A Rapid, Low-cost Technique for
Describing the Population Structure
of Reef Fishes

Hawaii
Biological
Survey

Final Report   January, 2008

COVER

Frame captures from videogrammetry transects conducted off Portlock, Oahu. Parallel laser beams (green dots) superimpose a measurement scale on the flank of fish and allow size estimation.

A Rapid, Low-cost Technique for Describing the Population Structure of Reef Fishes

Final Report

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EXECUTIVE SUMMARY

Attempts to manage exploited fish populations ideally incorporate information on the life history and demographic structure of the target species. In Hawaii, a complete set of the necessary information does not seem to exist for any one reef-fish species, making it nearly impossible to predict the outcome of new management strategies or evaluate the effectiveness of existing ones. We attempted to generate or find information on abundance, growth, sex-specific size-at-maturity, length-specific sex ratios, size-fecundity relationships, age structure, and forces of mortality for three exploited reef fishes (*Centropyge potteri*, *Dascyllus albisella*, and *Parupeneus multifasciatus*). This project included a novel approach to the study of reef fish biology: Estimation of mortality rates inside and outside a no-take marine reserve allowed fishery-independent estimation of natural and fishing mortality.

We used the life history and demographic information in a Ricker production model to predict or evaluate management strategies by examining effects on biomass and egg production. Low sample size prevented estimation of natural mortality for *Dascyllus albisella*, thus preventing production estimates for this fish inside the no-take marine reserve. Results varied between the other two species. The *Centropyge potteri* population inside Hanauma Bay (no-take reserve) appears to produce approximately triple the biomass, number of individuals, and number of eggs per reproductive event relative to the population in a nearby fished area (Maunalua Bay). For this species, the no-take reserve produces the raw material necessary for fishery enhancement in an equal-sized nearby area. The *Parupeneus multifasciatus* population in the same no-take reserve appears to produce roughly half the biomass and eggs of the population in a nearby fished area. Because of low abundance and high mortality inside the no-take reserve, the population there does not produce the raw materials necessary for fishery enhancement in Maunalua Bay. This study appears to be the first to use production estimates to empirically evaluate the fishery enhancement value of a no-take marine reserve.

We used the same production model to predict the effects of varying size limits and fishing pressure on the sex-changing *Centropyge potteri*. Results suggest a lower size limit protecting all females (~90 mm TL) would maximize egg production. Fishing pressure on individuals larger than 90 mm can increase. This would maintain maximum egg production, but also increase total yield, and drive the sex-ratio closer to the species average   Because of counterintuitive mortality rates (i.e., higher mortality in the reserve) generated for *Parupeneus multifasciatus*, we could not realistically model the effects of various fishing practices for this species but did determine that current fishing regulations appear to protect most mature females. The broad geographic range over which life-history-based fishing practices influence a fishery should be considered when evaluating the relative merits of management strategies.

INTRODUCTION

Sound fishery management decisions require a variety of life history and demographic information. The lack of one or more crucial bits of information can prevent proactive regulation and cloud evaluation efforts. Unfortunately, a complete set of life history and demographic information for any exploited Hawaiian coral reef fish species is virtually non-existent.

Often, the generation of life-history parameters is viewed as time-consuming and costly. Further, estimating demographic parameters is often fraught with unrealistic assumptions associated with fishery-dependent techniques.

We suggest that generating adequate life history and demographic information can be timely and cost-effective. Further, we suggest that the combination this life history information with the application of non-destructive, highly accurate size estimation methods in Hawaii's system of no-take marine reserves represents an unexploited and extremely valuable opportunity to generate fishery independent estimates of natural, and by extension, fishing mortality.

To demonstrate the feasibility of this approach, the goal of this project was to, within one year: 1) describe the growth and reproductive parameters for three coral reef fish species, 2) describe demographic patterns for each species inside and outside of a no-take marine reserve to estimate natural and fishing mortality, and 3) evaluate the fishery enhancement potential of various management techniques.

METHODS

1. Study System

Species

We studied three exploited species with a variety of life-history characteristics. The Potter's angelfish (*Centropyge potteri*) is an endemic, small-bodied, territorial, broadcast spawning species and is the number one aquarium fish collected on Oahu (DAR Records). The domino damselfish (*Dascyllus albisella*) is also a part of the ornamental fishery, but catch records suggest the fishery impact on this species may be negligible. Like the angelfish it is endemic, small-bodied, and site-attached, but rather than spawning in the water column, it lays demersal eggs in a nest which is typically guarded by males. Our third study species, the many-barred goatfish (*Parupeneus multifasciatus*), is targeted by commercial and recreational food fisheries, and is usually the most abundant goatfish wherever it occurs (Randall 2007). Creel surveys in Waikiki indicate it ranks second in number of fish caught by all methods (Meyer 2003). It is a broadcast spawner, but differs from the other two species in having a broader geographic distribution from Cocos-Keeling Islands in the Indian Ocean to Norfolk Island in the South Pacific and Hawaii in the North Pacific (Randall 2007) and being larger-bodied and less site-attached.

<u>Sites</u>

The majority of life history analysis was performed on specimens collected from the forereef of Kaneohe Bay, Oahu. This area can be difficult to access due to its exposure to trade winds (and resulting large waves). As such, fishing pressure is low (DAR catch records show that this is part of the least heavily fished region on Oahu for *Centropyge potteri*), and we assumed fishes collected in this area were from unfished populations. Where necessary (*e.g.*, reproductive analysis of *Parupeneus multifasciatus*, below) Hawaii-caught specimens from museum and university collections were also analyzed.

Demographic patterns were described at Hanauma and Maunalua Bays. These sites represent our best efforts to choose appropriate comparison sites for the three study species. Hanauma Bay encloses approximately 380,589 m^2 and fishing has been prohibited for 40 years. Our comparison site occupies an equivalent area in Maunalua Bay, adjacent to Portlock (N 21° 15'41.37" W, 157° 42'41.43"). This site lies approximately 3.2 km westward along the coast from Haunama Bay and contains, at least superficially, similar habitat types and depth distributions. Ornamental-catch records maintained by the Division of Aquatic Resources show that the majority of Potter's angelfish collected on Oahu come from this area. This shoreline is also a popular hook-and-line and spear-fishing location.

2. Life History Analysis

We collected specimens using nets or spears while on SCUBA from the forereef of Kaneohe Bay. Specimens were stored on ice until processing. We measured, to the nearest 0.5 mm, standard length, the distance between the origins of the dorsal and pelvic fins, and the length from the anterior-most part of the head to the end of the middle caudal rays. The latter measurements correspond to total length for *Centropyge potteri* and fork length for *Dascyllus albisella* and *Parupeneus multifasciatus*. We then measured total body mass (to 0.1 g), removed saccular otoliths (saggitae), and fixed gonads in Dietrich's fixative (60% distilled water, 28% absolute ethanol, 10% formaldehyde, and 2 % glacial acetic acid). Morphometric relationships were described using linear regression for lengths and a 2-parameter power function for length vs. weight. Growth and reproduction were described following the methods in Longenecker and Langston (2006), summarized below.

<u>Growth</u>

We prepared a single, transverse section of each saggita by mounting the otolith, lateral side down, on a glass microscope slide in thermoplastic glue (Crystal Bond #509 from Electron Microscopy Sciences, Hatfield, PA) then removing a section containing the core using an Isomet 11-1180 low-speed saw (Beuhler, Lake Bluff, IL). We affixed this section to a glass microscope slide, a cut side down, with thermoplastic glue; ground close to the core using a series of 600 and 1500 grit sandpaper; then polished the section with 0.3 and 0.05 µm alumina slurry on felt. We etched the polished surface with a 2.5% solution of unbuffered EDTA for 4-7 min, then rinsed with deionized water. We dissolved the thermoplastic glue with acetone and mounted prepared otolith sections on aluminum stubs. We coated these sections with a gold-palladium film in a Hummer II sputtercoater (Technics, Alexandria, VA), and viewed them on a Hitachi S-800 field

emission scanning electron microscope (Hitachi High Technologies America, Schaumburg, IL). We used Photoshop 7.0 (Adobe Systems, San Jose, CA) to examine digital images of the otolith sections (see Figure 1). Otolith preparations rarely included the primordium, so total number of rings were estimated by counting the number of increments past an easily identifiable check mark for each species, and adding an assumed number of days for the region inside the mark. For *Centropyge potteri*, the check mark corresponded to larval duration reported by Thresher & Brothers (1985), so we added the average value of 36 d. The mark on *Parupeneus multifasciatus* corresponded to 21 days (as indicated by counts on preparations including the primordium).
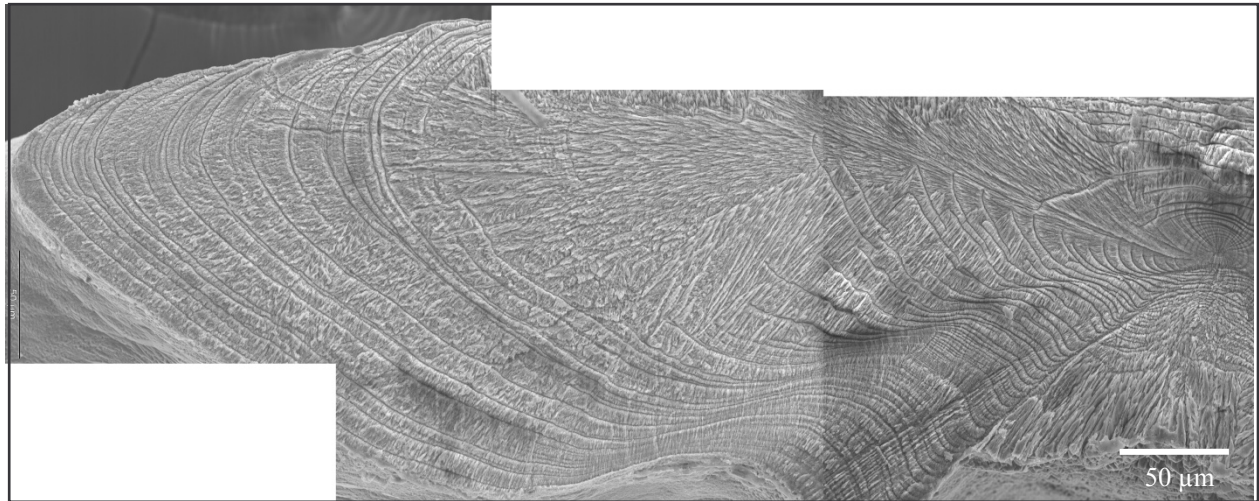

