



**A COMPENDIUM OF LIFE HISTORY INFORMATION FOR
SOME EXPLOITED HAWAIIAN REEF FISHES**

September, 2008

COVER

A haul of weke (*Mulloidichthys*) taken at Waimanalo, O'ahu, circa 1925. Photographer unknown. Image courtesy of Bishop Museum Archives.

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SOME EXPLOITED HAWAIIAN REEF FISHES**

Final Report Prepared for the Fisheries Local Action Strategy

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EXECUTIVE SUMMARY

Life history information is an important facet of fisheries management design and evaluation. Unfortunately, the information for exploited Hawaiian reef fishes is scattered and may be difficult to obtain. We conducted a systematic literature search for and provide in a standardized format a summary of life history information for 13 species (*Myripristis amaena*, *Sargocentron diadema*, *Caranx ignobilis*, *Caranx melampygyus*, *Pseudocaranx cheilio*, *Mulloidichthys flavolineatus*, *Parupeneus multifasciatus*, *Parupeneus porphyreus*, *Chlorurus spilurus*, *Scarus psittacus*, *Acanthurus triostegus sandvicensis*, *Ctenochaetus strigosus*, and *Naso unicornis*) from the five most heavily exploited reef fish families in Hawai'i (Holocentridae, Carangidae, Mullidae, Scaridae, Acanthuridae). Here we provide any information we could find on 21 categories: age at first reproduction, size at maturity, batch fecundity, sex ratio, egg size, oocyte development, spawning season, interspawning interval, spawning cue, spawning mode, reproductive mode, mating system, pelagic larval duration, larval development, maximum size, maximum age, growth equation, mortality estimates, length-length relationships, length-weight relationships, and diet. Hawai'i-based life history data was most complete for *Acanthurus triostegus sandvicensis* (20 of 21 parameters from Hawaiian populations), *Caranx melampygyus* (17 parameters) and the goatfishes *Parupeneus multifasciatus* and *P. poryphyreus* (14 parameters each). Life history information was particularly sparse for *Naso unicornis* (2 parameters) and *Sargocentron diadema* (3 parameters). Average coverage was greatest for families Mullidae and Carangidae (mean of 12 and 11.3 parameters respectively) and least for Holocentridae (7.5 parameters). The overall average was 10.3 (by family) to 10.5 (by species) parameters. All but three species (*Acanthurus triostegus sandvicensis*, *Caranx melampygyus*, and *Parupeneus multifasciatus*) lacked one or more pertinent pieces of life history information necessary to construct a surplus production model (e.g., age-growth data, mortality, or length-weight relationship). Only *C. melampygyus* and *A. triostegus sandvicensis* had sufficient information necessary to estimate annual reproductive output (batch fecundity data, sex ratio, L_{50} and inter-spawning interval). Recommendations for future work and to improve the reliability of existing information include histology-based analysis of reproduction, and validation of otolith increment periodicity.

INTRODUCTION

Hawaii's coral reefs support a large and diverse fishery benefiting commercial, recreational and subsistence fishers. Despite the cultural and economic importance of Hawaii's coral reef fisheries, life history information for many exploited species is fragmentary or, in some cases, completely unknown. A detailed knowledge of life history parameters is helpful in creating and essential for evaluating fisheries management policies.

The goal of this review is to compile and organize into a standardized format the existing life history information for representative species of Hawaii's most heavily exploited reef fish families. This compendium will be a useful reference for fisheries managers in Hawai'i, while helping to identify missing information that should be provided by future life history research efforts.

METHODS

Species names used here follow the taxonomy of Randall's most recent treatment of Hawaiian fishes [1]. Species names (in bold face) are followed by a reference to the taxonomic authority establishing the validity of the name. The current name is then followed by a list of synonyms (and a reference to their original descriptions). The reader is referred to Mundy's extensive checklist of Hawaiian fishes [2] for a list of authors using those synonymies in Hawai'i. First Hawai'i records are taken from Mundy [2].

A total thirteen species representing five families (Holocentridae, Carangidae, Mullidae, Scaridae, Acanthuridae) were selected for review. A systematic literature review was conducted in three stages: 1) a search of electronic resources (*e.g.*, Aquatic Sciences and Fisheries Abstracts, Google Scholar) was conducted using key word combinations of species names or synonyms plus the life history parameters listed on the following pages (see methods); 2) upon obtaining these references, we identified from their bibliographies and obtained additional relevant literature; 3) we then searched these bibliographies and obtained any additional references. We also conducted a manual search of the collection of theses and dissertations in the University of Hawai'i at Mānoa Department of Zoology. Finally, we contacted researchers doing life history work to identify species under investigation and for which there may be unpublished data.

All research describing one or more life history parameters for Hawaiian populations was included in this compendium. Results from studies outside Hawai'i were included only when data for Hawaiian populations were not available, were incomplete, or differed in quality from the outside studies. Studies containing only habitat or demographic information (*e.g.*, abundance, density and size-structure) were included when appropriate, but by no means is this compendium a comprehensive listing for these types of studies.

With few exceptions, we did not standardize units. Growth and morphometric equations appear as written in the original publication. This was done in order to reduce the possibility of transcriptional and computational errors and because a few authors did not specify units.

Description of life history parameters:

First Reproduction: The smallest size at which an individual of the species is reported to be sexually mature. Fish collected during the spawning season are considered mature when their gonads contain vitellogenic oocytes (females) or tailed sperm (males). Most studies contained herein use gross morphology of gonads or a gonadosomatic index (GSI) to estimate size at maturity.

L₅₀: The size-class at which 50% of individuals of a given sex are reproductively mature (see above).

Batch Fecundity: The mathematical relationship between female size and the number of eggs that can be spawned in a single reproductive event. In comparison, annual fecundity (number of eggs spawned each year) is a function of batch fecundity, inter-spawning interval, and the length of the spawning season.

Sex Ratio: Physical sex ratio is reported as the ratio of males to females, regardless of maturity. Operational sex ratio includes only reproductively mature individuals.

Egg Size: Diameter (in microns, μm) of ovulated or spawned oocytes along the longest axis. May also report average size of earlier-stage oocytes.

Oocyte Development: Describes the size-structure and growth of oocytes within the ovary of a mature female collected during the spawning season. Terminology follows Wallace and Selman [3]. Fish are classified as *asynchronous* if oocyte development is random and no dominant size class of oocytes is present within the ovary, *synchronous* if all oocytes grow and ovulate in unison, and *group synchronous* if at least two populations of oocytes can be distinguished at one time. The latter is the most common developmental scheme in reef fishes and is often assumed to indicate the ability to spawn multiple batches of eggs in a single spawning season.

Spawning Season: Indicates months during which spawning has been reported. In most cases, information on spawning seasonality comes from the gonadosomatic index (GSI) [calculated as gonad weight/(body weight-gonad weight) x 100] or, more rarely, histological examination of ovaries. In other cases, seasonality may be determined by direct observation of spawning fish.

Inter-spawning interval: Average or minimum time between successive spawns for an individual female. Determined by direct observation or inferred from gonad histology.

Spawning Cue: Environmental cues (*e.g.*, lunar, tidal or temperature) believed to induce spawning behavior.

Spawning Mode: Describes whether eggs are shed into the water column (*pelagic*) or laid on the substrate (*demersal*). With the exception of triggerfishes, most large-bodied (> 100 mm) reef fishes spawn pelagic eggs.

Reproductive Mode: A species is termed *gonochoristic* if the sexes are separate, and *hermaphroditic* if both ovarian and testicular tissue occur within a single individual. *Simultaneous hermaphrodites* can shed mature oocytes and sperm at the same time whereas *sequential hermaphrodites* change from one sex to another. Sequential hermaphrodites are classified by the direction of sex change: *protogynous hermaphrodites* change from female to male whereas *protandrous hermaphrodites* switch from male to female. Protogynous species are termed *monandric* if all males are derived from sex-changed females or *diandric* if males can also arise from juveniles. See Sadovy and Shapiro [4] for further description of reproductive mode.

Mating System: Indicates whether a male mates with several females (*polygyny*), a female with several males (*polyandry*) or if mating is *monogamous* or *random*. Mating system is usually determined by direct observation of fish spawning, though it can sometimes be inferred by the degree of sexual dimorphism.

Larval Development: May include a description of larval morphology, development and metamorphosis. In most cases, the description is representative of the subfamily, family, or tribe to which the species belongs (*i.e.*, not species-specific).

Maximum Size: Maximum reported weight or length for a species.

Maximum Age: Reports the age of the oldest known individual.

Growth Equation: The relationship between age and size, as determined by otolith-based or mark-recapture studies. Unless otherwise noted, growth parameters are reported using the von Bertalanffy growth equation $L_t = L_\infty(1 - e^{-k(t-t_0)})$ where L_t = length at time t , L_∞ = maximum (asymptotic) length, k = growth rate, and t_0 = time when length is theoretically zero.

Mortality: The predictable decline in numbers of individuals in successively older age-classes. *Total mortality* (Z) is the sum of *natural mortality* (M) and *fishing mortality* (F).

Morphometric Relationships: Mathematical relationship between various body lengths (length-length) or between body length and body depth (BD) or weight (Wt). Body lengths herein are reported as total length (TL), fork length (FL) or standard length (SL).

Diet: The majority of dietary information in this compendium comes from gut-content studies. Where possible, we report the total number of individuals examined for each study as well as the number of individuals with recognizable prey items. Dietary items may be reported in terms of percent *frequency of occurrence* (%FO), *volume* (%V), *number* (%N) and/or *index of relative importance* (IRI). The latter incorporates all three of the previous measurements: $IRI = [(\%N + \%V) \cdot \%FO]$ [5].

RESULTS

HOLOCENTRIDAE

***Myripristis amaena* (Castelnau, 1873) [6]**

Neomyripristis amaenus Castelnau, 1873 [7]

Myripristis symmetricus Jordan & Evermann, 1903 [8]

Myripristis argyromus Jordan & Evermann, 1903

Myripristis prasinus non Cuvier in Cuvier & Valenciennes, 1829 [9]

Myripristis pralinius non Cuvier in Cuvier & Valenciennes, 1829

Geographic range: Pacific Ocean from the Ryukyus, the Ogasawara Islands, Micronesia, Belau, New Guinea and the Caroline Islands to the Hawaiian Islands, the Line Islands, Society Islands, the Tuamotus, and Pitcairn Group [2]. No records from Indo-Malaya [2].

First Hawai'i record: Jordan & Evermann, 1903 as *Myripristis symmetricus* and *Myripristis argyromus* [8]

General Introduction

Commonly known as 'ū'ū (the generic Hawaiian name for *Myripristis* species), brick soldierfish, and menpachi.

Benthopelagic, in or near caves and crevices at 5-25 m [2]. Generally found in less than 10 m [1]. Occurs singly or in schools [10].

In a 1990 survey of the Johnston Atoll recreational fishery, it was typically the species caught in greatest abundance [11]. Fifty-one percent of the individuals in this survey were pre-reproductive, whereas 46% of individuals from a survey at Puako, Hawai'i were pre-reproductive [11].

Fishing is unregulated.

Reproduction and larvae

Assumed to spawn pelagically. Appearance at hatching is unknown. No species-level description of *M. amaena* larvae exist; however Leis & Carson-Ewart [12] illustrate the development of *Myripristis* larva and offer the following account of the soldierfishes: Deep head and trunk, but slender tail. Preanal length is 42-70% body length when gut is fully coiled. A small, pigment-covered gas bladder is above the anterior portion of gut. Head is only slightly compressed. Snout is initially short and truncate but becomes elongate and bulbous as rostral spine develops. Mouth does not reach to mid-eye, is initially terminal but becomes inferior as rostral complex develops. Gill membranes are free from the isthmus. At ~2.5 mm a large, bifurcate, serrate rostral spine begins to form and reaches maximum relative length shortly after notochord flexion. Larvae with this spine are called rhynchichthys larvae. The spine then decreases in size and disappears by 35 mm. At 1.9 mm, a smooth spine is located at the angle of the preopercle, and the supraoccipital crest has one posteriorly-directed and one small dorsal

spine. At 2.4 mm, transverse ribs and weak serrations develop on the posteriorly-directed supraoccipital spine and on the preopercular spine. By 18 mm, the supraoccipital crest has only a slightly raised ridge and a small posteriorly-directed spine. These disappear by 30 mm. Pelvic buds are present at 2.4 mm, with supporting elements appearing by 3.5 mm. Between 4.6 and 5.1 mm, the dorsal, anal and pectoral rays begin to form as dorsal spines ossify. All dorsal, pelvic and anal rays, and 3 of 4 anal spines, are complete by 7.6 mm. The 4th anal spine, pectoral fin and spinous dorsal are fully developed by 8.3 mm. Strongly ctenoid scales form at 6.0-7.5 mm. The lateral line forms at 10 mm. At settlement, the spine at the angle of the preopercle is short and smooth, and the opercular and preopercular margins are strongly serrate. Young larvae have a pigmented gut and several melanophores on the brain; and one to two dorsal, lateral and ventral melanophores on the tail. The tail melanophores disappear as rostral spines form. Pigment covers the whole body except for soft dorsal fin and posterior tail in postflexion larvae. The largest pelagic stages are blue and silver in life, but may become reddish just before settlement.

Based on an assumed settlement mark in a single otolith, Dee & Radtke [13] suggest a larval duration of 115-125 days.

	Male	Female	N	Range
First reproduction				
TL				
FL				
SL [11]	149 mm	154 mm	5♂, 11♀	
Age [11]	6 yr	6 yr		
L ₅₀				
TL				
FL				
SL				
Age				
Batch fecundity vs:				
Size [11]		$BF = 5.029 \cdot 10^{-20} (SL \text{ in mm})^{10.614}$	12	156-181
Age				
Weight [11]		$BF = 1.447 \cdot 10^{-7} (Wt \text{ in g})^{5.0038}$	12	~150-225
Sex ratio (M:F)				
Mature egg size/volume [11]		0.4 mm diameter		0.40-0.54
Egg development [11]		Group synchronous ^a		
Peak spawning season[11]		April-June	99	^b
Interspawning interval (# days)				
Spawning Cue				
Spawning mode				
Reproductive mode				
Mating system				

^a Based on interpretation of histological section presented in Dee & Parrish [11]

^b A second, smaller peak was seen in January at Johnston Island.

