Abstract—Networks of no-take fishery reserves have emerged as a tool for managing deepwater fish species. In Hawaii and elsewhere, such areas are used to manage deepwater snapper species. However, little is known regarding the movements of these species relative to protected areas. We used passive acoustic telemetry to track crimson jobfish (*Pristipomoides filamentosus*), also known as opakapaka, in one of Hawaii's bottomfish restricted fishing areas to understand the size required for a reserve to protect this species. From January 2017 through January 2018, 179 fish were tagged. Only 10 fish were classified as alive on the basis of movements indicated by detections in tracking data (tracks). For these fish, the median time between the first and last detection of an individual on an acoustic receiver array was 414.5 d with a mean number of detections per individual of 28,321. Linear estimates of home range averaged 3.7 and 6.0 km in conservative and optimistic scenarios, smaller than the median linear habitat dimension of Hawaii's reserves. Fish were detected within the reserve on 97% or more of the days they were tracked. These results indicate that current reserves in Hawaii are likely sufficient in scale to confer positive biological benefits to opakapaka that reside within their borders.

Evaluating movements of opakapaka (*Pristipomoides filamentosus*) relative to a restricted fishing area by using acoustic telemetry and a depth-constrained estimator of linear home ranges

Stephen R. Scherrer (contact author)[1]
Kevin C. Weng[2]

Email address for contact author: scherrer@hawaii.edu

[1] Department of Oceanography
School of Ocean and Earth Science and Technology
University of Hawaii at Manoa
1000 Pope Road
Marine Science Building 609
Honolulu, Hawaii 96822

[2] Virginia Institute of Marine Science
College of William and Mary
P.O. Box 1346
Gloucester Point, Virginia 23062-1346

Deepwater demersal fish species are typically characterized by slow growth and late maturity, making them vulnerable to overexploitation (Cailliet et al., 2001; Newman et al., 2016). Restricted fishing areas in deep water have emerged as a tool for rebuilding and maintaining the stocks of these species (Williams et al., 2009; Friedlander et al., 2014; Huvenne et al., 2016; Uehara et al., 2019). Key to understanding the benefits of these reserves is quantifying their ability to retain and protect fish species during critical life stages to confer positive, beneficial effects (Roberts et al., 2003). However, biological considerations are often unknown or neglected when reserve areas are designed, and those omissions can lead to uncertain outcomes (Halpern, 2003). Understanding the ecology and movements of these fish species in proposed or implemented areas is critical to planning and evaluation processes (Palumbi, 2004). Passive acoustic telemetry is a popular and versatile tool for tracking and quantifying fish movements in marine reserves (Crossin et al., 2017). However, deepwater fish species are more susceptible to postrelease mortality than shallow-water species because of barotrauma and other stressors (Edwards et al., 2019).

Deepwater demersal fish are a valuable resource throughout the Indo-Pacific (Kami, 1972; Williams et al., 2012; Newman et al., 2015, 2016; Wakefield et al., 2017; Hill et al., 2018). Multispecies complexes of such fish are both economically and culturally important, supporting commercial, recreational, and subsistence fishing (Craig et al., 1993; Pooley, 1993). In the Hawaiian Archipelago, these fish species are referred to as bottomfish, and management of the stock of these fish is focused on 6 species of eteline snappers and 1 endemic species of grouper. These species, known locally as the *Deep-7*, inhabit island slopes and banks at depths between 100 and 400 m (Kelley and Ikehara, 2006;

Oyafuso et al., 2017). The crimson jobfish (*Pristipomoides filamentosus*), called opakapaka in Hawaii, accounts for the largest fraction of commercial and recreational catch of bottomfish among the Deep-7 species. During the 2017–2018 fishing year, opakapaka accounted for over half of this fishery's $1.6 million ex-vessel value (Harding[1]).

An annual catch limit and a network of restricted fishing reserves were introduced to this fishery as a management strategy in 1998 in response to stock assessments indicating declines in the spawning potential ratio for onaga (*Etelis coruscans*) and ehu (*E. carbunculus*), the second- and third-most abundant species caught by this fishery, respectively, and 2 other species of the Deep-7 (Friedlander et al., 2014; Langseth et al., 2018). The state of Hawaii implemented bottomfish restricted fishing areas (BRFAs) to recover stocks with the goal of protecting 20% of bottomfish habitat in the main Hawaiian Islands (Friedlander et al., 2014). By using improved knowledge of preferred bottomfish habitat, in 2007 the BRFAs were restructured with a goal of further reducing fishing pressure and the number of reserve areas was reduced from 19 to 12 (Parke, 2007; Friedlander et al., 2014). Several studies conducted since have further documented the habitat associations of bottomfish species in the Hawaiian Islands (Misa et al., 2013; Moore et al., 2016; Oyafuso et al., 2017). In August 2019, 4 more reserves were reopened, leaving 8 closed areas.

The BRFAs are controversial among fishery stakeholders (Hospital and Beavers[2]). Studies have shown that fish size and abundance have increased within several of the BRFAs (Sackett et al., 2014), and there is some evidence that spillover to neighboring fished areas has occurred (Sackett et al., 2017). Despite these conservation benefits, some bottomfish fishermen in recent years have lobbied managers to do away with some or all of the protected areas (WPRFMC[3]). They argue that management measures do not adequately balance the economic effects experienced by fishermen with conservation benefits to the fish stocks (Oyafuso et al., 2019). The National Marine Fisheries Service, Hawaii Department of Land and Natural Resources, and Western Pacific Regional Fishery Management Council, who together oversee bottomfish resources in Hawaii, need data on the size of the home range and movement of bottomfish species to determine their future management strategies (WPRFMC[4]).

Prior to our study, there had been little empirical data to assess how the spatial scale of protection offered by the BRFAs compares to the routine movements of opakapaka and other bottomfish species (WPRFMC[4]). Coarse estimates of movements of opakapaka in the Hawaiian Archipelago were obtained through a mark-release-recapture tagging study (O'Malley[5]). As reported by O'Malley, researchers and fishermen partners tagged 4571 opakapaka. Only 113 of these individuals were later recaptured (2.5%). Individuals were recaptured up to 61 km from their tagging location; however, most individuals appeared to move shorter distances, with 86% of recaptured fish recovered less than 10 km from their tagging site (median time at liberty: 325 d).

In a handful of studies, passive acoustic telemetry has been used to track bottomfish in Hawaii. An active tracking study followed 2 juvenile opakapaka over 5-d and 6-d periods in Kaneohe Bay and described patterns of crepuscular movement between day and night habitats occurring within areas of 0.4 km^2 (Moffitt and Parrish, 1996). The habitat occupied by juveniles, however, differed significantly from that described for adults (Moffitt and Parrish, 1996). In another study, the movements of captive-bred and wild-caught juvenile fish (number of samples [n]=46) were tracked with an array of 6 receivers until their emigration from nursery grounds days to weeks after release (median time at liberty: 9 d). However, it was unclear if these individuals transitioned directly to adult habitat (Parrish et al., 2015). Adult opakapaka were tracked in 2004 (n=12; median time at liberty: 6 d; 5-receiver array), 2006 (n=5; median time at liberty: 0 d; 3-receiver array), and 2007 (n=10; median time at liberty: 1 d; 7-receiver array) as they moved over the boundary demarking the Kahoolawe Island Reserve, an area restricted to fishing but not a part of the BRFA system (Ziemann and Kelley[6,7,8]). Fish were again observed undertaking crepuscular movements, leaving the area at night and returning in the morning; however, the size and position of the acoustic array were insufficient to determine the extent of movements.

[1] Harding, K. 2018. Personal commun. Div. Aquat. Resour., Hawaii Dep. Land Nat. Resour., 1151 Punchbowl St., Rm. 330, Honolulu, HI 96813.

[2] Hospital, J., and C. Beavers. 2011. Management of the main Hawaiian Islands bottomfish fishery: fishers' attitudes, perceptions, and comments. NOAA, Natl. Mar. Fish. Serv., Pac. Isl. Fish. Sci. Cent. Admin. Rep. H-11-06, 46 p. [Available from website.]

[3] WPRFMC (Western Pacific Regional Fishery Management Council). 2013. Minutes of the 158th meeting of the Western Pacific Regional Fishery Management Council; 16–18 October, Honolulu, HI, 89 p. WPRFMC, Honolulu, HI. [Available from website.]

[4] WPRFMC (Western Pacific Regional Fishery Management Council). 2015. WPRFMC five-year research priorities under the MSRA 2014–2019, 12 p. WPRFMC, Honolulu, HI. [Available from website.]

[5] O'Malley, J. 2015. A review of the cooperative Hawaiian bottomfish tagging program of the Pacific Islands Fisheries Science Center and the Pacific Islands Fisheries Group. NOAA, Natl. Mar. Fish. Serv., Pac. Isl. Fish. Sci. Cent. Admin. Rep. H-15-05, 36 p. [Available from website.]

[6] Ziemann, D. A., and C. Kelley. 2004. Detection and documentation of bottomfish spillover from the Kahoolawe Island Reserve, 15 p. Final report. Oceanic Institute, Waimanalo, HI. [Available from Oceanic Institute, 41-202 Kalanianaole Hwy., Waimanalo, HI 96795.]

[7] Ziemann, D. A., and C. Kelley. 2007. Detection and documentation of bottomfish spillover from the Kahoolawe Island Reserve, 20 p. Final report. Oceanic Institute, Waimanalo, HI. [Available from Oceanic Institute, 41-202 Kalanianaole Hwy., Waimanalo, HI 96795.]

[8] Ziemann, D. A., and C. Kelley. 2008. Detection and documentation of bottomfish spillover from the Kahoolawe Island Reserve, Phase III final report, 25 p. Oceanic Institute, Waimanalo, HI. [Available from Oceanic Institute, 41-202 Kalanianaole Hwy., Waimanalo, HI 96795.]

Only one tagging study has described bottomfish movements in relation to the BRFAs. Weng (2013) passively tracked onaga (*n*=12; median time at liberty: 41 d; 8-receiver array) and ehu (*n*=6; median time at liberty: 28 d; 8-receiver array) in BRFA B, off Niihau, Hawaii (Fig. 1). The majority of tagged fish spent most of their time within the BRFA, indicating that the protected area was a reasonable size for bottomfish species.

