

Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve

Carl G. Meyer^{a,b}, Kim N. Holland^b, Bradley M. Wetherbee^c & Christopher G. Lowe^d

^aDepartment of Zoology, Edmonson Hall, University of Hawaii at Manoa, Honolulu, HI 98822, U.S.A. (e-mail: carlm@hawaii.edu)

^bHawaii Institute of Marine Biology, University of Hawaii at Manoa, P.O. Box 1346, Coconut Island, Kaneohe, HI 96744, U.S.A.

^cNOAA-NMFS-NESC, 28 Tarzwell Drive, Narragansett, RI 02882, U.S.A.

^dCalifornia State University, Long Beach, 1250 Bellflower Boulevard, Long Beach, CA 90840, U.S.A.

Received 28 October 1999

Accepted 10 June 2000

Key words: coral reef fishes, diel behavior patterns, acoustic telemetry, remote monitoring, hardwired array, management tools

Synopsis

Suitability of small (< 1 km²) marine reserves for protecting a commercially important endemic Hawaiian goatfish, *Parupeneus porphyreus*, was examined by quantifying goatfish habitat use, home range size and site fidelity in an existing marine reserve (Coconut Island in Kaneohe Bay, Hawaii). Five goatfish equipped with acoustic transmitters were tracked for up to 93 h each over 3–14 days. Daytime habitat use patterns of two of these fish were continuously monitored for one month using a fixed hydrophone hardwired to an onshore computer. Acoustically tagged fish showed consistent diel patterns of behavior, refuging in holes in the reef by day and moving over extensive areas of sand and coral rubble habitat at night. Remote monitoring of daytime habitat use by two goatfish revealed that the same daytime refuge was used by both fish for at least one month (the battery life of the transmitters). Home ranges of all fish were within the boundaries of the Coconut Island reserve suggesting that even small areas containing suitable habitat can make effective reserves for this species. A relatively low abundance of reproductive size *P. porphyreus* at Coconut Island in comparison with deeper areas may indicate an ontogenetic shift to deeper habitat in this species.

Introduction

The whitesaddle goatfish, *Parupeneus porphyreus* (family Mullidae) is an endemic Hawaiian goatfish. Often young are common on inshore reefs while adults are known to occur in depths of up to 140 m (Randall 1996). *P. porphyreus* occur close to cover during the day, often in groups of 2–10 individuals and very occasionally in groups of up to 100 individuals (Hobson 1974). At night, *P. porphyreus* are thought to move across the substrate probing for food with mandibular

barbels (Holland 1978). The major food items are benthic crustaceans and fish, the latter becoming more important in the diet of larger individuals (Hobson 1974, Mahi 1969).

Goatfish are of considerable commercial value throughout the Pacific Ocean, where they are noted as having soft, sweet flesh. *P. porphyreus* has long maintained a reputation for being the best tasting of the Hawaiian goatfishes and in ancient Hawaii *P. porphyreus* was used extensively as an offering to the gods and women were forbidden by kapu

(taboo) to eat its flesh (Titcomb 1972). *P. porphyreus* (Hawaiian name: kumu) is still highly esteemed in Hawaii (retailing for between US\$15–30 kg⁻¹) and, because it remains a favored target of both trap and spear fishermen, concern exists that the stock is over-fished and may have significantly declined.

In recent years, 'no-fishing' marine reserves have been increasingly suggested as viable fisheries management tools for exploited coral reef fish species (e.g., Bohnsack 1993, Dugan & Davis 1993, Roberts & Polunin 1993, Nowlis & Roberts 1997, 1999, Hastings & Botsford 1999). *P. porphyreus* is one of several important exploited Hawaiian reef fish species that may benefit from protection in marine reserves. This study aims to evaluate the potential suitability of marine reserves for protecting *P. porphyreus* by examining movement patterns, habitat utilization, home range size and site fidelity of this species in an existing reserve.

