



Estimating growth, size-dependent mortality, and tag loss in a mark–recapture study: demography of wavy turban snails in Southern California, USA

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ABSTRACT: Tagging studies are often used to measure survival and growth in wild populations. However, issues such as low returns of tagged animals, tag loss, and handling mortality can affect the precision and accuracy of demographic estimates if not accounted for. We conducted a mark–recapture study to measure the survival and growth of juvenile and adult wavy turban snails *Megastrea undosa*. Our study highlights several methodological advances, including a method for estimating a single growth function by analyzing the joint changes in length and weight of tagged animals; a simple method for estimating rates of tag loss when some animals are double tagged; and a way to estimate handling mortality by comparing encounter histories of animals immediately after tagging and after several weeks in the field. Tag loss was moderate ($\approx 15\%$ over a 100 d period) and handling mortality was substantial during the fall ($\approx 55\%$), but negligible during the spring. If we did not account for tag loss and handling mortality, our estimate of survival would have been severely underestimated ($\approx 46\%$ lower over a 100 d period). After accounting for such effects, our study revealed that survival probably increased sharply with body size, but survival did not differ among seasons. These snails are slow-growing, mature after approximately 6 yr, and can routinely grow to >10 yr old. There is an emerging fishery for this species, and because our results suggest that the oldest snails have a very high reproductive value, measures that protect these large individuals are likely to be beneficial for the resilience of these populations.

KEY WORDS: Handling mortality · *Megastrea undosa* · Predation · Reproductive value · Size-selective mortality · Tag recapture · Tag shedding · Type III survivorship · Von Bertalanffy growth function

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1. INTRODUCTION

Accurate measurements of species' demographic rates are critical for understanding the evolution of their life histories, the dynamics of their populations, and the effects that management actions can have on the long-term health of populations (reviewed by Coulson et al. 2006, Sandercock 2006, Metcalf & Pavard 2007). Demographic rates such as growth and mortality are important processes that often change throughout ontogeny (e.g. Krasne & Glanzman 1995, Gosselin & Qian 1997, Rochette et al. 1998). Because

of such changes, scientists need both an accurate description of what the average rates of growth and mortality are, and how these rates change throughout life in order to calculate key life history information such as the time it takes for organisms to grow to maturation, and the probability of a typical individual surviving to a reproductive age (Roff 2002). In addition, knowing the size- or age-dependent patterns of growth and survival can be useful when describing the dynamics of populations and evaluating the relative contribution of each age or life phase to properties such as average population

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size or population growth rate (Caswell 2001, Morris & Doak 2002).

In general, one of the most direct ways of measuring demographic rates in wild populations is to tag individuals and follow their fates over time (see reviews by Schwarz & Seber 1999, Pine et al. 2003, Sandercock 2006). Such mark–recapture studies have yielded a great deal of useful information on a large variety of species, and although a major goal of many mark–recapture studies is to estimate population size, here we concentrate on the estimation of demographic rates because analyzing the fates of tagged individuals is accompanied by a particular set of challenges. For example, it is often possible to tag only a small fraction of the population at large, and if tagged individuals intermix with non-tagged individuals, the probabilities of encountering tagged individuals after release can be low, thus leading to low effective sample sizes and imprecise estimates of demographic rates. In addition, issues such as tag loss and handling mortality may lead to a degree of bias in the estimates of demographic rates. To minimize the influence of these 3 issues (each of which we consider in more detail below), careful attention must be paid to both study design and data analysis.

Mark–recapture studies provide a direct means of measuring growth by comparing sizes of individuals at the time of tagging and recapture. However, field measurements of growth can be hampered by low probabilities of encountering previously tagged individuals. Even if animals can be readily tagged, it may still be difficult to find and recapture survivors, especially after long periods of time at liberty. Studies with long intervals between censuses may therefore have smaller sample sizes to measure growth, all else being equal (Gulland & Holt 1959). One obvious way to counter this effect is to make census intervals shorter. Such an adjustment can increase the effective sample size, but it may also mean that the expected magnitude of growth is relatively small, particularly if the animal being studied is naturally slow-growing. When census intervals are small, investigators may need to contend with a low ratio of signal to noise in the data (i.e. small average growth relative to measurement variability). This scenario can lead to low precision of growth estimates, although it should be noted that it does not necessarily introduce bias. Low signal to noise ratios present a challenge for making parameter estimates with a high degree of confidence, and in this context, it is desirable to extract information from the data as effectively as possible. With an eye toward that goal, in this study we outline a method for analyzing

growth patterns by considering changes in length and weight measurements jointly. Often, length and weight are measured concurrently in field studies, and although common growth models (e.g. the von Bertalanffy function) are typically estimated from a single measure of size (and length seems more commonly used, e.g. Jiao et al. 2010, Rypel 2012, Tang et al. 2014), using multiple measures of size can increase the precision of growth estimates and yield results that are more robust to measurement variability.

In contrast to a low rate of return of tagged individuals (which can affect the general precision of demographic estimates), tag loss can be a more insidious problem because it can lead to downward bias in estimates of survival. Even in studies that have multiple recapture events and can thus control for finite probabilities of recapture, estimates of survival probabilities will be biased if there is any tag loss (Arnason & Mills 1981). Most tagging methods can fail, and although tag retention will vary by method, species, and environment, many commonly used tags (e.g. floy tags, leg bands, numbered discs) are temporary and certainly experience some degree of loss. For example, tag loss has been estimated to be 75.2% yr⁻¹ for floy tags used on white bass, 16.0% yr⁻¹ for streamer tags used on lobsters, and 12.1% in 5 yr for passive integrated transponder (PIT) tags used on lemon sharks (Muoneke 1992, Rowe & Haedrich 2001, Feldheim et al. 2002). Other tagging methods that are meant to be more permanent, such as shell marks, toe clips, and subcutaneous injections of elastomer, are still susceptible to loss of recognition. For example, after 35 wk, the toes of some amphibians can regenerate, and fluorescent tags can be obscured as tissue grows over the tag (Davis & Ovaska 2001). Failure to account for a tag loss rate as small as 0.01 mo⁻¹ can result in a 25% underestimate in monthly survival probability (Henry & Jarne 2007), and despite the recognition of potentially large bias, relatively few studies consider tag loss explicitly. For example, a literature survey conducted by Henry & Jarne (2007) indicated that only 21% of mark–recapture studies of gastropods make mention of tag loss, and even fewer account for it in their analyses and conclusions.

One procedure to assess tag loss is to apply multiple tags to some individuals and follow their fates over time. For example, by tracking how many double-tagged individuals are recaptured later with a single tag, it is possible to make inferences regarding the probability of tag loss. Such a procedure works best when the fates of the tags are largely independ-

ent of one another. For example, when tags are attached to the organism at different locations, failure of one tag is unlikely to result in failure of the other. When an organism is given multiple tags, there are additional outcomes that can be observed in a mark–recapture study (alive with all tags retained, alive with only some tags retained), and the relative occurrence of these events can yield information on tag retention probabilities. Methods of analyzing tag loss in mark–recapture studies can be highly complex (e.g. Seber & Felton 1981, Wetherall 1982, Barrowman & Myers 1996) and can require explicit information on attributes such as sampling effort (e.g. Hyun et al. 2012). In this study, we highlight a simple approach to calculating rates of tag loss (and associated confidence intervals) from a study design in which individuals are given double tags of the same type. This approach uses information on the relative probabilities of double-tagged animals being recaptured with either one or both tags, and can be used to estimate tag retention as a single probability, or as a time-dependent process.

