

# Effects of age, size, and density on natural survival for an important coral reef fishery species, yellow tang, *Zebrasoma flavescens*

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**Abstract** Hundreds of thousands of juvenile yellow tang, *Zebrasoma flavescens*, are caught each year in the state of Hawai'i (USA) for the live aquarium trade. As part of an extensive adaptive management strategy built around a network of protected areas, an emphasis was placed on understanding this important species' life history. Multiple capture-mark-recapture techniques and a model selection approach to data analysis in Program MARK were used to estimate the effects of individual age and conspecific density on natural per-capita daily survival probabilities of yellow tang recruits (recently settled individuals, 30–50 mm total length) and the effects of body size and site on natural per-capita monthly survival probabilities for juveniles (58–127 mm total length). The models of recruit survival that included additive effects of density and age were best supported by the data and indicated an increase of survival with age and decrease of survival with increased conspecific density. At 1 day post-settlement, the model averaged daily per-capita survival probability ranged from 0.963 (95% CI: 0.932–0.981) at a low density of 0.1 recruits  $m^{-2}$  to 0.848 (95% CI: 0.752–0.911) at a high density of 1.3 recruits  $m^{-2}$ . The best supported model of juvenile survival had no effect of fish length or site, with a constant monthly per-capita survival of 0.939 (95% CI: 0.925–0.950). Only about 1% of recruits may survive to adulthood when protected from fishing. These results can be used to better analyze and interpret data from protected area monitoring surveys and refine management practices.

Continued long-term monitoring, combined with targeted life history studies and demographic modeling, is needed to further investigate the population level effects of fishing yellow tang juveniles.

**Keywords** Density dependence · Post-settlement mortality · Acanthuridae · Aquarium fishery management · Model selection · Program MARK

## Introduction

While coral reef fish have extremely high species and familial diversity compared to other vertebrate taxa (Sale 1991), life history characteristics of coral reef fish, including the relationship of natural survival with age, remain poorly understood (Caley 1998; Choat and Robertson 2002). Most studies of survival have been focused on small damselfishes (family Pomacentridae) and wrasses (family Labridae) (DeMartini 1998; Hixon and Webster 2002) and are particularly lacking for species commonly fished from coral reefs (Roberts 1996; DeMartini 1998). Survival has been estimated in a few species of surgeonfish (family Acanthuridae), but these results have been limited primarily to the night of settlement (Doherty et al. 2004) or relatively short time periods post-settlement (Planes and Lecaillon 2001; Almany 2004). Obtaining robust estimates of natural survival rates and identifying the processes that affect them over larger portions of the lifespan of more species of coral reef fish can increase our understanding of life history evolution (Caley 1998; Depczynski and Bellwood 2006), population dynamics (Roberts 1996; Sogard 1997; Hixon et al. 2002), and lead to more effective modeling of the effects of marine protected areas (MPAs)

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in fisheries management (DeMartini 1998; Lindholm et al. 2001; Gerber et al. 2003).

Yellow tang, *Zebrasoma flavescens*, juveniles are harvested along the west coast of Hawai'i Island for the live aquarium trade (fiscal year 2006 reported catch 421,012 individuals; Hawai'i Division of Aquatic Resources). Perceived declines in abundance, throughout the 1990s, led to stakeholder conflict. In 2000 the State of Hawai'i implemented a network of MPAs, which closed 35.2% of the 147 miles of the western coastline to fishing for aquarium species to manage this fishery. The State has carried out extensive monitoring since 1 year before implementation of the MPAs, and initial results indicated that juvenile abundance has increased by around 70% in areas closed to fishing (Tissot et al. 2004; Walsh et al. 2005). As part of this adaptive management effort, emphasis was placed on understanding the life history characteristics of yellow tang in order to better interpret monitoring data and refine current management practices. An important part of this process is estimating natural rates of survival soon after settlement and across the juvenile size range exploited in the fishery. This life history information will be valuable in future attempts to model yellow tang populations, as well as in interpreting data from visual surveys. The effects of density and high rates of predation just after settlement may render recruitment surveys inaccurate as estimates of true patterns of settlement (Connell 1985; Steele and Forrester 2002).

Model selection approaches for data analysis have become common in studies of ecology and evolution (Johnson and Omland 2004), and recently have been applied in studies of density-dependent survival of coral reef fish (Sandin and Pacala 2005; White and Warner 2007). The flexible model selection framework available in Program MARK has been commonly used in terrestrial and marine capture-mark-recapture (CMR) wildlife studies over the past decade to estimate population growth rates and survival probabilities (Morgan and Thompson 2002; Chaloupka and Limpus 2005; Hoolihan 2006). Use in studies of coral reef species, however, has been very limited (Curtis and Vincent 2006; Wormald and Steele 2008).

In the present study, a model selection approach was applied to estimate the effects of age and density on survival probability soon after settlement (recruit survival analysis) and the effects of size and site on the survival probability of larger juveniles (juvenile survival analysis). Maximum likelihood estimates of natural per-capita survival probabilities of yellow tang on reefs in West Hawai'i were produced using Cormack–Jolly–Seber (CJS) models (Lebreton et al. 1992) in Program MARK (White and Burnham 1999). Survival rates in coral reef fish studies are commonly estimated based on the fraction of whole cohorts or groups of aggregated individuals that survive

over time. For species which settle in discrete pulses, the effect of age on survival is assumed to be relatively uniform among groups (Hixon and Webster 2002). For reef fishes such as yellow tang, settlement occurs on a varied but consistent basis, and individuals end up living among conspecifics of multiple ages and under fluctuating densities. In the recruit survival analysis a method modified from Sale and Ferrell (1988) of following untagged individuals with high site fidelity was combined with a CJS modeling approach, allowing for the estimation of both age and density effects from these mixed-age groups. In the juvenile survival analysis, more standard CMR field techniques were used. However, since it is impossible to completely distinguish between death and emigration with most CMR methods, it is important to note that apparent rather than true survival estimates were produced (Lebreton et al. 1992).

