

Ocean warming and the demography of declines in coral body size

Robin Elahi*, Kenneth P. Sebens, Giulio A. De Leo

*Corresponding author: elahi@stanford.edu

Marine Ecology Progress Series 560: 147–158 (2016)

Methodological details regarding the sampling designs, coral measurements, the demographic model and its parameterization, and the relationship between coral surface area and biomass.

Historic and modern sampling designs

In October 1968, four permanent quadrats (0.25 m^2) separated by 4 – 6.5 meters were established by Charles Birkeland in a rock wall habitat at 13-15 m depth at Shady Cove. Each of these quadrats was divided into four contiguous quadrats (hereafter referred to as ‘subquadrats’), the corners of which were marked using epoxy putty. Photographs of subquadrats were taken using a Nikonos camera and strobe, and film slides were digitized prior to analysis. In December 2007, permanent horizontal transects (2.5 m long, $n = 6$) separated by at least five meters were installed haphazardly on rock walls between 12 and 18 m depth. Quadrats (0.09 m^2 , $n = 4$) were positioned randomly along transects with corners marked with marine epoxy to enable repeated sampling of the benthos. Photographs of quadrats were taken using an Olympus C-8080 digital camera with an Ikelite strobe attached to a $36 \times 25 \text{ cm}$ aluminum framer. Despite their age, the grain of the 35mm photographs provided comparable quality and resolution to the modern digital photographs. Further details on the sampling design of the two studies were provided in a previous manuscript testing the extent of change in community structure over the intervening four decades (Elahi et al. 2013).

Photographs were selected to span a three-year period beginning and ending in the winter (November – February). All quadrats were used to calculate coral density, but corals were not visible in all quadrats (or subquadrats). For historical time series, the census start dates included 11 November 1968 (1 quadrat; 2 subquadrats), 17 January 1969 (2 quadrats; 6 subquadrats), and 22 February 1969 (1 quadrat; 1 subquadrat). The end date was 6 January 1972 (8 subquadrats), and thus the realized time span ranged from 2.87-3.15 years for historical photographs. For all of the modern photos, the initial census was on 10 December 2007 and the final census on 3 December 2010 (2.98 years, 19 quadrats).

Measuring corals

We used NIH Image J to track the fate and estimate area (cm^2) of corals in photoquadrats.

To minimize measurement error, corals were included in size analyses only if the entire oral disk was visible and its tissue and tentacles were not expanded. Similarly, corals were not used if obscured by other organisms, or positioned at an angle relative to the substratum or camera. In the modern photos, a ruler was present in every photograph and used to set the scale for size estimations. In the historical photos, a ruler was present only in images taken on 11 November 1968. Using this photograph with the ruler, we were able to set a reference scale for each subquadrat by measuring the

distance between the oral discs of the same cup corals. Cup corals were the most reliable reference markers because they are sessile and resist overgrowth by other invertebrates (Bruno & Witman 1996). We tested the accuracy of using inter-coral distance as a scale with the modern photographs. We selected randomly one quadrat from each of six transects at Shady Cove. In each quadrat, we selected haphazardly a pair of corals (10-17.2 cm apart) that was visible in 2007 and 2010. Using the ruler in each modern photoquadrat as the scale, we measured the inter-coral distance for each pair of corals. Based on these six independent samples, we estimated $1.9 \pm 4.1\%$ error (mean \pm SD) in the measurement of inter-coral distance three years apart (calculated as the difference in inter-coral distance divided by the inter-coral distance in 2007). Therefore, we conclude that inter-coral distance is a reasonable proxy for a ruler because the magnitude of error was small and there was no directional bias (-0.6 to 1.0 mm absolute error).

