

Habitat- and sex-specific life history patterns of yellow tang *Zebrasoma flavescens* in Hawaii, USA

Jeremy T. Claisse^{1,*}, Marco Kienzle², Megan E. Bushnell¹, David J. Shafer¹,
James D. Parrish¹

¹University of Hawaii, Department of Zoology, 2538 McCarthy Mall, Edmondson 165, Honolulu, Hawaii 96822, USA

²CSIRO, Marine and Atmospheric Research Division, 233 Middle Street, Cleveland, Queensland 4163, Australia

ABSTRACT: Yellow tang *Zebrasoma flavescens* is the primary coral reef fish species taken in Hawaii for the aquarium trade. As part of an extensive adaptive management effort that included a network of marine protected areas that prohibited commercial aquarium fishing, an emphasis was placed on obtaining habitat- and sex-specific life history information for this valuable species. Using otolith and capture-mark-recapture methods we examined sexual differences in ontogenetic patterns of habitat use, growth rate, size dimorphism and longevity. Age validation using tetracycline to mark otoliths provided evidence that a single annulus formed each year. Yellow tang are a long-lived species (the oldest individual collected was 41 yr old) and display an asymptotic growth pattern typical of the family Acanthuridae. Median size and age at the transition between deeper coral-rich and shallow turf-dominated habitat use were about 20 mm longer and about 2 yr older for males than females and coincided with an increase in reproductive output. The sexual difference in size at habitat transition, combined with sexual size dimorphism (mean asymptotic maximum length — male: 179 mm; female 156 mm) results in differences in the size distributions of both sexes in the 2 habitats. Sexual size dimorphism resulted from a higher growth rate for males through the juvenile period.

KEY WORDS: Ontogenetic habitat use · Hawaiian aquarium fishery · Acanthuridae · Model selection · Otolith · Capture-mark-recapture · Growth · Coral reef fish

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Yellow tang *Zebrasoma flavescens* is a gonochoric (Bushnell 2007) surgeonfish (Acanthuridae) which accounts for approximately 80% of the fish caught for the live aquarium trade in Hawaii. The vast majority of this fishery occurs along the west coast of Hawaii Island (referred to hereafter as West Hawaii), where the reported yellow tang catch has increased from ~10 000 fish yr⁻¹ in the 1970s to ~400 000 fish in 2006 (Friedlander et al. 2008, Williams et al. 2009). In response to perceived declines in yellow tang abundance and conflicts among stakeholders in the 1990s, the State of Hawaii created a network of 9 marine protected areas (MPAs) on 31 December 1999 that, combined with existing MPAs, prohibited aquarium fishing in 35.2% of West Hawaii waters (Tissot et al.

2004, Williams et al. 2009). As part of this extensive adaptive management effort, an emphasis was placed on obtaining habitat- and sex-specific life history information for this valuable species.

Good information on age-based demographics (e.g. growth rates, longevity) of coral reef fishes can increase the capacity for successful management and conservation of reef fisheries (Choat & Robertson 2002). This is particularly important for species such as surgeonfish, where the characteristic square growth curve (fast initial growth that reduces rapidly after the first few years) and high longevity effectively decouple size and age for most of the lifespan (Hilborn & Walters 1992, Choat & Axe 1996, Berumen 2005, Trip et al. 2008). However, relatively little fine-scale age-based demographic information about coral reef fishes is available (Choat & Robertson 2002), and even less

*Email: claisse@hawaii.edu

information is combined with ontogenetic patterns of habitat use. Most studies on ontogenetic variation of habitat use have compared size distributions between habitats (Gillanders et al. 2003), and therefore have not considered age structure, sex-specific habitat use patterns or the duration of the lifespan spent in each habitat. When available, information about age-based habitat use can improve conservation planning and design of MPAs (Mumby 2006, Parnell et al. 2006) and lead to an understanding of how the amount of available juvenile and adult habitat may influence population size—a potential key to conservation and area-based fisheries management (Halpern et al. 2005).

Many species of coral reef fish, including several species of surgeonfish, make ontogenetic shifts in habitat use—an important factor in the organization of fish communities (Robertson 1988, Lawson et al. 1999, Lecchini & Galzin 2005, Robertson et al. 2005, Pratchett et al. 2008). Yellow tang in West Hawaii settle primarily into mid-depth (10 to 25 m) reef habitat with a high percentage of coral cover (hereafter deeper coral-rich habitat). At some as yet undetermined point in their lifespan, larger individuals shift to spending daytime foraging in adjacent, shallow, complex habitats (reef flats and boulders) characterized by a high percentage of exposed rock covered by turf algae (hereafter shallow turf-dominated habitat) (Walsh 1984, Ortiz & Tissot 2008). Because identification of sex in yellow tang is possible only through close examination of the gonadal opening or removal and examination of gonadal tissue (Bushnell 2007), sexual differences in ontogeny of habitat use were not explored in previous visual surveys of yellow tang habitat use (Walsh 1984, Ortiz & Tissot 2008).

Three types of sexual size dimorphism are found in the surgeonfish family: macroandry (larger males), isomorphism and macrogyny (larger females) (Robertson 1985, Trip 2004). Since the sister species to yellow tang, *Zebрасoma scopas* (Guriasu & Winterbottom 1998, Clements et al. 2003), is macroandric (Robertson 1985), we suspected that yellow tang could be as well. Sexual size dimorphism and sexual differences in habitat use can have important implications for proper evaluation of the effects of protection from fishing on populations in West Hawaii (Williams et al. 2009). Additionally, good estimates of demographic rates would permit future population modeling for the fishery. Therefore, quantifying these fine-scale life history characteristics was a high priority in the adaptive management strategy for the yellow tang fishery.

The objectives of the present study were to (1) quantify size-, age- and sex-specific ontogenetic patterns of habitat use for

yellow tang in West Hawaii, and (2) examine sexual dimorphism, including sex-specific patterns of growth, using otolith age-based methods and capture-mark-recapture length-based methods.

MATERIALS AND METHODS

Data collection. To investigate age-based characteristics of yellow tang life history, divers collected yellow tang using pole spears from sites along the West Hawaii coast (Table 1) between June 2003 and April 2007. Initially, limited collections were made of a representative size sample at each site to model size-at-age, but habitat was not recorded. To investigate the size and age of transition in habitat use, additional habitat-specific collections from deeper coral-rich and shallow turf-dominated habitats were made at 3 locations: Wawaloli, Kealakekua Bay and Keei (Table 1). Extensive habitat descriptions can be found in Walsh (1984) and Ortiz & Tissot (2008). Because of limitations on the total number of individuals that could be collected from some sites, and because initial collections made for growth modeling had already included smaller individuals, habitat-specific collections targeted the larger half of the size range present in the deeper coral-rich habitat. Collected fish were transported back to the laboratory on ice. Within 24 h, fish were weighed to the nearest 0.1 g, total length (TL) was measured to the nearest mm and gonads were removed for confirmation of sex. The gonads of recently settled individuals (32 to 45 mm TL, hereafter recruits) were not sufficiently developed for us to determine sex. Specimens were stored frozen and then thawed prior to removal of sagittal otoliths. Otoliths were cleaned with fresh water and stored dry.