## Materials and methods

### Study species

Yellow tang, *Z. flavescens*, is one of the most abundant herbivorous surgeonfishes (family Acanthuridae) along the west (Kona) coast of Hawai'i Island (Walsh et al. 2005; Tissot et al. 2004). They settle at ~30 mm total length (TL) after ~55 days as planktonic larvae (D. Shafer, pers. comm.). Settlement is highly variable in both time and space, but greatest during the summer (Walsh 1987; Walsh et al. 2005). Newly settled yellow tang retain some morphological characteristics (translucent pale yellow color and vertically extended body and fins) from their pelagic larval stage. These characteristics make them easy to identify up to 3 days after settlement. Yellow tang recruits are defined here as post-settlement individuals  $\leq 50$  mm TL. Results of pilot studies with tagged recruits proved manipulative experiments unfeasible, but indicated that recruits have very high site fidelity. Juveniles, defined here as yellow tang between 50 and 140 mm TL, also displayed very high site fidelity (this study).

### Study sites

Juvenile yellow tang were tagged and monitored at three sites along the west coast of Hawai'i Island: Wawaloli, 19°42'N, 156°03'W; North Keauhou Bay, 19°34'N, 155°58'W; and Ke'ei, 19°27'N, 155°55'W. Survival of recruits was estimated from visual censuses at fixed quadrats at Wawaloli. Since the goal of the study was to investigate natural probabilities of survival, all work was done at sites closed to aquarium collecting. Recruit and juvenile yellow tang are commonly found in mid-depth

(10–20 m) coral rich areas at these sites. Because of a positive correlation between abundance of *Porites compressa* and juvenile yellow tang at sites in West Hawaii, this coral has been regarded as important yellow tang habitat (Walsh 1987; Walsh et al. 2005; Ortiz and Tissot 2008). However, at Wawaloli, *P. compressa* is in relatively low abundance (7% of total substrate within our quadrats), and there were frequent personal observations of recruits using the other major coral species (*Porites lobata*, 33% and *Pocillopora meandrina*, 7% of the total substrate within our quadrats) for refuge. Therefore, total coral cover seemed to be an appropriate proxy for the amount of refuge habitat available to recruits in quadrats at Wawaloli.

#### Data collection

##### *Recruit survival*

In order to facilitate identification and track the survival of recently settled untagged yellow tang over time, habitat at Wawaloli was systematically surveyed using 12 permanent 10 m<sup>2</sup> quadrats. The layout consisted of two sets of six quadrats (two rows of three quadrats per set, each quadrat spaced 3.5-m apart). The two sets were placed ~30-m apart, at 14–18 m depth, in the coral rich zone of a continuous reef, along the upper edge of the outer drop-off.

Each set of quadrats was located within a large area of relatively homogeneous reef, to minimize habitat heterogeneity between individual quadrats. However, to assess whether differences in coral cover had substantial effects on the survival, benthic substrate was quantified in each quadrat at the start of the study. Nine digital photoquadrats, each with an image area of 60 × 40 cm, were taken at evenly spaced intervals throughout each quadrat. Photos were analyzed for benthic composition using *Coral Point Count with Excel extensions* (CPCe) to overlay a simple random distribution of 20 points over each photo (Kohler and Gill 2006). The type of substrate or taxon under each point was identified, and total percent coral cover was calculated for each quadrat.

Sampling took place over three consecutive summers. All 12 quadrats were sampled on each occasion on a single day. Sampling occurred on 18 occasions between July 3 and August 20 in 2004, on 10 occasions between June 18 and July 19 in 2005, and on 13 occasions between June 10 and July 8 in 2006. The mean interval between sampling during these periods was 2.8 days (±0.95 SD). Based on mean growth rate calculated from daily otolith rings back-calculated to settlement, it takes yellow tang recruits ~62 days post-settlement to reach 50 mm TL (D. Shafer pers. comm.). Sampling periods for recruit survival extended over 49, 31, and 38 days in 2004, 2005, and 2006, respectively; therefore even individuals that settled on the

first day of sampling in a given summer should not have grown to lengths greater than 50 mm TL during the sampling period. During each sampling occasion, a single observer on SCUBA spent 5 min per quadrat hovering ~2 m above the substrate to minimize disturbance. For each yellow tang recruit within the quadrat, the diver recorded whether it had the morphology of a new settler, made a size estimate, sketched each individual's home site, and also noted any distinguishing marks on the individual for future reference. Distinguishing marks were not common, but when present, they helped support the assumption that individuals maintained stable home sites. New settlers were identified only as those first seen with the new settler morphology. Yellow tang recruits first seen with new settler morphology and subsequently recorded with the appropriate size in the same location within each quadrat were assumed to be the same individuals.

##### *Juvenile survival*

Juvenile yellow tang were captured using a fine mesh barrier net and tagged at all three sites in 10–20 m depth. They were measured to the nearest mm TL and tagged under water to reduce stress on the fish. Each individual was tagged with a unique color/location combination of multiple elastomer tags, Northwest Marine Technology, Inc. (Frederick 1997). At Ke'ei, 49 juveniles were tagged in July 2004 and 35 more in December 2004. At Wawaloli, 20 juveniles were tagged in July 2004 and 17 more in December 2004. Sampling occurred at both these sites in August 2004, 1 month after tagging, and then every 2 months until October 2005. A third site was added in June 2005 when 82 individuals were tagged at North Keauhou. Sampling then occurred every 2 months until May 2006, except that the December 2005 sample was missed because of bad weather.

