Characterization and Assessment of the Main Hawaiian Island
Kona Crab (Ranina ranina) Fishery

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Introduction

In Hawaii, Kona crab (*Ranina ranina*) landings in Hawaii make up over 25% of all commercial crab landings and up to 5% of all commercially landed reef species (Smith 1993). In the Main Hawaiian Island (MHI) commercial Kona crab landings have declined over the last 18 years (DLNR unpublished data). Because the most recent stock assessment of the Kona crab fishery was conducted over 30 years ago (Vansant 1978) the need for a contemporary assessment of the stock and review of the fishery was identified at the 2008 National Oceanic and Atmospheric Administration (NOAA) Pacific Coral Reef Ecosystem Integrated Observing System (CREIOS) Workshop and prioritized within the Coral Reef Ecosystem Fishery Management Plan (CMFMGP).

The Kona crab, also known as frog crab, red frog crab, papa’i kua loa, krab ziraf and spanner crab is a large marine brachyuran which is targeted by both commercial and recreational fishers in Hawaii. Kona crabs are found in sandy substrata adjacent to coral reefs across the tropical and subtropical Indo-Pacific in depths ranging from 6 to 650 feet (Vansant 1978). The crabs spend a majority of time buried in the sand to avoid predators, which include sharks, rays, loggerhead turtles, large fish and occasionally marine mammals (Skinner and Hill 1986; Kennelly et al. 1990). Kona crabs emerge from the sand to feed and mate (Skinner and Hill 1986). Kona crabs are opportunistic scavengers but also feed on small fish and invertebrates (Onizuka1972).

While Hawaii represents the easternmost point of the Kona crab’s range (Brown 1985) commercial fisheries also exist in Australia, Japan, Philippines, Thailand, Seychelles Islands and Hawaii (Brown 1985; Tahil 1983; Boulle 1995; Krajangdara and Watanabe 2005). The largest fishery for Kona crabs is found in Queensland, Australia where annual landings can reach over six million pounds making it the largest single species fishery in the State (Dichmont and Brown 2010). A smaller Kona crab fishery also exists in New South Wales, Australia. Due to the economic importance of the fisheries in Australia, substantial research on Kona crabs has been performed in these regions.

This reports represents the first review of the Kona crab fishery in Hawaii in more than 30 years. The primary objective of this report is to assess the stock of the Kona crab fishery in the Main Hawaiian Islands. A summary of known life history characteristics is provided as well as an investigation of the historical data on temporal and spatial aspects of this fishery. A generalized linear model is used to standardize annual CPUE by removing potential effects of season and area on the distribution and catchability of Kona crabs. Three hypotheses are tested by the generalized linear model to determine possible area characteristics controlling Kona crab distribution: (1) Island in closest proximity to fishing area, (2) depth of fishing area (inshore or offshore) and (3) wave intensity experienced by fishing area. The commercial landings data and relative index of stock abundance (estimated by the generalized linear model) are then fit to a generalized surplus production model to estimate the model parameters of the fishery: maximum sustainable yield, fishing mortality at maximum sustainable yield, as well as a time trajectory of estimated stock biomass and fishing mortality. Stock biomass projections based on future potential catch scenarios are also provided.
Biology and Ecology of the Kona Crab

Taxonomy and Physical Description

*Ranina ranina* belongs to the Order Decapoda, Class Crustacea. Kona crabs vary in color from white to orange and have long, urn shaped bodies (Figure 1). The carapace can reach 5.5-10.4 inches in length and is covered with small, rounded spines that are used for protection (Tahil 1983; Brown 1985). Anterolateral areas of the carapace become armed with longer, sharper, spines as the crab reaches maturity. This characteristic that is especially prominent in males (Uchida and Uchiyama 1986). Kona crabs are sexually dimorphic with larger males than females (Fielding and Haley 1976; Minagawa 1993). The abdomen of the crab is divided into seven segments, which are much narrower in males than females (Uchida and Uchiyama 1986). In mature female crabs, spermatheca, are located between the third and fourth peripods. Mature males have a genital opening between the fifth pair of peripods.

*R. ranina* have five bilaterally symmetric pairs of limbs which are from anterior to posterior the chela, first walking leg, second walking leg, first swimming leg and second swimming leg (Figure 1.3). The chela, which form the claws, are larger in males. Large chelapeds are advantageous in male crabs as they help with both fighting and courtship (Minagawa 1993). Each limb has six segments. The most distal segment, the dactyl, is shaped like a paddle on the swimming legs and help form the claw on the chela. The dactyl is followed by the pompous, carpus, merus, ischium and the coxa segment. The most proximal segment, the coxa, attaches the limb to the body (...

Habitat and Behavior

Adult Kona crabs are found in sandy substrata adjacent to coral reefs in areas subject to strong currents (Vansant 1978). The habitat of small juveniles is unknown but assumed to be similar to the adult habitat (Brown 2001). Newly settled Kona crabs have been observed in the shallow waters of the surf break on a beach in west Maui (Layne Nakagawa pers. comm.) Kona crabs spend 90% of their time buried in the sand, emerging for an average of 1.7 hours a day to feed and/or mate (Skinner and Hill 1986). When food is available, the crabs will spend twice as much time emerged from the sand and will act aggressively towards one another. On average, males spend a significantly longer time emerged from the sand than females (Skinner and Hill 1986).
Life Cycle

Kona crabs exhibit a typical crab life cycle. The crabs begin life as planktonic larvae that eventually settle as benthic juveniles and grow into adults found in sandy habitats (Onizuka 1972; Minagawa and Murano 1993a). Mature females receive sperm from males via copulation and externally fertilize their eggs. Females externally brood their eggs until they hatch into larvae which, are released into the water column (Onizuka 1972).

Larval Development

Kona crab larvae spend several weeks as planktonic larvae which is their primary mechanism for dispersal (Brown 1985). The first molt, when the larvae develop into a zoea I stage, is typically 7-8 days after the larvae hatch (Fielding 1974). Six to seven days later a second molt occurs and the larvae develop into the zoea II stage. Prey density greatly affects the time between molts and the growth of these larval crabs (Minagawa and Murano 1993a) Larvae begin to settle on the bottom 5-6 weeks after they have hatched (Brown et al. 2008). The newly settled crabs typically have around a 0.40 inch carapace length (Brown et al. 2008). The settlement cue for the larvae is unknown but they are presumed to settle in sandy substrata (Brown et al. 2008). Larvae feed mostly during the day but little is known about the food preference of the larvae making aquaculture-rearing attempts unsuccessful to date (Minagawa and Murano 1993b). Changes in temperature will affect the feeding habits of the larvae as water temperature is correlated with feeding rates (Minagawa and Murano 1993b). Once the juvenile crabs settle their diet is similar to that of an adult crab (Brown et al. 2008).