Previous studies of bottomfish movement in Hawaii have used small tracking arrays, tagged small numbers of fish, tracked fish over short durations, or were limited to observations made only during marking and recapture. Therefore, the effectiveness of the BRFA network for retaining Deep-7 fish is unclear. The goal of this study was to use passive acoustic telemetry to determine if the movements of individual opakapaka were confined to one of these reserves or if they extended beyond the boundaries of the BRFA. The linear home ranges of tagged fish were then compared with the scale of protection provided by the current BRFA network. Finally, we looked at how individual fish spent time in and moved between protected and non-protected waters.
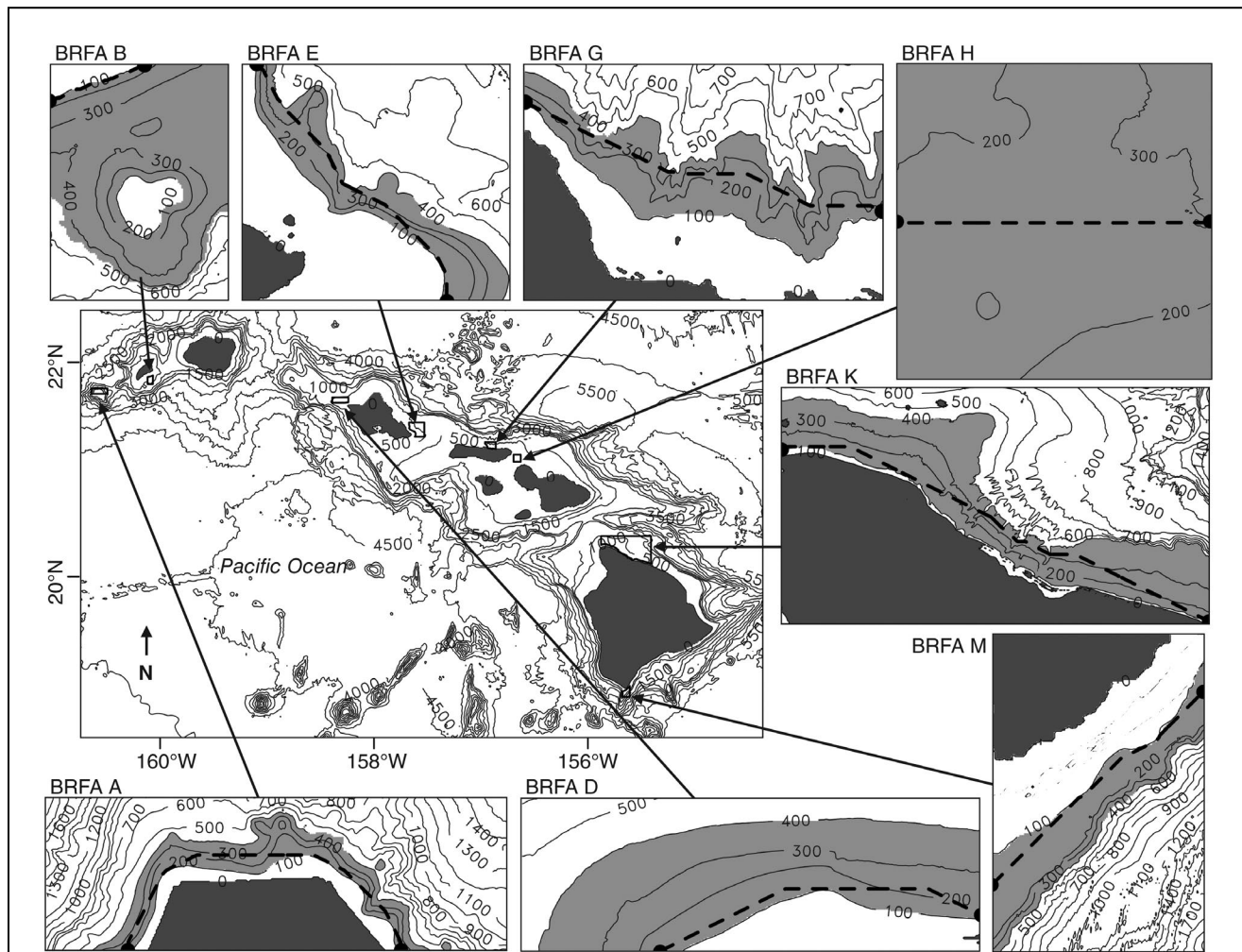
Figure 1

Map of the main Hawaiian Islands surrounded by plots of the 8 bottomfish restricted fishing areas (BRFAs) in which opakapaka (*Pristipomoides filamentosus*), as well as 5 other deepwater snapper species and 1 grouper species, are protected. The boundaries of each outer map correspond to BRFA boundaries except where nonlinear boundaries occur and none of the nonlinear BRFA boundaries intersect bottomfish habitat. A linear habitat dimension, or the distance across a habitat, was estimated for each BRFA by using a least-cost (shortest) path algorithm for comparison with the observed linear home ranges of individual opakapaka tagged in the Makapuu region off southeastern Oahu between 2017 and 2019. The start and end points for each path, indicated by black semicircles on the plot margins, are at a depth of 120 m, the preferred depth of opakapaka. The thick dashed line indicates the least-cost path through the BRFA in each plot. Paths are constrained by the depth range of 100–400 m, indicated by the light gray area in each plot. Solid black lines indicate depth contours in meters.

Materials and methods

Study area

The Makapuu region (21°33′30″N, 157°52′30″W) was selected as the study area because it contains both protected and non-protected habitat with sufficient area to capture the scale of bottomfish movements observed during a previous multi-island pilot study (Fig. 2). The area is important to the commercial fishery and in close proximity to the population center of Honolulu.

The region is located off Oahu's windward side and extends outward from Makapuu Point, the southeastern tip of the island of Oahu, north to the Lanikai Peninsula. A flat, broad shelf protrudes east from the island's

southern edge before terminating in a deep slope that forms the western edge of the Kaiwi Channel. The shelf narrows to the north, joining with a series of deeper shelves, and forms submarine canyons. The BRFA in this region (BRFA E) extends from 2.4 km offshore westward across the shelf in line with Koko Head crater to the south and Kailua to the north (Fig. 2). Within BRFA E, habitat between the 100- and 400-m depth contours encompasses an area of approximately 49 km^2.

Fish capture and tagging

Fish in this study were captured with the assistance of local fishermen by using vertical deep-drop hook-and-line gear and hydraulic or electric line pullers commonly
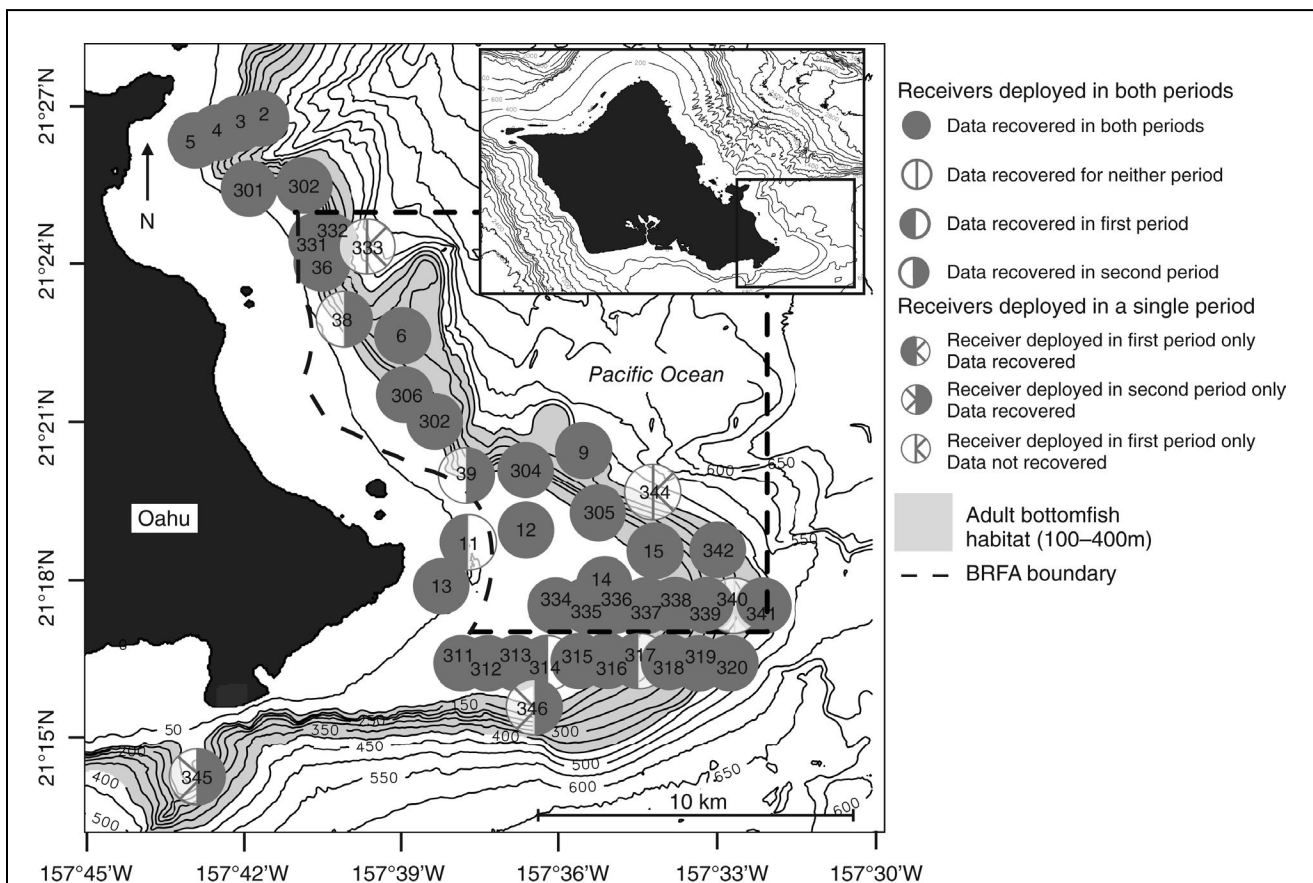
Figure 2

Map showing the acoustic receiver array deployed in the first analysis period (June 2017–April 2018) and second analysis period (May 2018–January 2019) during which the movements of tagged opakapaka (*Pristipomoides filamentosus*) were tracked in the Makapuu region off the southeastern coast of Oahu, Hawaii (inset). The black dashed line indicates the boundaries of the bottomfish restricted fishing area (BRFA) in this region. Solid gray circles roughly correspond to the detection footprints of individual receivers that were deployed and recovered and from which data were successfully downloaded. Open gray circles indicate stations that could not be recovered or have data downloaded from them (because of the station's loss or failure to log data). Half-shaded circles represent stations from which data were collected for only one period. Half circles containing one side of an X represent a period in which the receiver was not deployed. The light gray area represents adult bottomfish habitat (at depths of 100–400 m), and dark gray areas represent land. Black lines indicate depth contours in meters.

used to catch bottomfish in Hawaii (Glazier[9]). Hooks were baited with squid, anchovies, sardines, or saury for bait. Hook-and-line gear were configured with no more than 6 baited hooks at a time. Chum, or *palu* in the Hawaiian language, is used to attract bottomfish while fishing and consists of finely chopped bait (and sometimes a filler material, such wheat chaff, rice, or oats). Palu was released when the rig was at depth to attract and aggregate bottomfish. To reduce barotrauma, when possible after a fish was hooked, the rate at which the mainline was pulled was slowed, to allow some compensatory off-gassing of the swim bladder to occur, but was still fast enough to limit predation during ascent.

