

HISTORICAL AND PRESENT STATUS OF THE PEARL OYSTER, *Pinctada margaritifera*, AT PEARL AND HERMES ATOLL, NORTHWESTERN HAWAIIAN ISLANDS

BY

ELIZABETH E. KEENAN¹, RUSSELL E. BRAINARD², and LARRY V. BASCH³

ABSTRACT

Populations of the black-lipped pearl oyster, *Pinctada margaritifera*, at Pearl and Hermes Atoll in the Northwestern Hawaiian Islands were first reported in 1928 and heavily harvested over the next 2 years. Approximately 150,000 pearl oysters were either exported or killed during the exploitation. An expedition in 1930 to assess post-harvest population status found 480 *P. margaritifera* and determined the population to be severely depleted. Limited surveys in 1994 and 2000 found only a few pearl oysters and led to the conclusion that the population was still depleted. In 2003, the National Oceanic and Atmospheric Administration (NOAA)-led multi-agency marine debris removal team spent several months conducting surveys at Pearl and Hermes Atoll that included quantitative observations of *Pinctada margaritifera*. Data were collected on location, size, depth, habitat, and orientation of individual pearl oysters on the reef. Analyses of the 1930 and 2003 data sets revealed similar size-frequency distributions of the *P. margaritifera* population. The population has a spatial distribution within the Atoll similar to the 1930 post-harvest distribution, and some sustained level of reproduction. Density and depth distribution comparisons from the two survey periods suggest that pearl oysters are significantly more abundant in the shallow waters where they were harvested during the fishery but at a similar density overall as they were during the 1930 survey. Although no estimates of absolute population size are available for any time period, the large number of oysters harvested prior to the 1930 survey, together with estimates of oyster density in 1930 and 2003, suggest that the population may never have recovered to its pre-exploitation level.

INTRODUCTION

The pearl oyster, like other shellfish and many other marine animals (e.g., abalone; Tegner et al., 1996), has a long history of exploitation throughout the world.

¹Joint Institute for Marine and Atmospheric Research, University of Hawaii and NOAA Pacific Islands Fisheries Science Center, 1125-B Ala Moana Blvd, Honolulu, HI 96814 USA, E-mail: ekeen@mail.nmfs.hawaii.edu

²NOAA Pacific Islands Fisheries Science Center, 2570 Dole Street, Honolulu, HI 96822 USA

³U.S. National Park Service, Pacific Islands Coral Reef Program and University of Hawaii Manoa, Hawai'i-Pacific Islands Cooperative Ecosystem Studies Unit, Honolulu, HI USA

Records from the pearl industries in India and Venezuela document the discovery, harvest, and eventual over-exploitation of these populations (Arunachlam, 1952; Romero et al., 1999). Pearl oysters have been prone to exploitation due to the considerable value of the pearls and the nacre, or "mother of pearl", of the shell, and because of the animal's sessile nature and tendency to occur in sufficient densities at shallow depths for relatively easy collection.

The first documented discovery of *Pinctada margaritifera* at Pearl and Hermes Atoll in the Northwestern Hawaiian Islands (NWHI) (Fig. 1) was in May 1928 by Captain William B. Anderson of the Lanikai Fishing Company (Amerson et al., 1974). For the next 2 years, the pearl oysters were heavily harvested for their nacre. This shiny portion of the shell was exported to the U.S. mainland where it was used primarily to make buttons. Although documents concerning the harvest are wanting, conservative estimates are that the shells of approximately 100,000 oysters were exported (Galtsoff, 1933). It is estimated that about 50,000 more oysters were killed and discarded, some due to their poor shell quality and others in the search for pearls (Galtsoff, 1933). After the extent of the harvest was realized by the Hawaii Territorial government, an expedition was undertaken to assess the population and a temporary ban on harvesting was put in place. This six-week expedition, led by P. Galtsoff in the summer of 1930, utilized several Filipino divers and produced a lengthy report including data on pearl oyster size, weight, location (Fig. 2, modified from Galtsoff (1933)) and survey effort. Galtsoff (1933) found 480 *P. margaritifera* and pronounced the population too depleted to sustain further harvesting. At this time the Territory of Hawaii made the taking of pearl oysters illegal without permission, and a resurvey was suggested in five years to assess the recovery of the population. Subsequently the industry collapsed, coinciding with replacement of pearl shell with plastic for button making and the advent of commercial pearl oyster farms. Due to the lack of interest in further fishing of *P. margaritifera* in Hawaii, the suggested 5-year resurvey at Pearl and Hermes was not conducted; however, the species has remained under state protection since that time.