To obtain direct measurements of growth, 574 yellow tang between 58 and 200 mm TL were tagged in deeper coral-rich and shallow turf-dominated habitats in West Hawaii from July 2004 through August 2006. Fish were captured using a fine-mesh barrier net, measured to the nearest mm TL, tagged at depth and released in their capture location. Smaller individuals

Table 1. West Hawaii collection site location and management status

Site	Location	Management status
Wawaloli	19° 42' N, 156° 03' W	Closed to aquarium fishing since 1991
Kealakekua Bay	19° 29' N, 155° 56' W	No-take since 1969
Keei	19° 27' N, 155° 55' W	Closed to aquarium fishing since 2000
Wawaloli North	19° 43' N, 156° 03' W	Open to aquarium fishing

(<140 mm TL) were tagged with a unique color/location combination of elastomer tags (Northwest Marine Technology) (Frederick 1997) and larger individuals with T-bar tags through the dorsal musculature. After 221 to 656 d at liberty, 135 of these specimens were collected using pole spears and transported back to the laboratory on ice, where they were sexed and measured to the nearest mm TL.

Otolith preparation and interpretation. Analytical preparations of sagittal otoliths differed slightly for juveniles and adults compared to preparations for recruits. After at least 1 mo in dry storage, each juvenile and adult otolith was weighed to the nearest 0.1 mg. One otolith from each juvenile and adult was mounted on a glass slide using thermoplastic resin and sectioned transversely using a grinding wheel and 1000 grit wet/dry sand paper (Choat & Axe 1996, Choat et al. 2003). Annual increments in the sections were counted using a dissecting microscope with transmitted light. Annual periodicity of increment formation was validated using standard methods (Cappo et al. 2000) and details are available in Supplement 1 (Supplementary material available at: www.int-res.com/articles/suppl/m389p245_app.pdf). Each otolith was read twice by a single observer (J. T. Claisse); if counts did not agree, a third count was made. If 2 of the 3 counts did not agree but they differed by <10%, the median count was used. If counts differed by >10%, the otolith was discarded from analysis. Otoliths of recruits were not weighed due to their very small size and fragility. These recruit otoliths were also ground to produce a transverse section, but grinding was performed by hand and finished by polishing with alumina polish. Counts of daily increments were conducted by a single observer (D. J. Shafer) following standardized procedures (Shafer 2000). Only otolith preparations that provided clear transects from core to edge were used in analyses. While daily increment formation in yellow tang was not validated in the present study, we are confident in our interpretation because it has been validated for 2 congeners, *Zebrasoma scopus* and *Z. veliferum*, at Lizard Island, Australia (Lou & Moltschaniewskyj 1992), and for a number of other coral reef fishes in Hawaii (Danilowicz 1997, Shafer 2000, R. Langston unpubl. data).

Habitat use modeling. Median size and age at which yellow tang make an ontogenetic shift in daytime habitat use was estimated by adapting methods developed for estimating size or age at 50% reproductive maturity (Welch & Foucher 1988, Roa et al. 1999). The dichotomous response variable, not mature vs. mature, was replaced with collection habitat, deeper coral-rich habitat vs. shallow turf-dominated habitat. The proportion of individuals (P) at a given size or age (x) found in the shallow habitat was modeled (Roa et al. 1999):

$$P(x) = \frac{1}{1 + e^{\beta_0 + \beta_1 x}} \quad (1)$$

where β_0 and β_1 are intercept and slope parameters, respectively. This simplified logistic function assumes an asymptote of $P = 1$, and a linear relationship between the logit link function and a single predictor variable. β_0 and β_1 were estimated using a maximum likelihood approach based on the binomial error structure created from the dichotomous response variable (Welch & Foucher 1988). To calculate the median size or age at habitat transition $x_{P=50\%}$, Eq. (1) was solved for x with the maximum likelihood estimates of β_0 and β_1 , and $P(x) = 0.5$ (Roa et al. 1999).

Size-at-age modeling and longevity. Mean length (L_T , in mm) at age (T , in years) was modeled using the standard von Bertalanffy growth function (VBGF):

$$L_T = L_\infty [1 - e^{-k(T-t_0)}] \quad (2)$$

where L_∞ is the mean asymptotic maximum length, k describes the rate at which L_T reaches L_∞ (with units of yr^{-1}) and t_0 is the theoretical age at which the fish would have a length of 0 assuming that the larval fish followed the post-settlement growth pattern. This assumption is crude at best, and t_0 is essentially an arbitrary constant (Beverton & Holt 1957).

We also used the reparameterized version of the VBGF (rVBGF) (Francis 1988a, Moulton et al. 1992, Welsford & Lyle 2005, Trip et al. 2008):

$$L_T = I_y + \frac{(I_v - I_y) [1 - r^{2(T-y)(v-y)^{-1}}]}{1 - r^2} \quad (3)$$

where $r = \frac{I_v - I_w}{I_w - I_y}$

The rVBGF is defined by 3 mean lengths, I_y , I_v and I_w at ages y , v and $w = (y + v)/2$, respectively. Ages 2, 12 and 7, respectively, were chosen because they are well represented in our data and are dispersed throughout the period of growth (Francis 1988a). Estimates of I_y , I_v and I_w were obtained by minimizing the negative log-likelihood, assuming that length at age T is normally distributed, with mean L_T and standard deviation (σ). Examination of model residuals confirmed that these assumptions were appropriate.

When modeling growth, it is important to include recruit-sized individuals in the data set to obtain accurate estimates of mean size-at-age early in life (Craig 1999, Kritzer et al. 2001, Berumen 2005). Since sex was unidentifiable for the younger individuals, it was assumed that sexual differences in growth during the larval stage or during the first weeks post-settlement was negligible, and sex was assigned randomly using a 1:1 sex ratio rather than omitting these data when

fitting growth models to each sex separately. Furthermore, the ageing precision for juveniles and adults using annual increments was only to the nearest year: an individual showing x annual increments on its otoliths has, in reality, an age between x and $x + 1$ yr. As a consequence, mean size at $T = 0$ more accurately represents mean size of a yellow tang of roughly 0.5 yr of age. Therefore, daily ages of recruits were scaled so that mean size at $T = 0$ was consistent with the model being fitted to annual increments (i.e. recruit age = total daily increments – 365 d/2).

