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Use of a marine reserve in Kaneohe Bay, Hawaii by the giant trevally, *Caranx ignobilis*

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Abstract

Movement patterns, site fidelity and growth were studied for giant trevally (*Caranx ignobilis*) inhabiting a marine reserve surrounding Coconut Island in Kaneohe Bay, off the Island of Oahu, Hawaii. Short-term movements of fish were determined by acoustic telemetry and long-term movements and growth were investigated with conventional tag and release methods. Giant trevally appear to move to the Coconut Island marine reserve from the adjacent bay floor upon attaining a size of approximately 20–25 cm fork length. After several years spent frequenting the reserve, giant trevally move out of the bay into deeper water. Tracked fish spent considerable time within the marine reserve moving along the reef slope, but frequently ventured outside of the reserve boundaries. The recapture rate for tagged fish was 11%, with an average time at liberty of 346 days. Nearly one-third of recaptured fish were caught at distances greater than 3 km from the tagging site with maximum values demonstrating long-term (more than 7 years) and long-distance (30 km) movements. The protective function of the Coconut Island marine reserve for giant trevally is limited because the reserve is utilized by only a portion of the population, and even these fish regularly move outside of the refuge.

Keywords: Habitat use; Telemetry; Tagging; Movement patterns

1. Introduction

The giant trevally, *Caranx ignobilis* (Family: Carangidae) is widely distributed within the Indo-Pacific region, ranging from the Indian Ocean to waters of the Hawaiian and Marquesas Islands in the central Pacific Ocean (Talbot and Williams, 1956; Williams, 1958; Berry et al., 1981). This species occurs individually and in schools of up to several hundred fish, is generally found nearshore, at depths of less than 20 m, but occasionally to at least 100 m, and attains sizes as large as 165 cm (66 kg) (Forster, 1984; Sudekum et al., 1991; Randall, 1996). In the Hawaiian Islands, *C. ignobilis* is one of the most common carangids (Gosline and Brock, 1960). This species is a highly mobile predator, with a diverse diet, and hence has a significant role in the trophic ecology of nearshore communities in Hawaii (Major, 1978; Sudekum et al., 1991; Meyer et al., 2001).

Because of its abundance, large size, and palatability, *C. ignobilis* was caught by native Hawaiians in ancient times (Titcomb, 1972), and is presently targeted in commercial and recreational fisheries in

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the Hawaiian Islands (Williams, 1965; Kobayashi, 1993; Meyer et al., 2001). Because of its popularity, there has been considerable fishing pressure on the stocks in recent decades and populations in the main Hawaiian Islands have been depressed (Shomura, 1987).

The most extensive study on *C. ignobilis* was conducted by Sudekum et al. (1991) on the diet, reproduction, and age and growth of fish from the remote, uninhabited, Northwestern Hawaiian Islands. Smaller scale studies on the diet (Meyer et al., 2001), feeding behavior (Major, 1978) spawning and reproduction (von Westernhagen, 1974; Johannes, 1981; Lewis et al., 1983) and fisheries (Seki, 1986; Kobayashi, 1993) of *C. ignobilis* have also been reported. Despite its abundance and importance to fisheries, there have been few studies on the biology of this species in the main Hawaiian Islands and there is little information upon which to base management decisions aimed at recovering stocks and promoting wise utilization of this resource.

Marine reserves have received increasing attention as a management method for conservation and recovery of marine fish populations (Bohnsack, 1993; Roberts and Polunin, 1993; Pauly et al., 1998; Li, 2000). However, there is a lack of detailed and scientifically defensible knowledge regarding the effectiveness of marine refuges on current yields and future abundance of fish populations (Carr and Reed, 1993; Dugan and Davis, 1993; Soh et al., 2000). An important determinant of the effectiveness of marine reserves for enhancing fish populations is the movement patterns of fish in relation to protected areas (Polacheck, 1990). Coconut Island in Kaneohe Bay, Hawaii, has been a marine reserve for over 30 years (Randall, 1969) and has been the site of a number of studies on the efficacy of a small marine reserve for enhancing stocks of species of reef fishes that are important in commercial and recreational fisheries (Holland et al., 1993, 1996; Meyer et al., 2000). This study was undertaken to evaluate the effectiveness of the Coconut Island marine reserve for *C. ignobilis* through investigation of the extent that the reserve is used by this species. Holland et al. (1996) conducted similar studies on a closely related species (*Caranx melampygus*), which offers an opportunity to compare use of the Coconut Island reserve by these congeneric fishes.