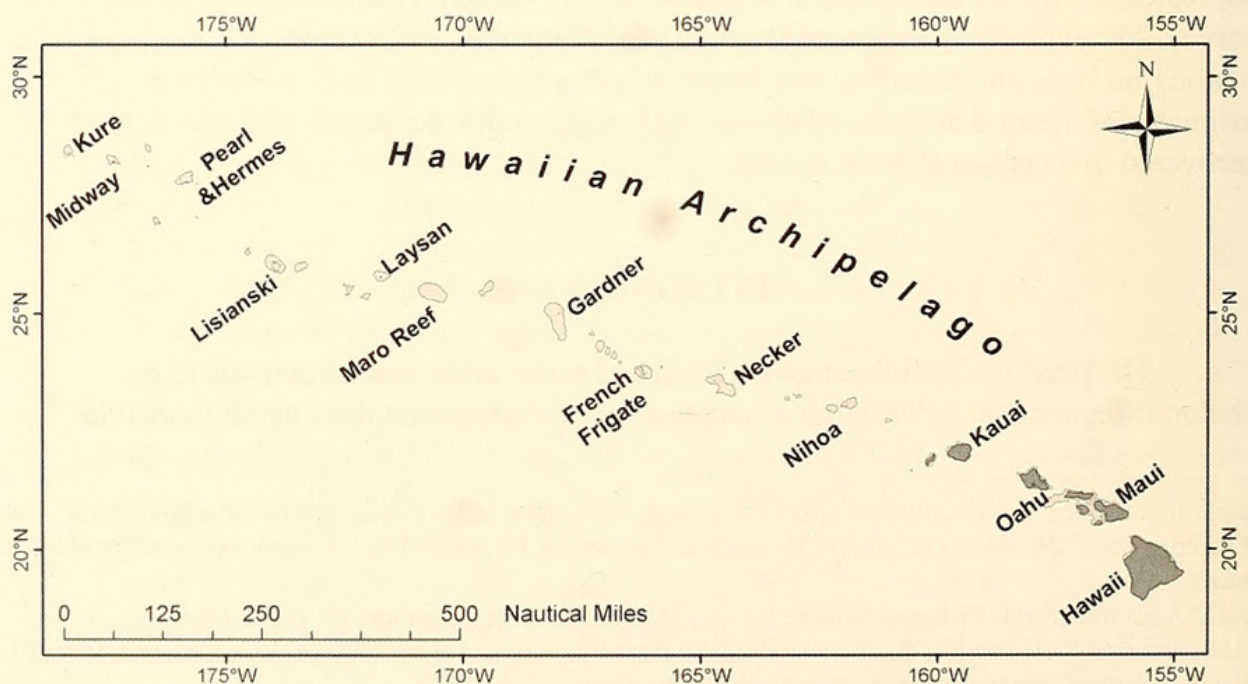


Figure 1. Map of the Hawaiian Archipelago.

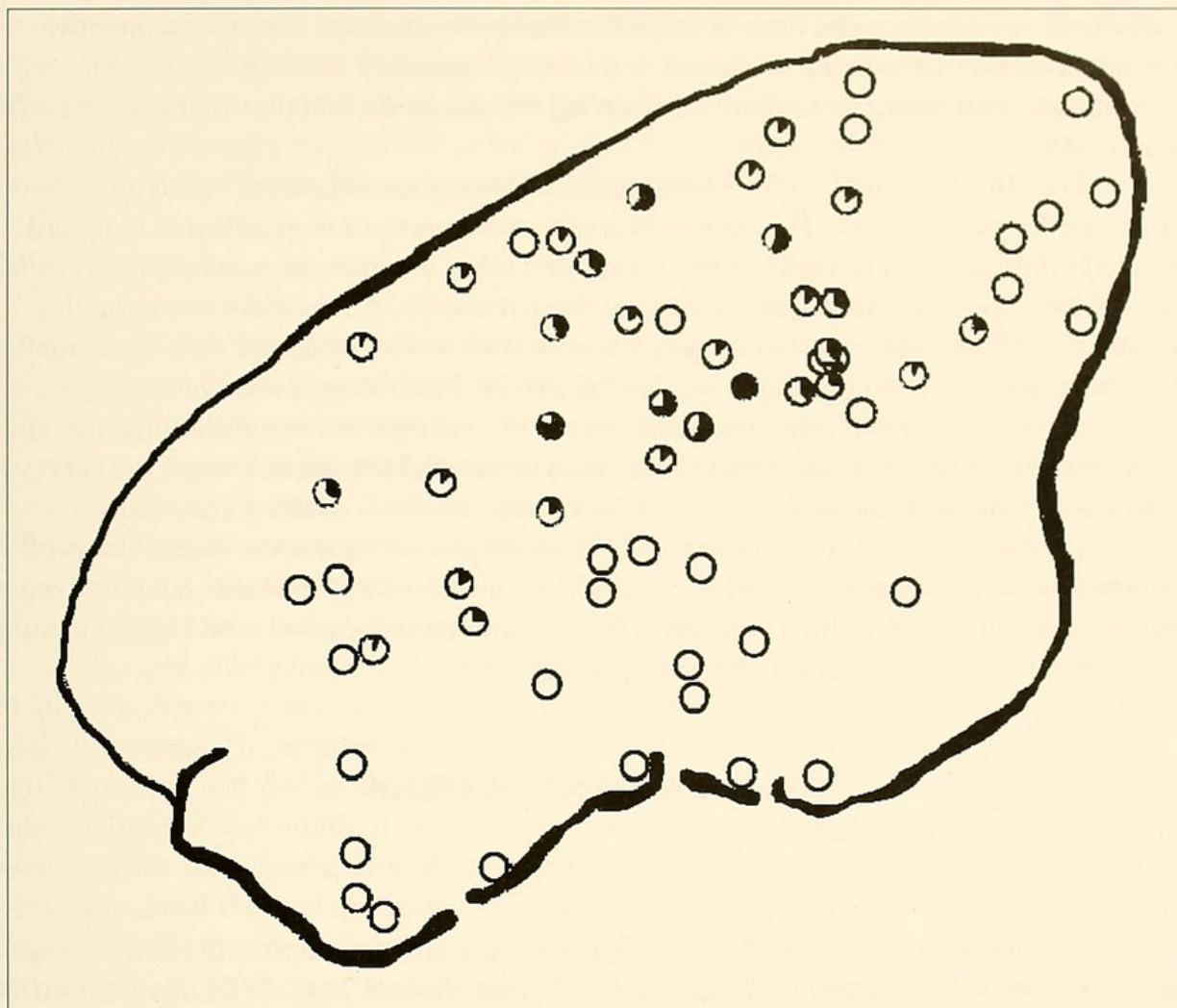


Figure 2. (From Galtsoff, 1933). Pearl oyster survey sites at Pearl and Hermes Atoll from the 1930 survey. The single black circle represents the highest relative abundance found (33 oysters / diver hour) and is represented as 100 percent. Other circles indicate the proportional relative abundance found at other sites in the 1930 survey. White circles are sites at which no oysters were found.