The demographic model

We modeled the number of individuals of size z' at time $t + 3$ as:

$$n(z', t + 3) = \int_{\Omega} k(z', z)n(z, t) dz \quad (\text{eqn S1})$$

where $n(z, t)$ is the probability density of individual size z at time t , with the integration being set over all possible sizes Ω (0.02-1.4 cm²). The function $k(z', z)$ is the kernel, a non-negative surface representing the probability density distribution of all possible transitions from size z to size z' . The kernel is analogous to a matrix of transition probabilities (Caswell 2001) with nonzero entries for survival $s(z)$, growth $g(z', z)$, and fecundity $f(z', z)$:

$$k(z', z) = s(z)g(z', z) + f(z', z) \quad (\text{eqn S2})$$

The kernel $k(z', z)$ of our IPM was consistent with the timing of censuses and the life history of our study organism (Rees et al. 2014). That is, censuses were performed between November and February, prior to planula release, which occurs primarily during winter months for *B. elegans* (Fadlallah & Pearse 1982; RE pers. obs.). Following the release of planulae, the surviving adults and recruits grow prior to the next census.

Equations and estimated parameters are provided in Table 1. Survival was modeled with a logistic regression, with survival (1) or death (0) as a function of size z . Growth was modeled as a linear regression of size z' as a function of size z . We chose not to use a log-transformation because the residuals from a regression using untransformed sizes displayed constant variance when plotted against size z , obviating the need for a log transformation (Appendix S2 in Rees et al. 2014). Further, as our primary question regarded the maximum size of populations, the use of a logarithmic scale for size would have compressed the axis region of greatest interest.

We modeled fecundity as:

$$f(z', z) = e(z, z_{mat})p_{recruit}c(z', z) \quad (\text{eqn S3})$$

where $e(z, z_{mat})$ is the number of embryos produced for a coral of size z , given a minimum size at maturity z_{mat} , the probability of recruitment $p_{recruit}$, and the size-distribution of recruits $c(z', z)$. Equation S3 describes a closed coral population refreshed solely by self-recruitment. This is a reasonable assumption for our IPM because *B. elegans* has internal fertilization and releases large (2mm), non-feeding, crawl-away larvae which settle within meters of their mother (Gerrodette 1981).

Model parameterization

The terms in Equation S3 were parameterized using size-dependent fecundity data from a coral population in central California (Fadlallah 1983) together with data on coral density and recruitment in the 24 modern quadrats. Size-dependent fecundity was presented originally as the number of embryos per female (Fadlallah 1983), but we did not know the sex of individual corals in the photoquadrats. Therefore, we halved the original number of embryos per female to obtain the number of embryos per individual, assuming a 1:1 sex ratio in the quadrats and that sperm were not limiting. Due to the fact that temperature influences size at maturity (Berrigan & Charnov 1994, Angilletta et al. 2004), we modified the original fecundity relationship to reflect the cooler temperatures observed in Washington State (see ‘Temperature Simulation of the IPM’).

We used an empirical relationship between calyx area (measured from photographs) and frustum volume (measured with calipers) using 50 corals collected at O’Neal Island ($\ln(\text{area}) = 0.57 + 0.58 * \ln(\text{volume})$; $t = 13.3$, $r^2 = 0.78$, $P < 0.001$) to calculate area from volume in Fadlallah (1983). The relationship between area and fecundity suggested a piecewise linear function with embryonic production increasing linearly with body size from size at maturity z_{mat} . Beyond z_{mat} , embryo number was assumed to be a linear function of size. This function was used to estimate the total number of embryos per quadrat in 2007, 2008, and 2009 ($\text{embryos}_{\text{year}}$), given the size-frequency distribution of corals present in the quadrat for a given year. The total number of embryos per quadrat over the three year time period ($\text{embryos}_{\text{total}}$) was the sum of the annual estimated number of embryos for 2007, 2008, and 2009.