Juvenile & Adult Growth Rates

Definitive growth rates of Kona crabs are not known but some partial information is available. In Australia two opposing hypotheses for the growth rates of Kona crabs have been proposed. The fast growth hypothesis estimates that crabs will reach a minimum legal size (4 inches) within 18 months will be 5.5 inches in 4 years and will attain maximum size within 8 to 9 years (Brown 1986; Boullé 1995). The slow growth hypothesis estimates that male crabs would take 4 years to reach minimum legal size (4 inches), nine years to attain 5.51-inch size and 14- 15 years to attain maximum size found in this species (de Moussac 1988; Chen and Kennelly 1999; Brown et al. 1999; Kirkwood et al. 2005). Aquarium-reared Kona crabs were found to grow approximately 0.25 inches per week from the time they settle, until the time they have reached the ninth instar (Brown et al. 2008).

The growth rates of Kona crabs are difficult to assess as their hard parts are lost during molting, and growth rates are stepwise between molts (Brown et al. 1999). Catch and recapture methods to determine growth provide an overestimation of time between molts as time since last molt of recaptured crabs cannot be determined (Chen and Kennelly 1999) and tagging can negatively affect growth rates (Brown et al. 1999). An attempt at analyzing lipofuscin in the brain and eyestalks of the crabs to determine age was unsuccessful (Browne et al. 2008) although this technique has been successful in other crustaceans (Sheehy and Prior 2008). Due to high mortality rates of Kona crabs in captivity future attempts using this
Overall, male Kona crabs grow faster than females and grow more per molt (Chen and Kennelly 1999; Brown et al. 1999). Smaller crabs molt much more often than larger crabs. However, larger crabs experience more growth per molt (Chen and Kennelly 1999). In Hawaii males grow on average 0.39 inches per molt and females grown an average of 0.30 inches per molt (Onizuka 1972). The growth rates found in Kona crabs vary by region, as is typical for many crustaceans (Kruse 1993). Factors such as temperature and food availability are correlated with the number of molts a crab experiences and how quickly a crab is able to grow (Brown et al. 1999).

Reproduction

The size at which Kona crabs reach sexual maturity varies by region and sex. Color of Kona crabs may be a general indicator of their sexual maturity; immature crabs are white and turn orange as they mature (Fielding and Haley 1976). In male crabs, there are several ways to define sexual maturity. Male crabs experience a physiological maturity when they first begin to produce spermatozoa (Kruse 1993). Spermatozoa are much easier to identify when males have begun to copulate successfully. Morphometric maturity occurs when the chela in the male, which plays a role in reproduction, becomes large and developed. Functional maturity occurs at the size in which males begin to participate in successful reproduction.

In Japan, physiological sexual maturity of males occurs at 1.5 inch carapace length (Minagawa et al. 1994) whereas in Thailand males are reported to reach sexual maturity at 2.9 inches (Krajandgdara and Watanabe 2005). In Hawaii, the majority of males were found to have mature spermatozoa at a 2.9 inch carapace length (Fielding and Haley 1976). In Japan, females reach sexual maturity (egg bearing) at a 2.6 inch carapace length (Minagawa et al. 1993). In Thailand, female Kona crabs reach sexual maturity 2.8 inch carapace length (Krajandgdara and Watanabe 2005). In Hawaii, over 87% of females were sexually mature with a 2.6 inch carapace length (Onizuka 1972).

In Hawaii, male crabs slightly outnumber female crabs (Onizuka 1972; Vansant 1978) and berried females (i.e., crabs that are bearing eggs) are found from May through September (Onizuka 1972). The highest frequency of egg bearing females occurs in June and July. Ovarian growth for female Kona crabs occurs from February to May resulting in increased feeding during these months (Fielding and Haley 1976). Feeding rates and thus emergence time in females has been found to be greatly correlated with their reproduction cycle (Kennelly and Watkins 1994). Berried (bearing eggs) females rarely emerge from the sand causing catch rates for females to drop dramatically during certain times of the year (Skinner and Hill 1987; Kennelly and Watkins 1994). In months prior to breeding, emergence of females increases, as they search for food (Skinner and Hill 1986).

In Kona crabs fertilization is external (Onizuka 1972). Large brachyuran male crabs may be able to fertilize multiple females (Kruse 1993). However, small male crabs may not be all of a female’s eggs. A unique characteristic of brachyuran crabs is the ability of females to store sperm in the
abdominal receptacle and successfully fertilize their eggs up to two years after copulation (Kruse 1993). Male Kona crabs must be large enough to dig female crabs out of the sand and copulate (Skinner and Hill 1986; Minagawa 1993).

Eggs are spherical in shape with an average 0.024 inch diameter (Krajangdara and Watanabe 2005). The eggs are orange in color until a few days before hatching, when they turn brown (Onizuka 1972). Eggs are brooded until they hatch 24 to 35 days after being fertilized (Onizuka 1972).

There are 78,000-169,000 eggs per brood in Kona crabs (Kennelly and Watkins 1994; Krajangdara and Watanabe 2005). The number of eggs per brood (i.e., fecundity) increases nonlinearly with size of the female crab (Fielding and Haley 1976). A 25% size increase in the female is associated with a 200% increase in the number of eggs per spawn (Fielding and Haley 1976). Larger females will spawn twice during the season while smaller crabs will only spawn once (Fielding and Haley 1976). The greatest spawning effort in larger females is always the first spawn. Females over 4 inch carapace length in Australia make up a small portion of the population, however, they contribute to over 13% of the annual egg production (Brown et al. 1999).