There have been three recent surveys at Pearl and Hermes which included documentation of pearl oyster presence: (1) by the U.S. National Marine Fisheries Service (NMFS) in 1993 (Moffitt, 1994); (2) the 2000 NWHI Reef Assessment and Monitoring Program (NOWRAMP) expedition (Maragos and Gulko, 2002); and (3) the 2002 NOWRAMP expedition (Basch, unpublished data). Each of these surveys reported only a few pearl oyster sightings, suggesting that the population did not rebound from the harvesting event and remained severely depleted. However, researchers had insufficient data to determine an accurate status of the pearl oyster population. The 1993 NMFS effort was a two-day survey of the general areas which had the highest pearl oyster densities in Galtsoff's (1933) survey. The densities at the three sites assessed in 1993 were found to be lower than in 1930 (Moffitt, 1994). One problem with the 1993 survey is that the methods used to determine the locations of survey sites in 1930 were not sufficiently accurate. They were comprised of calculations using triangulation of distant markers

and dead reckoning; moreover, these methods were made less accurate by the scientists' inability to navigate straight lines through the shallow, reticulated reef. Consequently, it is not possible to locate the 1930 sites with enough accuracy to make site-by-site comparisons over time, particularly considering the patchy distribution characteristic of pearl oysters.

The 2000 and 2002 NOWRAMP cruises were not specifically focused on surveying for pearl oysters. The relatively small areas surveyed were selected to record detailed information on the fish, algae, corals, and other invertebrate species present. Pearl oysters were also recorded on some of these transects. A report documenting the results of the 2000 cruise states that only a few oysters were found, and they were smaller than those taken in 1930 (Maragos and Gulko, 2002). The transects were purposely located on varying habitat types and many were not in preferred pearl oyster habitat. The few observations made on the status of the pearl oyster and the constraints of the surveys limit the usefulness of these surveys for determining the status of the population.

The purposes of this study were to: (1) accurately document the recent status of the pearl oyster population at Pearl and Hermes by means of a systematic, quantitative, and broad-scale survey of the *P. margaritifera* population at the Atoll, and (2) make initial comparisons between historical and recent survey results.

MATERIALS AND METHODS

Data Collection

As part of an ongoing NOAA-led multi-agency effort to remove derelict fishing gear and other marine debris from the coral reef ecosystems of the NWHI, divers from NOAA's Coral Reef Ecosystem Division (CRED) have methodically and systematically surveyed large areas of the shallow water reef habitats at Pearl and Hermes Atoll (Donohue et al., 2001). Since 2003, the survey protocols have included extensive pearl oyster observations. Divers surveyed reefs using snorkel gear while swimming or being towed along patch or reticulated reefs. Areas surveyed were recorded using a Garmin Geographic Positioning System (GPS) 12 (NAD84) in a small boat closely following diver tracks. For each pearl oyster observed, latitude, longitude, size, and depth were recorded. Maximum shell length and width were measured. Length was measured as the maximum dorsal ventral measurement (DVM), and width was recorded as the measurement of the shell perpendicular to the length. For a small number (approximately 10 percent) of the oysters no measurements, depths, or locations were recorded. Since identification of juvenile recruits to species requires more time and greater taxonomic skills than were available, and usually requires observation in the laboratory, juvenile oysters (<1.5 cm) were not included in the data analysis.

For a subset of observations, additional data were collected, when time allowed, on habitat (substratum, dominant biotic cover category), and orientation of individual oysters on the reef. For 40% percent of observations substrate was documented, and for 59% percent orientation was recorded. Habitat was characterized by percent cover of the

substratum types in the 1 m² area centered on an oyster. The substrate categories were recorded as algae, sand, coral, and coral cement. The algae category consisted of macroalgae only, which were not identified to species. The coral cement category encompassed coral rubble and dead coral either exposed or with associated turf or coralline algae. Orientation, the angle between the plane of the oyster's shell and the substrate it was attached to, was classified as horizontal, vertical or diagonal.

Data Analysis

Field data were transcribed daily to an Excel worksheet containing all parameters for each oyster. The GPS tracklines and waypoints were imported into ESRI Arcview[®] 3.2 Geographic Information System (GIS) software, where they were used to map both the reefs surveyed and the point location of oysters on those reefs (Fig. 3). The total area of the reef surveyed during 2003 was determined by creating polygons in ArcView which delineated the reef contours of areas where divers swam. These polygons were created using an Ikonis satellite image of the atoll (Fig. 4). The areas of all polygons were added to obtain total reef area surveyed.

Several manipulations of Galtsoff's (1933) observations were performed to enable comparison of his and our survey results. Galtsoff (1933) reported survey effort in diver minutes. He reported that the divers covered a reef at the speed of 42.7 ft/min (0.01 km/min), and that in order to cover the entire breadth of the reef the divers swam a zigzag pattern with a width of 60 to 100 ft. Galtsoff reported survey effort only for areas where oysters were found. In order to compensate for the rest of the survey area effort, we assumed that the average effort for a site with no oysters reported was approximately the same as for the sites where oysters were observed. There were 32 sites with oysters and 32 without, so the total minutes were doubled for a best approximation of survey effort. To estimate the distance surveyed from effort we multiplied the survey rate (0.01 km/min) by total minutes (4,562 min) for a result of 58.9 km. We multiplied this distance by the associated width (60 to 100 ft, or 0.01 to 0.03 km) to estimate the survey area covered, with a result of 1.1 km² to 1.8 km².