Longevity can be evaluated in a number of ways: (1) as the oldest individual in the sample (T_{\max}) (Beverton 1992), (2) as the mean age of the 25% older animal sampled ($T_{\max 25\%}$) (Choat & Robertson 2002) or (3) as the mean of the upper 10% of ages in the sample ($T_{\max 10\%}$) (Trip et al. 2008). Because precision of T_{\max} depends on sample size and the population age structure of the species at the location in question (Kritzer et al. 2001), the results for all 3 definitions for both sexes are reported so that the appropriate measure can be chosen for use in future comparative studies.

Length-based growth modeling. Estimates of annual growth at given sizes were obtained by using a maximum likelihood method to fit various parameterizations of the GROTAG model to capture-mark-recapture measurements of growth (Francis 1988b, Welsford & Lyle 2005). The GROTAG model estimates the change in length for the i th fish (ΔL_i) as a function of its initial length at release (L_i) and its length of time at liberty (ΔT_i):

$$\Delta L_i = \left(\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_i \right) \left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta} \right)^{\Delta T_i} \right] \quad (4)$$

This model, based on the rVBGF and the Fabens growth model (Francis 1988b), depends on 2 growth rates (g_α and g_β) at 2 specific lengths ($\alpha = 80$ mm TL, $\beta = 140$ mm TL) chosen from within the range of initial lengths in the data set. Variability in growth is parameterized within the likelihood and assumed to increase proportionally to the expected growth increment by a scaling factor (v). The remaining error, which incorporates any measurement error and lack of fit, is assumed to be normally distributed with mean zero and standard deviation s (Francis 1988b).

Model selection and confidence interval estimation. Hypotheses regarding sexual differences in (1) median size and age at ontogenetic habitat shift, (2) growth-at-age and (3) growth-at-length were investigated via model selection (Burnham & Anderson 2002) with sets of models containing various parameterizations of the models described previously in the methods. Akaike

weights (w_i) were calculated to assess the relative likelihood of each model in a set and were interpreted as a weight of evidence in favor of the hypothesis represented by the model (Burnham & Anderson 2002). Details of the model selection procedure and model parameterizations are given in Supplement 2 (available at: www.int-res.com/articles/suppl/m389p245_app.pdf).

Parameter estimates with first-order corrected 95% CIs (Haddon 2001) from 5000 bootstraps were produced for all models which received substantial support. Bootstrapping involved random resampling with replacement from the original data set so that an equivalent data set was constructed, and then re-estimating parameters for each new data set. A first-order bias correction in the percentiles used to calculate the CIs was made to account for any skew in the distribution of bootstrap parameter estimates (Haddon 2001, Welsford & Lyle 2005).

Sexual dimorphism in the relationship between weight and length is examined completely in Supplement 3 (available at: www.int-res.com/articles/suppl/m389p245_app.pdf).

All statistical analyses in the present study were coded in R (R Development Core Team 2008).

RESULTS

Sexual differences in patterns of ontogenetic habitat use

Both male and female yellow tang displayed a consistent pattern of ontogenetic shifts in daytime habitat use around a particular size and age (Table 2). Median size at habitat shift was about 20 mm larger for males than females. Median age at habitat shift was about 2 yr older in males. Model selection indicated there was strong evidence of sexual difference in the median size and age at habitat shift (Table S2.1, S2.2, available at: www.int-res.com/articles/suppl/m389p245_app.pdf). The highest ranked models (Table S2.1, S2.2, Model 1), where model parameters were fitted to each sex separately, received 100% of total w_i .

There were also clear, consistent differences in the size distributions of each sex sampled from each habitat (Fig. 1). Because females make the shift at a smaller size, nearly all individuals >140 mm in the deeper coral-rich habitat sample were males. In the shallow turf-dominated habitat sample, most individuals <150 mm were female and almost all individuals >165 mm were male, with some overlap between 150 and 165 mm (Fig. 1). There was, however, considerable overlap in age ranges of each sex from both habitat samples (Fig. 2).

Table 2. *Zebrasoma flavescens*. Estimated median size and age at habitat shift ($x_p = 50\%$) with first-order corrected 95% CIs. Because of lost otolith samples, median age at habitat shift was not estimated for deeper coral-rich habitat males at Wawaloli. NA: not available

	Length (mm)				Age (yr)			
	Median	CI	n		Median	CI	n	
			Shallow	Deep			Shallow	Deep
Male								
All sites	152	148 to 155	195	89	7.2	6.4 to 7.8	195	89
Wawaloli	150	145 to 155	81	18	NA	NA	81	4
Kealakekua	154	147 to 160	38	26	11.6	9.4 to 14.4	38	26
Keeki	158	153 to 163	40	43	10.3	8.7 to 12.4	40	43
Female								
All sites	132	129 to 135	202	48	5.1	4.7 to 5.6	202	48
Wawaloli	130	125 to 136	89	16	4.6	4.0 to 5.3	89	16
Kealakekua	132	127 to 136	29	13	7.2	5.6 to 9.3	29	13
Keeki	133	125 to 136	40	16	5.5	5.0 to 6.2	40	16

Size-at-age and longevity

Yellow tang from West Hawaii are long-lived, with a potential lifespan of at least 41 yr (Fig. 3). Model selection clearly supported the model of complete sexually dimorphic growth (Table S2.3, Model 1), which received almost all the support ($w_i = 0.95$). Parameter estimates from this model are displayed in Table 3. Yellow tang displayed rapid initial growth and approached L_∞ relatively early in life (Fig. 3).

Male L_∞ was 23 mm longer than that of females (Table 3). There were also clear differences in length at ages 7 and 12 yr. Mean size at age 2 was estimated to be 4 mm longer for males than females, although this difference was relatively small and the 95% CIs overlap slightly (Table 3).

While longevity or mean longevity varied from site to site and among the different methods of calculation, there was a consistent trend that males reached greater ages than females, i.e. 3 to 4 yr older in most cases (Table 4).

Length-based growth modeling

There is strong evidence in the capture-mark-recapture data that growth rate at length is sexually dimorphic. GROTAG growth parameter estimates (g_{80} and g_{140}), from the model ranked highest during model selection (Table S2.4, Model 1), indicated that mean male growth rate was higher over the size range examined and provided strong evidence of sexually dimorphic growth consistent with age-

length data. This model received 100% of total w_i . Parameter estimates from this model (with 95% CIs) are listed in Table 5, and the predicted growth increment (ΔL) at a given length are shown, together with the measured growth increments standardized to 1 yr of growth ($\Delta L_i/\Delta T_i$) vs. L_i (Fig. 4). It is important to note that while growth increments in Fig. 4 were standardized to 1 yr, they still do not include variation due directly to ΔT_i . Furthermore, predicted annual growth rates, particularly at both ends of the range of L_i , should be treated with some caution because of the lack of consistent sampling of both sexes throughout the range of L_i .