Growth and mortality

	Male	Female	N	Range
Maximum size TL [1] SL [13] FL Wt	30 cm 215 mm			
Maximum age [13]	14 years			
Growth equation [13]	$SL_t \text{ in mm} = 194.28(1 - e^{-0.219(\text{age in yearst} + 0.66)})$		15	44-187
Mortality Z M F				

Morphometric relationships

	Equation	N	Range
TL vs SL [14]	$SL \text{ in mm} = -16.61 + 0.88(TL \text{ in mm})$		
TL vs FL			
SL vs FL			
TL vs BD			
FL vs BD			
SL vs BD			
TL vs Wt			
FL vs Wt			
SL vs Wt [13]	$Wt \text{ in g} = 0.00003097(SL \text{ in mm})^{3.042}$	85	44-190

Diet

Dee & Parrish [11] presented results for 64 specimens for Johnston Atoll, 9 from the Northwestern Hawaiian Islands, 22 from Puako, Hawai'i; plus 14 specimens analyzed by Hobson [15] at Kona, Hawai'i. Megalops (crab larvae) dominated the diet in frequency of occurrence, number and volume. Next in importance were shrimp and fishes. Feeding is nocturnal.

Additional references

Hayes et al. [14] present the size structure of a recreational catch at Puako, Hawai'i.

***Sargocentron diadema* (Lacépède, 1802) [16]**

Holocentrus diadema Lacépède, 1802 [17]

Holocentrum diadema Lacépède, 1802 [17]

Adioryx diadema (Lacépède, 1802)

Geographic range: Indo-Pacific from South Africa, the Red Sea, and the Chagos Archipelago to Indonesia, southern Japan, the Ogasawara Islands, Australia, the Hawaiian Islands, French Polynesia and the Pitcairn Group [2].

First Hawai‘i record: Günther, 1873–1910 as *Holocentrum diadema* [18]

General Introduction

Commonly known as ‘ala‘ihi (the generic Hawaiian name for squirrelfishes, but see Titcomb [10]), ‘ala‘ihi kalalao (or ‘ala‘ihi kanalao or ‘ala‘ihi kakalao), and crown squirrelfish . Young are called ‘a ‘ala‘ihi [10].

Engyebenthic in or near crevices and caves of coral reefs from 3-77 m, often in lagoons or bays at < 20 m [2]. It is generally the most common species of *Sargocentron* wherever it is found.

Fishing is unregulated.

Reproduction and larvae

Assumed to be a pelagic spawner. Appearance at hatching is unknown. No species-level description of *S. diadema* larvae exist; however Leis & Carson-Ewart [12] illustrate the development of an unidentified squirrelfish larva and offer the following account of the squirrelfishes: Deep head and trunk, but slender tail. Preanal length is 42-70% body length when gut is fully coiled. A small, pigment-covered gas bladder is above the anterior portion of gut. Head is only slightly compressed. Snout is initially short and truncate but becomes elongate and bulbous as rostral spine develops. Mouth does not reach to mid-eye, is initially terminal but becomes inferior as rostral complex develops. Gill membranes are free from the isthmus. At ~2.5 mm a large, serrate rostral spine begins to form and reaches maximum relative length shortly after notochord flexion. Larvae with this spine are called rhynchichthys larvae. The spine then decreases in size and disappears by 35 mm. At 1.9 mm, a smooth spine is located at the angle of the preopercle, and the supraoccipital crest has one posteriorly-directed and one small dorsal spine. At 2.4 mm, transverse ribs and weak serrations develop on the posteriorly-directed supraoccipital spine and on the preopercular spine. By 18 mm, the supraoccipital crest has only a slightly raised ridge and a small posteriorly-directed spine. These disappear by 30 mm. Pelvic buds are present at 3.3 mm, with supporting elements appearing just after flexion. Between 4.6 and 5.1 mm, the dorsal, anal and pectoral rays begin to form as dorsal spines ossify. All dorsal, pelvic and anal rays, and 3 of 4 anal spines, are complete by 7.6 mm. The 4th anal spine, pectoral fin and spinous dorsal are fully developed by 8.3 mm. Strongly ctenoid scales form at 6.0-7.5 mm. The lateral line forms at 10 mm. At settlement, the spine at the angle of the preopercle is short and smooth, and the opercular and preopercular margins are strongly serrate. Young larvae have a pigmented gut and several melanophores on the brain. Pigment covers the whole body except for soft dorsal fin and posterior tail in postflexion larvae. The largest pelagic stages are blue and silver in life, but may become reddish just before settlement.

	Male	Female	N	Range
First reproduction TL FL SL Age				
L ₅₀ TL FL SL Age				
Batch fecundity vs: Size Age Weight				
Sex ratio (M:F)				
Mature egg size/volume				
Egg development				
Peak spawning season				
Interspawning interval (# days)				
Spawning Cue				
Spawning mode				
Reproductive mode				
Mating system				

Growth and mortality

	Male	Female	N	Range
Maximum size TL [1] SL FL wt	17 cm			
Maximum age				
Growth equation [19]	c			
Mortality Z M F				

^c Munro & Williams [19] describe k & L_∞ as 1.47 annually and 153 mm TL, respectively.

Morphometric relationships

	Equation	N	Range
TL vs SL			
TL vs FL			
SL vs FL			
TL vs BD			
FL vs BD			
SL vs BD			
TL vs Wt			
FL vs Wt			
SL vs Wt			

Diet

This squirrelfish is a nocturnal predator. Hobson [15] examined 28 specimens speared at night in Kona, Hawai'i. Xanthid crabs were eaten most frequently and in the highest volume. Next in importance (approximately equal to one another) were ophiuroids and megalops (crab larvae). Caridean shrimp and prosobranch gastropods were also eaten frequently, occupying ~6% each of the total prey volume consumed.

CARANGIDAE

***Caranx ignobilis* (Forsskål, 1775) [20]**

Scomber ignobilis Forsskål, 1775 [21]

Carangus hippoides Jenkins, 1903 [22]

Carangus ignobilis (Forsskål, 1775)

Geographic range: Tropical Indo-Pacific from South Africa and the Red Sea to southern Japan, the Ogasawara Islands, Australia, New Zealand, Micronesia, the Hawaiian Islands, the Marquesas Islands, and Pitcairn Island [2].

First Hawai‘i record: Jenkins, 1903 as *Carangus hippoides* [22]

General Introduction

Commonly known as ulua aukea (or ulua kea), giant trevally, white ulua, and giant ulua. Black ulua may be used by fishermen for dark individuals, which sometimes creates confusion with *C. lugubris*. Hawai‘ian names for stages of growth, from smallest to largest, for *Caranx* are: papiopio (usually shortened to pāpio today- young), pau u‘u (or pau‘u-individuals of intermediate size) and ulua (adult) [10]. Application of these common names varies by island, although most fishers consider specimens < 10-15 lbs to be papiopio and those greater than this to be ulua [23].

Pelagic over sand, rock, and reefs from 1-188 m [2]. Adults are most abundant on forereef [24], exposed fringing reefs and barrier reefs [25] whereas juveniles inhabit protected areas such as sandflats, backreef, lagoons and estuaries [26, 27]. Estuaries, in particular, may be important nurseries for this and other carangid species [26, 27]. May occur singly or in large groups [1, 24].

Growth rates of juveniles varies seasonally and may be correlated with availability of preferred prey items [28]. Young often forage in small schools [29]^d.

A number of acoustic tracking studies have been conducted on *C. ignobilis* in the main [26] and Northwestern Hawaiian Islands [30, 31]. The most comprehensive of these [31] tracked 28 individuals on five atolls over five and 12 month periods using passive acoustic telemetry. Individuals can range as far as 29 km from their capture site, but most (73%) movements are less than 5 km. Diel, lunar and seasonal patterns in movement occur, with lunar peaks around the full- and third-quarter moon phases during the summer months [31] when the species presumably spawns [32]. An active tracking study conducted on juvenile *C. ignobilis* (n=5 for max of 125 hours) in Kāne‘ohe Bay (O‘ahu, Hawai‘i) found home range size was from 0.173-0.768 km² and that kernel home range size increased with fish weight. These fish were most active at night and during the crepuscular periods. This same study analyzed mark and recapture data from 289 *C. ignobilis* (13.8-43 cm FL) from Kāne‘ohe Bay. Time at liberty ranged from

^d Major [29] found that juvenile *C. ignobilis* were more successful at capturing schooling anchovies when hunting in small groups than when hunting alone.

two days to approximately eight years with 32% of the recaptures within 0.5 km of the capture site, but one individual traveling 70 km in seven years.^e

In the Northwestern Hawaiian Islands, *C. ignobilis* is the dominant apex predator (up to 39% of the total fish biomass [25]) and is believed to have a profound influence in structuring fish assemblages there [33]. Populations of *C. ignobilis* in the main Hawaiian Islands are reported to be significantly depressed [34] as a result of fishing pressure. Although once part of a large commercial fishery, its availability and sale in local markets has declined in recent years due to concerns about ciguatera toxicity [23]^f. Despite these concerns, *Caranx ignobilis* remains prized among recreational anglers and spearfishermen, with the estimated value of the recreational fishery on this and other large Hawaiian carangids to be \$31 million annually [23]. An official “100 plus club” records the number of large ulua (> 100 pounds) caught and registered on each island [28]. The number of registered ulua has increased steadily since the 1980s [28], with the majority of large individuals taken from Hawai‘i, O‘ahu, and Maui [23].

Minimum legal harvest size in Hawai‘i is 10 inches (must be 16 inches for commercial sale). Daily bag limit is 20 (all ulua and papio species combined).

Reproduction and larvae

Forms large spawning aggregations of 100+ individuals [35]. Schools segregate by sex during pre-spawning period [36]. Males assume a dark coloration during spawning whereas females are lighter colored [35, 37]. Recruitment of 4” individuals to inshore areas occurs June-December, with peak recruitment August–December [28]. Young initially recruit to sheltered inshore areas such as estuaries then move to deeper water after 1-2 years [26, 27]. Hybridization with the congener *C. melampygus* has been reported [38].

Eggs of carangids are spherical, 0.7-1.5 mm in diameter, and pelagic [39]. Carangid larvae are usually 2.0-4.3 mm long, have a large yolk sac, unformed mouth, and unpigmented eyes [39]. Pigmentation of carangid larvae changed during the yolk absorption stage [39]. No species-level description of *C. ignobilis* larvae exist; however Leis & Trnski [39] illustrate the development of *Caranx* larva and offer the following account of the tribe Carangini: strongly compressed, with 24-25 myomeres. Gut initially straight, but begins to coil by 2.5 mm. The gut reaches 53-68% body length in preflexion larvae. The anus reaches 44-64% body length in postflexion larvae. The gas bladder is conspicuous and located over the gut coil. The snout is initially concave, but becomes convex by the postflexion stage. Small teeth form in preflexion larvae. Two rows of smooth preopercular spines form very early in the preflexion stage (1.8-2.5 mm). These are the last head spines to disappear during development. A supraoccipital crest is present during the early preflexion stage. There are no pterotic spines or ridges. Dorsal and anal fins form at the same time, with ossification occurring during flexion. The caudal peduncle is narrow after flexion is complete.

^e This study also provides size-frequency data for 321 *C. ignobilis* captured in Kāne‘ohe Bay.

^f Reported commercial landings and sales for *C. ignobilis* in 1998 were 10,149 lbs and 9,455 lbs respectively.

	Male	Female	N	Range
First reproduction TL FL SL [32] Age		550 mm SL	43	
L ₅₀ TL FL SL [32] Age		600 mm SL	43	
Batch fecundity vs: Size Age Weight				
Sex ratio (M:F) [32]	1:1.39 ^{gh}		119	
Mature egg size/volume [39]	700-1500 µm			
Egg development				
Peak spawning season [32]	May-August		43	April-Nov
Interspawning interval (# days)				
Spawning Cue	Lunar			
Spawning mode	Pelagic			
Reproductive mode [40]	Gonochoristic (assumed)			
Mating system				

Growth and mortality

	Sex Unknown	N	Range
Maximum size TL SL FL [32] Wt [32]	1,648 mm ⁱ 86.71 kg		
Maximum age	>9.27 yr [31,25]		
Growth equation [32] [27]	L in mm SL = 1838(1-e ^{-0.111(t in yr-0.097)}) ^j L in mm SL = 2129 (1-e ^{-0.082(t in yr+0.173)})	10 20	106-1180 mm 60-1180 mm
Mortality Z M F			

^g Based on macroscopic evaluation of fresh gonads. Immature individuals were apparently excluded from the count, so this estimate may be closest to an operational sex ratio.

^h Williams [36] reports male-biased sex ratios (1.68:1 M:F; n= 78) for *C. ignobilis* collected off East Africa.

ⁱ Max length estimated from weight of 86.71 kg.

^j Based on SEM counts of otolith increments. Otolith increments were assumed to be deposited daily, but this was not validated for *C. ignobilis*. The same study successfully validated daily increment formation in a congener from Hawai'i (*C. melampygyus*) and provides growth information for *C. ignobilis* based on a captive feeding study.

Morphometric relationships

	Equation	N	Range
TL vs SL [32]	$SL \text{ in mm} = -17.5 + 0.855(TL \text{ in mm})$	107	
TL vs FL [32]	$TL \text{ in mm} = 35.7 + 1.070(FL \text{ in mm})$	107	
SL vs FL [32]	$SL \text{ in mm} = 6 + 0.924(FL \text{ in mm})$	107	
TL vs BD			
FL vs BD			
SL vs BD			
TL vs Wt			
FL vs Wt			
SL vs Wt [26]	$W \text{ in kg} = 5 \cdot 10^{-5}(FL \text{ in cm})^{2.7498}$	65	
[32]	$W \text{ in g} = 2.30 \cdot 10^{-5}(SL \text{ in mm})^{2.977}$	118	

Diet

Caranx ignobilis feed primarily on fishes, cephalopods, and large crustaceans (including lobsters) [41]. In Hawai'i, they are believed to forage more frequently at night [42]. This is supported by the presence of several night-active prey items in their diet [32] as well as by tracking studies [26].

Several dietary studies have been conducted on *C. ignobilis* in both the Northwestern and Main Hawaiian Islands.