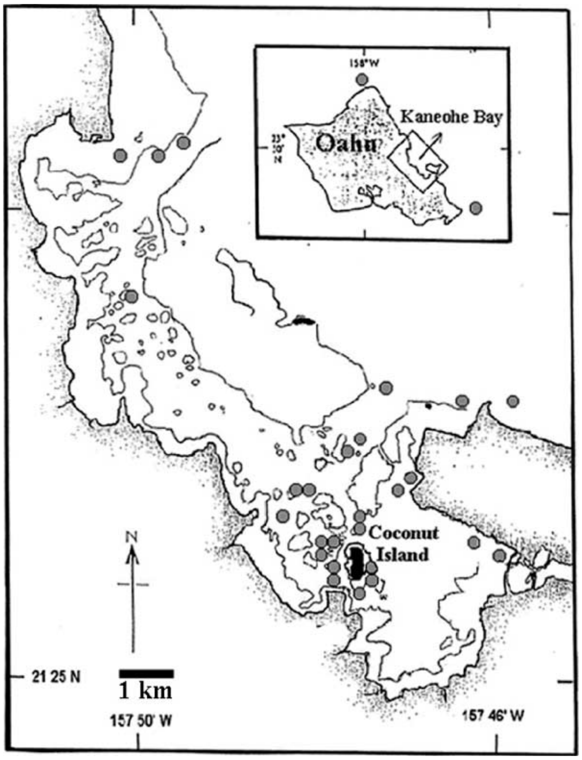

Fig. 1. Map of Oahu, Hawaii, with inset of the Kaneohe Bay study site. Recapture locations are shown for 28 *C. ignobilis* originally tagged and released at Coconut Island or the adjacent bay floor (contour line = 2 m reef depth).

2. Materials and methods

2.1. Study site

This study was conducted at the Hawaii Institute of Marine Biology, located on Coconut Island in Kaneohe Bay, Oahu, Hawaii (Fig. 1). Coconut Island is situated on a patch reef with a shallow (0.25–1.5 m) reef flat of sand and coral rubble that is interspersed with deeper pools and trenches (to 3 m). The total area of reef flat is roughly 137,000 m^2. The perimeter of the reef (approximately 2.4 km circumference) is surrounded by well-developed coral, which slopes steeply to the bay floor (mud and silt substratum) to a depth of about 13 m. Several dredged lagoons penetrate the interior of the reef flat and connect to the open bay. A major channel within the patch reef is 25–30 m wide, surrounded by mangroves and extends about 400 m into the interior of the reef. The nearest patch reef to Coconut Island is 40 m distant and is separated by deep water (13 m) and there are several other patch reefs within 1 km of the island. Coconut Island has been a marine reserve for over 30 years, with a no-fishing zone extending 8 m seaward of the reef edge.

2.2. Spatial segregation

To determine which segments of the *C. ignobilis* population frequented the Coconut Island vicinity, we compared length–frequency histograms of three groups of fish: (1) collected by research personnel with rod and reel from the Coconut Island reef and lagoons; (2) collected by research personnel with traps from the bay floor adjacent to the Coconut Island reef in deep (10–13 m) murky water and (3) collected by recreational fishermen using rod and reel in open water of Kaneohe Bay and nearby offshore areas. Fish in groups 1 and 2 were collected opportunistically at all times of the year between 1994 and 1998; fish in group 3 were collected during fishing tournaments held in September and October, 1991–1993 (see Meyer et al., 2001).

2.3. Long-term movement patterns

Long-term movements of *C. ignobilis* were investigated using conventional tagging. Tagged fish were captured either from Coconut Island with rod and reel, or from the bay floor adjacent to Coconut Island using traps set on the bottom at depths of 10–13 m. Fork length (FL) of captured fish was measured on a padded measuring board and weight was recorded with a hanging spring scale. All lengths reported in this study refer to fork length. Total length (TL) or standard length (SL) reported for fish recaptured by fishermen was converted to FL by the equations (Sudekum et al., 1991):

$$\mathrm{TL} = 1.070\,\mathrm{FL} + 35.7, \qquad \mathrm{SL} = 0.942\,\mathrm{FL} + 6.0$$

Fish were tagged with serially numbered plastic dart tags, 8 cm long, which contained reward information (Hallprint, South Australia). Tags of five different colors were used to allow for approximate determination of time at liberty for free-swimming fish that were re-sighted. Tags were applied into the musculature just below the dorsal fin and inserted so that the barb of the tag was placed between pterigiophores (see Holland et al., 1996). When large numbers of fish were captured in traps, they were transported in a holding tank to Coconut Island, where they were weighed, measured and tagged. They were then transported back to the site of capture and released. Posters advertising the tagging study were distributed within the community to increase the participation of local anglers. Tagged fish that were recaptured by scientific personnel were measured, weighed and released. For fish recaptured by anglers, date, time of day, location and length of the fish were recorded.