Figure 1. Scanning electron micrograph of a prepared *P. multifasciatus* otolith. We assigned a total age of 219 days to the fish that produced this otolith**.**

We assumed that each otolith increment represented one day, plotted age versus length, and described the relationship between these variables using a 3-parameter power function. We used this relationship to predict fish length for each otolith analyzed and used these data to construct a vonBertalanffy growth curve following the methods outlined in Everhart & Youngs (1992). Briefly, we estimated L_∞ (asymptotic length, or the length at which growth rate is theoretically zero) using a Ford-Walford plot, whereas t_o and K were estimated from a plot of ln ($L_\infty - 1_t$) versus estimated age (t_0 = the age when length is theoretically zero; K = rate of growth toward L_∞; l_t = the length at age t).

Reproduction

We dehydrated Dietrichs'-preserved gonads in a graded ethanol series, embedded them in glycol methacrylate (JB-4 Embedding Kit from Electron Microscopy Sciences, Hatfield, PA), and sectioned them at 2 - 5 µm on a rotary microtome (Sorvall Products, Newtown, CT) fitted with a glass knife. We affixed these sections to glass microscope slides, stained them in toluidine blue or hematoxylin and eosin and examined them for evidence of reproductive maturity. We classified ovaries according to Wallace & Sellman (1981) and testes according to Nagahama (1983). We considered female fish mature with the onset of vitellogenesis, and males mature

when the testes contained visible spermatozoa. We report size at sexual maturity as the size at which a regression equation (3-parameter, sigmoidal) of percent mature individuals in each 1 mm size class versus standard length indicates 50% of individuals are mature.

Ovaries selected for batch fecundity were weighed to the nearest 0.001 g on a digital microbalance. We collected 3-4 subsamples (chosen randomly from right or left lobe of ovary) of tissue (8-15 mg each) from the anterior, middle, and posterior of the gonad and weighed these to the nearest 0.01 mg on a CAHN 28 electrobalance. For *P. multifasciatus,* A biopsy of the remaining ovarian tissue was examined histologically (see above) to verify that the ovary contained vitellogenic or mature oocytes. We estimated batch fecundity from the sub-samples using the oocyte size-frequency method (Hunter et al. 1985; MacGregor 1957), assuming the largest mode of yolked oocytes formed the next spawning batch. We used a 2-parameter power equation to describe the relationship between batch fecundity and standard length.

3. Demographic Analysis

We estimated density, and ultimately abundance by using closed-circuit rebreathers to swim two-meter-wide belt transects along a compass heading and tallying all sightings of our study species. The start and stop points of each transect were recorded on a GPS unit towed on a surface float. Our goal was to uniformly survey each area, however currents often caused us to deviate from the planned course (Figure 2). For all transects, we assume that we swam in a straight line between the actual beginning and end points.

We used laser videogrammetry to describe the size distribution of the three study species at each site (Figure 3). Here, a video camera fitted with parallel laser beams was used to capture images of individuals when they were oriented perpendicular to the laser beam axes. We then reviewed the video with Windows Movie Maker® and captured still frames where both lasers appeared on the fish.   Because the beams are parallel, the lasers superimpose a reference scale on the side of the fish, allowing length estimates by solving for equivalent ratios.   Still images were analyzed using ImageJ (National Institutes of Health). In most cases, we were able to estimate total or fork length. However on occasion, the only reliable length estimate was "body depth" (the distance between the origins of the dorsal and pelvic fins). In these cases, we used morphometric relationships to convert this measurement to total or fork length.

For each species, we estimated mean length at each site. We also used length-weight relationships to estimate mean weight at each site.

Figure 2. Sampling areas in Hanauma Bay, a no-take marine reserve (right) and Maunalua Bay, an area open to fishing (left). Yellow lines indicate site boundaries, and white lines represent transects. Image from Google Earth.
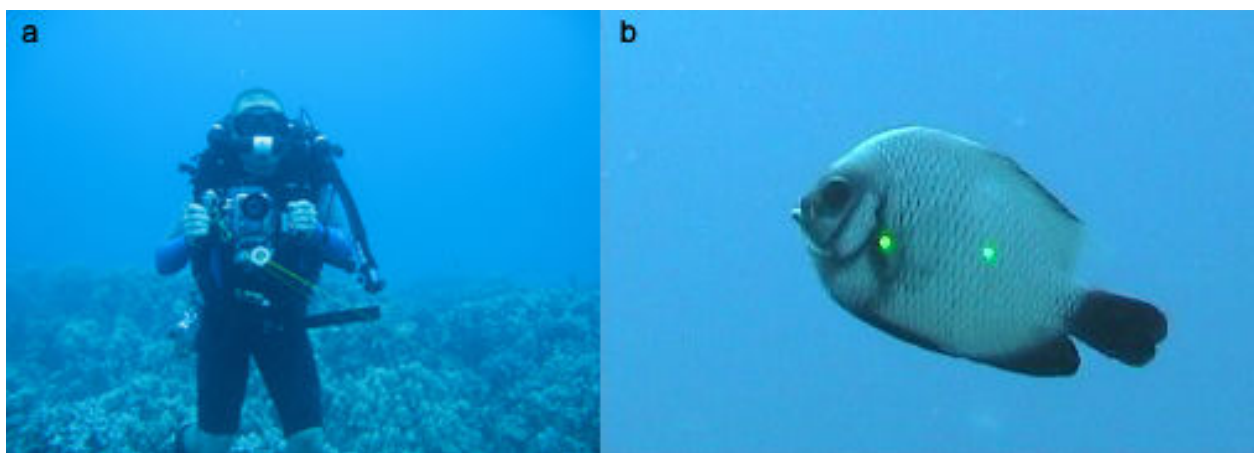

Figure 3. Laser videogrammetry, a non-destructive technique to estimate fish length. (a) a diver operates a video camera fitted with two parallel laser beams. (b) the laser beams superimpose a measurement scale on the side of *D. albisella*.

<u>Mortality</u>

We used vonBertalanffy growth equations to convert lengths to age estimates and constructed an age distribution for each species at each site. We then used regression analysis to describe the logarithm of the frequency of each age class as a function of age, and obtained total mortality (Z) from the negative slope of the line (Everhart & Youngs 1992). Because fishing is prohibited in Hanauma Bay, total mortality at this site is equivalent to natural mortality (M). At Maunalua Bay, total mortality is the sum of natural (M) and fishing mortality (F). Fishing mortality at Maunalua Bay was estimated by subtracting total mortality at Hanauma Bay from total mortality at Maunalua Bay. That is:

$$Z_{\text{Hanauma Bay}} = M$$
$$Z_{\text{Maunalua Bay}} = F + M$$

Therefore:

$$Z_{\text{Maunalua Bay}} - Z_{\text{Hanauma Bay}} = (F + M) - M = F$$

4. Production Modeling

We used vonBertalanffy growth equations, fishing and natural mortality estimates, length-weight regressions, size-at-maturity estimates, sex ratios, and size vs. batch fecundity relationships in a Ricker production model to estimate annual biomass production in kilograms and egg production per reproductive event at each site. The model was built assuming that mortality is constant over all age classes, including those smaller than used for mortality estimates. Production estimates were based on the hypothetical number of recruits (*i.e.*, frequency of the smallest age class) that would result in the estimated frequency of individuals in the smallest age class used for mortality estimates class frequency (*i.e.*, proportion of individuals in age class from videography times the estimated total population size). We then used the model to examine the effects of changing size limits and fishing pressure.

RESULTS

1. Life History Analysis

<u>Morphometric relationships</u>

We examined 195 *Centropyge potteri*, 136 *Dascyllus albisella*, and 96 *Parupeneus multifasciatus* to obtain morphometric relationships. All length-to-length relationships were linear, whereas length-weight relationships were best described by a two-parameter power function where weight was an approximately cubic function of length (

Table 1).

Table 1. Length conversions for three coral reef fishes. "TL" = the measurement used for videogrammetry analysis (total length for *C. potteri*, and fork length for *D. albisella* and *P. multifasciatus*; "BD" = the distance between dorsal and pelvic fin origins. Lengths are in mm, weight in g.