Mortality

Natural mortality rates for Kona crabs in Hawaii are unknown (Onizuka 1972). A preliminary estimate of natural mortality using the length converted catch curve was completed in the Seychelles Islands in the Indian Ocean. Natural mortality rates (M) in the Seychelles were estimated to be 0.8-0.9 yr⁻¹ for female crabs and 1.0 yr⁻¹ for males (de Moussac 1988). Predation on Kona crab released from fishers is expected to be a common occurrence. In the NWHI lobster fishery (now closed) predation of released lobsters was reported as a significant issue (Gooding 1985).

Unlike other brachyuran crabs Kona crab do not have the ability to regenerate limbs (Juanes and Smith 1995) or the ability to stop bleeding (Fielding 1974). Thus, mortality rates increase as the number of limb segments lost increases (Onizuka 1972; Kennelly et al. 1990). If an entire limb is lost the mortality rate can be up to 100% within 8 days. Present fishing methods likely result in elevated fishing mortality of released crabs due to limb loss and damage (Onizuka 1972; Kennelly et al. 1990; Sumpton et al. 1993; Juanes and Smith 1995; Kirkwood and Brown 1998).

A Description of the Main Hawaiian Island Kona Crab Fishery

Study Site

The Hawaiian Archipelago, the world's most isolated seamount chain, stretches over 1,800 miles, encompassing an area of over 16,000 km². The MHI are located between 19° and 22° N and 155° and 160° W, the southeastern most portion of the chain, and the focus region of this
study. The four major island platforms from south to north are: Big Island, Maui Nui (includes Molokai, Lanai, and Kahoolawe), Oahu, and Kauai (includes Niilau). On average, the 200 meter contour occurs approximately three miles from shore in the MHI (Smith 1993). Deep channels >3000 meters exist between the islands of Oahu and Kauai, as well as between Big Island and Maui Nui.

There is an estimated 3,227 square miles of potential Kona crab fishing grounds in Hawaii (Brown 1985). A small commercial fishery for Kona crabs has operated continuously in the MHI since 1938, with an annual peak in landings of 70,000 lbs occurred in 1972 (Vansant 1978). Additionally, a small number of crabs were landed in the Northwestern Hawaiian Islands (NWHI) and Kona crab were taken incidentally in the NWHI spiny lobster fishery (closed in 2000) (Brown 1985). Historically, the majority of Kona crab landings in Hawaii have come from either Penguin Bank, located off the southwest coast of Molokai, or from the northwest coast of Niihau (Onizuka 1972). Several fishermen also operate off the north coast of Oahu (Onizuka 1972). Kona crab is thought to be a popular target for recreational fishers (Smith 1993) however, the extent of the recreational fishery is not known.

In Hawaii, Kona crab fishers in small boats typically during day trips set strings of 30-40 ft tangle-nets on the sea floor (Brown 1985). The frames of tangle-nets are constructed with 3/16 inch fencing wire shaped into a circle or a square that is approximately 3 feet in diameter. The frame is then covered in 1-2 layers of small gauge mesh netting to entangle the crabs. Size and type of material used for crab tangle nets may vary by fishing location and fisher (Onizuka 1972). The nets are baited with whatever is available and set on the ocean floor for an average soak time of one hour (Kennelly and Craig 1989). Most commercial Kona crab fishing in Hawaii occurs from 50 to 150 feet (Vansant 1978). Upon net retrieval, fishers untangle the crabs and release crabs, which are not legal (undersized or female).

Currently the State of Hawaii Department of Aquatic Resources (HDAR) manages the MHI Kona crab stock as one management unit. No genetic information is currently available to determine the connectivity of Kona crabs across the Hawaiian Archipelago. The fishery is currently managed using four regulations that have been implemented at various times
throughout the fisheries history (Figure 2): (1) seasonal closure May-August, (2) a minimum legal size of 4 inch carapace length, (3) no taking/killing of female crabs and (4) no spearing of crabs. The same regulations apply to recreational fishers.

Restrictions on the Hawaii Kona crab fishery began in 1938 with a minimum 4-inch carapace size limit for selling of crabs, a no-take of berried female crabs and a closed season from June through August. In 1958 the spearing of crabs was prohibited. Beginning in January of 1993 the closed season for commercial Kona crab fishing was extended to include May. From June 1998 until September 2010 bottom-fishing vessels were not allowed to take crab nets on fishing trips. In 2002 the minimum size regulation was redefined to state no taking of crabs less than a 4-inch carapace length. Previously, undersized crabs could be kept for personal consumption. The most recent regulation prohibiting the taking of female crabs was implemented in September of 2006.

The State of Hawaii has required Kona crab fishers with a commercial fishing license to submit monthly landings reports since the 1930s, however, available data records begin in 1948. Fishers must renew commercial fishing license every fiscal year (July 1-June 30) and were assigned permanent license numbers beginning in July 1993. Landings reports with more detailed effort and release information began in 2002. All landings and dealer reports are manually entered into the State’s database by HDAR staff. Original reports prior to the 1990’s are stored as microfilm slides while copies of more recent reports have been scanned and are available as electronic copies. HDAR has recently implemented an on-line reporting system that allows commercial fishers to log in and fill out monthly landings reports. Three previous studies have been conducted on the Kona crab biology and fishery in Hawaii.

Onizuka (1972) studied the crabs spawning period, fecundity, molting, movement and growth in Hawaii by conducting tag and release studies in Wailua and Waimea Bay and by attempting to rear larvae in an aquaculture setting. Fielding (1973) conducted a study on the reproduction of Kona crabs in Hawaii by obtaining data from Penguin Bank that yielded similar results to Onizuka’s study. Vansant (1978) attempted to explain trends in the fisheries landings data by comparing historical landings data with landings data from a single fisher. He concluded that the Kona crab stock at Penguin Bank was stable and that any decrease observed in landings data could likely be explained by a decrease in fishing effort. In 1985, Dr. Ian Brown of Queensland, Australia came to Hawaii to investigate the Hawaiian Kona crab fishery and published a report on his trip containing information obtained from interviews with HDAR staff and long-time Kona crab fishers. Brown (1985) summarizes anecdotal information on the history of the Hawaii Kona crab fishery as well as major differences observed between the Queensland and Hawaii Kona crab fishery. Because few studies have been done on the Kona crab in Hawaii information is based largely on life history studies from other regions or other species.