2.4. Short-term movement patterns

Short-term movement patterns of giant trevally around Coconut Island were investigated using acoustic telemetry (active tracking). Fish were captured by rod and reel at several locations on the Coconut Island reef and transported to a holding tank where they were held for several days to ensure that no injuries had occurred during capture. The fish were anesthetized with MS222 (0.1 g l^{-1}), weighed, measured, and fitted with transmitters. Individually coded transmitters (8 mm × 30 mm, 5 g weight in water) with frequencies of 65.5–76.8 kHz (Model V-8-6L, Vemco Ltd., Nova Scotia) were attached externally to fish. Transmitters were attached by passing a large gauge hypodermic needle through the dorsal musculature immediately below the dorsal fin, inserting a nylon strap (0.3 mm width) into the needle and pulling the nylon strap through the body of the fish by retracting the needle. The nylon strap was passed through a metal ring on the transmitter, cinched tight and the excess length of nylon strap cut. Midway along the length of the transmitter the needle was used to pass a plastic coated wire through the musculature to secure the transmitter in place (see Holland et al., 1996).

This method of transmitter attachment has proved successful in previous studies (Holland et al., 1993, 1996; Meyer et al., 2000) and several fish subjected to this procedure that were subsequently recaptured appeared to be healthy and to have completely recovered from the procedure. Each fish was also tagged with a plastic dart identification tag. Following transmitter attachment, fish were transported to the site of capture, released and tracking commenced. Tracking was conducted from a 5.5 m boat equipped with an outboard engine, VR-60 receiver, V-10 directional hydrophone (Vemco Ltd.), and communication and navigation equipment (Holland et al., 1992). Position of the tracking boat was recorded at 15-min intervals on a map of the Coconut Island vicinity overlaid with an *x*–*y* coordinate grid.

2.5. Analysis of tracking data

Movement data were plotted and analyzed using the Animal Movement extension (Hooge and Eichenlaub, 1997) for ArcView® GIS software (ESRI, Redlands, CA). The Animal Movement site fidelity test was used to test the null hypothesis that the movements of each tracked fish were random. This test utilizes a Monte Carlo simulation to compare observed movements with 1000 random walks incorporating the actual sequence of distances traveled by fish during each 15 min interval (Okubo, 1980; Spencer et al., 1990; Hooge and Eichenlaub, 1997). Minimum convex polygons (MCP) were used to estimate the maximum area covered by each fish (MacDonald et al., 1980; Klimley and Nelson, 1984) and probabilistic Kernel Utilization Distribution (KUD) home range estimator was also calculated for each fish to increase spatial resolution (Worton, 1989; Seaman and Powell, 1996). KUD home ranges highlighted areas used most frequently by animals and thus provided higher resolution information on use of habitat and space. The total linear amount of reef face utilized by each fish was defined as the distance between the most distant points along the reef visited by each fish (regardless of frequency of the visits) during the entire track. This distance included the length of the sides of channels and lagoons visited by tracked fish.

3. Results

3.1. Spatial segregation

A total of 321 *C. ignobilis* was captured in our study, 231 were captured in traps on the bay floor adjacent to Coconut Island, 58 were caught from Coconut Island and 32 were caught in fishing tournaments (Fig. 2). Size of fish captured at Coconut Island ranged from 13.8 to 43.0 cm, with an average of 28.2 ± 6.2 cm. Only 5 of the 58 (8.6%) fish captured at Coconut Island were 20 cm or smaller, and 12 fish (20.6%) were less than 25 cm. Fish captured in traps tended to be smaller (range 15.5–36.7, average 22.3 ± 2.9 cm). Of 231 fish caught in traps, 21% were 20 cm or smaller, and 85% were less than 25 cm. The largest individuals, and greatest range of sizes resulted from fishing tournaments (range 15.0–87.7 cm, average 31.4 ± 12.9 cm). Only one fish caught in the tournaments was smaller than 20 cm and five (15.6%) tournament caught fish were less than 25 cm. Fig. 3 shows the relationship between body weight and fork length for the range of fish sizes weighed and measured in this study.

3.2. Long-term movements

Of 289 *C. ignobilis* tagged (231 from traps on the bay floor and 58 from rod and reel at Coconut Island) 33 fish (11.4%) were recaptured. The shortest time at liberty for recaptured fish was 2 days and the average time was 346 ± 582 days. The maximum time at liberty for an individual fish recaptured could not be determined precisely because the numbered part of the tag was missing when the fish was recaptured. However, this fish was 1 of 134 individuals tagged with a red-colored tag in our study and was therefore at liberty for a minimum of 7 years and 1 month and a maximum of 9 years and 6 months. There was a relatively large gap of time between tagging date for the 133rd and 134th fish tagged with red tags. Presuming that this recaptured fish was not the last fish (134th) released with a red tag, but one of the other 133 individuals carrying red tags, the fish would have been at liberty for a minimum of 8 years and 3 months.