Species	"TL" to SL	"BD" to "TL"	"TL" to weight
C. potteri	SL = 0.93 + 0.79(TL)	TL = 3.41 + 2.28(BD)	Wt = $1.73 \cdot 10^{-5}$(TL)$^{3.13}$
D. albisella	SL = 1.18 + 0.78(FL)	FL = 1.38 + 1.91(BD)	Wt = $1.38 \cdot 10^{-4}$(FL)$^{2.62}$
P. multifasciatus	SL = -1.98 + 0.92(FL)	FL = 16.96 + 3.32(BD)	Wt = $4.91 \cdot 10^{-6}$(FL)$^{3.23}$

Growth

We obtained 15 readable otoliths from *Centropyge potteri*. A vonBertalanffy growth equation fitted the observed data points well (Figure 4), with the predicted asymptotic length approximating the reported maximum length of 130 mm (Randall 2007). This species appears to have a maximum life span of approximately two years. Hill & Radtke (1988) described the growth of a *Dascyllus albisella* population from Johnston Atoll using annual growth increments, reporting a maximum life span of about 12 years. We use their growth equation for subsequent analyses ($l_t = 130[1 - e^{-0.23(t+1.466)}]$). We obtained 13 readable otoliths from *Parupeneus multifasciatus*. We did not find a tight fit between a vonBertalanffy growth equation and observed data points. Rather, the growth curve ran between what appears to be two distinct data series (Figure 5). We do not know the sex of individuals from which otoliths were obtained, so cannot determine whether the species exhibits sex-specific growth rates. The predicted asymptotic length is very close to the observed maximum length of 300 mm (Randall 2007). The specimens we examined appear to have lived to a maximum of approximately two years.
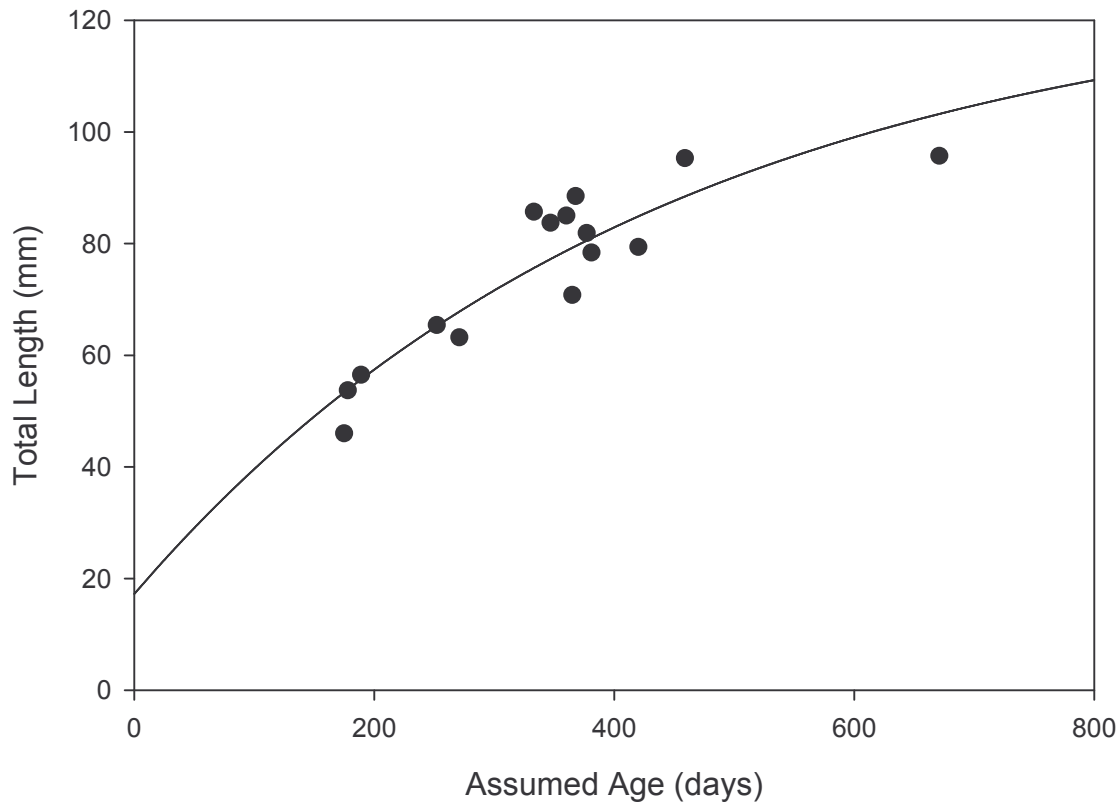
Figure 4. A scatterplot of age (assuming each otolith increment is equivalent to one day) versus total length for *Centropyge potteri*. The curve represents the resulting vonBertalanffy growth equation: $l_t = 127[1\text{-}e^{-0.00228(t+63.9)}]$.

Reproduction

Centropyge potteri has a rather complicated reproductive mode (Table 2). As protogynyous hermaphrodites (Lutnesky 1992; 1994; 1996), all males are derived from previously mature females, and the sex ratio varies by habitat, location (Lobel 1978) and body size.

We histologically examined gonads from 37 individuals to estimate size-at-maturity and sex ratio. Of these, 22 gonads were ovaries, 11 were testes, and four were ovotestes (Figure 6). Individuals with testes were significantly larger than those with ovaries (T-test, $p<0.05$), but did not differ significantly with those with ovotestes. Based on our analysis, fifty percent of individuals (as 100% females) mature at 54 mm TL. One-hundred percent of individuals between 54 and 67 mm TL are female, and the sex ratio between 68 and 89 mm can be described by the equation:

$$\% \text{ Females} = 405.5 - 4.439(TL)$$

One-hundred percent of individuals over 89 mm TL are male, with 50% of males maturing at 84 mm.
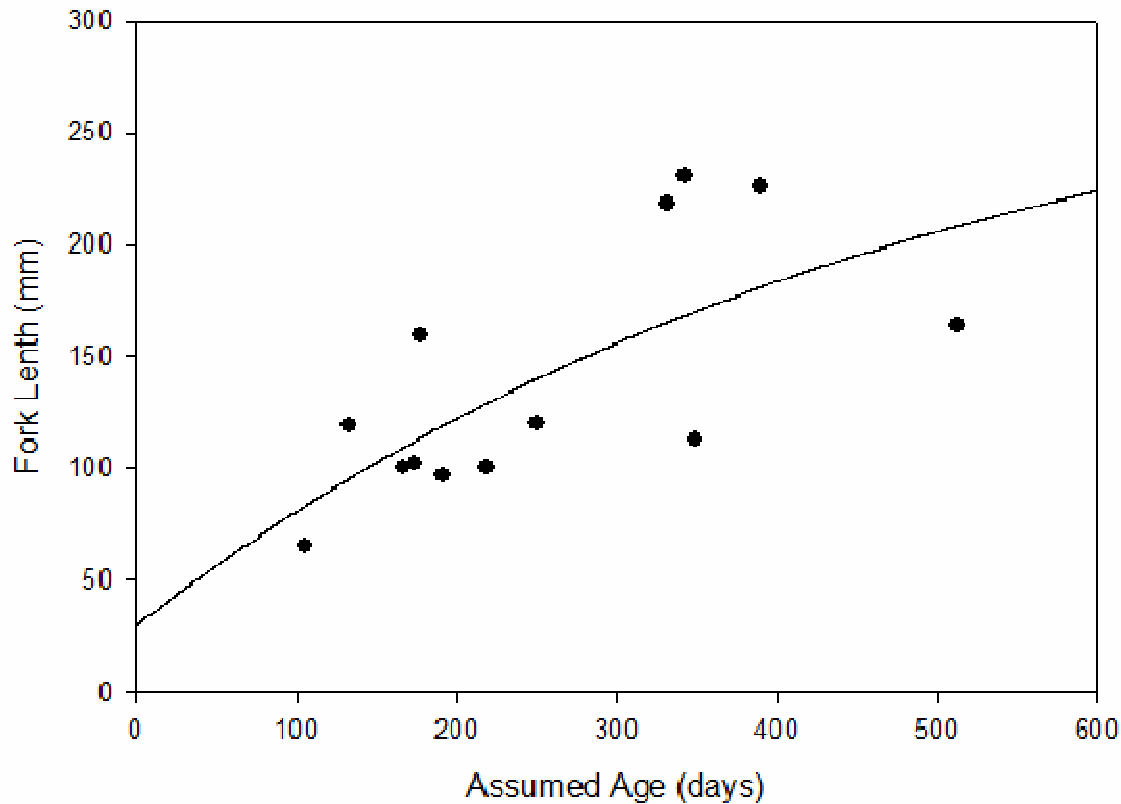

Figure 5. A scatterplot of age (assuming each otolith increment is equivalent to one day) versus total length for *Parupeneus multifasciatus*. The curve represents the resulting vonBertalanffy growth equation: $l_t = 303[1-e^{-0.00207(t+49.4)}]$.

Nine *C. potteri* ovaries were deemed appropriate for batch fecundity analysis. The largest size-mode of non-hydrated yolked (vitellogenic) oocytes ranged from 437.5-525 µm (mean 479 µm) which correspond to late vitellogenesis and final maturation (Collier et al. 2001). One individual contained hydrated oocytes (512-662 µm, mean 568); however, these were not included in the estimate as several had already been ovulated. Estimated fecundity ranged from 270 (for a 57 mm female) to 1,056 (75 mm female) eggs per spawn and is described by a power function (Table 2).