Another challenge associated with tagging studies is the potential for handling mortality. The capture and tagging of animals often involves procedures that impart some degree of stress to the organism (e.g. capture by nets, chemical sedation, implanting tags, exposure of aquatic organisms to air, etc.). Although most studies try to minimize the risk involved, handling mortality in a tagging study may upwardly bias the estimates of natural mortality, which is the process of interest to most researchers (Pollock 2000). When possible, handling mortality should be explicitly accounted for in the design and/or analysis of tagging studies. In this study, we assessed handling mortality by analyzing survival over several intervals between captures and comparing the survival during the interval immediately post-tagging to survival during other intervals. This approach can reveal a clearer picture of average survival in the wild since routine rates of survival can be separated from any effects of handling mortality.

To showcase these methodological advances, and to illustrate how they can improve field estimates of survival and growth in general, we analyzed data from a mark–recapture study that we conducted to evaluate growth and survival of a subtidal marine gastropod, the wavy turban snail *Megastrea undosa*. *M. undosa* is an example of a slow-growing species, and individual identity can be tracked with the aid of external tags affixed to the shell. A study of this species can thus serve as an example for highlighting processes that commonly pose a challenge for mark–

recapture studies (e.g. tag loss, a low signal to noise ratio in growth data, handling mortality), and for demonstrating how these processes can be accounted for to improve field estimates of demographic rates. In particular, we present a method for analyzing growth in length and growth in weight together in a single analysis; we derive a simple procedure to estimate rates of tag loss; and we show how field estimates of survival can be improved by incorporating estimates of tag loss and handling mortality into a standard, Cormack-Jolly-Seber analysis of encounter histories.

In addition to presenting these general, methodological advances, a further goal of this study was to test hypotheses about the survival of *M. undosa*. Specifically, we tested whether survival probabilities were dependent on size, whether there were seasonal differences in survival, whether the nature of size-dependent survival varied by season, and whether there was significant handling mortality associated with our tagging procedure. *M. undosa* may experience seasonal variation in survival because of seasonal variation in the frequency of storm events (Dayton & Tegner 1984) or because of a general, seasonal change in the abundance and activity of predators (Castañeda-Fernández-de-Lara et al. 2005, Villegas et al. 2014). Similarly, a general, size-dependent pattern of survival may be expected for *M. undosa* because of increases in speed or fortitude with body size (Bertness 1977, Schmitt 1981, Alfaro & Carpenter 1999). Finally, there is a small fishery for this species in California, and a larger fishery in Baja California, Mexico (Taniguchi & Rogers-Bennett 2001), but little is known about rates of survival in the field. It is expected that the California fishery will expand, and in order to anticipate the effects that an expanding fishery will have on these populations, a necessary first step is to estimate key demographic rates such as growth and survival.

2. MATERIALS AND METHODS

2.1. Study species

The wavy turban snail *Megastrea undosa*, previously known as *Astraea undosa* and *Lithopoma undosum* (Bouchet & Rosenberg 2016), is a large, subtidal marine gastropod that ranges from Point Conception, California (USA), to Isla Asuncion, Baja California (Mexico) (Taniguchi & Rogers-Bennett 2001). The wavy turban snail has a depth range from the low intertidal zone to 80 m, and in some locations,

population density of this species exhibits a negative relationship with depth (Alfaro & Carpenter 1999). The wavy turban snail is one of the largest gastropods found off the coast of California, and the shells of these animals can reach a basal diameter of up to 145 mm in our study area (pers. obs.). The wavy turban snail is a generalist herbivore known to eat macroalgae such as fleshy brown algae and coralline algae, but preferentially eats kelp (Cox & Murray 2006, Mazariegos-Villarreal et al. 2017). Predators of the wavy turban snail include the sea star *Pisaster giganteus*, Kellet's whelk *Kelletia kelletii*, the lobster *Panulirus interruptus*, and the octopus *Octopus bimaculatus* (Schmitt 1982, Alfaro & Carpenter 1999). Broken shells may indicate predation by lobsters, whereas empty shells may indicate death caused by octopuses, sea stars, Kellet's whelks, or disease (Schmitt 1982, Ambrose 1986). Predation by octopuses may be distinguished from other causes of death because octopuses carry snails back to their dens and discard the shells near the entrance to the dens (Ambrose 1983).

We conducted a mark–recapture study of a population near White's Point, Palos Verdes, California (33°42'37.2" N, 118°18'50.1" W). Our study location ranged from 8 to 12 m in depth and was accessed by boat. Wavy turban snails were collected by divers using SCUBA and carried in nylon mesh bags. Once snails were taken to the surface, they were held in a 75 l cooler filled with fresh seawater collected from the sea surface. Snails spent <30 min out of water while being measured and tagged before being returned to the water by divers. After initial collection, snails were marked with uniquely numbered, 3-digit tags that were made from 10 Mil waterproof paper (TerraSlate). The tags were affixed to the shells using ethyl cyanoacrylate (Krazy Glue) and finished with a clear nail polish topcoat. Before adhesion of the tags to the shell, shells were patted dry, and, if needed, a small (~1 cm²) section of the shell was cleared of any encrusting plants or animals. In general, this method of marking hard-shelled gastropods has been shown to have acceptably low rates of tag loss (Henry & Jarne 2007), although in this study we were able to estimate rates of tag loss directly (see Section 2.2).

The study was conducted from March to December 2019, and a total of 323 snails were tagged. Tagging was concentrated in 2 rounds. The first round took place in the spring of 2019, when 117 snails were tagged and released over 3 dates: 4 March, 15 March, and 20 May. The second round took place in the fall of 2019, when a total of 206 snails were tagged and

released on 13 September and 11 October. Recapture trips were made approximately 1 mo apart from April until December. It was exceedingly rare to recapture a tagged snail once it had been at liberty for more than 100 d, largely because of tag overgrowth (see Section 3). Our study thus consisted of a set of snails whose growth and survival rates were measured in the spring and early summer, and another set whose growth and survival rates were measured in the fall and early winter (see Table A1 in the Appendix).

To measure the growth of snails, we recorded their weights and shell diameters during each recapture. Weight was recorded to the nearest gram and measured using either mechanical spring hanging scales (Ajax Scientific) or a digital hanging scale (model SR-1, American Weigh Scales). The basal diameter was measured to the nearest 0.1 mm with dial calipers. Diameter was measured from the aperture edge (the site of most recent growth) to the opposite side of the shell.