Fish were brought aboard the vessel for surgical tagging and then immediately released into the water. Once the hook was removed, fish that were deemed acceptable for tagging were placed ventral side up in a padded v-board cradle. Seawater was pumped over the gill surface by using a saltwater hose or a recirculating pump to provide oxygen to the fish. Routine venting of the swim bladder is not recommended for this species (O'Malley[5]); therefore, venting was performed only when symptoms of barotrauma were severe and was conducted by puncturing the swim bladder or protruding stomach with an 18-gauge hypodermic needle stored in disinfectant. An incision between 1.5 and 2.5 cm in length was made with a sterile scalpel along the fish's ventral centerline anterior to the urogenital pore. An acoustic tag was inserted into the peritoneal cavity through this opening, along with triple antibiotic cream. The incision was closed with sutures (PDS Plus Antibacterial[10] monofilament, Ethicon US LLC, Bridgewater, NJ) and secured with a surgeon's knot. When conventional dart tags were available (10-cm PDS-2, Hallprint PTY Inc., Hindmarsh Valley, Australia), fish were tagged externally between the lateral line and the dorsal fin. Dart tags were provided by the Pacific Islands Fisheries Group as part of a long-term mark-recapture program. On-deck handling times were typically less than 5 min.

Two types of acoustic tags were used in the study, one with a depth sensor (Vemco V13P transmitter, Innovasea Systems Inc., Boston, MA) and one without (Vemco V13 transmitter). Each acoustic tag transmitted a unique ultrasonic ID code once every 90–200 s (nominal transmission interval: 145 s). V13 transmitters had an expected battery life of 2.25 years and provided only presence data, and V13P tags had an expected battery life of 1.63 years and provided records of both presence and depth.

As part of the determination of the size range of fish suitable for tagging, V13 and V13P tags were weighed. The minimum size of opakapaka eligible for tagging with each type of tag was calculated by using a conservative threshold of 2% of bodyweight and a species-specific allometric relationship between fork length (FL) and weight (Uchiyama and Kazama[11]). The minimum FL suitable for tagging was 31 cm for fish with V13 tags and 33 cm for fish with V13P tags.

Four main strategies for release were used in an attempt to balance rapid recompression and predator avoidance: 1) release at the seafloor by using a drop-shot device (Blacktip Catch and Release Recompression Tool, West Marine, Watsonville, CA; $n=74$), 2) midwater release (30–60 m) by using a drop-shot device (SeaQualizer Descending Device, SeaQualizer, Davie, FL; $n=70$), 3) surface or near-surface release ($n=18$), and 4) release, either at the surface ($n=8$) or by using a drop-shot device ($n=2$), after driving the vessel rapidly away from the fishing location. The method of release was not recorded for 3 individuals.

To directly assess the effect of barotrauma and surgery on 4 tagged opakapaka, we built a mid-water net pen (approximately 1.5 m high, with a diameter of 2.5 m) and used it to hold each individual at a depth of 20 m following capture and surgery. After 30–60 min, we descended to the net pen by scuba diving to observe the fish, noting condition and ability to orient and maintain neutral buoyancy. We then opened the net pen, allowing each fish to swim free, and observed its swimming ability.

Acoustic monitoring

The locations of fish in the study area were inferred from patterns of presence and absence at receiver stations. Each receiver station consisted of an acoustic receiver (Vemco VR2W or VR2AR, Innovasea Systems Inc.) and an acoustic release (Vemco VR2AR or Lightweight Release Transponder, Sonardyne International Ltd., Hampshire, UK) buoyed by 3 or 4 trawl floats and anchored to the seafloor with approximately 80 kg of concrete. Each mooring line was sheathed within a 38-mm-diameter PVC tube to minimize the potential for entanglement or fraying.

Individual receiver stations formed a larger tracking array that monitored the movement of tagged fish in the study area. The tracking array was made up of 5 sub-arrays representing either *fence* or *sparse* configurations (Fig. 2). A fence sub-array is a line of receivers deployed with overlapping detection regions so that a tagged fish transiting the line of receivers will be detected. A sparse sub-array is a group of receivers with detection regions that do not overlap and is used to detect movements around a region with much of the region unmonitored.

The fence sub-arrays, or fences, were designed to detect individuals crossing BRFA borders. Because a fence placed on the border would detect fish located inside or outside the BRFA, it was necessary to have 2 fences—one outside

[9] Glazier, E. 2007. Hawai'i pelagic handline fisheries: history, trends, and current status, 73 p. Final background document prepared for the Western Pacific Fisheries Management Council. Pac. Isl. Off., Impact Assessment Inc., Honolulu, HI. [Available from website.]

[10] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[11] Uchiyama, J. H., and T. K. Kazama. 2003. Updated weight-on-length relationships for pelagic fishes caught in the central North Pacific Ocean and bottomfishes from the Northwestern Hawaiian Islands. NOAA, Natl. Mar. Fish. Serv., Pac. Isl. Fish. Sci. Cent. Admin. Rep. H-03-01, 34 p. [Available from website.]

the BRFA at a distance from the border greater than the receiver's detection range and another located inside the BRFA's border by a similar distance. Four fences were deployed where the boundaries of the BRFA intersected with bottomfish habitat. One pair of fences was used to monitor the northern border, and the other pair was used to monitor the southern border. The placement of each fence was optimized by using an algorithm with respect to the following factors: the probability of detecting a tag transmission at a receiver across a range of depths, the bathymetry along the fence's transect, the height of the receiver from the seafloor, the desired height of the water column to be monitored, the swimming speed of individual opakapaka, and a probability of at least 25% for detecting any given transmission from a tag.

The probabilities of a receiver detecting transmissions from tags across a range of distances were determined through range testing experiments. Results of range experiments indicate that 5% of tag transmissions could be received at a distance of 847 m from the receiver. One quarter of tag transmissions were detectable at a distance of 545 m, and 12.5% of tag transmissions were detectable at a distance of 765 m (Scherrer et al., 2018). Therefore, to achieve a minimum detection rate of 25%, spacing between adjacent receivers in a fence configuration could not exceed 1530 m. To be conservative, the fence algorithm was initialized with a 12.5% detection range of 600 m and a 25% detection range of 500 m. Each receiver station was deployed from the vessel over its target location and was allowed to sink freely to the seafloor. By using the position of the vessel at the time of deployment as the station's position, the largest distance between 2 receivers in any of the fence configurations was 1232 m.

A single sparse sub-array was used to monitor individual movements between areas within the BRFA. The positions of individual receivers within the sparse sub-array were determined in iterative stages by using a telemetry optimization algorithm (Pedersen et al., 2014) and bathymetry of the Hawaiian Archipelago at resolutions of 50 m and 1 km (Johnson[12]). The locations of their deployment were selected within the bounds of BRFA E after constraining depth between 75 and 475 m. Aggregations of up to 100 opakapaka have been observed from manned submersibles 2–10 m above the seafloor in the Penguin Banks region, located just west of the island of Molokai (Haight, 1989; Haight et al., 1993; Kelley and Moriwake[13]). Therefore, a preferred depth of 6 m above the seafloor was selected. A maximum receiver detection range of 847 m was

determined by using results from deepwater range tests we have previously reported (Scherrer et al., 2018).

Receivers in deep water are particularly susceptible to close-proximity detection interference (CPDI), a phenomenon in which a receiver may fail to detect transmissions from tags at close distances (Kessel et al., 2015; Scherrer et al., 2018). Results from predictive modeling indicate that CPDI occurs for receivers in depths exceeding 200 m. However, CPDI is not believed to have affected the detection of fish transiting through fence sub-arrays because multiple transmissions would be sent by a tagged fish while it was within the detection range of the receiver before and after encountering the region affected by CPDI.
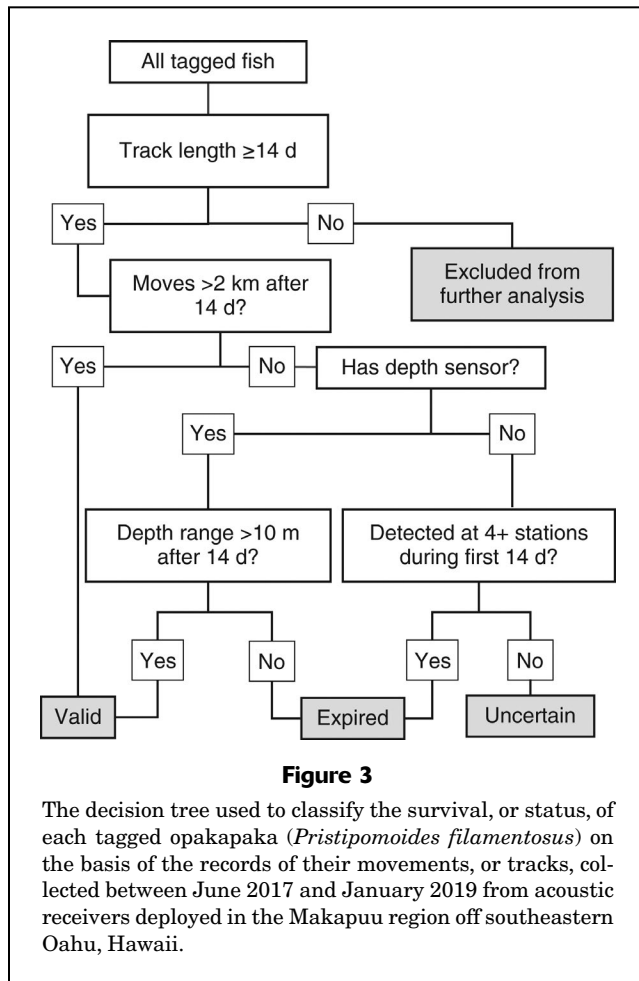
Data analysis

Categorizing fish status Data collected from acoustic receivers were downloaded and stored in the database application VUE, vers. 2.4 (Innovasea Systems Inc.). Potentially false detections were flagged by this software and subsequently removed from the data set. Data of the movements, or *tracks*, of fish were then exported to a comma-separated values file for further analysis in R, vers. 3.5.0 (R Core Team, 2018). A 30-s filter window was then used to flag any tags that were detected on multiple receivers to ensure that any movements detected represented real changes in position and not just periods particularly favorable to detection of acoustic signals.

