

INSIGHT INTO SEASONAL RECRUITMENT DYNAMICS OF JUVENILE
MULLOIDICHTHYS VANICOLENSIS AND *M. FLAVOLINEATUS*

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ABSTRACT

Goatfish were a culturally important food resource for early Hawaiians and their value is still sustained today as one of the highly sought reef fish in Hawaii's recreational and commercial fisheries. The most common juvenile goatfishes (oama), *Mulloidichthys flavolineatus* and *M. vanicolensis*, exhibit an annual pulse-type recruitment to near shore areas during the summer months in the Main Hawaiian Islands. These annual recruitment events provide food for pelagic and near shore fish as well as food and sport for recreational anglers. Growth rate, habitat preference, hatch date, CPUE, and size and age structure were used to compare recruitment characteristics between species, locations, and years. Oama during 2015 grew faster, were heavier on average, and hatched later than fish during the anomalously high 2014 recruitment. During a typical year, *M. vanicolensis* recruit earlier than *M. flavolineatus* and each species is directly linked with a hard or soft substrate type respectively. Limited information exists on these juvenile fishes even though these species have a significant role in the coastal ecology and near shore fisheries. This project aims to shed light on the early life history settlement characteristics of these goatfishes through the study of their annual recruitment patterns.

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BACKGROUND

Introduction

Commercial, recreational, and subsistence fishing are integral to the lifestyle of many people throughout Hawaii. Ocean resources and the ecosystem services they provide support the 50th state in economic and cultural ways that are unique to Hawaii. Early Hawaiians depended heavily upon the ocean for sustenance and in fulfilling cultural needs (Titcomb 1972). Today, commercial and recreational fishing are the predominant forms of harvest from the sea with decreased levels of subsistence fishing still occurring in some areas (Friedlander and Parrish 1997). The commercial sector, consisting mainly of longline and bottom fishing, provides high quality fresh fish locally and to buyers in the contiguous United States and other countries. Recreational fishing continues to expand and is difficult to quantify, but it may attain approximately 1.5 million person-hours annually (Garrod and Chong 1978, McCoy 2015). Goatfishes in Hawaii are a group of species that have prominent nearshore fisheries whilst maintaining cultural and traditional value.

Goatfish in Hawaii

The family Mullidae currently consists of 6 genera, including over 60 species inhabiting nearshore areas in tropical, sub-tropical, and temperate seas (Gosline 1984, Uiblein 2007). Goatfishes are easily distinguished by a unique pair of barbels equipped for probing the sediment in search of invertebrate prey (Krajewski et al. 2006, Kolasinski et al. 2009). Most goatfish species are bottom-foraging or associated with the benthos in some way (Krajewski and Bonaldo 2005). This group of fishes also serves as ecosystem engineers and indicators of environmental perturbations or other anthropogenic factors in temperate and tropical habitats (Uiblein 2007).

Early Hawaiians practiced sustainable harvesting methods for many species, including goatfishes, and respected the limits of their resources by only taking what they needed for food and ceremonial purposes (Titcomb 1972; Allen 2014). The endemic whitesaddle goatfish (*Parupeneus porphyreus*), locally known as kumu, was especially important in pre-contact Hawaii. It was often used for ritual offerings and could only be eaten by men (Titcomb 1972, Meyer et al. 2000). Early capture methods of goatfish mainly consisted of traps and nets (Mahi 1969, Titcomb 1972). Subsistence anglers currently harvest goatfishes by trap, spear, or hook

and line in many locations around Hawaii (Friedlander et al. 1997, Smith 1993), where they are prized for their flaky white meat.

Fishing pressure on goatfishes in Hawaii has transitioned from subsistence fishing to mainly commercial and recreational harvest. Since the 20th century, goatfishes have been an important component of commercial landings (Garrod et al. 1978). In 1900, over 80,000 kg of weke (adult goatfishes) was sold in the Honolulu fish market (Cobb 1905). An annual catch limit (ACL) for goatfishes in Hawaii for 2015 was set at 74,843 kg (WESTPAC 2015), reiterating the value of goatfish in Hawaii's nearshore fisheries. Landings of *Mulloidichthys* spp. often ranked third or fourth among all commercial reef fish species and averaged around 24,738 kg from 2000-2005 (Hawaii FEP 2009). Commercial fishers target weke, but the juveniles, locally known as oama, are exploited primarily by recreational and subsistence fishers.

The most common goatfish species in Hawaii are the yellow stripe goatfish (*Mulloidichthys flavolineatus*) and the yellowfin goatfish (*M. vanicolensis*). Recreational shoreline anglers target oama (a category that includes both species) during the summer and fall months, when they are abundant in nearshore habitats (Tagawa and Tam 2006). Popular fishing spots are often lined with people of all ages, using hook and line to test their luck at catching these prized species. Expected oama runs are often announced through local magazines, newspapers, and social media. They are considered a delicacy for fishers and their families, as well as popular bait for shore and boat anglers to catch larger predators such as the many jack species (family *Carangidae*; Holland et al. 1993). The annual activities of finding, catching, eating, and using oama for bait has been a tradition taught and propagated for many generations in Hawaii.

Oama life history characteristics

The term "oama" generally encompasses two species; *M. flavolineatus* and *M. vanicolensis* have similar morphology, but mainly differing in color (Hoover 1993). Despite their abundance, as well as their fisheries and ecological importance, there is limited information on the life history and biology of the two *Mulloidichthys* species. The limited research that does exist for goatfishes in Hawaii is almost exclusively focused on adults (Meyer et al. 2000; Holland et al. 1993). Kumu, one of only two endemic goatfish species in Hawaii, have attracted specific attention due to their prominence in Hawaiian history and their extremely high market value (~\$33/kg) (Meyer

et al. 2000; Mahi 1969; Moffit 1979). Most information on oama exists anecdotally or in unpublished “grey literature” and in the popular press.

There is scant information on the ecology of the juvenile oama stage. As is typical of most reef fishes, all goatfishes are broadcast spawners (Colin et al. 1978). Pelagic-larval duration (PLD) is relatively short, ranging from 25 to 33 days, after which time they metamorphose and settle in mass in nearshore areas (McCormick et al. 1993). Oama are known to recruit to inshore areas between June and September, and are found all around the island of Oahu ranging from boat harbors and canals to sandy bays and reef flats (Sato et al. 2008, Tagawa and Tam 2006). These areas likely serve as nursery areas for oama, providing protection from predators and feeding grounds. As adults, they utilize a wider range of habitat, including deeper areas, and can be found in large schools, in small groups, or even solitary individuals compared to oama that are mainly found in large schools (Uiblein 1991, Tagawa and Tam 2006).

Anecdotal information from local fishers indicates that *M. flavolineatus* and *M. vanicolensis* recruit to nearshore areas during different times of the year and at different sizes. Both species exhibit annual pulse recruitment during the summer months and are subsequently targeted by nearshore anglers. This recruitment pattern provides a unique opportunity to study the early life history of these very important and valuable species.

Recruitment dynamics

Recruitment is the addition of new fishes to a local population after their settlement from a larval pelagic phase or the transition that occurs from a juvenile stage to an adult susceptible to a fishery (Caley et al. 1996, Sponaugle 2015, Caselle and Warner 1996). Almost all reef fish species in Hawaii have this pelagic stage and oama have a silvery coloration during this time. There is little information on what occurs before the settlement event and the transition between habitats (McCormick and Makey 1997). Pelagic stage fish rely on a suite of different environmental and oceanographic cues to successfully migrate to a suitable nearshore habitat (Sponaugle 2015).

Examining recruitment is important in order to understand the life history characteristics of reef fishes. There are many physical and biological factors that influence the timing and duration of settlement, as well as survival and growth post-settlement (Bergenius et al. 2005; Smith et al. 2004; McCormick et al. 1995). Understanding recruitment patterns can provide insight into both the ecology of the pelagic phase and the temporal and spatial patterns in adult population structure (Smith et al. 2004; Sale 2004).

Oama recruitment dynamics, along with reproductive size and spawning of adults, are incompletely understood. There has been some characterization of spawning (Cole 2009), but few studies exist on oama recruitment. The predictable seasonal aspects of oama settlement facilitate the assessment of their recruitment dynamics (Robertson et al. 1998). The relatively short duration of these summer pulses can provide useful information on future adult populations, in addition to their direct value as fisheries species. This is valuable because understanding stock recruitment relationships and population dynamics are often difficult because demographic traits including, birth, death, immigration, and emigration are hard to characterize (Caley et al. 1996, Sale 2004). The determination of life history characteristics, such as otolith based age and growth, provides information to begin to understand some of these vital rates.

Otoliths: early life history

Examination of sectioned and polished otoliths provides valuable information on age and growth of fishes. Otoliths are calcium carbonate structures in the inner ear that progressively lay down daily and annual growth increments (rings) as a fish grows (Campana and Thorrold 2001). A single fish otolith can provide information on the age, size at age, growth, and hatch date (Begg et al. 2005; Green et al. 2009). Studies of fish otoliths date back over 100 years and continue to provide information fundamental to fisheries management (Campana et al. 2001; Begg et al. 2005).