2.2. Estimating tag loss

To estimate tag loss, we double-tagged a subset of 88 snails over several visits. Double-tagged snails were given a second tag on the opposite side of the shell from the first tag; this made the tags relatively independent. Throughout the study, we recorded how many of the double-tagged snails returned with both tags or with a single tag only, which permitted us to make inferences about the rate of tag loss. In our study, tag loss included both the detachment of tags and tag fouling, i.e. the complete covering of a tag by encrusting plants or animals. We derived a general procedure to estimate probability of tag retention (and relevant confidence intervals) from double-tagged animals in the field. We then applied this method to our data and estimated rates of tag loss over time for our study of *M. undosa*.

In the analysis of double-tagged and recaptured animals, we can consider the probabilities of each event in symbolic terms: ϕ is the probability of survival, p is the probability of recapture, and r is the probability that a tag was retained. We consider tags that have unique numbers but are otherwise the same and thus have the same average retention probabilities. If an animal was recaptured with 2 tags, we know that it survived, was recaptured, and both tags were retained. The probability that these 4 events occurred is:

$$\phi \times p \times r \times r \quad (1)$$

If an animal was recaptured with 1 tag, we know that it survived, was recaptured, 1 tag was retained, and 1 tag was lost. The probability of this set of events is:

$$\phi \times p \times r \times (1-r) \quad (2)$$

However, there are 2 possibilities here. Either the first tag is lost and the second is retained, or the first is retained and the second is lost. Therefore, the probability of recovering a double-tagged animal with a single tag is:

$$2[\phi \times p \times r \times (1-r)] \quad (3)$$

Given that a double-tagged snail was recaptured, and knowing that only those snails that retained 1 or more tags could be identified, the (conditional) probability of being recaptured with both tags is:

$$\frac{\phi pr^2}{(2\phi pr(1-r) + \phi pr^2)} \quad (4A)$$

and this probability reduces to:

$$\frac{r}{[2(1-r) + r]} \quad (4B)$$

Note that the probability of a double-tagged animal returning with both tags is a relatively simple function of the probability of tag retention (r). By this expression, if tag retention is high, the probability that a snail returns with both tags is relatively high. In contrast, if tag retention is low, the probability that a recaptured snail will have just a single tag is relatively high. To estimate r from field data consisting of double-tagged animals returning with either a single tag or both tags, one can reason that these counts will follow a Bernoulli distribution (binomial with number of trials = 1). Animals recaptured with both tags can be coded as a 1 and animals recaptured with a single tag can be coded as 0. Assuming these counts come from a Bernoulli distribution with the probability of success described by Eq. (4B), one can use maximum likelihood estimation to find the value of r that was most likely to have produced the observed counts of single and double tagged animals. Confidence intervals for r can be calculated from likelihood profiles. Specifically, the range of values whose log likelihood lies within $\frac{\chi^2_{\alpha,1}}{2}$ units of the maximum defines a confidence interval at the $\alpha - 1$ level, where χ^2_1 is a chi-squared probability distribution with 1 degree of freedom (Meeker & Escobar 1995).

In our study, double-tagged snails had been at liberty for varying periods of time before they were recaptured. This feature allowed us to model tag retention probability as a time-dependent process. Such an approach is appropriate for external tags like the ones we used. In general, it is expected that tag retention

will decrease over time as adhesives become weaker, or tags become obscured by abrasion or overgrowth (Treble et al. 1993, Rotella & Hines 2005). We modeled r as a decreasing function of time. Specifically, $r = \exp(-\lambda t)$, where λ is our tag loss rate (in units of d^{-1}) and t is time, measured in days. This expression of r was nested into Eq. (4B), and we used the likelihood procedure described above to estimate λ and 95% confidence limits. All statistical analyses were conducted in R (R Development Core Team 2020), and we used the package 'bbmle' for maximum likelihood estimation (Bolker & R Development Core Team 2020).

2.3. Length–weight relationship

To describe the relationship between the basal diameter (L) and mass of snails (W), we used the power function $W = aL^b$, where a and b are scaling parameters. These scaling parameters were estimated from a linear regression of the natural logarithm of weight (measured in grams) on the natural logarithm of length (measured in mm). In this analysis, the slope estimates b and the intercept estimates the natural log of a . Scaling parameters and their (co)variances were estimated from all of the snails tagged in this study, and we used only the measurements from the initial capture of snails so that recaptured snails were not included more than once.

2.4. Estimating growth

For gastropods and many other organisms (e.g. fishes, crustaceans, reptiles), growth in length often follows a decelerating pattern that is commonly described by a von Bertalanffy growth function:

$$L_t = L_\infty(1 - e^{-kt}) \quad (5)$$

where L_∞ is asymptotic size, k is a growth coefficient describing how quickly individuals approach their asymptotic size (on average), and t is time. In general, growth in weight does not follow this same form, and it can be a challenge to fit common growth models (e.g. von Bertalanffy curves) to mark-recapture data when growth is measured from changes in weight. However, lengths and weights are often measured simultaneously in growth studies and can be analyzed jointly to provide a more accurate and precise estimate of growth. In this study, we recorded changes in both length and mass during each interval, and we knew the average relationship between length and weight with a high degree of

certainty (see Section 3). Assuming snail growth in length follows a von Bertalanffy function, we can use a modified version of Fabens' method (Fabens 1965) to estimate L_∞ and k from mark–recapture data. In this approach, length at recapture (L_r) is a function of length at time of initial measurement (L_m) and the parameters of the growth curve. Specifically,

$$L_r = L_m + (L_\infty - L_m)(-k(\Delta t)) \quad (6)$$

where Δt is the interval of time between marking and recapture. In this same analysis, weight at time of recapture (W_r) can be modeled as a function of weight at initial measurement (W_m), the parameters of the von Bertalanffy function, and parameters describing the length–weight relationship. In this case:

$$W_r = a \left(\left(\frac{W_m}{a} \right)^{\frac{1}{b}} + \left(L_\infty - \left(\frac{W_m}{a} \right)^{\frac{1}{b}} \right) (-k\Delta t) \right)^b \quad (7)$$

where a and b are the parameters of a power function relating length (diameter) to weight. Assuming that measurements of length and weight follow a multivariate normal distribution with means described by Eqs. (5) and (6), one can use maximum likelihood estimation to find the values of L_∞ and k that were most likely to have produced the data, as well as the variances and covariances associated with observations of both length and weight. To estimate growth curves for *M. undosa*, we fit Eqs. (5) and (6) to the data using the 'mle2' function in the 'bbmle' package in R (Bolker & R Development Core Team 2020).

When using the estimated growth curves to project size at age, we calculated 95% confidence bands by simulation. In this procedure, we assumed that estimates of the growth curve parameters were distributed according to a multivariate normal distribution with means and variance–covariance matrices estimated by the 'mle2' function. We also assumed that the length–weight scaling parameters (a and b) were distributed as multivariate normal with means and covariances as estimated as described above. For a total of 5000 simulated parameter values, size was predicted at ages of 0 to 11 yr in 50 d increments. The 2.5th and 97.5th percentiles of the distribution were used to describe the lower and upper limits of the 95% confidence intervals for size at age.