RESULTS

A total of 1,057 pearl oysters were found at Pearl and Hermes Atoll during the 2003 summer survey. The pearl oysters were distributed primarily throughout the inner lagoon area (Fig. 2) with the exception of ten observations where individuals were found on the sand flats or outer fringing reefs. The lagoon habitat was surveyed by swimming only; we did not factor in the towed-diver survey areas in our density estimates as they were largely performed over sand and on habitat unsuitable for pearl oysters. This facilitated comparisons with Galtsoff's (1933) results as observers in the 1930 survey intentionally avoided the sand flats. Area computations using GIS resulted in a total lagoon survey area of 5.9 km². With an observed total of 1,047 pearl oysters in this area, we calculated an average density of 177 pearl oysters/km² in the lagoon area surveyed.

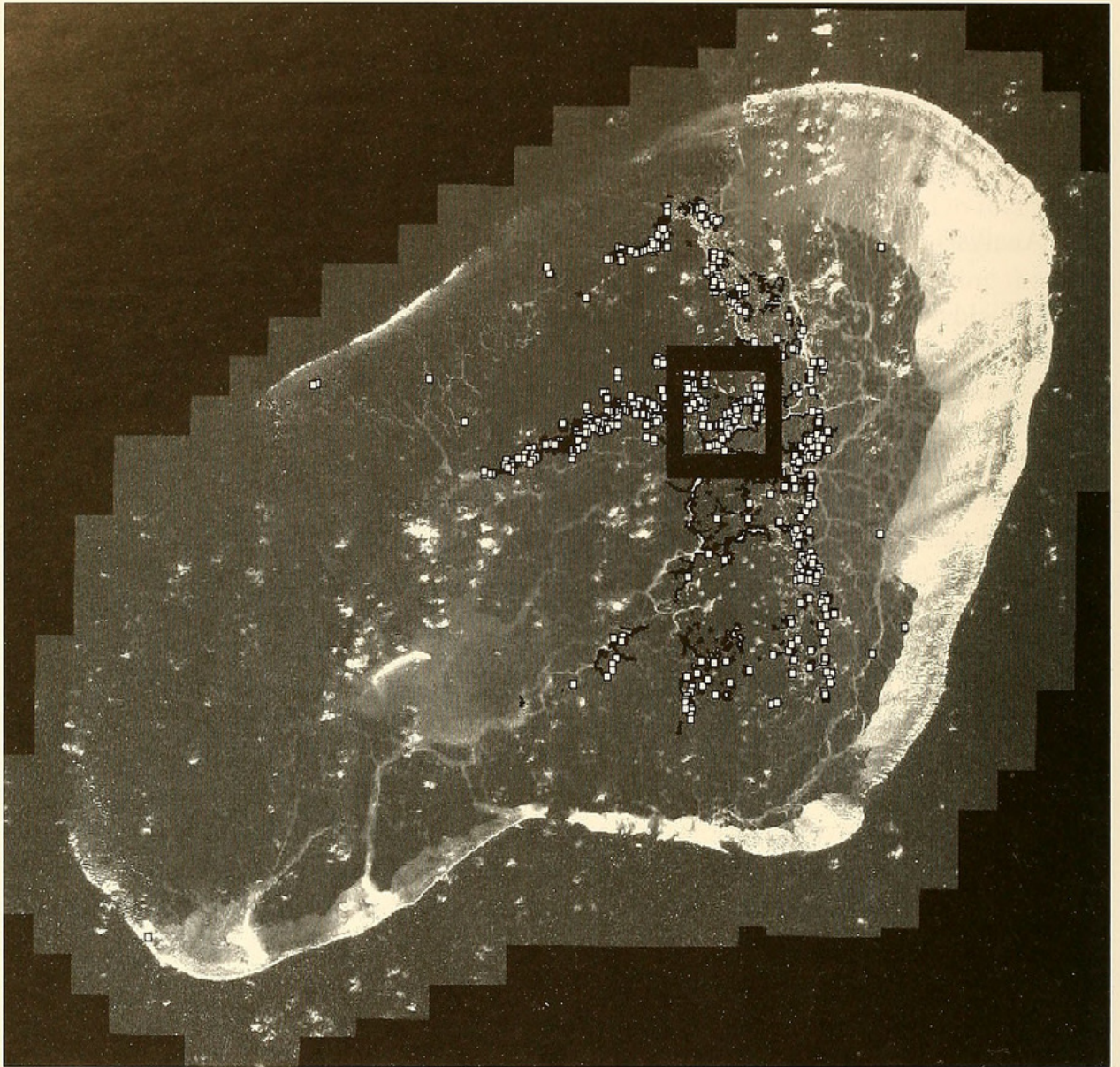


Figure 3. Distribution map of 2003 pearl oyster sightings, Pearl and Hermes Atoll. Areas surveyed by swimming are displayed as black lines, and oysters are represented as white squares. Only the survey areas and oysters in the inner lagoon were used in the density calculations. The black box represents the area portrayed in Figure 4.

This density estimate assumes that all oysters present were observed by the divers, when in reality some oysters were missed. Therefore, this is not an estimate of absolute oyster density, but a density estimate that can be compared to the 1930 survey, assuming that in each study there was the same probability that an oyster present in the surveyed area was observed by the divers. Pearl oysters were found at depths ranging from 0.31 m to 6.1 m with a mean of 1.36 m and standard deviation (sd) of 0.87 m (Fig. 5).