Methods

Commercial Data Description and CPUE Standardization
Commercial Kona crab landings data from January 1948 to December 2009 from the MHI were obtained from the State of Hawaii, Division of Aquatic Resources (HDAR). Submission of monthly commercial landings reports is required by all commercial fishers in the State of Hawaii. All reports include the date of fishing trip, commercial fisher license number, statistical fishing area where fishing occurred (Figure 3), species landed on each trip, pounds landed per trip, pounds sold, price received per pound, and number of individual crabs landed per trip. Beginning in October 2002, the format of commercial fishing reports was improved to include more detailed information. The new reports also include: type and number of gear(s) used on fishing trip, total soak time of gear (hours), number of landings lost to predation, and number of landed individuals released.

**Data Quality Control**

The data were screened to ensure that fishing reports had completed data fields and were reported according to HDAR instructions. The range and distributions of the all data were examined to identify any missing values or high value outliers. Fishing reports that appeared anomalously high (>{2\sigma} from \mu) or did not follow reporting instructions, were flagged. All reports that were flagged for not following reporting instructions, missing data, or high outliers were verified by contacting the reporting fisher. Data fields were corrected when possible. Reports that could not be verified were removed. Removed reports accounted for <3% of all reported landings and effort.

**Data Summary**

In total 12,152 commercial fishing reports were summarized and included in analyses. To meet HDAR confidentiality requirements, all data points were aggregated to include at least three fishers.

Catch per Unit Effort (CPUE) was defined as landings (lbs) per fishing trip. Although net set per trip likely vary, number of nets could not be used as a proxy for effort due to lack of data on number of nets prior to 2002 and inconsistencies in how number of nets were reported by fishers after 2002.

**Generalized Linear Model**

A generalized linear model (GLM; Nelder and Wedderburn 1972) was used to standardize
commercial Kona crab CPUE. Explanatory variables to include in the GLM were chosen based on factors that were expected to affect CPUE based on knowledge of the fishery and biology or the species. Explanatory variables that were considered for the model were: Year, season, depth of statistical fishing area, wave energy of statistical fishing area, and island platform associated with fishing area.

Seasonal changes in both environmental conditions and Kona crab behavior were expected to influence CPUE in the MHI Kona crab fishery. Kona crab behavior has been closely linked to their annual reproductive cycle (Skinner and Hill 1986), thus behavior and associated catchability of Kona crabs are expected to fluctuate throughout the year. Seasons for the GLM were defined by the five annual reproductive stages of female Kona crabs (Minagawa et al. 1993): season one = September to October; season two = November to December; season three = January to February; season four: March to April; season five = May to August (crab fishery closed in Hawaii). Reports occurring during season five were predominantly from May prior to 1993, before the closed season was extended.

Depth, type of bottom substrate, and local oceanographic conditions are all factors potentially controlling the spatial distribution of Kona crabs (Brown 1985; Brown et al. 2008). However, due to the spatial scale of the available fishery data, specific physical attributes present at a fishing location are unknown. In total, from 1948-2009, 83 statistical fishing areas were commercially fished for Kona crabs (Figure 4).

![Figure 4. Statistical fishing areas categorized by: a. depth, b. island platform, and c. wave intensity](image)

Each statistical fishing area was given a depth classification of “shallow” (occurring < 2 miles from shore), and “deep” (occurring >2 miles from shore) (Figure 4a). Each fishing area was also given an island classification based on the island platform it was associated with: Big Island, Oahu, Maui Nui, or Kauai, because the habitat available for Kona crabs is expected to vary by island (Figure 4b). Methods used by Friedlander et al. (2003) were used to give each statistical fishing area a wave intensity classification, based on the predominate swell direction it was exposed to: north, trade, south or sheltered from swell (Figure 4c). The intensity and height of waves an area experiences can be determined from the predominate swell direction it is exposed to (Fletcher et al. 2008). Wave height was found to significantly impact Kona crab CPUE in Australia (Brown et al. 2008). The intensity of a swell may affect the crab’s ability to detect bait or affect the stability of the fishing gear (Brown et al. 2008).
Annual CPUE from 1948-2009 were broken into 3 time timeseries, each representing a different management regime: 1948 to 1998 to represent the fishery prior to the 1998 “no taking of crab nets on bottomfishing trips regulation”; from June 1998 to August 2006, to represent the fishery prior to the “no-take of female crabs regulation” and after the aforementioned bottomfishing trip regulation); and September 2006 to December 2009 to represent the fishery following the “no take of females” regulation. Each timeseries of CPUE were standardized in the GLM separately to account for potential changes in catchability in the fishery due to management changes (Maunder 2006). By running three GLM’s, a different q was estimated for each management regime.

The CPUE data was transformed using the natural log. Although few zeros (< 5) were present in the CPUE data, a constant, c, equal to 10% of the average overall CPUE (c), was added to each observation to ensure proper data transformation (Campbell et al. 1996).

The GLM was run using Statistical Analysis Software ver. 9.2 (SAS). An identity link function was used for the model and a normal error distribution was assumed. A histogram of the residuals was examined and a Kolmogorov-Smirnov (K-S) test (Massey 1951) was performed to verify the assumption of a normal error distribution. A p-value of <0.001 was required to reject the null hypothesis of normality for the K-S test because GLM’s are moderately robust to violations of the normality assumption (Gill 2001). The GLM can be described as:

$$\ln(\text{CPUE}+c) = \mu + Y_i + S_j + A_k + \varepsilon_{ijk}$$

Where, $\mu$ is the overall mean, $Y_i$ is the effect of year $i$, $S_j$ is the effect of season $j$, $A_k$ is the effect of area $k$, and $\varepsilon_{ijk}$ is the error term with normal distribution. The area effect included either: 1. Island platform, 2. Depth, 3. Wave intensity, or 4. All three of the above. Six models were run for each of the CPUE indices, 15 models were run in total (Table 1).

Model selection was performed using Akaike’s Information Criterion (AIC; Akaike 1973; Burnham and Anderson 2002; Hinton and Maunder 2003):

$$\text{AIC} = -2\log(L(\hat{\theta} | y)) + 2K$$

where, $L(\hat{\theta} | y)$ is the numerical value of the log-likelihood at its maximum point, and $K$ is the number of parameters included in the model (Burnham and Anderson 2002). The model with the lowest AIC value is determined as the best fit of all candidate models, and represents a balance between the variance explained and the number of parameters included in the model (Burnham and Anderson 2002). Differences in AIC values ($\Delta_\text{AIC}$) were determined, and Akaike’s weights ($w_i$) were calculated for each model to determine the relative likelihood of each model, given the data and set of tested models (Burnham and Anderson 2002).
Table 1. Generalized linear models run in SAS to standardize MHI commercial Kona crab data from 1948-2009. The best-fit model was chosen using AIC values.