Sudekum et al. [32] examined the gut contents of 118 specimens from Northwestern Hawaiian Islands. Of these, 68.6% contained identifiable prey organisms. Fishes were most important (80.3% FO, 73.1% V). The top-five families of fishes were (in descending FO): Scaridae (13.6)^k, Carangidae, including opelu, *Decapterus macarellus* (8.6), Labridae (6.2%), Priacanthidae (6.2%), and eels of various families (14.8%). Cephalopods (mostly octopus) accounted for 24.7% and 15.9% frequency and volume respectively, whereas crustaceans (including palinurid lobsters) accounted for 17.3% and 11%.

Meyer et al. [43] examined 19 *C. ignobilis* collected from fishing tournaments on O'ahu. In contrast to the above study, they found fish accounted for only 7.3% of prey volume (22.2% frequency of occurrence) whereas crustaceans (especially the crab *Portunus japonicas*) were most important in terms of frequency of occurrence (88.9%) and volume (91.8%).

Smith and Parrish [27] examined the guts of 106 juvenile (50-177 mm FL) *C. ignobilis* collected from an estuary on Kaua'i. Fish were found in 43.4% of the guts and accounted for 95.1% of total percent volume. The majority of fish were not identifiable to family, though kuhliids, bothids, mugilids, and gobioids were present. Crustaceans were found in 71.1% of the guts, but accounted for only 3.3% of prey volume. These included amphipods, tanaids, isopods, shrimp, stomatopods, copepods and crabs

^k The authors state that scarids may be over-represented in their dietary analysis due to the ease of identification of this family due to their unique pharyngeal plates.

***Caranx melampygus* Cuvier in Cuvier & Valenciennes, 1833 [44]**

Caranx melampygus Cuvier in Cuvier & Valenciennes, 1833 [44]

Caranx stellatus Eydoux & Souleyet, 1850 [45]

Carangus melampygus (Cuvier, 1833)

Caranx hippos non (Linnaeus, 1766) [46]

Caranx latus non Agassiz in Spix & Agassiz, 1831 [47]

Carangus forsteri non Cuvier in Cuvier & Valenciennes, 1833

Caranx ascensionis non (Cuvier, 1833)

Caranx melampygus (Cuvier, 1833)

Geographic range: Tropical Indo-transpacific from South Africa and the Red Sea to the Ryukyu and Ogasawara Islands, Australia, New Caledonia, Micronesia, the Hawaiian Islands, Ducie Island, the offshore islands of the eastern tropical Pacific, and southern Baja California to Panama [2].

First Hawai‘i record: Eydoux & Souleyet, 1850 as *Caranx stellatus* [45]

General Introduction

Commonly called ‘ōmilu (or ‘omilumilu, but see Titcomb [10]), hoshi ulua, bluefin trevally, blue crevally, blue ulua, ulua omilu, and hoshi. Hawaiian names for stages of growth, from smallest to largest, for *Caranx* are: papiopio (usually shortened to pāpio today), pau u‘u (or pau‘u) and ulua [10].

Pelagic but reef-associated, often just above sand or reefs, at 1–190 m [2]. The young often use estuaries as nursery areas [27]. In Hanalei Bay (Kaua‘i), young reside in the estuary to about 0.7 years of age [27] then disappear, presumably moving into deeper [28] or more exposed habitats.

Growth rates of juvenile *C. melampygus* varies seasonally and may be correlated with recruitment of preferred prey items (e.g., small goatfishes) [28]. Adults most often seen foraging singly or in pairs; but occasionally forage in large groups [48]. May form inter-specific feeding associations with goatfishes [15] sharks, barracuda or rays [48].

A telemetry study [44] in Kāne‘ohe Bay indicates *C. melampygus* have modest (4596 ± 963 linear meters) home ranges and are more active during the day [49]. Further evidence of a modest home range is supported by mark and recapture data: 75% of fish were re-captured within 0.5 km of their release location. Time at liberty was not correlated with distance traveled [49]¹.

Caranx melampygus account for the majority of large jacks caught by fishers [28, 43]. Once part of a large commercial fishery, sale of *C. melampygus* and other carangids has decreased in the last 20 years due to concerns about ciguatera toxicity [23, 28]. Individuals > 6 inches FL (152 mm) are commonly caught by anglers [28]. Minimum take-home size in Hawai‘i is 10 inches (must be 16 inches for commercial sale). Daily bag limit is 20 (all ulua and papiro species combined).

¹ This latter statement is supported by our interpretation of data from Tagawa and Tam [28]; distance traveled does not correlate with fish length.

Reproduction and larvae

Eggs of carangids are spherical, 0.7-1.5 mm in diameter, and pelagic [39]. Carangid larvae are usually 2.0-4.3 mm long, have a large yolk sac, unformed mouth, and unpigmented eyes [39]. Pigmentation of carangid larvae changed during the yolk absorption stage [39]. No species-level description of *C. melampyus* larvae exists; however Leis & Trnski [39] illustrate the development of *Caranx* larva and offer the following account of the tribe Carangini: strongly compressed, with 24-25 myomeres. Gut initially straight, but begins to coil by 2.5 mm. The gut reaches 53-68% body length in preflexion larvae. The anus reaches 44-64% body length in postflexion larvae. The gas bladder is conspicuous and located over the gut coil. The snout is initially concave, but becomes convex by the postflexion stage. Small teeth form in preflexion larvae. Two rows of smooth preopercular spines form very early in the preflexion stage (1.8-2.5 mm). These are the last head spines to disappear during development. A supraoccipital crest is present during the early preflexion stage. There are no pterotic spines or ridges. Dorsal and anal fins form at the same time, with ossification occurring during flexion. The caudal peduncle is narrow after flexion is complete.

	Male	Female	N	Range
First reproduction TL [32] FL SL Age [32]		325 mm 2 years		
L ₅₀ TL [32] FL SL Age [32]		350 mm 2 years		
Batch fecundity vs: Size [32] Age Weight [32]		$F = 2.286 \cdot 10^{-9} (\text{SL in mm})^{5.359}$ $F = 0.923(\text{Wt in g})^{1.694}$	11	328-640 mm
Sex ratio (M:F) [32]		1:1.48 ^m	119	
Mature egg size/volume [50]		758 ± 17 μm ⁿ		721-787 μm
Egg development				
Peak spawning season [32]		May-July ^o		Apr-Nov
Interspawning interval (# days)		^p		
Spawning Cue [50]		Possibly lunar (new moon & 3 rd quarter)		
Spawning mode		Pelagic		
Reproductive mode		Gonochoristic		
Mating system				

^m In contrast, Williams [36] found male-biased (1.68:1) populations off East Africa.

ⁿ Although Moriwake *et al.* [50] report egg diameter to be 0.758 μm, we assume the diameters were given in mm, not microns.

^o Moriwake *et al.* [50] report that 75% of eggs spawned by *C. melampyus* in captivity were recovered in months May-August.

^p Moriwake *et al.* [50] report that captive female *C. melampyus* typically spawned eight times each season with interspawning intervals as short as five days.

Growth and mortality

	Sex Unknown	N	Range
Maximum size TL [1] SL FL Wt	100 cm		
Maximum age [32]	> 6 yrs		
Growth equation [32]	SL in mm = $897(1 - e^{-0.233(t \text{ in yr} + 0.044)})^q$	14	122-660 mm
[27]	SL in mm = $973(1 - e^{-0.194(t \text{ in yr} + 0.196)})^r$	20	70-660 mm
Mortality Z [51] M [51] F [51]	0.69 0.27 0.42		

Morphometric relationships

	Equation	N	Range
TL vs SL [32]	SL in mm = $-17.4 + 0.878(TL)$	140	
TL vs FL [32]	TL in mm = $24.3 + 1.052(FL)$	140	
SL vs FL [32]	SL in mm = $1.5 + 0.929(FL)$	141	
TL vs BD			
FL vs BD			
SL vs BD			
TL vs Wt			
FL vs Wt			
SL vs Wt [32]	W in g = $2.86 \cdot 10^{-5}(SL)^{2.974}$	140	

Diet

Caranx melampygus is a diurnal piscivore, with peak foraging at dusk and dawn [15, 48].

Hobson [15] examined six specimens from Kona, Hawai‘i. Only one individual (collected 3h after sunrise) contained readily identifiable prey items. It contained larval fishes and mysid shrimps.

Sudekum et al. [32] examined 147 individuals from the Northwestern Hawaiian Islands. Eighty-five percent contained identifiable prey items. Of these, 96% contained fish. The most important families were Labridae, Mullidae, Monacanthidae, Pomacentridae, Scaridae, and Priacanthidae.

Meyer et al. [43] examined 264 individuals collected from Kāne‘ohe Bay (O‘ahu, Hawai‘i) during fishing tournaments. Fish were most important, occurring in 86.3% of individuals and

^q Based on counts of otolith increments. Daily formation of otolith increment formation was validated by the authors using injected tetracycline.

^r Equation incorporates growth data from Sudekum *et al.* [32] and additional juveniles from a Kaua‘i estuary.

accounting for 95% of prey volume. Among fish families identified were Labridae, including *Thalassoma duperrey* (14.1% frequency of occurrence), Scaridae (9.86%), Mullidae, including *Mulloidichthys flavolineatus* (7%), Blenniidae (6.3%), Synodontidae (4.9%), Gobiidae (7.8%), Pomacentridae, mostly *Dascyllus albisella* (3.4%), and Acanthuridae (2.82%). Crustaceans (alpheid shrimps, stomatopods and crabs) were found in 22.7% of guts, but accounted for only 4.1% of prey volume.

Smith and Parrish [27] examined 90 juvenile (53-165 mm FL) *C. melampygyus* collected from a Kaua'i estuary. Fish were found in 43.4% of the guts and accounted for 95.1% of total prey volume. The majority of fish could not be identified, but kuhliids and gobioids were present. Crustaceans were found in 85.5% of guts, but accounted for 4.93% of prey volume. These included: tanaids, isopods, shrimp, amphipods, crabs and copepods.

Additional references

Honebrink [40] quite thoroughly reviews taxonomy and biology for this and other Hawaiian carangids, and will be helpful to anyone wishing for a more detailed description of the biology of *C. melampygyus* in a single reference. Gaffney [23] summarizes data on fishing pressure and management recommendations. Tagawa and Tam [28] provide tag and release data, and information on growth, recruitment and movement patterns. Masuda and Ziemann [52] state that *C. melampygyus* are important predators of cultured threadfin fingerlings (*Polydactylus sexfilis*) released into the wild. They describe the effects of fish size and stress level on predation.

***Pseudocaranx cheilio* (Snyder, 1904) [1]**

Scomber dentex Bloch & Schneider, 1801 [53]

Carangus cheilio Snyder, 1904 [54]

Caranx cheilio (Snyder, 1904)

Caranx delicatissimus Döderlein in Steindachner & Döderlein, 1884 [55]

Caranx dasson non Jordan & Snyder, 1907 [56]

Pseudocaranx dentex (Bloch & Schneider, 1801)

Geographic range: Hawaiian Islands [1].

First Hawai‘i record: Snyder, 1904 as *Carangus cheilio* [54].

General Introduction

This genus is in a state of taxonomic flux. Until Randall [1] recognized *P. cheilio* as a Hawaiian endemic in 2007, it was considered part of the Indo-Pacific and Atlantic, *P. dentex*. Much of the information presented below is based on studies of *P. dentex* performed outside Hawai‘i and should be viewed with caution.

Commonly called lehe (but see Titcomb [10]), ulua, white trevally, thicklipped jack, butaguchi, buta ulua, pig ulua.

Found midwater [57], and inhabiting reef edge by night [58]. More common in the Northwestern Hawaiian Islands [2] where most individuals inhabit depths between 73-181 m [59].

Juveniles exhibit strong schooling behavior [60] and are often found associated with flotsam. The sensory and developmental aspects of this behavior have been well-described [60-63].

In the Azores, *Pseudocaranx dentex* changes habitat use and schooling behavior ontogenetically. Immature individuals inhabit sheltered near-shore areas year-round, and typically occur in schools of < 10 individuals. Larger individuals (510-700 mm TL) are typically found on exposed off-shore reefs during the summer spawning season where they aggregate in schools of 20-70. These schools were assumed to be spawning aggregations, but this was not verified. After the spawning season, the aggregations break up and adults leave and presumably move to deeper habitats [64].

Afonso [65] studied the habitat use and site fidelity of *P. dentex* populations in the Azores using active tracking (n = 5 for 48 hrs each), passive acoustic telemetry (n = 32 for 3 years) and tag-recapture studies (n = 58). Results indicate *P. dentex* have large home ranges (up to 370 hectares in a 48 hr track) and can make large (> 10s of km) short-term movements. Recaptures (14%) from the tagging portion of the study indicate movements ranged from 100 m to 52 km over 11-416 days. Individuals inhabiting inshore reefs made predictable along-shore movements, moving northward during first 12 h and southward during the second 12. Fish movement likewise varied seasonally.

Counter to a previous hypothesis [64] there was no evidence of large aggregations during the summer spawning season [65]. Instead, adult fish ranged more widely during the summer and visited adjacent reefs. Afonso [65] hypothesizes that this “visiting” behavior increases mating opportunities and that the lack of spawning aggregations may be a result of fishing pressure.

Pseudocaranx dentex is cultured extensively in Japan [40] where it is among the more economically important carangid species [66]. It is also a popular food-fish in the Atlantic.

This species is rarely caught in the main Hawaiian Islands [24, 40]^s.

Minimum size for *P. cheilio* in Hawai‘i is 10 inches (must be 16 inches for commercial sale)^t. Daily bag limit is 20 (all species combined).

Reproduction and larvae

A description (in Japanese) of *P. dentex* development is given in Okiyama [67]. Masuda and Tsukamoto [63] describe chronology of sensory system development and associated behavioral changes: Retinas pigmented by day 2 (3.4 mm TL) becoming positively phototactic by 3 days (3.5 mm). Epithelium pigmented and free neuromasts also present by day 3 [66]. Fin spines complete by day nine. Vitreous humor forms at 10 days (4.3 mm). Seeks areas of low illumination by day 12. Cephalic canal complete by 18 mm. Outer retinal layer complete by 20-25 days (18-21 mm). Scale formation and trunk lateral line form at 23-30 mm.

In the Azores, juvenile *P. dentex* recruit to inshore habitats at 50-70 mm TL, move to deeper waters after reaching sexual maturity, and form aggregations around summits of offshore reefs during the spawning season [64].

^s Data from Tagawa and Tam [28] indicate that *P. cheilio* was the 7th most commonly collected carangid in a state-sponsored mark-recapture program, accounting for just 0.49 % fish captured

^t A total of 40,522 lbs was landed in 1998, of which 37,953 was sold for a value of \$53,643 [40].