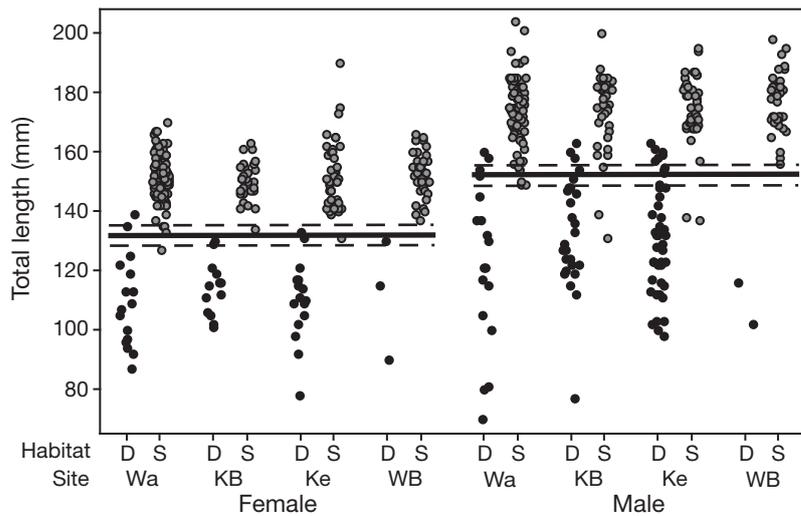


Fig. 1. *Zebrasoma flavescens*. Sizes of individual males and females collected in either deeper coral-rich habitat (D, black circles) or shallow turf-dominated habitat (S, grey circles) at 4 sites along the West Hawaii coast: Wawaloli (Wa), Kealakekua Bay (KB), Keeki (Ke) and Wawaloli Beach (WB). Collections from each site are consistent with median size at habitat shift estimated from pooled data (solid lines; 95% CIs: dotted lines). Note that few individuals were collected in the deeper coral-rich habitat at Wawaloli Beach due to lack of effort, not abundance

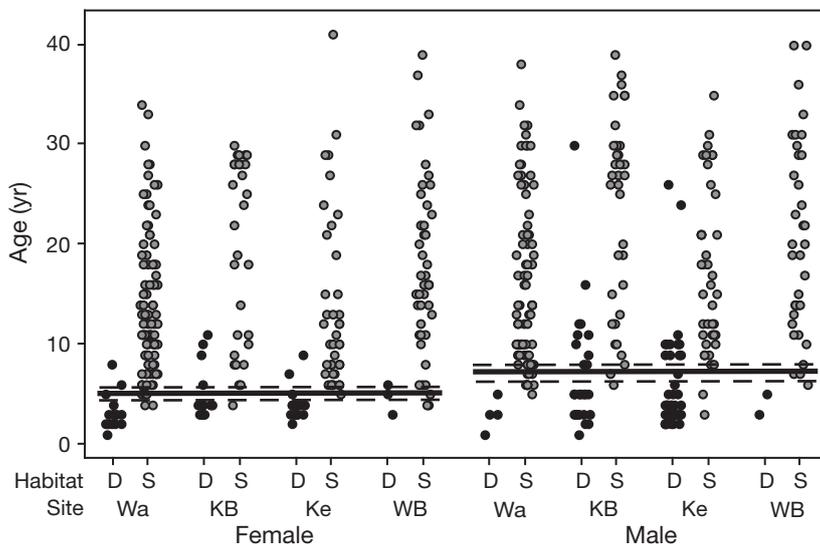


Fig. 2. *Zebrasoma flavescens*. Ages of individual males and females collected in either deeper coral-rich (D, black circles) or shallow turf-dominated (S, grey circles) habitats at 4 sites along the West Hawaii coast: Wawaloli (Wa), Kealakekua Bay (KB), Keei (Ke) and Wawaloli Beach (WB). Site-specific collections are consistent with median age at habitat shift estimated from pooled data (solid lines; 95% CIs: dotted lines). Note that very few individuals were collected in the deep habitat at Wawaloli Beach, and the sample of male ages from the deeper coral-rich habitat at Wawaloli was limited because of mishandled otoliths

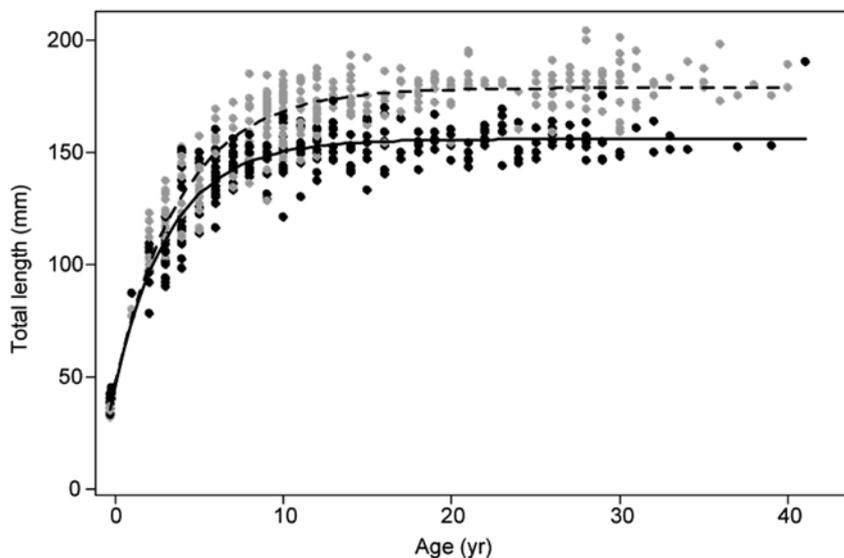


Fig. 3. *Zebrasoma flavescens*. Von Bertalanffy growth curves for males (---) and females (—) based on the model that assumes complete growth dimorphism. $n = 300$ males + 28 recruits assigned male (grey circles); $n = 280$ females + 28 recruits assigned female (black circles)

The highest ranked models, regardless of whether sexual dimorphism was assumed, both contained growth variability factor v (Table A2.4, Models 1 & 2). These models assume that growth variability increases with the predicted growth increment, and examination of model residuals confirmed this relationship.