Reproduction in the polygynous *Dascyllus albisella* has been studied extensively, and we use existing information for subsequent analyses. Asoh et al. (2001) report that the Hawaiian domino damselfish is a non-functional protogynous hermaphrodite: all males begin life with ovarian tissue but never shed eggs. Males mature at a larger size than females (Asoh et al. 2001), and the proportion of females in any given size class varies, but averages 62% (Stevenson 1963). Spawning occurs year-round, with peak activity from June and September (Danilowicz

1995). During this period, individual females spawn every 8.3-8.4 days, on average (Asoh 2003). Remarkably, batch fecundity is a function of length raised to the seventh power (Stevenson 1963). Data from Asoh et al. 2001 suggest the percent of females in a size class can be described by the equation:

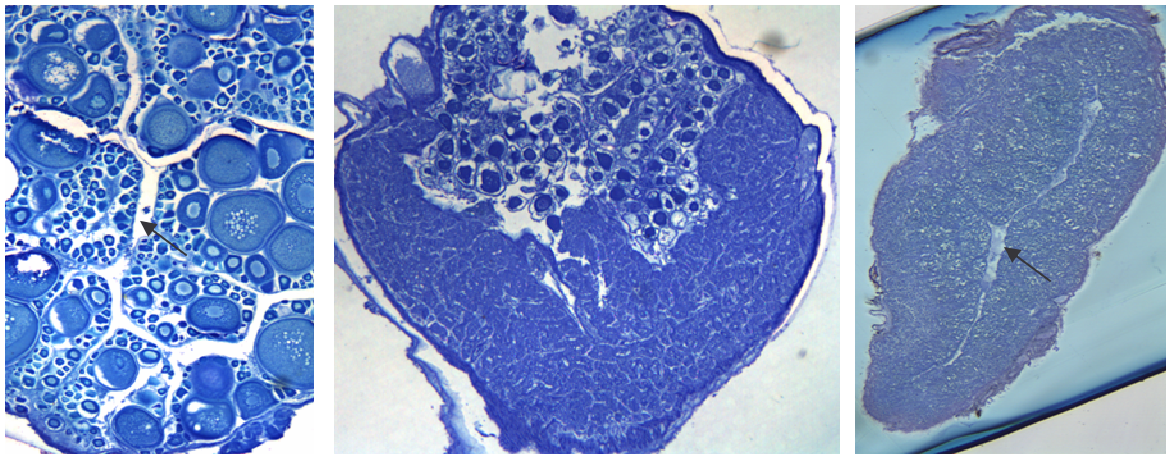$$\% \text{ Females} = 109.2 - 0.5349(FL)$$

Figure 6. Histological sections of *C. potteri* gonads (*Toluidine Blue*). Ovaries (left) consisted of parallel lamellae surrounding a central lumen (arrow). Several oocyte stages were present in reproductively active females indicating that this species has group-synchronous oocyte development. Ovotestes (center) consisted of mixed ovarian and testicular tissue and indicate individuals in transition from female to male. Individuals with ovotestes were considered males if the testicular portion contained visible spermatozoa and females if they contained vitellogenic oocytes. Testes (right) consisted of lobules or spermatogenic tissue. Several testes retained a non-functional lumen (arrow) suggesting that they had been derived secondarily from ovaries.

We could find little published information on the reproductive biology of the goatfish *Parupeneus multifasciatus*. Lobel (1978) observed spawning of *P. multifasciatus* in March, two days before the full moon, and briefly described spawning behavior. The Hawaii Division of Aquatic Resources reports the size at maturity to be 7.3 inches (185 mm FL) and has instituted a legal catch size of 7 inches (178 mm FL).

We histologically examined gonads from 50 individuals, of which 20 were ovaries and 30 were testes (Figure 7). As with *C. potteri* males were significantly larger than females (T-test $p<0.05$), although we found no histological evidence of hermaphroditism. This leaves the possibility that the size differences may instead reflect differences in growth rates between the sexes. The size at which 50% of individuals are mature also differs between sexes, with males maturing at a larger size than females (Table 2). Further, sex ratio varies in a predictable way throughout the reproductive size range of the species and can be described by the equation:

$$\% \text{ Females} = 141.3 - 0.6167(FL)$$

One-hundred percent of individuals larger than 225 mm FL are male.

Of the 20 ovaries we examined, only five contained late stage III (vitellogenic) or stage IV (mature) oocytes. Four of these individuals were collected between months of March to July and the fifth collected in November. Four of the five ovaries were deemed suitable for batch fecundity analysis. In these individuals, the largest size mode of oocytes ranged from 285-390 μm (mean 340 μm). Histological sections taken from the same ovaries indicate that these corresponded to stage IV (maturation) of Wallace and Selman (1981). Ovulated oocytes, found
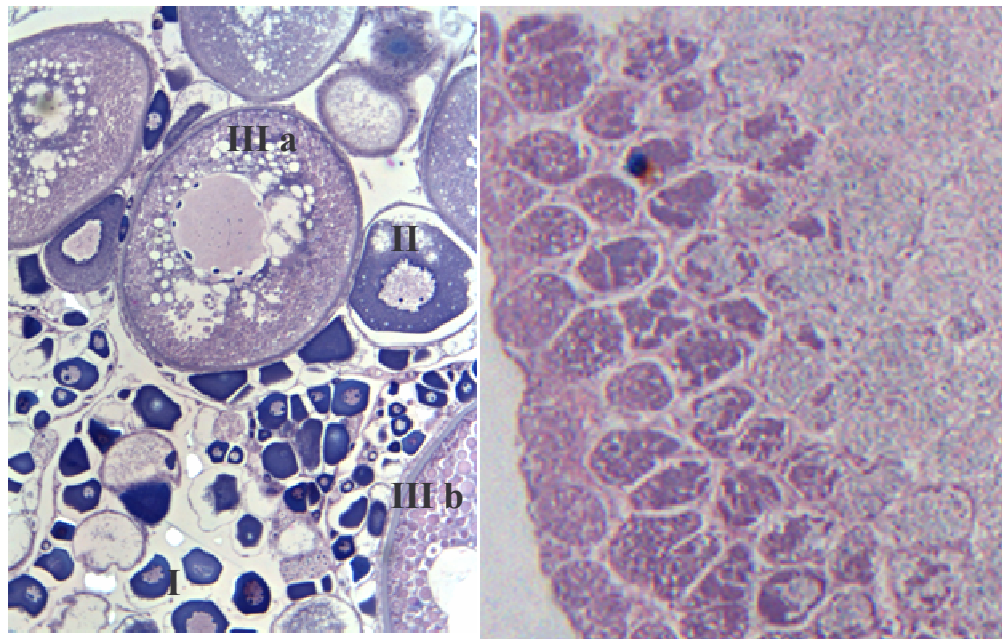

Figure 7. Histological sections of *P. multifasciatus* gonads *(Hematoxylin & Eosin)*. Ovaries of mature females (left) contained several stages including primary growth (I) cortical vesicle stage (II) early (III A) and late (III B) vitellogenesis, and maturation (not shown). Testes (right) were lobular and lacked an internal lumen.

in the ovarian lumen of one specimen, ranged from 330 to 450 μm in diameter (mean 389 μm). Together these data support the use of the above size class to estimate batch fecundity in this species. Estimated fecundity of *P. multifasciatus* ranged from 5,479 (155 mm specimen) to 21,530 (193 mm specimen). The latter was estimated from a museum specimen in which the ovary was ruptured during removal and thus may be inaccurate estimate. Due to the low number of samples, we could not generate a size-fecundity curve necessary for the production model. Instead, we used a curve for *P. ciliatus* (El-Agamy 1990), a similar-sized goatfish from Qatar. Figure 12 shows the fecundity estimates from the four individuals of *P. multifasciatus* along with the curve for *P. ciliatus*.

Demographic Analysis

We conducted 17 transects covering a total 13,520 m^2 in Hanauma Bay, whereas 23 transects covering a total 12,816 m^2 were conducted in Maunalua Bay. Of the three target species, we

recorded a total 585 fish. In Hanauma Bay we saw 48 *C. potteri*, 13 *D. albisella*, and 162 *P. multifasciatus*. In Maunalua Bay we saw 44 *C. potteri*, 74 *D. albisella*, and 244 *P. multifasciatus*. Estimates of density and abundance at each site are presented in
Table **3**. Of the three study species, only *Centropyge potteri* occurs in higher numbers in the no-take marine reserve (Hanauma Bay). A Mann-Whitney test on weighted densities of this species indicates that values are significantly different.

Table 2. Reproductive parameters for three reef fish species. L_{50} equals the size at which 50% of a given size class are mature. TL = total length; FL = fork length. Batch fecundity estimates are based on lengths in mm.

Species	Female L_{50}	Male L_{50}	Sex Ratio	Batch Fecundity[1]
C. potteri	54 mm TL	84 mm TL	varies predictably	# Eggs = $0.0118(TL)^{2.596}$
D. albisella	63 mm FL[2]	95 mm FL[2]	varies predictably[2]	# Eggs = $4.48 \cdot 10^{-11}(FL)^{7.134}$
P. multifasciatus	145 mm FL	152 mm FL	varies predictably	# Eggs = $0.0018(FL)^{3.092}$

(1) Results for *D. albisella* adapted from Stevenson 1963. (2) Adapted from Asoh et al, 2001.

Regression analysis of fish length estimated from laser videogrammetry versus actual fish length indicates a nearly 1:1 relationship throughout the size range of fish we captured on video during this study. Further, the prediction interval suggests 95% of our estimates will be within 0.5 cm of the actual fish length (Figure 8).

We captured on video a total 419 fishes suitable for size estimation. In Hanauma Bay we recorded 25 *C. potteri*, 9 *D. albisella*, and 126 *P. multifasciatus*. In Maunalua Bay we recorded 44 *C. potteri*, 65 *D. albisella*, and 150 *P. multifasciatus*. The information generated by laser videogrammetry allowed estimates of average lengths and weights at each site (
Table **3**). Again, only values for *Centropyge potteri* were higher in the no-take marine reserve (Hanauma Bay). T-tests indicate that average length and weight for *C. potteri* are significantly higher in the reserve area.

Mortality plots are presented in Figure 9–Figure 11, and estimates of total, natural, and fishing mortality are presented in
Table **3**. Sample size for *Centropyge potteri* was low, and resulting mortality estimates should be viewed with caution. However, as expected, we did find that total mortality in the no-take marine reserve (Hanauma Bay) was lower than that in the area open to ornamental collecting (Maunalua Bay), thus allowing fishery-independent estimation of fishing mortality. Sample size for *Dascyllus albisella* in the no-take marine reserve (Hanauma Bay) was too low to generate a mortality curve. Although total mortality was estimated for the open site (Maunalua Bay), lack of a natural mortality estimate prevented the generation of a fishing mortality estimate. Sample size for *Parupeneus multifasciatus* was suitably high for mortality estimates. However, contrary to expectation, total mortality in the no-take reserve

(Hanauma Bay) was higher than total mortality in the open site (Maunalua Bay). Calculation of a fishing mortality estimate would have resulted in a negative value (-0.1413), an unrealistic value for a site where fishing is known to occur.