The average shell length of pearl oysters measured was 20.2 cm (sd = 4.76 cm, $n = 963$). Shell length ranged from 1.5–33.0 cm. Pearl oysters smaller than 1.5 cm were excluded from analysis since oysters of that size could not be accurately identified

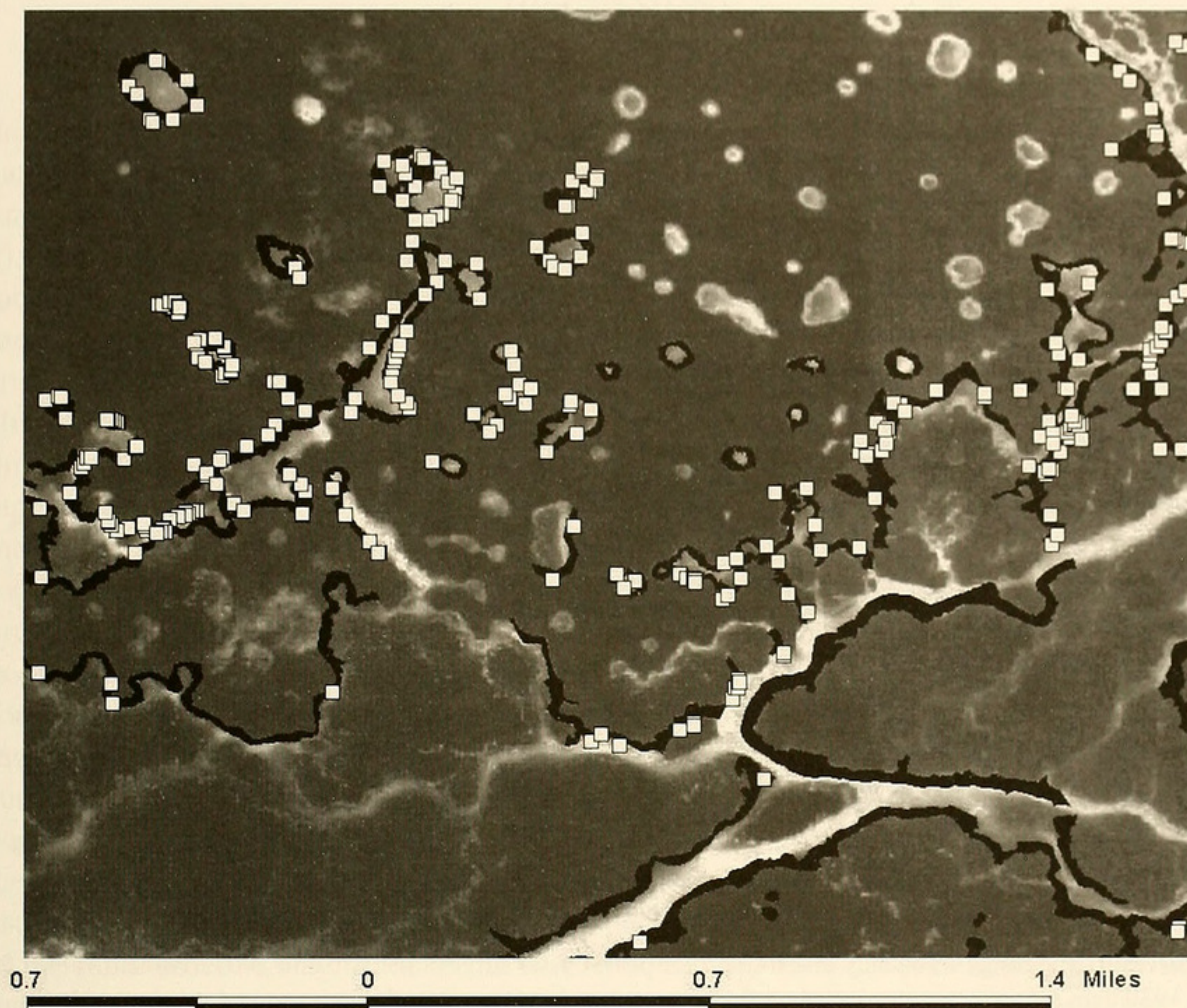


Figure 4. An enlargement of a section of the lagoon at Pearl and Hermes Atoll (Area portrayed is outlined by the black box in Figure 3). The black areas are the polygons created in Arcview 3.2 to delineate the surveyed reef area at Pearl and Hermes during 2003. Pearl oysters are represented by white squares.

to species in the field. The *P. margaritifera* size frequency distribution (Fig. 6) has a single mode. However, immature oyster recruits, or spat (shell length <5 cm), were excluded from the size-frequency data set. The mean shell length of 20.2 cm found in 2003 is remarkably similar to the mean shell length of 20.23 cm for the 164 adult pearl oysters measured by Galtsoff (1933), although the distributions have different shapes (Fig. 6). For 419 (40% of total surveyed) pearl oysters observed, data were recorded on substratum type. Within the lagoon, the typical substratum composition consisted of: sand 11% (sd = 24.8), coral 13% (sd = 17.3), algae 28% (sd = 32.1), and coral cement 48% (sd = 34.6). The oysters were found in various orientations. In the subset of oysters for which orientation data were collected (n = 624), most were horizontal (53%). Of the remaining oysters, 32% were vertical, and 15% were diagonal.