Methods

Study area

Coconut Island (Kaneohe Bay, Oahu, Hawaii) is surrounded by 137 000 m² of shallow patch reef (circumference of about 2.4 km) which descends steeply to a mud and silt bay floor (depth approximately 13 m). The top of the reef flat is comprised of sand and coral rubble and depth varies between 0.25 and 1.5 m, with a few deeper pools and trenches. The nearest adjacent reef is about 50 m away across a 13 m deep channel. The Coconut Island reef has been a no-fishing conservation zone for over 30 years and, consequently, animals remaining within its confines live in a virtually undisturbed environment.

Active tracking

Short term movement patterns, habitat use and home range size of *P. porphyreus* were determined using two types of acoustic telemetry; active tracking and continuous electronic monitoring of daytime habitat. The fish used in the telemetry studies were caught in the Coconut Island reserve using either traps or a fine-meshed surround net. The fish were maintained in captivity for several days following capture to ensure that they were healthy prior to tracking. Following

this observation period, the fish were anaesthetized with MS-222 (0.75 g l⁻¹) and sonic transmitters (0.8 cm diameter, 3.0 cm long, model V8, Vemco, Halifax, Nova Scotia) with individualized frequencies (ranging between 65.4 kHz and 76.8 kHz) were either attached to their dorsal surface or surgically implanted into the body cavity. Both methods of transmitter attachment proved satisfactory.

Dorsal attachment of the transmitter was similar to that previously used successfully with several species of jack and tuna (Holland et al. 1990, 1996). The cylindrical transmitters were attached to the fish with thin, 0.28 cm wide nylon straps ('cable ties'). These were installed by passing a 0.3 cm O.D. hypodermic needle completely through the dorsal musculature 1 cm below the dorsal surface of the fish, inserting the tip of the strap into the needle and then retracting the needle. In this way, the strap could be pulled completely through the fish. The strap was then passed through a ring on the front end of the transmitter and pulled tight, forming a complete loop. A thin piece of plastic covered wire was inserted in similar fashion at the other end of the transmitter to hold it snugly against the side of the first dorsal fin.

Surgically implanted transmitters were inserted through a 25 mm longitudinal incision in the abdominal wall, posterior to the rear ventral corner of the pectoral fin. The transmitter was smeared with antibiotic cream and pushed through the incision which was then closed with surgical staples. Each fish was kept in captivity for several days prior to release at its original point of capture.

Tracking commenced immediately following a fishes release and was conducted from a 5.5 m outboard-motor powered boat equipped with a directional hydrophone, and navigational and communications equipment. During tracking fish location was recorded at fifteen minute intervals as X,Y coordinates on a chart of the Coconut Island reef. More frequent positional fixes were recorded if the fish showed a distinct change in the direction or speed of movement. These tracking methods are described in greater detail in Holland et al. (1992). Minimum convex polygons were used to describe the maximum area covered by each animal (MacDonald et al. 1980, Klimley & Nelson 1984, Spencer et al. 1990). To increase spatial resolution, fish movements were also analyzed using grid-square analysis (Winter & Ross 1982, Holland et al. 1993, 1996) which compiles the number of times a fish visits a particular grid cell during the tracking period,

thereby displaying the extent of its movements and highlighting areas most frequently visited.

Continuous remote monitoring of daytime habitat

To determine medium-term (up to 1 month) fidelity of *P. porphyreus* to daytime habitat and the patterns of usage of this habitat, two fish carrying transmitters were continuously monitored over the course of a month using an omni-directional hydrophone placed in daytime habitat and connected via a 30 m cable to a laptop computer located on shore. The computer was equipped with software for logging transmitter pulse signal strength at 1 min intervals. Individual fish were identifiable from the different output frequencies of their transmitters.

Long-term site fidelity and dispersal

Between 1991 and 1995, all specimens of *P. porphyreus* caught in the Coconut Island refuge 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. Each tag carried a reward notice and a phone number, and posters were distributed locally to increase public awareness of the tag-and-release program. Tagged fish recaptured within the Coconut Island refuge by scientific personnel were remeasured and released.