The chronological properties of otolith rings to determine age, and using back calculation techniques to determine size-at-age, are unique phenomena in fisheries science. A less obvious application is in the examining of the microstructure in otoliths to reveal additional life history information. Only annuli, or yearly rings, were counted until Pannella (1971) discovered that fish

also deposit daily growth increments. These daily rings can therefore provide information on juvenile fishes less than one year in age.

Life history traits such as pelagic larval duration (PLD), timing of settlement, and hatch date can be identified through the examination of daily growth rings (Sponagule 2009). Much research has focused on the settlement marks in otoliths because they can reveal how long a fish was in its pelagic larval stage and how growth varied before and after settlement (Wilson et al. 1997; 1999). PLD also serves as a proxy of dispersal ability and connectivity between regions or populations because a longer or more mobile pelagic stage allows for further dispersal (Victor et al. 1986; 2000; but see Selkoe et al. 2014).

Catch rate interpretation

Catch per unit effort (CPUE) is often used as an index of fish abundance after some type of standardization to account for biases (Haggarty et al. 2006; Harley et al. 2001; Maunder et al. 2006). Biases can be manifested through changes in gear efficiency, species targeting, environmental factors, or fluctuations in the populations of the species of interest (Maunder et al. 2006). Regardless of the issues in the relationship between abundance and CPUE, this index is still useful because of the cost and feasibility of obtaining other types of fishery data (Walsh et al. 2015). Oama CPUE data may reflect relative abundance in the local area and provides a time series from when the larval goatfishes recruited to the population, and when oama recruit to the weke population. A data series of this type reveals time-specific ontogenetic shifts, especially for habitat, and a time table of when oama are accessible by recreational anglers.

OBJECTIVES

The objectives of the following thesis were to describe the recruitment dynamics of juvenile *Mulloidichthys flavolineatus* and *M. vanicolensis* (oama) during the summer of 2014 and 2015. Oama recruitment was characterized by fish age, length, weight, habitat preference, hatch date, and catch per unit effort (CPUE) over the course of each summer.

METHODS

Samples sites and target species

The two juvenile stage (oama) goatfish species of interest were, *Mulloidichthys flavolineatus* and *M. vanicolensis*. Oama often frequent the same nearshore locations during the summer months (June-September) every year. Haleiwa Harbor and Kawela Bay on the north shore of Oahu were chosen based on prior knowledge that oama of both species were present at each location (Figure 1). It was also imperative to choose locations that would not be overly crowded and therefore interfere with sampling. A south shore site in Aina Haina was opportunistically added during 2015 to accommodate a separate genetics project.

Oama collections

Sampling was carried out from June through October in 2014 and 2015. Each site was visited at least once a week at the beginning of the season, with sampling completed when oama were no longer present or the winter swells restricted access to sampling locations. Visits to the north shore started relatively early in the season (May) to ensure that the first recruitment wave was sampled. Typical oama fishing gear was used at all locations and consists of a retractable fiberglass hand pole, two-pound test fluorocarbon fishing line, a clamp split shot lead, and a size 20 limerick hook. Bait mainly consisted of tuna scraps, skipjack tuna belly, or previously frozen oama.

Haleiwa Harbor and Kawela Bay both have soft bottom habitats, consisting of mud and sand adjacent to hard bottom rock and reef habitat. After every sampling trip at each habitat type, the date, number of each species caught, fishing duration, location, and catch per unit effort (CPUE=number of oama caught per fishing hour) were recorded. Captured oama were kept in an aerated bucket of water until sampling was concluded. Oama were euthanized and chilled to be processed later in the lab. Weight (g), fork length (FL in cm), total length (TL in cm), species, date, and location were recorded for each specimen kept. A specific ID was designated for each oama and the head was removed, placed in a Whirl Pak bag, and stored in the freezer.

Dissections and otolith analysis

Head dissections began upon the completion of North Shore sampling season. A small serrated knife was used to cut the oama head above the eye sockets through the back of the skull. Forceps were used to remove tissue and Kimwipes were used to remove excess fluid to reveal the pockets where the otoliths were located. Both sagittae otoliths were removed and cleaned with water and a small paintbrush. After the otoliths were dried, they were placed in small vials along with their label ID.

Otoliths were mounted concave side up on glass slides with Crystal Bond (Wilson et al. 1997; 1999). The distal end of the otolith that protruded over the slide edge was ground to the edge of the slide with 40M (micron) lapping film. The glue was reheated and the polished face was then placed face down on the slide and the rostral end was ground with 40M film again. This second round of grinding stops when a thin cross section remained. A series of manual polishing was done using 3M lapping film, followed by 0.3M film until daily rings were visible from the core (the focus where the otolith originated) to the edge of the otolith. Otolith readings were conducted under 40X objective magnification and a 10x eye piece on a compound microscope. Preference was given to read the daily rings from the core to the dorsal end.

Growth

Each fish was aged by counting the daily otolith rings with a second reading conducted to ensure consistency and deviation $\leq 10\%$ (Zerbi et al. 2001) (Figure 2). One fish was removed from the analysis because the second read deviated by $\geq 10\%$ from the first reading. Individual otolith growth per fish was calculated by measuring the radial distance from the core to the distal edge of the otolith and dividing that distance by the age (days) of the fish. Otolith length and fish length were also regressed to confirm that the assumption of a linear relationship was not violated. Oama growth was modeled with a linear relationship between age (days) and fork length:

$$Y = mx + b \tag{1}$$

where Y is fork length (cm), x is age (days), m is a scaling parameter for the slope, and b is the y-intercept (theoretical length at age 0). Multiple linear regression was used to determine if age, location, year, or species were effective indicators of fork length. Starting with all interactions and main effects, backward elimination identified significant variables when estimating species

and location specific parameters. A large sample size (>500) and visual inspection of residuals to confirm homogeneity of variances permitted further analysis. ANOVA was used to compare growth rates between years (2014 and 2015) and between species (*M. flavolineatus* and *M. vanicolensis*).

Length-weight relationship

Length and weight data were fit to the following function to estimate the relationship between length and weight:

$$W = aL^b \quad (2)$$

where W is fish weight (g) and L is fork length (cm) (Froese et al. 2011). The scaling parameter a is derived from the intercept and b from the slope of the linear log-transformed version as outlined in Froese 2006:

$$\log(W) = \log(a) + b \log(L) \quad (3)$$

Multiple linear regression and backward elimination were used in the same manner as with the linear growth analysis to determine which variables and/or interactions were important in predicting fish weight.

CPUE

CPUE was calculated by dividing the number of oama caught by the duration (in hours) of each fishing trip. CPUE data were collected on each substrate type at all locations. Due to the nature of the data and various zero values, a moving average analysis was conducted over a moving window of three values. This type of analysis softened the extremely high values and reduced the impact of the zero values.

RESULTS

Oama Collections

Oama were collected from May through October in 2014 and 2015. A total of 548 oama were caught and retained for analysis, including 346 *M. flavolineatus* and 202 *M. vanicolensis*. Ten *M. flavolineatus* were excluded from the analyses because they exceeded the 17.8 cm FL (7 in) cutoff for adults. The fork length range of *M. flavolineatus* was 8.3 to 17.6 cm ($\mu=10.1$ cm \pm 1.0 sd) and 9.0 to 15.0 cm ($\mu=11.9$ cm \pm 1.0 sd) for *M. vanicolensis* (Figure 3). A total of 376 oama were aged, and consisted of 245 *M. flavolineatus* and 131 *M. vanicolensis*. Ages ranged from 58 to 232 days ($\mu=80.8$ days \pm 14.3 sd) for *M. flavolineatus* and 72 to 167 days ($\mu=101.5$ days \pm 13.3 sd) for *M. vanicolensis*. Habitat type was almost exclusively linked with one species, with all but three *M. flavolineatus* (<1%) captured on soft substrate, and all but three *M. vanicolensis* (1.5%) captured on hard substrate. Pelagic larval duration data for both species was unavailable because of the difficulty in identifying a settlement mark or region in the sagittal otolith sections.

Early life history characteristics

A strong linear relationship was found between FL and age ($r^2 = 0.82$, $p<0.001$). All oama combined in 2015 grew significantly faster than in 2014 ($F_{1,367}=22.84$, $p<0.001$) (Figure 4), but there was no significant difference in growth rates (regression slopes) between species (Figure 5). However, *M. flavolineatus* were smaller at a given age compared to *M. vanicolensis* ($F_{1,367}=98.1$, $p<0.0001$). Regionally, mean size from Haleiwa were smaller at a given age than mean size fish from Aina Haina or Kawela ($F_{1,367}=5.16$, $p<0.001$).

Oama also showed a strong relationship between FL and weight ($r^2 = 0.96$, $p<0.001$) (Table 1, Figure 6). Oama in 2015 were heavier, on average, than 2014 oama ($F_{1,519}=7.79$, $p<0.0001$) and *M. vanicolensis* were heavier at a given length than *M. flavolineatus* ($F_{1,519}=37.19$, $p<0.0001$). A comparison of mean FL revealed no significant differences between years and revealed that *M. vanicolensis* were larger than *M. flavolineatus* ($F_{1,538}=420.25$, $p<0.001$) (Figure 6). *M. vanicolensis* from Kawela were significantly larger than those from Haleiwa ($F_{1,538}=65.22$, $p<0.0001$).

