurus crocodilus*)	1	0.2	-	-	-	-
Bothidae (*Bothus mancus*)	1	0.2	2	1.5	-	-
Carangidae	10	2.0	13	9.6	-	-
Carangoides orthogrammus	1	0.2	-	-	-	-
Caranx melampygus	5	1.0	7	5.2	-	-
Scomberoides lysan	4	0.8				
Selar crumenopthalmus	-	-	6	4.4	-	-
Caranx sp.	-	-	10	7.4	-	-
Chanidae (*Chanos chanos*)	1	0.2	-	-	-	-
Cirrhitidae	7	1.4	1	0.7	-	-
Cirrhitus pinnulatus	7	1.4				
Paracirrhites arcatus	-	-	1	0.7	-	-
Clupeidae (*H. quadrimaculatus*)	-	-	20	14.8	-	-

/ctd.

Table 4.8. (Continued) Summary of catches observed at Waikīkī.

Species Captured	Gear Type					
	Spear		Pole		Other	
	N	%	N	%	N	%
Congridae (*Conger cinereus*)	1	0.2	1	0.7	-	-
Dasyatidae (*Dasyatus sp.*)	-	-	1	0.7	-	-
Fistulariidae (*Fistularia commersonii*)	-	-	5	3.7	-	-
Holocentridae	19	3.8	1	0.7	-	-
Myripristis amaena	8	1.6	-	-	-	-
Neoniphon sammara	-	-	1	0.7	-	-
Sargocentron sp.	11	2.2	-	-	-	-
Kuhliidae (*Kuhlia sandvicensis*)	23	4.6	10	7.4	1	5.9
Kyphosidae (*Kyphosus bigibbus*)	20	4.0	1	0.7	-	-
Labridae	9	1.8	6	4.4	-	-
Anampses cuvier	4	0.8	1	0.7	-	-
Cheilio inermis	-	-	2	1.5	-	-
Stethojulis balteata	1	0.2	-	-	-	-
Thalassoma ballieui	3	0.6	-	-	-	-
Thalassoma duperrey	1	0.2	3	2.2	-	-
Lethrinidae (*Monotaxis grandoculis*)	1	0.2	-	-	-	-
Lutjanidae (*Lutjanus kasimira*)	3	0.6	-	-	-	-
Monacanthidae (*Aluterus scriptus*)	1	0.2	-	-	-	-
Mugilidae (*Mugil cephalus*)	-	-	6	4.4	1	5.9
Mullidae	96	19.0	19	14.1	-	-
Mulloidichthys flavolineatus	9	1.8	4	3.0	-	-
Mulloidichthys vanicolensis	3	0.6	1	0.7	-	-
Parupeneus bifasciatus	1	0.2	-	-	-	-
Parupeneus cyclostomus	2	0.4	-	-	-	-
Parupeneus multifasciatus	46	9.1	14	10.4	-	-
Parupeneus pleurostigma	1	0.2	-	-	-	-
Parupeneus porphyreus	34	6.7	-	-	-	-
Muraenidae	1	0.2	2	1.5	1	5.9
Gymnothorax meleagris	-	-	-	-	-	-
Gymnothorax undulatus	1	0.2	-	-	1	5.9
Muraenid sp.	-	-	2	1.5	-	-
[Octopodidae (*Octopus cyanea*)]	[110]					

/ctd.

Table 4.8. (Continued) Summary of catches observed at Waikīkī.

Species	Gear Type					
	Spear		Pole		Other	
	N	%	N	%	N	%
Pomacentridae	5	1.0	4	3.0	3	17.6
Abudefduf abdominalis	3	0.6	2	1.5	-	-
Abudefduf sordidus	2	0.4	2	1.5	3	17.6
Priacanthidae	35	6.9	1	0.7	-	-
Heteropriacanthus cruentatus	20	4.0	1	0.7	-	-
Priacanthidae sp.	15	3.0	-	-	-	-
Scaridae	73	14.5	-	-	-	-
Calotomus carolinus	38	7.5	-	-	-	-
Chlorurus perspicillatus	7	1.4	-	-	-	-
Chlorurus sordidus	2	0.4	-	-	-	-
Scarus dubius	1	0.2	-	-	-	-
Scarus psittacus	11	2.2	-	-	-	-
Scarus rubroviolaceus	14	2.8	-	-	-	-
Scarid sp.	12	2.4	1	0.7	-	-
Serranidae (*Cephalopholis argus*)	4	0.8	-	-	-	-
Sphyraenidae (*Sphyraena barracuda*)	-	-	5	3.7	-	-
Synodontidae (*Synodus sp.*)	-	-	1	0.7	-	-
Tetraodontidae (*Arothron hispidus*)	-	-	5	3.7	1	5.9
Total Fish Catch	**505**		**135**		**17**	

Table 4.9. Catch Per Unit Effort$_2$ (Mean number of fishes captured per fishing activity observed) calculated from shoreline patrol data.

Gear Type	Permanently Fished Area	Pulse Fished Area	Reserve
Spear	0.19	0.09	0.13
Pole	0.07	0.03	0.06
Other	0.11	0.23	0.00
Total	0.08	0.05	0.07

Table 4.10. Estimated annual catch (t) of reef fishes by area and gear type at Waikīkī. Annual yield estimates (t km^{-2}) for each area are given below catch totals.

Gear Type	Permanently Fished Area	Pulse Fished Area*	Reserve
Spear	0.228	0.539	0.023
Pole	0.210	0.031	0.005
Other	0.020	0.011	0.000
Total	0.457	0.581	0.028
Total Yield (t km^{-2})	0.199	0.581	0.091

*Catch and yield calculated for open years only.

Table 4.11. Summary of catch rates (CPUE, catch per unit effort) and catch composition from spear and pole & line fishing on reefs in Hawai'i and the South Pacific. Adapted from Dalzell (1996).