DISCUSSION

Sexual differences in patterns of ontogenetic habitat use

Male and female yellow tang in West Hawaii each showed a clear ontogenetic pattern of habitat use. Males were larger (median size 152 vs. 132 mm TL) and older (median age 7.2 vs. 5.1 yr) than females when they shifted from daytime use of deeper coral-rich habitat to shallow turf-dominated habitat (Figs. 1 & 2, Table 2). To confirm that these differences were consistent across sites, $x_{P=50\%}$ for both size and age was estimated for each sex from the 3 sites where suitable sample sizes were available. Median age at habitat shift was older at some sites when the model was fitted to these smaller samples (Table 2). This is probably due to the stronger influence that the few much older males (15 to 30 yr) collected in the deeper coral-rich habitat had on these smaller samples. Interestingly, none of these older males was exceptionally large (Fig. 1), which may suggest that size more than age determines when the habitat shift occurs. Additionally, there appears to be less variability in size at transition for females compared to males (Fig. 1).

The sexual differences in median size at habitat shift, combined with highly asymptotic growth (Figs. 3 to 5) and macroandric sexual size dimorphism (Table 3, Fig. 3), translate to clear differences in the size distribution of each sex in the 2 habitats. In the shallow turf-dominated habitat, larger individuals were almost all males and smaller individuals almost all females, with substantial overlap only between 150 and 165 mm TL (Fig. 1). In the deeper coral-rich juvenile habitat, almost all individuals >140 mm TL were males.

The ontogenetic habitat shift in yellow tang coincides with the size at which there is a clear increase in reproductive output (for females: Bushnell 2007; for males: J. T. Claisse unpubl. data) and is consistent with

the hypothesis that habitat use patterns represent a tradeoff between mortality risk and growth or foraging rate (Gilliam & Fraser 1987, Dahlgren & Eggleston 2000, Gillanders et al. 2003). Yellow tang initially settle into the more structurally complex, deeper coral-rich habitat and then shift into habitat with more food resources, i.e.

Table 3. *Zebrasoma flavescens*. Parameter estimates with 95 % first-order corrected CIs (parentheses) for rVBGF and VBGF parameterizations that assume sexual dimorphism in all parameters and for the model fitted to combined data from both sexes. See 'Materials and methods: Size-at-age modeling and longevity' for parameter descriptions

	l_2 (mm)	l_7 (mm)	l_{12} (mm)	l_∞ (mm)	k (yr ⁻¹)	t_0 (yr)	σ (mm)
Male	100 (97 to 102)	156 (154 to 159)	172 (171 to 174)	179 (177 to 180)	0.25 (0.24 to 0.27)	-1.2 (-1.3 to -1.2)	10.4 (9.6 to 11.3)
Female	96 (93 to 98)	142 (141 to 144)	153 (152 to 154)	156 (154 to 157)	0.3 (0.28 to 0.32)	-1.2 (-1.3 to -1.1)	8.9 (8.1 to 9.8)
Both sexes	97.0 (95 to 99)	149 (148 to 150)	163 (162 to 164)	168 (166 to 170)	0.27 (0.25 to 0.28)	-1.2 (-1.25 to -1.31)	13 (12.5 to 13.6)

abundant turf algae (Ortiz & Tissot 2008). The median size at habitat shift as a percentage of l_∞ is almost identical for the 2 sexes (84.9% for males, 84.6% for females). The increased food resources in shallow habitats may translate into increased reproductive ability. However, energy is also probably redirected from growth toward reproduction as the growth rate slows during this period (Fig. 3) (Day & Taylor 1997). Regarding the sexual differences in size and age at

habitat transition, further research is needed to examine whether ecological factors (e.g. potentially the balance between mortality risk and potential benefits of switching habitats) differ between the sexes and/or whether larger males exclude smaller males, but not females, from shallow daytime habitat.

Sexual differences in ontogenetic patterns of habitat use can produce misleading or skewed sex ratios in samples if not accounted for in sampling protocols of life history studies of demersal fishes. In the present study, the sex ratio of yellow tang collected in shallow turf-dominated habitat was close to unity (M:F, 1:0.96), while the sex ratio of yellow tang collected in deeper coral-rich habitat was highly skewed toward males (1.85:1). This ratio was due to smaller size at habitat shift in females and was amplified by a sampling bias toward the larger (>100 mm TL) fish in the deeper habitat. However, below median female size at habitat shift (132 mm TL) the sex ratio in our sample was almost 1 (1:0.98). Skewed sex ratios are not uncommon in life history studies of surgeonfishes: *Zebrasoma scopas* (1:0.61), *Ctenochaetus striatus* (1:0.32) (Dalzell 1989), *Acanthurus triostegus* collected with fish traps (1:0.47) and *Acanthurus triostegus* samples from museum collections (1:1.56) (Randall 1961). Some of these differences may result from sexual differences in habitat use rather than actual skewed sex ratios.

Effects of aquarium collecting on habitat use patterns were not directly investigated in the present study, but presence or absence of collecting did not appear to influence our results. While sample size at

Table 4. *Zebrasoma flavescens*. Longevity and mean longevity calculated for each sex as oldest individual (T_{max}), mean of upper 25% of ages in the sample ($T_{max\ 25\%}$) and mean of upper 10% of ages in the sample ($T_{max\ 10\%}$)

Site	Male			Female		
	T_{max}	$T_{max\ 25\%}$	$T_{max\ 10\%}$	T_{max}	$T_{max\ 25\%}$	$T_{max\ 10\%}$
All	40	31	34	41	27	31
Wawaloli	38	28	32	34	24	28
Kealakekua	39	34	37	30	29	29
Keei	35	28	31	41	27	32
North Wawaloli	40	34	37	30	29	29

any given site was limited, the pattern of yellow tang habitat use at the site open to fishing, Wawaloli Beach, appeared to be consistent with other sites (Figs. 1 & 2). Also, there were no obvious differences between sites that had been under protection for different lengths of time (Table 1). High spatial and temporal variation in annual recruitment (Tissot et al. 2004, Walsh et al. 2005) may mask the effects, if any, of removal of juveniles on these habitat use patterns.