A high percentage of recaptured fish (78.8%) had been originally tagged at Coconut Island, but only 15.1% of fish were both tagged and recaptured at Coconut Island. Of 28 fish for which capture locations were reported, 32.1% were captured within 0.5 km of the tagging site, 14.3% between 0.5 and 1 km, 21.4% between 1 and 3 km, and 32.1% over 3 km from the tagging site (Fig. 1). One fish tagged at Coconut Island was recaptured more than 70 km away at Kaena Point, Oahu, after more than 7 years at liberty. Fish recaptured at Coconut Island or adjacent reefs tended to be smaller (mean FL = 31.7 ± 8.9 cm, $n = 12$) and

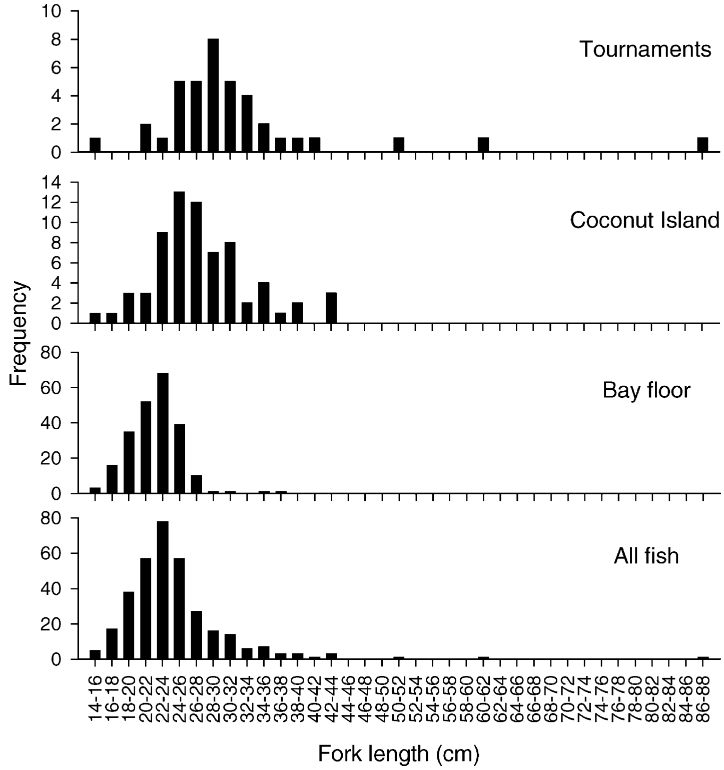

Fig. 2. Length–frequency histograms for all *C. ignobilis* examined in this study and for fish from three sources.

were at liberty for shorter amounts of time (mean = 145.8 ± 168.3 days, $n = 13$) than fish recaptured at distant locations (mean FL = 45.8 ± 25.2 cm, mean days at liberty = 509.1 ± 739.0 days, $n = 12$), although differences were not significant (t-test, $0.05 < P < 0.10$, d.f. = 11).

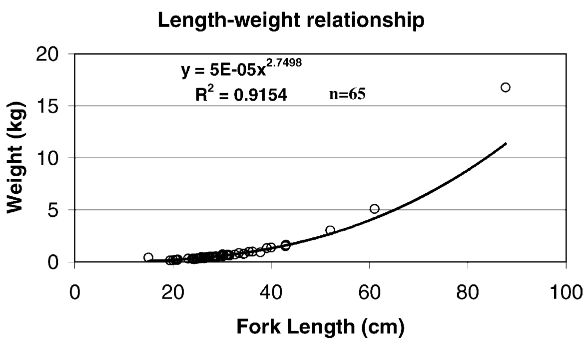

Fig. 3. Length–weight relationship for *C. ignobilis* weighed and measured in this study.