	Male	Female	N	Range
First reproduction TL FL SL Age	u			
L ₅₀ TL FL SL Age	v			
Batch fecundity vs: Size Age Weight				
Sex ratio (M:F) [59]	1:1.14		62	
Mature egg size/volume				
Egg development				
Peak spawning season [68]	January, July ^w			
Interspawning interval (# days)				
Spawning Cue				
Spawning mode	Assumed to be pelagic			
Reproductive mode [40]	Assumed Gonochorist			
Mating system				

Growth and mortality

	Sex Unknown	N	Range
Maximum size TL [23] SL FL [69] Wt	940 mm 131.4 cm		
Maximum age [69]	7 yrs ^x		
Growth equation [69]	FL in mm = 1085 (1-e ^{-0.258(t+0.12yr)}) FL in mm = 1232 (1-e ^{-0.307(t-0.77yr)})	8 37	340-960 mm FL
Mortality Z M F			

^u Tagawa and Tam [28] report that *P. cheilio* reach sexual maturity between 18.8-33.7 inches TL (478-856 mm), but we could not find a primary reference for this information.

^v Afonso *et al.* [64] estimated L₅₀ for male and female *P. dentex* to be 278 and 300 mm FL respectively.

^w Afonso *et al.* [64] found that *P. dentex* in the Azores spawned June-September, with peak spawning in August.

^x Tagawa and Tam [28] report a maximum life span of 48.1 years in a DAR technical report; however we could not find primary reference for this information.

Morphometric relationships

	Equation	N	Range
TL vs SL			
TL vs FL			
SL vs FL			
TL vs BD			
FL vs BD			
SL vs BD			
TL vs Wt			
FL vs Wt [70]	Wt in kg = 0.0000309675FL ^{2.86839 y}	509	33-89 cm FL
SL vs Wt			

Diet

Pseudocaranx cheilio is an opportunistic carnivore that feeds primarily on benthic fishes and invertebrates [59].

Seki [59] examined the guts of 64 *P. cheilio* from the Northwestern Hawaiian Islands. Fishes occurred in 68.8 percent of guts and accounted for 64.2% total volume. Twenty families of fishes were identified from gut contents. Most important were Congeridae, Priacanthidae, and Serranidae. Crustaceans occurred in 53.1% of sampled individuals but accounted for only 4.3% total volume. Crabs (Reptantia) were the most important crustaceans, followed by shrimp (Natantia). Molluscs (mostly cephalopods) were found in 34.4 % individuals and accounted for 9.4% total volume.

Sazima [71] observed ram feeding in a school of 10 individuals (250 mm FL) of *P. dentex* off the coast of Sao Paulo, Brazil. In a subsequent examination of guts of three museum specimens, she found that two smaller individuals (132-141 mm FL) contained remains of small fishes and benthic crustaceans, whereas a third, large individual (184 mm FL) contained only planktonic mysids. Based on these data, she concludes that *P. dentex* feeds primarily on benthic fishes and invertebrates, but may also occasionally filter-feed on planktonic organisms.

^y The authors also found significant differences in log-transformed weight-length relationships between males and females

MULLIDAE

***Mulloidichthys flavolineatus* (Lacépède, 1801) [72]**

Mullus flavolineatus Lacépède, 1801 [73]

Upeneus preorbitalis Swain & Swain, 1882 [74]

Mulloides samoensis Günther, 1874 [75]

Pseudupeneus preorbitalis (Swain & Swain, 1882)

Mulloidichthys samoensis (Günther, 1874)

Mulloides flavolineatus (Lacépède, 1801)

Geographic range: Indo-Pacific from South Africa and the Red Sea to the Ryukyu and Ogasawara Islands, Australia (to southern New South Wales), Lord Howe Island, Micronesia, the Hawaiian Islands, the Marquesas, and the Pitcairn Group [1, 2].

First Hawai‘i record: Swain & Swain, 1882 as *Upeneus preorbitalis* [74]

General Introduction

Commonly called weke‘ā, weke, weke ‘ā‘ā, yellowstripe goatfish, and white goatfish. Young (to about 6 inches) are called oama.

Engybenitic over coral and sand at 1–97 m [2], but usually seen from near shore to about 20 m [1]. Unlike other Hawaiian goatfishes, this species may be found high in the water column [76]. During the day, this species forms inactive aggregations. In shallow waters, these typically consist of 20 to >100 individuals in shallow inlets and channels [77], often with many individuals at rest on the bottom [1]. In deeper waters, the aggregations may contain >1,000 individuals extending more than five meters from the bottom [76].

Mulloidichthys flavolineatus has high site fidelity, foraging on sand-flats at night and returning to the same sheltering habitat by first light [77]. Mean nighttime range was 8,267 m² (range 5,200–11,600 m²) whereas daytime range was 2,533 m² (range 1,200–3,200 m²) for three fish tracked in an O‘ahu marine life conservation district [77]. This same study provides size-frequency data for 323 individuals caught with a purse seine in the marine live conservation district.

M. flavolineatus was the most abundant goatfish in a visual survey of Midway Atoll with 0.71% abundance and 35% occurrence in visual transects. Size ranged from 70–250 mm [78].

In the Red Sea, wrasses frequently accompany *M. flavolineatus* while foraging in the daytime [79]. The goatfish spends more time foraging when accompanied by wrasses than when wrasses are not present. Goatfish may be less efficient when feeding with wrasses because of harassment and frequent forced location changes. Small *M. flavolineatus* tend to feed in larger groups than large individuals.

Young individuals (to about 6 in) are prized as baitfish [77]. Combined daily bag limits for young (under 7 inches) *Mulloidichthys* and *Upeneus* species is 50. There is no bag limit for fishes longer than 7 inches.

Reproduction and larvae

Eggs and larvae of *M. flavolineatus* have not been described; however Leis & Carson-Ewart [12] provide the following generalized account of mullid development, based on at least three unidentified goatfish species plus *Upeneus tragula*: Larvae hatch at 1.6-3.4 mm with unpigmented eyes, unformed jaws and a large yolk sac. Larvae are laterally compressed, with 23-25 myomeres. Early preflexion larvae have 5-6 preanal myomeres, early postflexion larvae have ~8, and 10 mm larvae have ~10. The preflexion gut is 30-40% of body length, and postflexion gut is 60% body length. The gas bladder is covered by heavy pigment. The head is rounded dorsally, with a short, steeply-sloped snout. The terminal, slightly oblique mouth extends to the anterior margin of the pupil. At 8-9 mm, small teeth form in the upper jaw, followed closely by teeth in the lower jaw. At the same size, chin barbels originate at the hypohyal symphysis as thickenings along the edge of the branchiostegal membrane, these do not occupy the position under the tip of the lower jaw until settlement. Gill openings are free from the isthmus. Anal-fin elements begin forming during flexion (~4 mm), followed by dorsal rays. Both fins are ossified by 6 mm. During flexion there is a gap of approximately 50% head length between the anus and anal fin origin. This gap closes by 10 mm. The spinous dorsal fin forms after flexion (5.6 mm) and is fully ossified by ~7 mm. Pectoral rays form during flexion and are completely developed by ~8 mm. Pelvic fin buds appear at 5.5 mm and fins are fully formed by 7 mm. Scales appear in larvae ≤ 13 mm. Body pigment changes substantially during yolk absorption: Preflexion larvae have pigment on the dorsal surface of the gut, small melanophores along the ventral midline of the tail, and three melanophores in a triangular pattern on the midbrain; brain pigmentation becomes more extensive during development; a midlateral stripe on the tail and internal melanophores over the notochord form just before flexion; after flexion, rows of melanophores form on the mid-dorsal and mid-ventral tail and trunk, then pigment spreads such that, until settlement, larvae are blue dorsally and silver laterally.

Pelagic larval duration in the southwestern Indian Ocean is estimated at 45-50 days based on counts of pre-settlement otolith rings (n= 118) [80].

	Male	Female	N	Range
First reproduction TL FL SL Age				
L ₅₀ TL FL SL [14] Age	160 mm	160 mm		116-278 mm
Batch fecundity vs: Size Age Weight				
Sex ratio (M:F)	z			
Mature egg size/volume				
Egg development				
Peak spawning season	aa			
Interspawning interval (# days)				
Spawning Cue				
Spawning mode	Pelagic			
Reproductive mode	Gonochoristic (assumed)			
Mating system				

Growth and mortality

	Sex Unknown	N	Range
Maximum size TL [1] SL FL [77] Wt	40 cm 336 mm		
Maximum age [77]	12 years		
Growth equation [77]	$FL_t \text{ in cm} = 34.2(1 - e^{-0.564(t - 0.36)})^{bbcc}$	53	
Mortality Z M F			

^z Wahbeh [84] estimated sex ratio for a Red Sea population to be 1:1.55 M:F.

^{aa} In the Red Sea, peak spawning occurs June-August [84].

^{bb} Above growth rates from a mark-recapture study in a Hawaii MLCD (Coconut Island). An alternate growth rate calculated was $k = 0.557$.

^{cc} Wahbeh [84] calculated sex-specific growth rates for *M. flavolineatus* in the Red Sea: for males TL in cm = $31.7(1 - e^{-0.213(t + 0.78 \text{ yr})})$ whereas for females TL in cm = $35(1 - e^{-0.168(t + 0.97 \text{ yr})})$.

Morphometric relationships

	Equation	N	Range
TL vs SL [77]	$SL \text{ in mm} = -4.78 + 0.84(TL \text{ in mm})$		116-278 mm
TL vs FL			
SL vs FL			
TL vs BD			
FL vs BD			
SL vs BD			
TL vs Wt			
FL vs Wt [77]	$W \text{ in kg} = 0.0087(FL \text{ in cm})^{3.21}$	97	
SL vs Wt			

Diet

Mulloidichthys flavolineatus feeds on sand-dwelling invertebrates, primarily during nighttime [15]. In the Marshall Islands, fish were the most dominant prey item [81]. However, in Kona, Hawai'i bivalves, polychaetes, and amphipods appeared to be most important [15]. The most taxonomically detailed study to date was conducted at Midway Atoll [82]. Of the 31 individuals examined, 18 contained food and a total 21 prey categories were present. Polychaetes^{dd} were most abundant in terms of percent number, volume, frequency and index of relative importance. Other important prey groups include xanthid crabs, bivalves, gammaridean amphipods, and the tanaid *Leptochelia dubia*. Most taxa consumed occur in sand, and sand was frequently found in the guts.

Additional references

Pothin [80] described sagittal otoliths and found stocks of juvenile fishes could be reliably distinguished based on Fourier analysis of shape. Wahbeh [83] reports on food and feeding behavior in the Red Sea. Wahbeh [84] reports on reproduction in the Red Sea. Al-Absy [85] reports on growth and morphometric relationships from the Red Sea. H. Leba and K. Cole (University of Hawai'i Department of Zoology) are currently working on a reproductive study of this species. Their analysis is expected to include information on size-at-maturity, sex-ratio, oocyte development, and batch fecundity for Hawaiian specimens.

^{dd} Sorden [82] identified 23 species of polychaetes from 16 families in the guts of *M. flavolineatus* with *Armandia intermedia* (Opheliidae) and *Nothria holobranchia* (Onuphidae) comprising 2/3 of the polychaetes eaten.

Parupeneus multifasciatus (Quoy & Gaimard, 1825) [86]
Mullus multifasciatus Quoy & Gaimard, 1825 [87]
Mullus trifasciatus non Lacépède (ex Commerson), 1801 [73]
Upeneus trifasciatus non (Lacépède, 1801)
Upeneus velifer Smith & Swain, 1882 [74]
Parupeneus trifasciatus non (Lacépède, 1801)
Pseudupeneus multifasciatus (Quoy & Gaimard, 1825)
Upeneus multifasciatus (Quoy & Gaimard, 1825)
Parupeneus moana (Jordan & Seale, 1906) [88]

Geographic range: Eastern Indian Ocean (Northwestern Australia and Cocos-Keeling Islands) and Pacific from Christmas Island and Indonesia to southern Japan, the Ogasawara Islands, Australia (to New South Wales), Lord Howe Island, Micronesia, the Hawaiian Islands, the Tuamotu Archipelago, and the Marquesas, Norfolk Island and the Pitcairn Group [1, 2].

First Hawai‘i record: Quoy & Gaimard, 1825 as *Mullus multifasciatus* [87]

General Introduction

Commonly called moano, manybar goatfish, and multibarred goatfish. Hawai‘ian names for the young are ‘ahua or ‘ohua [10].

Engybenitic over sand, rock, and reef from 1-161 m [2]. Rarely found more than ½ meter above the bottom [76]. Primarily day-active, though some specimens may forage at twilight [15].

This species forages singly or in groups of two to three [76, 82] and is occasionally accompanied by other goatfish species including *P. pleurostigma* [82]. It is usually the most common reef-associated goatfish wherever it is found [1].

Minimum take-home size in Hawai‘i is 7 in. There is no bag limit.

Reproduction and larvae

Little is known of the reproductive behavior of this species. Lobel [89] observed spawning in March, two days before the new moon. Spawning occurs 1900-2000 [90]. Males hold territories during reproductive season [90]. K. Longenecker & R. Langston (unpublished observation) observed larger fishes (presumably males) ‘herding’ smaller fish (presumably females) during periods when gonadal analysis revealed active spawning.