Location	Gear Type	Mean CPUE (kg/h)[#]	Principal catch components	Source
Hawai'i (Kāne'ohe Bay)	Pole & Line*	0.31	Carangidae, Mullidae, Lutjanidae	Everson (1994)
Hawai'i (Hanalei Bay)	Pole & Line[a]	0.07	Carangidae, Mullidae, Sphyrnidae	Friedlander & Parrish (1997)
Hawai'i (Waikīkī)	Pole & Line[a]	0.04	Carangidae, Mullidae, Albulidae	This Study
Hawai'i (Kāne'ohe Bay)	Spear	0.87	Octopodidae, Scaridae, Acanthuridae, Mullidae	Everson (1994)
Hawai'i (Hanalei Bay)	Spear	0.87	Scaridae, Acanthuridae, Kyphosidae, Mullidae	Friedlander, Parrish & Peterson (1995)
Hawai'i (Waikīkī)	Spear	1.13	Acanthuridae, Octopodidae, Mullidae, Scaridae	This study
Philippines (Cape Bolinao)	Spear	1.30	Siganidae, Mullidae, Labridae, Scaridae	Acosta and Recksiek (1989)
Philippines (Malalison Island)	Spear	1.10	Acanthuridae	Amar, Cheong & Cheong (1996)
Papua New Guinea (Kavieng)	Spear	2.40	Scaridae, Serranidae, Lutjanidae, Haemulidae	Wright and Richards (1985)
Nauru	Spear	2.00	Lutjanidae, Holocentridae, Serranidae, Acanthuridae	Dalzell and Debao (1994)
Guam	Spear	0.40	Scaridae, Kyphosidae, Siganidae, Acanthuridae	Katnik (1982)
Micronesia (Woleai)	Spear	1.20	Acanthuridae, Scaridae, Balistidae, Labridae	Smith and Dalzell (1993)
Tonga	Spear	1.4	Acanthuridae, Scaridae, Holocentridae, Serranidae	Halapua (1982)
Fiji (Dravuni)	Spear	1.2	Serranidae, Acanthuridae, Lutjanidae, Carangidae	Emery and Winterbottom (1991)

*Includes vessel based fishing

[a]Shore based only

[#]Per line hour for pole & line, per man hour for spear

Table 4.12. Estimated annual yields (t km^{-2} $year^{-1}$) from fisheries operating in relatively small (<10 km^2) areas of fringing reef habitat around the Pacific. Adapted from Dalzell (1996).

Location	**Area fished (km^2)**	**Maximum depth fished (m)**	**Yield (t km^{-2} $year^{-1}$)**	**Source**
American Samoa	3	40	8.6-44.0	Wass (1982)
Nauru	7.5	100	4.5	Dalzell & Debao (1994)
Niue	6.2	60	9.3	Dalzell et al. (1993)
Philippines (Apo)	1.5	20-60	11.4-24.9	Alcala (1981), Alcala and Luchavez (1981)
Philippines (Sumilon)	0.5	40	14.0-36.9	Alcala & Gomez (1985), Lopez (1986)
Philippines (Panilacan)	1.8	29	10.7	Savina & White (1986), Bellwood (1988)
Fiji (Koro and Lakeba)	8.4	n.a.	5.0	Bayliss-Smith (MS)
Waikīkī	3.3	15	0.2-0.58	This study

Annual exploitation rate (u) is the fraction of a population at the beginning of the year that is caught during the year. Annual exploitation rates at Waikīkī were calculated using the formula $u=C/P$, where P = standing stock estimate of 17 to 36 t km^{-2} (Brock and Kam, 1993) and C = annual yield (harvest) estimate of 0.2 to 0.58 t km^{-2} (this study). Thus the upper estimate of annual exploitation rate (u_{max}) at Waikiki = 0.58/17 = 0.034 or 3.4%.

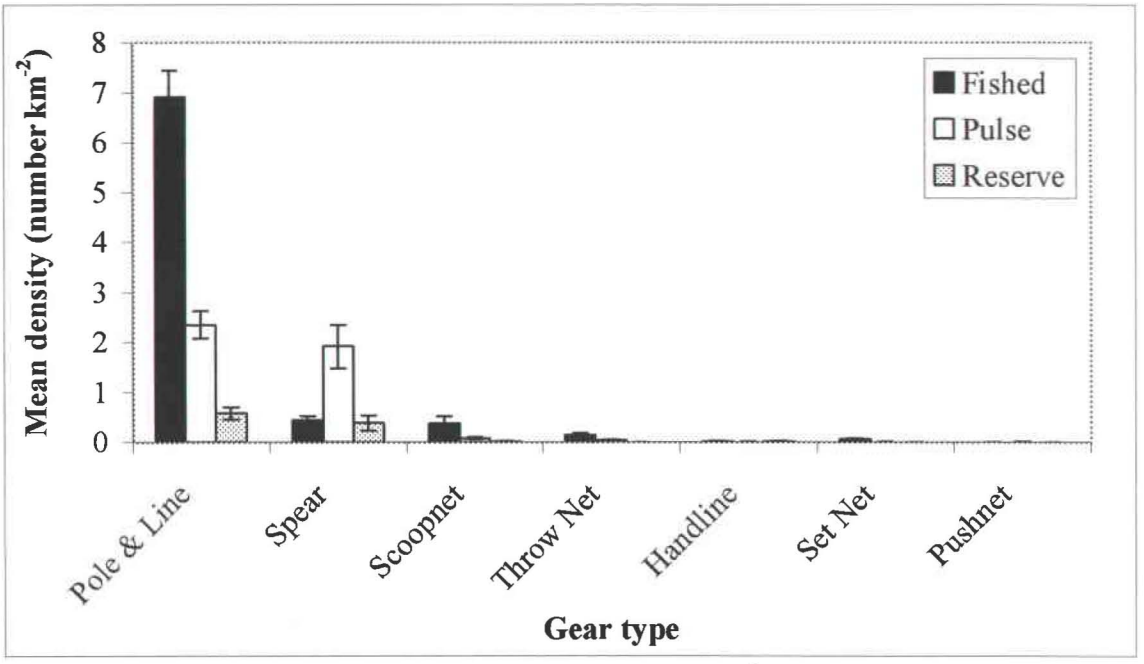

Figure 4.1. Mean density of fishing activities (number km^{-2}) in permanently fished (solid bars), pulse fished (open bars) and reserve (shaded bars) areas at Waikīkī. Error bars are ± 1 S.E.M.