Sexual differences in age, size and growth

Yellow tang are a very long-lived species and display the typical acanthurid square growth curve (Fig. 3), with high initial growth rates that rapidly decrease after the first few years (Choat & Axe 1996, Choat & Robertson 2002). The oldest individuals col-

Table 5. *Zebrasoma flavescens*. Parameter estimates with 95 % first-order corrected CIs (parentheses) from the GRO-TAG model which assumes sexual dimorphism and a proportional increase in growth variability with the expected growth interval. g_{80} and g_{140} : growth rates at 80 and 140 mm TL; v : growth variability scaling factor; s : SD of the remaining error

	g_{80}	g_{140}	v	s
Male	19 (16 to 23)	8 (6 to 9)	0.54 (0.39 to 0.71)	2.6 (1.6 to 7.1)
Female	12 (9 to 14)	3 (2 to 4)	0.59 (0.46 to 0.75)	2.3 (1.6 to 3.1)

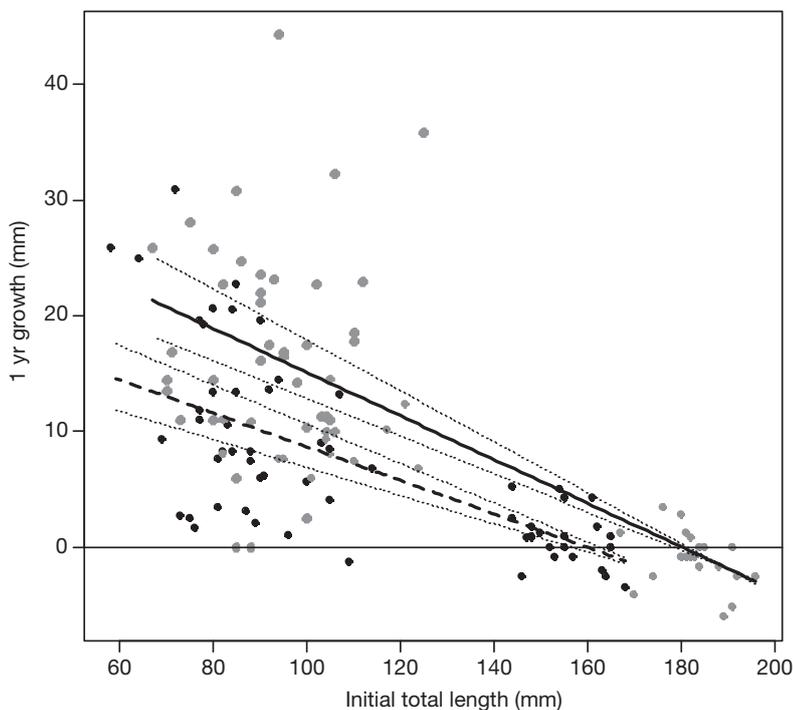


Fig. 4. *Zebrasoma flavescens*. Measured growth increments from capture-mark-recapture data standardized to 1 yr of growth ($\Delta L_i/\Delta T_i$) vs. initial total length at release (L_i) for males (grey circles) and females (black circles). Predicted growth increments from the highest ranked model are plotted as a solid line for males and a dashed line for females with 95% first order corrected CIs (dotted lines)

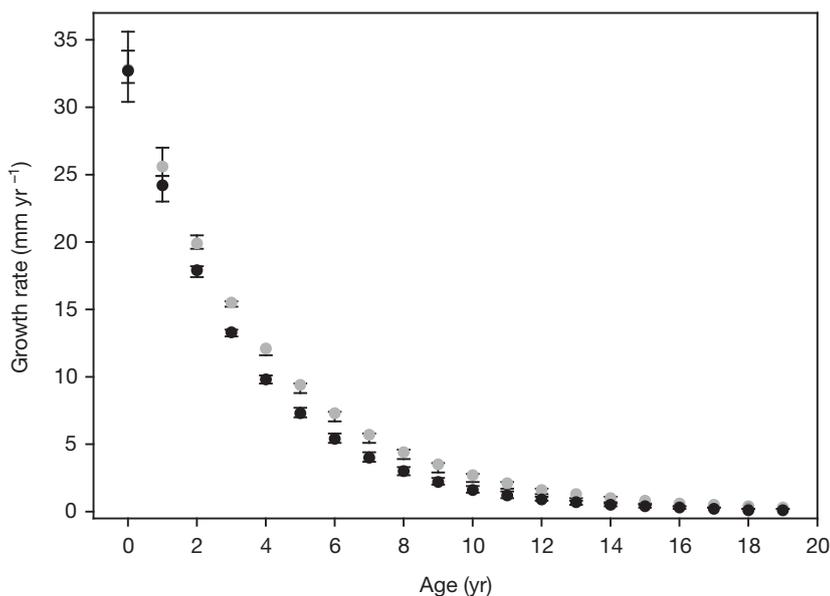


Fig. 5. *Zebrasoma flavescens*. Male (grey circles) and female (black circles) mean annual instantaneous growth rates (derivative of VBGF model with each parameter estimated separately for each sex) vs. age with 95% first-order corrected CIs. The growth rate at age x approximates the average growth rate from age x to $x + 1$

lected in the present study were a 41 yr old female and a 40 yr old male, although mean longevity was consistently greater in males than females (Table 4). The macroandric sister species of yellow tang, *Zebrasoma scopas*, had a similar $T_{\max 25\%}$ of 29 to 34 yr among different locations on the Great Barrier Reef, but sexual differences in longevity were not investigated (Choat & Robertson 2002, Trip et al. 2008). While survival rates of juveniles in the deeper coral-rich habitat appear to be independent of size (Claisse et al. 2009), the presence of size- and sex-dependent survival rates of yellow tang adults, either of which could lead to the slightly higher male longevity, has not been empirically tested.

The hypothesis of sexual growth dimorphism was supported by both age-based (Table S2.3, Model 1) and length-based capture-mark-recapture data (Table S2.4, Model 1). These 2 methods are not directly comparable, but complementary; the first models mean growth rate for a given age (averaging across a range of sizes) and the second estimates mean growth rate for fish of a given size (averaging across a range of ages) (see Fig. 1 in Francis 1988a). To further examine the actual growth rates (as k in the VBGF is not a growth rate, but a rate with unit inverse of time), the instantaneous mean annual growth rate for each sex was calculated with first-order corrected 95% CIs (as described in 'Materials and methods') by calculating the derivative of the VBGF version of Model 1 (Table S2.3) at each year. Growth rates for both sexes are $>30 \text{ mm yr}^{-1}$ during the first year of life (0 to 1 yr), but males grow substantially faster than females from year 2 to 3, a trend that continues until the asymptotic size is approached (Figs. 3 & 5). Because we did not determine sex in the yellow tang recruits (up to 102 d total age), our age-based growth methods assumed that differences in growth rates between the sexes were negligible through this period. Therefore, it is possible that growth rates actually begin to differentiate between the sexes earlier than the model describes.

Sexual size dimorphism in another macroandric surgeonfish, *Ctenochaetus striatus*, was also derived from comparatively faster male growth from an early age (~ 1 yr) at locations across much of the Indo-

Pacific region (Trip 2004). For yellow tang, the sexual difference in growth rate may coincide with an increased allocation of energy toward reproduction at around 90 mm, when females achieve the ability to produce eggs, albeit in very small batches (Walsh 1984, Bushnell 2007). However, in 2 macrogynic surgeonfish species, *Acanthurus leucosternon* and *A. nigricans*, comparatively faster early post-settlement growth by females led to sexual size dimorphism. This appears contrary to the idea that relatively slower female growth results from the greater cost to females of reproductive development. This may imply that direction and magnitude of sexual dimorphism in surgeonfish depend more on selection acting on male size (Trip 2004). If so, relative male size may be largely a function of the social aspects of the reproductive system in surgeonfish, and macroandry may result primarily from agonistic competition between males (Robertson 1985).