There was a strong linear relationship between FL and otolith radius ($F_{1,306}=775.4$, $p<0.001$) (Figure 8). Individual growth rates ranged from 0.16-0.0064 mm/day, with a mean of 0.010 mm/day (± 0.001). No significant relationships were apparent between individual growth rates and time, even when data were split by species.

Based on back calculations by subtracting age from date captured, hatch dates for oama were clustered during the spring and summer months (March through September) (Figure 9). Oama in 2014 hatched earlier than in 2015 ($\chi^2=80.08$, $p<0.001$) and *M. vanicolensis* hatched earlier than *M. flavolineatus* overall ($\chi^2=57.78$, $p<0.001$).

CPUE

CPUE data were collected from June to October for both years with a total of 165 values between both habitat types and among all three locations. Values ranged from 0 to 36 oama/hour for *M. flavolineatus* and 0 to 55 oama/hour for *M. vanicolensis*. CPUE values were lower in 2015 compared to 2014 and peaks were earlier in 2014 compared to 2015 (Figure 10). *M. vanicolensis* peaked earlier than *M. flavolineatus* at Kawela and Haleiwa in 2014 (Figure 10) and the *M. vanicolensis* peak was delayed in 2015 compared to 2014 (Figure 10).

DISCUSSION

This project documents the unique pulse recruitment of oama around the island of Oahu by examining early life history characteristics. Most of the previous goatfish research in Hawaii focused on adults or high market value species like the kumu (*Parupeneus porphyreus*). Oama and weke are important ecosystem forage components for marine predators and highly valued by both the recreational and commercial fisheries. Researching recruitment is important for understanding population dynamics, connectivity, spawning, and settlement (Sponaugle 2015). This study is one of few to examine the recruitment dynamics, age, and growth rates of oama, and is therefore valuable for understanding the population dynamics of these two species. Quality data can promote responsible fishing practices and support sound conservation and management of natural resources.

The results showed that early life history characteristics and recruitment patterns varied among species and between years. Not many differences were observed between locations (except for a size difference in *M. vanicolensis*), and therefore much of the discussion is framed in a species or year comparison. The two oama species showed different peaks in CPUE, hatch date, habitat preference, and size structure, while the two years showed different growth rates, hatch date, and CPUE peaks.

It is not uncommon for species to coexist in close proximity yet exhibit different life history characteristics (Ross 1986, Nagelkerken et al. 2006, Donovan et al. 2015, Bay et al. 2001). In the case of oama, the two species recruit to nearshore habitats at different times, with *M. vanicolensis* recruiting earlier than *M. flavolineatus* by about one month. This was documented with both the early hatch dates and earlier CPUE peaks for *M. vanicolensis*. Perhaps the spawning populations have evolved unique spawning peaks in order to stagger the incoming waves of juvenile fishes to nursery areas, or they may have different pelagic larval durations.

Oama not only recruited at different times, but also settled onto different habitats. *M. vanicolensis* preferentially settled onto hard bottoms, while *M. flavolineatus* chose soft bottoms. These separate habitat preferences reduce competition for space and other resources, while

allowing them occupy the same area (bay, harbor, etc). Other related species have been known to exhibit this habitat separation phenomenon. For example, two goatfish species in the Mediterranean exhibit niche separation through depth preferences (Golani 1994). Damselfish on the Great Barrier Reef segregate based on habitat and life stage (adult or juvenile) (Bay et al. 2001). The color of each species also matches the type of substrate where they congregate (Figure 11). The tan-yellow color of *M. flavolineatus* allows them to blend in with the sand and silt, while the darker red-orange hue of *M. vanicolensis* helps them camouflage on hard bottom, usually consisting of rock, coral, crustose coralline algae, and turf algae.

There was a significant difference in size structure between the two species. *M. vanicolensis* are longer at a given age and heavier at a given length compared to *M. flavolineatus* which is expected based on habitat considerations. Compared to *M. flavolineatus*, which settle in relatively protected sandy habitats, *M. vanicolensis* settle in waters with greater wave exposure where their larger morphology might be beneficial (Friedlander et al. 2003). This is also supported by a location comparison where *M. vanicolensis* from Kawela were significantly larger than *M. vanicolensis* from Haleiwa. The rocky ledges where *M. vanicolensis* school at Kawela are subjected to constant wave action and fronts incoming swells. Different pelagic larval durations and consequently different times in nursery habitats could also explain why *M. vanicolensis* are larger.

Yearly differences in growth can be attributed to density dependent factors. Many areas in the Central Pacific experienced a huge recruitment pulse of a variety of reef fish species in 2014 and it was described as a “biblical” fish arrival by some sources (Talbot 2014). Our sampling in 2014 captured this large recruitment event and was a valuable comparison with 2015, which seemed to be a more “typical” recruitment year in terms of magnitude. We observed high recruitment at both study sites in 2014, seen in the greater CPUE magnitudes for both species. Recruitment was also earlier in 2014 compared to 2015. Pelagic stage larvae depend on currents and environmental cues to locate a suitable location to settle (Sponaugle 2015). This 2014 recruitment pulse was possibly due to favorable oceanographic conditions that affected the timing and magnitude of recruitment, but cannot explain why certain species, and not others, attained such high recruitment levels.

There were no significant differences in growth rate between species, however 2014 fish grew significantly slower than fish in 2015. The nearshore areas that oama recruit to normally serve as protection from predators and provide habitat to feed and grow (Dahlgren et al. 2006). However, the dramatically higher densities in 2014 likely increased competition for food and available refuges leading to increased post-settlement mortality (Hixon et al. 2012). Experienced anglers agreed that the 2014 oama season was the best in 20-30 years. Even though the increased abundance benefited anglers, this likely reduced the fitness of individuals, manifested in reduced growth rates that year. Oama typically are consistent in their spatial recruitment patterns, but in 2014 there was such a large influx of fishes that many schools occupied poorer quality habitats, such as canals and runoff channels.

Anomalous recruitment years, like 2014, are known to occur in both Hawaii and other locations. Large episodic recruitment events for *Pervagor spilosoma*, *Priacanthus meeki*, and Acanthuridae species has been documented previously in Hawaii (Stimson 2003, Tagawa and Tam 2006). Effects of these events can be deleterious, such as increased mortality, for species experiencing an unusually high recruitment. Classic density-dependent mechanisms affect recruitment by minimizing the number of refuges and create more stress, which can also lead to stunted growth or increased predation (Forrester 2015).

Oama showed differences in growth, recruitment peaks, hatch date, habitat preference, and size on a spatial and temporal scale. This study was the first step in collecting juvenile life history characteristics on two poorly-known species. It is important to recognize that oama encompass two species with different life history characteristics, and contemporary regulations do not distinguish between species. The current bag limit of 50 oama per day per person is quite high and can affect each species differently. Understanding the variation that occurs on small spatial scales and the year to year variation has important management implications for the ecosystem and resource users.

In addition to fishery concerns, Hawaii's marine ecosystems are influenced by oama abundance. A large number of nearshore and pelagic fishes feed and depend upon strong oama recruitment

to ensure proper growth and healthy populations of their own species, according to both angler accounts and literature (Tagawa and Tam 2006, Meyer et al. 2001). Prominent nearshore predators of oama include multiple jack species (e.g., *Caranx melampygus*, *C. ignobilis*, *Seriola dumerili*), bonefishes (*Albula spp.*), and Pacific threadfin (*Polydactylus sexfilis*). In addition, pre-settlement oama are often found in the stomachs of pelagic predators such as skipjack tuna (*Katsuwonus pelamis*), wahoo (*Acanthocybium solandri*), and dolphinfish (*Coryphaena hippurus*), and seabirds. Recruitment and movement of these predators may be intertwined with the dynamics of their prey. Therefore, oama recruitment, abundance, and growth patterns can have direct effects on higher trophic levels. These oama-dependent predators are also ecologically, recreationally, and economically important to the state of Hawaii.

Oama recruit at relatively small spatial scales, and occupy habitats close to shore, making them highly susceptible to habitat alteration, pollution, and fishing. The critical several months that oama use these habitats allows them to fully develop before recruiting to the adult fishery. Habitat alteration, such as dredging and shoreline armoring has a direct effect by minimizing the area of quality habitat that oama utilize during this pivotal post-settlement stage. Illegal fishing activities, mainly small-eye gillnets, can also have a dramatic impact on oama due to their preference for shallow nearshore areas. Anecdotal information from anglers indicates that the number of locations where oama are found has declined over time. Oama are highly dependent on these nearshore habitats, and may not have the same capacity as their adult counterparts to migrate to deeper habitats or areas further offshore. Protecting habitats encompassing their range will greatly benefit oama especially since relatively small reserves are able to benefit weke that have a larger range (Holland et al. 1993, Meyer et al. 2000).

This study revealed that variations in oama abundance occur on a yearly scale at different locations. A longer time series would reveal the long-term effects of fishing, climate change, and reveal natural variation of fish populations and recruitment. These long-term effects can cause shifts in body size distribution, reduced abundance, or changes in reproductive output (DeMartini and Smith 2015, Pratchett et al. 2015). However, the oama fishery is unique because anglers are not specifically seeking large individuals but rather fishing a specific life stage (post-settlement juveniles). Harvesting large quantities of oama may result in removing too many fish before they

have the opportunity to reach maturity (recruitment overfishing). The short time period and small spatial scale at which oama recruitment occurs may benefit from a more dynamic management regime. An adaptive management strategy that occurs on small spatial scales, such as a community regulated area, or a local monitoring program could account for the inter-annual and spatial fluctuations that occur for these species (Zanre 2014). However, it would be helpful to have a longer time series to examine the natural fluctuations in timing of recruitment, size, and age among locations.