High postrelease mortality and moderate to high rates of residency at a single station made determining fish status important. Simply, it is difficult to distinguish a fish with a small home range near a single receiver from a tag laying on the bottom near a receiver. A decision tree was developed to assist in classifying fish detected on the receiver on the basis of features of their tracks (Fig. 3). Tracks were assigned to 1 of 3 categories: *expired tracks* of fish that were believed to be dead, *valid tracks* of fish believed to be alive, and *uncertain tracks* of fish for which status could not be determined. Following this initial classification, we reviewed records of each tag and made adjustments to status when appropriate.

It is similarly difficult to distinguish the tracks of a rapidly moving tagged fish from the movements of a shark that has eaten a tagged fish; therefore, we tagged individuals of several predator species to assist in determining parameters for track classification. We tagged 8 sandbar sharks (*Carcharhinus plumbeus*), 1 silky shark (*C. falciformis*), and 1 Galapagos shark (*C. galapagensis*). All tagged sharks were detected on the receiver array during the analysis period. Their behavior patterns were characterized by frequent movement between stations (mean movements per day: 8.9 [standard deviation (SD) 10.7]), detection at multiple stations in a single day (mean number of stations detected per day: 3.5 [SD 1.6]), and movement over large distances (mean linear home range: 18.1 km [SD 5.7]). Because a tagged fish eaten by a predator is likely to be digested and its tag regurgitated within about 1 week (Medved, 1985), we doubled this time period to be

[12] Johnson, P. 2011. Main Hawaiian Islands multibeam bathymetry synthesis: 50-meter bathymetry and topography. Hawaii Mapping Res. Group, Sch. Ocean Earth Sci. Tech., Univ. Hawaii Manoa, Honolulu, HI. [Data available from website, accessed May 2011.]

[13] Kelley, C. D., and V. N. Moriwake. 2012. Appendix 3. Essential fish habitat descriptions, part 1: Hawaiian bottomfish. *In* Final fishery management plan for coral reef ecosystems of the western Pacific region, vol. 3. Essential fish habitat for management unit species, p. A3-02–A3-111. [Available from West. Pac. Reg. Fish. Manage. Counc., 1164 Bishop St., Ste. 1400, Honolulu, HI 96813.]

Figure 3

The decision tree used to classify the survival, or status, of each tagged opakapaka (*Pristipomoides filamentosus*) on the basis of the records of their movements, or tracks, collected between June 2017 and January 2019 from acoustic receivers deployed in the Makapuu region off southeastern Oahu, Hawaii.

conservative and defined *shark-like* movement as detection at 4 or more stations during the first 14 d of the track. A predation event was identified when tag data indicated movements with shark-like qualities followed by cessation of movement. Tracks shorter than 14 d were discarded (because these movements might be those of opakapaka that were inside shark stomachs).

Further classification was based on movement. Results of range testing indicate that, under optimal conditions, receivers could detect tag transmissions at distances up to 1.0 km. Therefore, detections on 2 receivers less than 2 km apart could be detections of a stationary tag laying between them. Consequently, tracks of fish that moved between 2 stations separated by more than 2.2 km 14 d after tagging were considered valid. However, if no horizontal movements were observed for a given individual, its status could still be classified if its tags were capable of reporting changes in depth greater than those that could be attributed to tidal fluctuations. Following the 14th day after tagging, a valid classification was assigned to tracks from individuals with depth-sensing tags if vertical movement ranges exceeded 10 m. This threshold was selected because it is greater than the maximum fluctuation in depth that could be explained by tidal changes alone.

Tracks from tags lacking depth sensors that did not indicate movement after 14 d were classified as expired if they had a strong shark-like movement pattern at the beginning of the track. The track of a fish detected at fewer than 4 stations during the first 2 weeks was classified as uncertain. Visual inspection of the tracks of such fish were indistinguishable from tracks of stationary tags attached to fish that were known to be dead but also resembled highly resident fish that were known to be alive from depth records.

Analysis scenarios Two scenarios were developed by using the classification of each fish's track, to select which tracking data would be included in further analyses. The first scenario included only valid tracks and represents a conservative outlook on the data. The second scenario included both valid and uncertain tracks. The group of tracks with an uncertain classification likely includes a mixture of both valid tracks from highly resident fish that were detected consistently at a single receiver and detections of stationary tags belonging to fish that died after they were tagged. For this reason, the second scenario should be considered an optimistic outlook.

Testing for size-selective survivorship bias Correlation between body size and survivorship outcome for tagged opakapaka was tested by comparing the distribution of FLs from fish with valid tracks to that of the total population of tagged fish. A subset of lengths equal in number to the fish with valid tracks was selected at random without replacement from the measured FLs of all sampled fish. The mean and SD of this subset of lengths were recorded, and the process was repeated 10,000 times. These summary statistics were used to calculate 95% confidence intervals (CIs) for comparing the size of surviving opakapaka with the size of all of the opakapaka that were tagged.

Analysis periods The receiver array was deployed and recovered twice during the study (Fig. 2). Five stations were lost midway through the study and were replaced; therefore, the data for these replacement stations exist only for the later period after the second deployment. Three receiver stations were lost later in the study, such that data for these sites exist only for the earlier period. Because the stations lost during these periods differed, the data were split into 2 periods for analysis corresponding with each realized array configuration. The first analysis period began on 26 May 2017 and ended on 15 April 2018. The second analysis period was from 6 May 2018 through 6 January 2019.

Calculating individual home range A number of methods for quantifying home range have been proposed with application varying depending on the study environment and the technology and method used (Stickel, 1954; Stumpf and Mohr, 1962; Schadt et al., 2002; Börger et al., 2006; Dwyer et al., 2015). Because adult opakapaka are associated with a narrow depth band, their habitat can be thought of as

a river winding along island slopes and flanked by areas where individuals are unlikely to occur. In river systems, a constrained linear home range estimator provides a more robust estimate of space use when compared with estimates from the use of a minimum convex polygon, kernel utilization, and other common methods used to quantify home range; therefore, we used a constrained linear home range estimator to calculate the size of the home range for each individual on the basis of its known locations from detection records (Dwyer et al., 2015).

The home range distance for each individual was calculated as the least-cost path between receivers that detected that fish's tag. Least-cost paths were constrained to depths between 100 and 400 m by using the marmap package, vers. 1.0.3, in R (Pante and Simon-Bouhet, 2013). In effect, if the linear path between 2 stations crossed a depth falling outside this range, the path would shift to the nearest point with a depth inside the acceptable range, resulting in a longer path consistent with present knowledge of habitat use of bottomfish. Home range distances calculated for the 2 analysis periods were compared by using nonparametric sign-rank tests.

Comparing home range distance to size of reserves   Least-cost estimates of home range for opakapaka were compared with the size of the BRFAs by using a metric of the linear habitat available within each of the 8 reserves. Because BRFAs include both preferred and non-preferred habitat, we quantified a linear habitat dimension for each BRFA by using the same depth-constrained least-cost path approach that was used to calculate individual fish home ranges. For the 7 BRFAs located along slopes, a path was calculated between the 2 sides of the BRFA's boundary intersecting bottomfish habitat by using bathymetry with a 50-m resolution. The start and end points for each path were at a depth of 120 m, the preferred depth of opakapaka. The east–west distance across the rectangular area was used to define the linear habitat dimension of the BRFA containing depths exclusively within those defined as bottomfish habitat.

Quantifying movement frequency and site fidelity   Detections of fish on receiver fences were used to determine the proportion of time individuals spent within protected areas of the study area and the frequency of movements across the reserve's boundaries. When a fish moved into the reserve, a tag was first detected at a receiver outside of the reserve, followed by detection at a receiver inside the reserve. Similarly, when a fish moved out of the reserve, it was detected first at a receiver inside the reserve, followed by detection at a receiver located outside the reserve. The fraction of time an individual spent within the reserve was standardized by the total time that individual was tracked to calculate its proportional time of protection. The number of movements across reserve boundaries was then standardized by the track duration, defined as the number of days elapsed between the first and final detections of a tag on the array during each analysis period, to estimate the frequency at which they moved between protected and non-protected areas. The correlation between the proximity of a fish's tagging location to the boundary of the reserve and the frequency with which that fish crossed the boundary was also quantified, by using Pearson's correlation coefficient (r).

Results

Fish capture and tagging

Between 9 January 2017 and 11 January 2018, 179 opakapaka were tagged and released within the Makapuu region. Of those fish, 125 were also tagged with conventional dart tags. All fish tagged were larger than the minimum size requirement of 31 cm FL, ranging in size from 34 to 76 cm FL (median: 45.5 cm FL; interquartile range [IQR]: 41–53 cm FL). Tags attached to 168 fish were detected at least once on the receiver array between 26 June 2017 and 6 January 2019. Of those detected tags, 68 tags included a depth sensor and transmitted pressure data in addition to their unique ID codes.

None of the fish held in the net pen had symptoms of severe barotrauma, with all 4 individuals maintaining neutral buoyancy and proper orientation. Each fish swam away once the net pen was opened. However, 2–5 sharks were observed in near proximity within 10 min of each deployment of the pen.

Categorizing fish status

The classifications of tracks were used to determine the status of the 168 tagged opakapaka detected on the array between 26 June 2017 and 6 January 2019: 10 tracks were classified as valid, 35 tracks were classified as uncertain, and 83 tracks were classified as expired. Tracks of 40 individuals with durations less than 14 d were excluded from analysis, and no tracks were available for 11 fish with tags that were not detected on the array during either analysis period (Table 1). Using the decision tree, we initially assigned a valid classification to 30 tracks; however, 20 of these tracks were later reclassified. These tracks were reclassified because of faulty depth sensors, detection patterns that could be otherwise explained by a tag on the seafloor detected only under optimal acoustic conditions, or daily depth patterns that closely resembled those of the bluntnose sixgill shark (*Hexanchus griseus*) (Comfort and Weng, 2015). Twelve of the tracks initially considered to be valid were reclassified as uncertain, and 8 tracks were reclassified as expired.

With the assumption that only the fish with valid tracks survived after tagging, the estimated survivorship rate was 5.6%. Including uncertain tracks raises this estimate to 25.1%. Because some fish were tagged prior to the start of the study, track duration was used to compare and standardize results between individuals. In contrast, time at liberty, which encompasses the period from an individual's tagging to the last detection of its tag, would be inappropriate for standardizing analysis

Table 1

The number of tracks, algorithmically determined and after reclassification, for 179 tagged opakapaka (*Pristipomoides filamentosus*) detected on an acoustic receiver array between 26 June 2017 and 6 January 2019 in the Makapuu region off Oahu, Hawaii. The survival or status of detected fish was determined by using an algorithm to classify their tracks into 3 categories: *valid tracks* of fish believed to be alive, *uncertain tracks* of fish for which status could not be determined, and *expired tracks* of fish that were believed to be dead. Tracks of 40 fish with durations less than 14 d were excluded from analysis, and no tracks were available for 11 fish that were not detected on the array.