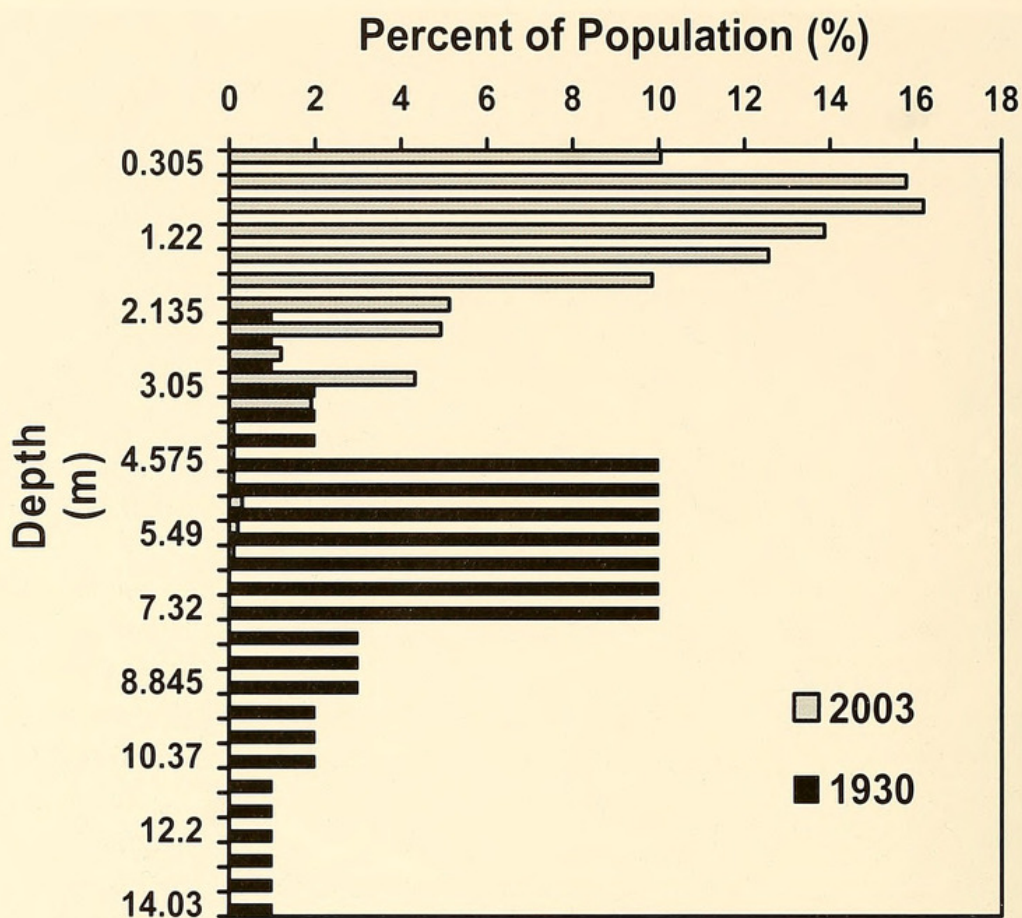


Figure 5. Depth range frequency distribution for pearl oyster surveys in 1930 and 2003. Percent values for the 1930 data set are estimates based on the given mean depth range and minimum and maximum depths from Galtsoff (1933).

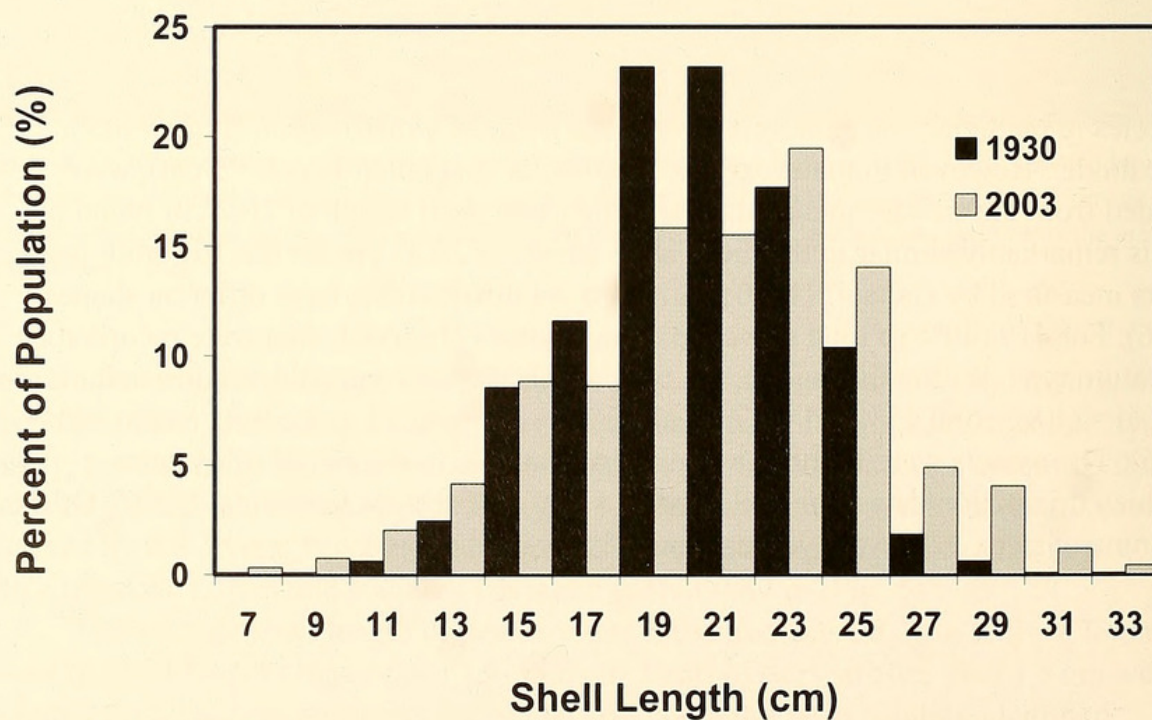


Figure 6. Size-frequency distribution of the pearl oyster population at Pearl and Hermes Atoll, Northwestern Hawaiian Islands in 1930 (N =197) and 2003 (N =963).