Oama will continue to have a strong cultural significance and recreational fishery in Hawaii. Defining their life history characteristics and understanding their recruitment dynamics are essential to promoting responsible fishing practices and management. Unlocking oama life history characteristics will also benefit the weke fishery as well as the suite of predators that depend upon oama as an important prey source. These goatfish could also serve as a model for studying other species that have large fisheries and are ecologically significant, such as the halalu (*Selar crumenophthalmus*). It is important to understand the ecology of species such as oama, owing to their significance in the economy, ecosystem, and culture of contemporary Hawaiian society.

Table 1: Number of oama sampled, aged, and length-weight (L/W) parameters for all species, sites, and years. MUFL – *M. flavolineatus*. MUVA – *M. vanicolensis*.

Year	Location	Species	N		L/W	
			Collected	Aged	a	b
2014	Haleiwa	MUFL	68	33	0.0027	3.69
	Haleiwa	MUVA	66	39	0.0029	3.69
	Kawela	MUFL	68	34	0.0029	3.69
	Kawela	MUVA	39	23	0.0029	3.69
2015	Haleiwa	MUFL	55	47	0.0048	3.45
	Haleiwa	MUVA	57	44	0.0052	3.45
	Kawela	MUFL	71	57	0.0046	3.45
	Kawela	MUVA	40	25	0.0049	3.45
	Paiko	MUFL	84	74	0.0046	3.45
Totals			548	376		

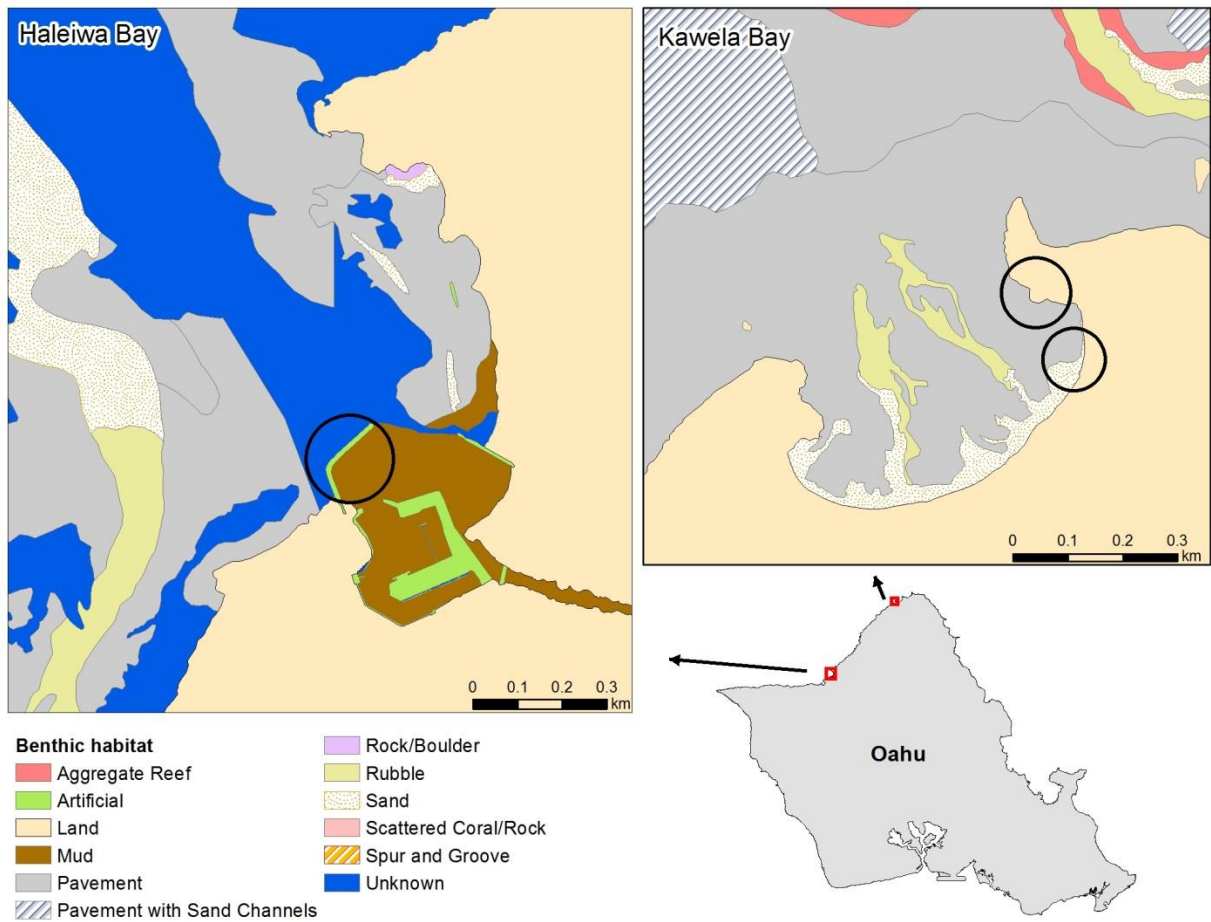


Figure 1: The two oama sampling sites were located on the north shore of Oahu. Detailed benthic habitat maps are presented for Haleiwa Harbor and Kawela Bay with black circles representing sampling locations.

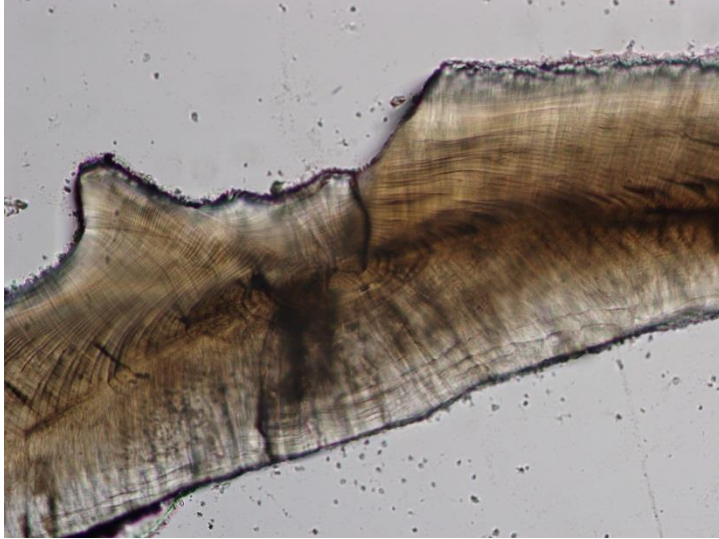


Figure 2: Images taken from portions of sectioned and polished otoliths showing daily growth increments for a) *Mulloidichthys flavolineatus* and b) *M. vanicolensis*.

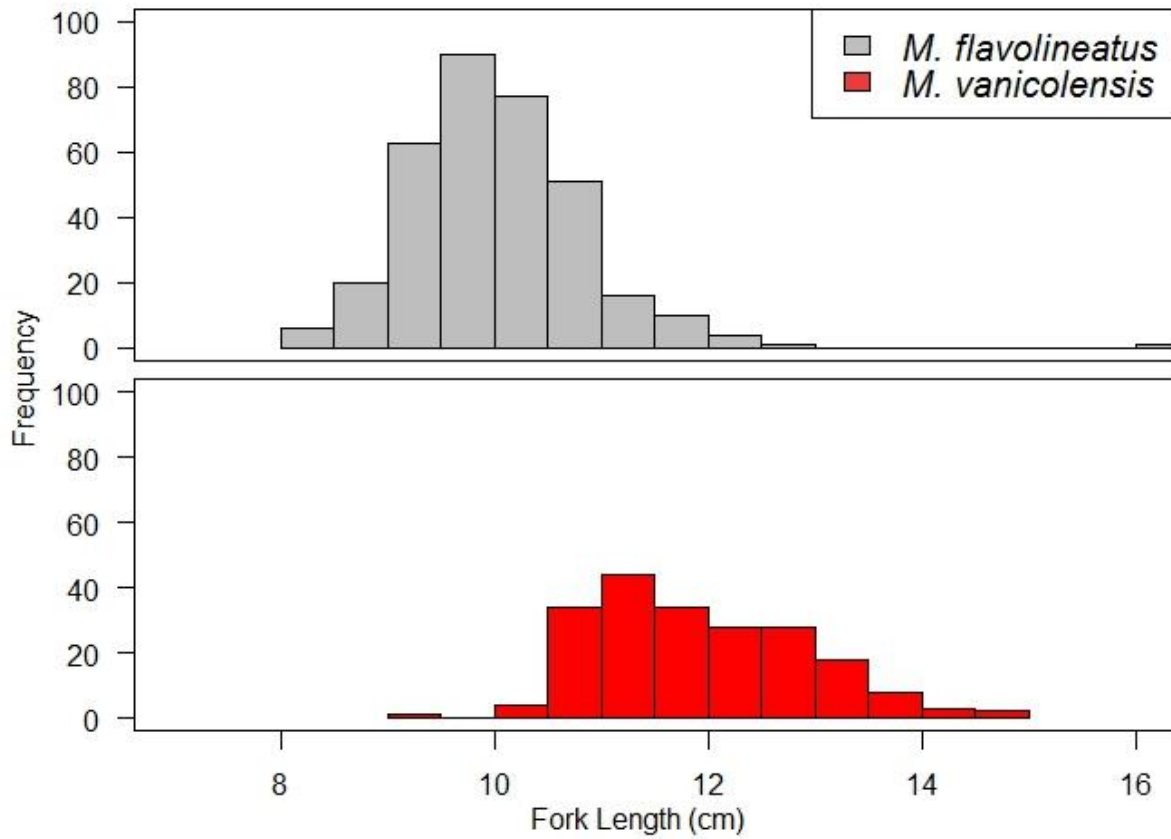


Figure 3: Length frequency histogram of *Mulloidichthys flavolineatus* and *M. vanicolensis* sampled during the summer of 2014 and 2015 on the north shore of Oahu. Mean sizes for *M. flavolineatus* was significantly shorter compared to *M. vanicolensis*.