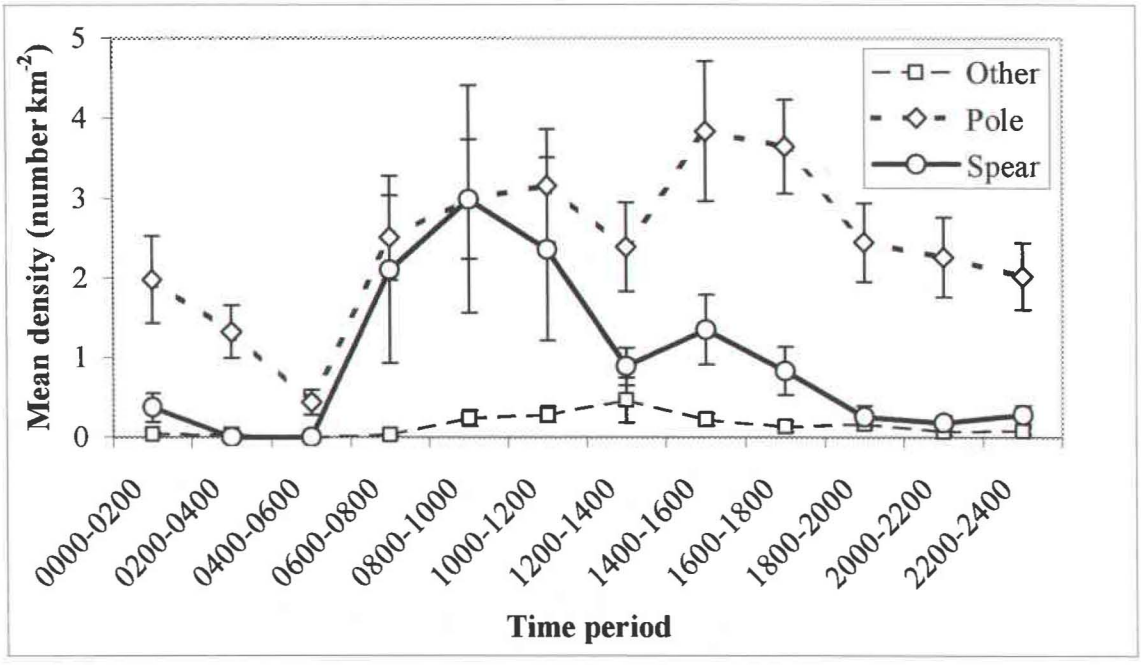

Figure 4.2. Diel variation in mean density (number km^{-2}) of pole & line (dotted line), spear (solid line) and other (dashed line) fishing activities at Waikīkī. Error bars are ± 1 S.E.M.

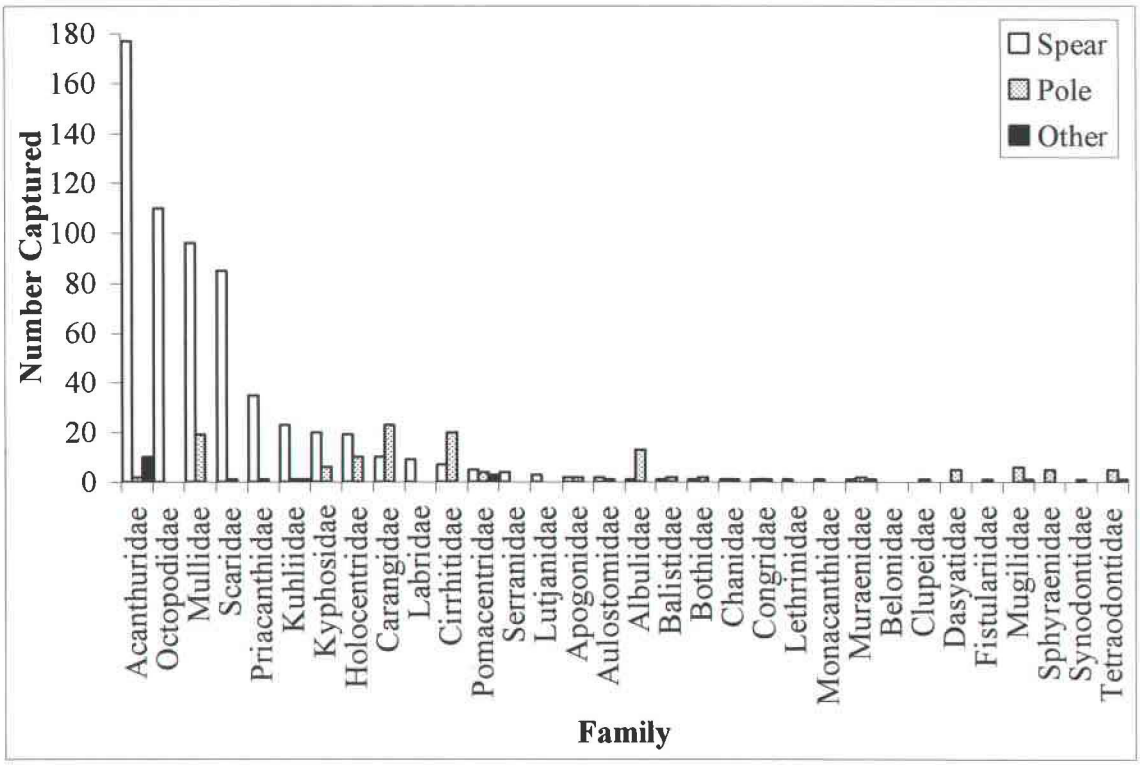

Figure 4.3. Frequency of reef fish families (and octopus) in catches taken by spear (open bars), pole (shaded bars) and other gear types (solid bars) at Waikīkī.

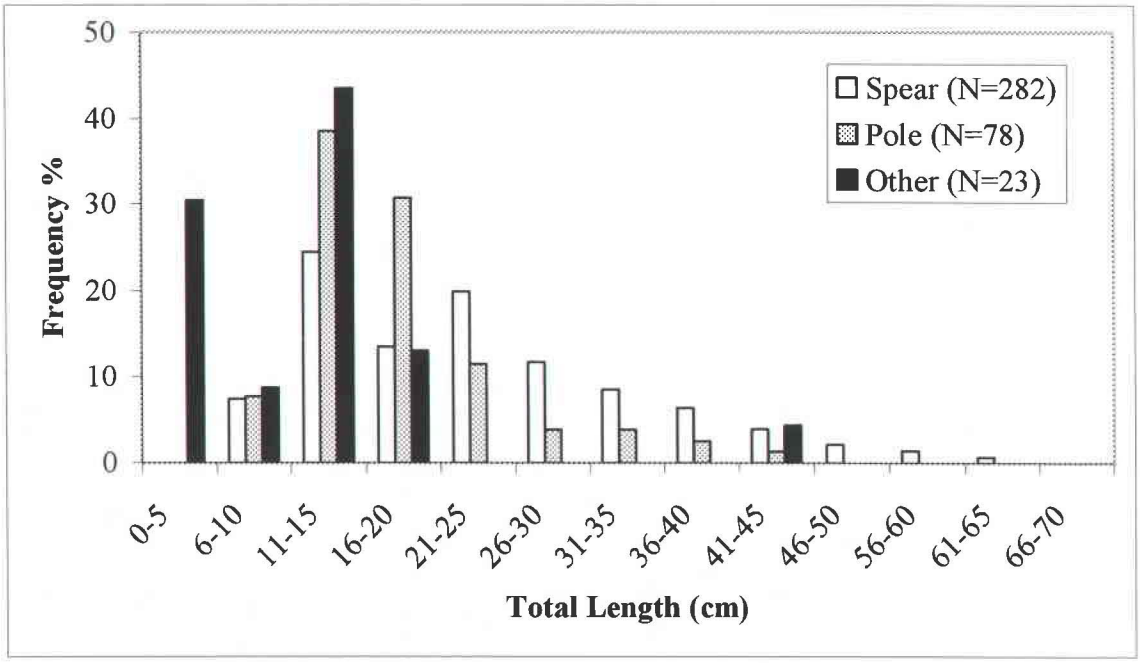

Figure 4.4. Size frequency distribution of catches of reef fishes taken by spear (open bars), pole & line (shaded bars) and other gear types (solid bars) at Waikīkī.