On each sampling occasion, the location of each individual within a grid of 5 × 7.5 m quadrats was recorded to confirm the level of site fidelity. Concurrent growth and movement studies indicated that individual females made an ontogenetic habitat shift to shallower water habitats at ~140 mm TL. Robertson (1988) reported that relocation could be an important factor in structuring reef populations of surgeonfish, such that numbers of surgeonfish settling on a patch reef did not reflect future abundance in local adult populations. Therefore, individuals >127 mm TL were removed from subsequent survival analysis to minimize the chance of emigration via ontogenetic habitat shift during our 10–15 month sampling period. Males make an ontogenetic habitat shift at ~165 mm TL; therefore male emigration during the sampling period was not an issue.

During each sampling occasion, approximately 240 total diver minutes were spent recording the location of each

tagged juvenile observed within the sampling grid. Divers made an effort to standardize their observation time uniformly across the grid during each sampling occasion. Also, the area roughly 50 m in all directions away from the grid was searched for individuals that might have shifted their home site. Over the course of this study, only one individual was observed that shifted its home site outside the grid ~20 m from its original site and was then seen at the new home site on multiple occasions over the following 6 months. In an attempt to quantify short-term loss due to handling and tagging, sampling was also done at each site 1 week after tagging. The surveys 1 week after tagging were not included in the survival analysis, although any individuals lost during this period were left in the sample because it would not be possible to separate handling/tagging from natural mortality over that time period.

#### Analysis of survival and resight probability

An encounter history (resighted or not resighted during each sampling occasion) was compiled for each individual. Individual encounter histories were then combined to construct a Program MARK input file for each analysis (White and Burnham 1999). Cormack–Jolly–Seber (CJS) models were used to calculate apparent survival ( $\Phi$ ) and resight probability ( $p$ ; Lebreton et al. 1992). Each model contained a unique parameterization including various combinations of individual covariates to evaluate their affect on  $\Phi$ . To reduce the chance of obtaining spurious results, the “all possible models” approach was avoided (Anderson et al. 2001) and a set of candidate models was chosen a priori for each analysis based on biological reasoning. Instead of creating and testing null hypotheses, the model selection approach implemented in Program MARK simultaneously confronts each model in a set with the data (i.e., the program MARK input file). Biological inference is then made by comparing the level of support for each model (Burnham and Anderson 2002).

When incorporating individual covariates into the CJS models,  $\Phi$  was parameterized as having a linear relationship with one or more individual covariates on the logistic scale in the following form:

$$\Phi_i = \frac{e^{\beta_0 + \sum_{j=1}^N \beta_j X_{ji}}}{1 + e^{\beta_0 + \sum_{j=1}^N \beta_j X_{ji}}}$$

where  $\Phi_i$  denotes the survival parameter for an individual  $i$ .  $X_{ji}$  is the  $j$ th covariate value for individual  $i$ .  $N$  is the number of covariates in the model.  $\beta_0$  is the common intercept parameter, and  $\beta_j$  is the slope or categorical offset parameter for the  $j$ th covariate. Using this logistic form

allows survival which is on the probability scale [0 to 1] to be expressed as a linear function of the vector of covariate values measured on the real scale  $[-\infty, +\infty]$ . Estimates of  $\Phi$  or  $p$  were scaled over an appropriate time period for each analysis, daily for recruits and monthly for juveniles.

#### Candidate models: recruit survival analysis

A set of candidate models was formulated to investigate the effects of individual age, conspecific recruit density, and habitat on the per-capita survival of yellow tang recruits (Table 1). Survival was modeled first as a single parameter  $\Phi(\cdot)$ , a constant probability across all individuals and sampling occasions in the study. Age, calculated as days since a recruit was first observed exhibiting remnant larval morphology, was modeled in two forms. First, age was modeled as categorical variable representing two age classes: (1) 0 to 3 days old; (2) 3 days and older, denoted by  $\Phi(A_{0-3,3+})$ , because some coral reef fish species exhibit measurably higher mortality for settling individuals in the hours or few days immediately following settlement (Caselle 1999; Planes and Lecaillon 2001; Hixon and Webster 2002; Steele and Forrester 2002; Almany and Webster 2006). Second, age was modeled as an individual covariate denoted by  $\Phi(A)$ , because survival may increase as a more consistent trend over the few weeks after settlement (Sale and Ferrell 1988; Caley 1998). Recruit density was calculated for each individual at the start of each interval as the number of yellow tang recruits in the individual's quadrat at each sampling occasion and modeled as an individual covariate denoted by  $\Phi(D)$ . To examine whether habitat differences between our quadrats

**Table 1** Summary of *Zebrasoma flavescens* recruit survival analysis model selection statistics

| #  | Model                             | QAICc | $\Delta$ QAICc | $w_i$ | $N_p$ | QDeviance |
|----|-----------------------------------|-------|----------------|-------|-------|-----------|
| 1  | $\Phi(D + A)p(\cdot)$             | 716.5 | 0              | 0.68  | 4     | 708.5     |
| 2  | $\Phi(D + A_{0-3,3+})p(\cdot)$    | 718.4 | 1.90           | 0.26  | 4     | 710.4     |
| 3  | $\Phi(D + \%CC)p(\cdot)$          | 723.3 | 6.73           | 0.02  | 4     | 715.2     |
| 4  | $\Phi(D)p(\cdot)$                 | 723.6 | 7.10           | 0.02  | 3     | 717.6     |
| 5  | $\Phi(A + \%CC)p(\cdot)$          | 725.6 | 9.05           | <0.01 | 4     | 717.6     |
| 6  | $\Phi(A)p(\cdot)$                 | 726.1 | 9.59           | <0.01 | 3     | 720.1     |
| 7  | $\Phi(A_{0-3,3+} + \%CC)p(\cdot)$ | 730.9 | 14.40          | <0.01 | 4     | 722.9     |
| 8  | $\Phi(A_{0-3,3+})p(\cdot)$        | 732.1 | 15.58          | <0.01 | 3     | 726.1     |
| 9  | $\Phi(\%CC)p(\cdot)$              | 738.9 | 22.32          | <0.01 | 3     | 732.8     |
| 10 | $\Phi(\cdot)p(\cdot)$             | 740.6 | 24.11          | 0     | 2     | 736.6     |