<table>
<thead>
<tr>
<th>Model #</th>
<th>Explanatory Variable(s)</th>
<th>Timeseries of Data</th>
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<td>year</td>
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<td>year, season</td>
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<td>6</td>
<td>year, season</td>
<td>2006-2009</td>
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<tr>
<td>7</td>
<td>year, season, depth</td>
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<tr>
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<td>year, season, depth</td>
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<td>Year, season, wave intensity</td>
<td>1998-2006</td>
</tr>
</tbody>
</table>

Production Model

A Stock-Production Model Incorporating Covariates (ASPIC) (ver. 5) software was used (Prager 1992; Prager 1994; Prager 2011) to estimate parameters of a nonequilibrium, generalized production model (Pella and Tomlinson 1969; Fletcher 1978; Prager 1994). The generalized production model is considered more robust than other production models because by including one additional parameter, the model makes no assumption about the relationship of B_{MSY} to K, or model shape (Maunder 2003). The model was conditioned on annual yield (landings) data and standardized CPUE (see section) (Prager 1994; Prager 2011). Yield data was chosen over effort data because landings data is generally observed more precisely than effort (Prager 1994; Prager 2011). The generalized production model used by ASPIC is described as:

\[
\frac{dB_t}{dt} = \gamma m B_t/K - \gamma m (B_t/K)^n - F_t B_t.
\]

Where \( m \) is the maximum sustainable yield, \( B \) is biomass at time \( t \), \( K \) is carrying capacity of the population, \( F \) is the fishing mortality at time \( t \), \( n \) is an exponent that determines the shape of the curve, and \( \gamma \) is a function of \( n \) (Pella and Tomlinson 1969; Fletcher 1978; Prager 1994; Prager 2002):

\[
\gamma = nn/(n-1)/n-1
\]

The shape of the production curve (\( n \)) is characterized by the \( B_{MSY} \) to \( K \) ratio (\( \Phi \)):

\[
\Phi = (1/n)1/(n-1)
\]
The model is linked the observed data (standardized CPUE) by: 

$$CPUE_t = qB_t$$

CPUE at time $t$, is equal to the product of $m$ $q$ is the catchability coefficient, and biomass ($B$) of the stock at time $t$ (Fletcher 1978; Prager 1994; Prager 2002; Williams and Prager 2002). The ASPIC model accumulates residuals in CPUE and assumes a log normal distribution (Prager 1992; Prager 1994; Williams and Prager 2002). The objective function used by the model is sum of squares, to provide maximum likelihood estimates. The model convergence criteria, $\varepsilon 1$, was set at 1 x 10-8 and defined as:

$$2|L_1-L_0|/L_1+L_0 < \varepsilon 1$$

Where $L_1$ is the highest objective-function value and $L_0$ is the lowest.

Although commercial data for this fishery was available from 1948-2009 only data from 1970-2006 was included in the model. Data prior to 1970 were not included in the model because landings during the early phases of the fishery are suspected to be underreported by as much as 50% (Brown 1985). In September of 2006, a no taking of female Kona crabs regulation was implemented for the fishery. Data after August 2006 was not included because no quantitative information is available on how a male-only harvest would impact the catchability and production of the stock. In June 1998 a regulation was implemented that prohibited the use of crab nets on bottomfishing vessels. The 1998 regulation is suspected to have a significant impact on the catchability of the fishery (Maunder et al. 2006). To account for the possible change in catchability the data was broken into two fisheries, each with equal statistical weight, from 1970 to 1998 (before regulation) and from 1998 to 2006 (after regulation). ASPIC is able to estimate a separate $q$ for each fishery.

Bias-corrected 90% confidence intervals were calculated for each estimated parameter from 1,000 bootstrap runs (Efron and Tibshirame 1986; Prager 1994).

The initial biomass parameter ($B_{1970}/K$) is considered a nuisance parameter, difficult to estimate (Prager 2005) and thus, was fixed at 0.7 because the Kona crab stock was likely lightly exploited prior to 1970 (Vansant 1978). A sensitivity analysis was performed to determine the effect of fixing $B_{1970}/K$ at 0.7. The model was run with fixed $B_{1970}/K$ values ranging from 0.1 to 1.0, and Akaike’s Weight ($w_i$) for each run was compared.

To ensure including two fisheries and two $q$ parameters improved model fit, AIC values were compared between a model run as a single fishery and the model run as two fisheries. A t- test was used to test the null hypothesis that $q1=q2$ (Prager 2011). If the model fit was not substantially (>2 AIC units) better with the single fishery model and if the catchability coefficients for both fisheries are significantly different, the break in the fishery will be validated.

| Model                      | AIC       | $|I_{0}$  | W_i  |
|---------------------------|-----------|--------|------|
| Year                      | 26236.25  | 2115.80| 0    |
| Year, season              | 26206.27  | 2085.81| 0    |
| Year, season, island area | 24120.46  | 0      | 0    |
| Year, season, depth       | 26045.85  | 1925.39| 0    |
| Year, season, swell exposure | 25378.56 | 1258.10| 0    |

| Model                      | AIC       | $|I_{0}$  | W_i  |
|---------------------------|-----------|--------|------|
| Year                      | 4432.44   | 468.11 | 0    |
| Year, season              | 44310.02  | 445.68 | 0    |
| Year, season, island area | 3964.34   | 0      | 0    |
| Year, season, depth       | 4408.06   | 443.72 | 0    |
| Year, season, swell exposure | 4108.43 | 144.10 | 0    |

| Model                      | AIC       | $|I_{0}$  | W_i  |
|---------------------------|-----------|--------|------|
| Year                      | 2006.48   | 494.94 | 0    |
| Year, season              | 203.95    | 492.42 | 0    |
| Year, season, island area | 1511.53   | 0      | 0    |
| Year, season, depth       | 2005.52   | 493.98 | 0    |
| Year, season, swell exposure | 1841.56 | 330.03 | 0    |

**Biomass projections**

To determine potential impacts of different catch scenarios on the Main Hawaiian Island Kona crab stock, the ASPIC generalized production model was used to calculate biomass projections from 2010-2030 based on theoretical future catch scenarios (Goodyear 2001; Prager 2011). To ensure that the projected landings would not change the production function estimated from the historical fishery data all production parameters, except carrying capacity ($K$), were fixed to values estimated by the general production model with data Kona crab fishery data from 1970-2006 (Table 4.1). $K$ was not fixed in order to calculate confidence intervals for the projected biomass estimates because it was associated with the highest variance of the parameter estimates by the ASPIC model.