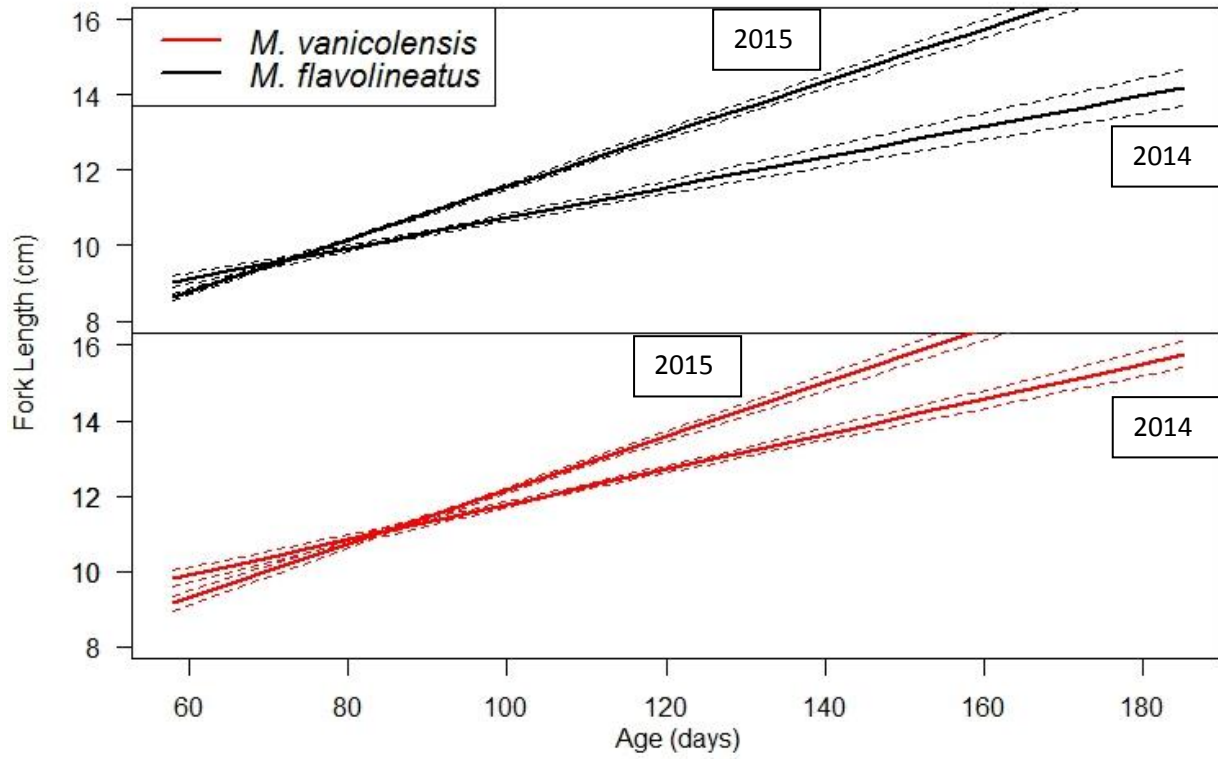


Figure 4: Growth curves for 2014 vs 2015 with separate lines by species. Growth rate (regression slope) was significantly lower in 2014 compared to 2015 for both species combined. Dotted lines represent standard error.

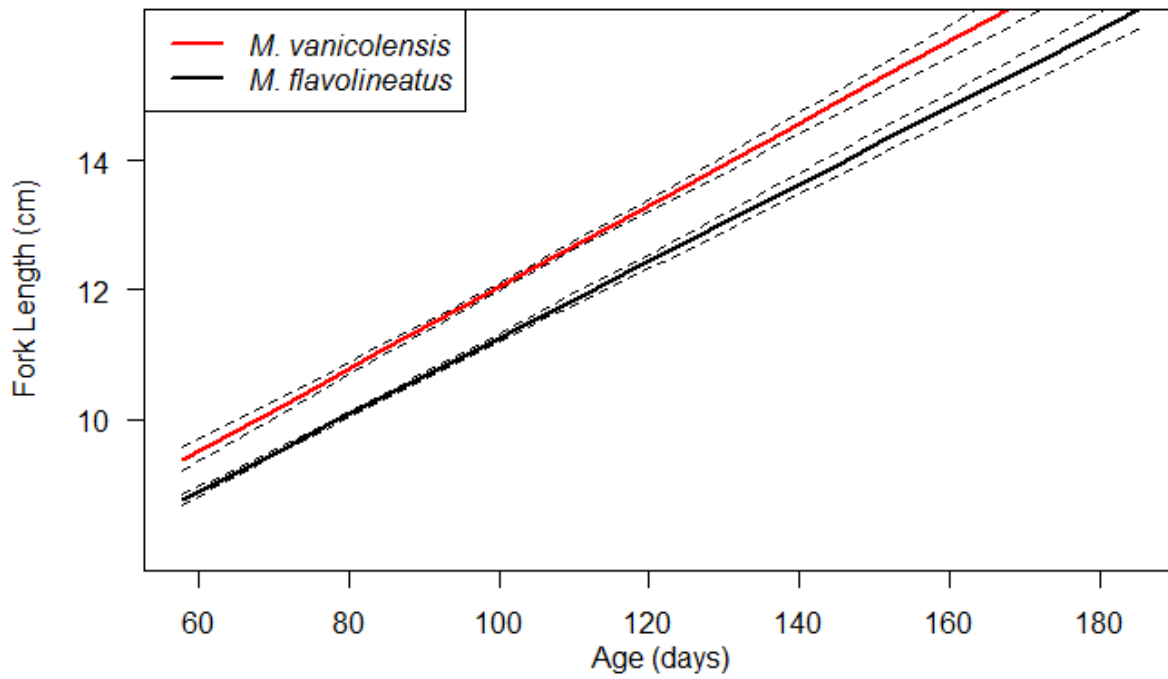


Figure 5: Growth curves for both oama species from 2014 and 2015. Growth rate (regression slope) was not significantly different between species. However, *Mulloidichthys vanicolensis* were significantly longer at a given age compared to *M. flavolineatus* (significantly different intercepts). Dotted lines represent standard error.

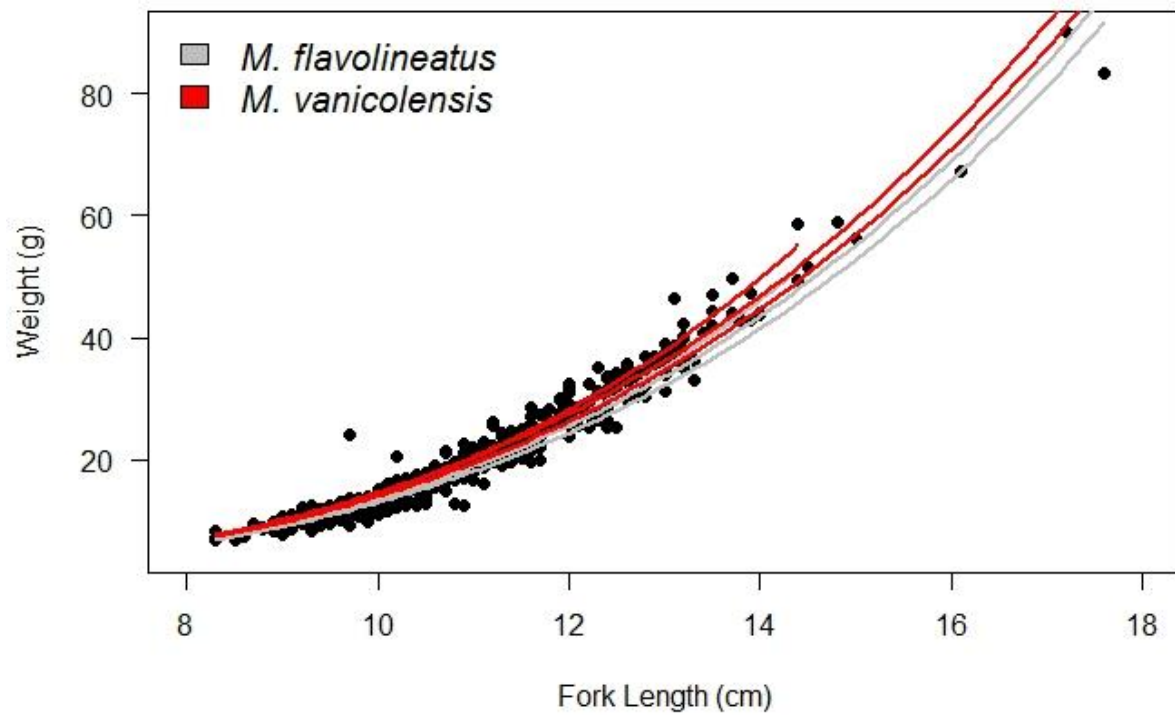


Figure 6: Length weight relationships for *Mulloidichthys flavolineatus* and *M. vanicolensis*. Individual lines within a species color represent different locations. On average, *M. vanicolensis* was heavier at a given length than *M. flavolineatus*.