Eggs of *Parupeneus* are 0.63-0.93 mm in diameter, spherical and pelagic [12]. Larvae of *P. multifasciatus* have not been described; however Leis & Carson-Ewart [12] provide the following generalized account of mullid development, based on at least three unidentified goatfish species plus *Upeneus tragula*: Larvae hatch at 1.6-3.4 mm with unpigmented eyes, unformed jaws and a large yolk sac. Larvae are laterally compressed, with 23-25 myomeres. Early preflexion larvae have 5-6 preanal myomeres, early postflexion larvae have ~8, and 10 mm larvae have ~10. The preflexion gut is 30-40% of body length, and postflexion gut is 60% body length. The gas bladder is covered by heavy pigment. The head is rounded dorsally, with a short, steeply-sloped snout. The terminal, slightly oblique mouth extends to the anterior margin

of the pupil. At 8-9 mm, small teeth form in the upper jaw, followed closely by teeth in the lower jaw. At the same size, chin barbels originate at the hypohyal symphysis as thickenings along the edge of the branchiostegal membrane, these do not occupy the position under the tip of the lower jaw until settlement. Gill openings are free from the isthmus. Anal-fin elements begin forming during flexion (~4 mm), followed by dorsal rays. Both fins are ossified by 6 mm. During flexion there is a gap of approximately 50% head length between the anus and anal fin origin. This gap closes by 10 mm. The spinous dorsal fin forms after flexion (5.6 mm) and is fully ossified by ~7 mm. Pectoral rays form during flexion and are completely developed by ~8 mm. Pelvic fin buds appear at 5.5 mm and fins are fully formed by 7 mm. Scales appear in larvae ≤ 13 mm. Body pigment changes substantially during yolk absorption: Preflexion larvae have pigment on the dorsal surface of the gut, small melanophores along the ventral midline of the tail, and three melanophores in a triangular pattern on the midbrain; brain pigmentation becomes more extensive during development; a midlateral stripe on the tail and internal melanophores over the notochord form just before flexion; after flexion, rows of melanophores form on the mid-dorsal and mid-ventral tail and trunk, then pigment spreads such that, until settlement, larvae are blue dorsally and silver laterally.

	Male	Female	N	Range
First reproduction				
TL				
FL [91]	151 mm ^{ec}	138 mm	50	72-228 mm
SL				
Age				
L ₅₀				
TL				
FL [91]	152 mm	145 mm	50	72-228 mm
SL				
Age				
Batch fecundity vs:				
Size [91]		5,479-21,530 eggs ^{ff}	4	155-193 mm
Age				
Weight				
Sex ratio (M:F) [91]		3:2 ^{eg}	50	72-228 mm
Mature egg size/volume [91]		389 μ m	4	330-450 μ m
Egg development [91]		Group Synchronous		
Peak spawning season		^{hh}		
Interspawning interval (# days)				
Spawning Cue				
Spawning mode		Pelagic		
Reproductive mode [91]		Gonochoristic		
Mating system				

^{ec} Histology-based study. Males were also significantly larger than females.

^{ff} El Agamy [92] provides a fecundity curve for *P. ciliatatus*, a similar-sized goatfish from Qatar: # Eggs = $0.0018(\text{FL})^{3.092}$

^{eg} Physical sex ratio (counting mature and immature individuals) for 50 speared specimens from Kāneʻohe Bay. This study found that the proportion of females in the population described varied predictably with body length [% Females = $141.3 - 0.67(\text{FL in mm})$], and that all individuals larger than 197 mm FL were male.

^{hh} Unknown, but Longenecker & Langston [91] found mature females in March-July and November.

Growth and mortality

	Male	Female	N	Range
Maximum size TL [1] SL [86] FL [91] Wt	30 cm 260 mm	179 mm 197 mm	50	72-228 mm
Maximum age [91]	>2 years ⁱⁱ		13	
Growth equation [91]	FL in mm = $303(1 - e^{-0.00207(t \text{ in days} + 49.4)})^{jj}$		13	
Mortality Z [91] M [91] F	0.3025 per 16 weeks ^{kk} 0.4439 per 16 weeks		150 126	

Morphometric relationships

	Equation	N	Range
TL vs SL			
TL vs FL			
SL vs FL [91]	SL in mm = $-1.98 + 0.92(\text{FL in mm})$	50	72-228 mm
TL vs BD			
FL vs BD ^{ll} [91]	FL in mm = $16.96 + 3.32(\text{BD in mm})$	50	72-228 mm
SL vs BD			
TL vs Wt			
FL vs Wt [91]	Wt in g = $4.91 \cdot 10^{-6}(\text{FL in mm})^{3.23}$	50	72-228 mm
SL vs Wt			

Diet

Parupeneus multifasciatus feeds diurnally on benthic invertebrates, although juveniles may feed on plankton [15].

Hobson [15] examined the guts of 31 individuals from Kona, Hawai'i. Twelve of 14 individuals collected before or during morning twilight were empty [15]. In the remaining individuals, (2 collected at twilight and 15 in the afternoon) xanthid crabs and caridean shrimps were most important (30.6 and 15.4% volume respectively) followed by crab larvae in the megalops stage (8.6%).

The most taxonomically detailed study, was conducted on 20 individuals at Midway Atoll [82]. This study likewise found that crabs and shrimp were most important in terms of percent

ⁱⁱ Age estimates based on counts of otolith increments. Daily deposition of otolith increments is assumed but has not been successfully validated.

^{jj} Authors note that growth in males and females may differ but this has not been tested.

^{kk} Natural mortality was calculated from age structure in a marine reserve, total mortality from age structure in a nearby fished area. Counter-intuitively, total mortality appeared lower than natural mortality alone. Work to increase the range of sites and number of individuals studied is underway.

^{ll} BD, as used by Longenecker & Langston [91] was the distance between the origins of the dorsal and pelvic fins.

number, volume, frequency, and index of relative importance. In descending order of importance: Xanthidae, caridean shrimp, Alpheidae, Portunidae, and *Rhynchinocetes rugulosus*.

A more recent study of 40 individuals also found crabs (raninids and galatheids) and shrimp to be most important, accounting for 70% of the total volume. These were followed by fishes (16.4%, including *Ptereleotris heteropterus*) and stomatopods (3.2%) [93].

Additional references

Longenecker and Langston (in progress) are currently working on completing a more detailed life-history study of *P. multifasciatus* which will include additional growth, fecundity, mortality, and sex ratio data.

***Parupeneus porphyreus* (Jenkins, 1903) [86]**

Pseudupeneus porphyreus Jenkins, 1903 [22]

Parupeneus dispilurus non (Playfair in Playfair & Günther, 1867) [94]

Parupeneus fraterculus non (Valenciennes in Cuvier & Valenciennes, 1831) [95]

Upeneus porphyreus (Jenkins, 1903)

Parupeneus pleurotaenia non (Playfair in Playfair & Günther, 1867)

Geographic range: Hawaiian Islands and Johnston Atoll [2].

First Hawai'i record: Steindachner, 1900 as *Parupeneus dispilurus* [96].

General Introduction

Commonly called kŭmŭ, whitesaddle goatfish, and red goat fish. Hawaiian names include kolokolopao (or kolokolopā or makolokolopao) for the spawn; ahuluhulu for small juveniles, kŭmŭ a'e for larger juveniles, and kŭmŭ for adults [10].

Engyebenthic over sand, rock, and reef from 2-140 m [2]. Most typically found low in the water column, < 2 m from the bottom [76]. Adults shelter in holes in the reef during day and forage over sand and rubble at night, returning to the same hole in the morning. The young feed during the day [97].

Five fish tracked with acoustic tags at Coconut Island had home ranges from 9,070-35,163 m² [98].

This is the most valuable reef fish in Hawai'i [97]; it can fetch \$15-30/kg [98]. Aquaculture of this species was attempted at the Hawai'i Institute of Marine Biology in the 1970s, but the project was stopped when a suitable feed could not be developed [99].

Historically, this species was forbidden to women because the red color suggested menstruation, during which time women were isolated [10]. Today, Hawaii's fishing regulations require a minimum size of 10 in. There is no bag limit.

Reproduction and larvae

Eggs of *Parupeneus* are 0.63-0.93 mm in diameter, spherical and pelagic [12]. Except for the observation of sharply-pointed pharyngeal teeth [97], larvae of *P. porphyreus* have not been described; however Leis & Carson-Ewart [12] provide the following generalized account of mullid development, based on at least three unidentified goatfish species plus *Upeneus tragula*: Larvae hatch at 1.6-3.4 mm with unpigmented eyes, unformed jaws and a large yolk sac. Larvae are laterally compressed, with 23-25 myomeres. Early preflexion larvae have 5-6 preanal myomeres, early postflexion larvae have ~8, and 10 mm larvae have ~10. The preflexion gut is 30-40% of body length, and postflexion gut is 60% body length. The gas bladder is covered by heavy pigment. The head is rounded dorsally, with a short, steeply-sloped snout. The terminal, slightly oblique mouth extends to the anterior margin of the pupil. At 8-9 mm, small teeth form in the upper jaw, followed closely by teeth in the lower jaw. At the same size, chin barbels originate at the hypohyal symphysis as thickenings along the edge of the branchiostegal

membrane, these do not occupy the position under the tip of the lower jaw until settlement. Gill openings are free from the isthmus. Anal-fin elements begin forming during flexion (~4 mm), followed by dorsal rays. Both fins are ossified by 6 mm. During flexion there is a gap of approximately 50% head length between the anus and anal fin origin. This gap closes by 10 mm. The spinous dorsal fin forms after flexion (5.6 mm) and is fully ossified by ~7 mm. Pectoral rays form during flexion and are completely developed by ~8 mm. Pelvic fin buds appear at 5.5 mm and fins are fully formed by 7 mm. Scales appear in larvae ≤ 13 mm. Body pigment changes substantially during yolk absorption: Preflexion larvae have pigment on the dorsal surface of the gut, small melanophores along the ventral midline of the tail, and three melanophores in a triangular pattern on the midbrain; brain pigmentation becomes more extensive during development; a midlateral stripe on the tail and internal melanophores over the notochord form just before flexion; after flexion, rows of melanophores form on the mid-dorsal and mid-ventral tail and trunk, then pigment spreads such that, until settlement, larvae are blue dorsally and silver laterally.

Estimated larval duration 41-56 days (mean = 47.4) [99]. Recruitment begins in March [100] with no new settlers visible after June [97]. New recruits are 31-37 mm [97].

	Male	Female	N	Range
First reproduction TL FL [99] SL Age		238	125	
L ₅₀ TL FL SL Age				
Batch fecundity vs: Size [99] Age Weight		mm	6	11991-25953
Sex ratio (M:F)	^{mm}			
Mature egg size/volume [99]	800 μ m			500-900
Egg development [99]	Group synchronous			
Peak spawning season [99]	December-July		125 ♀, 395 ♂	
Interspawning interval (# days)				
Spawning Cue				
Spawning mode	Pelagic			
Reproductive mode	Gononchorist			
Mating system				

^{mm} Moffitt [99] measured the batch fecundity for six *P. porphyreus* specimens. Range for the data are listed above, however, the data are suspect as they suggest that fecundity decreases with body size.

ⁿⁿ No sex ratio given, however, Moffitt [99] collected 395 male and 125 females in his life history study.

Growth and mortality

	Sex Unknown	N	Range
Maximum size TL [1] SL FL[99] Wt	51 cm 470 mm		
Maximum age [99]	6 years (Estimated)		
Growth equation [99]	$FL_{t \text{ in cm}} = 49.2(1 - e^{-0.538(t+0.0446)})$	36	36-385
Mortality Z M F			

Morphometric relationships

	Equation	N	Range
TL vs SL			
TL vs FL			
SL vs FL [99]	SL = -0.21+0.91(FL) FL = 0.24 + 1.10(SL)	91	40-408 FL
TL vs BD			
FL vs BD			
SL vs BD			
TL vs Wt			
FL vs Wt [99]	$W = 1.31 \cdot 10^{-2} (FL)^{3.153}$	167	None given
SL vs Wt			

Diet

This species feeds nocturnally on benthic crustaceans [15]. Six of 11 specimens speared during the afternoon in Kona, Hawai'i, were empty or contained only trace amounts of well-digested prey [15]. Five specimens speared within one hour of sunrise had full stomachs. Xanthid crabs accounted for 65.2% of volume followed by hippid crabs (10%) and caridean shrimps (2%) [15].

Mahi [97] described digestive anatomy and examined guts of 198 specimens collected from O'ahu. She identified 23 different prey items. Twenty-five percent of all guts were empty, with the majority of these collected later in the day. Guts contained the most food in early morning, suggesting this species feeds nocturnally. Fish <60 mm feed mostly on copepods, gammarids, megalops larvae and caprellids. For fish > 110 mm, crabs were most important, followed by isopods, alpheid shrimps, and *Stenopus hispidus*.

Additional references

Holland [101] described the chemosensory system of *P. porphyreus*. H. Leba and K. Cole (University of Hawai'i Department of Zoology) are currently working on a reproductive study of this species. Their analysis is expected to include information on size-at-maturity, sex-ratio, oocyte development, and batch fecundity.

SCARIDAE

***Chlorurus spilurus* (Valenciennes, 1840) [1]**

Scarus sordidus Forsskål, 1775 [21]

Scarus spilurus Valenciennes in Cuvier & Valenciennes, 1840 [102]

Pseudoscarus sumbawensis (Bleeker, 1848) [103]

Callyodon erythrodon (Valenciennes in Cuvier & Valenciennes, 1840)

Pseudoscarus vitriolinus Bryan, 1906 [104]

Callyodon sordidus (Forsskål, 1775)

Scarus erythrodon Valenciennes in Cuvier & Valenciennes, 1840

Chlorurus sordidus (Forsskål, 1775)

Geographic range: Central and Western Pacific from the Ryukyu and Ogasawara Islands, Australia (Queensland), Micronesia, the Hawaiian Islands, the Line Islands, east to the Pitcairn Islands and Rapa [1, 2].

First Hawai‘i record: Steindachner, 1900 as *Pseudoscarus sumbawensis* [96].

General Introduction

Formerly included in the Indo-Pacific species *Chlorurus sordidus*, the Hawaiian population was recognized in 2007 as part of a distinct Central and Western Pacific species [1], therefore reports for *C. sordidus* (or synonyms) outside of this range do not apply to the Hawaiian species.

Commonly called bullethead parrotfish. Hawaiian names for growth stages of parrotfishes are, from spawn to adults: ‘ohua, ponuhunuhunu (or panuhunuhunu), and uhu [10].

Engybenitic over reefs and rubble from 1-9 m [2]. During the day this fish is an active swimmer, often in groups, over coral-rich reefs, migrates in schools at twilight, and is solitary at night, resting in reef crevices (sometimes encased in mucus) [15]. Juveniles may school with other scarids [105].

Occurs in three color phases: juveniles are grey to dark brown and often have four narrow whitish stripes on the head and body; the initial phase (which may be females or small, reproductively mature “sneaker” males) is dark reddish brown, with the ventral part of the head and the area around the mouth red, the dental plates are white (this phase can display two longitudinal series of small white spots on the side of the body and a broad white zone posteriorly with a large, round black spot on the base of the caudal fin); terminal males are green with a pink bar on each scale except for on the caudal peduncle, the dental plates are blue-green, the edges of the lips are pink with a submarginal green joining the corner of the mouth and extending across the head below eye level, above this band the head is lavender to pale green, two green bands extend posteriorly from the eye, a broad zone of the body may be suffused with yellow [1].