*QAICc* Akaike information criterion corrected for overdispersion and small sample size,  $\Delta$ *QAICc* QAICc difference of a model from the minimum QAICc,  $w_i$  Akaike weight,  $N_p$  number of independently estimable parameters in the model, *QDeviance* model deviance adjusted for overdispersion. See text for a description of model notation

had substantial effects on the survival, percent coral cover for each quadrat was modeled as an individual covariate denoted by  $\Phi(\%CC)$ . Additive models were included to investigate effects of covariate combinations and denoted by  $\Phi(covariate1 + covariate2)$ . Resight probability was modeled as a constant parameter denoted by  $p(\cdot)$  in combination with each parameterization of  $\Phi$ , because we had no a priori reason to suspect the ability to resight recruits varied over time or space.

#### Candidate models: juvenile survival

A set of candidate models was formulated to investigate the effects of individual body size and site on the per-capita survival for juvenile yellow tang (Table 2). Juvenile survival was first modeled as a single constant parameter, denoted by  $\Phi(\cdot)$ . Total length, measured at the time of initial capture, was used as an individual covariate to estimate the effect of size on survival, denoted by  $\Phi(TL)$ . Mark and recapture studies have commonly shown increased survival of larger juvenile fishes (Sogard 1997). It was not possible to estimate age of juvenile individuals in the present study since otolith methods would have been destructive and settlement date of juveniles was unknown. Site differences, which probably reflect some combination of differences in habitat and predator abundance, were modeled as a separate parameter for each site, denoted by  $\Phi(s)$ . The additive model of both covariates was also included, denoted by  $\Phi(s + TL)$ . Resight probability was modeled as a constant parameter  $p(\cdot)$  in combination with each parameterization of  $\Phi$ , because we had no a priori reason to suspect the ability to resight tagged yellow tang varied over time or space.

#### Goodness of fit testing and model selection

The CJS models used in this study assume only binomial variation (Lebreton et al. 1992), yet commonly CMR data can be overdispersed, which can lead to underestimated variances. Overdispersion can be caused by a lack of

independence between individuals, which can be common in CMR data (Anderson et al. 1994). To assess the amount of overdispersion (i.e., lack of fit) in our data, the median  $\hat{c}$  approach in MARK was used to estimate the variance inflation factor  $\hat{c}$ . A  $\hat{c}$  value of 1.0 means data exhibit little overdispersion; the greater  $\hat{c}$ , the more overdispersion in the data. This approach is currently considered to be the most general and robust available (White and Burnham 1999; Cooch and White 2007). The current version of MARK is not able to include individual covariates in the median  $\hat{c}$  procedure, so for each analysis, the most parameterized model in the respective candidate model set without covariates was used to estimate  $\hat{c}$ . This remains a conservative approach because overdispersion in the data is likely to be explained by one or more of the individual covariates which would lead to a smaller estimate of  $\hat{c}$ . Model selection statistics, standard errors and confidence intervals of the maximum likelihood parameter estimates (MLEs) were adjusted according to the  $\hat{c}$  generated by the median  $\hat{c}$  procedure.

Model selection using the complete model set for each analysis was performed in Program MARK using quasi-likelihood QAICc. QAICc is a form of Akaike's information criterion (AIC), corrected for both overdispersion with the estimate of  $\hat{c}$  (QAIC) and for the sample size (AICc; Akaike 1973; Burnham and Anderson 2002). The best model in the set is defined by the lowest QAICc value. QAICc differences ( $\Delta QAICc$ ) were computed and reported to compare relative difference between the models. Akaike weights ( $w_i$ ), normalized so they sum to one for the model set, were calculated to assess the relative likelihood of each model in the candidate model set and can be interpreted as a weight of evidence (Burnham and Anderson 2002). Greater weights indicate greater confidence in the selection of a model. The number of independently estimable parameters was also reported for each model.

If no single model in a candidate set was highly supported ( $w_i > 0.90$ ), a model averaging procedure was used to account for this model selection uncertainty. This procedure weighs the impact of all models for a given parameter according to its  $w_i$  and produces a single estimate and the associated 95% CIs for each specified parameter (Burnham and Anderson 2002). This variance estimate incorporates both the sampling variance and the variation from the model selection uncertainty (Buckland et al. 1997).

## Results

### Recruit survival

A total of 168 yellow tang recruits were first observed with the new settler morphology within the quadrats during our

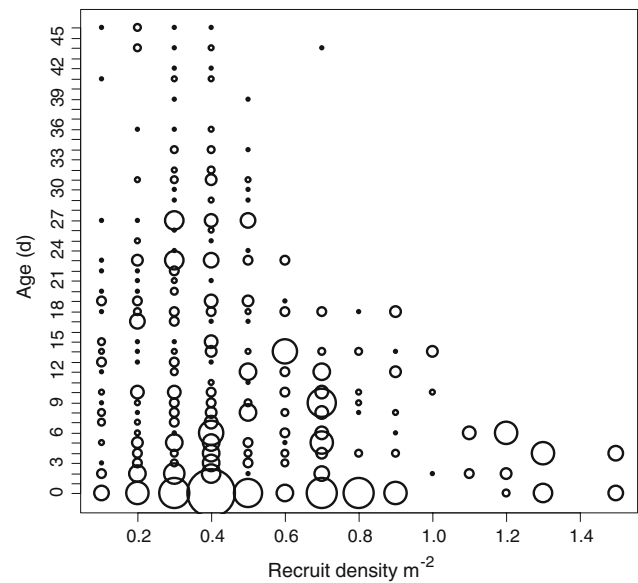
**Table 2** Summary of *Zebrafish* juvenile survival analysis model selection statistics

| # | Model                  | QAICc | $\Delta QAICc$ | $w_i$ | Np. | QDeviance |
|---|------------------------|-------|----------------|-------|-----|-----------|
| 1 | $\Phi(\cdot)p(\cdot)$  | 852.2 | 0              | 0.58  | 2   | 848.3     |
| 2 | $\Phi(TL)p(\cdot)$     | 854.0 | 1.73           | 0.24  | 3   | 848.0     |
| 3 | $\Phi(s)p(\cdot)$      | 855.4 | 3.14           | 0.12  | 4   | 847.3     |
| 4 | $\Phi(s + TL)p(\cdot)$ | 857.1 | 4.81           | 0.05  | 5   | 847.0     |