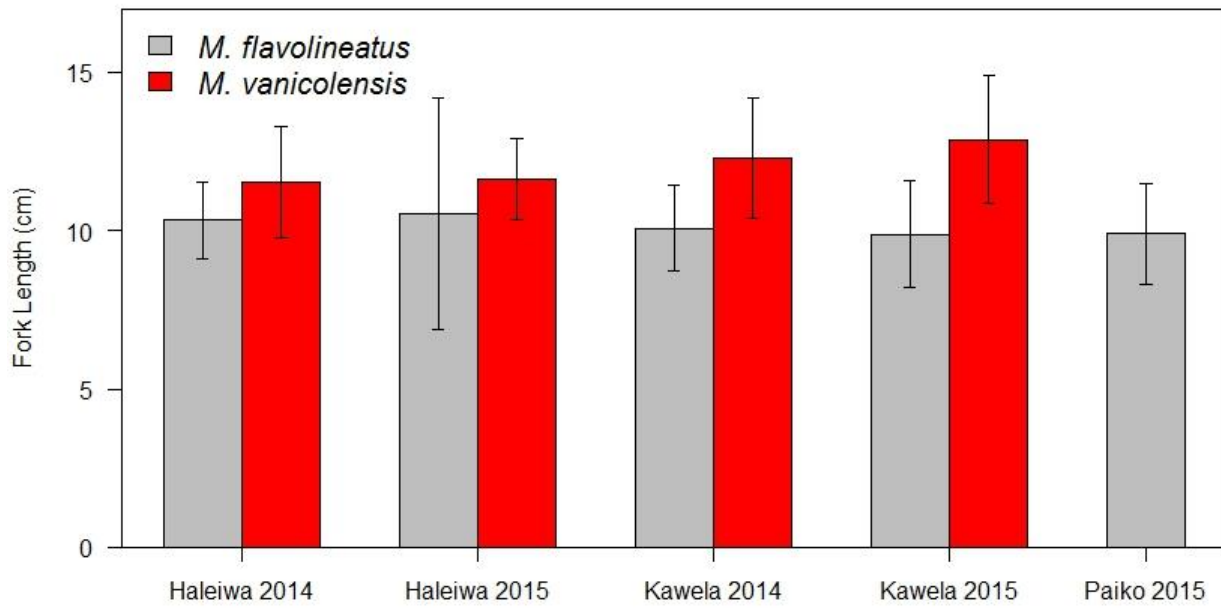


Figure 7: Mean fork length comparisons (with error bars) by species, location, and year. Mean size of *Mulloidichthys vanicolensis* is consistently larger than *M. flavolineatus*. Paiko (Aina Haina) consisted of only one habitat type and therefore only *M. flavolineatus* were present.

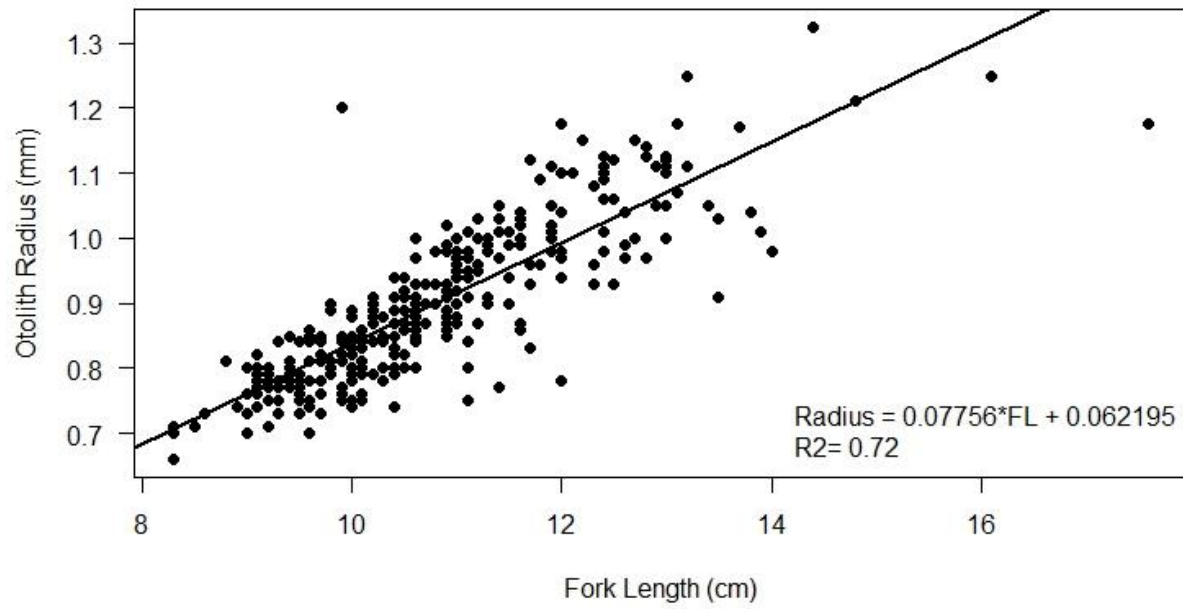


Figure 8: Linear relationship between fish fork length and otolith radius. Otolith radius was measured from the core (focus) to the dorsal end of the otolith.

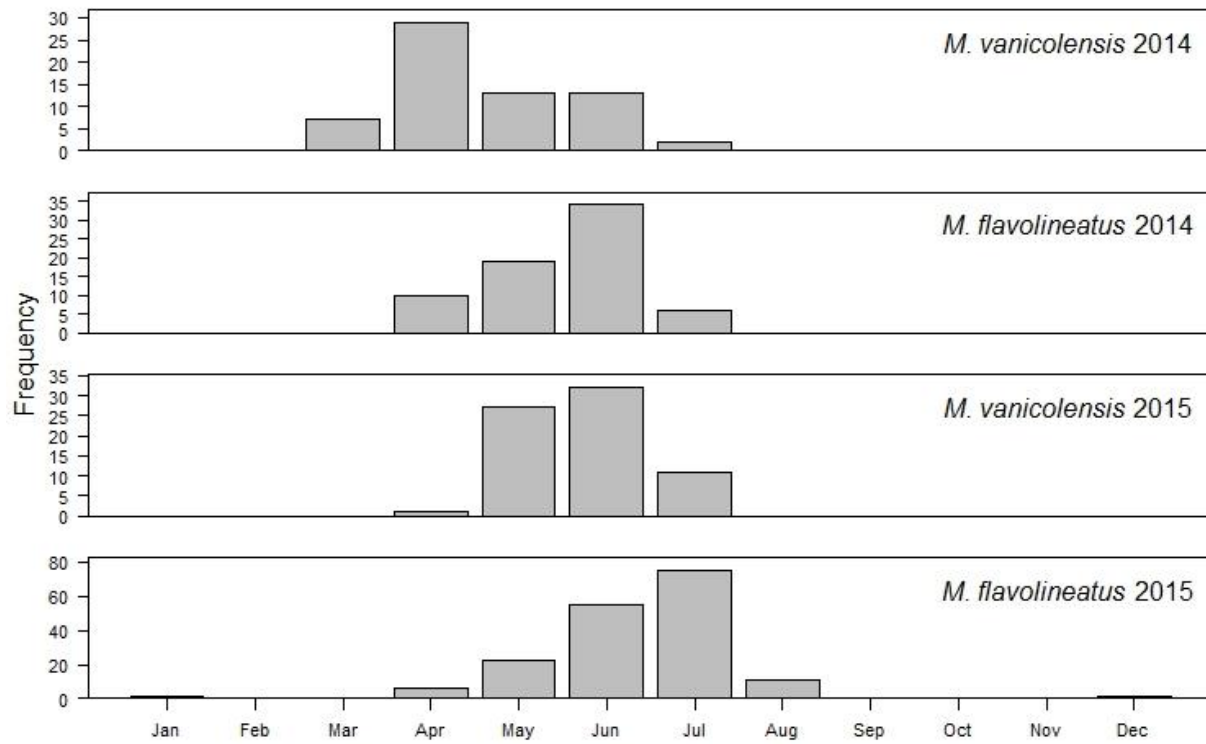


Figure 9: Oama hatch dates separated by species and year. Hatch dates represent a birthdate by subtracting fish age from date collected. *Mulloidichthys vanicolensis* “hatch” earlier than *M. flavolineatus* and 2015 hatch dates were delayed compared to 2014.