3.3. Short-term movements

Five *C. ignobilis* were tracked for up to 125 h, over periods spanning up to 14 days. The hypothesis that the observed movements were random was rejected for all fish tracked, indicating that each tracked fish showed some degree of site fidelity (Table 1). The home ranges of tracked fish, expressed as minimum convex polygon, KUD home range, and linear reef used were variable among individual fish (Table 1). The MCP home ranges, incorporating all positional fixes, ranged from 0.173 to 0.768 km^2. Activity of the fish was centered on Coconut Island, however, the island represented a large portion of the interior of the MCPs, and much of the space inside the polygons was not utilized (Fig. 4). For example, the KUD incorporating 95% of positional fixes occupied only 4.8–28.0% of their respective MCP home ranges, and the core activity spaces (50% KUD) occupied only 0.4–1.8% of their respective MCP home ranges (Table 1). Linear reef used by

Table 1
Summary of tracking data from *C. ignobilis* captured and released at the Coconut Island marine reserve

Fish #	Fork length (cm)	Weight (g)	Track duration (h)	MCP home range (km^2)	KHR (m^2)		KHR as % of MCP		Linear reef used (m)	MSD (m)	Site fidelity (*P*)
					95%	50%	95%	50%			
2	29.1	495	69	0.702	33658	3342	4.8	0.5	3702	63,650	99.9
3	33.3	748	125	0.173	41967	3188	24.3	1.8	2707	37,269	99.9
4	32.8	683	72	0.768	44380	2778	5.8	0.4	3863	151,961	99.9
5	36.5	960	9	0.326	91089	3604	28.0	1.1	1380	116,014	99.9

MCP: minimum convex polygon and KHR: kernel home range. MSD is the mean squared distance from the center of activities. *P* is the proportion of Monte Carlo simulated movement paths with higher MSD values than the observed data.

tracked fish ranged from 1380 to 3863 m (mean = 2913 ± 1142 m). None of the three measures of home range size were significantly correlated with track duration (Pearson Correlation coefficient, $P > 0.05$).

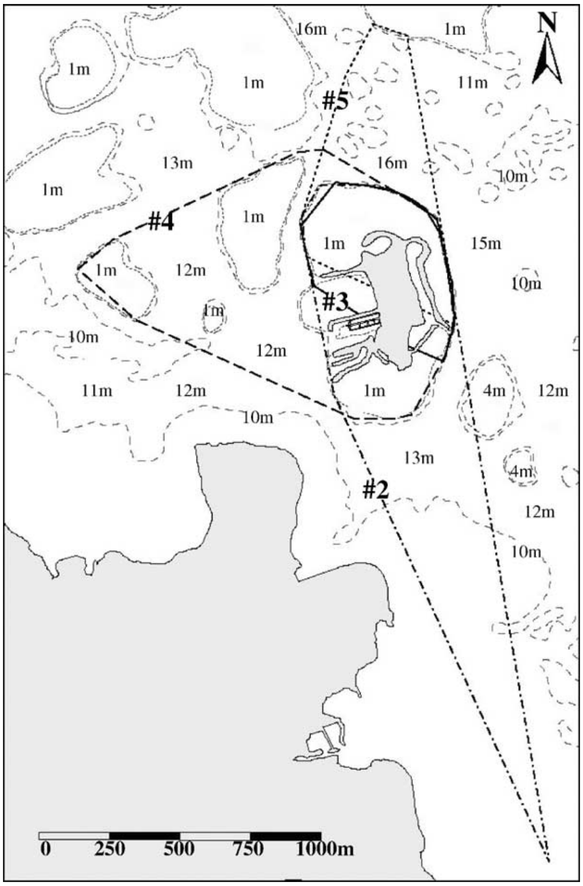

Fig. 4. Minimum convex polygons for four *C. ignobilis* tracked in the Coconut Island marine reserve. Each MCP encloses all positional fixes during an individual track. Shaded areas = land.

There was a significant ($P < 0.05$) positive correlation between fish size (weight) and 95% KUD size, but fish size was not significantly correlated with MCP or linear reef used. The home ranges (MCP) of three fish extended from 610 to 1750 m beyond the boundaries of the Coconut Island reserve. Home range habitat included primarily patch reef wall (live coral) and lagoon areas (mangrove), and to a much lesser extent the nearby reef flats (sand and coral rubble), and the deep, flat muddy areas between patch reefs (Figs. 5 and 6).

Tracked fish were generally more active at night and during crepuscular periods than during the day.

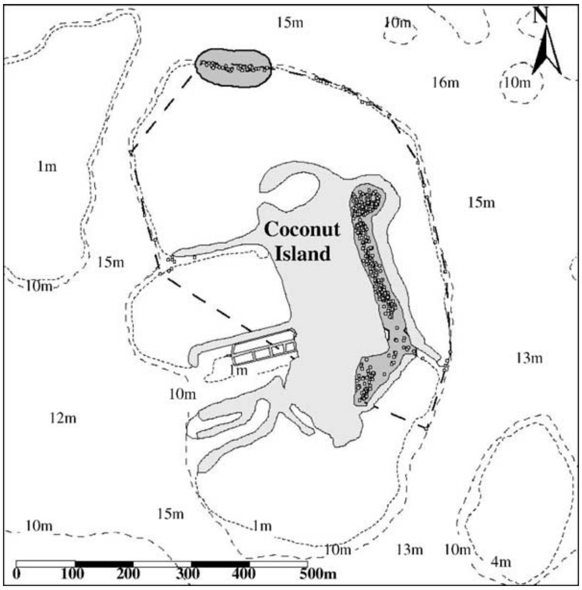

Fig. 5. Minimum convex polygon (dashed line) and kernel home ranges for fish #3 (33.3 cm FL) during 125 h of tracking. Small circles: positional fixes, shaded area within bold contour of 95% kernel home range.