QAICc Akaike information criterion corrected for overdispersion and small sample size,  $\Delta QAICc$  QAICc difference of a model from the minimum QAICc,  $w_i$  Akaike weight, Np. number of independently estimable parameters in the model, QDeviance model deviance adjusted for overdispersion. See text for a description of model notation

sampling period. Settlement occurred consistently across all three summers, i.e., new recruits with the recently settled morphology were counted in the quadrats on 66% of sampling occasions. Variation in settlement led to a large range densities and ages within the quadrats over the sampling period (Table 3). Mortality naturally led to relatively fewer individuals reaching older ages and a low level of colinearity between age and density. However, there was adequate overlap through moderate densities and ages (Fig. 1) and substantial unexplained variation (Pearson correlation coefficient =  $-0.296$ ) to explore differences between density and age effects. The median  $\hat{c}$  procedure estimated  $\hat{c}$  to be 1.32, suggesting that there is little extra-binomial variation in the recruit data.

There is strong evidence that density and age both affect recruit survival (Table 1). The models best supported by the data were those that included the additive effects of density and either form of age. The two highest ranked models (Table 1, model 1, 2) combined received 94% of the overall support from summing the Akaike weights. In both models, daily survival was density dependent, decreasing with increasing conspecific density (i.e., negative  $\beta$  for the density individual covariate with confidence intervals that did not overlap 0; Table 4). In model 1 (Table 1), survival increased as a linear function of age on the logistic scale (Table 4), and in model 2 (Table 1) survival was decreased during the first 3 days following settlement (Table 4). Comparing the top two models in Table 1 to their reduced single covariate counterparts (Table 1, models 4, 6, 8), it is clear that the additive models fit the data substantially better. To illustrate the relationship of the estimates of age and density effects from the highest ranked model, survival estimates were plotted against age and density to create an age–density surface (Fig. 2). There was very little evidence in the data that differences in total percent coral cover between quadrats affected survival



**Fig. 1** Sampling distribution of individual combinations of *Zebrosoma flavescens* recruit density  $m^{-2}$  and age (d). The size of the circle reflects the number of individuals sampled over the course of the study at that age and density combination, ranging from 1 (for example, age 3 and density  $0.1 m^{-2}$ ) to 36 (at age 0 and density  $0.4 m^{-2}$ )

probabilities relative to the effects of density and age (Table 1).

The model averaging procedure was used to produce estimates of per-capita daily survival probability with 95% confidence intervals, which incorporate model selection uncertainty among all the models in our recruit survival candidate model set (Table 1). This uncertainty stemmed primarily from the two different ways age was parameterized in the top two models because they accounted for over 95% of the total  $w_i$ . Daily survival estimates were produced at four densities ( $0.1, 0.5, 0.9,$  and  $1.3$  recruits  $m^{-2}$ ) and

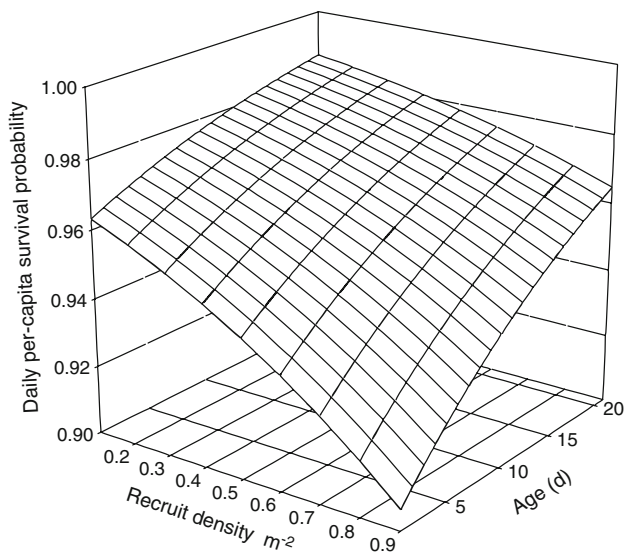
**Table 3** Summary of recruit and juvenile *Zebrosoma flavescens* individual covariates

|                 | Mean | SD   | Min. | Max. |
|-----------------|------|------|------|------|
| <b>Recruit</b>  |      |      |      |      |
| A               | 11.7 | 10.2 | 0    | 48   |
| D               | 0.50 | 0.32 | 0.1  | 1.5  |
| %CC             | 48.3 | 8.7  | 30.7 | 57.1 |
| <b>Juvenile</b> |      |      |      |      |
| TL—Wawaloli     | 85.5 | 19.6 | 58   | 123  |
| TL—Keauhau      | 88.6 | 14.8 | 66   | 127  |
| TL—Ke’ei        | 99.7 | 11.5 | 68   | 126  |
| TL—Total        | 92.6 | 15.7 | 58   | 127  |

Recruit: A age (d), D density (recruits  $m^{-2}$ ), %CC total percent coral cover in a quadrat; and juvenile: TL—(site): total length (mm) measured at time of capture for each site and across all sites (Total)