Minimum legal size in Hawai‘i 12 in. There is no bag limit.

Reproduction and larvae

This species is a diandric protogynous hermaphrodite: sex changes from female to male, however some individuals in the initial (and typically female) phase develop directly into reproductively active males. The initial:terminal phase ratio is 120:1 around Oahu [106]. Based on macroscopic examination, 6.7% of initial phase individuals were male [106]. Based on a plot of gonadosomatic index [106], sex changes begins at ~27 cm SL.

Chlorurus eggs are spindle-shaped, 1.5-3.0 mm long, ~0.5-1.0 mm wide, and spawned pelagically [12]. Larvae of *C. spilurus* have not been described; however Leis & Carson-Ewart [12] offer the following account of parrotfish development: Larvae hatch at 1.6-1.7 mm, and have a large yolk sac, unpigmented eyes, and an unformed mouth. Preflexion larvae are elongate, ovoid in cross-section, with a deep caudal peduncle and 25 myomeres. Larvae become increasingly compressed during development. The gut is rugose and extends slightly beyond the midbody. Before flexion, the gut is straight, with a slight constriction at the posterior end. After flexion, the anterior portion of the gut coils. A large gas bladder is located above mid-gut, but moves to the posterior end of the gut before settlement. The mouth is small, nearly horizontal, and no teeth appear before settlement. There are no spines on the head or pectoral girdle. Shortly before flexion, the dorsal rays begin to form in a posterior to anterior direction. Anal rays form shortly after. Ossification of dorsal spines begins by 5.5 mm, again from posterior to anterior. Anal spines and dorsal rays form at 6-7 mm. Pelvic buds develop ~5.8 mm, but elements are not complete until 8-14 mm. All fin spines are short, slender, weak, and unornamented. Scales do not form until after settlement. Larvae have pigment over the gut, immediately anterior to the anus, and 1-12 melanophores along the ventral midline of the tail.

	Male	Female	N	Range
First reproduction TL FL SL [106] Age		~20 cm ^{oo}		
L ₅₀ TL FL SL Age	pp			
Batch fecundity vs: Size Age Weight				
Sex ratio (M:F) ^{qq}	1:12.4		364	
Mature egg size/volume				
Egg development				
Peak spawning season[106]	June ^{rr}		75	May-Jul [107]
Interspawning interval (# days)				
Spawning Cue [108]	Temporal		4078	14:00-15:00
Spawning mode [12]	Pelagic			
Reproductive mode [106]	Diandric, protogynous			
Mating system [108]	Promiscuous or male territory, group		4078	Some pairs

^{oo} We estimated this parameter based on increased gonadosomatic index with length and may have overestimated minimum size at first reproduction.

^{pp} Gust *et al.* [109] report geographic variation in size and age at maturity for populations on the Great Barrier Reef.

^{qq} Estimated from Howard & Parrish [106] initial:terminal phase ratio of 120:1, with 6.7% of initial phase as males.

^{rr} This estimate is based on increased gonadosomatic index of individuals that are assumed to have reached reproductive size; however, reproductive size has not been verified. This peak does correspond nicely with observed scarid spawning by Poepoe *et al.* [107].

Growth and mortality

	Male	Female	N	Range
Maximum size				
TL [1]	40 cm			
SL ^{ss}	40 cm	32 cm		
FL				
Wt				
Maximum age [110]	9 years ^{tt}			
Growth equation [110] ^{uu}	SL _t in mm = 192.95(1-e ^{-1.083(t in years+0.05)})		70	98-245
Mortality				
Z				
M				
F				

Morphometric relationships

	Equation	N	Range
TL vs SL [106]	SL in cm = 0.820(TL in cm)	91	
TL vs FL			
SL vs FL [106]	SL in cm = 0.821(FL in cm)	91	
TL vs BD			
FL vs BD			
SL vs BD			
TL vs wt			
FL vs wt			
SL vs wt [106]	Wt in g = 0.04989(SL in cm) ^{2.934}	98	11.1-33.3

Diet

This fish scrapes algae from the surface of dead coral. Hobson [15] examined the gut contents of seven specimens from Kona, all were full of fine benthic algae (constituting <20% of volume), calcareous powder, organic slurry and sand. Hobson saw no evidence of coral feeding.

^{ss} These estimates are based on maximum sizes from a gonadosomatic index plot by Howard & Parrish [106] the value for males corresponds nicely with a maximum reported size of 40 cm in Randall [1].

^{tt} Estimated for populations on the Great Barrier Reef.

^{uu} This equation should be viewed with caution. Gust *et al.* [109] found significant geographic variation (K values varied by a factor of ~2, and L_∞ by 43 mm) in growth on the Great Barrier Reef. Munday *et al.* [111] also report sex-based growth differences.

***Scarus psittacus* Forsskål, 1775 [112]**

Scarus psittacus Forsskål, 1775 [21]

Pseudoscarus bataviensis (Bleeker, 1857) [113]

Scarus oviceps non Valenciennes in Cuvier & Valenciennes, 1840 [102]

Scarus gilberti Jenkins, 1901 [114]

Scarus brunneus Jenkins, 1901

Scarus jenkinsi Jordan & Evermann, 1903 [8]

Callyodon gilberti (Jenkins, 1901)

Callyodon brunneus (Jenkins, 1901)

Callyodon jenkinsi (Jordan & Evermann, 1903)

Callyodon bataviensis (Bleeker, 1857)

Scarus galena Jordan, 1925 [115]

Callyodon forsteri (Valenciennes in Cuvier & Valenciennes, 1840)

Scarus forsteri Valenciennes in Cuvier & Valenciennes, 1840

Scarus taeniurus Valenciennes in Cuvier & Valenciennes, 1840

Geographic range: Indo-Pacific from South Africa and the Red Sea to southern Japan, Australia, Micronesia, the Hawaiian Islands, the Tuamotu Archipelago, and the Marquesas [2].

First Hawai‘i record: Steindachner, 1900 as *Pseudoscaras bataviensis* [96]

General Introduction

Commonly called palenose parrotfish. Hawaiian names for growth stages of parrotfishes are, from spawn to adults: ‘ohua, ponuhunuhunu (or panuhunuhunu), and uhu [10].

Engyrbenthic over rock and reef from 1-5 m [2]. During the day juveniles and females tend to occupy shallow reef flats, usually in aggregations, whereas males tend to be solitary on the reef face [15]. At night, this fish rests encased in a mucus envelope in reef crevices [15].

Occurs in two distinct color phases: juveniles are similar to initial phase, which is reddish brown to gray with a dark spot at the base of the first membrane of the dorsal fin and a small black and blue spot at the upper base of the pectoral fins; the terminal male is green posteriorly, with pink edges on the scales (more pink and less green on scales anteriorly), the abdomen is pink with a longitudinal series of green spots following the scale rows, a green bands edges each lip, these bands join at the angle of the mouth and continue below the eye, two additional green band extend from the posterior of the eye, the snout is dark purple to lavender-gray [1].

Minimum legal size in Hawai‘i is 12 in. There is no bag limit.

Reproduction and larvae

This species is a diandric protogynous hermaphrodite: sex changes from female to male, however some individuals in the initial (and typically female) phase develop directly into reproductively active males. The initial:terminal phase ratio is 77:1 around O‘ahu [106]. Based on macroscopic examination, 28.6% of intitial phase individuals were male [106]. Based on a plot of gonadosomatic index [106], sex changes begins at ~16 cm SL.

Scarus eggs are spindle-shaped, 1.5-3.0 mm long, ~0.5-1.0 mm wide, and spawned pelagically [12]. Larvae of *S. psittacus* have not been described; however Leis & Carson-Ewart [12] offer the following account of parrotfish development: Larvae hatch at 1.6-1.7 mm, and have a large yolk sac, unpigmented eyes, and an unformed mouth. Preflexion larvae are elongate, ovoid in cross-section, with a deep caudal peduncle and 25 myomeres. Larvae become increasingly compressed during development. The gut is rugose and extends slightly beyond the midbody. Before flexion, the gut is straight, with a slight constriction at the posterior end. After flexion, the anterior portion of the gut coils. A large gas bladder is located above mid-gut, but moves to the posterior end of the gut before settlement. The mouth is small, nearly horizontal, and no teeth appear before settlement. There are no spines on the head or pectoral girdle. Shortly before flexion, the dorsal rays begin to form in a posterior to anterior direction. Anal rays form shortly after. Ossification of dorsal spines begins by 5.5 mm, again from posterior to anterior. Anal spines and dorsal rays form at 6-7 mm. Pelvic buds develop ~5.8 mm, but elements are not complete until 8-14 mm. All fin spines are short, slender, weak, and unornamented. Scales do not form until after settlement. Larvae have pigment over the gut, immediately anterior to the anus, and 1-12 melanophores along the ventral midline of the tail.

	Male	Female	N	Range
First reproduction				
TL				
FL				
SL [106]		~10 cm ^{vv}		
Age				
L ₅₀				
TL				
FL				
SL				
Age				
Batch fecundity vs:				
Size				
Age				
Weight				
Sex ratio (M:F) [106] ^{ww}		1:2.4	1397	
Mature egg size/volume				
Egg development				
Peak spawning season [106]	August-November ^{xx}			May-Nov ^{yy}
Interspawning interval (# days)				
Spawning Cue				
Spawning mode [12]		Pelagic		
Reproductive mode [116]		Diandric, protogynous		
Mating system		Polygyny		

^{vv} We estimated this parameter based on increased gonadosomatic index with length and may have overestimated minimum size at first reproduction.

^{ww} Estimated from Howard & Parrish [106] initial:terminal phase ratio of 120:1, with 28.6% of initial phase as males.

^{xx} Based on peaks in sparse gonadosomatic index plots by Howard & Parrish [106].

^{yy} This adds *Scarus* spawning observations by Poepoe *et al.* [107], which do not overlap with gonadosomatic index plots of Howard & Parrish [106].

Growth and mortality

	Male	Female	N	Range
Maximum size TL [1] SL [106] ^{zz} FL wt	30 cm ~26 cm	~22 cm		
Maximum age [110]	5 years ^{aaa}			
Growth equation [110] ^{bbb}	$SL_t \text{ in mm} = 172.10(1 - e^{-1.190(t \text{ in years} + 0.05)})$		57	104-215
Mortality Z M F				

Morphometric relationships

	Equation	N	Range
TL vs SL [106]	$SL \text{ (cm)} = 0.784 \text{ TL (cm)}$	99	4.6-31.3
TL vs FL [106]	$FL \text{ (cm)} = 0.957 \text{ TL (cm)}$	99	4.6-31.3
SL vs FL [106]	$SL \text{ (cm)} = 0.819 \text{ FL (cm)}$	99	4.6-31.3
TL vs BD			
FL vs BD			
SL vs BD			
TL vs wt			
FL vs wt			
SL vs wt [106]	$Wt \text{ in g} = 0.03934(SL \text{ in cm})^{3.005}$	99	4.6-31.3

Diet

This species scrapes benthic algae from rock surfaces during the day. Hobson [15] examined two specimens and found <20% algae mixed with calcareous powder, organic slurry and sand. There was no evidence of coral tissue or mucus.

^{zz} These estimates are based on maximum sizes from a gonadosomatic index plot by Howard & Parrish [106].

^{aaa} Estimated from a Great Barrier Reef population.

^{bbb} This equation should be viewed with caution. Choat & Robertson [110] report geographic variation on the Great Barrier Reef.

ACANTHURIDAE

***Acanthurus triostegus sandvicensis* Streets, 1877 [1]**

Chaetodon triostegus Linnaeus, 1758 [117]

Acanthurus triostegus var. *sandvicensis* Streets, 1877 [118]

Teuthis triostegus (Linnaeus, 1758)

Hepatus triostegus (Linnaeus, 1758)

Teuthis sandvicensis (Streets, 1877)

Acanthurus sandvicensis Streets, 1877

Acanthurus triostegus (Linnaeus, 1758)

Geographic range: The subspecies is endemic to the Hawaiian Islands and Johnston Atoll; however the species occurs throughout the Indo-Pacific region (except around the Arabian Peninsula) and the eastern tropical Pacific [1, 2].

First Hawai'i record: Broussonet, 1782 as *Chaetodon triostegus* [119]

General Introduction

Commonly called manini or convict tang. Young were called 'ōhua liko (tender leaf bud) when transparent and about the size of a postage stamp, 'ōhua kani'o when bars appear about a day after settlement, 'ōhua pala pohaku (stone slime) or 'ōhua ha'eka'eka (grimy looking) when the skin begins to darken, and kakala manini when about half grown [10].

Engyobenthic over rock, coral, rubble, or sand from 1-46 m, throughout the rest of its range, the species occurs to 90m [2]. Newly settled fish are abundant in tidepools [1]. Juveniles, which are gregarious and often seen in groups, move into deeper water. Adults can be solitary, in small groups, or in large, dense feeding aggregations. Manini are found close to coral or rocks and a source of algae (food). They are not abundant in areas of heavy coral cover. Schooling behavior is seen during spawning. At night, manini rest on the substrate in a state of torpor [120].

Titcomb [10] reports that Hawaiians would catch the 'ōhua "by the million", mix them with salt, and scatter them on lava rocks to dry in the sun. These were stored for future consumption or taken inland for trade. In the 1960s, manini was described as the most abundant and commercially important surgeonfish in Hawai'i [120]. It was the second-most abundant species encountered in a recent creel survey of recreational fishers in Waikiki [121].

Minimum take-home size in Hawai'i is 5 in. There are no bag limits.

Reproduction and larvae

Development has been illustrated and described in detail by Randall [120]: Eggs float in seawater, are transparent, spherical (0.58-0.70 mm in diameter), and contain a single 0.165 mm diameter oil globule. Eggs fertilized and reared in vitro at an average 24°C, hatched ~26 h post-fertilization at a length of ~1.7 mm, had a large yolk sac, unformed mouth, and no eye pigment. Aquarium-kept larvae 42.5-hours-old could maintain (or decrease) depth and avoid approaching objects, whereas 5-day-old larvae were capable of oriented swimming. The 5-day-old larvae had resorbed all yolk and about half of the oil globule. 5.5-day-old larvae appeared to exhibit

feeding behavior. Positive phototaxis is inferred for the acronurus stage; this behavior disappears as settlement begins.