Results

Home range location, size and habitat content

Five *P. porphyreus* (205 to 257 mm FL) were tracked for up to 92 hours over periods spanning 3 to 14 days (Table 1). The home ranges of all five fish were within the boundaries of the Coconut Island refuge (Figure 1). Home range habitat included areas of reef flat (sand, coral rubble) and live coral but did not include the flat, muddy bottom surrounding the Coconut Island patch reef. Home range size calculated from convex polygons varied for each fish from 9070 to 35 163 m² (Table 1).

Table 1. Summary of tracking data from five *P. porphyreus* captured and released within the Coconut Island marine reserve.

Fish no.	Fork length (cm)	Weight (g)	Duration of track (h)	Home range size (m ²)	Transmitter placement
1	23.3	—	45	9070	Internal
2	25.7	413	48	35163	Internal
3	20.5	186	92	16763	External
4	22.5	—	42	12098	External
5	24.1	336	74	22909	External



Figure 1. Home range size of five *P. porphyreus* tracked in the Coconut Island marine reserve. Shaded area = terrestrial habitat, light dashed line = 1 m depth contour, bold lines = minimum convex polygons (MCP) denoting home range borders of each fish. MCP's include all positional fixes. Split home range of fish no. 5 is indicated by two separate polygons.

A general trend of increasing home range size with increasing fish size was apparent but these variables were not significantly correlated ($r = 0.72$, $df = 3$, $p > 0.05$). Several fish had overlapping home ranges and shared the same daytime habitat.

Daily movement patterns

Tracked fish exhibited a clear diel pattern of movement. During daytime, the fish remained in holes in the reef (typically with 2 to 10 other conspecifics) and made small, highly localized movements in the immediate vicinity of their holes. They typically showed high fidelity to their daytime habitat, returning to the same holes each day. Within 15–30 min after sunset, each fish left its daytime habitat and moved several hundred meters to nocturnal habitat on sand flats 0.5–1.5 m deep. Although each fish returned to the same general area of sand flats each night, there was some variability in specific areas visited by each fish. The fish typically remained in nocturnal habitat until 30 min before sunrise when they returned directly to their daytime holes. To further illustrate this pattern, a synopsis of the movements of four of the tracked fish is given below.

Fish no. 2 (FL = 257 mm) was the largest animal tracked (Table 1). This fish was trapped and released in the 2.5–3.5 m deep entrance channel to the Coconut Island lagoon (Figure 2), and tracked continuously for 48 h (2 day–night cycles). During all daylight hours, the fish remained largely quiescent in the lagoon entrance channel. Within 15 min after sunset (18:03 h) this fish left the channel and swam approximately 500 m N over the adjacent sand flats to shallow (< 1 m) habitat consisting of sand and coral rubble, where it moved around over approximately 10 000 m² of flats for up to 9 h. On both nights, this fish returned temporarily to its daytime habitat before again swimming up to 300 m N over the flats, where it moved around over approximately 3600 m² of sand and rubble until shortly before sunrise when it returned to the lagoon entrance channel.

Fish no. 3 (FL = 205 mm, Wt = 186 g) and fish no. 4 (FL = 225 mm FL) were captured simultaneously by surround-netting at a known daytime habitat on the east side of Coconut Island (Figures 3, 4). On two occasions (totaling 42 hours) both fish were tracked simultaneously and, although these fish shared the same daytime habitat, their nocturnal activities were centered in different areas. Remote monitoring of daytime habitat revealed that both fish maintained fidelity to their daytime habitat for at least one month (the lifespan of the transmitter batteries) and during this time each maintained a clear pattern of behavior; remaining in their hole by day, departing at sunset and returning at sunrise. A description of the individual movements of these two fish follows.