**Table 4**  $\beta$  estimates, standard error (SE), and 95% lower (LCI) and upper (UCI) confidence intervals for the two highest ranked models in the *Zebrosoma flavescens* recruit survival analysis

| $\beta$ Parameter              | Estimate | SE    | LCI    | UCI    |
|--------------------------------|----------|-------|--------|--------|
| $\Phi(D + A)p(\cdot)$          |          |       |        |        |
| $\Phi$ Intercept               | 3.335    | 0.334 | 2.681  | 3.990  |
| $\Phi$ D slope                 | -0.124   | 0.036 | -0.194 | -0.055 |
| $\Phi$ A slope                 | 0.052    | 0.019 | 0.015  | 0.089  |
| p                              | 2.297    | 0.164 | 1.976  | 2.619  |
| $\Phi(D + A_{0-3,3+})p(\cdot)$ |          |       |        |        |
| $\Phi$ Intercept               | 3.401    | 0.336 | 2.742  | 4.059  |
| $\Phi$ D slope                 | -0.145   | 0.035 | -0.214 | -0.076 |
| $\Phi$ A <sub>3+</sub>         | 0.778    | 0.274 | 0.240  | 1.316  |
| p                              | 2.316    | 0.165 | 1.992  | 2.640  |



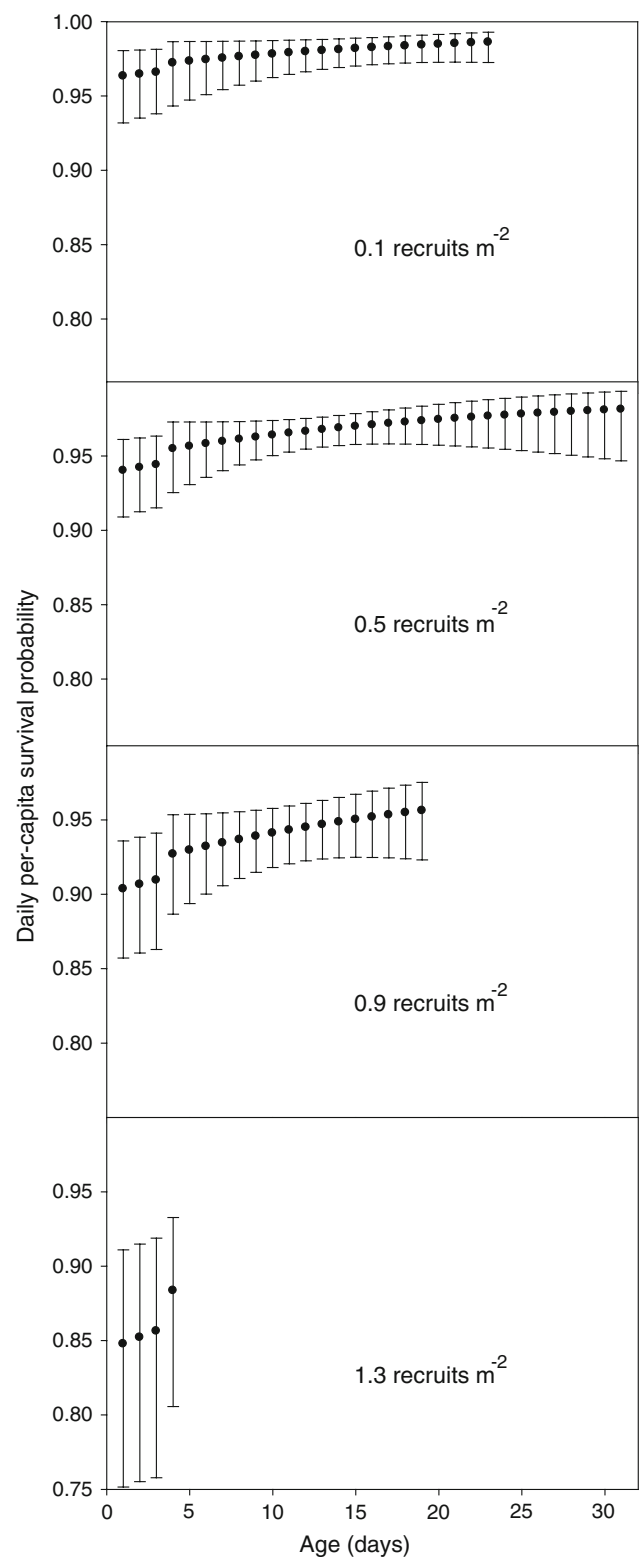
**Fig. 2** Age–density surface of survival probability for *Zebrasoma flavescens* recruits. Daily per-capita survival probability estimates from highest ranked recruit survival model [ $\Phi(D + A)p(\cdot)$ ]: additive effects of age (d) and recruit density  $m^{-2}$ . Estimates are truncated to a range of covariate values well represented in the data

plotted in Fig. 3 across an age range for each density that was well represented in our data (Fig. 1). While each of these plots is for a given density, individuals typically will experience changes in density due to mortality and new settlement from day to day. However, these plots do illustrate that density had a greater effect on survival than age over the range of each variable in this sample. At 1 day post-settlement the daily survival probability ranged from 0.963 (95% CI: 0.932–0.981) at a low density of 0.1 recruits  $m^{-2}$ , to 0.848 (95% CI: 0.752–0.911) at a high density of 1.3 recruits  $m^{-2}$ .

Estimates of resight probability were high and very similar for the two highest ranked models: model 1 (Table 1) resight probability was 0.909 (95% CI: 0.878–0.932); model 2 (Table 1), resight probability was 0.910 (95% CI: 0.880–0.933).

**Juvenile survival**

The size distribution of the 203 tagged juvenile yellow tang varied somewhat among sites (Table 3). Mortality over the week post-tagging, possibly due to handling and tagging, was very low (<2%) and not greater than estimated natural mortality during this period. The loss of a single elastomer tag each was observed in three individuals. However, the remaining tag(s), plus scar tissue at the site of the missing tag allowed for proper identification in all cases. The median  $\hat{c}$  procedure estimated  $\hat{c}$  to be 1.20, suggesting that little extra-binomial variation is present in the juvenile data.