CHAPTER 5

GENERAL DISCUSSION

There are many reasons for creating marine reserves, but one of the main reasons is their potential effectiveness as tools for the conservation and management of fishery target species (Roberts 1991, Roberts & Polunin 1991, 1993, Roberts et al. 1995, Bohnsack 1996, Russ 2002). There are two different scales of marine reserve 'effectiveness' (local and regional). Local effectiveness is the ability of individual reserves to maintain or increase the abundance and size of target species within reserve boundaries (Roberts, 1991, 1993, Bohnsack 1996, Russ 2002). These increases may in turn lead to net export of target species from reserves to adjacent fished areas, and greater reproductive output from reserves than from fished areas of equivalent size (Roberts, 1991, 1993, Bohnsack 1996, Russ & Alcala 1996b, Russ 2002). Regional effectiveness is the contribution made by reserves to the overall stability and productivity of regional fisheries. Theoretical analyses have generally indicated that relatively large portions (>40%) of total fished areas would need to be set aside as reserves in order to produce any meaningful regional increase in fisheries (Nowlis & Roberts 1999, Nowlis 2000). Thus, even if all existing shallow-water marine reserves in Hawai'i were locally effective, their regional effectiveness would still be negligible because they cover less than 1% of Main Hawaiian Islands coastal reefs.

There is growing political resolve to increase the proportion of reef area that is protected inside marine reserves (pers. obs.). Vociferous opposition from fishers makes the creation of large reserves, or numerous smaller reserves, an unlikely prospect in the

Main Hawaiian Islands and many other populated coastal areas. The most likely scenario is the enlargement of some existing reserves and establishment of a few additional, relatively small reserves. One important question that remains unanswered in this process is how large reserves need to be in order to ensure effective protection of target species (Dugan & Davis 1993, Bohnsack 1998). Perhaps a more pertinent question might be 'how small can reserves be and still maintain local effectiveness?'

Most previous studies of reserve effectiveness implicitly assumed that greater abundance and size of target species inside reserves than in surrounding fished areas (or than before reserve establishment) indicated that reserve size was adequate (Polunin & Roberts 1993, Roberts 1993, Roberts 1995, Jennings et al. 1995, McClanahan & Kaunda-Arara 1996, Rakitin & Kramer 1996, Wantiez et al. 1997, Russ & Alcala 1998b). Some authors have even concluded that 'reserve size doesn't matter' because greater abundance and size of target species within reserve boundaries was found across a wide spectrum of reserve sizes (Halpern, in press). The great majority of these studies lacked replication in space and time, and therefore cannot unequivocally prove that the presence of the reserve was the causal factor underlying the observed patterns of target species abundance and size (Edgar & Barrett 1997, Russ 2002, Halpern in press). Intrinsic differences between reserve and fished areas are an equally plausible explanation for these patterns, particularly as 'special' locations are generally chosen as sites for marine reserves (Roberts 1993, 2000, Woodley 1985, Kenchington 1988).

The present study empirically demonstrated that greater abundance and size of mobile target species could still occur in a reserve that is too small to fully contain their routine short-term movements (Chapter 2). A combination of intrinsic habitat differences between the Waikīkī reserve and surrounding fished areas (Chapter 3), and low fishing mortality in areas immediately adjacent to the reserve boundaries (Chapter 4) are probably responsible for this apparent paradox. Increased fishing mortality in the areas around the Waikīkī reserve would presumably reduce target species abundance inside the reserve. Reserves need to be large enough so that changing patterns of fishing activity outside their boundaries do not negatively impact target species abundance and size inside the reserve.

The present study also demonstrated that 'highly mobile' species (e.g., *Caranx sp.*) show site fidelity to well defined home ranges and have predictable, repeated patterns of daily movement and habitat use in contiguous fringing reef (Chapter 2). These characteristics, which have been previously demonstrated in patch reef habitat (Holland et al. 1996), make even these mobile species well suited to protection in marine reserves. In order to protect the widest range of species possible, reserves must be large enough to contain the larger home ranges of these more mobile species. This approach will automatically ensure protection of more sedentary target species (e.g., Acanthuridae and Scaridae). The existing reserve area at Waikīkī (0.32 km^2) would need to be at least tripled in size (1 km^2) to begin to effectively protect more mobile species such as jacks and goatfishes (Chapter 2). This estimate of minimum effective reserve size is derived from fish movements that are determined by the spatial distribution of critical habitat at

Waikīkī, and caution should therefore be exercised when applying it to other areas. Nevertheless, comparisons of fish movement data from Waikīkī with published results from other areas and other reef-associated species suggest that there is some generality to the patterns and scale of daily movements (Chapter 2). Many species exhibit a crepuscular 'commute' between foraging and refuge habitats in the order of 250-1000 meters. These movements are generally oriented along well-defined reef features (e.g., the reef crest) and are frequently parallel to the shoreline. Some species utilize structurally complex habitat for both foraging and refuging, whereas others refuge in complex habitat and forage in soft substrate. This suggests that some general size and habitat guidelines could be applied to reserve design. Reserves should contain both structurally complex habitat and areas of soft substrate; boundaries should be placed along natural breaks in habitat rather than across contiguous habitat; reserves should cover at least 1 km of coastline and enclose a minimum of 1 km^2 of marine habitats.

The question of whether reserves cause greater target species abundance and size can only be answered by using a Before After Control Impact Pair (BACIP) study design (Stewart-Oaten et al. 1986, Underwood 1993, Edgar & Barret 1997, Tissot & Hallacher 1999, Russ 2002, Halpern in press). This design includes paired reserve and fished areas before and after reserve establishment. The important test with this design is not whether a variable (e.g., mean biomass) is greater inside or outside marine reserves, but how the variable changes with time within the reserve relative to outside (Edgar & Barret 1997, Russ 2002). Reserve size could be incorporated as a treatment in a BACIP study but it may be more practical to use reserve design guidelines described above to plan the

experimental 'plots' for these studies. Compliance with no-fishing regulations should also be considered in BACIP studies. The bias introduced by illegal fishing inside reserves will always be in the direction of a reduced effect of "protection" and will act to reduce differences between reserve and fished areas.