	No. of tracks	
Status	Algorithmically determined	After reclassification
Valid	30	10
Uncertain	24	35
Expired	74	83
Excluded from analysis	40	40
Undetected	11	11
Total	179	179

results because it includes days before the analysis period began. The durations of tracks for fish believed to be alive ranged between 161 and 560 d (median: 414.5 d; IQR: 297–496 d), and the durations of uncertain tracks were between 66 and 560 d (median: 357 d; IQR: 219–491 d) (Table 2).

Analysis scenarios

The status of each fish was used to construct conservative and optimistic analysis scenarios. The conservative scenario included only 10 tracks, those of fish determined to be alive. The optimistic scenario used tracks of 45 fish, including 35 tracks classified as uncertain in addition to the 10 tracks used in the conservative scenario.

Testing for size-selective survivorship bias

The mean length of opakapaka considered under both conservative and optimistic scenarios fell within the 95% CIs obtained from simulation data sampled without replacement: the mean length from the conservative scenario, for example, was 42.6 cm FL (95% CI: 42.1–54.5). However, the SD of mean lengths for fish included under both scenarios was smaller than the 95% CI obtained from simulation data sampled without replacement: the SD from the conservative scenario was 2.8 cm FL (95% CI: 4.9–14.4), and the SD from the optimistic scenario was 7.2 cm FL (95% CI: 8.15–11.8). These results indicate that the mean size of fish included in each scenario did not significantly differ from that of the tagged sample;

however, the smallest and largest tagged fish were under-represented in the data (Fig. 4).

Analysis periods

Receivers were recovered and downloaded twice, once mid-study and once at the end of the study, separating the analysis into 2 periods. Under the conservative scenario, all 10 fish with valid tracks were detected on the receiver array during the first period and 8 fish were detected on the array during the second period. Under the optimistic scenario, 45 fish were detected on the receiver array in total, with 44 fish detected during the first period and 37 fish detected during the second period.

Equipment losses affected the array's overall performance. During the first analysis period (26 June 2017–15 April 2018), 2 receiver stations from the fence sub-arrays were lost, station 333 (depth: 325 m) and station 340 (depth: 324 m) (Fig. 2). Losing station 333 truncated the northern fence so that the 25% minimum detection threshold extended to an estimated depth of 370 m rather than 400 m as planned. Losing station 340 left a gap in the southern boundary fence inside the BRFA. The possibility that individuals could move into the BRFA through this gap undetected cannot be ruled out. During the second analysis period (6 May 2018–6 January 2019), 3 stations from the fence sub-arrays were lost (Fig. 2). Stations 314 (depth: 78 m) and 317 (depth: 150 m) were part of the southern fence outside the BRFA. The receiver at station 340 (depth: 331 m), part of the southern fence inside the BRFA, once again broke free of its mooring and was later recovered. The logs from this receiver indicate that it broke free of its mooring within 3 weeks of deployment. The gaps caused by receiver losses in the second period mean that it was possible for tagged individuals to move into and out of the BRFA undetected during this time.

Calculating individual home range distance

Estimates of linear home range varied between 3.2 and 9.4 km under the conservative scenario and between 0.0 and 19.7 km under the optimistic scenario during the first analysis period. The median observed home range distance during this time was 5.8 km (IQR: 3.2–8.1 km) for the conservative scenario and 3.2 km (IQR: 1.6–6.1 km) under the optimistic scenario. Home ranges observed during the second period were between 1.7 and 8.1 km with a median distance of 3.7 km (IQR: 2.4–6.0 km) under the conservative scenario and between 0.0 and 8.1 km with a median distance of 2.4 km (IQR: 1.7–3.7 km) under the optimistic scenario.

Observed home ranges were mostly consistent between both periods. Results of nonparametric sign-rank tests indicate that home range did not significantly differ across these 2 periods for either scenario ($P > 0.05$). Regardless of period, the median home range calculated for any fish during the study was 6.0 km (IQR: 5.5–8.1 km) under the conservative scenario and 3.7 km (IQR: 1.7–7.2 km) under the optimistic scenario.

Table 2

Summary information for movement data, or tracks, of tagged opakapaka (*Pristipomoides filamentosus*) that were monitored with an acoustic receiver array during the first analysis period (P1), June 2017–April 2018, and the second analysis period (P2), May 2018–January 2019, within and near the bottomfish restricted fishing area (BRFA) in the Makapuu region off Oahu, Hawaii. Information includes the number of days during which detections were made and the number of movements across BRFA boundaries that were detected. Tracks of fish believed to be alive were classified as valid, tracks of fish for which status could not be determined were considered uncertain.

Tag ID code	Status	Fork length (cm)	Tagging date	Time at liberty (d)	Track duration (d)	No. of transmissions detected	No. of days with detections	Home range (km) P1	P2	Total no. of boundary movements detected	Time in BRFA (%) P1	P2
2122	Uncertain	47.0	2018-01-09	216	95	483	16	5.5	4.7	4	93	100
2127	Uncertain	49.5	2018-01-09	96	95	950	68	5.1	0.0	14	96	0
2133	Valid	43.0	2018-01-09	190	35	457	28	5.5	1.7	6	99	100
2136	Valid	42.0	2018-01-09	452	335	21,062	301	6.0	2.4	0	100	100
2139	Uncertain	50.0	2018-01-09	456	338	470	127	3.8	5.1	0	100	100
2140	Uncertain	39.5	2018-01-09	234	49	68	13	3.4	4.7	0	100	100
2157	Uncertain	52.5	2018-01-10	66	66	515	35	5.5	0.0	18	56	0
28171	Uncertain	52.0	2018-01-11	446	331	2351	212	2.4	2.4	0	100	100
28175	Uncertain	48.0	2018-01-11	391	276	920	125	11.8	3.7	0	100	100
28177	Uncertain	42.5	2018-01-11	437	144	679	41	13.2	3.8	4	100	16
28178	Uncertain	50.0	2018-01-11	352	158	19	11	3.4	5.1	0	100	100
28179	Valid	45.0	2018-01-11	454	339	60,130	339	5.5	3.8	69	98	98
28181	Uncertain	53.0	2018-01-11	446	331	9716	170	1.7	0.0	0	100	100
28185	Uncertain	34.0	2018-01-11	453	338	549	163	3.2	1.6	0	0	0
30683	Uncertain	41.5	2017-08-28	714	463	18,651	397	1.6	0.0	0	0	0
30684	Uncertain	43.0	2017-08-28	726	475	77,111	475	3.7	2.4	28	0	0
30690	Uncertain	42.0	2017-08-28	725	474	44,580	467	6.0	0.0	0	100	100
30694	Uncertain	36.0	2017-08-28	725	474	44,364	457	6.1	0.0	2	100	100
30695	Valid	36.5	2017-08-28	716	453	3605	297	7.1	2.4	2	100	100
30703	Uncertain	54.0	2017-08-28	681	429	577	94	2.4	2.4	0	100	100
30705	Valid	40.5	2017-08-29	724	474	17,055	462	6.1	8.1	86	99	97
30707	Uncertain	53.0	2017-08-29	724	474	33,067	456	0.0	1.7	0	100	100
30714	Uncertain	47.0	2017-06-24	764	410	12,364	152	0.0	1.7	0	100	100
30715	Uncertain	38.0	2017-06-24	856	538	57,792	535	0.0	1.7	0	100	100
30717	Uncertain	36.5	2017-06-24	73	71	277	7	0.0	0.0	0	100	0
30721	Valid	45.0	2017-06-24	856	538	64,477	538	3.2	6.0	0	100	100
30722	Uncertain	45.0	2017-06-24	856	538	99,377	522	0.0	1.7	0	100	100
30729	Uncertain	49.5	2017-06-25	187	186	1175	60	8.4	0.0	0	100	0
30734	Uncertain	55.5	2017-06-25	772	435	570	75	1.6	2.4	0	100	100
30739	Uncertain	40.0	2017-06-26	121	121	77	24	1.6	0.0	0	100	0
30742	Uncertain	47.0	2017-06-26	505	116	199	25	1.6	2.4	0	100	100
30743	Uncertain	43.0	2017-08-28	726	475	63,462	465	1.6	2.4	0	100	100
30747	Uncertain	44.0	2017-08-28	176	176	22,474	172	3.2	0.0	0	100	0
30749	Uncertain	61.0	2018-01-11	201	78	111	42	2.4	2.4	0	100	100
30751	Uncertain	70.0	2018-01-11	364	249	11,103	221	1.6	4.7	0	100	100
36810	Unknown	44.0	2017-06-24	637	319	1558	61	0.0	1.7	0	100	100
51581	Unknown	61.5	2017-01-13	1012	370	22,062	276	0.0	0.0	0	100	100
51582	Alive	41.0	2017-03-18	380	280	8109	222	3.8	0.0	0	100	0
51584	Unknown	51.0	2017-03-18	813	299	5446	234	1.7	0.0	0	100	100
51585	Unknown	44.0	2017-03-18	820	234	152	50	1.6	1.6	0	100	100
51586	Alive	46.0	2017-03-18	961	447	39,084	447	3.2	3.7	0	100	100
51587	Unknown	48.0	2017-03-18	982	397	629	139	1.6	1.6	0	100	100
51588	Alive	44.0	2017-03-18	286	186	16,105	186	7.1	0.0	6	80	0
51596	Alive	42.5	2017-08-28	726	475	44,371	475	3.2	6.0	0	100	100
51598	Unknown	44.5	2017-08-29	514	256	114	59	1.7	0.0	0	100	100

Figure 4

Frequency distributions of fork lengths for all opakapaka (*Pristipomoides filamentosus*) tagged and measured in the Makapuu region off the coast of Oahu, Hawaii, between January 2017 and January 2018 (number of samples [*n*]=179, light gray bars) and those for fish used in 2 survivorship scenarios. The conservative scenario includes only valid tracks, from tags on fish determined to be alive (*n*=10, black bars). The optimistic scenario includes uncertain tracks, from tags on fish for which survival could not be determined, as well as valid tracks (*n*=45, dark gray bars).

Comparing home range distance to size of reserves

The median linear habitat dimension of the BRFA network was 11.40 km (IQR: 8.32–16.02 km) (Fig. 1). Under the conservative survivorship scenario, with the exception of BRFA B, home ranges observed for opakapaka were less than the linear habitat dimension of the BRFAs (Fig. 5). Three individuals (6.7% of 45) included in the optimistic scenario had home range estimates greater than the median linear habitat dimension of the BRFAs.