DISCUSSION

In distribution maps (Figs. 3 and 4) we indicate that pearl oysters are widespread throughout the Atoll lagoon. When comparing our results with Galtsoff's (1933) post-harvest data, we considered whether changes in the population occurred since that time. By visually comparing the maps from the 1930 and 2003 surveys (Figs. 2 and 3), a general idea of the difference in spatial distribution can be obtained. Although the locations from the 1930 map (Galtsoff, 1933) are only roughly estimated, no oysters were recorded in 1930 for the reefs in the southeast and south ends of the islands. When those areas were surveyed in 2003, relatively high levels of pearl oysters were observed on almost all reefs. It is likely there has been new recruitment and population expansion into this region since the 1930 survey. Moreover, reefs in the south central and north central lagoon, where some oysters were seen in 1930, were not surveyed in 2003; some oysters may be present in these areas.

Determining whether *Pinctada margaritifera* populations have recovered to pre-harvest levels is complicated by the fact that there are no estimates of pre-harvest population density, and no estimates of absolute oyster abundance at Pearl and Hermes for any time period. Comparisons between early and recent post-harvest data sets are facilitated by the fact that Galtsoff (1933) did report numbers of oysters found and the survey effort, which can be used to estimate oyster density in the 1930 survey. After converting Galtsoff's (1933) reported effort into survey area, we determined an average density of 209 to 349 pearl oysters/km² during his surveys. In our 2003 survey, we estimated an average density within the lagoon areas of 177 pearl oysters/km², lower but of the same order of magnitude as the density found in 1930, and presumably lower than the density just prior to exploitation. Given the lack of data between the two surveys, changes in pearl oyster abundance during the intervening 73 years cannot be determined. However, if abundance has not reached pre-exploitation levels, it is useful to ask why. One explanation for this would be that adult pearl oyster densities were reduced by exploitation below a threshold where Allee effects (or inverse density dependence) came into play (Levitan, 1995). *Pinctada margaritifera* is a broadcast spawner with planktonic larvae (Pouvreau et al. 2000); consequently, reduced adult densities could have imposed a direct bottleneck on fertilization success, and subsequent embryonic, larval, and recruitment success (Pouvreau et al., 2000). With a lowered adult density there would be less likelihood that female gametes would become fertilized in the water column, as has been shown for octocorals, sea urchins, abalone, and other sessile or sedentary benthic marine invertebrates (Levitan, 1995; Tegner et al., 1996; Coma and Lasker, 1997). Subsequently, if a larva was produced and dispersed proximate to a suitable settlement site, the likelihood that it would encounter a settlement cue associated with an adult shell also would be more remote. In other words, Allee effects would be further enforced given that pearl oyster larvae tend to settle gregariously on the shells of adult oysters (Pascal and Zampatti, 1995; Zhao et al., 2002).

Comparison of the pearl oyster population depth distribution between the 1930 and 2003 surveys shows some intriguing differences (Fig. 5). In 1930, oysters were reported as ranging from 2.5 to 15.0 m, and were most abundant from 4.4 to 8.3 m.

Galtsoff (1933) also reports that, according to Captain Anderson, when the oysters were first discovered they were very abundant in water depths of 1 to 3 m. In our 2003 survey, we found oysters from 0.3 to 6.0 m depth, but animals were most abundant in the 0.5 to 2.2 m range (determined using the mean of $1.36 \text{ m} \pm 0.87 \text{ m sd}$). In Figure 5, we illustrate the difference in the depth ranges between the two studies. The absence of any oysters in waters shallower than 2.5 m in 1930 is evidence of the heavy harvesting effort at these shallow depths in the immediately preceding years. Seventy-three years later, we found oysters to be very abundant at these shallow depths, suggesting that the remaining population contributed to a reseeding of shallow areas of the reef. What remains elusive at this time is an explanation for the apparent scarcity of oysters at deeper depths in our survey. The most likely explanation is that oysters still occur in higher abundance at these greater depths but that our sampling did not detect them. Since the lagoon surveys were performed by snorkeling, the divers spent most of their time at or near the surface while surveying. Oysters which may have been on the deeper reef slopes may have been missed because of their smaller size in relation to other search images (since the primary mission was to locate generally larger marine debris) and the greater distance with depth from the divers. We have no reason to believe that the lagoonal reefs have changed in a way that would impose biological limits to the depth range of the oysters.

Alternatively, though less likely, pearl oysters may recruit preferentially to shallower depths and may be less abundant in deeper areas due to this preference in combination with (1) reduced adult densities at depth sustained over the post-harvest period and (2) Allee effects. A directed survey for pearl oysters at Pearl and Hermes conducted along multiple-depth contours would help determine the distribution and other population parameters of oysters at deeper depths.

The present study indicates that the *Pinctada margaritifera* population at Pearl and Hermes Atoll is reproducing at some level, as indicated by individuals of a broad range of size classes, including recruits. The mean shell length of the 963 pearl oysters measured in the 2003 survey was 20.2 cm. The oysters were found predominantly on coral cement and macro-algae dominated habitat. This observation contrasts with Galtsoff's (1933) report that most oysters were found "confined exclusively to those sections where the bottom is covered with corals." Initially, we thought that the difference between surveys in composition of oyster-occupied habitat might be attributed to differences in the depth range, but examination of the data showed similar coral percent cover at all depths.

The shell orientation of the oysters was measured in our survey because our initial observations of orientation were inconsistent with a comment in Galtsoff's (1933) report. Galtsoff (1933) noted that oysters were found in a vertical or slightly inclined position, while we commonly observed oysters in a horizontal position. Our results indicate that only about 1/3 of oysters were oriented vertically, and $\geq 1/2$ were horizontal. These differences in orientation may be a residual artifact of harvesting, or may reflect depth-related differences in the nature of near-boundary layer water movements which the animals may respond to by orienting themselves, either to minimize drag due to sheer forces, or to optimize filter-feeding efficiency in different flow regimes.