Although target species abundance is generally higher in the Waikīkī reserve than in adjacent fished areas (Chapter 3), results of the present study do not support the existence of density-dependent net export ('spillover') of juvenile and adult fish from the reserve to fished areas (Chapter 2). The pattern of recaptures and resightings of conventionally tagged reef fish at Waikīkī was generally consistent with tracking results and strongly suggested that most individuals are highly site attached to permanent home ranges, whereas a few disperse to distant locations. The existence of genetically 'resident' and 'nomadic' fish in reef fish populations appears to be a more likely explanation for the dispersal patterns of fish observed at the Waikīkī reserve (and Coconut Island) than density-dependent emigration. Evidence of spillover claimed by previous authors (e.g., Rakitin & Kramer 1996, Russ & Alcala 1996b, Chapman & Kramer 1999) is on a small spatial scale (a few hundred meters), consistent with the sighting or capture of resident individuals within home ranges that straddle a reserve boundary. If 'boundary-straddling' is the primary mechanism of spillover, then export of adult biomass from reserves will be restricted to areas within close proximity of reserve boundaries. Reserves that are too small to fully contain the routine movements of target species will have high proportions of these 'boundary-straddling' individuals in the reserve

population and may be susceptible to target species depletion if fishing mortality adjacent to reserve boundaries is high.

In conclusion, the question of whether small marine reserves are effective has two answers: (1) Small reserves may be locally effective in increasing target species abundance and size if they are large enough to contain the home ranges of the key target species. The present study suggests that this requires reserves in Hawai'i to cover a minimum of 1 km of coastline and an area of 1 km^2; (2) The regional effectiveness of small reserves will be contingent on the number established. Theoretical studies suggest that optimum effects of marine reserves will only be achieved by closing a large percentage (>40%) of the fished area. Less than 1% of coastal reefs in the Main Hawaiian Islands are currently protected within small reserves. This suggests that the current regional effect of Hawai'i's marine reserves is negligible.

LITERATURE CITED

Acosta AR, Recksiek CW (1989) Coral reef fisheries at Cape Bolinao, Philippines: an assessment of catch, effort and yield. Asian Mar Biol 6:101-114.

Alcala AC (1981) Fish yields of coral reefs of Sumilon Island, central Philippines. Bull Nat Res Council Philippines 36:1-7.

Alcala AC, Gomez ED (1985) Fish yields of coral reefs in Central Philippines. Proc 5th Int Coral Reef Symp 5:521-524.

Alcala AC, Russ GR (1990) A direct test of the effects of protective management on the abundance and yield of tropical marine resources. J Cons CIEM 46:40-47.

Alcala, AC, Luchavez T (1981) Fish yield of the coral reef surrounding Apo Island, Negros Oriental, Central Visayas, Philippines. Proc 4th Int Coral Reef Symp 1:69-74.

Amar EC, Cheong RM, Cheong MVT (1996) Small scale fisheries of coral reefs and the need for community-based resource management in Malalison Island, Philippines. Fish Res 25:265-277.

Atkins P (1981) Behavioral determinants of the nocturnal spacing pattern of the yellow tang *Zebrasoma flavescens* (Acanthuridae). Pac Sci 35:263-264.

Attwood CG and Bennett BA (1994) Variation in dispersal of Galjoen (*Coracinus capensis*)(Teleostei: Coracinidae) from a marine reserve. Can J Fish Aquat Sci 51:1247-1257.

Barrett NS (1995) Short- and long-term movement patterns of six temperate reef fishes (Families Labridae and Monacanthidae). Mar Freshwat Res 46:853-860.

Bayliss-Smith T (MS) The price of protein: marine fisheries in Pacific subsistence. Unpubl. MS Dept Geography, University of Cambridge, Cambridge CB2 3EN, UK. 29pp.

Bellwood DR (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.

Bohnsack JA (1990) The potential of marine fishery reserves for reef fish management in the US Southern Atlantic. Miami. NOAA tech Memo NMFS-SEFC-261. 40pp.

Bohnsack JA (1993) Marine Reserves: They enhance fisheries, reduce conflicts and protect resources. Oceanus 36:63-71.

Bohnsack, JA (1996) Maintenance and recovery of fishery productivity. Chapter 11. Pages 283-313 in NVC Polunin and CM Roberts (Eds.) Tropical Reef Fisheries. Fish and Fisheries Series 20. Chapman and Hall. London. 477 pp.

Bohnsack JA (1998) Application of marine reserves to reef fisheries management. Aust J Ecol 23:298-304.

Bradbury C, Green JM, Bruce-Lockhart M (1995) Home ranges of female cunner, *Tautogolabrus adspersus* (Labridae), as determined by ultrasonic telemetry. Can J Zool 73:1268-1279.

Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. Bull Mar Sci 32:269-276.

Brock RE, Kam AKH (1993) Fishing and its impact on coral reef fish communities. Final report to Department of Land and Natural Resources, Division of Aquatic Resources, State of Hawai'i. 35 pp.

Brock VE (1954) A preliminary report on a method of estimating reef fish populations. J Wildl Manage 18:297-308.

Burke NC (1995) Nocturnal foraging habitats of French and bluestriped grunts, *Haemulon flavolineatum* and *H. sciurus*, at Tobacco Caye, Belize. Env Biol Fish 42:365-374.

Carr MH, Reed DC (1993) Conceptual issues relevant to marine harvest refugia: Examples from temperate reef fishes. Can J Fish Aquat Sci 50:2019-2028.

Chapman MR, Kramer DL (2000) Movements of fishes within and among fringing coral reefs in Barbados. Env Biol Fish 57:11-24.

Chapman MR, Kramer DL, (1999) Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: Effects of reserve protection and habitat characteristics. Mar Ecol Prog Ser 181:81-96.

Chiappone M, Sullivan Sealey KM (2000) Marine reserve design criteria and measures of success: Lessons learned from the Exuma Cays land and sea park, Bahamas. Bull Mar Sci 66:691-705.

Chitty D (1967). The natural selection of self regulatory behavior in animal populations. Proc Ecol Soc Aust 2:51-78.

Choat JH, Bellwood DR (1985) Interactions amongst herbivorous fishes on a coral reef: *Influence of spatial variation*. Mar Biol 89:221-234.

Cole RG, Villouta E, Davidson RJ (2000) Direct evidence of limited dispersal of the reef fish *Parapercis colias* (Pinguipedidae) within a marine reserve and adjacent fished areas. Aquat Conserv Mar Freshwat Ecosyst 10:421-436.