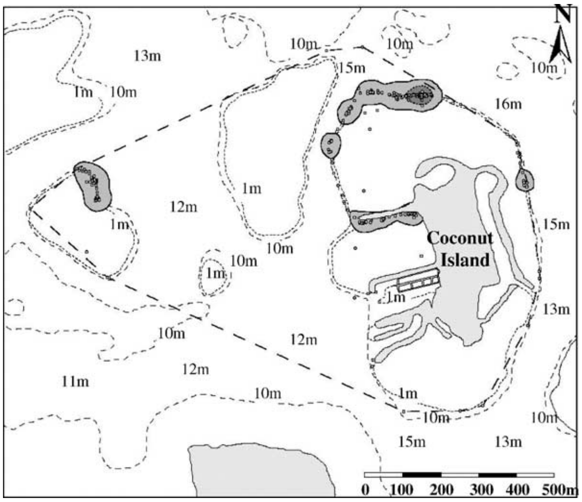

Fig. 6. Minimum convex polygon (dashed line) and kernel home ranges for fish #4 (32.8 cm FL) during 72 h of tracking. Small circles: positional fixes, light shaded area within bold contour of 95% kernel home range, dark shaded area within dotted contour of 50% kernel home range.

Although the fish were often active during both day and night, they tended to patrol greater distances along the reef edge at night and long quiescent periods usually occurred during the day. Shifts between locations were also more common at night and at dawn and dusk. One particular 150 m stretch along the north reef wall of Coconut Island was used by all five *C. ignobilis* tracked, even though the fish were tracked at different times of the year and were captured at several different locations around Coconut Island (Figs. 5 and 6). Two fish spent long periods (up to 48 h) in the recesses of the lagoon that extends within the Coconut Island reef (Fig. 5). Although tracked fish often revisited locations within their home ranges, the timing of these repeat visits did not appear to be related to temporal or tidal cycles.

To illustrate specific examples of the general behavioral patterns described above, a more detailed account of two tracks is presented. Fish #3 was tracked on three occasions, spanning 9 days, for a total of 125 h, and spent a large amount of time in the Coconut Island lagoon (Fig. 5). Upon release in the Coconut Island lagoon at 1030 h the fish moved about actively within the lagoon. At 2100 h the fish exited the lagoon and swam around the perimeter of the Coconut Island reef to the location at the north end of the island reef visited by all five tracked fish. The fish remained within a small area at this location until 1400 h the next day, when it swam along the reef perimeter and returned to the lagoon. The fish was relatively active within the lagoon until termination of the track at 1100 h the next morning. Three days later fish #3 was relocated in the lagoon and tracked for an additional 72 h. The fish spent the first 48 h of the supplemental track moving within in the lagoon. The fish made limited movements at the northern extreme of the lagoon between sunset and mid-afternoon, and more extensive movements within the south portion of the lagoon between mid-afternoon and sunset. The fish left the lagoon at sunset the following day, swam around the perimeter of the Coconut Island reef to the west side of the island, and returned to the lagoon at 2215 h (Fig. 5), after which it was relatively inactive in the northern extreme of the lagoon until termination of the track at 1000 h the following morning.