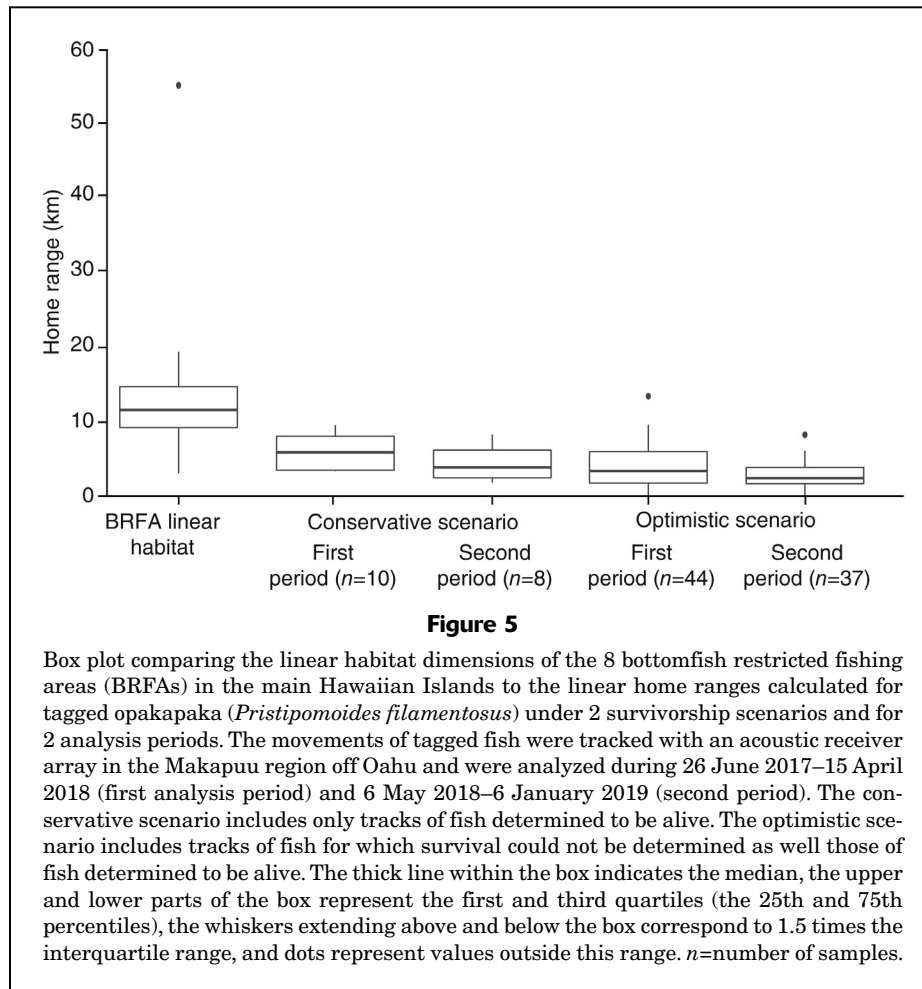### Quantifying movement frequency and site fidelity

Tracked fish generally stayed within the boundaries of the protected reserve. Under the conservative scenario, 5 of the 10 fish with valid tracks were detected crossing BRFA boundaries a combined 39 times during the first analysis period. This group had a high degree of site fidelity; on average, these fish spent 97.7% (SD 6.2) of their time within the BRFA during this period. Under the optimistic scenario, 11 of the 45 fish with valid or uncertain tracks were detected crossing BRFA boundaries a combined 94 times. Site fidelity was similarly high for these fish; on average, fish detected in this period spent 91.6% (SD 25.8) of their time within the BRFA.

Fish were rarely observed crossing reserve boundaries. Under the conservative scenario, the median number of total movements across BRFA boundaries for fish detected moving between protected and unprotected areas was 6 crossings/fish (IQR: 6–12 crossings/fish) over a track duration of 280 d (IQR: 230–293 d). Standardized by track

duration, the median number of movements into or out of the BRFA for the 5 fish that crossed boundaries was 0.043 crossings·d^{-1}·fish^{-1} (IQR: 0.021–0.057 crossings·d^{-1}·fish^{-1}), a rate equivalent to 1 crossing every 23.3 d. However, rates for individuals were as high as 0.064 crossings/d, equivalent to 1 crossing every 15.7 d. Under the optimistic scenario, the median number of total movements across BRFA boundaries was 6 crossings/fish (IQR: 3.5–13.5 crossings/fish) over a median track duration of 95 d (IQR: 76.5–224.5 d). Standardized by track duration, the median number of movements into or out of the BRFA for the 11 fish that crossed boundaries was 0.061 crossings·d^{-1}·fish^{-1} (IQR: 0.028–0.168 crossings·d^{-1}·fish^{-1}), equivalent to 1 crossing every 16.4 d. However, rates for individuals were as high as 0.273 crossings/d, equivalent to 1 crossing every 3.6 d.

Under the conservative scenario, 2 of 8 fish considered to be alive and detected during the second analysis period crossed BRFA boundaries a combined total of 130 times (74 times and 56 times) over a track duration of 245 d. On average, the 8 fish spent the majority of their time (mean: 99.3% [SD 6.2]) within the BRFA. Standardized by their track lengths, these 2 fish moved into or out of the BRFA with 0.229 and 0.302 crossings/d, equivalent to 1 crossing every 4.4 and 3.3 d, respectively. Under the optimistic scenario, 5 of the 37 fish detected during the second period crossed the BRFA boundaries 145 times total. Similar to that of fish in the conservative scenario, site fidelity was high; on average, fish detected in this period spent 89.8% (SD 28.9) of their time within the BRFA. The median fish in this group crossed the BRFA boundaries at an average rate of 0.028 crossings/d (IQR: 0.003–0.149 crossings/d) over a mean track duration of 245 d (IQR: 245–245 d). Standardized by track duration, this rate was equivalent to 1 movement over reserve boundaries every 35.4 d. However, rates of individuals were as high as 0.156 crossings/d, equivalent to 1 crossing every 6.4 d.

Irrespective of analysis period or array shape, the 10 fish with tracks used in the conservative scenario were detected within the BRFA on 97.6% (SD 6.2) of days they were tracked, compared with 91.6% (SD 25.7) of tracked days for the 45 fish in the optimistic scenario. Under the conservative scenario, 226 total detected movements between protected and non-protected areas were made by 5 fish over a median track duration of 339 d (IQR: 186–453 d). These fish moved across boundaries at a rate of 0.17 crossings·d^{-1}·fish^{-1} (IQR: 0.03–0.18 crossings·d^{-1}·fish^{-1}) or 1 crossing every 5.8 d. Eleven of the 45 fish for which tracks were considered under the optimistic scenario were detected crossing the reserve boundaries a combined 301 times. The median fish spent 100% (1st quartile: 100; 3rd quartile: 100) of their time within the BRFA. The median fish detected moving across boundaries crossed BRFA boundaries 6 times (IQR: 3.5–24) over a median track duration of 350 d (IQR: 173.5–495.5 d), corresponding to 0.04 crossings/d

Figure 5

Box plot comparing the linear habitat dimensions of the 8 bottomfish restricted fishing areas (BRFAs) in the main Hawaiian Islands to the linear home ranges calculated for tagged opakapaka (*Pristipomoides filamentosus*) under 2 survivorship scenarios and for 2 analysis periods. The movements of tagged fish were tracked with an acoustic receiver array in the Makapuu region off Oahu and were analyzed during 26 June 2017–15 April 2018 (first analysis period) and 6 May 2018–6 January 2019 (second period). The conservative scenario includes only tracks of fish determined to be alive. The optimistic scenario includes tracks of fish for which survival could not be determined as well those of fish determined to be alive. The thick line within the box indicates the median, the upper and lower parts of the box represent the first and third quartiles (the 25th and 75th percentiles), the whiskers extending above and below the box correspond to 1.5 times the interquartile range, and dots represent values outside this range. *n*=number of samples.

(IQR: 0.015–0.21 crossings/d) and equivalent to 1 movement over reserve boundaries every 27 d. Rates of individuals were as high as 0.27 crossings/d, equivalent to 1 crossing every 3.7 d. Under both conservative and optimistic scenarios, there was a moderate correlation between the distance an individual's tagging location was from the reserve boundary and the probability that an individual was detected leaving the reserve (conservative: $r=-0.43$; optimistic: $r=-0.36$). Across both scenarios, only 1 fish (tag ID code: 28179) was detected leaving the reserve and did not return.

Discussion

In this study, opakapaka were monitored by using acoustic telemetry to compare home ranges of individual fish to estimates of the scale of protection under Hawaii's BRFA system. All of the linear home ranges calculated for fish under a conservative survivorship scenario were similar to each other in magnitude and smaller than the linear habitat dimension of BRFA E, where the fish were tracked. Only 2 fish included in the optimistic survivorship scenario had linear home ranges that exceeded the linear

habitat dimension of BRFA E; however, it is possible that these fish had been eaten by predators. We were unable to detect any long-range movements of opakapaka because it was not possible to detect acoustic tags beyond the range of the receiver array. However, our findings are supported by the results of conventional tagging experiments for this species in which the majority of fish (>85%) were recaptured within 10 km of their tagging location (O'Malley[5]; Uehara et al., 2019). Despite minor differences, tracks of fish were similar under both conservative and optimistic survivorship scenarios. The median home range was relatively small (6.0 km for the conservative scenario and 3.6 km for the optimistic scenario). This result is not surprising because significant movement was a key requirement to qualify for the conservative scenario.

When broadening our comparison to include the 7 additional BRFAs, we found that the typical home range for tagged opakapaka under both scenarios was smaller than the minimum linear habitat dimension for all but 1 BRFA. It should be noted that the small linear habitat estimated for this reserve, BRFA B off the island of Niihau, is not representative of the total habitat within the area because the method used to quantify linear habitat uses the shortest path across the reserve and does not account for the

large offshore pinnacle within this reserve (Fig. 1). When a similar least-cost path approach is applied around the pinnacle, the linear habitat of this BRFA increases from 3.0 km to 9.2 km. Our results are broadly consistent with those of studies that used baited underwater camera stations, indicating that the BRFAs do provide protection for bottomfish (Sackett et al., 2017). Our findings are also in agreement with those of aforementioned conventional tagging work done in the region in which the majority of fish were recaptured in close proximity to their tagging location (Kobayashi, 2008; O'Malley[5]).