Yellow tang in West Hawaii make crepuscular migrations away from daytime shallow turf-dominated foraging habitat to spawn at sunset in the deeper coral-rich habitat, primarily along the edge of the deeper reef slope (Walsh 1984). Each evening males return repeatedly to the same temporary spawning territory (J. T. Claisse unpubl. data) and court passing females in what has been described as a linear lek (Loiselle & Barlow 1978, Walsh 1984). Selection for larger male size could result from competition between males for a preferred temporary spawning territory, or females could choose to spawn with larger males, although selection strength may be complicated by sperm competition from streaker males (Walsh 1984, J. T. Claisse pers. obs.).

CONCLUSIONS

Yellow tang *Zebrasoma flavescens* from West Hawaii displayed clear sexual differences in growth, mean maximum size and ontogenetic patterns of habitat use. Relatively soon after settlement, males grew faster than females of the same age or size until asymptotic size was approached, consistent with sexual size dimorphism in other surgeonfish species (Trip 2004). Habitat-specific age-based life history information that accounted for sexual differences provided increased management capabilities. Based on results from the present study, monitoring protocols for the West Hawaii MPA network were enhanced in 2006 to include additional surveys of the shallow turf-dominated habitat to properly account for changes to the adult reproductive stocks (Williams et al. 2009). The science of MPAs is currently in transition from the basic understanding that MPAs increase numerical density,

biomass and average size of fishes within their boundaries (Halpern & Warner 2002) toward a more explicit understanding of MPAs as a fisheries management tool (Kellner et al. 2007, White & Kendall 2007). Obtaining and using age-based life history information at a finer scale (e.g. habitat- and sex-specific) will continue to support a more complete understanding of the system and lead to improved design of appropriate long-term monitoring protocols and management measures.

Acknowledgements. This research was funded in part by NOAA, Center for Sponsored Coastal Ocean Science, under award nos. NA03NOS4260044, NA04NOS4260172 and NA160A2412 to the University of Hawaii for the Hawaii Coral Reef Initiative. This research was also funded in part by a grant/cooperative agreement from NOAA, project no. R/FM-20, sponsored by the University of Hawaii Sea Grant College Program, SOEST, under Institutional Grant no. NA05OAR4171048 from the NOAA Office of Sea Grant, Department of Commerce. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. Major equipment and logistical support were provided by the Hawaii Cooperative Fishery Research Unit, US Geological Survey and the University of Hawaii. Financial and logistical support was provided by the Hawaii Division of Aquatic Resources and generous logistical support by the US National Park Service Kaloko-Honokohau National Historical Park. The use of trade, firm or corporation names in this publication is for the convenience of the reader. Such use does not constitute an official endorsement or approval by the US Government of any product or service to the exclusion of others that may be suitable. The University of Hawaii Ecology, Evolution and Conservation Biology Program also provided funding. An NSF Graduate Research Fellowship provided support for J.T.C. We thank Team Tang members S. McTee and T. Clark who provided top-notch field assistance; J. Eble for additional help collecting samples; and J. Choat, W. Robbins and E. Trip for help with everything otolith. T. Carvalho and M. Dunlap at the Biological Electron Microscope Facility at the University of Hawaii assisted with visualization of the tetracycline bands for validation purposes. D. Ortiz, A. Taylor, W. Walsh, C. Birkeland, C. Smith, I. Williams, S. Beavers, L. Basch and B. Schumacher provided logistical and scientific support throughout the study. We also thank 2 anonymous referees for their comments.

LITERATURE CITED

- Berumen ML (2005) The importance of juveniles in modeling growth: butterflyfish at Lizard Island. *Environ Biol Fishes* 72:409–413
- Beverton RJH (1992) Patterns of reproductive strategy parameters in some marine teleost fishes. *J Fish Biol* 41: 137–160
- Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food, London
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference, a practical information-theoretic approach. Springer Science, New York
- Bushnell ME (2007) Reproduction of *Zebrasoma flavescens*: oocyte maturation, spawning patterns and an estimate of reproductive potential for female yellow tang in Hawaii. MS thesis, University of Hawaii, Manoa, HI