Corless M, Hatcher BG, Hunte W, Scott S (1997) Assessing the Potential for Fish Migration From Marine Reserves to Adjacent Fished Areas in the Soufriere Marine Management Area, St. Lucia. Proc Gulf Caribb Fish Inst 49:71-98.

Craig P (1996) Intertidal territoriality and time-budget of the surgeonfish, *Acanthurus lineatus*, in American Samoa. Env Biol Fish 46:27-36.

Dalzell P (1996) Catch rates, selectivity and yields of reef fishing. Chapter 7. Pages 161-192 in NVC Polunin and CM Roberts (Eds.). Tropical Reef Fisheries. Fish and Fisheries Series 20. Chapman and Hall. London. 477 pp.

Dalzell P, Debao A (1994) Coastal fisheries production on Nauru. South Pacific Commission, Nouméa, New Caledonia, Inshore Fish Res Proj Tech Doc 2. 299 pp.

Dalzell P, Lindsay SR, Patiale H (1993) Fisheries resources survey of the island of Niue. South Pacific Commission, Nouméa, New Caledonia, Inshore Fish Res Proj Tech Doc 3. 68 pp.

DeMartini EE (1993) Modeling the potential of fishery reserves for managing Pacific coral reef fishes. Fish Bull 91:414-427.

Dubin RE, Baker JD (1982) Two Types of Cover-Seeking Behavior at Sunset by the Princess Parrotfish, *Scarus taeniopterus*, at Barbados, West Indies. Bull Mar Sci 32:572-583.

Dugan JE, Davis GE (1993) Applications of marine refugia to coastal fisheries management. Can J Fish Aquat Sci 50:2029-2042.

Edgar GJ, Barrett NS (1997) Short term monitoring of biotic change in Tasmanian marine reserves. J Exp Mar Biol Ecol 213:261-279.

Emery AR, Winterbottom R (1991) Lagoonal fish and fisheries of Dravuni, Great Astrolabe Reef, Fiji, South Pacific. University of the South Pacific, Marine Studies Programme, Suva, Fiji, Tech Rep 3. 22 pp.

Everson A (1994) Fishery data collection system for fishery utilization study of Kāne'ohe Bay: two-year interim report. Department of Land and Natural Resources, Division of Aquatic Resources, State of Hawai'i. Technical Report 94-01, 45 pp.

Fricke HW (1986) Pair swimming and mutual partner guarding in monogamous butterflyfish (Pisces, Chaetodontidae): A joint advertisement for territory. Ethology 73:307-333.

Friedlander AM (2001) Essential Fish Habitat and the Effective Design of Marine Reserves: Application for Marine Ornamental Fishes. Aquarium Sci Conserv 3:135-150.

Friedlander AM, Parrish JD (1997) Fisheries harvest and standing stock in a Hawaiian Bay. Fish Res 32:33-50.

Friedlander AM, Parrish JD (1998a) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J Exp Mar Biol Ecol 224:1-30.

Friedlander AM, Parrish JD (1998b) Temporal dynamics of fish communities on an exposed shoreline in Hawai'i. Env Biol Fish 53:1-18.

Friedlander AM, Parrish JD, Peterson JD (1995) A survey of the fisheries of Hanalei Bay, Kauai. Final report submitted to Department of Land and Natural Resources, Division of Aquatic Resources, State of Hawai'i. 93 pp.

Grigg RW (1994) Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawai'i. Mar Ecol Prog Ser 103:25-34.

Guénette S, Lauck T, Clark C (1998) Marine Reserves: from Beverton and Holt to the Present. Rev Fish Biol Fish 8:251-272.

Halapua S (1982) Fishermen of Tonga: their means of survival. University of the South Pacific, Suva, Fiji, 100 pp.

Halpern BS (2002) The impact of marine reserves: do reserves work and does reserve size matter? Ecol Appl 12. In press.

Helfman GS (1978) Patterns of community structure in fishes: summary and overview. Env Biol Fish 3:129-148.

Helfman GS (1986). Fish behavior by day, night and twilight. Pages 366-387 In: Pitcher TJ (Ed.) The behavior of teleost fishes. Johns Hopkins University Press. 554 pp.

Helfman GS, Meyer JL, McFarland WN (1982) The Ontogeny of Twilight Migration Patterns in Grunts (Pisces: Haemulidae). Anim Behav 30:317-326.

Holland KN, Lowe CG, Peterson JD (1992) Tracking coastal sharks with small boats: hammerhead sharks as a case study. Aust J Mar Freshwater Res 43:61-66.

Holland KN, Lowe CG, Wetherbee BM (1996) Movement and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. Fish Res 25:279-292.

Holland KN, Peterson JD, Lowe CG, Wetherbee BM (1993) Movements, distribution and growth rates of the white goatfish *Mulloides flavolineatus* in a fisheries conservation zone. Bull Mar Sci 52:982-992.

Hooge PN, Eichenlaub B (1997) Animal movement extension to arcview. ver. 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK, USA.

Hooge PN, Eichenlaub WM, Solomon EK (2000) Using GIS to Analyze Animal Movements in the Marine Environment. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska. 20 pp.

Jennings S (2000) Patterns and prediction of population recovery in marine reserves. Rev Fish Biol Fish 10:209-231.

Jennings S, Grandcourt EM, Polunin NVC (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. Coral Reefs 14:225-235.

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. Adv Mar Biol 34:1-70.

Jennings S, Lock JM (1996) Population and ecosystem effects of reef fishing. Chapter 8. Pages 193-218 in N.V.C. Polunin and C.M. Roberts (Eds.) Tropical Reef Fisheries. Fish and Fisheries Series 20. Chapman and Hall. London. 477 pp.

Jennings S, Polunin NVC (1996) Impacts of fishing on tropical reef ecosystems. Ambio 25:44-49.

Jennings SE, Grandcourt M, Polunin NVC (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. Coral Reefs 14:225-235.

Johannes B, Riepen M (1996) Environmental and social implications of the fishery for live coral reef food fish in Asia and the Western Pacific. Live Reef Fish Inf Bull 1:18-22.

Katnik SE (1982) Effects of fishing pressure on the reef flat fisheries of Guam. M.Sc. thesis, University of Guam, 62 pp.

Kenchington RA (1988) Managing reefs and inter-reefal environments for sustained exploitive, extractive and recreational uses. Proc Sixth Int Coral Reef Symp 1:81-87.

Klimley AP, Nelson DR (1984) Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. Behav Ecol Sociobiol 15:45-54.

Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. Env Biol Fish 55:65-79.

Lee RYG (1982) A statistical analysis of Ala Moana surf heights. NOAA Tech Memo NWSTM PR-26. 16 pp.