Fish no. 3 was tracked on three successive occasions, at approximately weekly intervals, for a total of 92 h

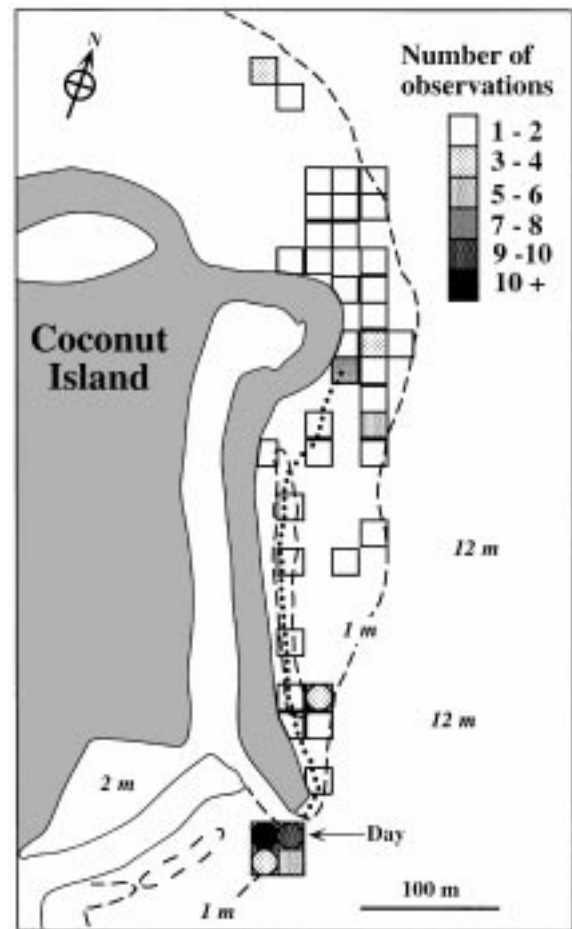


Figure 2. Grid square analysis of the diel movements of fish no. 2. Daytime (circles) was spent refuging in the 2 to 3 m deep entrance channel to the Coconut Island lagoon. Nighttime (squares) was spent on shallow sand flats approximately 500 m N of daytime habitat. Dotted line denotes route taken between daytime and nighttime habitats. Shading of grid squares denotes the number of times that the fish was observed in each 20 × 20 m cell.

(5 day–night cycles). This fish left its daytime hole within 15 min of sunset (19:00 h) each evening, and traveled up to 220 m N to shallow (< 1 m) nighttime habitat (Figure 3). Nocturnal movement patterns varied between nights. On the first two nights, it moved around in a 3200 m² area of sand and rubble flats approximately 100 m N of the daytime hole. On the third night of tracking (one week later) the fish was relocated in this area of flats but at 1:30 h it moved to an adjacent area of high coral cover on the reef edge where it remained quiescent until returning to its daytime hole just before sunrise. On the fourth night, the fish returned to this

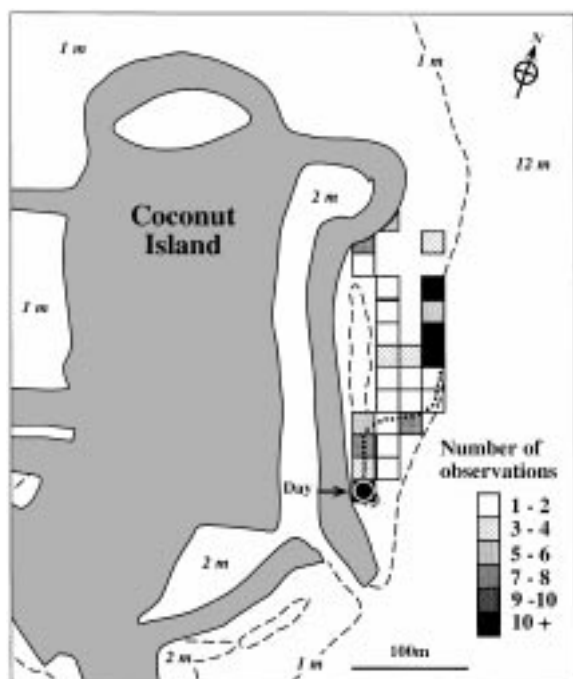


Figure 3. Diel habitat use by fish no. 3. Daytime (circles) was spent in a hole under coral heads in a 2.5 m deep depression in sand flats on the east side of Coconut Island. Nighttime (squares) was spent moving across the sand flats to 100–200 m N of the daytime habitat. Dotted line = route taken between daytime and nighttime habitats. Grid squares = 20 × 20 m.