Table 3. Estimates of density, abundance, length and weight (±SD) for three species in a no-take marine reserve (Hanauma Bay) and a fished area (Maunalua Bay). TL = total length, FL = fork length.

| Species	Estimate	Haunama Bay	Maunalua Bay
C. potteri			
	Density (m^{-2})	0.00355(0.00743)	0.00328(0.00538)
	Abundance (n)	1351	1247
	Mean TL (mm)	84.3(12.1)	70.0(12.8)
	Mean Weight (g)	19.3(8.0)	11.2(6.6)
D. albisella			
	Density (m^{-2})	0.00096(0.00253)	0.00577(0.01659)
	Abundance (n)	366	2198
	Mean FL (mm)	97.5(13.6)	102.0(18.3)
	Mean Weight (g)	30.7(9.5)	35.4(14.8)
P. multifasciatus			
	Density (m^{-2})	0.01198(0.00627)	0.01904(0.03532)
	Abundance (n)	4560	7246
	Mean FL (mm)	138.7(32.1)	148.9(35.6)
	Mean Weight (g)	49.3(40.5)	62.8(53.3)
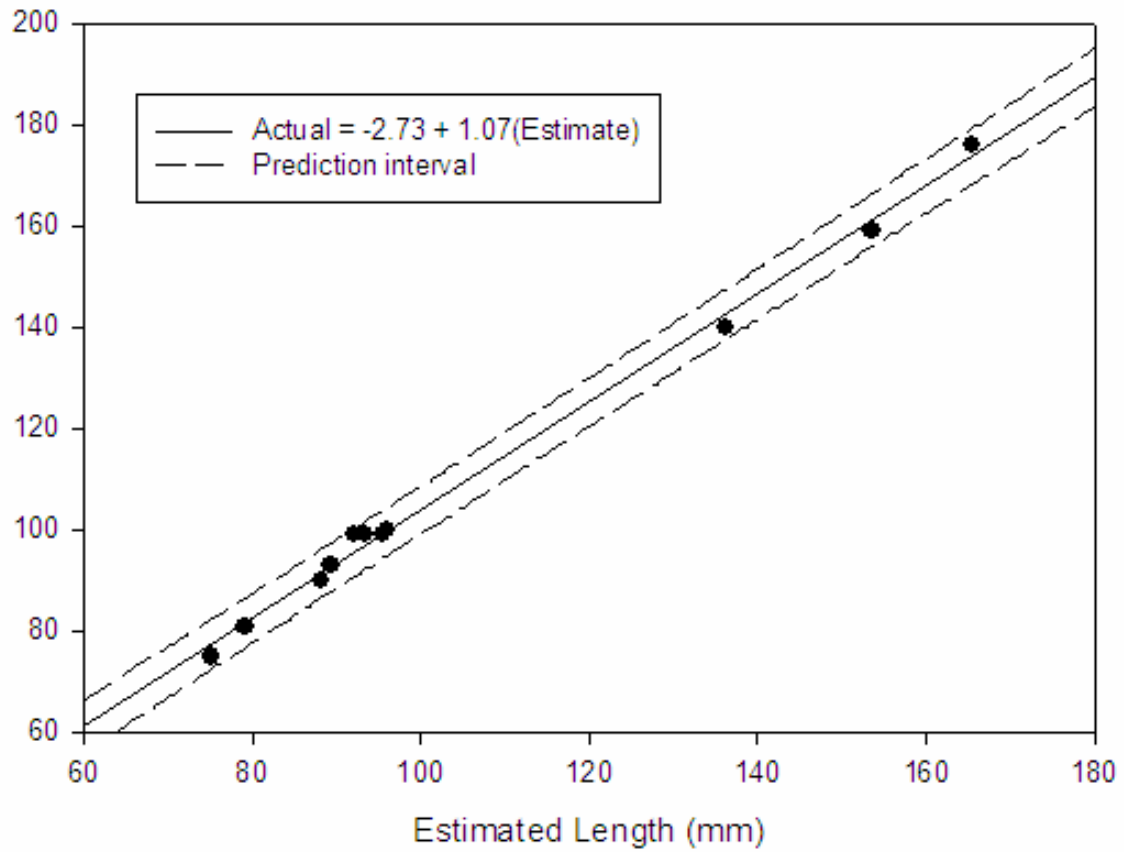
Figure 8. The relationship between estimated and actual lengths of specimens "captured" on videotape for laser videogrammetry and subsequently speared. The prediction interval suggests that 95% of length estimates will be within 0.5 cm of actual fish length.
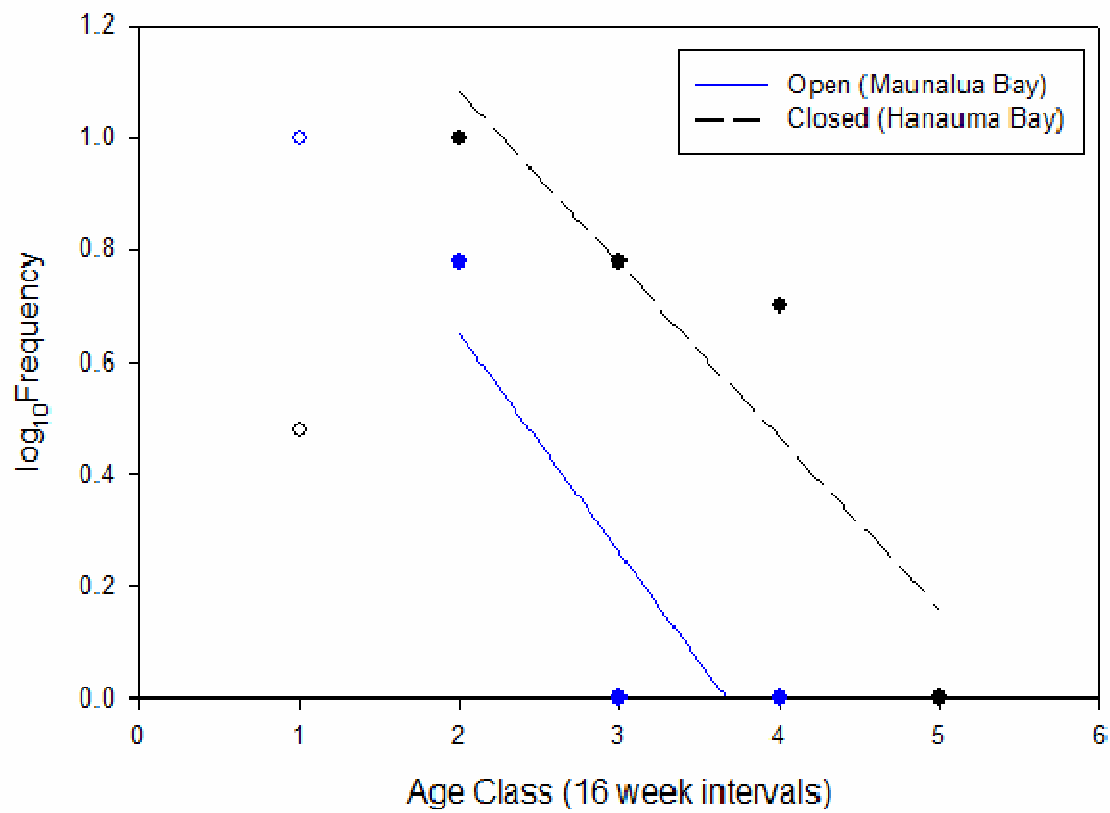
Figure 9. Mortality plots for *Centropyge potteri*. Age Class 1 is composed of fishes 28 – 45 weeks old, only data represented by filled circles were used for regression analysis.
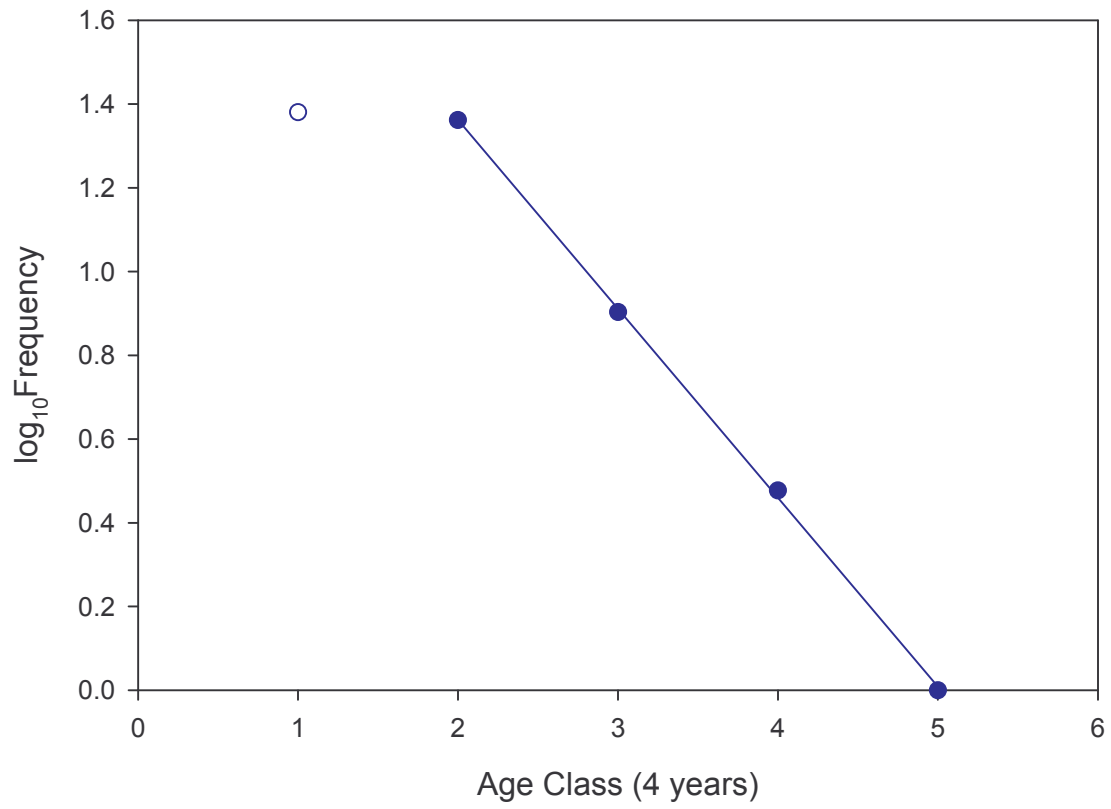
Figure 10. Mortality plot for *Dascyllus albisella* in Maunalua Bay, open to fishing. Due to low sample size, a plot could not be constructed for Hanauma Bay, a no-take marine reserve. Age Class 1 is composed of fishes 1 – 4 years old, only data represented by filled circles were used for regression analysis.
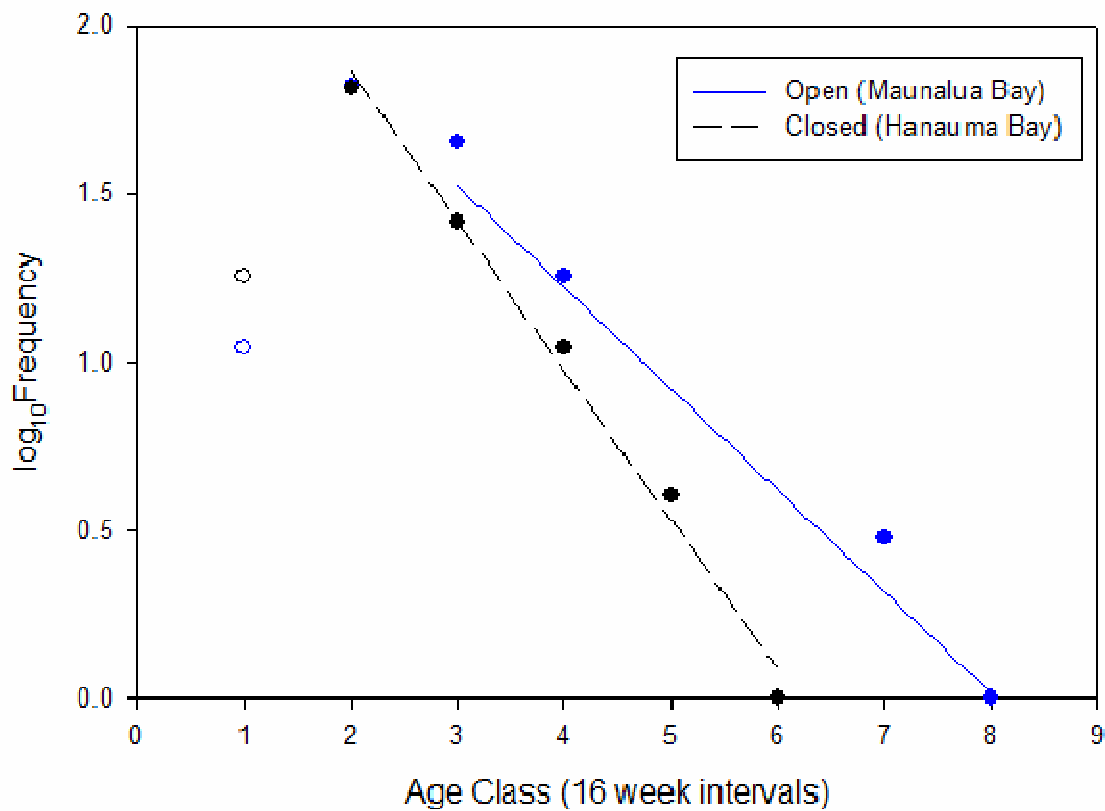
Figure 11. Mortality plots for *Parupeneus multifasciatus*. Age Class 1 is composed of fishes 7 – 22 weeks old. This species has a size limit of 178 mm FL, fishes can legally be caught beginning at Age Class 3, only data represented by filled circles were used for regression analysis.