2.5. Survival

To estimate survival and recapture probabilities, we analyzed the encounter histories of the tagged snails. The encounter histories are a record of whether or not each snail was present during recap-

ture. In the encounter history, a value of 1 indicates an animal was found and 0 means an animal was not found at the time of recapture. We followed the general procedure of mark–recapture analysis that uses encounter histories to estimate both survival and recapture probabilities (ϕ and p , respectively; see Lebreton et al. 1992, Sandercock 2006 for reviews of the general approach), but with a few differences to accommodate the specifics of our study. Because our estimates of tag loss were restricted to a period of ~100 d at liberty (see Section 3), we analyzed individual encounter histories over a period less than 100 d. Although it was likely that many of the tagged snails remained in the general vicinity for much longer, tag overgrowth made it unreliable to use encounter histories to estimate survival after ~100 d in the field. The snails were tagged in 5 groups, and within the 100 d limit, each group experienced 4 recapture periods (the fifth group experienced 3 recaptures). For each group with 4 recaptures, there were 8 possible encounter histories, and each encounter history can be expressed as a function of survival and recapture probabilities (Table 1). For the group with 3 recaptures, there were 4 possible encounter histories (Table 1). In our analyses, we used maximum likelihood estimation to find the survival and recapture parameters that were most likely to have produced the encounter histories we observed. The encounter histories were assumed to come from a multinomial distribution with the probability of each encounter history specified by both the chosen values of survival and recapture probabilities and the events that could lead to each of the encounter histories (Table 1).

Survival and recapture probabilities can be influenced by many factors, including attributes of the animal (e.g. body size), field conditions, and personnel. Instead of treating ϕ and p as static, we fit several different models of ϕ and p to the data and compared the relative support for each model using Akaike's information criterion (AIC). Each model represents a competing hypothesis for how and why survival and recapture probabilities varied. Models to be considered were decided upon before the study was completed, and the set of candidate models was determined by both prior information and the need for a systematic examination of how survival varied. For our study, we had strong prior information that recapture probability would vary among recapture events and would vary with snail size. In particular, the number of divers searching for snails ranged from 2 to 4, and water clarity varied substantially. In addition, previous studies indicate that larger snails exhibit greater movement (Bertness 1977, Schmitt

Table 1. Encounter histories that were possible in this study. See Table A1 for the frequency of encounter histories observed in this study. ϕ : probability of survival; r : tag retention given the snail survived; p : probability of recapture

Encounter history	Probability of occurring
1111	$\phi_0\phi_1r_1p_1\phi_2r_2p_2\phi_3r_3p_3$
1110	$\phi_0\phi_1r_1p_1\phi_2r_2p_2(1-\phi_3)$ + $\phi_0\phi_1r_1p_1\phi_2r_2p_2\phi_3r_3(1-p_3)$ + $\phi_0\phi_1r_1p_1\phi_2r_2p_2\phi_3(1-r_3)$
1101	$\phi_0\phi_1r_1p_1\phi_2r_2(1-p_2)\phi_3r_3p_3$
1100	$\phi_0\phi_1r_1p_1(1-\phi_2) + \phi_0\phi_1r_1p_1\phi_2(1-r_2)$ + $\phi_0\phi_1r_1p_1\phi_2r_2(1-p_2)(1-\phi_3)$ + $\phi_0\phi_1r_1p_1\phi_2r_2(1-p_2)\phi_3(1-r_3)$ + $\phi_0\phi_1r_1p_1\phi_2r_2(1-p_2)$
1001	$\phi_0\phi_1r_1(1-p_1)\phi_2r_2(1-p_2)\phi_3r_3p_3$
1011	$\phi_0\phi_1r_1(1-p_1)\phi_2r_2p_2\phi_3r_3p_3$
1010	$\phi_0\phi_1r_1(1-p_1)\phi_2r_2p_2\phi_3r_3(1-p_3)$ + $\phi_0\phi_1r_1(1-p_1)\phi_2r_2p_2(1-\phi_3)$ + $\phi_0\phi_1r_1(1-p_1)\phi_2r_2p_2\phi_3(1-r_3)$
1000	$\phi_0\phi_1(1-r_1) + \phi_0\phi_1r_1(1-p_1)(1-\phi_2)$ + $\phi_0\phi_1r_1(1-p_1)\phi_2(1-r_2)$ + $\phi_0\phi_1r_1(1-p_1)(1-\phi_3)$ + $\phi_0\phi_1r_1(1-p_1)\phi_2r_2(1-p_2)\phi_3(1-r_3)$ + $\phi_0\phi_1r_1(1-p_1)\phi_2r_2(1-p_2)\phi_3r_3(1-p_3)$ + $(1-\phi_0\phi_1)$
111	$\phi_0\phi_1r_1p_1\phi_2r_2p_2$
110	$\phi_0\phi_1r_1p_1\phi_2r_2(1-p_2) + \phi_0\phi_1r_1p_1(1-\phi_2)$ + $\phi_0\phi_1r_1p_1\phi_2(1-r_2)$
101	$\phi_0\phi_1r_1(1-p_1)\phi_2r_2p_2$
100	$\phi_0\phi_1(1-r_1) + \phi_0\phi_1r_1(1-p_1)\phi_2r_2(1-p_2)$ + $\phi_0\phi_1r_1(1-p_1)(1-\phi_2)$ + $\phi_0\phi_1r_1(1-p_1)\phi_2(1-r_2) + \phi_0(1-\phi_1)$ + $(1-\phi_0\phi_1)$

1981, Alfaro & Carpenter 1999) and thus may be more difficult to detect on a given survey. To account for this variation, in all models we described the logit-transformed recapture probability as:

$$\log\left(\frac{p}{1-p}\right) = \alpha_i - \beta L \quad (8)$$

where β is a parameter that describes how recapture probability declines with snail body size (L), and α_i represents the baseline recapture probabilities that were allowed to differ for each recapture event, indexed by the subscript i .

The main hypotheses we were interested in concerned survival. In particular, we wanted to know whether survival depended on size (as it does in other gastropod species, e.g. Paine 1976, Nakaoka 1996, Shima et al. 2016), whether there were seasonal differences in survival, and whether there was any handling mortality. In the analyses, we modeled daily survival probabilities. To account for the fact that time intervals between recaptures differed, daily survival probability was raised to the power of the number of

days between sightings to calculate ϕ for a particular interval. Size-dependent survival was modeled as:

$$S_{\text{Max}}(1 - \exp(-cL)) \quad (9)$$

where L is the basal diameter of the snail, c is a parameter that describes how quickly survival changes with size, and S_{Max} describes the survival probability attained as snails get larger and larger. This is a relatively flexible function, and depending on the parameters, it can be flat (in the case of no size-dependence) or it can describe a curved pattern where survival changes with size and approaches an asymptotic value.