Fish #4 was captured by pole and line at a channel entrance on the west side of Coconut Island and tracked on two occasions, spanning 7 days, for a total of 72 h. This fish did not enter the Coconut Island lagoon, but spent nearly the entire track moving along the perimeter of the Coconut Island reef and the edge of a nearby patch reef (Fig. 6). Following release at 1130 h, the fish swam around the reef perimeter to the location visited by all fish at the north end of the island, where it remained relatively quiescent until sunset. At sunset the fish moved back and forth along a 400 m stretch of reef wall on the north side of the island until shortly after sunrise. Then the fish briefly left the Coconut Island patch reef, but returned to the Coconut Island reef and completely circled the island before settling at the north end of the island from 0745 h until sunset. Just after sunset the fish again swam back and forth along the reef wall on the NW edge of Coconut Island and at 2130 h moved to a patch reef 500 m west of Coconut Island. The fish made occasional limited movements along the NE corner of the patch reef until several hours before sunrise. Just prior to sunrise the fish moved more actively along the reef edge. Thereafter, the fish remained quiescent at the patch reef until the track was terminated at 1200 h. Two days later this fish was detected at the common area at the north end of the Coconut Island reef at 1345 h and in the same location again the next morning at 0920 h, when it was tracked for an additional 24 h. During the day it made limited excursions along the north reef wall, and just after sunset moved to a mangrove-lined channel along the western edge of Coconut Island. It moved actively within the channel and briefly moved to the north end of Coconut Island at 0330 h, before returning to the channel, where it remained quiescent for approximately 3 h. Shortly before sunrise it left the channel and moved to the NE side of the Coconut Island reef where it swam actively along the reef perimeter for roughly 2 h, before becoming relatively inactive and remained at this location until 0900 h when the track was terminated.

4. Discussion

4.1. Spatial segregation

There was clearly a limited size range of *C. ignobilis* that utilized the Coconut Island marine reserve. Our catch data for *C. ignobilis* indicate that small fish (<25 cm) were most common in the murky parts of the bay, that the majority of fish captured at Coconut Island ranged between 25 and 40 cm, and that fish larger than 40 cm were uncommon around Coconut Island or elsewhere near the patch reefs in Kaneohe Bay. The largest fish were caught outside the bay or on the outskirts of the bay during tournaments. These patterns of size distribution for *C. ignobilis* in Kaneohe Bay suggest an ontogenetic shift in habitat use, from deep, murky waters, to more reef-associated locations and finally to the outer limits of the bay and into deeper waters outside of the bay. Although size selectivity of the different fishing methods used to collect fish in our study may have contributed to the distribution patterns described above, we believe that the size range of fish caught by various means in our study are reflective of the size range of fish that were actually present at the various locations and were not an artifact of fishing method. No such differential distribution was observed for *C. melampygus* captured in Kaneohe Bay by the same methods during a concurrent study. Evidence supporting our findings was also reported by Blaber and Cyrus (1983), who noted that juveniles of *C. ignobilis* just under 20 cm were common in highly turbid water in South Africa.

According to age at length estimates of Sudekum et al. (1991), average length at age 1 for *C. ignobilis* is 19.6 cm and at age 2 is 36.5 cm. Using these estimates, fish inhabiting the deep, murky part of Kaneohe Bay were largely fish less than 1-year-old (20 cm), and fish most frequently captured at Coconut Island were between 1- and 2-year-old (20–40 cm). This species appears to spend at least the later part of year 1 in the deep murky parts of Kaneohe Bay, then apparently moves to patch reefs such as those near Coconut Island during the second year. By the end of the second year of life the majority of fish have moved to the outer bay or have left the bay altogether. Size at maturity for *C. ignobilis* has been reported as 55–65 cm, which they reach in approximately 3.5 years (Williams, 1965; Lewis et al., 1983; Sudekum et al., 1991). Thus, the Coconut Island marine reserve offers refuge for immature *C. ignobilis* during approximately 1 year of their lives. Although the size range of fish commonly found at Coconut Island was limited, this size range is especially vulnerable to recreational and commercial net fisheries in Hawaii, which target *C. ignobilis* between 24 and 40 cm (Kobayashi, 1993).

4.2. Long-term movements

Results from the tagging portion of this study suggest a life history pattern of limited residence in the Coconut Island vicinity and within Kaneohe Bay. There was a relatively low recapture rate of fish tagged in the deep, murky parts of the bay, which might indicate higher emigration or mortality levels than for fish at Coconut Island. Based on movements of recaptured fish, Coconut Island appears to represent a reef-type habitat occupied by a portion of the fish that have left the deep parts of the bay upon reaching approximately 20 cm or 1 year of age. Tagging data also support the presumption that residence time at these reef locations is limited to the first few years of life for *C. ignobilis* and that there is a progression out of the bay as fish increase in size. Fish recaptured at Coconut Island or nearby reefs tended to be smaller fish, which had been at liberty for short periods of time, whereas fish at liberty for longer periods of time, were on average larger and were more often captured by recreational fishers at channels near the outside of Kaneohe Bay, or long distances from the bay.