Movements of opakapaka with valid tracks in this study are within the range of those reported for other snappers of the family Lutjanidae, species that have high site fidelity and limited home ranges with rare long-distance movements. Tinhan et al. (2014) reported that amarillo snapper (*Lutjanus argentiventris*) were detected in the Gulf of California within a 0.61-km^2 marine reserve on 49% (SD 30) of the days after they were tagged, and red snapper (*L. campechanus*) in the Gulf of Mexico have been associated within 26.3 m (SD 35.4) of artificial reefs (Piraino and Szedlmayer, 2014). In Hawaii, no discernable movement was observed for over 83.5% of tagged common bluestripe snapper (*L. kasmira*), and 95% of those fish were recaptured within 150 m of the location of their initial release (Friedlander et al., 2002). In another study, individual ehu and onaga tracked relative to BRFA B off the island of Niihau spent almost all of their time within the reserve and were detected moving distances up to 8.9 km (Weng, 2013). Even larger ranges have been described for green jobfish (*Aprion virescens*), a bottomfish species not included in the Deep-7 management unit, with individuals observed moving up to 18 km (Meyer et al., 2007). Movements of opakapaka deemed to be alive in this study fall between these reported ranges. However, we used range testing experiments to determine that 2.2 km would be used as the movement criteria to categorize fish status. Therefore, any tracks from surviving individuals with movements that were exclusively of shorter distances were classified as uncertain and included only in the optimistic scenario.

Estimates of postrelease survivorship of fish tagged in this study are low, between 5.6% and 25.1% depending on the inclusion of tracks classified as uncertain. These low survivorship rates mirror those of conventional mark-recapture work in which observed recapture rates for this species were 2.5% (O'Malley[5]), 12.0% (Kobayashi, 2008), and 8.7% (Uehara et al., 2019). Survivorship rates as high as 66.7% have been reported for opakapaka tagged with acoustic transmitters in the Kahoolawe Island Reserve (Ziemann and Kelley[8]); however, assumption of an individual's survival in that study was based on detection of a tag on at least one receiver, and no further steps to ascertain survivorship were performed. In our study, we applied a rigorous approach to determining the status of our fish and included in our analysis only tracks with durations of at least 14 d. If our approach to classifying tagged fish were applied to fish in the study conducted in the Kahoolawe Island Reserve, only 30.8% of tagged opakapaka would have been included. When we discussed approaches with

authors of this other study, one of them told us that tagged fish were evaluated at the surface upon release and that those in poor condition were recaptured and their tag was removed (Kelley[14]).

Mortality following tagging is a major challenge to study of the movements of deepwater fish species (Edwards et al., 2019). The 2 major causes of mortality in our study are believed to be barotrauma and predation. Deep-7 species are physoclistic, that is, the gas bladder is not open to the gastrointestinal tract, making them particularly susceptible to barotrauma injuries from expansion of the swim bladder during rapid ascent following hooking (DeMartini et al., 1996; Edwards et al., 2019). Severe injury may result in organ damage and death (Rogers et al., 2011). Results from studies of methods that can mitigate barotrauma in deepwater rockfish species (*Sebastes* spp.) indicate that slow ascent rates, limited on-deck handling times, and rapid recompression improve survivorship outcomes (Rogers et al., 2011). External symptoms of barotrauma observed during this project included esophageal eversion and exophthalmia due to swim bladder expansion. Rapid release of air and deflation of the body cavity while the peritoneal incision was made was not uncommon and was likely caused by a rupture in the swim bladder. Barotrauma can also lead to physical and behavioral impairment that can result in subsequent predation (Rankin et al., 2017).

Sharks, marine mammals, and other potential predators were also a significant source of mortality. During our sampling, a number of opakapaka were consumed partially or totally by predators during ascent following hooking. Detection records for 65 tagged fish indicate a series of rapid movements between receivers immediately after tagging followed by no further detections or persistent detections at a single receiver. This type of tracking record is consistent with a tagged fish being inside the stomach of a predator with movement cessation occurring with expulsion of the tag. We suspect that the pulu used to aggregate bottomfish for capture in our study also attracted predators and exacerbated this issue. For future studies, it would be wise to first consider how variation in tagging methods may offset the mortality associated with tagging this and other deepwater fish species. Given the high rates of postrelease mortality observed in our study, protocols that reliably improve survivorship for this species should be explored.

Acoustic telemetry is an established tool for evaluating animal movements relative to marine reserves. Its application in this study at depths greater than 200 m is relatively novel and presented a number of challenges that studies in shallower environments do not have to address (Arnold and Dewar, 2001; Heupel et al., 2006; Pedersen et al., 2014; Edwards et al., 2019). A considerable amount of hardware associated with each receiver station was deployed over the duration of this study at operational depths that exceeded those accessible by scuba diving. Deployment at these depths necessitated servicing of

---

[14] Kelley, C. 2019. Personal commun. Dep. Oceanogr., Sch. Ocean Earth Sci. Tech., Univ. Hawaii Manoa, 1000 Pope Rd., Honolulu, HI 96822.

receiver stations from a suitably sized vessel and introduced additional points of failure for each station and uncertainty to the data retrieved from them.

Close-proximity detection interference is a factor that must be accounted for when deploying acoustic tracking arrays at depths exceeding 200 m (Scherrer et al., 2018). Using a conservative model for predicting CPDI and a detection range of 847 m, we estimated that at 20 m above the seafloor, CPDI effects could extend between 70 and 451 m from the receiver depending on the receiver's depth. This model assumes that no energy is lost at the seafloor and sea surface and should be considered a worst-case scenario. Given the nominal transmission rate of the tags used and assuming an average swimming speed of 1 body length/s, we do not believe CPDI affected our ability to detect the passage of tagged fish transiting through fence receiver subarrays. However, if tagged individuals spent extensive time in the vicinity of deeper receivers, CPDI may have led to an underestimation of residency rates.

The loss of several stations reduced the capacity of the acoustic receiver array to monitor fish within and transiting into or out of the BRFA. Theoretical detection rates were calculated by using a telemetry optimization algorithm and the locations of receivers recovered during each analysis period (Pedersen et al., 2014). We estimated that receiver losses reduced the proportion of monitored habitat (100–400 m) within BRFA E from the planned 27.0% to 23.2% during the first analysis period. During the first period, the loss of receiver stations 333 and 340 from fence sub-arrays within the BRFA introduced the potential for undetected passage of individuals that transited into the BRFA, and such missed detections would result in an underestimation of site fidelity within the BRFA. Because observed site fidelity within the BRFA was quite high, it is unlikely that undetected movements significantly altered the conclusions of this analysis. During the second analysis period, loss of stations 314 and 317 from the outer southern fence sub-array and station 340 from the interior southern fence sub-array created a path where fish could theoretically swim undetected between protected and nonprotected waters. The loss of these stations means that detected movements between protected and non-protected regions may underestimate true movement frequency and site fidelity within the reserve during this period.

Although genetic panmixia has been reported for opakapaka across the Hawaiian Archipelago, there is growing evidence to support spatially structured approaches to management (Gaither et al., 2011). Panmixia can occur even through a limited exchange of larvae and adult individuals, but large-scale exchanges are required to support spatially distinct populations (Wright, 1931; Botsford et al., 2003). Long-range movements greater than 300 km have been reported for tagged opakapaka, but the high degree of site fidelity observed in our study and reported from conventional mark-recapture studies indicates that such movements are rare for this species (Kobayashi, 2008; O'Malley[5]). These observations are consistent with those of baited-camera studies that indicate disproportionate measures of abundance and population structure between opakapaka inside and outside of reserve boundaries (Sackett et al., 2017). Furthermore, results from the use of simulation models of larval dispersal across the archipelago indicate that larvae are primarily retained in 4 self-sustained zones with only limited advection (Vaz, 2012). These observations support the use of spatially structured approaches to assessment and management of this species.

Acknowledgments

Literature cited

Arnold, G., and H. Dewar.
  2001. Electronic tags in marine fisheries research: a 30-year perspective. *In* Electronic tagging and tracking in marine fisheries (J. R. Sibert and J. L. Nielsen, eds.), p. 7–64. Kluwer Academic Publishers, Dordrecht, Netherlands.

Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson.
  2006. Effects of sampling regime on the mean and variance of home range size estimates. J. Anim. Ecol. 75:1393–1405. Crossref

Botsford, L. W., F. Micheli, and A. Hastings.
  2003. Principles for the design of marine reserves. Ecol. Appl. 13:25–31. Crossref

Cailliet, G. M., A. H. Andrews, E. J. Burton, D. L. Watters, D. E. Kline, and L. A. Ferry-Graham.
  2001. Age determination and validation studies of marine fishes: do deep-dwellers live longer? Exp. Gerontol. 36:739–764. Crossref

Comfort, C. M., and K. C. Weng.
  2015. Vertical habitat and behaviour of the bluntnose sixgill shark in Hawaii. Deep-Sea Res., II 115:116–126. Crossref

Craig, P., B. Ponwith, F. Aitaoto, and D. Hamm.
  1993. The commercial, subsistence, and recreational fisheries of American Samoa. Mar. Fish. Rev. 55(2):109–116.

Crossin, G. T., M. R. Heupel, C. M. Holbrook, N. E. Hussey, S. K. Lowerre-Barbieri, V. M. Nguyen, G. D. Raby, and S. J. Cooke.
  2017. Acoustic telemetry and fisheries management. Ecol. Appl. 27:1031–1049. Crossref

DeMartini, E. E., F. A. Parrish, and D. M. Ellis.
  1996. Barotrauma-associated regurgitation of food: implications for diet studies of Hawaiian pink snapper, *Pristipomoides filamentosus* (family Lutjanidae). Fish. Bull. 94:250–256.

Dwyer, R. G., H. A. Campbell, T. R. Irwin, and C. E. Franklin.
  2015. Does the telemetry technology matter? Comparing estimates of aquatic animal space-use generated from

GPS-based and passive acoustic tracking. Mar. Freshw. Res. 66:654–664. Crossref

Edwards, J. E., J. Pratt, N. Tress, and N. E. Hussey.
2019. Thinking deeper: uncovering the mysteries of animal movement in the deep sea. Deep-Sea Res. Oceanogr., I 146:24–43. Crossref

Friedlander, M., J. D. Parrish, and R. C. DeFelice.
2002. Ecology of the introduced snapper *Lutjanus kasmira* (Forsskal) in the reef fish assemblage of a Hawaiian bay. J. Fish Biol. 60:28–48. Crossref

Friedlander, A. M., K. A. Stamoulis, J. N. Kittinger, J. C. Drazen, and B. N. Tissot.
2014. Chapter five—understanding the scale of marine protection in Hawai'i: from community-based management to the remote Northwestern Hawaiian Islands. Adv. Mar. Biol. 69:153–203. Crossref

Gaither, M. R., S. A. Jones, C. Kelley, S. J. Newman, L. Sorenson, and B. W. Bowen.
2011. High connectivity in the deepwater snapper *Pristipomoides filamentosus* (Lutjanidae) across the Indo-Pacific with isolation of the Hawaiian Archipelago. PLoS ONE 6(12):e28913. Crossref

Haight, W. R.
1989. Trophic relationships, density and habitat associations of deepwater snappers (Lutjanidae) from Penguin Bank, Hawaii. M.S. thesis, 89 p. Univ. Hawaii Manoa, Honolulu, HI.