Lowry MB, Suthers IM (1998) Home range, activity and distribution patterns of a temperate rocky-reef fish, *Cheilodactylus fuscus*. Mar Biol 132:569-578.

MacDonald DW, Ball FG, Hough NG (1980) The evaluation of home range size and configuration using radio tracking data. Pages 40-426 In: Amlaner CJ, MacDonald DW (Eds.) Handbook of biotelemetry and radio tracking, Pergamon Press, Oxford. 804 pp.

Malvestuto SP, Davies WD, Shelton WL (1978) An evaluation of the roving creel survey with nonuniform probability sampling. Trans Am Fish Soc 107:255-262.

Mazeroll AI, Montgomery WL (1995) Structure and organization of local migrations in brown surgeonfish (*Acanthurus nigrofuscus*) Ethology 99:89-126.

Mazeroll AI, Montgomery WL (1998) Daily migrations of a coral reef fish in the Red Sea (Gulf of Aqaba, Israel): Initiation and orientation. Copeia 4:893-905.

McClanahan TR (1994) Kenyan coral reef lagoonal fishes: Associations with reef management, complexity, and sea urchins. Coral Reefs 13:231-241.

McClanahan TR, Kaunda-Arara B (1996) Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. Conserv Biol 10:1187-1199.

McClanahan TR, Muthiga NA (1988) Changes in Kenyan coral reef community structure and function due to exploitation. Hydrobiology 166:269-276.

McClanahan TR, Shafir SH (1990) Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. Oecologia 83:362-370.

McManus JW (1988) Coral reefs of the ASEAN Region: Status and management. Ambio 17:189-193.

Meyer CG, Holland KN (2001) A kayak method for tracking fish in very shallow habitats. Pages 289-296 In: Sibert JR and Nielsen J (Eds.) Electronic Tagging and Tracking in Marine Fisheries. Kluwer Academic Publishers, The Netherlands. 484 pp.

Meyer CG, Holland KN, Wetherbee BM, Lowe CG (2000) Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. Env Biol Fish 59:235-242.

Montgomery WL, Myrberg AA Jr, Fishelson L (1989) Feeding ecology of surgeonfishes (Acanthuridae) in the northern Red Sea, with particular reference to *Acanthurus nigrofuscus* (Forsskaal). J Exp Mar Biol Ecol 132:179-207.

Nagelkerken I, Dorenbosch M, Verberk WCEP, De la Moriniere EC, van der Velde G (2000) Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. Mar Ecol Prog Ser 194:55-64.

Nowlis JS (2000) Short- and long-term effects of three fishery-management tools on depleted fisheries. Bull Mar Sci 66:651-662.

Nowlis JS, Roberts CM (1999) Fisheries benefits and optimal design of marine reserves. Fish Bull 97:604-616.

Ogden JC, Buckman NS, (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus criosensis* Bloch (Scaridae). Ecology 54:589-596.

Ogden JC, Ehrlich PR (1977) The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae) Mar Biol 42:273-280.

Okubo A (1980) Diffusion and ecological problems : mathematical models. Springer-Verlag, New York. 254 pp.

Overholtzer KL, Motta PJ (1999) Comparative resource use by juvenile parrotfishes in the Florida Keys. Mar Ecol Prog Ser 177:177-187.

Parker GA (1984) Evolutionarily stable strategies. Pages 30-61 In: Krebs JR, Davis NB (Eds.) Behavioral Ecology: An Evolutionary Approach. Blackwell Scientific Publications, Oxford. 494 pp.

Pet J (1997) Destructive fishing methods in and around Komodo National Park. Live Reef Fish Inf Bull 2:20-24.

Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral reef fishes in two small Caribbean marine reserves. Mar Ecol Prog Ser 100:167-176.

Quinn TP, Ogden JC (1984) Field evidence of compass orientation in migrating juvenile grunts (Haemulidae). J Exp Mar Biol Ecol 81:181-192.

Rakitin A (1994) The effect of a marine reserve on the abundance and size of coral reef fishes in Barbados. West Indies. M.Sc. Thesis. McGill University. Montreal. 80 pp.

Rakitin A, Kramer DL (1996) Effect of a marine reserve on the distribution of coral reef fishes in Barbados. Mar Ecol Prog Ser 131:97-113.

Randall JE (1985) Guide to Hawai'i Reef Fishes. Harrowood Books, Philadelphia. 79 pp.

Randall JE (1996) Shore fishes of Hawai'i. Natural World Press, Honolulu. 216 pp.

Reese ES (1989) Orientation behavior of butterflyfishes (family Chaetodontidae) on coral reefs: Spatial learning of route specific landmarks and cognitive maps. Env Biol Fish 25:79-86.

Righton D, Miller M, Ormond R (1998) Correlates of territory size in the butterflyfish *Chaetodon austriacus* (Rueppell). J Exp Mar Biol Ecol 226:183-193.

Roberts CM (1991) Larval mortality and the composition of coral reef fish communities. Trends Ecol Evol 6:83-87.

Roberts CM (1995) Rapid build-up of fish biomass in a Caribbean marine reserve. Conserv Biol 9:815-826.

Roberts CM (2000) Selecting marine reserve locations: Optimality versus opportunism. Bull Mar Sci 66:581-592.

Roberts CM, Ballentine WJ, Buxton CD, Dayton P, Crowder LB, Milon W, Orbach MK, Pauly J, Trexler J, Walters CJ (1995) Review of the use of marine fishery reserves in the U.S. southeastern Atlantic. NOAA Technical Memorandum NMFS-SEFSC-376. 31 pp.

Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. Science 294(5548):1920-1923.

Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar Ecol Prog Ser 41:1-8.

Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? Rev Fish Biol Fish 1:65-91.

Roberts CM, Polunin NVC (1993) Marine reserves: Simple solutions to managing complex fisheries? Ambio 22:363-368.

Robertson DR (1983) On the spawning behavior and spawning cycles of eight surgeonfishes (Acanthuridae) from the Indo-Pacific. Env Biol Fish 9:193-223.

Russ GR (2002) Yet another review of marine reserves as reef fishery management tools. Chapter 19. Pages 421-433 in PF Sale (ed). Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. Academic Press. London. 500 pp.

Russ GR, Alcala AC (1989) Effects of intense fishing pressure on an assemblage of coral reef fishes. Mar Ecol Prog Ser 56:13-27.

Russ GR, Alcala AC (1996a) Marine reserves: rates and patterns of recovery and decline of large predatory fish. Ecol Appl 6:947-961.

Russ GR, Alcala AC (1996b) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Mar Ecol Prog Ser 132:1-9.

Russ GR, Alcala AC (1998a) Natural fishing experiments in marine reserves 1983-1993: community and trophic responses. Coral Reefs 17:383-397.