We report the first systematic, quantitative survey for pearl oysters throughout

the lagoon at Pearl and Hermes Atoll since Galtsoff's 1930 post-harvest expedition. By comparing the estimated densities of post-harvest and present populations, it would appear that the abundance of oysters in 2003 is similar to the population size in 1930. Given the lack of data during the intervening 73 years, we cannot determine whether the population ever recovered to its pre-exploitation abundance, but all available observations suggest it has remained at a reduced level. However, because we found the majority of pearl oysters at depths where the historical exploitation was focused, we conclude that the pearl oyster population has increased in density at shallower depths since the 1930 survey. In addition, it seems likely that the oyster density in deeper waters may be comparable to historical densities, if not higher. Depth-stratified surveys of pearl oysters at Pearl and Hermes are needed for a more thorough understanding of current population status; these additional surveys likely would yield a higher present population density.

ACKNOWLEDGEMENTS

We wish to thank the 2003 marine debris team for their significant and essential contribution of field time and effort in collecting the data used in this paper. The 2003 team was G. Schorr, K. Koyanagi, J. Asher, A. Hall, C. Kistner, J. Stephenson, J. Jones, K. Shepley, K. Curtis, K. Hogrefe, M. Defley, M. Moews, M. Timmers, M. Kalson, S. Holzwarth, and S. Charrette. Special thanks to C. Navarro for acting as data manager for a portion of the field time. Funding for this project came from the NOAA Coral Reef Conservation Program, with strong support by Tom Hourigan of the NOAA Fisheries Office of Habitat Conservation. Shipboard and logistical support in the field were provided by the captains and crews of the M/V *Ocean Fury* and M/V *American Islander*. We appreciate the support and permits to conduct this research within the Hawaiian Islands National Wildlife Refuge by the U.S. Fish and Wildlife Service and the State of Hawaii Department of Land and Natural Resources.

LITERATURE CITED

- Amerson, A.B., R.B. Clapp, and W.O. Wirtz
 1974. The natural history of Pearl and Hermes Reef, Northwestern Hawaiian Islands. *Atoll Research Bulletin* 174:26-39.
- Arunachalam, S.
 1952. The history of the pearl fishery of the Tamil Coast. *Annamalai University Historical Series*, no. 8, 206pp.
- Coma, R., and H.R Lasker
 1997. Small-scale heterogeneity of fertilization success in a broadcast spawning octocoral. *Journal of Experimental Marine Biology and Ecology* 214:107-112
- Donohue, M.J., R.C. Boland, C.M. Stramek, and G.A. Antonelis
 2001. Derelict fishing gear in the Northwestern Hawaiian Islands: diving surveys and debris removal confirm threat to coral reef ecosystems. *Marine Pollution Bulletin* 42(12):1301-1312

Galtsoff, P. S.

1933. Pearl and Hermes Reef, Hawaii hydrographical and biological observations. *Bernice P. Bishop Museum Bulletin* no. 107:49pp.

Levitan, D.R.

1995. The ecology of fertilization in free-spawning invertebrates. *In*: L. McEdward (ed.), *Ecology of marine invertebrate larvae*, pp. 123-156. CRC Press, Boca Raton, Fl.

Maragos, J., and D. Gulko, (eds.)

2002. Coral reef ecosystems of the Northwestern Hawaiian Islands: Interim results emphasizing the 2000 surveys. U. S. Fish and Wildlife Service and the Hawai'i Department of Land and Natural Resources, Honolulu, Hawai'i. 46 pp.

Moffitt, R. B.

1994. Pearl oysters in Hawaii. *Hawaiian Shell News*, May, 3-4.

Pascal, M. S., and E.A. Zampatti

1995. Evidence of a chemically mediated adult-larval interaction triggering settlement in Ostrea puelchana: applications in hatchery production. *Aquaculture* 133: 33-44.

Pouvreau, S., A. Gangnery, J. Tiapari, F. Lagarde, M. Garnier, and A. Bodoy

2000. Gametogenic cycle and reproductive effort of the tropical blacklip pearl oyster, Pinctada margaritifera (Bivalvia: Pteriidae), cultivated in Takapoto Atoll (French Polynesia). *Aquat. Living Resources* 13(1): 37-48.

Romero, A., S. Chilbert, and M.G. Eisenhart

1999. Cubagua's pearl-oyster beds: the first depletion of a natural resource caused by Europeans in the American continent. *Journal of Political Ecology* 6:57-78

Tegner, M.J., L.V. Basch, and P.K. Dayton

1996. Near extinction of an exploited marine invertebrate. *Trends in Ecology and Evolution* 11, 7: 278-279.

Zhao, B., S. Zhang, and P.Y. Qian

2002. Larval settlement of the silver- or goldlip pearl oyster *Pinctada maxima* (Jameson) in response to natural biofilms and chemical cues. *Aquaculture* 62216:1-19.



Keenan, Elizabeth E, Brainard, Russell, and Basch, Larry V. 2006. "Historical and present status of the pearl oyster, *Pinctada margaritifera*, at Pearl and Hermes Atoll, Northwestern Hawaiian Islands." *Atoll research bulletin* 543, 333–344.

View This Item Online: <https://www.biodiversitylibrary.org/item/123669>

Permalink: <https://www.biodiversitylibrary.org/partpdf/83087>

Holding Institution

Smithsonian Libraries and Archives

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: In Copyright. Digitized with the permission of the rights holder

Rights Holder: National Museum of Natural History, Smithsonian Institution

License: <https://creativecommons.org/licenses/by-nc-sa/4.0/>

Rights: <http://www.biodiversitylibrary.org/permissions/>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.