Haight, W. R., D. R. Kobayashi, and K. E. Kawamoto.
1993. Biology and management of deepwater snappers of the Hawaiian Archipelago. Mar. Fish. Rev. 55(2):20–27.

Halpern, B. S.
2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecol. Appl. 13(sp1):117–137. Crossref

Heupel, M. R., J. M. Semmens, and A. J. Hobday.
2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar. Freshw. Res. 57:1–13. Crossref

Hill, N. J., T. Peatman, C. B. Wakefield, S. J. Newman, T. Halafihi, J. Kinch, C. T. T. Edwards, S. J. Nicol, and A. J. Williams.
2018. Improving guidelines for implementing harvest strategies in capacity-limited fisheries—lessons from Tonga's deepwater line fishery. Mar. Policy 98:85–91. Crossref

Huvenne, V. A. I., B. J. Bett, D. G. Masson, T. P. Le Bas, and A. J. Wheeler.
2016. Effectiveness of a deep-sea cold-water coral marine protected area, following eight years of fisheries closure. Biol. Conserv. 200:60–69. Crossref

Kami, H. T.
1972. The *Pristipomoides* (Pisces: Lutjanidae) of Guam with notes on their biology and fisheries aspects. M.S. thesis, 140 p. Univ. Guam, Mangilao, Guam.

Kelley, C. D., and W. Ikehara.
2006. The impacts of bottomfishing on Raita and West St. Rogatien Banks in the Northwestern Hawaiian Islands. Atoll Res. Bull. 543:305–318.

Kessel, S. T., N. E. Hussey, D. M. Webber, S. H. Gruber, J. M. Young, M. J. Smale, and A. T. Fisk.
2015. Close proximity detection interference with acoustic telemetry: the importance of considering tag power output in low ambient noise environments. Anim. Biotelem. 3:5. Crossref

Kobayashi, D. R.
2008. Spatial connectivity of Pacific insular species: insights from modeling and tagging. Ph.D. thesis, 215 p. Univ. Technol. Sydney, Sydney, Australia. [Available from website.]

Langseth, B., J. Syslo, A. Yau, M. Kapur, and J. Brodziak.
2018. Stock assessment for the main Hawaiian Islands Deep 7 bottomfish complex in 2018, with catch projections through 2022. NOAA Tech. Memo. NMFS-PIFSC-69, 217 p.

Medved, R. J.
1985. Gastric evacuation in the sandbar shark, *Carcharhinus plumbeus*. J. Fish Biol. 26:239–253. Crossref

Meyer, C. G., Y. P. Papastamatiou, and K. N. Holland.
2007. Seasonal, diel, and tidal movements of green jobfish (*Aprion virescens*, Lutjanidae) at remote Hawaiian atolls: implications for marine protected area design. Mar. Biol. 151:2133–2143. Crossref

Misa, W. F. X. E., J. C. Drazen, C. D. Kelley, and V. N. Moriwake.
2013. Establishing species-habitat associations for 4 eteline snappers with the use of a baited stereo-video camera system. Fish. Bull. 111:293–308. Crossref

Moffitt, R. B., and F. A. Parrish.
1996. Habitat and life history of juvenile Hawaiian pink snapper, *Pristipomoides filamentosus*. Pac. Sci. 50:371–381.

Moore, C., J. C. Drazen, B. T. Radford, C. Kelley, and S. J. Newman.
2016. Improving essential fish habitat designation to support sustainable ecosystem-based fisheries management. Mar. Policy 69:32–41. Crossref

Newman, S. J., C. B. Wakefield, A. J. Williams, J. M. O'Malley, S. J. Nicol, E. E. DeMartini, T. Halafihi, J. Kaltavara, R. L. Humphreys, B. M. Taylor, et al.
2015. International workshop on methodological evolution to improve estimates of life history parameters and fisheries management of data-poor deep-water snappers and groupers. Mar. Policy 60:182–185. Crossref

Newman, S. J., A. J. Williams, C. B. Wakefield, S. J. Nicol, B. M. Taylor, and J. M. O'Malley.
2016. Review of the life history characteristics, ecology and fisheries for deep-water tropical demersal fish in the Indo-Pacific region. Rev. Fish Biol. Fish. 26:537–562. Crossref

Oyafuso, Z. S., J. C. Drazen, C. H. Moore, and E. C. Franklin.
2017. Habitat-based species distribution modelling of the Hawaiian deepwater snapper-grouper complex. Fish. Res. 195:19–27. Crossref

Oyafuso, Z. S., P. S. Leung, and E. C. Franklin.
2019. Evaluating bioeconomic tradeoffs of fishing reserves via spatial optimization. Mar. Policy 100:163–172. Crossref

Palumbi, S. R.
2004. Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. Annu. Rev. Environ. Resour. 29:31–68. Crossref

Pante, E., and B. Simon-Bouhet.
2013. marmap: a package for importing, plotting and analyzing bathymetric and topographic data in R. PLoS ONE 8(9):e73051. Crossref

Parke, M.
2007. Linking Hawaii fisherman reported commercial bottomfish catch data to potential bottomfish habitat and proposed restricted fishing areas using GIS and spatial analysis. NOAA Tech. Memo. NMFS-PIFSC-11, 37 p.

Parrish, F. A., N. T. Hayman, C. Kelley, and R. C. Boland.
2015. Acoustic tagging and monitoring of cultured and wild juvenile crimson jobfish (*Pristipomoides filamentosus*) in a nursery habitat. Fish. Bull. 113:231–241. Crossref

Pedersen, M. W., G. Burgess, and K. C. Weng.
2014. A quantitative approach to static sensor network design. Methods Ecol. Evol. 5:1043–1051. Crossref

Piraino, M. N., and S. T. Szedlmayer.
2014. Fine-scale movements and home ranges of red snapper around artificial reefs in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 143:988–998. Crossref

Pooley, S. G.
    1993. Economics and Hawaii's marine fisheries. Mar. Fish. Rev. 55(2):93–101.

R Core Team.
    2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from website, accessed June 2018.]

Rankin, P. S., R. W. Hannah, M. T. O. Blume, T. J. Miller-Morgan, and J. R. Heidel.
    2017. Delayed effects of capture-induced barotrauma on physical condition and behavioral competency of recompressed yelloweye rockfish, *Sebastes ruberrimus*. Fish. Res. 186:258–268. Crossref

Roberts, C. M., G. Branch, R. H. Bustamante, J. C. Castilla, J. Dugan, B. S. Halpern, K. D. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, et al.
    2003. Application of ecological criteria in selecting marine reserves and developing reserve networks. Ecol. Appl. 13(sp1):215–228. Crossref

Rogers, B. L., C. G. Lowe, and E. Fernández-Juricic.
    2011. Recovery of visual performance in rosy rockfish (*Sebastes rosaceus*) following exophthalmia resulting from barotrauma. Fish. Res. 112:1–7. Crossref

Sackett, D. K., J. C. Drazen, V. N. Moriwake, C. D. Kelley, B. D. Schumacher, and W. F. X. E. Misa.
    2014. Marine protected areas for deepwater fish populations: an evaluation of their effects in Hawai'i. Mar. Biol. 161:411–425. Crossref

Sackett, D. K., C. D. Kelley, and J. C. Drazen.
    2017. Spilling over deepwater boundaries: evidence of spillover from two deepwater restricted fishing areas in Hawaii. Mar. Ecol. Prog. Ser. 568:175–190. Crossref

Schadt, S., F. Knauer, P. Kaczensky, E. Revilla, T. Wiegand, and L. Trepl.
    2002. Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. Ecol. Appl. 12:1469–1483. Crossref

Scherrer, S. R., B. P. Rideout, G. Giorli, E.-M. Nosal, and K. C. Weng.
    2018. Depth- and range-dependent variation in the performance of aquatic telemetry systems: understanding and predicting the susceptibility of acoustic tag–receiver pairs to close proximity detection interference. PeerJ 6:e4249. Crossref

Stickel, L. F.
    1954. A comparison of certain methods of measuring ranges of small mammals. J. Mammal. 35:1–15. Crossref

Stumpf, W. A., and C. O. Mohr.
    1962. Linearity of home ranges of California mice and other animals. J. Wildl. Manage. 26:149–154. Crossref

Tinhan, T., B. Erisman, O. Aburto-Oropeza, A. Weaver, D. Vázquez-Arce, and C. G. Lowe.
    2014. Residency and seasonal movements in *Lutjanus argentiventris* and *Mycteroperca rosacea* at Los Islotes Reserve, Gulf of California. Mar. Ecol. Prog. Ser. 501:191–206. Crossref

Uehara, M., A. Ebisawa, I. Ohta, and Y. Aomuma.
    2019. Effectiveness of deepwater marine protected areas: implication for Okinawan demersal fisheries management. Fish. Res. 215:123–130. Crossref

Vaz, A. C.
    2012. Here today, gone tomorrow: flow variability, larval dispersal and fisheries management in Hawai'i. Ph.D. diss., 122 p. Univ. Hawaii Manoa, Honolulu, HI. [Available from website.]

Wakefield, C. B., J. M. O'Malley, A. J. Williams, B. M. Taylor, R. S. Nichols, T. Halafihi, R. L. Humphreys, J. Kaltavara, S. J. Nicol, and S. J. Newman.
    2017. Ageing bias and precision for deep-water snappers: evaluating nascent otolith preparation methods using novel multivariate comparisons among readers and growth parameter estimates. ICES J. Mar. Sci. 74:193–203. Crossref

Weng, K. C.
    2013. A pilot study of deepwater fish movement with respect to marine reserves. Anim. Biotelem. 1:17. Crossref

Williams, A., N. J. Bax, R. J. Kloser, F. Althaus, B. Barker, and G. Keith.
    2009. Australia's deep-water reserve network: implications of false homogeneity for classifying abiotic surrogates of biodiversity. ICES J. Mar. Sci. 66:214–224. Crossref

Williams, A. J., S. J. Nicol, N. Bentley, P. J. Starr, S. J. Newman, M. A. McCoy, J. Kinch, P. G. Williams, F. Magron, G. M. Pilling, et al.
    2012. International workshop on developing strategies for monitoring data-limited deepwater demersal line fisheries in the Pacific Ocean. Rev. Fish Biol. Fish. 22:527–531. Crossref

Wright, S.
    1931. Evolution in Mendelian populations. Genetics 16:97–159.