Despite bias that might have resulted from differential fishing effort at various locations and under-reporting of recaptured fish by recreational fishers, tagging data also suggested that use of the Coconut Island refuge by *C. ignobilis* differs from that of *C. melampygus*. The recapture rate for *C. ignobilis* (11.4%) was only half that of *C. melampygus* (20.7%) (Holland et al., 1996). Only 32% of *C. ignobilis* were recaptured within 0.5 km of Coconut Island and 32% were also recaptured at distances greater than 3 km from the island. For *C. melampygus* 75% of recaptures were within 0.5 km of Coconut Island and only 5% were at distances greater than 3 km (Holland et al., 1996). In addition, only one *C. ignobilis* was recaptured more than once, whereas 11 *C. melampygus* were recaptured many times. The recapture rate in our study was still relatively high, however, in comparison to other tagging studies. Okamoto and Kawamoto (1980) recaptured only one *C. ignobilis* of 343 tagged in the Northwestern Hawaiian Islands, and James (1980) reported a recapture rate of 4.9% for *Caranx georgianus* off New Zealand.

Although several *C. melampygus* were also recaptured long distances from Kaneohe Bay, *C. melampygus* captured at Coconut Island included individuals that were sexually mature and approaching the maximum size attained by this species. The *C. melampygus* captured from Coconut Island would have been 2–8-year-old, compared to a maximum of just over 2 years estimated for *C. ignobilis* (Sudekum et al., 1991). Both species may be far ranging, as indicated by long distance recaptures, but at least a portion of the *C. melampygus* population remains close to Coconut Island for prolonged periods of time, whereas *C. ignobilis* within the reserve are largely immature 1–2-year-old fish.

4.3. Short-term movements

Short-term movement patterns of *C. ignobilis* were variable. Several fish remained within the Coconut Island reserve continuously for days, whereas others spent comparatively little time within the reserve. Additionally, some individuals alternated between these patterns. Other fishes tracked within the refuge at Coconut Island have demonstrated fairly repeatable and predictable behavior (Holland et al., 1993, 1996; Meyer et al., 2000). However, Winter and Ross (1982) found that it was common for fish within a species to fall into different behavioral groups.

Short-term movement patterns of *C. ignobilis* shared several characteristics with those of *C. melampygus* described by Holland et al. (1996). Both species tended to actively patrol along reef edges and both showed periods of reduced activity concentrated within small areas. Activity of both species was also centered within the Coconut Island reserve. There were also marked differences between these two species; *C. ignobilis* showed less site fidelity, spent considerable time in the Coconut Island lagoon and also occasionally ranged to reef flats and deep, murky portions of the bay. Movements of *C. melampygus* were much more limited within the Coconut Island reserve, and were also almost exclusively along reef walls (Holland et al., 1996). Tracked *C. ignobilis* tended to be more active at dawn and dusk, and usually shifted locations near sunrise or sunset. Holland et al. (1996) found that *C. melampygus* tracked within the Coconut Island reserve were most active during the day and were quiescent for long periods of time at night. Similar observations of activity levels have been recorded for these two species in other studies (Major, 1978; Potts, 1980). Overall, movement patterns of *C. ignobilis* were more variable and less predictable than *C. melampygus* tracked at Coconut Island by Holland et al. (1996), which showed very consistent behavior, both within individuals tracked for consecutive days, and among different fish.

4.4. Relevance to the Coconut Island marine reserve

Based on size distribution, recapture rates and locations, and short-term movements, it appears that *C. ignobilis* utilize the Coconut Island refuge for a short span of their lives and do not limit their movements to within the refuge even during this time. Therefore, the Coconut Island refuge would provide relief from fishing pressure for *C. ignobilis* within a narrow size range. However, even a short time spent by *C. ignobilis* within the Coconut Island refuge provides a brief respite from fishing pressure, helps to interrupt long periods of overfishing, and ultimately may enhance the fishery (Carr and Reed, 1993; Dugan and Davis, 1993). The movement patterns observed for *C. ignobilis* differ from those of another carangid and several species of goatfish also studied within the Coconut Island refuge. These fishes either utilized the refuge up through maximum sizes attained (*C. melampygus* and *Mulloides flavolineatus*; Holland et al., 1993, 1996), or remain extremely site attached to the refuge reef during a particular life history stage (*Parupeneus porphyreus*) (Meyer et al., 2000).

Information gathered in a combination of studies, such as those conducted at Coconut Island (Holland et al., 1993, 1996; Meyer et al., 2000; this study), would be helpful for the design of marine reserves aimed at enhancing populations of multiple species of fishes (Polacheck, 1990; Dugan and Davis, 1993; Soh et al., 2000). For example, establishment of a small fishery reserve on the scale of the Coconut Island reserve may be expected to be sufficient for protection of a number of relatively large and mobile fish species, but would offer more limited refuge to a species with more extensive movement patterns such as *C. ignobilis*. The type of information obtained in such studies also has applications for empirically testing and improving models designed to evaluate the effectiveness of fisheries reserves based on estimates of movement patterns and habitat requirements (DeMartini, 1993).

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