Table 4. Mortality estimates for three reef fish species. Fishing mortality could not be determined for *D. albisella* due to low sample size in the no-take marine reserve (Hanauma Bay), or for *P. multifasciatus* because total mortality appeared to be lower in the open area (Maunalua Bay), which would have resulted in negative fishing mortality.

Species	Interval	$Z_{Hanauma}$ (= M)	$Z_{Maunalua}$ (=F+M)	F
C. potteri	16 wk	0.3079	0.3891	0.0812
D. albisella	4 yr	--------	0.4511	--------
P. multifasciatus	16 wk	0.4439	0.3025	--------

2. Production Modeling

The size-fecundity relationship for *Parupeneus multifasciatus* presented in Table 2 is based on a low sample size. We opted to use a relationship for a congener (El-Agamy 1990), which may systematically overestimate reproductive output (Figure 12). Production values under current mortality estimates are presented in Table 5. Sites could not be compared for *Dascyllus albisella* because too few individuals were observed in the no-take reserve to allow mortality estimates. Values for number (the unit of concern for ornamental collectors), biomass, and egg production are all higher in the no-take reserve for *Centropyge potteri*. Values for *Parupeneus multifasciatus* show the opposite pattern. Biomass (the unit of concern to fishers) and egg production were lower in the no-take reserve.

Figure 13 provides a visualization of one modeling effort predicting the effects of imposing various size limits on the *Centropyge potteri* fishery, but holding fishing mortality at current levels. Additional models, also investigating the effects of size limits, but with increased fishing pressure were also built. These suggested that both yield in numbers and reproductive output can be increased if individuals below 90 mm TL are not collected. Models for *D. albisella* and *P. multifasciatus* could not be constructed due to lack of natural mortality estimates and counter intuitively low fishing mortality estimates, respectively.
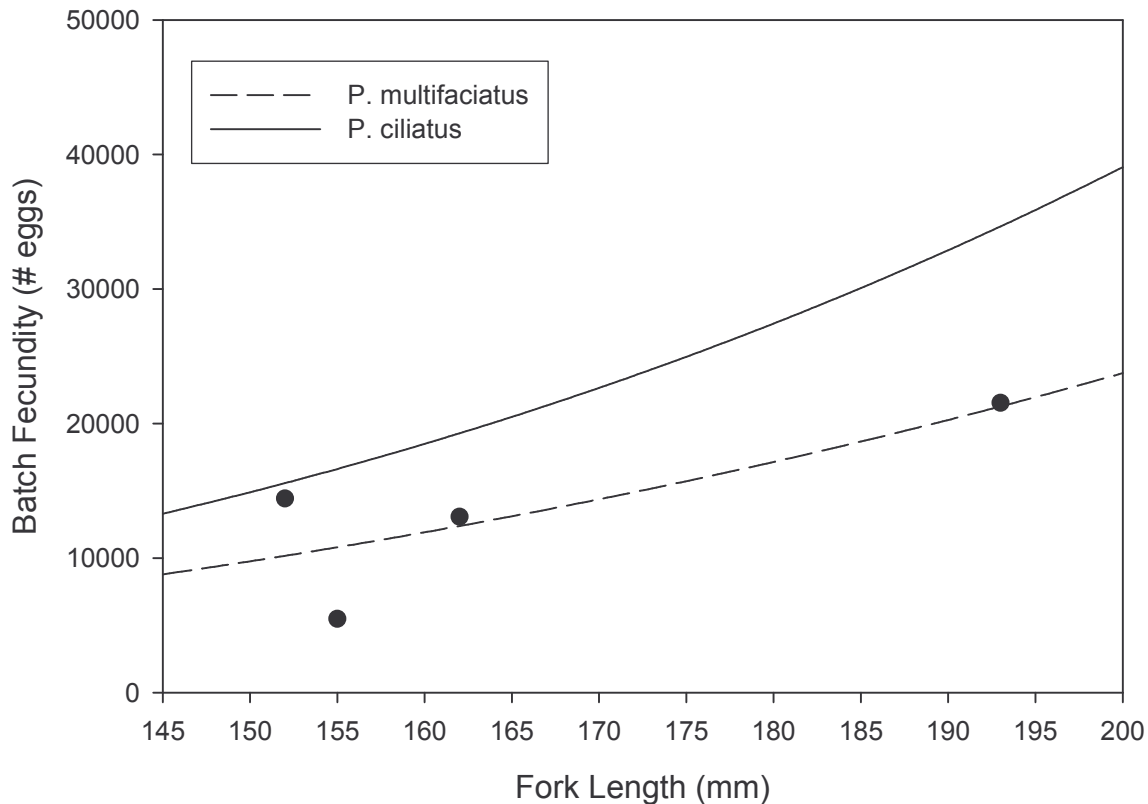

Figure 12. A comparison of relationships between length and batch fecundity for *P. multifasciatus* and *P. ciliatus*. Because few gravid females were obtained during this study, we used the *P. ciliatus* relationship (adapted from El-Agamy 1990) for production modeling.

Table 5 Production estimates for three species in a no-take marine reserve (Hanauma Bay) and a fished area (Maunalua Bay). Egg production estimates assume each mature female spawns a single time (*i.e.*, values do not reflect spawning frequency).