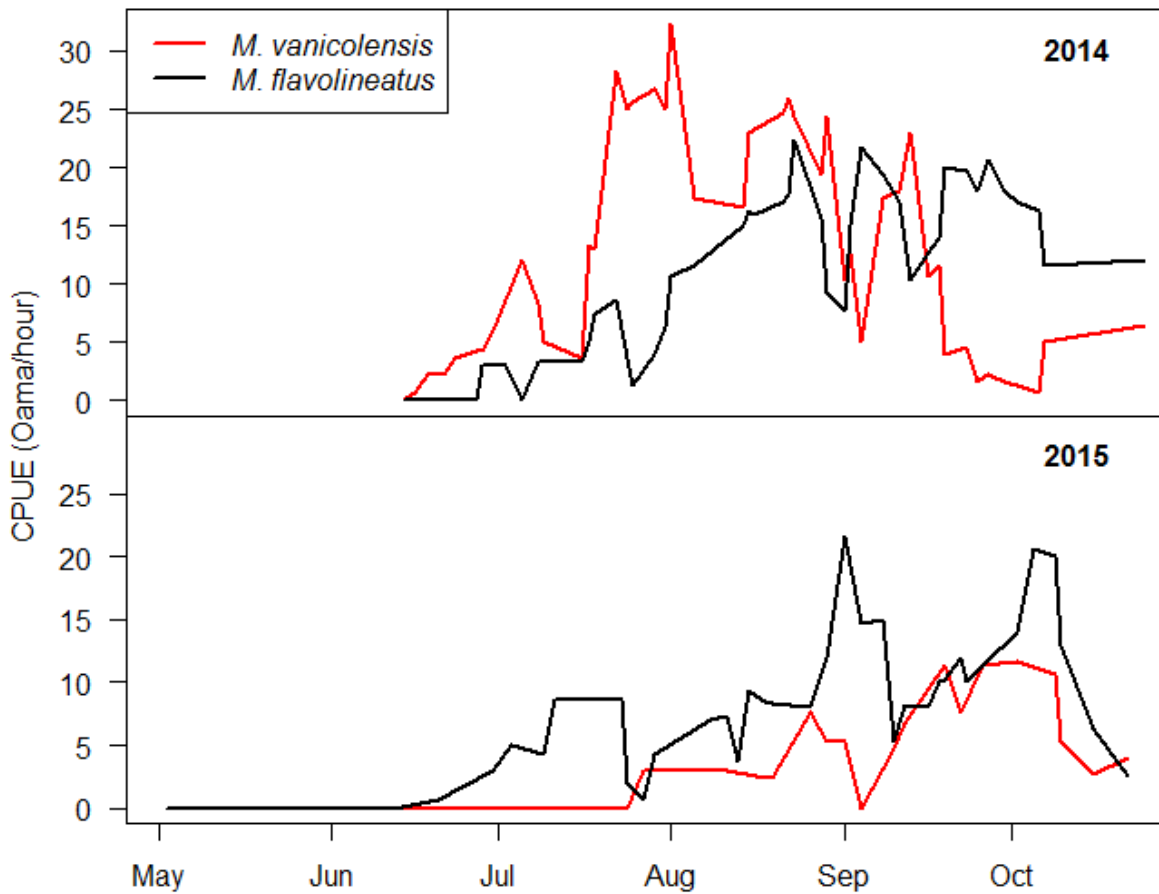


Figure 10: Moving average of catch per unit effort (CPUE= oama hr⁻¹) for *Mulloidichthys flavolineatus* and *M. vanicolensis* for A) 2014 and B) 2015. A moving window of three CPUE values was used to calculate the moving average.

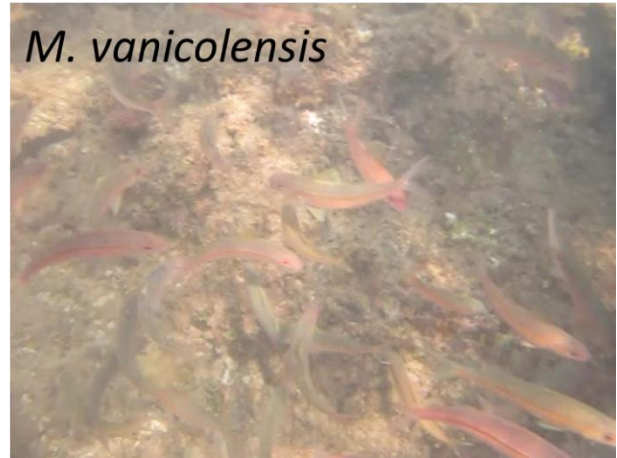


Figure 11: Results showed that species was linked with substrate type. *Mulloidichthys flavolineatus* recruited to soft substrate (sand, silt, mud) and *M. vanicolensis* recruited to hard substrate (rock, coral, CCA, etc).

REFERENCES

- Allen, M.S. (2014). The historical role of bonefishes (*Albula* spp.) in Polynesian fisheries. In Hawaiian Archaeology pp 51-72.
- Bay, L. K., Jones, G. P. & McCormick, M. I. (2001). Habitat selection and aggression as determinants of spatial segregation among damselfish on a coral reef. *Coral Reefs* **20**, 289-298.
- Begg, G. A., Campana, S. E., Fowler, A. J. & Suthers, I. M. (2005). Otolith research and application: current directions in innovation and implementation. *Marine and Freshwater Research* **56**, 477-483.
- Bergenius, M. A. J., McCormick, M. I., Meekan, M. G. & Robertson, D. R. (2005). Environmental influences on larval duration, growth and magnitude of settlement of a coral reef fish. *Marine Biology* **147**, 291-300.
- Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P. & Menge, B. A. (1996). Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* **27**, 477-500.
- Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**, 197-242.
- Campana, S. E. (2005). Otolith science entering the 21st century. *Marine and Freshwater Research* **56**, 485-495.
- Campana, S. E. & Thorrold, S. R. (2001). Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 30-38.
- Caselle, J. E. & Warner, R. R. (1996). Variability in recruitment of coral reef fishes: The importance of habitat at two spatial scales. *Ecology* **77**, 2488-2504.
- Cobb, J.N. (1905). Commercial fisheries in the Hawaiian Islands. In: Jordan, D.S. & B.W. Evermann. The aquatic resources of the Hawaiian Islands. *Bulletin United States Commercial Fisheries* **23**, 577-765.
- Cole, K.S. (2009). Size-dependent and age-based female fecundity and reproductive output for three Hawaiian goatfish (Family Mullidae) species, *Mulloidichthys flavolineatus*, *M. vanicolensis*, and *Parupeneus porphyreus*. Report to the DAR Dingell-Johnson Sport Fish Restoration.
- Colin, P.L. and Clavijo, I.E. (1978). Mass spawning by the spotted goatfish *Pseudupeneus-maculatus* (Bloch) (Pices: mullidae). *Bulletin of Marine Science* **28**, 780-782.
- Dahlgren, C. P., Kellison, G. T., Adams, A. J., Gillanders, B. M., Kendall, M. S., Layman, C. A., Ley, J. A., Nagelkerken, I. & Serafy, J. E. (2006). Marine nurseries and effective juvenile habitats: concepts and applications. *Marine Ecology Progress Series* **312**, 291-295.
- DeMartini, E.E. & Smith, J.E. (2015) Effects of fishing on the fishes and habitat of coral reefs. In *Ecology of Fishes on Coral Reefs*, Vol. 1 (Mora, C.), pp. 135-144. Cambridge, UK: Cambridge University Press.
- Donovan, M. K., Friedlander, A. M., Harding, K. K., Schemmel, E. M., Filous, A., Kamikawa, K. & Torkelson, N. (2015). Ecology and niche specialization of two bonefish species in Hawai'i. *Environmental Biology of Fishes* **98**, 2159-2171.
- Donovan, M.K., Friedlander, A.M., Usseglio, P., Goodell, W., Iglesias, I., Schemmel, E.M., Stamoulis, K., Filous, A., Giddens, J., Kamikawa, K., Koike, H., McCoy, K., Wall, C.B. (In review). Effects of gear restriction on the abundance of juvenile fishes along sandy beaches in Hawaii.
- Forrester, G.E. (2015) Competition in reef fishes. In *Ecology of Fishes on Coral Reefs*, Vol. 1 (Mora, C.), pp. 34-40. Cambridge, UK: Cambridge University Press.