Acronuri, ranging from 22.0-29.5 mm SL, move inshore to settle in tidepools at night during May through September, with peaks at the new moon [120]. Otolith increment analysis indicates larval duration is 54 days (L. Basch, D. Shafer, & B. Walsh, unpublished data). Transformation takes 4-5 days [120].

Leis & Carson-Ewart [12] offer the following generalized account of surgeonfish development: Preflexion larvae are strongly compressed and moderate in depth, becoming deep in head and trunk at ~2.3 mm and even deeper following flexion. The tail is much less deep than the trunk. Myomere count is 21-23. The gut is coiled and reaches 44-61% of body length before flexion. A small gas bladder is located above the anterior portion of the gut. Brain case is vaulted. The snout is long and head shape is triangular. The terminal mouth does not reach the eye; small, conical teeth form in both jaws at ~4 mm. Eyes are round, gill membranes are broadly attached to the isthmus, and head spination is extensive. The smallest larvae (~1.8 mm) have a serrate supraoccipital crest. The second dorsal spine and the pelvic spine are first to form (at ~2.3 mm). Both of these are serrate by 2.8 mm, when more dorsal spines form. An anal spine ossifies at 3 mm and becomes serrate shortly thereafter. Dorsal and anal rays form immediately after flexion, and a second anal spine ossifies. Pectoral rays form at 4.6 mm. All supporting elements of pectoral, anal and dorsal fins are present by 5-6 mm. All pelvic elements are present by 8mm. The first dorsal and anal spines are markedly short. At ~5 mm, scales form as small, broad-based lamina projecting upright from a basal plate. At ~ 8 mm, these are arranged in vertical rows. The acronurus stage begins at ~ 17 mm with the formation of the peduncular spine. The lateral line is complete by 24 mm. Before settling, larvae are extremely compressed with head serrations (relatively) reduced in size. Preflexion larvae are moderately pigmented on the brain and gut. The acronurus stage has a silvery gut and the beginnings of bars.

	Male	Female	N	Range
First reproduction TL FL SL [120] Age		101 mm		
L ₅₀ TL FL ^{ccc} [122] SL Age [122]	<70 mm <168 d	164 mm 440 d	52♂, 70♀	
Batch fecundity vs: Size [122] Age Weight		-648,588.17 + (FL in mm)4226.06	18	158-223
Sex ratio (M:F) [122]	1:1.33 ^{ddd}		122	
Mature egg size/volume [120]	~0.70 mm			0.66-0.70
Egg development [122]	Group synchronous			
Peak spawning season [120]	February – June		193	Dec-Jul
Interspawning interval [120]	29.5 days			
Spawning Cue [120]	Full moon		3,863	-12 to +2 d
Spawning mode [120]	Pelagic, group spawning ^{ccc}			
Reproductive mode [122]	Gonochorist			
Mating system				

Growth and mortality

	Females	Males	N	Range
Maximum size TL [122] SL [122] FL [122] wt [122]	234 mm 183 mm 223 mm 332 g	227 mm 181 mm 271 mm 290.5 g	188 187 188 115	
Maximum age [122]	>4 years ^{fff}		297	
Growth equation [122]	l_t in mm = 202.798(1-e ^{-0.0039276(age in days-18.6533)}) ^{ggg}		45	54-819
Mortality Z [122] M [122] F [122]	0.68170, quarterly 0.53549, quarterly 0.14621, quarterly		73 224	

^{ccc} Manini do not have forked tails; FL as used here is the length to the end of the middle ray of the tail.

^{ddd} ~2/3 of 291 adults caught in unbaited fish traps in 30-90' of water off O'ahu were male [120].

^{eee} Observations from the Tuamotu Archipelago.

^{fff} Likely much longer. Specimens up to 223 mm were reported, but ages could only be estimated for specimens up to the L_∞ of 200 mm FL.

^{ggg} Otolith increments are assumed to form daily. Although not statistically tested, growth did not appear to vary by sex or location.

Morphometric relationships

	Equation	N	Range
TL vs SL			
TL vs FL [122]	$FL \text{ in mm} = 1.796 + (TL \text{ in mm})0.939$	188	29.5-234.0
SL vs FL [122]	$FL \text{ in mm} = 1.922 + (SL \text{ in mm})1.196$	187	24.0-183.0
TL vs BD			
FL vs BD [122]	$FL \text{ in mm} = 9.397 + (SL \text{ in mm})2.190^{hhh}$	153	14.0-106.7
SL vs BD			
TL vs wt			
FL vs wt [122]	$Wt \text{ in g} = 0.00001214(FL \text{ in mm})^{3.1557}$	115	85.0-223.0
SL vs wt			

Diet

Juvenile and adult manini feed almost constantly during the day on fine filamentous algae. Animals in experimental studies preferred the red alga, *Polysiphonia*, and the green *Enteromorpha* [120, 121].

Additional references

Hayes *et al.* [14] provide the size distribution of recreational catch at Puako, Hawai‘i. Poepoe *et al.* [107] describe the spawning season at Mo‘omomi Bay, Moloka‘i. Sale [123] performed experiments on depth and shelter use by juveniles.

^{hhh} As the distance between the origins of the dorsal and pelvic fins.

***Ctenochaetus strigosus* (Bennett, 1828)** [124]

Acanthurus strigosus Bennett, 1828 [125]

Ctenochaetus striatus non (Quoy & Gaimard, 1825) [87]

Geographic range: Hawaiian Islands and Johnston Atoll [2].

First Hawai‘i record: Bennett, 1828 as *Acanthurus strigosus* [125]

General Introduction

Some fragmentary life-history information is reported for *C. strigosus* from throughout the Indo-Pacific. However, a 2001 revision of the genus by Randall & Clements [124] recognized *Ctenochaetus strigosus* as a Hawaiian endemic, making the relevance of studies from the South Pacific and Indian oceans suspect.

Commonly called kole, goldring surgeonfish, or goldring bristletooth.

Engyobenthic over coral, rock, and rubble at 6–113 m [2]; however, it is usually shallow [124] and found in the sub-surge zone [126]. Individuals are usually solitary [124].

It is commercially important, ranking second in aquarium catch records [127]. It also important in recreational/subsistence fishing, and was the most abundant fish in Waikiki creel surveys [121], all were taken by spear.

Fishing is unregulated.

Reproduction and larvae

Recruitment begins in May and is heaviest June through September [128, 129]. Juvenile stage is yellow [1].

Eggs are pelagic [12]. An acronurus larva and recently transformed juvenile were illustrated by Randall [130]. Leis & Carson-Ewart [12] offer the following generalized account of surgeonfish development: Preflexion larvae are strongly compressed and moderate in depth, becoming deep in head and trunk at ~2.3 mm and even deeper following flexion. The tail is much less deep than the trunk. Myomere count is 21-23. The gut is coiled and reaches 44-61% of body length before flexion. A small gas bladder is located above the anterior portion of the gut. Brain case is vaulted. The snout is long and head shape is triangular. The terminal mouth does not reach the eye; small, conical teeth form in both jaws at ~4 mm. Eyes are round, gill membranes are broadly attached to the isthmus, and head spination is extensive. The smallest larvae (~1.8 mm) have a serrate supraoccipital crest. The second dorsal spine and the pelvic spine are first to form (at ~2.3 mm). Both of these are serrate by 2.8 mm, when more dorsal spines form. An anal spine ossifies at 3 mm and becomes serrate shortly thereafter. Dorsal and anal rays form immediately after flexion, and a second anal spine ossifies. Pectoral rays form at 4.6 mm. All supporting elements of pectoral, anal and dorsal fins are present by 5-6 mm. All pelvic elements are present by 8mm. The first dorsal and anal spines are markedly short. At ~5 mm, scales form as small, broad-based lamina projecting upright from a basal plate. At ~8 mm, these are arranged in vertical rows. The acronurus stage begins at ~17 mm with the formation of the

peduncular spine. The lateral line is complete by 24 mm. Before settling, larvae are extremely compressed with head serrations (relatively) reduced in size. Preflexion larvae are moderately pigmented on the brain and gut. The acronurus stage has a silvery gut.

	Male	Female	N	Range
First reproduction TL [131] ⁱⁱⁱ FL SL Age	140	100		
L ₅₀ TL FL SL Age				
Batch fecundity vs: Size Age Weight				
Sex ratio (M:F) [131]	1.53:1 ⁱⁱⁱ			74-196 mm TL
Mature egg size/volume				
Egg development				
Peak spawning season [132]	March-June		160♂, 101♀	Mar-Aug
Interspawning interval (# days)				
Spawning Cue [128]	Sunset			-55 to +5 min
Spawning mode				
Reproductive mode				
Mating system [108]	Promiscuous, group		870	Some pairs

ⁱⁱⁱ Parrish & Claisse [131] base these estimates on gonadosomatic index values and warn that the values are estimates.

ⁱⁱ Parrish & Claisse [131] note that males dominate the sex ratio at 130 mm TL and that a large majority of individuals >150 mm TL are male; however, they warn that this pattern may be depth-based.

Growth and mortality

	Male	Female	N	Range
Maximum size ^{kkk} TL [1] SL FL Wt	24 cm			
Maximum age [131]	18 years ^{lll}		136	
Growth equation ^{mmm}			136	74-188 mm TL
Mortality Z M F				

Morphometric relationships

	Equation	N	Range
TL vs SL [131]	TL in mm = -2.40 + 1.36(SL in mm)	202	~62-122 mm
TL vs FL			
SL vs FL			
TL vs BD			
FL vs BD			
SL vs BD			
TL vs wt			
FL vs wt			
SL vs wt [131]	Wt in grams = 0.000045(SL in mm) ^{3.05}	202	~50-150 mm

Diet

Additional references

Poepoe et al [107] describe the spawning season at Mo‘omomi Bay, Moloka‘i. Sancho et al. [90] describe pre-settlement behavior of and predation on larvae.

^{kkk} Randall [1] reports a maximum size of 240 cm.

^{lll} Parrish & Claisse [131] base this estimate on otolith analysis, assuming increments are formed annually.

^{mmm} Parrish & Claisse [131] constructed sex-based growth equations but did not provide parameters. Both sexes grow rapidly for the first few years, then much slower for the duration of the lifespan. Small males appear to grow faster than small females, and males reach a larger size than females.

***Naso unicornis* (Forsskål, 1775) [133]**

Chaetodon unicornis Forsskål, 1775 [21]

Naseus fronticornis Lacépède, 1801 [73]

Naseus unicornis (Forsskål, 1775)

Monoceros unicornis (Forsskål, 1775)

Acanthurus unicornis (Forsskål, 1775)

Geographic range: Indo-Pacific from South Africa and the Red Sea to southern Japan, the Ogasawara Islands, Australia, Micronesia, the Hawaiian Islands, the Tuamotu Archipelago, and the Marquesas [2].

First Hawai'i record: Commerson *in* Cuvier & Valenciennes, 1835 as *Naseus fronticornis* [134]

General Introduction

Commonly called bluespine unicornfish. The generic Hawaiian name for *Naso* species is kala; young are called pakalakala [10].

Engybenitic over coral and rock from 1-33 m [2]. Primarily an inshore species and will enter shallow water [1]. Typically forms large schools on reef crests, but is solitary in less rugose habitats [135]. Individuals <20 cm TL dominate the backreef, whereas larger individuals dominate the reef crest [135].

Usually most active during the day [135]. Home range size (minimum convex polygon) averages 3,717 m² (range: 325-7650) [135]

Minimum catch size in Hawai'i is 14 in. There is no bag limit.

Reproduction and larvae

Eggs are pelagic [12]. Larvae of *N. unicornis* have not been described; however Leis & Carson-Ewart [12] illustrate the development of a *Naso* species and offer the following generalized account of surgeonfish development: Preflexion larvae are strongly compressed and moderate in depth, becoming deep in head and trunk at ~2.3 mm and even deeper following flexion. The tail is much less deep than the trunk. Myomere count is 21-23. The gut is coiled and reaches 44-61% of body length before flexion. A small gas bladder is located above the anterior portion of the gut. Brain case is vaulted. The snout is long and head shape is triangular. The terminal mouth does not reach the eye; small, conical teeth form in both jaws at ~4 mm. Eyes are round, gill membranes are broadly attached to the isthmus, and head spination is extensive. The smallest larvae (~1.8 mm) have a serrate supraoccipital crest. The second dorsal spine and the pelvic spine are first to form (at ~2.3 mm). Both of these are serrate by 2.8 mm, when more dorsal spines form. An anal spine ossifies at 3 mm and becomes serrate shortly thereafter. Dorsal and anal rays form immediately after flexion, and a second anal spine ossifies. Pectoral rays form at 4.6 mm. All supporting elements of pectoral, anal and dorsal fins are present by 5-6 mm. All pelvic elements are present by 8mm. The first dorsal and anal spines are markedly short. At ~5 mm, scales form as small, broad-based lamina projecting upright from a basal plate. At ~ 8 mm, these are arranged in vertical rows. The acronurus stage begins at ~ 17 mm with the formation of the peduncular spine. The lateral line is complete by 24 mm. Before settling,

larvae are extremely compressed with head serrations (relatively) reduced in size. Preflexion larvae are moderately pigmented on the brain and gut. The acronurus stage has a silvery gut. The keris larval stage is about 40 mm total length [1].

Doherty et al. [136] report density-independent settlement mortality of ~61%. Density-dependent post-settlement mortality, ranging from 9-20%, was seen over the following two weeks in a population from Moorea.

Spawning occurred near the surface of a 2.1 m deep aquarium [137].

	Male	Female	N	Range
First reproduction				
TL				
FL				
SL				
Age				
L ₅₀				
TL				
FL				
SL				
Age				
Batch fecundity vs:				
Size				
Age				
Weight				
Sex ratio (F:M)				
Mature egg size/volume				
Egg development				
Peak spawning season				
Interspawning interval (# days)				
Spawning Cue				
Spawning mode				
Reproductive mode				
Mating system				

Growth and mortality

	Male	Female	N	Range
Maximum size TL [1] SL FL wt	70 cm			
Maximum age [138]	30 years			
Growth equation [110] ^{nmn}	$SL_t \text{ in mm} = 385.77(1 - e^{-0.489(\text{age in years} + 0.14)})$		59	176-494
Mortality Z M F				

Morphometric relationships

	Equation	N	Range
TL vs SL			
TL vs FL			
SL vs FL			
TL vs BD			
FL vs BD			
SL vs BD			
TL vs wt			
FL vs wt			
SL vs wt [138] ^{ooo}	$Wt = 0.00008495(SL \text{ in mm})^{2.843}$	56	50-457 mm

Diet

Five specimens, 298-440 mm long, from the Marshall Islands ate frondose algae (*Dictyota* and *Padina*) [81].