Handling mortality is a concern in any tagging study, and in our study, we removed snails from the water for up to 30 min while we measured and tagged them. Although we studied a fully subtidal population, some individuals of *M. undosa* are found in intertidal habitats and routinely survive temporary exposure to air (Taniguchi & Rogers-Bennett 2001). For example, based on the tide profiles in our study region, sedentary organisms at 0.305 m (1 foot) above Mean Lower Low Water are routinely exposed for 3–5 h during daytime in both the spring and fall (Flater 2020). We suspected that handling mortality would be minimal, but we could test for it explicitly. Handling mortality would result in lower than expected survival during the interval between initial tagging and initial recapture, and would manifest as an excess of encounter histories of 1, 0, 0, 0. To evaluate handling mortality, we included an additional term, ϕ_0 , which describes probability of surviving the tagging event. For example, the probability of observing an encounter history of 1, 1, 1 would be $\phi_0\phi_1p_1r_1\phi_2p_2r_2$, etc. (Table 1). Finally, we evaluated seasonal variation by systematically allowing 1 or more parameters describing survival and/or handling mortality to differ between the group of snails tagged in the spring, and the group tagged in the fall. This led to 10 different models describing how survival and recapture probabilities varied (see Table 2 for model details). Models were fit to the data using maximum likelihood estimation, and AIC values were compared to evaluate model support.

3. RESULTS

3.1. Tag loss

Double-tagged snails tended to retain both of their tags over the course of the study, but some tag loss occurred, and losses accumulated over time. The first

instances of tag loss were observed after 42 d, and after approximately 80 d, it was increasingly common to observe snails that were originally double-tagged returning with a single tag only (Fig. 1). When cumulative tag loss was described by an exponential model, our estimate of tag loss rate, λ , was $1.55 \times 10^{-3} \text{ d}^{-1}$ (95 % CI: 5.42×10^{-4} to 3.48×10^{-3}).

3.2. Length–weight relationship

The length–weight relationship for the snails is depicted in Fig. 2. The regression coefficient b value for the ln-transformed length–weight relationship was estimated to be 2.980, indicating that weight scales approximately with the cube of length. When converted back to the natural scale, the relationship between the basal diameter (L) and mass of snails (W) was estimated to be $W = 0.0003L^{2.980}$. The standard errors of scaling parameters a and b were estimated to be of 0.00005 and 0.02889, respectively. The r-squared value for the (ln-transformed) regression was 0.967, suggesting a close relationship between length and weight (Fig. 2).

3.3. Growth

Growth in length decreased as snails got larger (Fig. 3A), and growth in weight decreased as snails got heavier (Fig. 3B). The growth curves estimated

from the changes in size were expressed as plots of size at age (Fig. 3C,D). Growth in length was asymptotic; the average snail nearly reached the asymptote at approximately 11 yr old (Fig. 3C). Growth in weight showed a sigmoidal pattern (Fig. 3D). This reflects the fact that that growth in weight of the average snail peaked at intermediate size (cf. Fig. 3A). The von Bertalanffy growth coefficient (k) for the snails was 0.00055 (95 % CI: 0.00038–0.00080). The asymptotic size (L_{∞}) was 118.29 mm (95 % CI: 100.71–135.87 mm). The smallest snails we encountered (~27 mm diameter) were estimated to be 1.33 yr old, on average.

3.4. Survival and recapture probability

Of the 117 snails tagged in the spring and the 206 snails tagged in the fall, 39.3 and 31.1 % were recaptured at least once. The proportion that was recaptured was highest for snails of intermediate size, and relatively low for the smallest and largest snails (Fig. 4). Recapture depends on both survival and detection, and in our analyses we used a model comparison approach to draw inferences about the various processes that may have affected probabilities of survival and detection of our study animals. The models we used to describe the data varied in their degree of complexity (Table 2), and changes in model support (AIC scores) reflected the importance of including various processes when describing survival. For example, the drop in AIC values between

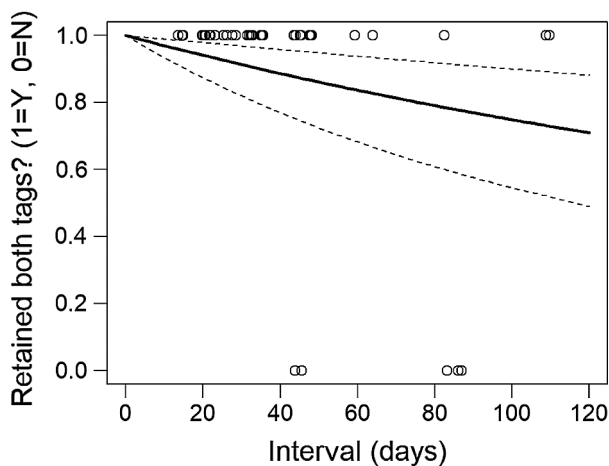


Fig. 1. Data used to evaluate tag retention in *Megastraea undosa* over time. Curves represent the probability of a double-tagged snail retaining both tags and are described as $r/(2-r)$, where the probability of tag retention (r) is described as an exponential function of time (t): $r = \exp(-\lambda t)$. Solid curve represents our mean estimate of tag loss rate (λ), dashed lines represent 95 % CI. $n = 84$

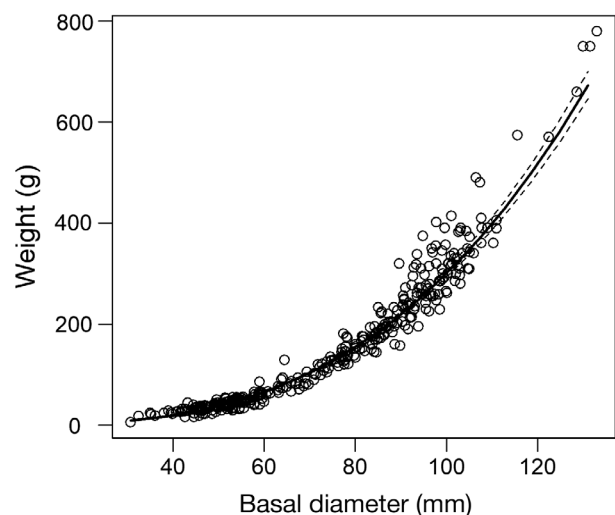


Fig. 2. Relationship between basal diameter and weight of *Megastraea undosa*. r -squared value for the regression of weight on diameter (both log-transformed) was 0.967. Dashed lines represent 95 % CI