reef edge location and moved back and forth along a 100 m stretch of live coral. On the fifth night of tracking (again, one week later), the fish returned to the same area of reef edge habitat for several hours before moving to an area of sand flats approximately 200 m N of its daytime habitat. The fish moved around this area of sand flats for approximately 5 h then moved back to the previously visited reef edge location where it remained stationary until returning to daytime habitat shortly before sunrise.

Fish no. 4 (FL = 225 mm FL) was tracked on 2 occasions, spanning one week, for a total of 42 h (Table 1). Fish no. 4 spent the majority of daylight hours in the same hole as No. 3 but also hid underneath a coral head 50 m N of this location for up to several hours around sunrise each morning (Figure 4). This fish left the hole shortly after sunset (19:00 h) each evening and traveled 200 m N to a shallow (0.5–1 m) area of sand flats and coral heads where it moved around over approximately 1600 m² of habitat until returning to daytime habitat shortly before sunrise.

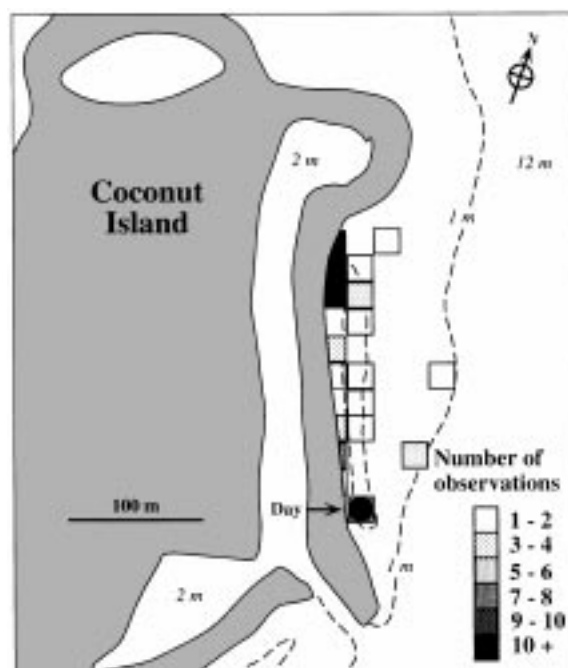


Figure 4. Diel movements of fish no. 4. Daytime (circles) was spent in the same hole as fish no. 3. Nighttime (squares) was spent moving over sand flats 200 m N of the daytime habitat. Dotted line indicates route taken between daytime and nighttime habitats. Grid squares = 20 × 20 m.

Fish no. 5 (FL = 241 mm, Wt = 336 g) was caught in a fish trap set on the reef wall on the west side of Coconut Island and tracked for 74 h over the course of a week during which time it showed a possible shift in home range. Following release it moved south along the reef wall into a 3–8 m deep channel on the west side of Coconut Island where it remained for the following 48 h (Figure 5). Four days later, this fish was relocated in a different daytime habitat (a 2.5 m deep, live coral fringed depression in sand flats on the south side of Coconut Island). During the remaining portion of the track, daylight hours were spent in this depression and nights were spent moving over approximately 6800 m² of sand flats immediately southeast of daytime habitat. Subsequent daytime spot checks, carried out every 2–3 days over 10 days, located the fish in the depression on each occasion.