The number of surviving recruits was counted for each quadrat in 2010 (recruits_{2010}), and we calculated $p_{recruit} = \text{recruits}_{2010}/\text{embryos}_{\text{total}}$. This estimated probability of recruitment was associated with considerable uncertainty for several reasons. First, it assumed that every (female) mature coral spawned annually over the three-year period, because *Balanophyllia elegans* has a 12-month gestation period as well as overlapping oogenic and brooding cycles (Fadlallah & Pearse 1982). However, it is possible that some females didn’t reproduce every year during the study period; this source of error would underestimate recruitment probability. Second, it assumed that unobserved recruits in 2007 or observed recruits in 2008 did not successfully reproduce and contribute to the surviving pool of recruits measured in 2010. This source of error would overestimate recruitment probability. Third, embryos produced by reproductive corals in the quadrat may have settled outside the quadrat and vice versa. We assumed that larval immigration was balanced by larval emigration, but this source of error could overestimate or underestimate recruitment probability depending on the density and distribution of corals. To address the first two concerns, we also calculated annual recruitment probability for each quadrat in 2008, 2009, and 2010 (recruits_{t+1}) as $p_{annual} = \text{recruits}_{t+1}/\text{embryos}_t$, but we used $p_{recruit}$ in the IPM to match the temporal scale (three years) of the other vital rates.

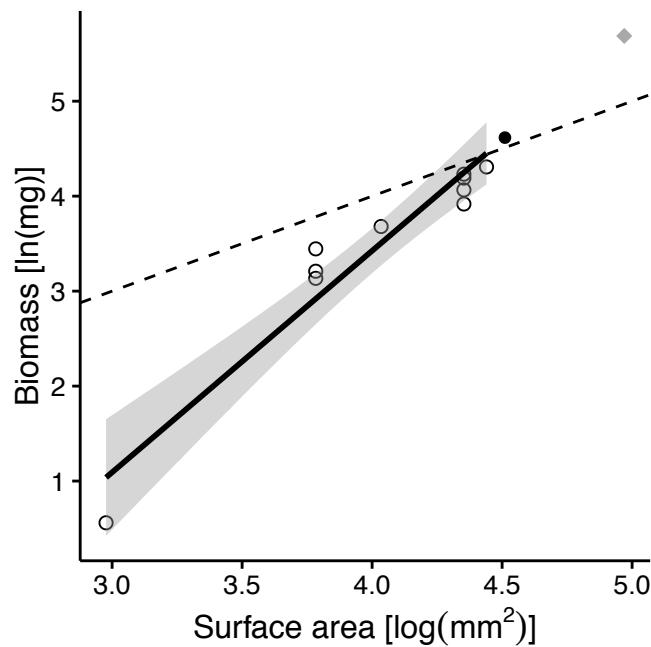


Figure S1. The relationship between biomass ($\ln(\text{mg})$) and surface area ($\ln(\text{mm}^2)$) for ten corals (open points) sampled at Shady Cove, WA in fall 2013. Biomass was estimated using an analysis of the C:H:N ratios in corals. Using the estimated ordinary least squares relationship, we also plot the predicted biomass of the maximum surface area (99th percentile) observed in the historic (1969-1972; gray diamond) and modern (2007-2010; filled circle) populations. A reduced major axis regression supported the hypothesis that tissue biomass scales allometrically with surface area ($\beta = 2.4$, 95% limits = 1.9, 3.0; $P < 0.0001$). The dashed line represents unity.

References

- Angilletta MJ, Steury TD, Sears MW (2004) Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integr Comp Biol* 44:498-509
- Berrigan D, Charnov EL (1994) Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos* 70:474-478
- Bruno JF, Witman JD (1996) Defense mechanisms of scleractinian cup corals against overgrowth by colonial invertebrates. *J Exp Mar Biol Ecol* 207:229-241
- Caswell H (2001) Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA
- Elahi R, Birkeland C, Sebens KP, Turner KR, Dwyer TR (2013) Limited change in the diversity and structure of subtidal communities over four decades. *Mar Biol* 160:3209-3219
- Fadlallah YH (1983) Population dynamics and life history of a solitary coral, *Balanophyllia elegans*, from Central California. *Oecologia* 58:200-207
- Fadlallah YH, Pearse JS (1982) Sexual reproduction in solitary corals: overlapping oogenic and brooding cycles, and benthic planulas in *Balanophyllia elegans*. *Mar Biol* 71:223-231
- Gerrodette T (1981) Dispersal of the solitary coral *Balanophyllia elegans* by demersal planular larvae. *Ecology* 62:611-619
- Rees M, Childs DZ, Ellner SP (2014) Building integral projection models: a user's guide. *J Anim Ecol* 83:528-545