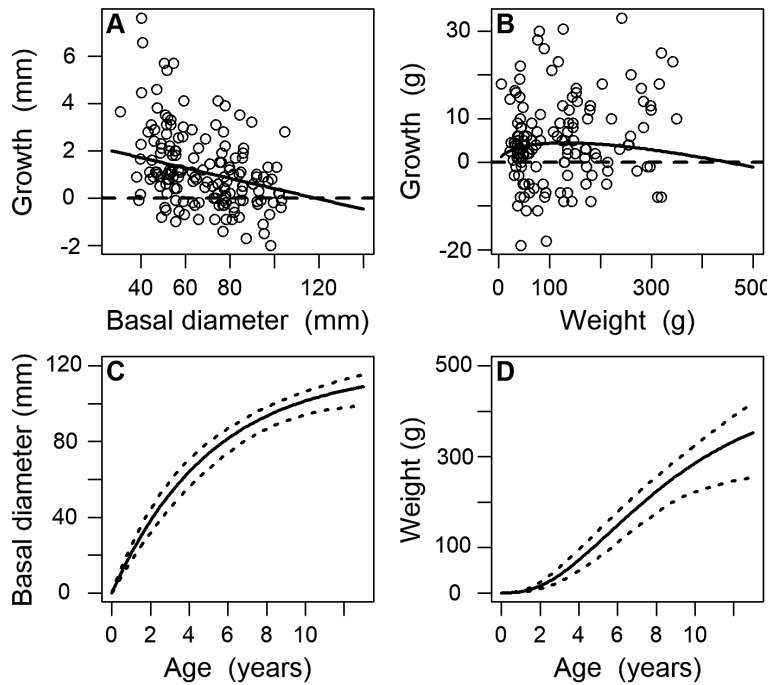


Fig. 3. (A,B) Relationships between *Megastraea undosa* size at capture and subsequent growth in (A) length and (B) weight. Average interval = 41 d. (C,D) Estimated patterns of size-at-age for both (C) length and (D) weight as estimated from the data displayed in panels A and B. All curves are derived from a single von Bertalanffy growth function that was estimated from a joint analysis of length and weight (see Section 2.4 of the main text). Curves in the top panels indicate average growth with size; curves in lower panels illustrate size at a given age. Solid curves represent the mean, and dashed curves indicate 95% CI

model 2 and model 1 suggested that handling mortality was important. The differences in AIC scores between models 3 and 4 further indicated that handling mortality was different between seasons. The best-fit model with the lowest AIC score was one that included size-dependent mortality, and handling mortality that varied by season (model 8; Table 2). Further refinements of this model in which either the baseline survival parameter or both the baseline survival and parameter describing size dependence were allowed to vary seasonally did not produce a substantial improvement in model fit (see models 9 and 10 in Table 2). Subsequent inferences about survival were based on the model with the greatest support (model 8; Table 2). From the estimated parameters of this model, it could be seen that handling mortality was only significant in the fall. The S_0 parameter was approximately 1 for spring, which indicates little to no handling mortality. In contrast, in the fall this value was 0.450, a value that indicated significant handling mortality. In general, there was no evidence that more complex functions were

needed to describe size-dependent recapture (data not shown).

Survival increased sharply with size (Fig. 5). Daily survival probability was quite low for newly recruited snails (≈ 0.94), but by the time they reached 50 mm in size (approximately 1000 d old), survival probability was greater than 0.995. The rate of size-dependence (c) was estimated to be 0.106 (95% CI: 0.087–0.132), and the maximum survival probability (S_{max}) was estimated to be 1.000 (95% CI: 1.000–1.000 when rounded to 3 decimal places). Recapture probability decreased with size. Average recapture probability for the smallest snails in this study (approximately 27 mm in diameter) was 0.330, whereas the recapture probability for snails that were 120 mm in diameter was 0.138 on average (Fig. 6).

4. DISCUSSION

Our results highlight the importance of carefully accounting for the effects of tag loss and handling mortality when conducting mark-recapture studies.

In general, estimates of survival can be biased downward if tag retention is imperfect, and although the rate of tag loss was moderate in our study (0.00155 d^{-1} , or $\approx 85\%$ chance of retaining a tag over a 100 d period), accounting for tag loss was essential for obtaining an accurate estimate of survival in the field. For example, if we assumed 100% tag retention, our estimate of the probability of an 80 mm snail surviving 100 d would have been 0.863. In contrast, when correcting for tag loss, the corresponding estimate was 0.980, i.e. a value 1.13 times larger. Ignoring handling mortality would have introduced an even larger bias in our field estimates of survival. Even though handling mortality was appreciable only in the fall season, our estimate of the probability of an 80 mm snail surviving 100 d would have been 0.415 if we had assumed no handling mortality. Such effects of tag loss on estimates of survival are consistent with other studies exploring this issue (e.g. Treble et al. 1993, Henry & Jarne 2007), and the value of survival corrected for tag loss and handling mortality is much more consistent with the observation that these snails can live 10–12 yr in the wild,

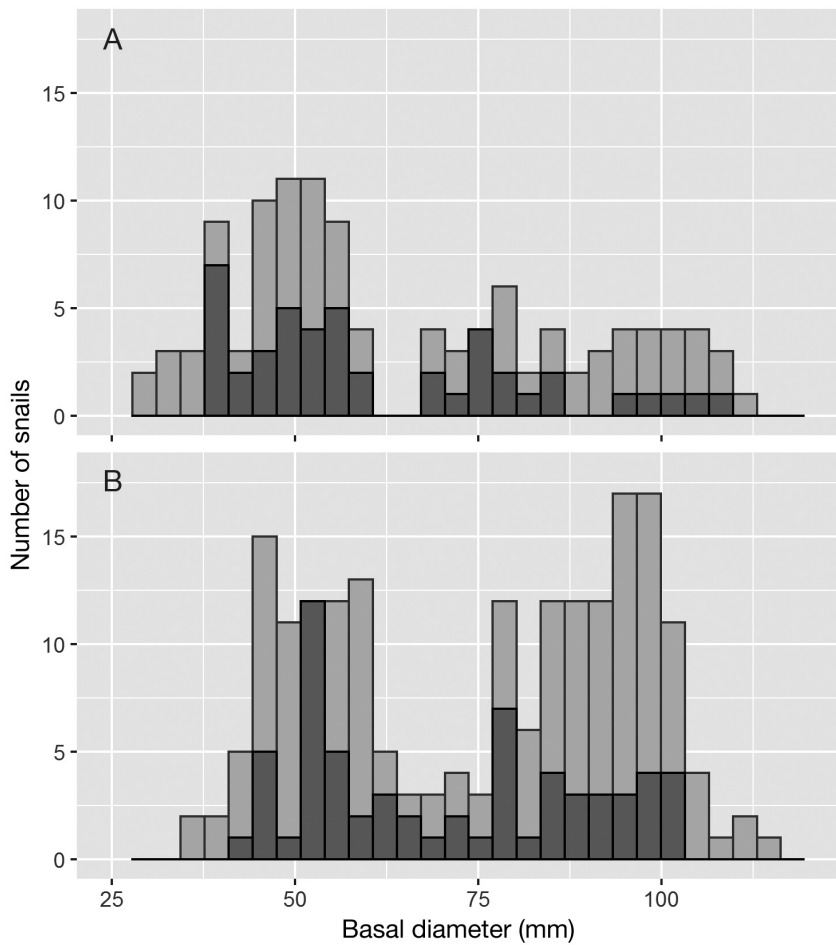


Fig. 4. Size-frequency distributions for all *Megastraea undosa* measured in each tagging event (light gray bars), and snails that were recaptured at least once (darker gray bars) in (A) spring and (B) fall. Within each size bin, the relative heights of the bars illustrate the relative probability of recapture, a process influenced by both survival and detectability

and possibly longer (Cupul-Magana & Torres-Moye 1996). Without accounting for tag loss and handling mortality, we would expect survival to 9 yr to be less than 0.001%. If we account for tag loss and handling mortality, we expect survival to 9 yr to be ~21%. Given the ages of snails regularly found in the field (e.g. ~30% of snails in a random sample were >9 yr old; Cupul-Magana & Torres-Moye 1996), the latter estimate is likely to be much more accurate. On a similar note, Martone & Micheli (2012) estimated survival of *Megastraea undosa* adults at 3 different locations and reported apparent survival probabilities of 0.536–0.759 (when converted to a 100 d period). These authors did not account for tag loss and handling mortality, and their reported values likely underestimated the true values of survival, although it is important to note that the goal of their study was a spatial comparison of relative, rather than absolute, survival rates, and the effects of tag loss and handling mortality were likely the same across locations.