Reported landings for the fishery from 2007-2009 were used in the projection model despite the unknown production and catchability change associated with 2006 prohibition of females regulation. From 2010 until 2030 constant annual landings of 0 lbs, 7,000 lbs, 8,000 lbs were used to project future biomass trends.

**Results**

**Generalized Linear Model**

The models for each management regime that contained year, season, and area by island had the lowest Akaike’s information criterion (AIC), a strong weight of evidence, and were chosen as the relatively best fit models (Table 2a-c). Year, season, and area were found to explain a significant portion of variability in CPUE for the 1948-1998 and 1998-2006 management regimes (Table 2a). Area was the only significant variable found for the 2006-2009 management regime (Table 2b). The final models explained 29% of the variation in CPUE from 1948-1998 and 52% of the variation from 1998-2006 and 2006-2009 (Table 2c).
A decline in the standardized CPUE over the last 18 years was found in the MHI Kona crab fishery (Figure 5). A histogram of the residuals and the associated skewness and kurtosis values indicated that the models’ did not violate any normality assumptions (Figure 6). A Kolmogorov-Smirnov (K-S) test confirmed that the model residuals were normally distributed. Standardized CPUE peaked in 1972, which was followed by a drastic decline from 1972-1977 (Figure 5). Throughout the 1980’s and early 1990’s, CPUE fluctuated but remained relatively stable (Figure 5). Standardized CPUE for the fishery followed a general pattern of decline from 1992-2006 (Figure 5). From 2006-2009 the standardized CPUE appears relatively stable with a small, local peak occurring in 2007 (Figure 5).

**Generalized Production Model**

Parameters estimated by the ASPIC generalized production model are presented in Table 3. $B_{MSY}$ was estimated to occur at 73% of the population’s carrying capacity (Table 3). Time trajectories of the model’s estimated stock status, or $B$ ratio (biomass relative to $B_{MSY}$) and $F$ ratio (fishing mortality relative to $F_{MSY}$) are presented in Figures 7 and 8.
For the 39 years of data analyzed, model estimates indicate biomass of the MHI Kona crab stock never reached $B_{\text{MSY}}$ (Figure 7). High fishing mortality persisted in the early seventies, and by 1975 the biomass of the stock was below 50% of $B_{\text{MSY}}$ (Figure 7). Fishing mortality dropped below $F_{\text{MSY}}$ during most of the 1980s, allowing the biomass of the stock to slightly rebuild (Figure 8). From 1989 to 1997 the stock’s biomass was over 50% of $B_{\text{MSY}}$ (Figure 7).

The largest spike in fishing mortality ($F$) the MHI Kona crab stock has experienced occurred in 1998, when $F$ was estimated at over four times $F_{\text{MSY}}$ (Figure 8). Fishing mortality declined after 1998, and was estimated at only 92% of $F_{\text{MSY}}$ in 2006 (Figure 8). The stock biomass shows a gradual decline from 1998 to 2006. In 2006 the biomass was estimated to be only 18% of $B_{\text{MSY}}$ (Figure 7). A Kobe plot of the entire time series is presented in Figure 9.

The CPUE estimated by the model fit the observed CPUE well (Figure 10). The distributions of residuals did not appear to violate any assumptions of a log normal distribution (Figure 11). Model convergence was achieved for all 1,000 bootstrap runs. Parameters estimated by the base model are presented in Table 3 with bias-corrected 90% confidence intervals calculated from 1,000 bootstrap runs.

The AIC value for the model including two fisheries was substantially (>2 AIC units) less than the AIC value for the single fishery model indicating the use of two fisheries improved model fit. The two-tailed t-test revealed the two catchability coefficients estimated by the model were significantly (p<0.05) different. The estimated $q$ for the latter fishery (1998-2006) was over 50% higher than the $q$ estimated for the earlier time series (1970-1998) (Table 3).

Sensitivity analyses on the fixed $B_{1970}/K$ parameter indicated that both the fit of the model and the ending status estimated by

### Table 3. Parameter point estimates and 90% confidence intervals estimated for the MHI Kona crab stock by a generalized production model using ASPIC.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Point estimates</th>
<th>90% Confidence Intervals</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>$B_1/K$</td>
<td>0.70 (fixed)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>MSY</td>
<td>40,400.00</td>
<td>25,900.00-48,430.00</td>
<td></td>
</tr>
<tr>
<td>$K$</td>
<td>218,000.00</td>
<td>153,700.00-261,100.00</td>
<td></td>
</tr>
<tr>
<td>$B_{\text{MSY}}$</td>
<td>159,500</td>
<td>72,360.00-198,500.00</td>
<td></td>
</tr>
<tr>
<td>$F_{\text{MSY}}$</td>
<td>0.2534</td>
<td>0.1963-0.3825</td>
<td></td>
</tr>
<tr>
<td>B-ratio (2007)</td>
<td>0.1810</td>
<td>0.1054-0.3341</td>
<td></td>
</tr>
<tr>
<td>F-ratio</td>
<td>0.9218</td>
<td>0.4995-1.638</td>
<td></td>
</tr>
<tr>
<td>q1</td>
<td>0.0006294</td>
<td>0.0005187-0.008917</td>
<td></td>
</tr>
<tr>
<td>q2</td>
<td>0.0009660</td>
<td>0.00007441-0.01072</td>
<td></td>
</tr>
</tbody>
</table>

![Figure 7](image_url)

**Figure 7.** Relative biomass ($B/B_{\text{MSY}}$) estimated by a generalized production model in ASPIC for the MHI Kona crab stock from 1970-2006 with 90% confidence intervals.
the model were insensitive to fixed values of 0.7 (Table 4). AIC values were not substantially different between models run with $B_{1970}$ values ranging from 0.1 to 1.5 (Table 4). For all models $\Delta_i$ were less than one indicating, the fit of the model was insensitive to the fixed value of $B_{1970}/K$ (Burnham and Anderson 1998) (Table 4). The $w_i$ for all models were also similar indicating the likelihood of one model occurring over another was not substantial (Table 4).