^{nmn} Data from Great Barrier Reef.

^{ooo} Choat & Axe [138] provide a relationship from Australian specimens, but do not indicate the unit of measurement for weight.

DISCUSSION

Table 1 summarizes the status of life history work for the 13 species covered in this compendium. Hawai‘i-based life history data was most complete for *Acanthurus triostegus sandvicensis* (20 of 21 parameters from Hawaiian populations), *Caranx melampygyus* (17 parameters) and the goatfishes *Parupeneus multifasciatus* and *P. porphyryreus* (14 parameters each). Life history information was particularly sparse for *Naso unicornis* (2 parameters) and *Sargocentron diadema* (3 parameters). Average coverage was greatest for families Mullidae and Carangidae (mean of 12 and 11.3 parameters respectively) and least for Holocentridae (7.5 parameters). The overall average was 10.3 (by family) to 10.5 (by species) parameters.

All but three species (*Acanthurus triostegus sandvicensis*, *Caranx melampygyus*, and *Parupeneus multifasciatus*) lacked one or more pertinent pieces of life history information necessary to construct a surplus production model (e.g., age-growth data, mortality, or length-weight relationship). Only *C. melampygyus* and *A. triostegus sandvicensis* had sufficient information necessary to estimate annual reproductive output (batch fecundity data, sex ratio, L_{50} and inter-spawning interval).

First Reproduction and L_{50}

Of the 28 regulated Hawaiian reef-fish species^{PPP}, 17 are regulated by size alone. For most, the minimum landing size coincides with the purported minimum size at maturity or L_{50} . The majority of studies in this compendium determined size at first maturity or L_{50} by macroscopic or gravimetric examination and did not list distinct values for males and females. In cases where sexes mature at different sizes, using an averaged L_{50} may be misleading to managers, particularly if a goal of management is to maximize female reproductive output. Similarly, the use of macroscopic classification system may introduce excessive error in maturity and sex-ratio estimates [139], particularly for small-bodied fishes. Longenecker and Langston (unpublished) examined gonads of *A. triostegus sandvicensis* by gross morphology, histological classification, and GSI. Of the 93 individuals for which they provided both gross and histological classifications, six percent were assigned the wrong gender (classified male when female or vice-versa) and 18% were misclassified by maturity (called mature when immature or vice versa) when using gross classification alone. The use of histological sections also allowed them to resolve the gender and maturity of an additional fifteen fish (16%) from smallest size-classes that had been classified as juvenile or undifferentiated via macroscopic examination. They also found that plotting changes in gonadosomatic index (GSI) vs. size was accurate at predicting

^{PPP} Includes *Kuhlia sandvicensis*, *K. xenur*, *Mugil cephalus*, *Chanos chanos*, *Naso unicornis*, *N. brevirostris*, *N. annulatus*, *N. hexacanthus*, *Acanthurus triostegus sandvicensis*, *Parupeneus multifasciatus*, *P. porphyryreus*, *Polydactylus sexfilis*, *Albula glossodonta*, *Scarus dubius*, *S. psittacus*, *S. rubroviolaceus*, *Chlorurus sordidus*, *C. perspicillatus*, *Caranx ignobilis*, *C. lugubris*, *C. melampygyus*, *C. sexfasciatus*, *Carangoides equula*, *C. ferdau*, *C. orthogrammus*, *Aprion virescens* and *Mulloidichthys flavolineatus*

Table 3. Checklist of known life history parameters for thirteen species of exploited Hawaiian fishes. Closed circles indicate that the information comes from Hawaiian studies whereas open circles indicate information from locations outside Hawai‘i. Triangles indicate that the information supplied is not specific to the indicated species, but is assumed to be similar to others in the family. Asterisks indicate parameters which are undergoing current work in Hawai‘i.

	1st Reproduction	L50	Batch Fecundity	Sex Ratio	Egg Size	Oocyte Development	Spawning Season	Inter-Spawning Interval	Spawning Cue	Spawning Mode	Reproductive Mode	Mating System	Pelagic Larval Duration	Larval Development	Maximum Size	Maximum Age	Growth Equation	Mortality	Length vs. Length	Length vs. Weight	Diet
<i>Myripristis amaena</i>	●		●		●	●	●		▽				●	△	●	●	●		●	●	●
<i>Sargocentron diadema</i>									▽	▽				▽	●		●				●
<i>Caranx ignobilis</i>	●	●		●	▽		●			●	●			△	●	●	●		●	●	●
<i>Caranx melampygus</i>	●	●	●	●	●		●	●	●	●	●			△	●	●	●	●	●	●	●
<i>Pseudocaranx cheilio</i>	△	△		●	△		△			△				△	●	●	●			●	●
<i>Mulloidichthys flavolineatus</i>	*	●	*	○	*	*	○			●	*		○	△	●	●	●		●	●	●
<i>Parupeneus multifasciatus</i>	●	●	*	●	●	●				●	●		*	△	●	●	●	●	●	●	●
<i>Parupeneus porphyreus</i>	●	*	*	●	●	●	●			●	●		●	△	●	●	●		●	●	●
<i>Chlorurus spilurus</i>	●			●	△		●			●	●	●		△	●	●	○		●	●	●
<i>Scarus psittacus</i>	●			●			●			●	●	●		△	●	○	○		●	●	●
<i>Acanthurus triostegus sandvicensis</i>	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●
<i>Ctenochaetus strigosus</i>	●	*	*	●			●		●	△		●		△	●	●	*		●	●	●
<i>Naso unicornis</i>										●				△	●	○	○		○	○	○

female L_{50} but was grossly inaccurate for predicting male L_{50} . We suggest that future studies should report separate L_{50} for males and females and that researchers “spot check” macroscopic gonadal classifications with histological data. Not only can the use of gonad histology improve accuracy of L_{50} estimates, but it will also result in more reliable estimates of sex ratio (particularly operational sex ratio) and can be used to determine interspawning interval and evaluate ovaries for suitability for batch fecundity analysis.

Spawning Seasonality

Studies on spawning seasonality from Hawaiian populations were available for eight species (Table 2). Data reported for two additional species (*P. cheilio* and *P. multifasciatus*) were too fragmented to plot seasonality. For most species, spawning began in the winter or early summer months and declined or abated during the late summer (August-November). These data are similar to the pattern documented by Walsh [128]. Overall, overlap of peak spawning was greatest in May and June. Only the parrotfish *S. psittacus* showed peak spawning during September-November.

All but one of the studies determined spawning seasonality by gonadosomatic index (GSI) or macroscopic classification of the gonads. Macroscopic classification is problematic for the reasons mentioned previously. In contrast, GSI is among the most efficient and widely-used method to assess spawning seasonality; however, it can only detect relative changes in reproductive investment over time. In some species, spawning may continue at reduced levels during periods of low GSI (e.g., Langston [140]). With proper histological validation, GSI values can be correlated with oocyte stages (see Brewer *et al.* [141]), resulting in a more informative data set. Histology can also be used selectively to investigate extremes in GSI values. For example, Dee and Parish [11] plotted GSI by season for *M. amaena* but also used ovarian histology to double-check their data. By doing this, they were able to validate that no spawning occurred during months with low GSI.

Batch Fecundity

Hawai‘i-based batch fecundity equations were available for only three of the 13 species investigated. A curvilinear relationship was evident for *M. amaena* [11] and *C. melampygyus* [32] whereas in *A. triostegus sandvicensis* [122] the relationship was linear. Predictably, maximal fecundity was greatest for the larger-bodied *C. melampygyus* (up to 4,270,000 eggs/spawn vs. 70,000 for *M. amaena*). Limited fecundity data was also provided for the goatfishes *P. porphyreus* [99] and *P. multifasciatus* [91], but were insufficient to generate curves. The small sample-size (<20) for the above species and complete lack of information for others emphasizes the need for additional fecundity studies in Hawaiian reef fishes.

Table 4. Reported spawning seasonality for eight species of exploited Hawaiian fishes. Methods used to determine spawning seasonality are histology (Histo), gonadosomatic index (GSI), and visual (Vis). Open circles indicate months when spawning is reported. Closed circles indicate maximal peak spawning. “X” indicates months for which no data are available.

Species	Method	J	F	M	A	M	J	J	A	S	O	N	D
<i>Myripristis amaena</i> ^{qqq}	GSI, Vis. Histo	●			●	○	●			X	○		
<i>Caranx ignobilis</i> ^{rrr}	Vis.	X	X			X	●	●	○	○		○	
<i>Caranx melampygus</i> ^{sss}	Vis.		X		○	○	●	●			○		
<i>Parupeneus porphyreus</i> ^{ttt}	GSI	●	○	○	○	○	●	○					○
<i>Chlorurus spilurus</i> ^{uuu}	GSI	X	X	X		○	●	X	X	X	○	○	
<i>Scarus psittacus</i> ^{vvv}	GSI	X	X	X		X	X	X	●	X	●	○	○
<i>Acanthurus triostegus sandvicensis</i> ^{www}	Vis.	○	●	●	●	●	○	○					○
<i>Ctenochaetus strigosus</i> ^{xxx}	GSI		○	●	●	●	○	○	○				

^{qqq} Based on our interpretation of Fig. 5 from Dee and Parrish [11].

^{rrr} Based on our interpretation of Fig. 5 from Sudekum *et al.* [32].

^{sss} Based on our interpretation of Fig. 5 from Sudekum *et al.* [32].

^{ttt} Based on our interpretation of Fig. 6 from Moffitt [99].

^{uuu} Based on our interpretation of Fig. 12 from Howard and Parrish [106].

^{vvv} Based on our interpretation of Fig. 13 from Howard and Parrish [106].

^{www} Based on plot and interpretation of female gonad length from table 5 of Randall [120].

^{xxx} Based on the combined data of Parrish and Claisse [131] and Lobel [132].

Age-Growth

Hawai'i-based age-growth information was available for 9 of 13 species. Growth information for three additional species (*N. unicornis*, *C. spilurus* and *S. psittacus*) was provided from studies conducted elsewhere. With the exception of *M. flavolineatus* [77], growth parameters were estimated from counts of otolith increments. Otolith increment periodicity was successfully validated for *M. amaena* [13] and *C. melampygyus* [32] and attempted for *C. strigosus* [131] and *A. triostegus sandvicensis* [122]. Although otolith validation can be difficult and time consuming, it is imperative to interpreting otolith-derived growth data. Misinterpretation of increment formation may result in inaccurate age estimates [142] and lead to overexploitation of fish stocks [143]. This is particularly important for Hawaiian studies, as estimates of longevity vary widely depending on the assumed periodicity of otolith increments. For example, maximum age estimates for *A. triostegus sandvicensis* were 4+ years (assumed daily increments) [122] whereas the confamilial *C. strigosus* is reported to live 18+ years (annual increments [131]).

Mortality

Mortality estimates were available for only three species. Despite this, a number of studies [11, 13, 14, 26, 28, 43, 77] contain or reference large sets of size-frequency data. When combined with existing growth equations [13, 27, 32, 77], these data could be used to estimate mortality for an additional three species: *C. ignobilis*, *M. amaena* and *M. flavolineatus*.

Sampling Bias

Much of the existing growth and reproductive information for carangids (especially *P. cheilio*) comes from populations in the Northwestern Hawaiian Islands. These populations occur at different latitudes (with temperature, hydrographic regimes, primary productivity, etc.) than Main Hawaiian Island specimens and are most are not subject to significant fishing pressure. As such, this information should be applied with caution to Main Hawaiian Island populations. When possible, we recommend life history studies from Main Hawaiian Island to tease-out differences in natural vs. fishing mortality and to examine the role that fishing may play in driving-down L_{50} .

Need for a Life History Network

Several studies collected but did not analyze otoliths or gonadal tissues. Creating a central repository for life history specimens would increase the usefulness of collected specimens (e.g., from Northwestern Hawaiian Islands cruises). Quality assurance could be achieved with the production of a manual for the standardized collection, preservation, and cataloging of incoming samples.

Literature Sources for Life History Data

Approximately 51% of the key Hawai‘i-based life history references cited in this compendium came from peer-reviewed journals. The remainder came from non-peer-reviewed books (6%) technical reports (35%) and theses or dissertations (8%). Although the lack of peer review may cause some to question the quality of the information, we feel the limited availability of these publications is of greater concern. Because they are not indexed in literature databases, grey literature references may lie undiscovered by most researchers. Even if grey literature references are located, the publications have limited circulation, are seldom available electronically and are usually inaccessible to researchers outside the state. This problem could be corrected by encouraging state and federal laboratories to publish pertinent information from technical reports in peer-reviewed journals. In addition, the Hawai‘i Department of Land and Natural Resources may be able to institute a policy requiring all recipients of scientific collecting permits to submit electronic copies of publications (both peer-reviewed and grey literature) to their office at the completion of the study. These titles could be indexed online and electronic copies could be made available by request under a fair-use policy.

SUMMARY OF RECOMMENDATIONS

- 1) Update methodology used to estimate key life history parameters (*i.e.*, incorporate histological studies to estimate sex ratio, minimum size at maturity and L_{50}).
- 2) Encourage additional life history studies for the Main Hawaiian Islands.
- 3) Re-evaluate current size-restrictions for species for which L_{50} is known.
- 4) Push for increased effort in estimating batch and annual fecundity for important target species.
- 5) Validate rate of otolith increment deposition for key species using chemical marking techniques.
- 6) Analyze *existing* data sets to fill in the gaps (for example, estimate total mortality of *M. amaena* using existing age-growth and size-frequency data).
- 7) Encourage publication in peer-reviewed journals.
- 8) Create a repository and database for Hawai‘i-based life history studies. This repository could:
 - i) provide a set of written guidelines for the collection of life history data (see #1);
 - ii) store and catalog unused specimens for future analysis;
 - iii) track specimens collected under Special Activities Permits;
 - iv) house an electronic library of life history information;
 - v) post an up-to-date bibliography of life history publications on the internet;

- vi) where allowed by copyright and fair-use laws, provide electronic copies of hard-to-find life history publications and technical reports;
and
- vii) cross-reference life history studies with relevant demographic studies

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