**Fig. 3** Model averaged daily per-capita survival probability estimates with 95% confidence intervals, which incorporate model selection uncertainty for *Zebrasoma flavescens* recruits at four representative densities (0.1, 0.5, 0.9, and 1.3 recruits  $m^{-2}$ ). For each density, estimates were plotted for the age range that was well represented in our data

The highest ranked model, which kept survival and resight probability constant, received 58% of the total weight (Table 2, model 1). Monthly per-capita survival from this model was 0.939 (95% CI: 0.925–0.950), and the resight probability was 0.911 (95% CI: 0.882–0.933). The model with survival as a function of length ranked second, however, the added slope parameter ( $\beta$  associated with TL) did little to increase the fit of the model (i.e., very small change in QDeviance), and examination of that  $\beta$  estimate shows it was effectively 0 ( $-0.003$ , 95% CI =  $-0.02$  to  $0.01$ ). Since there was some model selection uncertainty, model averaged daily per-capita survival estimates were produced (using the mean TL) with 95% CIs to account for the potential difference in survival probability between sites: Wawaloli 0.936 (0.913–0.955), Keauhou 0.940 (0.923–0.953), and Ke'e'i 0.938 (0.923–0.951).

## Discussion

Natural probabilities of survival were estimated for yellow tang, *Zebrasoma flavescens*, from soon after settlement, through the juvenile stage targeted in the aquarium fishery. Model selection illustrated that conspecific recruit density and individual age affected recruit survival over the first few weeks post-settlement (Table 1). Probability of survival increased with increasing age and decreased with increasing density (Table 4, Figs. 2, 3). In juvenile yellow tang, natural probabilities of survival were constant across the range of body lengths and the different sites in the study (Table 2).

The three main relevant assumptions from CMR studies using CJS models (Burnham et al. 1987) appear to be valid for both analyses in this study. They are: (1) tagging/marking has no acute effect on survival, (2) marks are not lost or missed, and (3) every surviving marked animal has the same probability of recapture or detection during a sampling occasion. Assumptions related to the direct effects of tagging are not applicable to recruits because they were untagged. For elastomer tagged juveniles, there was no apparent increase in mortality over the first week after tagging. Further, this method has had little effect on survival when used with other fishes of similar size (Frederick 1997; Malone et al. 1999; Imbert et al. 2007; Wormald and Steele 2008). Elastomer tag loss was also minimal and using multiple tags per individual allowed for proper identification in the few instances when tags were lost. Finally, the visual resighting methods removed much of the potential bias common to trapping or other fishing recapture methods (Wormald and Steele 2008). Furthermore, since individual heterogeneity in resight/recapture probability can lead to high  $\hat{c}$  values (Cooch and White 2007), the low

$\hat{c}$  values (i.e., near 1.0) estimated in this study also support the validity of these assumptions.

It is possible, however, that the natural probabilities of recruit and juvenile survival for either were slightly underestimated, or in the case of recruit survival, slightly overestimated. Yellow tang exhibited very high site fidelity, but if some low level of emigration were occurring undetected, true survival probabilities would be even higher than the apparent survival probabilities calculated here. On the contrary, in the recruit survival analysis, the earliest that yellow tang recruits were recorded was during the morning following nocturnal settlement; however, given the frequency of sampling, it is possible that some recruits were  $\sim 36$  h and rarely  $\sim 60$  h post-settlement when first recorded at age 0. Therefore, the age effect in this study may be somewhat underestimated, and overall estimates of natural daily survival probability for the younger ages could be slightly high.

Survival during the process of settlement is generally low for coral reef fishes (Doherty et al. 2004; Almany and Webster 2006). These estimates of yellow tang recruit survival (Fig. 1) are higher than most published estimates for other young coral reef fishes (Planes and Lecaillon 2001; Hixon and Webster 2002; Doherty et al. 2004; Almany and Webster 2006). A meta-analysis of 24 species of coral reef fish estimated that 55.7% were consumed within 1–2 days post-settlement (Almany and Webster 2006). Only 39% of *Naso unicornis* settlers were estimated to survive the period from their nocturnal arrival on the reef (settlement) to the following morning (Doherty et al. 2004). A caging experiment using two other surgeonfish species, *Zebrasoma scopas* and *Ancanthurus triostegus*, implicated predators as a main cause of mortality during the settlement process (Planes and Lecaillon 2001). However, their caging methodology probably prevents comparisons of their estimates with estimates of natural unmanipulated survival.

The inclusion of a resight parameter in the CJS models may also have led to estimates of natural survival that are somewhat higher than estimates from previous studies. Usually resight parameters have not been estimated and/or incorporated into the models in studies of coral reef fish survival. It is typically assumed that individuals are seen or correctly counted on every sampling occasion (Sale and Ferrell 1988; Hixon and Webster 2002). In the present study, estimates of  $p$  were high. Therefore, incorporating  $p$  only slightly increased the estimates of daily survival probability. However, in cases where an observer's ability to resight a tagged individual may be lower for some reason (e.g., low visibility, cryptic coloration, and large home range), and especially where variation occurs in environmental sampling conditions over time, including estimates of  $p$  in the survival model can lead to more accurate

estimates of survival and variance estimation (Lebreton et al. 1992; Cooch and White 2007).

While many studies have reported detecting density-dependent survival in recently settled coral reef fish using traditional null hypothesis testing techniques (Hixon and Webster 2002), the meta-analysis of Osenberg et al. (2002) suggests that there is a greater ability to detect an effect of density when the focal species are at higher densities, even when per-capita effects of density on survival are similar. Yellow tang recruit density from the present study (mean density 0.5 recruits  $m^{-2}$ ; SD 0.3) would have fallen into the lower density range in their analysis, where detecting density dependence was less common. Furthermore, in some cases where it was detected, the effect sizes may be so low that they would have very little impact on population regulation. Therefore, the model selection approach used here, which focuses on estimation of effect sizes and model parameters, including their uncertainty, may be a more effective alternative to null hypothesis testing, particularly when densities are low (Burnham and Anderson 2002; Osenberg et al. 2002).