Another issue that can be a challenge for mark–recapture studies concerns the measurement of growth when the time between measurements is small relative to the lifespan of the animal.

Table 2. A summary of the relative support for the various models describing survival of *Megastraea undosa* in the field. Values of Akaike's information criterion (AIC) are listed for each of 10 candidate models that describe variation in survival. Models are arranged in increasing order of complexity, and the lowest AIC score was used to select the simplest model (highlighted in **bold**) that adequately described variation in survival

Model	Details regarding survival	Parameters	Log likelihood	AIC	ΔAIC
1	Constant survival	9	−69.24	156.47	41.28
2	Handling mortality, constant survival	10	−59.68	139.35	24.16
3	Handling mortality, survival differed between seasons	11	−57.63	137.25	22.06
4	Seasonal difference in handling mortality, constant survival	11	−50.16	122.32	7.13
5	Seasonal difference in both handling mortality and survival	12	−49.86	123.71	8.52
6	Size-dependent mortality, no handling mortality	10	−57.31	134.62	19.43
7	Size-dependent mortality, handling mortality	11	−55.21	132.42	17.23
8	Size-dependent mortality, seasonal differences in handling mortality	12	−45.6	115.19	0
9	Seasonal difference in handling mortality, seasonal differences in baseline mortality; size-dependent mortality	13	−45.11	116.21	1.02
10	Seasonal difference in handling mortality, seasonal differences in both baseline mortality and size-dependent mortality	14	−45.04	118.07	2.88

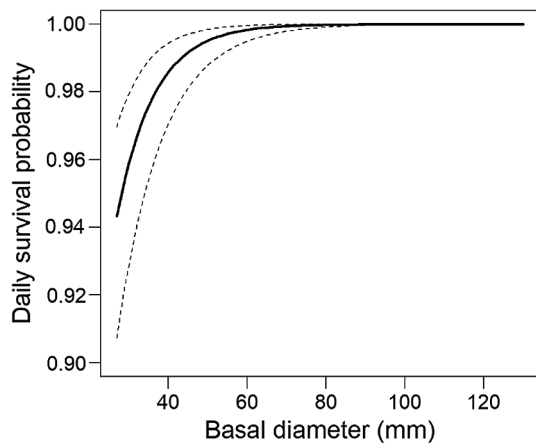


Fig. 5. Estimated relationship between daily survival probability of *Megastrea undosa* and size. Size-dependent survival was best described by an asymptotic model ($S_{\text{Max}}(1 - \exp(-cL))$), where S_{Max} is the survival probability as snails increase in size, L is the basal diameter of the snail, and c is a parameter that describes how quickly survival changes with size. Mean and 95% CIs (dashed lines)

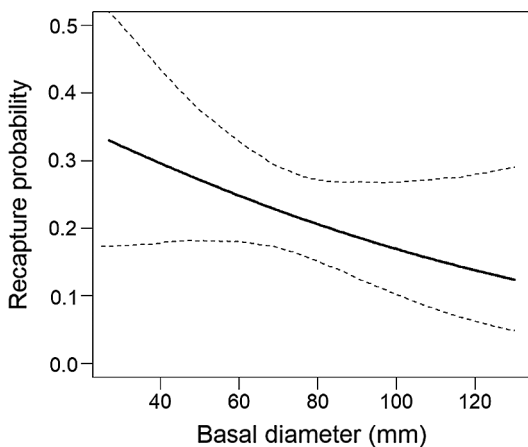


Fig. 6. Estimated relationship between average recapture probability of *Megastrea undosa* and size. Recapture probability is described by a logistic model. Mean and 95% CIs (dashed lines)

M. undosa can live 12 yr or more and are relatively slow growing. Our average interval between measurements was 41.4 d—a period over which growth increments are not expected to be large. Combining this with natural variability in measurement (e.g. due to chipped shells and difficulties of weighing specimens at sea) resulted in a relatively low signal to noise ratio in the data (cf. Fig. 3A,B). In such situations, it will be beneficial to analyze growth in length and growth in weight all within a single analysis (as described in Section 2). Doing so increases precision and can yield more accurate descriptions of growth. For example, if growth were estimated using data on diameter only or

weight only, the estimated diameter of a 10 yr old snail would have been 94.4 mm (95% CI: 86.6–101.1 mm) or 117.1 mm (95% CI: 45.4–126.7 mm), respectively. Together, these estimates would yield a 95% CI of 58.3–124.1 mm. In contrast, combining data on growth in length and weight into a single analysis yielded greater precision and a narrower 95% CI (mean = 104.5, 95% CI: 96.2–111.1). Although it is common for studies of growth to estimate growth functions for length, it is relatively rare to describe growth functions for weight (Hopkins 1992). Measurements of lengths and weights are often taken simultaneously, and ways to analyze these measures together are straightforward. We recommend that future studies consider joint analyses of length and weight as 2 related aspects of growth.

Regarding the survival of *M. undosa*, we found that survival probabilities were strongly dependent on size, but we found little evidence that baseline values of survival differed between the spring and fall, and little evidence that the pattern of size dependence differed between seasons. Size-dependent increases in survival were strongest during the juvenile phase. For example, even a medium-sized snail (50 mm diameter) was 5.01 times more likely to survive a 1 mo period than a small snail (27 mm diameter). Such a change in survival within ontogeny is common pattern for many marine invertebrates (Gosselin & Qian 1997), and one implication of the strong size dependence observed for *M. undosa* is that any variation in overall survival rates or rates of growth during the first 2 yr post recruitment will likely be important for determining the abundance of adults. Processes that affect growth and survival (e.g. food availability: White 1978, Chen et al. 2005; predator abundance: Navarrete & Menge 1996, Nakaoka 2000) are therefore likely to be important drivers of variation in the size of these populations.

The observed patterns of size-dependent survival are likely because smaller snails are more vulnerable to predation. In general, snails may be able to avoid predation by attaining a larger size (McClanahan 1990, Navarrete 1996), but the exact mechanisms leading to a refuge with body size are seldom known. For instance, larger snails may have thicker, stronger shells that offer a better defense against predators (Boulding et al. 1999, Zuschin et al. 2003, Kosloski et al. 2017), but large snails may also be able to escape predation because of greater speed and mobility. For *M. undosa*, we believe that increased speed with body size is likely to be the major reason for the size-dependent increase in survival that we detected in the field. Previous studies have shown that escape

speed of *M. undosa* increases sharply with the size of the snail (Schmitt 1981), which is consistent with the size-dependent survival we observed in the field. In addition, there is evidence to suggest that the fortification of shells that comes with larger size is not enough by itself to deter most predators. Alfaro & Carpenter (1999) conducted tethering experiments to compare relative rates of predation in the wild. In these experiments where the effects of escape speed were negated, the authors found no significant differences in survival of snails of different size classes.