For $B_{1970}/K$ values from 0.4-1.0 the model estimated the ending fishing mortality ($F_{2006}$) to be less than $F_{MSY}$ (Table 4). For $B_{1970}/K$ values < 0.4 $F_{2006}$ was estimated to exceed $F_{MSY}$, however, an initial starting biomass equal to 40% of $K$ is not suspected as likely at the beginning of the time series.

**Biomass Projections**

The estimated biomass from 1970-2006 by the generalized production model is shown from 1970-2006 and from 2010-2030 the projected biomass for each of the predicted constant annual landings is presented (Figures 12a-c). Both the mean and median of the projected biomass is shown to correct for any bias caused by the error associated with $K$. Upper and lower 90% confidence intervals were calculated using 1,000 bootstrap runs to estimate the variability associated with $K$ (Jones 1998).

The projection model results predicted that biomass would reach 50% of $B_{MSY}$ by 2015 and $B_{MSY}$ by 2020 if the fishing mortality from 2010-2020 was zero (Figure 12a). At an annual harvest of 7,000 lbs, the projection model estimated the stock may take over 18 years to reach 50% of $B_{MSY}$ (Figure 12b). The projection model estimated a decline in biomass at an annual harvest of 8,000 lbs beginning in 2010 (Figure 12 c).
Figure 10 (left). Observed and estimated CPUE (lbs/trip) from ASPIC’s generalized surplus production model for two time periods: Jan. 1970- May 1998 and June 1998- August 2006.

Figure 11 (right). Model residuals from CPUE fit.

Table 4. Results to determine how sensitive model AIC value and ending relative fishing mortalities were to starting fixed B1970/K values.
Figure 12 a-c: ASPIC generalized production model projections estimated of mean and median biomass from 2010-2030 assuming annual harvest level from 2010-2030 of: a. 0 pounds, b. 7,000 pounds, and c. 8,000 pounds. 90% confidence intervals of projections are also presented (dashed brown line).
Discussion

Our results estimated a decline in fishery CPUE and kona crab biomass over 18 years despite advancements in technology. Advancements in technology such as the widespread use of GPS, plotters, and hydraulic winches likely had substantial impacts on effort efficiency in the Kona crab fishery. A critical factor in landing Kona crabs is fishing in areas that contain habitat suitable for Kona crabs, and fishing in areas free of coral and rubble to avoid gear entanglement and damage (Brown et al. 2008). The use of GPS to precisely navigate to fishing locations would increase the efficiency of fishing effort and allow fishers to return to the exact locations that have previously yielded high landings. A fishing trip to Penguin Bank in 1985 by fishers unfamiliar with the area and without GPS resulted in a CPUE of one crab per 80 nets, due to the majority of nets being set in areas of coral and algae (Brown 1985).

The cause of the estimated decline in the Kona crab commercial fishery standardized CPUE that began in the late 1991, and the estimated decline in biomass that occurred after 1995 is unclear, but several leading causes are suspected. If the stock was overexploited in the mid-seventies as suggested by experienced Kona crab fishers (Brown 1985), overfishing could explain at least part of the decline in estimated stock biomass and standardized CPUE. Another potential explanation is a negative fluctuation in recruitment associated with environmental changes. Model results must be interpreted with caution and consideration of all assumptions.

Average size of individuals over time is often used as an indicator of stock exploitation status (Erhanhart and Ault 1998). Spatial patterns in the observed size of Kona crabs may suggest the stock has been overexploited in certain areas. On average, Kona crabs landed in MHI weight just over one pound (DLNR; unpublished data). However, crabs weighing up to 4.3 pounds, the heaviest ever reported, were found in the relatively unexploited NWHI Kona crab population in the 1980s, where large size crabs made up to 25% of the total landings (Brown 1985). Over the last the seven years, Kona crabs landed at Penguin Bank have been significantly larger than crabs landed in the other island areas (DLNR; unpublished data). The relatively low effort at Penguin Bank due to it’s distance from shore may explain why significantly heavier crabs are found at Penguin Bank. On average, two to three commercial Kona crab fishers target Penguin Bank per year, and Maui Nui (including Penguin Bank) was the last of major Kona crab fishing areas to be commercially exploited. The required distance and transit time to Penguin Bank, may also relieve this area from some recreational fishing pressure.

A change in environmental and oceanographic conditions during the 1990’s may have had an impact on Kona crab recruitment and adversely affected CPUE in the fishery. In the NWHI, a local depletion of spiny lobsters (Panulirus marginatus) occurred at Penguin Bank when a large scale Pacific wide regime shift caused a weakening in the South Equatorial Current (SEC) (Polovina and Haight 1999). Changes in local currents were observed with the weakening of the SEC and recruitment of lobsters to Maro Reef no longer occurred (Polovina and Haight 1999). In 1997-1998 a major El Niño event took place (Peterson and Schwing 2003). Following the El Niño, a rapid shift to La Nina and negative PDO conditions occurred (Peterson and Schwing 2003). In Hawaii, negative temperature anomalies of up to -0.5 °C was observed from 1999-2002 (Peterson and Schwing 2003).
Resource limitation specifically, available habitat, is a likely a density-dependent factor affecting the overall biomass and carrying capacity of the MHI Kona crab stock. A much larger Kona crab fishery is supported off the coast of Queensland, Australia where the continental shelf extends over 45 km off the coast providing a large area of potential Kona crab habitat (Brown 1985). The relatively narrow island shelves around the MHI (~4 Km offshore) limits the habitat available for Kona crabs in their preferred depth range (Brown 1986). Though never documented in Kona crabs other crab species commonly experience both disease and egg parasitism at high densities, which can cause a substantial reduction in a stock’s productivity (Cobb and Caddy 1989). Due to the high mortality rates associated with Kona crab limb loss and their display of inter-specific aggression in aquaria situations (Skinner and Hill 1987), increased mortality at high densities is also a likely scenario for Kona crabs.