- Friedlander, A. M., Brown, E. K., Jokiel, P. L., Smith, W. R. & Rodgers, K. S. (2003). Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* **22**, 291-305.
- Friedlander, A. M. & Parrish, J. D. (1997). Fisheries harvest and standing stock in a Hawaiian bay. *Fisheries Research* **32**, 33-50.
- Froese, R. (2006). Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* **22**, 241-253.
- Froese, R., Tsikliras, A. C. & Stergiou, K. I. (2011). EDITORIAL NOTE ON WEIGHT-LENGTH RELATIONS OF FISHES. *Acta Ichthyologica Et Piscatoria* **41**, 261-263.
- Garrod, P.V. and Chong, K.C. (1978). The fresh fish market in Hawaii. Hawaii Agricultural Experiment Station, College of Tropical Agriculture C3: 1-24.
- Golani, D. (1994). NICHE SEPARATION BETWEEN COLONIZING AND INDIGENOUS GOATFISH (MULLIDAE) ALONG THE MEDITERRANEAN COAST OF ISRAEL. *Journal of Fish Biology* **45**, 503-513.
- Gosline, W. A. (1984). STRUCTURE, FUNCTION, AND ECOLOGY IN THE GOATFISHES (FAMILY MULLIDAE). *Pacific Science* **38**, 312-323.
- Green, B.S., Mapstone, B.D., Carlos, G., and Begg, G.A. (2009). Tropical otoliths-where to next (eds.) in *Tropical Fish Otoliths: Information for Assessment, Management and Ecology*. (Hawaii FEP 2009) Western Pacific Regional Fishery Management Council. Fishery Ecosystem Plan for the Hawaii Archipelago.
- Hixon, M.A., Anderson, T.W., Buch, K.L., Johnson, D.W., McLeod, J.B. & Stallings, C.D. (2012). Density dependence and population regulation in marine fish: a large-scale, long-term field manipulation. *Ecological Monographs* **82**, 467-489.
- Holland, K. N., Peterson, J. D., Lowe, C. G. & Wetherbee, B. M. (1993). MOVEMENTS, DISTRIBUTION AND GROWTH-RATES OF THE WHITE GOATFISH *MULLOIDES-FLAVOLINEATUS* IN A FISHERIES CONSERVATION ZONE. *Bulletin of Marine Science* **52**, 982-992.
- Hoover, J.P. (1993). *Hawaii's Fishes: A Guide for Snorkelers, Divers, and Aquarists*. Honolulu: Mutual Pub. Print.
- Kolasinski, J.A., Frouin, P., Sallon, A., Rogers, K., Bruggemann, H.J. & Potier, M. (2009) Feeding ecology and ontogenetic dietary shift of yellowstripe goatfish *Mulloidichthys flavolineatus* (Mullidae) at Reunion Island, SW Indian Ocean. *Marine Ecology Progress Series* **386**, 181-195.
- Krajewski, J.P. & Bonaldo, R.M. (2005) Plankton-picking by the goatfish *Pseudupeneus maculatus* (Mullidae), a specialized bottom forager. *The Fisheries Society of the British Isles* **68**, 925-930.
- Krajewski, J.P., Bonaldo, R.M., Sazima, C. & Sazima, I. (2006) Foraging activity and behaviour of two goatfish species (PerciformesL Mullidae) at Fernando de Noronha Archipelago, tropical West Atlantic. *Environmental Biology of Fishes* **77**, 1-8.
- Mahi, C.A. (1969). The food and feeding habits of the kumu, *Parupeneus porphyreus*. Hawaii Cooperative Fishery Unit-Directed Research Report.
- Maunder, M. N., Sibert, J. R., Fonteneau, A., Hampton, J., Kleiber, P. & Harley, S. J. (2006). Interpreting catch per unit effort data to assess the status of individual stocks and communities. *Ices Journal of Marine Science* **63**, 1373-1385.
- McCormick, M. I. & Kerrigan, B. A. (1996). Predation and its influence on the condition of a newly settled tropical demersal fish. *Marine and Freshwater Research* **47**, 557-562.
- McCormick, M.I. & Makey, L.L. (1997) Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. *Marine Ecology Progress Series* **153**, 247-257.

- McCormick, M. I. & Milicich, M. J. (1993). LATE PELAGIC-STAGE GOATFISHES - DISTRIBUTION PATTERNS AND INFERENCES ON SCHOOLING BEHAVIOR. *Journal of Experimental Marine Biology and Ecology* **174**, 15-42.
- McCormick, M. I. & Molony, B. W. (1995). INFLUENCE OF WATER TEMPERATURE DURING THE LARVAL STAGE ON SIZE, AGE AND BODY CONDITION OF A TROPICAL REEF FISH AT SETTLEMENT. *Marine Ecology Progress Series* **118**, 59-68.
- McCoy, K. (2015) Estimating nearshore fisheries catch for the main Hawaiian Islands. Master's thesis, The University of Hawaii at Manoa, Honolulu, Hawaii.
- Meyer, C. G., Holland, K. N., Wetherbee, B. M. & Lowe, C. G. (2000). Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. *Environmental Biology of Fishes* **59**, 235-242.
- Meyer, C. G., Holland, K. N., Wetherbee, B. M. & Lowe, C. G. (2001). Diet, resource partitioning and gear vulnerability of Hawaiian jacks captured in fishing tournaments. *Fisheries Research* **53**, 105-113.
- Moffit, R.B. (1979). Age, growth and reproduction of the Kumu, *Parupeneus porphyreus* Jenkins M.S. Thesis, University of Hawaii, Honolulu.
- Nagelkerken, I., Velde, G.V.D., Verberk, W.C.E.P. & Dorenbosch, M. (2006) Segregation along multiple resource axes in a tropical seagrass fish community. *Marine Ecology Progress Series* **308**, 79-89.
- Pannella, G. (1971). Fish otoliths: daily growth layers and periodic patterns. *Science* **173**, 1124-1127.
- Robertson, D. R. & Kaufmann, K. C. (1998). Assessing early recruitment dynamics and its demographic consequences among tropical reef fishes: Accommodating variation in recruitment seasonality and longevity. *Australian Journal of Ecology* **23**, 226-233.
- Ross, P. M., Thrush, S. F., Montgomery, J. C., Walker, J. W. & Parsons, D. M. (2007). Habitat complexity and predation risk determine juvenile snapper (*Pagrus auratus*) and goatfish (*Upeneichthys lineatus*) behaviour and distribution. *Marine and Freshwater Research* **58**, 1144-1151.
- Ross, S. T. (1986). RESOURCE PARTITIONING IN FISH ASSEMBLAGES - A REVIEW OF FIELD STUDIES. *Copeia*, 352-388.
- Sale, P. F. (2004). Connectivity, recruitment variation, and the structure of reef fish communities. *Integrative and Comparative Biology* **44**, 390-399.
- Sato, N., Asahida, T., Terashima, H., Hurbungs, M. D. & Ida, H. (2008). Species composition and dynamics of larval and juvenile fishes in the surf zone of Mauritius. *Environmental Biology of Fishes* **81**, 229-238.
- Selkoe, K.A., Gaggiotti, O., ToBo Laboratory, Bowen, B.W. & Toonen, R.J. (2014) Emergent patterns of population genetic structure for a coral reef community. *Molecular Ecology* **23**, 3064-3079.
- Smith, M.K. (1993) An ecological perspective on inshore fisheries in the Main Hawaiian Islands. *Marine Fisheries Review* **55**, 34-49.
- Smith, K. A. & Sinerchia, M. (2004). Timing of recruitment events, residence periods and post-settlement growth of juvenile fish in a seagrass nursery area, south-eastern Australia. *Environmental Biology of Fishes* **71**, 73-84.
- Sponaugle, S. (2015) Recruitment of coral reef fishes: linkages across stages. In *Ecology of Fishes on Coral Reefs*, Vol. 1 (Mora, C.), pp. 28-33. Cambridge, UK: Cambridge University Press.
- Stimson, J. (2005). Archipelago-wide episodic recruitment of the file fish *Pervagor spilosoma* in the Hawaiian Islands as revealed in long-term records. *Environmental Biology of Fishes* **72**, 19-31.

- Tagawa, A. and Tam, C. (2006). Hawaii's Ulua and Papio Tagging Project 2000 to 2004. Division of Aquatic Resources: Hawaii. 06-01.
- Talbot, R. (2014) "Biblical" spawning event on Hawaiian reefs. *CORAL Magazine* Nov/Dec 2014.
- Titcomb, M. (1972). Native Use of Fish in Hawaii. Honolulu: U of Hawaii. Print.
- Uiblein, F. (1991) Ontogenetic shifts in resource use and shoaling tendency related to body size in Red Sea goatfish (*Parupeneus forsskali*, Mullidae). *Marine Ecology* **12**, 153-161.
- Uiblein, F. (2007). Goatfishes (Mullidae) as indicators in tropical and temperate coastal habitat monitoring and management. *Marine Biology Research* **3**, 275-288.
- Victor, B. C. (1986). DURATION OF THE PLANKTONIC LARVAL STAGE OF 100 SPECIES OF PACIFIC AND ATLANTIC WRASSES (FAMILY LABRIDAE). *Marine Biology* **90**, 317-326.
- Victor, B. C. & Wellington, G. M. (2000). Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. *Marine Ecology Progress Series* **205**, 241-248.
- Walsh, W. A. & Brodziak, J. (2015). Billfish CPUE standardization in the Hawaii longline fishery: Model selection and multimodel inference. *Fisheries Research* **166**, 151-162.
- Wilson, D. T. & McCormick, M. I. (1997). Spatial and temporal validation of settlement-marks in the otoliths of tropical reef fishes. *Marine Ecology Progress Series* **153**, 259-271.
- Wilson, D. T. & McCormick, M. I. (1999). Microstructure of settlement-marks in the otoliths of tropical reef fishes. *Marine Biology* **134**, 29-41.
- Zanre, E. (2014) Community-based subsistence fishing area designation procedures guide. Division of Aquatic Resources, Hawaii Revised Statutes 188-22.6.
- Zerbi, A., Aliaume, C. & Joyeux, J. C. (2001). Growth of juvenile tarpon in Puerto Rican estuaries. *Ices Journal of Marine Science* **58**, 87-95.