Russ GR, Alcala AC (1998b) Natural fishing experiments in marine reserves 1983-1993: roles of life history and fishing intensity in family responses. Coral Reefs 17:399-416.

Sadovy Y (1989) Caribbean fisheries: problems and prospects. Progress in Underwater Science 13:169-184.

Sadovy Y (1997) Live reef-fish species feature prominently in first marine fish IUCN Red List. Live Reef Fish Inf Bull 2:13-14.

Sakai Y, Kohda M (1995) Foraging by mixed-species groups involving a small angelfish, *Centropyge ferrugatus* (Pomacanthidae). Jap J Ichthyol 41:429-435.

Sakurai M, Nakazono A (1995) Twilight migrations of the temperate Japanese surfperch *Neoditrema ransonneti* (Embiotocidae). Jap J Ichthyol 42:261-267.

Sale PF (1989) Diversity of the Tropics: Causes of High Diversity in Reef Fish Systems. Pages 1-20 In: Harmelin-Vivien ML, Bourliere F (Eds.) Vertebrates in Complex Tropical Systems. New York, Springer-Verlag. 200 pp.

Sale PF, Douglas WA (1981) Precision and accuracy of visual census techniques for fish assemblages on coral reef patch reefs. Env Biol Fish 6:333-339.

Sancho G (2000) Predatory behaviors of *Caranx melampygus* (Carangidae) feeding on spawning reef fishes: A novel ambushing strategy. Bull Mar Sci 66:487-496.

Sancho G, Petersen CW, Lobel PS (2000) Predator-prey relations at a spawning aggregation site of coral reef fishes. Mar Ecol Prog Ser 203:275-288.

Sarramegna S (2000) Contributions à l'étude des réserves marines du lagon sud-ouest de Nouvelle-Calédonie : influence des différents statuts sur la structure des peuplements ichtyologiques . Thèse de doctorat : Biologie des populations : Université de la Nouvelle-Calédonie. 436 pp.

Savina GC, White AT (1986) Reef fish yields and non-reef catch of Pamilacan Island, Bohol, Philippines, Pages 497-500 In: Maclean JL, Dizon LB, Hosillos LV (Eds.) Proceedings of the first asian fisheries forum. Asian Fisheries Society, Manila. 727 pp.

Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.

Shapiro DY (1987) Patterns of space use common to widely different types of social groupings of a coral reef fish. Env Biol Fish 18:183-194.

Shulman MJ (1985) Coral reef fish assemblages: Intra- and interspecific competition for shelter sites. Env Biol Fish 13:81-92.

Sinclair ARE (1984) The function of distance movements in vertebrates. Pages 240-258 In: Swingland IR, Greenwood PJ (Eds.) The ecology of animal movement. Clarendon Press, Oxford. 328 pp.

Sluka R, Chiappone M, Sullivan KM (1994) Comparison of juvenile grouper populations in southern Florida and the central Bahamas. Bull Mar Sci 54:871-880.

Sluka R, Chiappone M, Sullivan KM (1996) Habitat preferences of groupers in the Exuma Cays. Bahamas J Sci 4:8-14.

Sluka R, Chiappone M, Sullivan KM (1997) The benefits of a marine fishery reserve for Nassau grouper *Epinephelus striatus* in the central Bahamas. Proc 8th Int Coral Reef Symp 2:1961-1964.

Smith A, Dalzell P (1993) Fisheries resources and management investigations in Woleai Atoll, Yap State, Federated States of Micronesia. South Pacific Commission, Nouméa, New Caledonia. Inshore Fish Res Proj Tech Doc 4. 64 pp.

Sokal RR, Rohlf FJ (1995) Biometry: The principles and practice of statistics in biological research. W. H. Freeman Company, New York. 887 pp.

Spencer SR, Cameron GN, Swihart RK (1990) Operationally defining home range: temporal dependence exhibited by hispid cotton rats. Ecology 71:1817-1822.

Stewart-Oaten A, Murdoch WM, Parker KR (1986) Environmental impact assessment: 'Pseudo-replication' in time? Ecology 67:929-940.

Swingland IR (1984) Intraspecific differences in movement. Pages 102-115 In: Swingland IR, Greenwood PJ (Eds.) The ecology of animal movement. Clarendon Press, Oxford. 328 pp.

Thresher RE (1979) Social behavior and ecology of two sympatric wrasses (Labridae: Halichoeres spp.) off the coast of Florida. Mar Biol 53:161-172.

Tissot BN, Hallacher LE (1999) Impacts of aquarium collectors on coral reef fishes in Hawai'i. Final Report. Honolulu, HI: Division of Aquatic Resources, Department of Land and Natural Resources, State of Hawai'i, 32 pp.

Tricas TC (1989) Determinants of feeding territory size in the corallivorous butterflyfish, *Chaetodon multicinctus*. Anim Behav 37:830-841.

Tupper M, Juanes F (1999) Effects of a Marine Reserve on Recruitment of Grunts (Pisces: Haemulidae) at Barbados, West Indies. Env Biol Fish 55:53-63.

Underwood AJ (1993) The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. Aust J Ecol 18:99-116.

Walsh WJ III (1984) Aspects of nocturnal shelter, habitat space, and juvenile recruitment in Hawaiian coral reef fishes. Ph.D. dissertation. University of Hawai'i Department of Zoology. 475pp

Wantiez L, Thollot P, Kulbicki M (1997) Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. Coral Reefs 16:215-224.

Wass RC (1982) The shoreline fishery of American Samoa: past and present. Pages 51-83 In: JL Munro (ed). Marine and Coastal Processes in the Pacific: Ecological Aspects of Coastal Zone Management. UNESCO Special Publication. UNESCO Seminar on Marine and Coastal Processes in the Pacific. Motupore Island Research Centre, Papua New Guinea, July 14-17, 1980.

Woodley SJ (1985) The Great Barrier Reef Marine Park: The management challenge. Proc Fifth Int Coral Reef Congress 4:259-264.

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Wright A, Richards AH (1985). A multispecies fishery associated with coral reefs in the Tigak Islands, Papua New Guinea. Asian Mar Biol 2:69-84.

Yabuta S, Kawashima M (1997) Spawning behavior and haremic mating system in the corallivorous butterflyfish, *Chaetodon trifascialis*, at Kuroshima Island, Okinawa. Ichthyol Res 44:183-188.

Zeller DC (1997) Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). Mar Ecol Prog Ser 154:65-77.

Zeller DC, Russ GR (1998) Marine reserves: Patterns of adult movement of the coral trout (*Plectropomus leopardus* (Serranidae). Can J Fish Aquat Sci 55:917-924.