The magnitude of a density effect on survival can be dependent on the combination of level of settlement (i.e., local settler density) and the amount of available shelter. In many cases predators facilitate competition for shelter between conspecifics of prey species when shelter is limited (Holbrook and Schmitt 2002; Forrester and Steele 2004; Hixon and Jones 2005). In the present study, quadrats were located in the habitat likely to receive natural settlement. Results indicated that differences in coral cover (the proxy for amount of refuge habitat available) had less effect than differences in age or density, but this was expected because of the relatively limited amount of habitat heterogeneity between quadrats (Table 3). Observations during the current study of yellow tang recruits taking refuge in the protected spaces provided by coral suggest that habitat refuge limitation facilitated by predators is the most probable explanation for density dependence of yellow tang recruits. However, additional experiments would be needed to confirm whether this is the case.

Whether local conspecific density of coral reef fish is more likely to have a positive or negative effect on survival may depend on the combination of habitat type and intraspecific social behavior. Studies have frequently demonstrated density-dependent mortality on isolated patch reefs (Forrester et al. 2002; Hixon and Webster 2002), but along continuous reef structures there has been evidence for inverse density-dependent mortality or “safety in numbers,” in species which displayed coordinated predator avoidance (Sandin and Pacala 2005; White and Warner 2007). Sandin and Pacala (2005) postulated that if there is a cost to predators of moving between patch

reefs, then it would be advantageous for them to spend more time at patch reefs with higher prey densities. Conversely, on a continuous reef, predators would exploit the easiest targets, i.e., smallest groups. However, in the current study, yellow tang recruits on a continuous reef showed the opposite effect, i.e., lower survival when in larger groups. While the home ranges of yellow tang recruits tended to overlap, individuals appear to react independently to predators and divers. Therefore, a negative effect of density on survival may be more prevalent on continuous reefs for fishes that do not display coordinated predator avoidance or schooling/shoaling behavior (as defined by Pitcher and Parrish 1993).

The best supported model of juvenile survival in this study (Table 2, model 1), suggests constant monthly survival across the juvenile size range. This is contrary to other CMR studies of juvenile teleosts (Sogard 1997) that have commonly supported a positive relationship between body size and survival rates during the juvenile stage (Anderson 1988). However, such studies were usually done with tagged, hatchery raised juveniles, which may have introduced some bias (Sogard 1997). In Hawai'i, smaller hatchery raised striped mullet, *Mugil cephalus*, were less likely to survive after release into the wild (Leber 1995). However, a similar CMR study with wild caught fish showed that smaller individuals survived at a rate similar to larger individuals (Leber et al. 1995). The data from the juvenile survival analysis in this study appear to support the conclusion that using hatchery fish in CMR studies may introduce bias leading to an apparent positive relationship of size and survival over the juvenile size range.

Caley (1998) reviewed mortality schedules from studies of coral reef fish. As defined in that paper, Type 2 mortality refers to constant per-capita mortality throughout the lifespan, while Type 3 curves (concave up) indicate high mortality early in life followed by a relatively low and constant rate. Combining our recruit and juvenile survival analysis produces a result for yellow tang similar to a Type 3 curve. Daily post-settlement survival increased over the age range in the recruit analysis (at the mean density model averaged estimate: day 1 survival was 94%, up to ~98% at 30 days post-settlement) and continued to a much higher (~99.8%, converted from the monthly survival probability) and constant probability through the juvenile size range. Of the studies Caley (1998) reported, 75% had Type 2 mortality. However, many of the studies that found Type 2 mortality appear to have missed very early days soon after settlement, producing results generally similar to this study if based only on the juvenile survival analysis result. Therefore, if both the period immediately after settlement and more of the juvenile size/age range are included, Type 3 mortality may be demonstrated more often in coral reef fishes.

Local coral reef fisheries managers should take into account both the effects of age and density on survival in their analysis and interpretation of monitoring data. Because of the low initial rates of survival post-settlement, the smallest size class (recruits) should probably be disregarded in analysis of monitoring data. Estimates of recruit abundance are probably strongly dependent on timing of surveys relative to larger pulses of settlement, rather than accurately reflecting the amount of settlement at a given site. Sampling is further complicated because yellow tang recruits have lower probability of survival at higher recruit densities. This pattern tends to homogenize or reduce the patchiness of high density settlement. Thus surveys, particularly those covering a relatively small area, may not reflect the actual density or distribution of settlement (Connell 1985; Steele and Forrester 2002).

CMR methods combined with the model selection framework available in Program MARK provide great potential for obtaining important demographic information for coral reef species (Wormald and Steele 2008). The daily and monthly survival probabilities estimated in the present study can be multiplied out, yielding the probability of survival over longer time periods that may be more biologically relevant. For example, yellow tang reach sexual maturity at about 14 cm TL (about 5 years of age) (M.E. Bushnell pers. comm.), and therefore only approximately 1% of recruits may be surviving to adulthood when protected from fishing. Protected area monitoring data have shown that the added juvenile mortality in open areas from fishing, in combination with natural mortality, produces reduced juvenile abundance compared to protected populations (Tissot et al. 2004; Walsh et al. 2005). There is also recent evidence suggesting that over time fishing juveniles also impacts adult abundance (W. J. Walsh pers. comm.). While density effects on survival of recruits were detected in the present study, future research should explore whether density affects survival and growth of the larger juveniles that are targeted in the fishery, possibly with a removal experiment that mimics commercial fishing practices. Although compensatory increases in survival and growth in response to fishing pressure are commonly assumed in traditional fisheries management, further research is needed to confirm these assumptions, particularly for coral reef species.

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