A key assumption of the production model is that the index of a stock abundance is proportional to the stock biomass by a constant the catchability coefficient (Prager 1994; Prager et al. 1996). Catchability is very difficult parameter to estimate. ASPIC’s quantitative estimates of q are usually imprecise because it is used as a scaling parameter (Sissenwine 1978; Prager 1994; Maunder et al. 2006; Wilberg et al. 2010; Prager 2011). Changes in regulations, fishing methods, vessel capacity, environment, stock density and fisher experience are all factors associated with potentially changing the catchability of a stock (Arreguin-Sanchez 1996; Maunder et al. 2006). Although, we accounted for two significant changes in catchability likely due to regulation changes, other factor may have also influenced catchability that were not accounted for. The index of abundance for the Kona crab stock used by the model only represents crabs landed over a 4-inch carapace length. If the proportion of undersize crabs in the stock has changed over time the index of abundance will not be consistent representation of stock biomass (Breen and Kendrick 1998).

Another factor our model did not consider is recreational landings. In Hawaii, recreational fishers outnumber commercial fishers, and an estimated 19-35% of all Hawaii residents participate in recreational fishing (Smith 1993). Recreational fishers make up approximately 20% of all fisheries landings in Hawaii, while commercial fisher makeup to 80% (Pooley 1993). Recreational fishing is suspected to be highest in areas with large populations and therefore, greatest on the island of Oahu (Smith 1993). Increased levels of resource extraction due to recreational fishing could be responsible for the relatively low CPUE Oahu experiences. Beginning in 2001, State of Hawaii, has begun conducting random telephone surveys and interviews at boat ramps, to estimate the level of recreational fishing in Hawaii (http://www.hawaii.gov/dlnr/dar/surveys/). Creel surveys thus far have resulted in little Kona crab data.

The impact of recreational landings and effort in Hawaii fisheries is unknown, as recreational fishers are not required to obtain a fishing license or report landings (Friedlander and Parrish 1997). Recreational fishing has significantly impacted stock abundance in other fisheries (Cardona et al. 2007), and the number of recreational crab fishers participating in the MHI
Kona crab fishery is expected to be substantial (Brown 1985; Pooley 1993). If the Hawaiian Kona crab fishery is indeed over-exploited, assuming recreational fishing effort is stable or increasing, the addition of recreational data to the standardized CPUE model could likely further accentuate the downward trend in catch rates over the last ten years.

The fishing methods typically used in the Kona crab fishery may offer the stock some protection from overfishing. In the Seychelles Islands, the preferred Kona crab habitat was reported to be both sandy and coral substrata (Boule 1995). Coral areas are avoided by Kona crab fishers as setting nets in areas other than sandy substrate result in gear damage or loss (Brown 1985). If Kona crabs utilize coral substrate as habitat in Hawaii, the coral areas may offer the species a refuge from fishing pressure. In Australia, tangle-nets used in the Kona crab fishery have a very low retention rate and only an estimated 7% of all crabs attracted to bait on a net will be entangled and successfully landed (Hill and Waasenberg 1999), resulting in maximum catch rates of about 10 crabs per hour per net (Kennelly 1989). In Australia, even lower catch rates are observed for fishers using crab traps to land Kona crabs (Sumpton et al. 1995). The low retention rate and targeted habitat of the gear used in the Kona crab fishery may provide a refuge for Kona crabs from fishing gear.

Our production model did not include data following the 2006 regulation that banned the taking of female crabs because the effect this regulation may have had on the stock’s production is unknown. The aim of a male only harvest fishery is to protect the large, fecundant female crabs, in hopes of avoiding recruitment overfishing and to minimize the risk of recruitment failure (Wenner and Kuris 1991). If the 2006 regulation was beneficial to the production of the stock, as intended, continuing the production model through 2009 would represent a worst case scenario. The model would not account for the potential increase in stock productivity after 2006 and model parameters would be estimated assuming both males and females were being harvested and a constant stock production. However, in certain crustacean fisheries (i.e. Spink King crab, Dungeness crab, Blue crab, and Alaska King crab) prohibitions on taking females have negatively impacted the production of the stock, by reducing the overall reproductive success (MuMullen and Yoshihara 1969; Smith and Jamieson 1991; Hines et al. 2003; Carver et al. 2005; Sat et al. 2007). Prohibitions on taking females might hinder reproductive success by decreasing the number of males, the average size of males, and the overall sperm availability in a stock (MuMullen and Yoshihara 1969; Smith and Jamieson 1991; Sato et al. 2007).

The mating behavior of Kona crabs may cause them to be particularly sensitive to a male-only harvest. In order to unbury females and successfully copulate, male Kona crabs must be larger than females (Skinner and Hill 1987). Selecting only large males may decrease their size relative to females (Sato and Goshima 2006). Because fecundity in Kona crabs increases exponentially with linear size, large females contribute disproportionately to the population relative to their abundance (Fielding and Haley 1976; Brown et al. 1999). If large males are unavailable to fertilize large females, the reproductive potential of the Kona crab stock would decrease causing a decrease in stock production. However, because male Kona crabs do grow faster and are capable of fertilizing multiple females (Brown et al. 1999; Kruse 1993), the population may be able to sustain a higher male harvest. Single sex harvest was proven as an effective tool for avoiding recruitment failure without decreasing the stock’s reproduction potential in the Bonne Bay
(Newfoundland) Snow crab (*Chionoecetes opilio*) fishery (Ennis et al. 1988). Understanding the impact of a male only harvest on the Kona crab stock should be a management priority and is essential for a complete assessment of the current status of the stock.

**Conclusion**

Although the best information available suggests the Kona crab stock has been experiencing a substantial decline in biomass over the last 18 yrs., over-exploitation of the stock may not be the sole explanation. The long term impacts of the recent no take of female crabs regulation and no taking of crab nets on bottomfishing trips regulation on the Kona crab stock in the Main Hawaiian Islands have yet to be determined, and CPUE should be monitored in coming years to assure the reproductive potential of the stock has not been affected. New fisher reporting requirements implemented in 2002 will continue to increase knowledge about the fishery and will continue to increase knowledge about the fishery and help provide better estimates of current catch rates. More information on the biology of the crab, recreational fishing effort and landings, the Hawaii Kona crabs response to environmental changes, discard mortality rates, genetic connectivity of the stock, and the range in characteristics of vessels participating in the fishery could help future management decisions and help better assess the state of the stock.

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