Speed of movement

Mean minimum speeds of movement of each fish were calculated from straight line distance moved

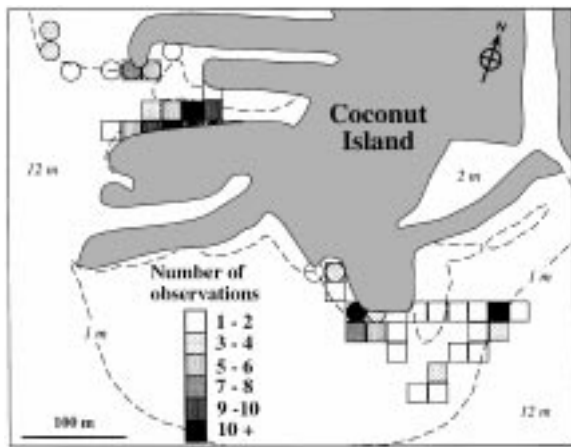


Figure 5. Diel habitat use by fish no. 5. Activities were split between two areas of the Coconut Island reef: a – The initial 48 h were spent in a 3–8 m deep channel on the west side of Coconut Island. b – Subsequent activities were restricted to the SE corner of Coconut Island reef. Daytime (circles) was spent among coral heads in a 2.5 m deep depression in the sand flats. Nighttime (squares) was spent on shallow (1 m) sand flats east of this pool. Grid squares = 20 × 20 m.

between positional fixes. Repeated stationary fixes were eliminated from calculations. During daylight hours, movement patterns were so restricted that swimming speeds are irrelevant. Nighttime mean minimum speed of movement of different fish ranged from 1.76–5.37 $\text{m}^{-1} \text{min}^{-1}$ (mean = 2.59 $\text{m}^{-1} \text{min}^{-1}$). Analysis of variance indicated no significant effect of fish size on movement speed ($F_{4,4} = 1.85$, $p < 0.05$).

Long-term dispersal patterns

Forty-six tagged *P. porphyreus* were released in the Coconut Island refuge between 1991 and 1995. Seven (15.2%) fish were subsequently recaptured from Coconut Island after times at liberty ranging from 24 to 112 days (mean 58 days). None were reported captured outside Coconut Island. The size frequency distribution of 64 *P. porphyreus* caught in traps ($n = 42$), seine nets ($n = 12$) and gill nets ($n = 10$) is illustrated in Figure 6. *P. porphyreus* caught in the Coconut Island refuge ranged from 157 mm to 303 mm FL (mean 217 mm FL) with a distinct mode at 210 mm. Seventy-five percent of these were smaller than the size at first reproduction (SFR) of approximately 240 mm FL (Moffit 1979).

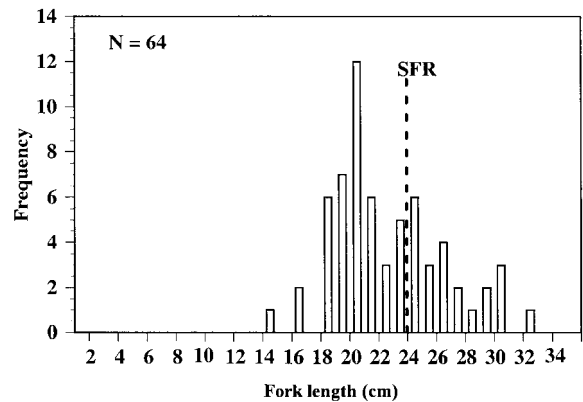


Figure 6. Length frequency composition of *P. porphyreus* captured in the Coconut Island marine reserve 1991–1995. Dashed vertical line indicates size at first reproduction (SFR) according to Moffit (1979).

Discussion

The whitesaddle goatfish tracked in this study showed patterns of behavior that were broadly similar to the nocturnally active yellowfin goatfish, *Mulloides flavolineatus*, that are also found within the Coconut Island marine reserve (Holland et al. 1993). Both goatfish species were largely quiescent by day, became active at around sunset and moved to distant nocturnal feeding areas where they remained active throughout the night. They returned to daytime habitat around sunrise. Both goatfish species utilized similar sized areas of shallow, flat sand and rubble habitat at night, with individuals frequently revisiting the same areas on successive nights.