Regarding growth of *M. undosa*, our study determined that average diameters of snails at the benchmark ages 5 and 10 yr are 84.02 and 105.4 mm, respectively. In Todos Santos Bay, Mexico, Cupul-Magana & Torres-Moye (1996) determined that the average basal diameter of snails at the same ages are approximately 44.5 and 67.5 mm, respectively. In addition, another study was conducted in Bahia Tortugas and Punta Abrejo by Martone & Micheli (2012). At their northern site (Bahia Tortugas), snails at 5 yr were 82.9 mm and snails at 10 yr were 105 mm, while at their southern site (Punta Abrejo), snails at 5 yr were 88.0 mm and snails at 10 yr were 116 mm. Differences in growth among these populations may be explained by differences in coastal upwelling and productivity. Populations studied by Martone & Micheli (2012) were in a region of high productivity; populations studied by Cupul-Magana & Torres-Moye (1996) were in an area of relatively low productivity; and our study population is located in a region of intermediate productivity (Lluch-Belda et al. 2003, Wingfield et al. 2011).

Our analyses revealed a seasonal difference in handling mortality. In the spring, handling mortality was negligible, but in the fall, handling mortality was surprisingly high. The tagging procedures were similar between spring and fall, and although handling mortality was inferred indirectly (by analyzing patterns in encounter histories), there is some additional evidence to support these conclusions. In our final tagging event that took place in late fall, we observed several mortalities that were likely the result of handling. Seven snails that were all tagged at the beginning of the day's procedure were found as empty shells during the next recapture. There was no damage to the shells and the snails were in the vicinity of the release point, suggesting that these snails were weakened or dead upon release. The reason for higher mortality in the fall may be due to higher air and/or water temperatures than in the spring. In the fall, there was a more distinct thermocline, and water at the sea surface was notably warmer than water at

depth. As part of the collection and tagging procedure, snails were temporarily housed in coolers full of water from the sea surface. It is possible that the warmer water exacerbated the stress associated with handling, which contributed to handling mortality. For future studies, we suggest that efforts be made to match the temperature of water in containers to the temperature snails experience at depth.

Recapture probability of the snails we studied decreased with body size. This may be the result of larger snails having greater mobility (Schmitt 1981, Hemmert & Baltzley 2016) and larger home ranges (Paine 1969, Gaston & Blackburn 1996). Snails with larger home ranges would be more likely to wander to the periphery of our study area where they would have a lower chance of being detected by a diver. In our study there were hundreds of tagged snails, and it was difficult for the divers to search as much ground as the snails, especially larger ones, were likely to be distributed over. To maximize searching efficiency, divers concentrated on the core area of the study site. This means snails on the edge of the study area would have a lower chance of recapture than those that stayed within the core area. A decrease in recapture probability with body size may be common in mark-recapture studies. For many species, home range increases with body size (e.g. Turner et al. 1969, Gittleman & Harvey 1982, Reiss 1988) and search effort is often concentrated in core areas (Royle et al. 2013, Peterson et al. 2015). Fortunately, it is relatively straightforward to analyze size-dependent recapture probability and to account for this phenomenon when estimating survival in wild populations.

5. CONCLUSIONS

There are 2 sets of advances made by this study. The first includes estimates of growth and survival of *Megastrea undosa*, and the implications that these patterns of growth and survival have for an emerging fishery on this species. Our results confirm that *M. undosa* is a relatively slow-growing species and reveal that relatively few individuals survive to maturation. For example, in our Southern California study population, it takes approximately 6 yr for a snail to reach a size consistent with full maturity (taken to be ~90 mm in diameter, based on Martone & Micheli 2012). Furthermore, very few snails survive to maturity because mortality during the early juvenile phase is particularly high. In contrast to juveniles, large adults have a favorable survival out-

look (cf. Fig. 4), and studies of relative fecundity suggest that high rates of fecundity are achieved only after snails grow to sizes larger than 90 mm diameter (Martone & Micheli 2012). The largest adults of this species have high reproductive value and are thus very important for the replenishment of populations (see Caswell 2001, Morris & Doak 2002 for a general discussion of these effects). Management strategies that preserve these large individuals (e.g. marine protected areas that restrict all fishing; slotted size limits) will thus be highly beneficial for preserving reproductive capacity of these populations and helping to ensure their long-term health (Berkeley et al. 2004, Hixon et al. 2014, Marshall et al. 2019).

The second set of advances made by our study focuses on 3 issues that are common in mark–recapture studies: tag loss, handling mortality, and the challenge of measuring growth over relatively short intervals of time. The methods we describe to account for these phenomena are broadly applicable and can be used to improve estimates of survival and growth in wild populations. Estimating tag loss requires 2 tags attached to the organism, but double-tagging can be done for a wide variety of species and tag types (e.g. Adam & Kirkwood 2001, Shaffer et al. 2005, Heard et al. 2008). Our method is simple, allows the estimation of confidence intervals, and can be used to estimate tag loss as a time-dependent function. Estimating handling mortality is also fairly straightforward, and we believe this is an important step to take. In our study, visual signs of handling mortality were not noticeable until very late in the study, and the magnitude of handling mortality revealed by the analysis was somewhat surprising. We suspect that handling mortality might be similarly underappreciated in other studies if handling imparts a degree of stress. Even if tagged animals are not monitored closely after release, handling mortality can be inferred from the pattern of encounter histories as outlined above. Finally, estimating growth through the joint analysis of changes in multiple measures of body size can increase both the accuracy and precision of the estimates of growth functions for wild populations.

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Appendix. Additional data

Table A1. Frequency of encounter histories (see Table 1) that were observed for *Megastrea undosa* in this study. Dates are given as mo/d/yr

Group	Season	Encounter history				Frequency
		3/4/2019	3/15/2019	4/29/2019	5/30/2019	
1	Spring	1	1	1	1	0
		1	1	1	0	1
		1	1	0	1	1
		1	1	0	0	19
		1	0	0	1	1
		1	0	1	1	0
		1	0	1	0	5
		1	0	0	0	16
2	Spring	3/15/2019	4/29/2019	5/30/2019	6/20/2019	
		1	1	1	1	0
		1	1	1	0	1
		1	1	0	1	0
		1	1	0	0	8
		1	0	0	1	0
		1	0	1	1	0
		1	0	1	0	0
3	Spring	5/30/2019	6/20/2019	7/3/2019	7/17/2019	
		1	1	1	1	0
		1	1	1	0	0
		1	1	0	1	0
		1	1	0	0	3
		1	0	0	1	3
		1	0	1	1	1
		1	0	1	0	3
4	Fall	9/13/2019	10/11/2019	11/1/2019	12/6/2019	
		1	1	1	1	4
		1	1	1	0	2
		1	1	0	1	5
		1	1	0	0	16
		1	0	0	1	7
		1	0	1	1	17
		1	0	1	0	6
5	Fall	10/11/2019	11/1/2019	12/6/2019		
		1	1	1		3
		1	1	0		2
		1	0	1		2
		1	0	0		34

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