- Cappo M, Eden P, Newman SJ, Robertson S (2000) A new approach to validation of periodicity and timing of opaque zone formation in the otoliths of eleven species of *Lutjanus* from the central Great Barrier Reef. *Fish Bull* 98:474–488
- Choat JH, Axe LM (1996) Growth and longevity in acanthurid fishes; an analysis of otolith increments. *Mar Ecol Prog Ser* 134:15–26
- Choat JH, Robertson DR (2002) Age-based studies. In: Sale P (ed) *Coral reef fishes*. Elsevier Science, San Diego, CA, p 57–80
- Choat JH, Robertson DR, Ackerman JL, Posada JM (2003) An age-based demographic analysis of the Caribbean stoplight parrotfish *Sparisoma viride*. *Mar Ecol Prog Ser* 246: 265–277
- Claisse JT, McTee SA, Parrish JD (2009) Effects of age, size, and density on natural survival for an important coral reef fishery species, yellow tang, *Zebrasoma flavescens*. *Coral Reefs* 28:95–105
- Clements KD, Gray RD, Choat JH (2003) Rapid evolutionary divergences in reef fishes of the family Acanthuridae (Perciformes: Teleostei). *Mol Phylogenet Evol* 26:190–201
- Craig PC (1999) The von Bertalanffy growth curve: when a good fit is not good enough. *ICLARM Q* 22:28–29
- Dahlgren CP, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81:2227–2240
- Dalzell P (1989) The biology of surgeonfishes (Family: Acanthuridae), with particular emphasis on *Acanthurus nigricauda* and *A. xanthopterus* from northern Papua New Guinea. PhD thesis, University of Newcastle upon Tyne
- Danilowicz BS (1997) A potential mechanism for episodic recruitment of a coral reef fish. *Ecology* 78:1415–1423
- Day T, Taylor PD (1997) Von Bertalanffy's growth equation should not be used to model age and size at maturity. *Am Nat* 149:381–393
- Francis RICC (1988a) Are growth parameters estimated from tagging and age-length data comparable. *Can J Aquat Sci* 45:936–942
- Francis RICC (1988b) Maximum likelihood estimation of growth and growth variability from tagging data. *NZ J Mar Freshw Res* 22:42–51
- Frederick JL (1997) Evaluation of fluorescent elastomer injection as a method for marking small fish. *Bull Mar Sci* 61:399–408
- Friedlander A, Aeby G, Brainard R, Brown E and others (2008) The state of coral reef ecosystems of the Main Hawaiian Islands. NOAA/NCOS Center for Coastal Monitoring and Assessment, Biogeography Branch, Silver Spring, MD
- Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Mar Ecol Prog Ser* 247:281–295
- Gilliam JF, Fraser DF (1987) Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68:1856–1862
- Guiasu RC, Winterbottom R (1998) Yellow juvenile color pattern, diet switching and the phylogeny of the surgeonfish genus *Zebrasoma* (Percomorpha, Acanthuridae). *Bull Mar Sci* 63:277–294
- Haddon M (2001) *Modeling and quantitative methods in fisheries*. CRC Press, Boca Raton, FL
- Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. *Ecol Lett* 5:361–366
- Halpern BS, Gaines SD, Warner RR (2005) Habitat size, recruitment, and longevity as factors limiting population size in stage-structured species. *Am Nat* 165:82–94
- Hilborn R, Walters CJ (1992) *Quantitative fisheries stock assessment: choice, dynamics, and uncertainty*. Chapman & Hall, New York
- Kellner JB, Tetreault I, Gaines SD, Nisbet RM (2007) Fishing the line near marine reserves in single and multispecies fisheries. *Ecol Appl* 17:1039–1054
- Kritzer JP, Davies CR, Mapstone BD (2001) Characterizing fish populations: effects of sample size and structure on the precision of demographic parameter estimates. *Can J Fish Aquat Sci* 58:1557–1568
- Lawson GL, Kramer DL, Hunte W (1999) Size-related habitat use and schooling behavior in two species of surgeonfish (*Acanthurus bahianus* and *A. coeruleus*) on a fringing reef in Barbados, West Indies. *Environ Biol Fishes* 54:19–33
- Lecchini D, Galzin R (2005) Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). *Mar Biol* 147:47–58
- Loiselle PV, Barlow GW (1978) Do fishes lek like birds? In: Reese ES, Lighter FJ (eds) *Contrasts in behavior adaptations in the aquatic and terrestrial environments*. Wiley Interscience, New York
- Lou DC, Moltschanivskyj NA (1992) Daily otolith increments in juvenile tropical parrotfishes and surgeonfishes. *Mar Freshw Res* 43:973–981
- Moulton PL, Walker TI, Saddler SR (1992) Age and growth studies of gummy shark, *Mustelus antarcticus* (Gunther), and school shark, *Galeorhinus galeus* (Linnaeus), from southern Australian waters. *Mar Freshw Res* 43: 1241–1267
- Mumby PJ (2006) Connectivity of reef fish between mangroves and coral reefs: algorithms for the design of marine reserves at seascape scales. *Biol Conserv* 128:215–222
- Ortiz DM, Tissot BN (2008) Ontogenetic patterns of habitat use by reef-fish in a Marine Protected Area network: a multi-scaled remote sensing and *in situ* approach. *Mar Ecol Prog Ser* 365:217–232
- Parnell PE, Dayton PK, Lennert-Cody CE, Rasmussen LL, Leichter JJ (2006) Marine reserve design: optimal size, habitats, species affinities, diversity, and ocean microclimate. *Ecol Appl* 16:945–962
- Pratchett M, Berumen M, Marnane M, Eagle J, Pratchett D (2008) Habitat associations of juvenile versus adult butterflyfishes. *Coral Reefs* 27:541–551
- Randall JE (1961) A contribution to the biology of the convict surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*. *Pac Sci* 15:215–272
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, available at: www.r-project.org
- Roa R, Ernst B, Tapia F (1999) Estimation of size at sexual maturity: an evaluation of analytical and resampling procedures. *Fish Bull* 97:570–580
- Robertson DR (1985) Sexual-size dimorphism in surgeon fishes. *Proc Fifth Int Symp Coral Reefs* 5:403–408
- Robertson DR (1988) Abundances of surgeonfishes on patch-reefs in Caribbean Panama: due to settlement, or post-settlement events? *Mar Biol* 97:495–501
- Robertson DR, Ackerman JL, Choat JH, Posada JM, Pitt J (2005) Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. *Mar Ecol Prog Ser* 295: 229–244
- Shafer DJ (2000) Evaluation of periodic and aperiodic otolith structure and somatic-otolith scaling for use in retrospective life history analysis of a tropical marine goby, *Bathygobius coalitus*. *Mar Ecol Prog Ser* 199:217–229
- Tissot BN, Walsh WJ, Hallacher LE (2004) Evaluating effectiveness of a marine protected area network in West

- Hawai'i to increase productivity of an aquarium fishery. *Pac Sci* 58:175–188
- Trip EL (2004) A multi-scale analysis of population dynamics and sexual size dimorphism in a widely distributed coral reef fish family (Acanthuridae). MS thesis, James Cook University, Townsville
- Trip EL, Choat JH, Wilson DT, Robertson DR (2008) Inter-oceanic analysis of demographic variation in a widely distributed Indo-Pacific coral reef fish. *Mar Ecol Prog Ser* 373:97–109
- Walsh WJ (1984) Aspects of nocturnal shelter, habitat space, and juvenile recruitment in Hawaiian coral reef fishes. PhD thesis, University of Hawaii, Manoa, HI
- Walsh WJ, Tissot BN, Hallacher L (2005) A report on the findings and recommendations of effectiveness of the West Hawaii Regional Fishery Management Area. Hawaii State Department of Land and Natural Resources, Honolulu, HI (available at: www.coralreefnetwork.com/kona/FRA%205%20yr.%20Report%20to%20Legislature.pdf)
- Welch DW, Foucher RP (1988) A maximum likelihood methodology for estimating length-at-maturity with application to Pacific cod (*Gadus macrocephalus*) population dynamics. *Can J Fish Aquat Sci* 45:333–343
- Welsford DC, Lyle JM (2005) Estimates of growth and comparisons of growth rates determined from length- and age-based models for populations of purple wrasse (*Notolabrus fucicola*). *Fish Bull* 103:697–711
- White C, Kendall BE (2007) A reassessment of equivalence in yield from marine reserves and traditional fisheries management. *Oikos* 116:2039–2043
- Williams ID, Walsh WJ, Claisse JT, Tissot BN, Stamoulis KA (2009) Impacts of a Hawaiian marine protected area network on the abundance and fishery sustainability of the yellow tang, *Zebrasoma flavescens*. *Biol Conserv* 142: 1066–1073

*Editorial responsibility: John Choat,
Townsville, Queensland, Australia*

*Submitted: January 29, 2009; Accepted: May 16, 2009
Proofs received from author(s): July 20, 2009*