Although nighttime behavior and habitat utilization for the two goatfish species are similar, there are significant differences in daytime behavior and habitat preference. Yellowfin goatfish form large daytime schools (> 100 individuals) loosely associated with reef structure and individual fish occasionally switch from one daytime school to another. By contrast, *P. porphyreus* typically refuged alone or in small groups (2–10 individuals) in holes in the reef and displayed strong fidelity to these holes; two tracked fish used the same hole daily for at least a month.

Strong fidelity to daytime holes may make *P. porphyreus* particularly vulnerable to spear fishermen because this behavior concentrates these fish in predictable locations where they can be found repeatedly and where they are comparatively easy targets.

Grigg (1994) suggests that the predictable occurrence of aggregations of Hawaiian reef fish in areas of high relief (known in the Hawaiian language as 'koa' or 'fish house'), increases their catchability and may partially explain why some coral reef fishes are vulnerable to overexploitation.

Diel movement and habitat use patterns of *P. porphyreus* and *M. flavolineatus* are similar to those observed in Caribbean grunts (Haemulidae), which also undertake crepuscular foraging migrations between daytime reef and nocturnal sand flat habitats (Burke 1995, McFarland & Wahl 1996). They also exhibit individual site fidelity to both daytime and nighttime habitat (Burke 1995). The use of structurally complex reef habitat for refuging and the use of sand flat habitat for foraging is a behavioral style shared by several families of coral reef fish. Grigg (1994) observed that in Hawaii, reef fish biomass exceeds theoretically predicted carrying capacities in areas of high relief and suggested that the fish inhabiting these areas must forage over much larger areas at night to meet their metabolic needs. The current data support that contention.

The data from this study indicate that small (< 1 km²) marine reserves could be effective in protecting this highly targeted goatfish. First, the home ranges of all the tracked *P. porphyreus* were within the boundaries of the Coconut Island patch reef, indicating that even this comparatively small marine reserve contains sufficient suitable daytime and nighttime habitat to support individuals of this species. Second, two of the *P. porphyreus* tracked (and 25% of all those captured at Coconut Island) were above SFR indicating that a refuge the size of Coconut Island can protect both large juveniles and some spawning size individuals.

The rate and extent of dispersal of *P. porphyreus* from Coconut Island remains unclear because of the small number of tagged fish released and recaptured within the marine reserve (maximum time at liberty 112 days) and the absence of recaptures from remote locations. However, the low proportion of adult fish in trap catches from Coconut Island in comparison to commercial trap catches from deeper areas (Moffit 1979) suggests that *P. porphyreus* may disperse from Coconut Island after reaching sexual maturity and move to deeper habitat. If this is the case, harvest refugia designed to protect large adult whitesaddle goatfish should include deeper habitat than is available at the Coconut Island patch reef. Similar ontogenetic shifts in tropical reef habitat

have been demonstrated for french grunt, *Haemulon flavolineatum* (McFarland 1979, Quinn & Ogden 1984) and data from a variety of coastal shelf fisheries also suggest that fish commonly move offshore as they increase in size (e.g. Smale 1988).

Acknowledgements

The authors wish to thank the tracking volunteers who assisted during this study, especially Aaron Bush, Filiesha Le Rand and Fred Farell. This work was funded by the Main Hawaiian Islands Marine Resources Investigation, Division of Aquatic Resources, Department of Land and Natural Resources, State of Hawaii.