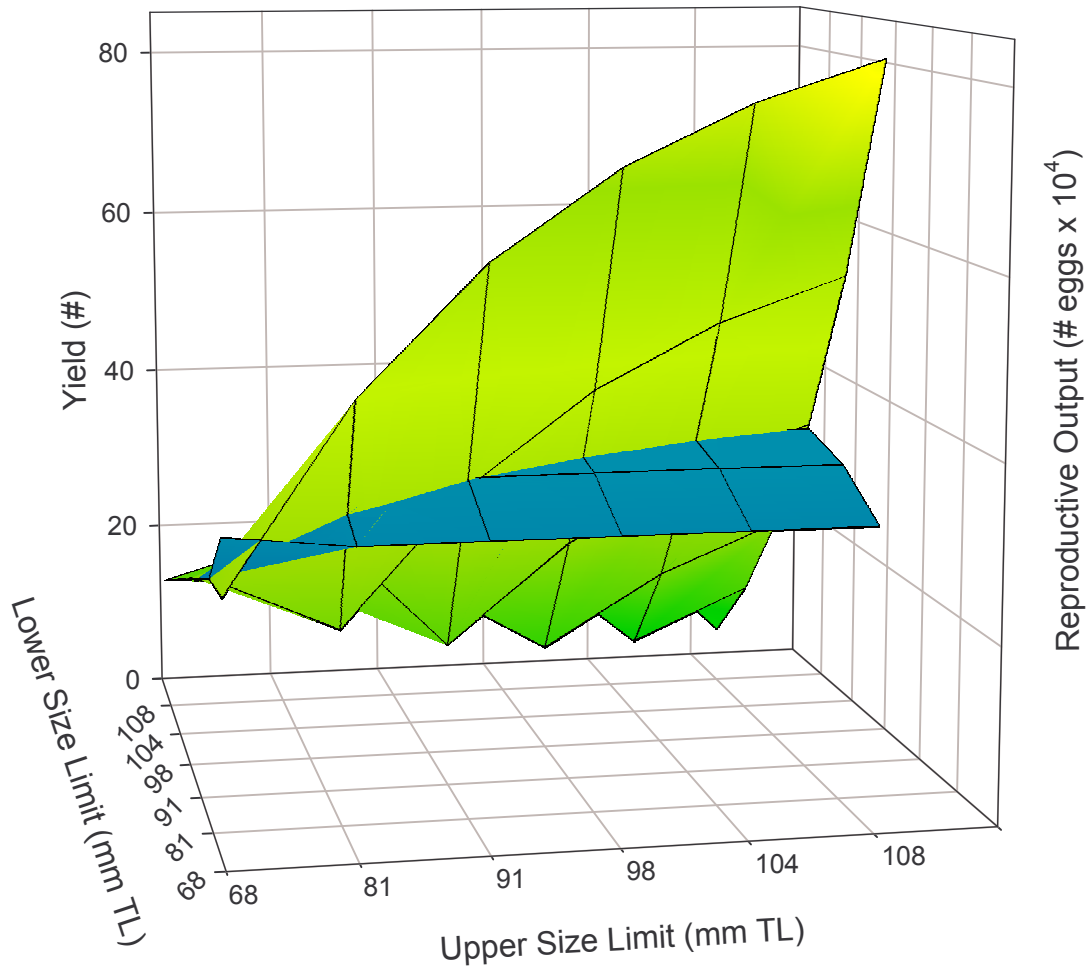| Species	Estimate	Hanauma Bay	Maunalua Bay
C. potteri			
	n	3149	1024
	kg	64.6	19.7
	# eggs	1,024,873	337,474
D. albisella			
	n	---------	2971
	kg	---------	104.5
	# eggs	---------	3,532,421
P. multifasciatus			
	kg	959.6	2,656.8
	# eggs	24,290,147	44,938,763

Figure 13. Yield (in green) versus reproductive output (in blue) as a function of size limits for *Centropyge potteri* in a fished area with constant fishing mortality. The leading edge of each plot corresponds to the smallest size of entry into the fishery, in this case 68 mm. Each plot then fades back from the reader, with each more or less horizontal line representing larger sizes. The relatively vertical lines represent the upper size limit. Estimated yield and reproductive output under current fishing pressure, in this case fishing mortality of 0.0812 from 68 through 108 mm, is indicated by the upper right point on the yield plot (83 individuals per cohort) and the lower right of the reproductive output plot (337,474 eggs when each female in a cohort reproduces once per size class).

DISCUSSION

The overarching goal of this project was to demonstrate that the life history and demographic information necessary to evaluate fishery management strategies can be obtained quickly and inexpensively. We attempted to do so by generating data and modeling production for three common reef fish species. The results presented above were accomplished in a single person-year. Importantly, this time period includes project initiation and the setbacks associated with

almost any new line of research. We think this project should provide strong motivation for continued research on the life history and population structure of Hawaii's exploited reef fishes, most of which are poorly understood.

Despite the quantity of information generated in a single year, we suspect that in many cases the quality could have been improved with larger sample sizes and a broader geographic focus. Several examples deserve mention.

Although we attempted to chemically marking otoliths, we were not able to validate the periodicity of increment formation in *Centropyge potteri* or *Parupeneus multifasciatus*. In both cases, we assumed the increments we observed were formed on a daily basis. The growth curve we generated for *C. potteri* fitted observed data quite well, but the curve for *P. multifasciatus* did not. In the latter case, the vonBertalanffy growth curve ran through the middle of what appeared to be two distinct growth trajectories (Figure 5). We observed sex-based size differences in this goatfish, as did Randall (2004), but found no histological evidence that the species is hermaphroditic. These results suggest the possibility of sex-specific growth rates for *P. multifasciatus*. Unfortunately, we do not know the sex of individuals that were used in our growth analysis. Further research is warranted and has the potential to alter apparent mortality rates.

Mortality estimates for all species were based on the assumptions of constant survival and constant recruitment. These assumptions cannot be evaluated without larger sample size and/or a longer study period. Regardless of whether the assumptions are valid, small sample size is reason for concern about *Centropyge potteri* mortality estimates. Mortality plots with few age classes can be profoundly influenced by the presence of one or a few individuals in the largest age class(es), thus mortality estimates for *C. potteri* are likely in need of revision. The same applies to *Dascyllus albisella*, for which numbers in Hanauma Bay were too low to generate a preliminary mortality estimate. Results for *Parupeneus multifasciatus* were counterintuitive, with mortality appearing higher in a no-take marine reserve (Hanauma Bay) than at a popular fishing site (Maunalua Bay). Including more sites in videogrammetry survey efforts could alter these values such that fishery independent estimates of fishing mortality can be obtained and would certainly provide more confidence in the broader applicability of the results.

Finally, we attempted to model reproductive output at all sites by incorporating size-at-maturity data, variable sex-ratios, and length-batch fecundity relationship into a Ricker production model. Despite intensive sampling for gravid *Parupeneus multifasciatus*, we collected too few specimens for a reliable length-fecundity regression. We opted to use a published fecundity equation (El-Agamy 1990) for a congener. This relationship approximated the observed data distribution for *P. multifasciatus*, but may have systematically overestimated egg production. The reproductive output estimates we present assume each mature female spawns only once per age class. This is certainly incorrect because spawning occurs from December to May for *C. potteri* (Lobel 1978; Collier et al. 2003), and year-round for *D. albisella*, with individual females spawn every 8.3 - 8.4 days (Asoh 2003) during a peak from June and September (Danilowicz 1995). Actual reproductive output is likely to be higher than estimated, and apparent differences in site-specific values may change dramatically if spawning periodicity varies by location.

Given the above caveats, we compared estimated production values in an attempt to better understand the fishery enhancement potential of a variety of management techniques. The following discussion should be viewed with appropriate caution.

No-take marine reserves are often promoted as fishery enhancement tools (Russ & Alcala 1996; Roberts 1997; Roberts & Sargant 2002; Russ et al. 2004; Gaylord et al. 2005; Roberts et al. 2005; Friedlander et al. 2007). Although no-take reserves do have some undisputed fishery management value (*e.g.*, overexploitation cannot occur in the absence of fishing), whether they can enhance a fishery, defined here as total fish catch above pre-reserve levels, remains a matter of some contention (Hilborn 2007). Remarkably, very few empirical analyses of the latter question exist, and results are often contradictory (Willis et al. 2003; Sale et al. 2005).

At the center of this debate is whether to-take reserves can compensate for lost fishing habitat. Imagine a simple example where fishing occurs in a well-defined area and the exploited population is uniformly distributed. If half of this fishing ground is converted to a no-take marine reserve, the number of catchable fish has suddenly been halved. To compensate for the lost fishing ground, production in the reserve must double that of baseline values and all production increase must be exported to the fishable habitat. If either of these events does not occur, a reserve cannot enhance fish catch.

We were able to estimate production in terms of biomass, # of individuals (depending on the unit of interest to fishers) and eggs in a no-take marine reserve and a nearby fished area for two exploited reef fishes. We believe this is the first time production estimates have been used to evaluate the fishery enhancement potential of a no-take reserve. We emphasize that we did not determine whether export (or spillover) occurs. We simply evaluated whether enough raw material was produced inside the reserve to increase total fish catch *if 100% of "excess" production is exported*. We also emphasize that this analysis assumes our study sites originally held identical populations.

Our results varied between species. *Centropyge potteri* appears to produce three times more biomass, individuals, and eggs in the no-take reserve than in the fished area. Based on our argument, above, it appears that enough raw material is produced to enhance a fishery in an equal-sized adjacent area. We reiterate that spillover rates of settled individuals and eggs/larvae must be determined before final conclusions are drawn. The *Parupeneus multifasciatus* population in the no-take reserve appears to produce half the biomass and eggs of that in the fished area, suggesting that the fishery for this species is not enhanced. The production values for *P. multifasciatus* appear to be driven by low abundance and high mortality in the no-take reserve. Speculation on the cause(s) of these trends is not warranted until more robust estimates are obtained.