References cited

- Bohnsack, J.A. 1993. Marine reserves they enhance fisheries, reduce conflicts, and protect resources. *Oceanus* 36: 63–71.
- Burke, N.C. 1995. Nocturnal foraging habitats of French and bluestriped grunts, *Haemulon flavolineatum* and *H. sciurus*, at Tobacco Caye, Belize. *Env. Biol. Fish.* 42: 365–374.
- Dugan, J.E. & G.E. Davis. 1993. Applications of marine refugia to coastal fisheries management. *Can. J. Fish. Aquat. Sci.* 50: 2029–2042.
- Grigg, R.W. 1994. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Mar. Ecol. Prog. Ser.* 103: 25–34.
- Hastings, A. & L.W. Botsford. 1999. Equivalence in yield from marine reserves and traditional fisheries management. *Science* 284: 1537–1538.
- Hobson, E.S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona Hawaii. *U.S. Fish. Bull.* 72: 915–1031.
- Holland, K.N. 1978. Chemosensory orientation to food by Hawaiian goatfish (*Parupeneus porphyreus*, Mullidae). *J. Chem. Ecol.* 6: 173–186.
- Holland, K.N., R.W. Brill & R.K.C. Chang. 1990. Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregation devices. *U.S. Fish. Bull.* 88: 493–507.
- Holland, K.N., C.G. Lowe & J.D. Peterson. 1992. Tracking coastal sharks with small boats: hammerhead sharks as a case study. *Aust. J. Mar. Freshwater Res.* 43: 61–66.
- Holland, K.N., J.D. Peterson, C.G. Lowe & B.M. Wetherbee. 1993. Movements, distribution and growth rates of the white goatfish *Mulloidés flavolineatus* in a fisheries conservation zone. *Bull. Mar. Sci.* 52: 982–992.
- Holland, K.N., C.G. Lowe & B.M. Wetherbee. 1996. Movement and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. *Fish. Res.* 25: 279–292.
- Klimley, A.P. & D.R. Nelson. 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.

- MacDonald, D.W., F.G. Ball & N.G. Hough. 1980. The evaluation of home range size and configuration using radio tracking data. pp. 40–426. *In*: C.J. Amlaner & D.W. MacDonald (ed.) Handbook of Biotelemetry and Radio Tracking, Pergamon Press, Oxford.
- Mahi, C.A. 1969. The food and feeding habits of the Kumu, *Parupeneus porphyreus*. M.S. Thesis, University of Hawaii, Honolulu. 188 pp.
- McFarland, W.N. 1979. Observations on recruitment in haemulid fishes. Proceedings of the Gulf Caribbean Fisheries Institute, University of Miami 32: 132–138.
- McFarland, W.N. & C.M. Wahl. 1996. Visual constraints on migration behavior of juvenile French grunts. *Env. Biol. Fish.* 46: 109–122.
- Moffit, R.B. 1979. Age, growth and reproduction of the Kumu, *Parupeneus porphyreus* Jenkins. M.S. Thesis, University of Hawaii, Honolulu. 272 pp.
- Nowlis, J.S. & C.M. Roberts. 1997. You can have your fish and eat it too: theoretical approaches to marine reserve design. *Proc. 8th Int. Coral Reef Symp.* 1–4.
- Nowlis, J.S. & C.M. Roberts. 1999. Fisheries benefits and optimal design of marine reserves. *U.S. Fish. Bull.* 97: 604–616.
- Quinn, T.P. & J.C. Ogden. 1984. Field evidence of compass orientation in migrating juvenile grunts (Haemulidae). *J. Exp. Mar. Biol. Ecol.* 81: 181–92.
- Randall, J.E. 1996. *Shore Fishes of Hawaii*. Natural World Press, Honolulu. 216 pp.
- Roberts, C.M. & N.V.C. Polunin. 1993. Marine reserves: simple solutions to managing complex fisheries? *Ambio* 22: 363–368.
- Smale, M.J. 1988. Distribution and reproduction of the reef fish *Petrus rupestris* (Pisces: Sparidae) off the coast of South Africa. *S. Afr. J. Zool.* 23: 272–287.
- Spencer, S.R., G.N. Cameron & R.K. Swihart. 1990. Operationally defined home range: temporal dependence exhibited by hispid cotton rats. *Ecology* 71: 1817–1822.
- Titcomb, M. 1972. *Native Use of Fish in Hawaii*. University Press of Hawaii, Honolulu. 175 pp.
- Winter, J.D. & M.J. Ross. 1982. Methods in analyzing fish habitat utilization from telemetry data. pp. 273–279. *In*: N. Armantrout (ed.) Proceedings of the Symposium on Acquisition and Utilization of Aquatic Habitat Inventory Information, American Fisheries Society, Western Division, Portland.