Low sample size prevented us from estimating mortality for *Dascyllus albisella* in the no-take reserve, and unexpectedly high estimates of mortality for *Parupeneus multifasciatus* in the no-take reserve prevented an estimate of fishing mortality. Because of these difficulties, we could not model the effects of changing size limits or fishing pressure for these species. We were able to model changes in yield (as individuals, the measurement of concern to ornamental collectors) and reproductive output with changing size limits and fishing mortality for *Centropyge potteri*.

Current fishing effort in Maunalua Bay, based on our mortality estimates, appears to result in the removal of 83 fish per cohort or 8% of individuals. Our static reproductive output estimates suggest that 337,473 eggs are released per population-level reproductive event. Importantly, we estimate that 46% of the population is female (This estimate assumes the sex-ratio vs size relationship generated for Kaneohe Bay is applicable to the Maunalua and Hanauma Bay populations. Although the L_{50} for females is probably developmentally fixed, sex change could occur at different sizes in different habitats). This value is a large deviation from the average of ~75% females reported by Lobel (1978). This difference may be driven by fishing because small individuals are targeted in the aquarium trade (Ogawa & Brown 2001). Because *C. potteri* is a protogynous hermaphrodite, this practice removes a disproportionate number of females from the population.

Interestingly, our analyses suggest that targeting large individuals (which are assumed to be almost exclusively male) would result in increased yield, increased egg production, and a sex ratio closer to the species average. For instance, if no fishing occurs up to 91 mm SL, all females in the population would have the chance to reproduce and change sex. This results in maximum production of 395,184 eggs (an increase of 17%), the exact number that would be produced if no collecting occurred. Heavier collecting effort can be directed toward the larger size classes. An additional 50% fishing mortality on the size classes $\geq$ 91 mm TL (equivalent to collecting 16% of the population) results in an 89% increase in yield. This scenario would also drive the sex ratio of this population toward the species average, we predict 65% of individuals would be female under this scenario.

Although we could not model yield under various management regimes for *Parupeneus multifasciatus*, the above discussion indicates that management can capitalize on reproductive patterns. Interestingly, the current size limit for *P. multifasciatus* appears to confer disproportionate protection to females, which mature at 145 mm FL. These cannot be harvested until they reach 178 mm, at which point only 31% of the population is female. Thus current regulations appear to promote high population-level reproductive output.

Providing they are based on sound scientific data, species-based management approaches, as outlined in the last two paragraphs, have the added benefit of protecting exploited fish populations over a broad geographic area. This simple but important part of life-history-based management practices should not be overlooked when evaluating the relative merits of fishery management techniques.

MANAGEMENT CONSIDERATIONS

(1) Laser videogrammetry allows size estimates with the accuracy and precision needed to evaluate fishery management techniques for smaller-bodied reef fishes, many of which are exploited in Hawaii. Importantly, the technique provides an archival record of natural populations, and images of numerous species can be captured during the same transect.

(2) By employing laser videogrammetry, no-take marine reserves have incredible scientific value in allowing the fishery independent estimation of fishing and natural mortality.

Mortality values may be site specific, and a larger number of site comparisons than conducted in this study should be completed before final conclusions are drawn.

(3) Given the warning in (2), it appears that the fishery enhancement value of no-take marine reserves varies between species. More species-specific research is needed.

(4) The research advised in (3) also provides a basis for modeling life-history-based management strategies. As such, it should result in a win-win situation for fishery management.

(5) Each of the species studied here has somewhat complicated reproductive patterns. These should be considered when modeling fishery production. For *Centropyge potteri*, establishing a minimum size of ~9 cm would result in maximum population-level reproductive output, while allowing increased collecting effort and yield in terms of numbers of individuals.

(6) Species-specific management strategies have a far wider geographic impact than site-based management strategies.

ACKNOWLEDGMENTS

REFERENCES

Asoh, K., Yoshikawa, T. & M. Kasuya. 2001. Gonadal development and non-functional protogyny in a coral-reef damselfish, *Dascyllus albisella* Gill. Journal of Fish Biololgy 58:1601-1616.

Asoh, K. 2003 reproductive parameters of female Hawaiian damselfish *Dascyllus albisella* with comparison to other tropical and subtropical damselfishes. Marine Biology 143:803-810.

Collier, J.T., T. Kaneko, T. Hirano, and E.G. Grau. 2003. Seasonal changes in reproductive activity in the Potter's angelfish (*Centropyge potteri*) in Kaneohe Bay, Hawaii. Environmental Biology of Fishes 68:49-57.

Dannilowicz, B.S. 1995. Spatial patterns of spawning in the coral reef damselfish *Dascyllus albisella*. Marine Biology 122:145-155.

El-Agamy, A.E. 1990. On the fecundity of the goatfish *Parupeneus pleurotaenia* Playfair. Journal of the Marine Boilogicl Association of India 32:85-89.

Everhart, W., & W. Youngs. 1992. Principles of fishery science. Ithaca, Comstock.

Friedlander, A.M., E.K. Brown & M.E. Monaco. 2007. Coupling ecology and GIS to evaluate efficacy of marine protected areas in Hawaii. Ecological Applications 17:715-730.

Gaylord, B., S.D. Gaines, D.A. Siegel & M.H. Carr. 2005. Marine reserves exploit population structure and life history in potentially improving fisheries yields. Ecological Applications 15:2180-2191.

Hilborn, R. 2007. Moving to sustainability by learning from successful fisheries. Ambio 36:296-303.

Hill, K.T., & R. L. Radtke. 1988. Gerotological studies of the damselfish *Dascyllus albisella*. Bulletin of Maring Science 42:424-434.

Hunter , J.R., N.C.H. Lo, and R.J.H. Leong. 1985. Batch fecundity in multiple spawning fishes. NOAA Technical Report NMFS 36:67-77.

Lobel, P.S. 1978. Diel, lunar, and seasonal periodicity in the reproductive behavior of the pomacanthid fish, *Centropyge potteri*, and some other reef fishes in Hawaii. Pacific Science 32: 193-207.

Lutnesky, .M. F. 1992. Behavioral ecology of reproduction in the pomacanthid angelfish, *Centropyge potteri*. PhD. dissertation, University of Hawaii at Manoa, Honolulu. 155 pp.

Lutnesky, .M. F. 1994. Density-dependent protogynous sex change in territorial-haremic fishes: models and evidence. Behavioral Ecology 5:375-383.

Lutnesky, .M. F. 1996. Size-dependent rate of protogynous sex change in the pomacanthid angelfish, *Centropyge potteri*. Copeia 1996:212-216.

Longenecker, K., & R.C. Langston. 2006. Life History Characteristics of a Small Cardinalfish, *Ostorhinchus rubrimacula* (Percoidei: Apogonidae), from Koro, Fiji. Pacific Science 60:223–231.

MacGregor, J.S. 1957. Fecundity of the Pacific sardine (*Sardinops caerulea*). Fishery Bulletin 57:427-449.

Meyer, C.G. 2003. An empirical evaluation of the design and function of a small marine reserve (Waikiki Marine Life Conservation District) PhD dissertation. University of Hawaii at Manoa, Honolulu. 134 pp.

Nagahama, Y. 1983. The functional morphology of teleost gonads. Fish Physiology, Academic Press. IXA: 223-275.

Ogawa,T., & C.L. Brown. 2001. Ornamental reef fish aquaculture and collection in Hawaii. Aquarium Sciences and Conservation 3:151-169.

Randall, J.E. 2004. Revision of the goatfish genus *Parupeneus* (Perciformes: Mullidae), with descriptions of two new species. Indo-Pacific Fishes 36:1-64.

Randall, J.E. 2007. Reef and shore fishes of the Hawaiian Islands. Sea Grant College Program. University of Hawaii, Honolulu. 546 pp.

Roberts, C.M. 1997. Ecological advice for the global fisheries crisis. Trends in Ecology and Evolution 12:35-38.

Roberts, C.M., & H. Sargant. 2002. Fishery benefits of fully protected marine reserves: why habitat and behavior are important. 15:487-507.

Roberts, C.M., J.P. Hawkins & F.R. Gell. 2005. The role of marine reserves in achieving sustainable fisheries. Philosophical Transactions of the Royal Society B 360:123-132.

Russ, G.R., & A.C. Alcala. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Marine Ecology Progress Series 132:1-9.

Russ, G.R., A.C. Alcala, A.P. Maypa, H.P. Calumpong, & A.T. White. 2004. Marine reserve benefits local fisheries. Ecological Applications 14:597-606.

Sale, P.F., R.K. Cowen, B.S. Danilowicz, G.P. Jones, J.P. Kritzer, K.C. Lindeman, S. Planes, N.V.C. Polunin, G.R. Russ, Y.J. Sadovy, & R.S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution 20:74-80.

Stevenson, R.A. 1963. Life history and behavior of *Dascyllus albisella* Gill, a pomacentrid reef fish. PhD. dissertation. University of Hawaii at Manoa, Honolulu. 221 pp.

Thresher, R.E., & E.B. Brothers. 1985. Reproductive ecology and biogeography of Indo-West Pacific angelfishes (Pisces: Pomacanthidae). Evolution 39:878-887.

Wallace, R.A., & K. Sellman. 1981. Cellular and dynamic aspects of oocyte growth and maturation in teleosts. American Zoologist 21:325-343.

Willis, T.J., R.B. Millar, R.C. Babcock, & N. Tolimieri. 2003. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? Environmental Conservation 30:97-103.